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Cover Photograph: Female Prairie Warbler (*Setophaga discolor*) on fruiting Buffalo Top Palm (*Thrinax morrisii*) inflorescence. Photo taken near Owl Hole and Lucayan National Park, Grand Bahama, 6 October 2013. Photograph © Janet Franklin.

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Winter Bird Communities in Pine Woodland vs. Broadleaf Forest on Abaco, The Bahamas

Janet Franklin[1,*] and David W. Steadman[2]

Abstract - We assessed the relative abundance of winter resident birds (species that breed in North America but spend the winter in The Bahamas) through 115 point counts conducted during December and January 2007–2012 on Abaco, The Bahamas. We also analyzed structure and composition of the woody vegetation in Abaco's two widespread terrestrial habitats: Pineland, an open woodland of *Pinus caribaea* var. *bahamensis* (Bahamas Pine) that covers most of the island; and Coppice, a broadleaf, relatively diverse forest that covers <10% of Abaco. Winter resident birds were more abundant in Pineland (8.61 individuals/point) than in Coppice (2.28 individuals/point). *Setophaga palmarum* (Palm Warbler) and *S. coronata* (Yellow-rumped Warbler) dominated the winter bird communities in Pineland (44.6% and 37.4% of all detected individuals, respectively), with the next three most common species (*S. discolor* [Prairie Warbler], *Dumetella carolinensis* [Gray Catbird], and *Geothlypis trichas* [Common Yellowthroat]) ranging from 6.5 to 2.0%. The winter species composition in Coppice was more even than in Pineland, featuring *S. ruticilla* [American Redstart] (39.8%), Prairie Warbler (16.2%), Gray Catbird (13.1%), and the next five most common species (*S. americana* [Northern Parula], *Seiurus aurocapillus* [Ovenbird], *S. caerulescens* [Black-throated Blue Warbler], *Mniotilta varia* [Black-and-white Warbler], and *S. citrina* [Hooded Warbler]) ranging from 7.3 to 3.1%. In Pineland, bird community composition varied with overstory cover and height, understory cover and type, and ground cover. In contrast, patterns of bird community composition in Coppice were not associated strongly with variation in habitat structure or forest composition. This may reflect that Coppice, experiencing frequent hurricane disturbance, has considerable small-scale heterogeneity in the availability of food for winter resident birds. Comparing our data with those from previous surveys of winter birds conducted 5–40 years earlier in the northern Bahamas, we see little evidence of major changes in this bird community.

Introduction

Interest in assessing declines of Nearctic-Neotropical migratory bird populations during the 1980s led to studies of these species on their wintering grounds, including the Caribbean region. Research on migratory birds in the Caribbean has ranged from single-species studies over short time frames (Hallworth et al. 2011, Latta and Faaborg 2009) to community-level analyses over decades (Faaborg et al. 2007, 2013). We augment this research by presenting results from recent surveys of the winter resident bird community on Abaco, an island in the northern Bahamas where similar surveys were done nearly 20 years ago.

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The northern Bahamian islands are particularly important wintering and passage areas for Nearctic-Neotropical migratory landbirds because of their proximity to North American breeding areas (Kale et al. 1969, Wunderle and Waide 1993). During the winter (here defined as December through February), songbirds (mostly warblers) that nest in North America make up as many as one-half of the species and individuals in bird communities in the northern Bahamas (Currie et al. 2005b, Emlen 1977).

Two distinctive terrestrial forest communities are found in the northern Bahamas. The first is a woodland (i.e., no closed canopy) of *Pinus caribaea* var. *bahamensis* (Griseb.) W.H. Barrett & Golfari (Bahamas Pine) called Pineland. The second is a broadleaf, evergreen forest (i.e., closed or nearly closed canopy) called Coppice. These two plant communities have been recognized as conservation targets in The Bahamas because they are globally rare, sustain indigenous plants and animals (including migratory birds), and are historically or currently threatened by logging, clearing for agriculture and commercial/residential development, invasive plants, human-set fires, and non-native grazing and browsing ungulates (Sullivan-Sealey et al. 2002).

Pineland occurs only on four islands in the northern Bahamas, namely Grand Bahama and Abaco on the Little Bahama Bank, and Andros and New Providence on the Great Bahama Bank. Pineland may have been less common than today on Abaco in the Late Holocene (ca. 5000 to 1000 years ago), when broadleaf forest (Coppice) elements were more prominent (Steadman et al. 2007). Although Pineland undoubtedly has been present on Abaco (and the other three islands) throughout the Holocene (the past 10,000 years), its extent appears to have expanded (at the expense of Coppice) when people first arrived (ca. 1000 year ago) because of increased frequency and extent of fire (Kjellmark 1996, Lee 1996b, Slayton 2010). Today, Pineland is the most extensive terrestrial habitat on Abaco (Sullivan-Sealy et al. 2002), whereas Coppice is restricted mostly to limestone ridges and covers less than 10% of the island.

In this study, we evaluated the distribution and abundance of wintering landbirds in the two main terrestrial habitats (Pineland vs. Coppice) on Abaco based on surveys of birds and vegetation (e.g., Franklin and Steadman 2010) conducted from 2007 to 2012. We predicted, based on previous studies (Currie et al. 2005a, b; Emlen 1977; Wunderle and Waide 1993), that bird species composition, diversity, and abundance would differ between these habitats and would also be correlated with vegetation structure. To examine regional patterns and possible temporal change, we then compared our Pineland survey results with those from similar studies conducted in Pineland on Andros (Currie et al. 2005a) and Grand Bahama (Emlen 1977) as well as on Abaco (Lee 1996a, b). Our Coppice survey results were compared to those from similar studies carried out on Andros (Currie et al. 2005a) and Eleuthera (Currie et al. 2005b).

