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Woodland size and vegetation effects on resident and non-resident woodland birds in Bermuda

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Miguel Mejías¹ and Erica Nol²

Abstract Human colonization on oceanic islands typically has disastrous consequences for indigenous flora and fauna. Since settlement in 1612, the native evergreen forest on the island of Bermuda has been fragmented by development and largely replaced by exotic trees, with unclear consequences for woodland birds. We quantified the number of woodland birds using modified point counts in 28 woodlands on Bermuda, from 24 March to 9 April 2014. We examined the impact of woodland size and vegetation features on total species richness and abundance of resident and non-resident woodland birds, and on abundance of the Bermuda population of White-eyed Vireos (*Vireo griseus bermudianus*). Woodland area had significant positive relationships with total species richness, total woodland bird abundance, and abundance of White-eyed Vireos. Similarly, species richness and abundance of non-resident woodland birds significantly increased with woodland area. None of the vegetation characteristics explained any of the woodland bird abundance metrics. Our results suggest that larger woodlands are essential habitats for supporting diverse and large communities of resident and non-resident woodland birds in Bermuda. Our study also highlights the adaptability of woodland birds, particularly the White-eyed Vireo, to exotic vegetation.

Keywords avian conservation, Bermuda woodland birds, exotic vegetation, island birds, woodland fragment size

Resumen Efectos del tamaño del parche de bosque y la vegetación en paseriformes residentes y no residentes en Bermudas—La colonización de islas oceánicas por el hombre tiene consecuencias desastrosas para la flora y la fauna indígenas. Desde el asentamiento en 1612, los bosques siempreverdes de las islas Bermudas han sido fragmentados por la urbanización y reemplazados principalmente por especies exóticas, con consecuencias poco claras para las aves de bosque. Desde el 24 de marzo al 9 de abril de 2014, este grupo de aves fue monitoreado con puntos de conteo modificados en 28 parches de bosque en Bermudas. Examinamos el impacto del tamaño del parche de bosque y las características de la vegetación en la riqueza de especies total, la abundancia de las aves de bosque residentes y no residentes y la abundancia de la población de Bermudas de *Vireo griseus bermudianus*. El tamaño del parche de bosque tuvo un efecto positivo significativo con la riqueza y la abundancia de especies totales y la abundancia de *Vireo griseus bermudianus*. De igual manera, la riqueza de especies total y la abundancia de aves de bosque no residentes aumentaron significativamente con el tamaño del parche de bosque. Ninguna de las características de la vegetación fue capaz de explicar los valores de abundancia de las aves de bosque. Nuestros resultados sugieren que parches de bosque más grandes son hábitats esenciales para mantener comunidades grandes y diversas de aves de bosque residentes y no residentes en Bermudas. Nuestro estudio también destaca la adaptabilidad de estos grupos, particularmente de *Vireo griseus bermudianus*, a la vegetación introducida.

Palabras clave aves de bosque de Bermudas, aves de islas, conservación de aves, tamaño del parche de bosque, vegetación introducida

Résumé Taille des zones forestières et effets de la végétation sur les oiseaux forestiers résidents et non résidents aux Bermudes — La colonisation humaine des îles océaniques a généralement eu des conséquences désastreuses sur la flore et la faune indigènes. Depuis la colonisation de l'île des Bermudes en 1612, la forêt sempervirente indigène a été fragmentée par le développement et largement remplacée par des arbres exotiques, ce qui a eu des conséquences incertaines sur les oiseaux forestiers. Nous avons quantifié le nombre d'oiseaux forestiers par des comptages par points modifiés dans 28 zones forestières des Bermudes, du 24 mars au 9 avril 2014. Nous avons examiné l'impact de surface forestière et des caractéristiques de la végétation sur la richesse spécifique totale et l'abondance des oiseaux forestiers résidents et non résidents, ainsi que sur l'abondance de la population du Viréo aux yeux blancs, sous-espèce des Bermudes (*Vireo griseus bermudianus*). Il existe une corrélation positive significative de la surface forestière avec la richesse spécifique totale, l'abondance totale des oiseaux forestiers et l'abondance du Viréo aux yeux blancs. De même, la richesse spécifique et l'abondance des oiseaux forestiers non résidents augmentent de manière significative avec la superficie forestière. Aucune des caractéristiques de la végétation n'explique les mesures de l'abondance des oiseaux forestiers. Nos résultats suggèrent que

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les grandes forêts sont des habitats essentiels pour le soutien des communautés diverses et importantes d'oiseaux forestiers résidents et non résidents aux Bermudes. Notre étude souligne également la capacité d'adaptation des oiseaux forestiers, en particulier du Viréo aux yeux blancs, à la présence d'une végétation exotique.