Field-site Description

Lying at the northern limit of the West Indian biogeographical region, the Bahamas archipelago includes The Commonwealth of the Bahamas (where our research took place; also known as "The Bahamas") and The Turks and Caicos Islands (TCI). The Bahamian islands consist of limestone from indurated calcareous sand deposited on massive, shallow carbonate banks. Abaco, which lies on the Little Bahama Bank, is the second largest island in the group (1214 km^2), with a maximum elevation of 44 m. Our coordinated bird and vegetation surveys in Pineland and Coppice were conducted throughout Great and Little Abaco (Fig. 1). The transect locations were selected to represent geographical variation of plant communities on Abaco and a range of disturbance types; the levels of habitat fragmentation were especially variable in Coppice, for which only two tracts >10 km^2 still exist on Abaco (Table 1). We did not survey other non-marine habitats found on Abaco (mangrove, scrubland, wetlands, abandoned agriculture) in this study.

Pineland, also known as pine woodland, pine rockland, pineyard, or subtropical needle-leaved evergreen woodland (Areces-Mallea et al. 1999), is dominated by Bahamas Pine (a variety endemic to the Bahamian islands). Second-growth Pineland dominates Abaco, where intensive commercial logging took place island-wide

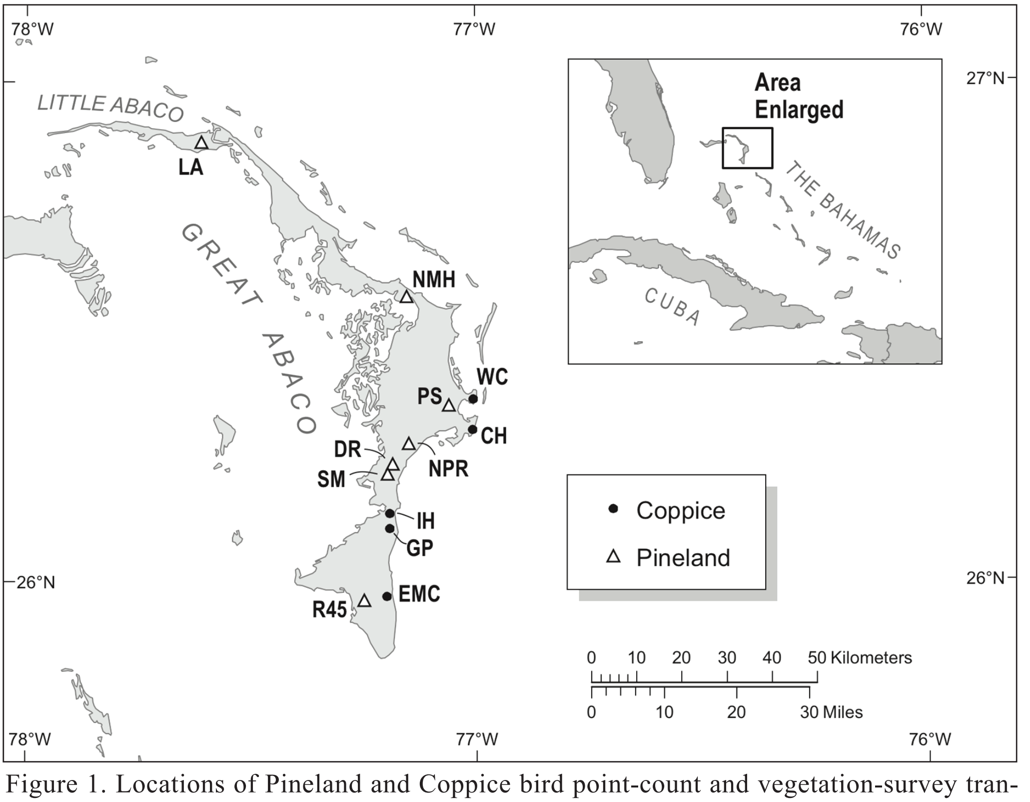

Figure 1. Locations of Pineland and Coppice bird point-count and vegetation-survey transects on Abaco Island, The Bahamas. Transect names indicated by abbreviations are shown in Table 1.

Table 1. Transect characteristics including mean (± SE) forest structure attributes. Date = month and year bird surveys were conducted for each transect. Transects are ordered by increasing height and basal area and decreasing density within Coppice, and by increasing height, density, and basal area within Pineland (from more to less disturbed). Types of disturbance and degree of fragmentation are described. ANP = Abaco National Park; No. Points = number of bird point-count stations and forest-structure plots [in brackets the number of 10-m radius plots where DBH, BA, and density were measured]; hemi = estimated from hemispherical photos; DBH = tree diameter at 1.3 m height for trees >5 cm; BA = basal area (sum of cross sectional area) based on DBH; cover estimated visually except Tree Cover (hemi) based on hemispherical photo (1 - average canopy openness); Understory = woody layer 1–4 m tall; Ground = herbaceous layer of graminoids, ferns, forbs.