Mots clés avifaune insulaire, conservation des oiseaux, oiseaux forestiers des Bermudes, taille des fragments de forêt, végétation exotique

The native terrestrial flora and fauna of Bermuda has been severely altered since human settlement in the early 1600s (Wingate 1990, Sterrer *et al.* 2004). Prior to settlement, Bermuda was covered by a dense evergreen forest that consisted largely of Bermuda cedar (*Juniperus bermudiana*), Bermuda palmetto (*Sabal bermudana*), and a handful of native shrub species (Britton 1918). European settlers rapidly altered the landscape through large-scale burning and deforestation (Wingate 1990). In the 1940s, Bermuda cedar was nearly pushed to extinction with the accidental introduction of two scale insects (Hemiptera) that killed 90–95% of the junipers within 10 yr (Challinor and Wingate 1971, Wingate 1990, Rueger and von Wallmenich 1996). Vegetation on the island now consists almost entirely of exotic plant species. This catastrophic near-extinction event following human settlement is typical of island biota, which are notoriously sensitive to mainland invaders (Showler *et al.* 2002, Courchamp *et al.* 2003, Sterrer *et al.* 2004). In general, island biodiversity is also threatened by mammalian predators that accompanied human settlers, including cats (*Felis catus*; Burns *et al.* 2013), rats (*Rattus* spp.; Verrill 1902), and pigs (*Sus scrofa*; Strachey 1625), all of which decimate populations of native birds, reptiles, and plants (Le Corre and Jouventin 1997, García 2000).

Fossil records reveal that Bermuda was previously inhabited by a relatively rich community of endemic land-birds, including an endemic genus of hawk (*Bermuteo avivorus*; Olson 2008), a dove (*Zenaida* sp.; Olson 2011), a towhee (*Pipilo naufragus*; Olson and Wingate 2012), a small owl (*Aegolius gradyi*; Olson 2012), and the Bermuda Flicker (*Colaptes oceanicus*; Olson 2013). The present resident land-bird community of Bermuda comprises 13 species, at least 6 of which are human introductions (Amos 1991, Avery *et al.* 2013). Among Bermuda's avifauna, only one land-bird is currently recognized as an endemic: the local subspecies of White-eyed Vireo (*Vireo griseus bermudianus*), believed to be a descendant of the North American White-eyed Vireo (Amos 1991). The local vireo population in Bermuda has shorter wings, duller plumage, and a different repertoire of songs than its North American counterpart (Amos 1991). Currently, Bermudian White-eyed Vireos are classified as a level 1 protected species and considered to be Vulnerable under the Bermuda Protected Species Amendment Order (2016). Although no current estimates of its abundance are available, its status as the last endemic land-bird in Bermuda makes it of extreme conservation importance. While Bermuda has a depauperate resident avifauna, migrant songbirds are regularly recorded. Nearly 400 species of birds have been documented throughout the island's ornithological history, with an average of 200 migrant species seen annually (Amos 1991).

Human development pressures have influenced the extent of both native and exotic vegetation. By 1982, new housing units

were being built at a rate of 300 units/yr; in the present day, Bermuda is one of the most densely populated oceanic islands in the world, with a population surpassing 62,000 (1,275 people/km²; Wingate 1990, Dobson 2002). Much of Bermuda's land area has been converted into urban development, with approximately 14% of the island covered by impermeable surfaces (Dobson 2002). Consequently, such development has resulted in the fragmentation of Bermuda's forest (hereafter "woodlands") into discrete patches of various sizes.