Forest type/Transect	Date	No. points [plots]	% tree cover	% tree cover (hemi)	Tree height (m)	Tree density (ha^{-1})	DBH (cm)	BA ($cm^2 m^{-2}$)	% understory cover	Understory height (m)	% ground cover
Coppice											
Gilpin Point (GP); roads, hunting trails	Jan 2012; Dec 2012	4 [2]	69 (± 6.2)	84 (± 1.3)	7.64 (± 0.7)	3263 (± 2307)	9.4 (± 0.3)	27.4 (± 6.6)	48 (± 4.1)	2 (± 0.2)	0
Island Homes (IH); dense roads, recent residential development	Dec 2007; Jan 2009	6 [3]	84 (± 1.8)	89 (± 0.3)	7.89 (± 0.1)	4011 (± 2316)	9.6 (± 0.2)	35.3 (± 4.9)	75 (± 5.1)	3 (± 0.1)	0
Cherokee (CH); roads, residential development	Dec 2007; Jan 2009	7 [3]	86 (± 1.7)	88 (± 0.2)	9.32 (± 0.7)	2525 (± 1458)	10.7 (± 0.4)	29.1 (± 9.0)	67 (± 4.4)	2 (± 0.1)	0
Eight Mile Cave (EMC); roadless, protected	Dec 2007; Jan 2009	9 [4]	74 (± 3.4)	88 (± 0.7)	9.77 (± 0.6)	3072 (± 1536)	10.7 (± 0.3)	35.3 (± 7.7)	78 (± 3.1)	3 (± 0.1)	0
Wilson City (WC); recent clearing; hunting trails	Jan 2010	16 [8]	73 (± 3.0)	86 (± 1.1)	9.47 (± 0.5)	2606 (± 921)	11.0 (± 0.2)	32.0 (± 6.3)	50 (± 3.5)	3 (± 0.1)	0
Pineland											
Dan's and Ralph's (DR); second growth	Dec 2007; Jan 2009	11 [5]	31 (± 3.7)	46 (± 2.1)	13.66 (± 0.3)	388 (± 174)	16.9 (± 0.7)	9.7 (± 4.3)	51 (± 4.4)	2 (± 0.1)	50 (± 4.4)
Sawmill (SM); second growth	Dec 2007; Jan 2009	11 [5]	30 (± 2.2)	46 (± 1.6)	13.46 (± 0.3)	420 (± 188)	17.8 (± 0.8)	11.7 (± 5.3)	53 (± 5.0)	2 (± 0.1)	45 (± 4.8)
Power Station Road (PS); second growth; recent roads	Jan 2010	9 [5]	30 (± 2.6)	44 (± 1.6)	14.82 (± 0.5)	579 (± 259)	15.7 (± 0.6)	12.6 (± 5.6)	46 (± 2.6)	2 (± 0.1)	47 (± 2.5)
Road 45 ANP (R45); second growth, protected	Dec 2012	22 [11]	29 (± 1.7)	50 (± 1.7)	14.64 (± 0.3)	749 (± 256)	15.0 (± 0.4)	15.2 (± 4.6)	43 (± 2.8)	1 (± 0.1)	81 (± 1.8)
New Pine Road (NPR); second growth	Jan 2010	10 [5]	25 (± 2.4)	49 (± 2.2)	13.87 (± 0.7)	770 (± 344)	14.8 (± 1.2)	24.9 (± 11.1)	31 (± 2.3)	3 (± 1.3)	45 (± 3.0)
North Marsh Harbour (NMH); second growth	Dec 2007	2 [-]	20 (± 3.5)	42 (± 2.8)	17.32 (± 0.1)	-	-	-	35 (± 3.5)	2 (± 0.1)	65 (± 3.5)
Little Abaco (LA); old growth	Jan 2010	8 [10]	-	30 (± 2.7)	17.80 (± 1.9)	178 (± 56)	27.8 (± 1.0)	11.6 (± 3.7)	56 (± 2.9)	2 (± 0.1)	34 (± 2.3)

from the early 20th century through the 1940s (Dodge 2005). Tree cover and height in Pineland vary with disturbance history (Table 1). The Pineland understory often is dominated by shrubby *Metopium toxiferum* (Poisonwood) and other woody taxa; the understory species composition varies with fire history (Currie et al. 2005b). *Pteridium aquilinum* (Bracken Fern) dominates the herbaceous layer in some locations.

Coppice, the second upland forest type on Abaco, is also classified as dry evergreen or subtropical seasonal (broadleaf) evergreen forest (Areces-Mallea et al. 1999, Smith and Vankat 1992). The structure and composition of the Coppice we surveyed on Abaco (Table 1) are similar to "Blackland Coppice" (Correll and Correll 1982), "Inland Coppice" on Andros (Smith and Vankat 1992), and "Tall Coppice" on Eleuthera (Currie et al. 2005b). Coppice typically lacks pines, and is dominated by broadleaf hardwoods such as *Bursera simaruba* (Gum-elemi), *Coccoloba diversifolia* (Pigeon-plum), *Eugenia confusa* (Red Stopper), *Exothea paniculata* (Inkwood), *Mastichodendron foetidissimum* (Mastic), and Posionwood. The Coppice understory consists of saplings of the overstory tree species as well as small trees and shrubs. Evidence of repeated storm damage is ubiquitous, with many tree trunks snapped off or tipped over.

Methods

Bird point counts

The terrestrial bird communities on Bahamian islands consist of four seasonal categories of species: (1) winter residents (species that breed in North America but spend the winter in the Bahamas); (2) passage migrants (species that breed in North America and migrate through the Bahamas during the spring and/or autumn but generally spend the winter south of the Bahamas); (3) summer residents (species that breed in the Bahamas but that migrate southward after breeding); and (4), permanent residents (species that breed in the Bahamas and remain there year-around). This paper concerns only the winter resident species (category 1), which comprised ≈50% of the 1444 total detections in our surveys and included 17 species.

Data for the 32 species of permanent residents (category 4) are included in Supplemental File 1 (available online at http://www.eaglehill.us/CANAonline/suppl-files/c105-Franklin-s1), which also includes data for winter residents and forest-structure variables. Because some breeding species of birds do not typically occur on Abaco in December or January (category 3, summer residents), and the category 4 species may be less vocal (and therefore less detectable) in winter than during the main April–June breeding season, our data for these species do not accurately assess breeding populations, and thus are not directly comparable to data from breeding bird surveys (e.g., Lloyd and Slater 2011).

The location of each bird point-count station was recorded with a Garmin global positioning system (GPSMAP 60CSx, Garmin International, Inc., Olathe, KS, USA). We conducted 13-minute, double-observer, unlimited-radius, circular-plot point counts (Emlen 1971, Ralph et al. 1993) on 11–16 Dec 2007, 12–17 Jan 2009, 7–12 Jan 2010, 5–10 Jan 2012, and 1–5 Dec 2012. Each point count was done by the authors. Double-observer point counts record avian abundance with high levels of precision (Nichols et al. 2000). Point counts with an unlimited-radius are believed generally to provide better estimates of actual population size than those with a fixed radius (Simons et al. 2007). Each point-count station (73 in Pineland, 42 in Coppice, in 12 transects; Table 1) was at least but close to 200 m apart; every point on each transect was sampled during times of little or no rain, wind <10 km/hr, and within 4 hours of daybreak. The points in Pineland were along straight, grassy, single-lane former logging roads that allowed quiet, rapid travel through this homogeneous habitat. The points in Coppice were along narrow foot-trails. Some trails were pre-existing; others we cut ourselves, never counting birds on the same day that we cut the trail.