Woodland area can have implications for the composition of bird communities (Freemark and Collins 1992, Donnelly and Marzluff 2004, Dolman *et al.* 2007). For example, the reduction of woodland area increases the amount of available edge habitat, leaving some species vulnerable to avian predators, such as American Crows (*Corvus brachyrhynchos*), that are more abundant along forest edges (Whitcomb *et al.* 1981, Donovan *et al.* 1995, Burke and Nol 2000). Thus, larger woodlands can reduce nest predation and increase reproductive success (Burke and Nol 2000, Aquilani and Brewer 2004). Food abundance can also be higher in larger woodlands, making them more suitable to woodland birds (Burke and Nol 1998). Other studies, however, suggest that small woodlands may not be detrimental to fitness of breeding woodland birds (Friesen *et al.* 1999, Zanette and Jenkins 2000, Zanette 2001).

Although the effect of woodland area on birds is well documented on continents, studies on remote oceanic islands are limited. Here we report results of a study on the effects of woodland area on the woodland bird community of Bermuda. In this paper, we define woodland birds as terrestrial birds, passerines and non-passerines, that are known to occur within Bermuda's woodlands. Our objective was to determine if woodland size was a good predictor of the species richness or abundance of all woodland bird species or the abundance of Bermudian White-eyed Vireos in particular. We were also interested in any relationship between woodland area and the species richness and abundance of migrant and wintering woodland birds (hereafter "non-resident woodland birds"). Because larger woodlands may exhibit higher food availability (in the form of insects and berries) for woodland birds (Burke and Nol 1998), we predicted that total species richness and woodland bird abundance, as well as abundance of White-eyed Vireos, would increase with increasing woodland area. We also predicted that species richness and abundance of non-resident woodland birds would increase with woodland area. Finally, we tested if vegetation structure (i.e., density of forest layers) of the woodlands could help to explain total species richness or woodland bird abundance, abundance of White-eyed Vireos, or species richness or abundance of non-resident woodland birds. We also provide a description of tree species composition of woodlands to investigate how

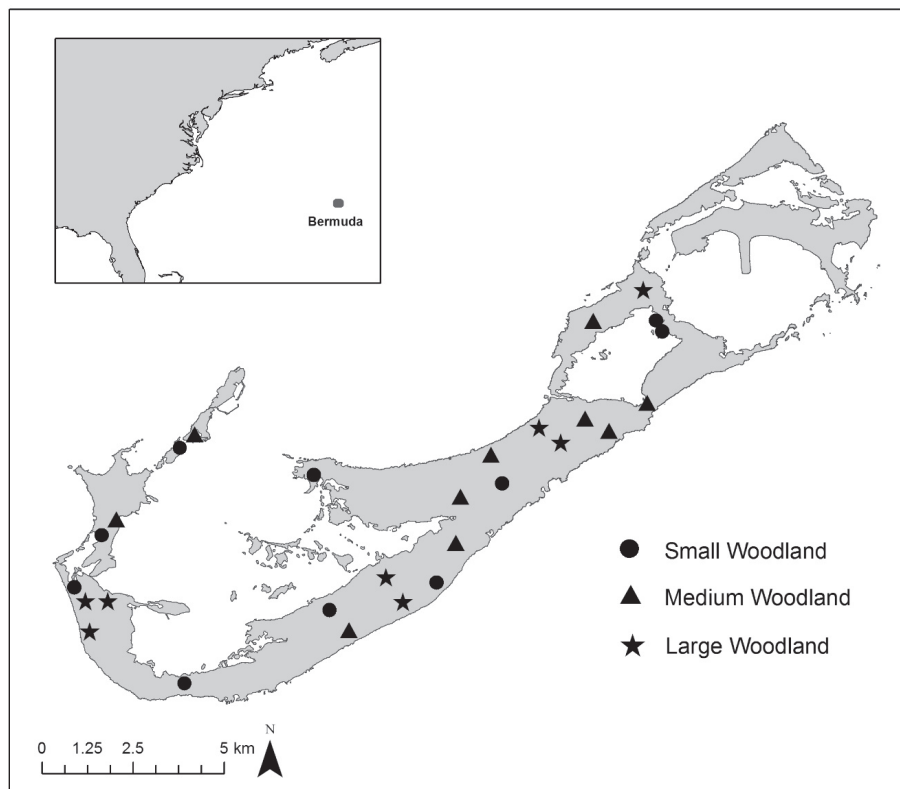


Fig. 1. Locations of all woodlands where point counts were conducted on the island of Bermuda between 24 March and 9 April 2014.

Bermuda's woodland birds utilize native and non-native vegetation.

Methods

This study was conducted on the island of Bermuda (32°18'N, 64°47'W) in the Atlantic Ocean, from 24 March to 9 April 2014. The topography of the island consists of hills and valleys, and its rocks originate from beach-derived calcareous sediments, deposited initially as dunes that have since cemented into aeolianite limestone (Bretz 1960, Land 1970). The soil supporting woodland flora originated from the erosion of this limestone by weathering over time (Britton 1918). We initially identified 100 woodlands throughout Bermuda and randomly selected 28 woodlands under the constraints of an approximate equal number in each of the following three size categories: small woodlands averaging 0.79 ha \pm 0.05 SE, $n = 10$; medium woodlands averaging 1.77 ha \pm 0.1 SE, $n = 10$; and large woodlands averaging 3.28 ha \pm 0.6 SE, $n = 8$ (Fig. 1). Vegetation in woodlands was primarily comprised of non-native plant species with allspice (*Pimenta dioica*), fiddlewood (*Citharexylum spinosum*), Brazilian pepper (*Schinus terebinthifolius*), and Chinese fan palm (*Livistona chinensis*) as dominant trees. Woodlands were all second growth, and between 53 and 63 yr old. Permission to survey woodlands on privately owned land was obtained directly from landowners.

We conducted modified 50-m radius point counts in each woodland during morning hours between 0700 and 1000. A single survey point was established within each woodland. Point count locations were chosen by identifying the approximate

center point within each woodland with high resolution aerial photographs generated within ESRI ArcMap 10 geographic information system (GIS) software (Esri, Redlands, CA, USA). Although our 50-m radius was contained even within our smallest woodlands, the periphery of our circle within smaller sites was sometimes close to edge habitat and is an unavoidable consequence of their small areas. Modified point counts consisted of regular listening and observing surveys for two successive 4-min periods, and then for the next 3 min we alternated between 6 s of pishing and 24 s of listening and observing to determine if we could lure in any quiet birds. We performed these 11-min surveys twice in each woodland during the study period. To reduce biases from temporal effects, we conducted the second point count at each woodland's center point at a different time within our 3-hr timeframe. We did point counts only on days when there was no rain and light to no wind (Austen *et al.* 2001).

In each woodland, we also conducted a single vegetation survey using a 11.3 m radius plot centered on our bird survey point. Within this plot, we visually estimated the percent cover of the herbaceous (< 0.5 m), canopy (0.5–2 m, > 2–10 m), and supercanopy (> 10 m) vegetation layers. We then randomly selected a 6 m \times 6 m sub-plot within the larger plot, and identified and counted all mature trees (those with a diameter at breast height [DBH] > 2.5 cm). Within this sub-plot, we further selected a 3 m \times 3 m square and identified and counted all saplings therein, when they were present. Using 10-cm resolution aerial photographs taken in May 2012 and provided by the Bermuda Government, we identified and calculated the areas of our study woodlands in Bermuda. The areas were measured in hectares using ESRI

ArcMap 10 GIS software. Although we selected and mapped our study woodlands in 2013, a year prior to this study, the forest composition remained unchanged for 27 of the 28 sample sites. One large woodland was downgraded to a smaller category due to moderate forest clearing.

Statistical Analysis

We used general linear models to test for relationships between the predictor variables (woodland area, and herbaceous, canopy, and supercanopy cover) and all avian species metrics (total species richness, total woodland bird abundance, White-eyed Vireo abundance, non-resident species richness, and non-resident abundance). For regressions, we plotted the residuals of each model and checked for any violation of homogeneity. If assumptions of homogeneity were violated, we applied a generalized linear model with a Poisson error structure (McCullagh and Nelder 1989). To avoid counting birds attracted to our lure, we only included woodland birds seen or heard within the first 8 min of point counts in our estimate of total woodland bird abundance, while woodland birds seen or heard during the remaining 3-min “pishing phase” counted towards total species richness only. Birds seen or heard flying overhead were excluded from the analysis. All general and generalized linear models are presented with respective regression coefficients, *t* statistics, and *p*-values. Results from all tests were considered significant if $p < 0.05$.