Each species of bird detected by sight or sound was noted by time interval of first detection (0–5 minutes vs. 5–10 minutes vs. 10–13 minutes [during this last interval we made a "pish" call to attract birds]). The 3-minute "pish" call was done to lure in nearby silent birds not detected during the point count (especially important for wintering warblers, which often are vocally inconspicuous; Steadman et al. 2009), and to confirm the identities of certain birds detected during the first 10 minutes. For each individual bird, we recorded the distance (estimated to the nearest 5 m for 0–50 m, and to the nearest 10 m for >50 m) and direction (to nearest 45º) at first detection. Each observer registered individual birds separately. We then compared our independent detections immediately following the point count to derive the counts used for analysis. The number of each species per point was recorded; we did not correct for potential differences in auditory detectability (see Waide and Narins 1988). Seabirds, shorebirds, raptors, and landbirds observed flying over the point-count stations were recorded but not included in this analysis. Our nomenclature for warblers follows the substantial revisions in Lovette et al. (2010).

Vegetation surveys

Vegetation structure and composition data were gathered later on many of the same days when point counts had been conducted and on 5–11 May 2009, 10–16 Jul 2009, 2–7 May 2012, and 29 Nov–5 Dec 2012. At each point-count station, the overstory (trees >4 m tall) canopy cover was estimated visually by two observers for a 50-m radius area, as well as from hemispherical photographs. Percent canopy openness, a measure of the light environment, was calculated from the hemispherical photos (Nikon Coolpix 4500 with FC-E8 fisheye converter) using Gap Light Analyzer (Frazer et al. 2001), and the inverse of canopy openness was used as an estimate of canopy cover. Canopy height was estimated with an Impulse laser rangefinder (Laser Technology Inc., Centennial, CO, USA) based on the average height of five overstory trees selected randomly from five different compass directions (Currie et al. 2005a). The understory (woody stratum from 1–4 m tall) was classified as mixed shrub, palms, or saplings (of overstory tree species), and over- and understory heights were estimated visually to the nearest 0.5 m. If an herbaceous ground layer was present it was classified as fern or graminoid-dominated. To describe species composition, density, and basal area of the tree layer, we established 10-m radius plots (41 in Pineland, 20 in Coppice) within 20 m of every other point-count station. For every tree >5 cm diameter in each plot, we identified the species and measured its diameter at 1.3 m height (DBH). Nomenclature for plants follows Correll and Correll (1982) with taxonomic updates from the Taxonomic Name Resolution Service.

Analyses

For winter resident species recorded in both Pineland and Coppice, the difference in relative abundance (right skewed) between the two habitats was tested using non-parametric Wilcoxon rank sum tests. Subsequently, multivariate clustering and ordination of bird relative density (percent of individuals at the point for each species) and forest-structure variables were carried out separately for winter resident species in Pineland and Coppice points. Clustering, based on the Jaccard distance measure and average linkage clustering (Peet and Roberts 2013), was used to detect any subgroups of points within forest types showing similar winter resident bird assemblages. Analysis of similarity (ANOSIM; Clarke 1993), a non-parametric test based on permutation of among- and within-group similarities, was used to test for the significance of bird species composition difference among groups. Indicator species analysis (Dufrêne and Legendre 1997) identified those winter resident species having strong association (high abundance within the group) and fidelity (occurring at many points within the groups and few points outside the group) with those groups identified by clustering. Finally, unconstrained ordination using detrended correspondence analysis (DCA; Hill and Gauch 1980), which describes continuous variation in bird composition among points, was used to determine the correlations of forest structure variables with variation in bird composition.

Unlike Pineland with its monospecific overstory, Coppice has many tree species. Therefore, the same methods of clustering and ordination, applied to tree species data from the 10-m radius plots, were used to evaluate whether continuous variation in tree species composition was correlated with bird composition within Coppice. We carried out statistical analyses using R (R Development Core Team 2012), in particular the vegan package (Oksanen et al. 2011), and with PC-Ord (McCune and Mefford 1999).

Results

Pineland vs. Coppice

Winter resident birds were detected much more often in Pineland (8.61 individuals/point) than Coppice (2.28 individuals/point; Table 2). Two species (*Setophaga palmarum* [Palm Warbler] and *Setophaga coronata* [Yellow-rumped Warbler]) dominated in Pineland (82.0% of all detections), with only two other species (*Setophaga discolor* [Prairie Warbler] and *Dumetella carolinensis* [Gray Catbird]) exceeding 3%. The winter species composition in Coppice was much more even than in Pineland, featuring *Setophaga ruticilla* (American Redstart, 39.8%), Prairie Warbler (16.2%), Gray Catbird (13.1%), and five other species (*Setophaga americana* [Northern Parula], *Seiurus aurocapillus* [Ovenbird], *Setophaga caerulescens* [Black-throated Blue Warbler], *Mniotilta varia* [Black-and-white Warbler], and *Setophaga citrina* [Hooded Warbler]) with >3% of detections. Yellow-rumped Warbler, *Geothlypis trichas* (Common Yellowthroat), *Passerculus sandwichensis* (Savannah Sparrow), and *Sphyrapicus varius* (Yellow-bellied Sapsucker) were recorded exclusively in Pineland, whereas Ovenbird, Black-throated Blue Warbler, *Setophaga virens* (Black-throated Green Warbler), Hooded Warbler, and *Helmitheros vermivora* (Worm-eating Warbler) were recorded only in Coppice. Of species found in both habitats, there was a greater relative abundance of Palm Warblers in Pineland, and American Redstarts and Northern Parula in Coppice (see Table 2).

Pineland

When birds from Pineland points were considered alone, five groups of points resulted from clustering (ANOSIM: $R = 0.971$, $P = 0.001$). The Palm Warbler, an in-

Table 2. Point-count data for winter resident birds, Abaco, Bahamas, 11–16 Dec 2007, 13–18 Jan 2009, 7–12 Jan 2010, 5–10 Jan 2012, and 1–5 Dec 2012. Ind./point = average individuals per point; (S) = species of conservation concern (US Fish and Wildlife Service 2008). Abbreviations for species names used in Figure 2 are given in parentheses. Primary feeding guilds: F = frugivore; G = granivore; I = insectivore. Significantly greater abundance in one habitat for species recorded in both habitats indicated by Wilcoxon rank sum test, with $^{***} = P << 0.0001$; $^{**} = 0.0001 < P < 0.001$.

	Pineland		Coppice	
Species	Ind./ point	% total	Ind./ point	% total
Yellow-bellied Sapsucker *Sphyrapicus varius* L. (yesa) I	0.01	0.2	-	-
Gray Catbird *Dumetella carolinensis* L. (grca) F	0.56	6.4	0.30	13.1
White-eyed Vireo *Vireo griseus* Boddaert (wevi) F	0.01	0.1	0.01	0.5
Northern Parula *Setophaga americana* L. (nopa) I	0.01	0.1	0.17^{**}	7.3
Cape May Warbler *Setophaga tigrina* Gmelin (cmwa) I	0.03	0.3	0.01	0.5
Black-throated Blue Warbler *Setophaga caerulescens* Gmelin (bbwa) I	-	-	0.12	5.2
Yellow-rumped Warbler *Setophaga coronata* L. (yrwa) F	3.22	37.4	-	-
Black-throated Green Warbler *Setophaga virens* Gmelin (S) (bgwa) I	-	-	0.02	1.0
Prairie Warbler *Setophaga discolor* Viellot (S) (prwa) I	0.51	6.5	0.37	16.2
Palm Warbler *Setophaga palmarum* Gmelin (pawa) I	3.84	44.6^{***}	0.01	0.5
Black-and-white Warbler *Mniotilta varia* L. (bwwa) I	0.12	1.4	0.11	4.7
American Redstart *Setophaga ruticilla* L. (amre) I	0.13	1.5	0.90^{***}	39.8
Worm-eating Warbler *Helmitheros vermivora* Gmelin (S) (wowa) I	-	-	0.04	1.6
Ovenbird *Seiurus aurocapillus* L. (ovbi) I	-	-	0.14	6.3
Hooded Warbler *Setophaga citrina* Boddaert (howa) I	-	-	0.07	3.1
Common Yellowthroat *Geothlypis trichas* L. (coye) I	0.17	2.0	-	-
Savannah Sparrow *Passerculus sandwichensis* Gmelin (sasp) G	0.01	0.2	-	-
Total species	12	-	13	-
Total individuals/point	8.610	-	2.276	-
Number of points counted	73	-	42	-

sectivore, was the indicator species for most Pineland surveyed (53 of 70 points in this analysis; 76%). The eight points of the old-growth pine transect (Little Abaco; Table 1) made up another group, with two frugivores (Yellow-rumped Warbler, Gray Catbird) as indicators (Table 3). Three smaller groups of points were differentiated from other Pineland points by the occurrence of several wintering warbler species (all insectivores) that are found more routinely in Coppice.

Variation in the composition of the migrant bird community was correlated with vegetation structure in Pineland. Yellow-rumped Warbler and Gray Catbird were associated with taller trees, lower tree cover, higher understory cover, and a low ground cover of ferns (high scores on axis 1; Fig. 2A). These attributes characterize the points of the old-growth pine transect on Little Abaco, where the understory also uniquely had abundant *Myrica cerifera* (Bay-berry) shrubs as well many small trees of Gum-elemi, Poisonwood, and others. The Bay-berry (and other shrubs and small trees) was a prolific source of small fruits for the Yellow-rumped Warblers and Gray Catbirds. Conversely, the Common Yellowthroat, Northern Parula, and American Redstart (insectivores) and Savannah Sparrow (a granivore) tended to be found in Pineland sites with higher tree cover, lower understory cover (often palm type with *Sabal palmetto* [Pond-top] dominating), and higher ground cover of graminoids (low on axis 1; Fig 2A).

Coppice

Winter residents in Coppice points showed some spatial variation in composition based on clustering (ANOSIM: $R = 0.746$; $P = 0.001$), although the largest

Table 3. Indicator species for groups of points derived from clustering relative abundances of winter resident birds (Table 2) stratified by Pineland and Coppice. Indicator Value = relative frequency ´ relative abundance. *P*-values based on permutation test. Transects described in Table 1. Note: two surveyed points removed from Coppice and three from Pineland analyses because similarity was 1 with another point.

Group/Transect(s) (No. points analyzed)	Species	Indicator value (*P*)
Pineland points (70)		
All transects (53)	Palm Warbler	0.453 (0.001)
Power Station Road (3)	No indicators	-
Power Station Road (3)	Black-and-white Warbler	0.777 (0.004)
Road 45 Abaco National Park (3)	Prairie Warbler	0.516 (0.020)
	Common Yellowthroat	0.436 (0.071)
	Cape May Warbler	0.326 (0.082)
Little Abaco (8)	Gray Catbird	0.957 (0.001)
	Yellow-rumped Warbler	0.465 (0.055)
Coppice points (40)		
From all transects (19)	No indicators	-
From all transects (13)	American Redstart	0.606 (0.001)
Wilson City, Cherokee (4)	Gray Catbird	0.864 (0.001)
Eight Mile Cave (1)	Black-and-white Warbler	0.907 (0.002)
Eight Mile Cave, Wilson City, Cherokee (3)	Northern Parula	0.822 (0.008)
	Cape May Warbler	0.333 (0.091)

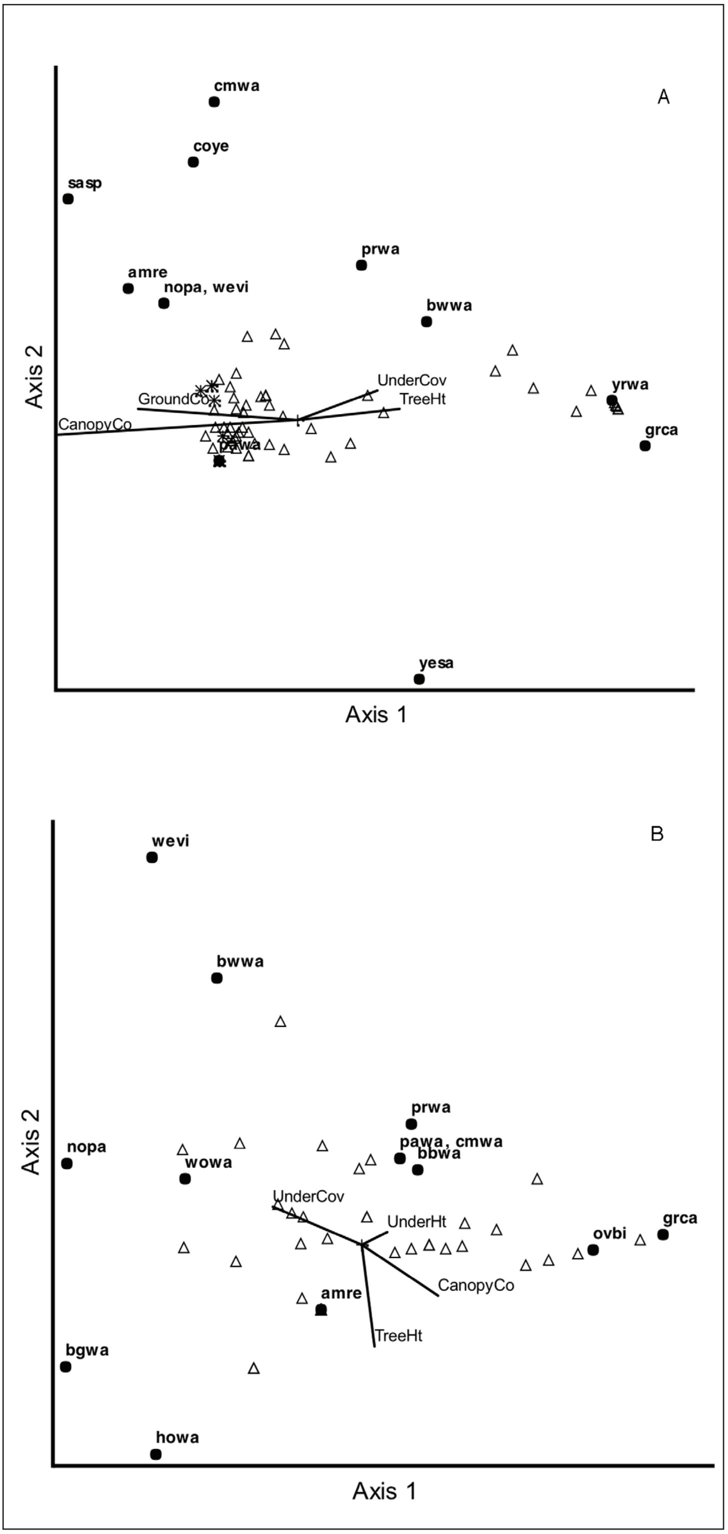

Figure 2. Ordination diagram showing point count stations arranged according to similarity in winter resident bird species composition based on DCA Axes 1 and 2 for A) Pineland (open triangles indicating mixed shrub understory type, asterisks indicating palm understory type) and B) Coppice. Bird species' position in ordination shown with labeled solid circles (abbreviations given in Table 2). Vectors indicate direction and strength of correlation of forest structure variables (Table 1) with trends in bird species composition among points. Squared correlation coefficient assessing significance of fitted environmental factors (significance was determined by permutation). A) Pineland: CanopyCo (Percent Tree Cover) r^2 = 0.292, P = 0.001; TreeHt (Tree Height) r^2 = 0.124, P = 0.025; UnderCov (Percent Understory Cover) r^2 = 0.094, P = 0.033; GroundCo (Ground Cover) r^2 = 0.193, P = 0.001. B) Coppice: CanopyCo r^2 = 0.057, P = 0.327; TreeHt r^2 = 0.029, P = 0.590; UnderCov r^2 = 0.047, P = 0.392; UnderHt (Understory Height) r^2 = 0.025, P = 0.615.

group of points (19 of 40 included in this analysis) had a diverse set of winter residents with no clear indicator species (Table 3). The next largest group of Coppice points (13) was characterized by the presence of American Redstart, whereas three smaller groups of points featured either Gray Catbird, or Black-and-white Warbler, or Northern Parula and *Setophaga tigrina* (Cape May Warbler). Most groups included points from different transects (Table 3), indicating that migrant species composition did not vary in any systematic way across Abaco.

When variation in Coppice winter resident species composition was examined in relation to variation in habitat structure, *Vireo griseus* (White-eyed Vireo), Worm-eating Warbler, Black-and-white Warbler, and Northern Parula were characteristic of sites with relatively high understory cover and low tree cover (low scores on the first ordination axis and high scores on the second; Fig. 2B). Gray Catbird and Ovenbird were associated with sites with somewhat taller trees, greater tree cover, and lower understory cover (high scores on axis 1; Fig. 2B). Hooded Warbler and Black-throated Green Warbler were associated with sites having a shorter understory canopy layer (low scores axis 2; Fig. 2B). Nevertheless, correlations of habitat structure with the ordination axes (describing main patterns of bird species differences among points) were very weak for Coppice sites (shown by short vectors; Fig. 2B). Finally, our lack of detections of Yellow-rumped Warbler in Coppice is surprising given its regular occurrence in this habitat in other studies in the northern Bahamas (Currie et al. 2005a, b; Wunderle and Waide 1993).

The trees Pigeon-plum, Mastic, Poisonwood, and Gum-elemi tend to dominate in Coppice. Clustering of relative basal area for 47 tree species in 20 Coppice plots suggested five groups (Table 4) varying in their species composition (ANOSIM: $R = 0.770$, $P = 0.001$). In addition to indicator species, these groups of Coppice plots can be defined from patterns of tree species dominance, similar to variations described for Andros by Smith and Vankat (1992). The largest group (B; 10 plots) included plots from three of five Coppice transects (throughout Abaco) with diverse species composition; only Mastic was a weak indicator species (IV = 0.318, $P = 0.131$). The other four groups, however, comprised plots from within a single transect; Mahogany (Group B) can dominate in less-disturbed forest whereas Poisonwood (Group E) is more abundant in disturbed Coppice (Table 1). This spatial clustering of species suggests that variation in Coppice tree composition is geographically structured. Nevertheless, we found no clear association between winter resident bird community composition and variation in tree species composition.

Discussion

The loss and degradation of wintering habitats in the Neotropics (mostly forests of highly varied successional histories) have been cited as potential threats to populations of migratory species (Arendt 1992, Askins et al. 1992), a concept best evaluated through long-term studies (Faaborg et al. 2013, Steadman et al. 2009). Coppice covers a limited extent of Abaco, but supports a diverse and unique

Table 4. Average basal area (cm^2 m^{-2}) for the 18 most abundant trees (including all indicator species) in Coppice plots within groups identified by clustering. Transect abbreviations: CH = Cherokee; EMC = Eight Mile Cave; GP = Gilpin Point; IH = Island Homes; WC = Wilson City. Indicator species ($P < 0.1$) shown in bold.

Species	Group A n = 2 (WC)	Group B n = 10 (EMC, IH,WC)	Group C n = 3 (CH)	Group D n = 2 (GP)	Group E n = 3 (IH)
Coccoloba diversifolia Meisn. (Pigeon-plum)	6.634	8.279	1.637	6.404	3.851
Mastichodendron foetidissimum (Jacq.) H.J. Lam (Mastic)	4.194	**6.496**	3.728	0.643	4.239
Metopium toxiferum (L.) Krug & Urb (Poisonwood)	0.633	3.727	0.236	5.611	**14.653**
Bursera simaruba (L.) Sarg. (Gum-elemi)	1.142	2.580	6.871	7.635	0.332
Swietenia mahagoni (L.) Jacq (Mahogany)	-	2.896	-	1.591	0.227
Exothea paniculata (Juss.) Radlk. (Inkwood)	2.478	1.807	3.144	0.350	2.432
Ficus aurea Nutt. (Golden Wild Fig)	-	1.585	3.636	-	-
Guapira obtusa (Jacq.) Little (Beefwood)	4.197	1.162	1.013	0.410	1.908
Hypelate trifoliata Sw. (White Ironwood)	1.437	0.765	0.330	-	-
Sideroxylon salicifolium (L.) Lam. (Cassada-wood)	-	0.762	**3.483**	0.065	1.398
Eugenia axillaris (Sw.) Willd. (White Stopper)	-	0.662	**1.347**	0.073	-
Nectandra coriacea (Sw.) Griseb. (Lancewood)	0.369	0.412	-	**0.925**	0.114
Eugenia confusa DC. (Red Stopper)	**11.224**	0.293	0.028	0.584	0.258
Acacia choriophylla Benth. (Cinnecord)	-	0.290	-	**0.718**	0.232
Piscidia piscipula (L.) Sarg. (Jamaica Dogwood)	-	0.164	**2.707**	-	0.960
Amyris elemifera L. (White Torch)	**0.521**	0.146	0.171	-	0.059
Coccoloba swartzii Meisn. (Bastard Pigeon-plum)	-	0.082	-	**1.072**	0.191
Simarouba glauca DC. (Paradise Tree)	-	0.011	-	-	**0.076**

winter resident bird community, including three species of conservation concern (Table 2). On Abaco (and elsewhere in The Bahamas), Coppice has become more threatened, especially in coastal areas, as land uses have changed from historically extensive (selective logging, agriculture) to currently intensive (resorts, second homes, and energy development; Sullivan-Sealy 2002). Bahamian Pineland is fire-adapted (O'Brien et al. 2008), and human-set fires have been frequent and widespread on Abaco (based on a 75-year record; Miller 2007); increasing fire frequency in the past 300–400 years corresponds to increasing dominance of pine on Abaco (Slayton 2010). Coppice already threatened by land clearing may be further lost if high-intensity fires burn from Pineland into the edges of Coppice (e.g., during drought).

Winter residents were more abundant in Pineland than Coppice, as was also found on Andros (Currie et al. 2005a). In Pineland, we found that bird community composition varied systematically with overstory cover and height, and understory cover and type, as Emlen (1977) discovered on Grand Bahama. In Coppice, we found no clear association of bird community composition with observed variation in habitat structure or tree species composition. This finding may reflect that Coppice occurs mainly on windward ridges that experience the full force of Abaco's frequent hurricanes (Caribbean Hurricane Network 2013), which results in considerable heterogeneity in habitat structure and food availability on small spatial scales. This structuring of Coppice by frequent natural disturbance may also explain why we did not detect trends in bird community composition related to the degree of anthropogenic disturbance and fragmentation by roads and other clearings (Table 1). Even small patches of disturbed Coppice supported a diverse winter bird community.

The four species (Gray Catbird, Cape May Warbler, Prairie Warbler, and White-eyed Vireo) without a statistically significant difference in relative abundance in Pineland vs. Coppice (Table 2) were detected in Pineland mainly where the understory, consisting of shrubs and small trees (<5 cm DBH) characteristic of Coppice, was tall and/or dense (Fig. 2A). Gray Catbird and Prairie Warbler have been classified as mid-successional or forest-edge species in the Caribbean (Wunderle and Waide 1993). Thus, the presence of these four species in Pineland may depend on patches of broadleaf species in the understory. The Prairie Warbler, however, has been observed to be a habitat generalist elsewhere in the Caribbean, including pine forest (Latta and Faaborg 2001).

By Neotropical standards, the general distribution and relative abundance of both migratory and resident species of birds are fairly well known in the Bahamian islands (Buden 1987, Hallett 2006, White 1998). Even so, surveys of Bahamian bird communities are available for breeding species only on Grand Bahama (Emlen 1977, Lloyd and Slater 2011), and for winter resident species just on Grand Bahama (Emlen 1977), Abaco (Lee 1996a, b), Andros (Currie et al. 2005a), and Eleuthera (Currie et al. 2005b). Thus, we remain in the early stages of learning about long-term trends in Bahamian winter bird communities.

The study most directly comparable to ours took place in the second growth Pineland of Abaco National Park in December 1995 (Lee 1996a, b). Lee's surveys included 60 counted points, the results of which we compared to our own 65 counted points in Pineland (Table 5; we excluded our eight counted points from the relatively mature Pineland of Little Abaco to make our data more comparable to his). Each of the six most common winter residents recorded in December 1995 was recorded by us in 2007–2012; similarly, the five most commonly recorded species in our surveys also were found by Lee. Overall, we see no evidence of major changes in species composition over the 12 to 17 years that separate the Pineland bird surveys on Abaco. The largest change in relative abundance of a single species involved the Palm Warbler; while ranked first in abundance during each time period, ≈3.3 more individual Palm Warblers were detected per point in 2007–2012 than in 1995. Two other species (both frugivores) showed notable changes in relative abundance, with the Yellow-rumped Warbler gaining ≈0.5, and the Gray Catbird

Table 5. Comparison of point-count data for winter resident birds in Pineland habitat, Bahamas. Data for Andros (February 2002; rank order only) are from the three Pineland habitat categories of Currie et al. (2005a). Data for Grand Bahama (1968–1971; Jan, Feb; rank order only) are from Emlen (1977). Data for Abaco (Dec 1995) are from Lee (1996a, b). Data for Abaco (2007–2012; Dec, Jan) are our own, but exclude the eight points from the relatively mature Pineland transect on Little Abaco. To make the Abaco data sets more comparable, we eliminated Lee's data from walked transects and car surveys. The Abaco data are in individuals per point, with rank order in parentheses. Because of major methodological differences, individuals per point are not given for Andros or Grand Bahama. T = tied for; (S) = species of conservation concern (US Fish and Wildlife Service 2008). Scientific names given for species not previously mentioned.

Species	Andros 2002	Grand Bahama 1968–1971	Abaco 1995	Abaco 2007–2012	Difference
Sharp-shinned Hawk (*Accipiter striatus* Viellot)	-	-	0.02 (T7)	-	-0.02
Merlin (*Falco columbarius* L.)	-	-	0.02 (T7)	-	-0.02
Yellow-bellied Sapsucker	-	9	-	0.02 (T9)	+0.02
Gray Catbird	-	6	0.52 (2)	0.02 (8)	-0.50
White-eyed Vireo	-	-	0.03 (6)	0.01 (T11)	-0.02
Northern Parula	-	11	-	0.01 (T11)	+0.01
Cape May Warbler	-	12	-	0.03 (7)	+0.03
Black-throated Blue Warbler	-	13	0.02 (T7)	-	-0.02
Yellow-rumped Warbler	4	2	-	0.54 (2)	+0.54
Black-throated Green Warbler (S)	-	8	-	-	-
Prairie Warbler (S)	2	3	0.28 (4)	0.53 (3)	+0.25
Palm Warbler	1	1	0.97 (1)	4.26 (1)	+3.29
Black-and-white Warbler	T6	4	0.02 (T7)	0.13 (6)	+0.11
American Redstart	3	7	0.22 (5)	0.15 (5)	-0.07
Ovenbird	-	10	-	-	-
Common Yellowthroat	5	5	0.45 (3)	0.19 (4)	-0.26
Savannah Sparrow	-	-	-	0.02 (T9)	+0.02
Total species	7	13	10	12	+2
Total individuals/point	-	-	2.43	5.90	+3.47
Number of points counted	90	- (transects)	60	65	-

declining by ≈0.5 individuals/point. Owing to spatial and temporal variation in fruit availability (both between and within years), localized variation in the abundance of frugivorous species is not unexpected.

Looking at the winter resident birds from Pineland surveyed on other Bahamian islands (Andros in 2002, Grand Bahama in 1968–1971), the Palm Warbler ranked number one in abundance in every data set (Table 5). We note as well that the six most common species in any given Pineland survey were also typically in the top six species of the other Pineland surveys. This same consistency in rank abundance is apparent when comparing the results of Coppice surveys on Andros, Eleuthera, and Abaco, where four species (Gray Catbird, Prairie Warbler, American Redstart, and Ovenbird) were always in the top five (Table 6). In Coppice, the Yellow-rumped Warbler ranked high on Andros and Eleuthera, but we did not detect it in this habitat on Abaco. The lack of Bay-berry in our Coppice plots may account for this difference.

Before any potential changes in relative abundance of Bahamian winter resident birds can be detected, data are needed from larger geographic areas and over longer time intervals (Latta 2012, Latta and Faaborg 2009). Based on current evidence,

Table 6. Rank order of point-count data for winter resident birds in Coppice habitat, Bahamas, where 1 is the most abundant. Data for Andros (Feb 2002) and Eleuthera (Jan-Mar 2003) are from the "Short coppice" and "Tall coppice" categories of Currie et al. (2005a, 2005b). Data for Abaco (2007–2012; Dec, Jan) are our own. Only rank order is given because of major methodological differences in the surveys. T = tied for; (S) = species of conservation concern (US Fish and Wildlife Service 2008). Scientific names given for species not previously mentioned.

Species	Andros 2002	Eleuthera 2003	Abaco 2007–2012
Gray Catbird	4	1	3
White-eyed Vireo	-	T11	T11
Northern Parula	T9	T9	4
Magnolia Warbler *Setophaga magnolia* Wilson	T9	-	-
Cape May Warbler	T9	T7	T11
Black-throated Green Warbler (S)	-	-	10
Black-throated Blue Warbler	T5	-	6
Yellow-rumped Warbler	T5	2	-
Kirtland's Warbler (S) *Setophaga kirtlandi* Baird	T9	-	-
Prairie Warbler (S)	1	4	2
Palm Warbler	T9	6	T11
Black-and-white Warbler	T5	T9	7
American Redstart	2	3	1
Worm-eating Warbler (S)	T9	T7	9
Ovenbird	3	5	5
Northern Waterthrush *Parkesia noveboracensis* Gmelin	T9	-	-
Common Yellowthroat	-	T11	-
Hooded Warbler	T5	-	8
Indigo Bunting *Passerina cyanea* L.	T5	-	-
Total species	16	12	13
Number of points counted	60	60	42

there appears to have been little change in the winter resident bird communities of the Bahamas in recent decades. Given modern trends in land use (Sullivan-Sealey et al. 2002), some protection of these forested habitats from clearing would help to maintain habitats for winter resident landbirds in the northern Bahamas in the coming decades.

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