Vegetation variables (herbaceous, canopy, and supercanopy cover) were chosen to represent the structural diversity of each woodland. We first tested for correlations among vegetation variables. As no significant correlations were detected, we subsequently used all three vegetation variables in our analyses. We used the species composition only in descriptions of habitat. We used paired *t*-tests to compare mean abundance of native trees to exotic trees per 6 m × 6 m sub-plot and to compare mean abundance of native saplings to introduced saplings in the smaller 3 m × 3 m squares.

In addition to general and generalized linear models, we also used a model selection approach to determine the relative importance of woodland area and vegetation variables on all five response variables (Burnham and Anderson 1998, Anderson and Burnham 2002). We tested all combinations of additive models on each response variable. We evaluated the AIC_c weight of top-ranked models and compared them to weaker ones. Significant model selection results are presented as beta (β) ± standard error (SE) and 95% confidence intervals (CI). All statistical analyses were conducted in R (R Core Team 2010), including using the MuMIn package (Bartoń 2011) to generate AIC_c tables.

Results

Avian Species Composition

We detected 442 woodland birds comprising 17 species across all woodlands; 400 (90%) individuals were residents and 42 (10%) were non-residents (Table 1). Of the resident woodland birds detected, 190 (48%) were native and 210 (53%) were introduced. The non-resident guild included five (83% of all non-resident species) species of New World wood-warblers (family Parulidae). Five of the 17 woodland bird species found in woodlands are recognized as invasive species (i.e., species that have

Table 1. Total abundance (sum of all point counts) and status (resident or non-resident) of all woodland birds recorded during point counts within Bermuda woodlands from 24 March to 9 April 2014. (N) native species, (I) introduced species, (*) invasive species, and (P) species detected only because they responded to pishing.

Common Name	Scientific Name	Status	Total
Feral Chicken ^{I*}	<i>Gallus gallus</i>	resident	13
Common Ground-Dove ^N	<i>Columbina passerina</i>	resident	11
Mourning Dove ^N	<i>Zenaidura macroura</i>	resident	46
Great Kiskadee ^{I*}	<i>Pitangus sulphuratus</i>	resident	105
White-eyed Vireo ^N	<i>Vireo griseus bermudianus</i>	resident	59
American Crow ^{I*}	<i>Corvus brachyrhynchos</i>	resident	14
Gray Catbird ^N	<i>Dumetella carolinensis</i>	resident	55
European Starling ^{I*}	<i>Sturnus vulgaris</i>	resident	19
House Sparrow ^{I*}	<i>Passer domesticus</i>	resident	6
European Goldfinch ^I	<i>Carduelis carduelis</i>	resident	30
Ovenbird ^N	<i>Seiurus aurocapilla</i>	non-resident	31
Black-and-white Warbler ^{N,P}	<i>Mniotilta varia</i>	non-resident	1
American Redstart ^N	<i>Setophaga ruticilla</i>	non-resident	2
Northern Parula ^N	<i>Setophaga americana</i>	non-resident	5
Black-throated Green Warbler ^{N,P}	<i>Setophaga virens</i>	non-resident	1
Northern Cardinal ^I	<i>Cardinalis cardinalis</i>	resident	42
Indigo Bunting ^N	<i>Passerina cyanea</i>	non-resident	2

become superabundant and have been observed competing with, harming, and displacing native birds). The Great Kiskadee (*Pitangus sulphuratus*) was by far the most abundant bird detected. Other common species across woodlands included the Bermudian White-eyed Vireo and Gray Catbird (*Dumetella carolinensis*). Non-resident woodland birds were virtually absent from all small woodlands.

Woodland Area and Vegetation Effects

A strongly significant positive relationship was found between woodland area and total species richness ($R^2 = 0.44$, $t = 4.72$, $p < 0.0001$; Fig. 2). None of our vegetation variables explained total species richness ($p > 0.05$ for all tests). Total woodland bird abundance increased significantly with woodland area ($R^2 = 0.71$, $t = 7.90$, $p < 0.0001$; Fig. 2). To ensure that the relationship between our predictor variables and total woodland bird abundance was not skewed by the numbers of the highly abundant kiskadee, we initially ran a generalized linear model excluding kiskadees. Despite excluding kiskadees from the analysis, total woodland bird abundance still increased significantly with woodland area. Therefore, we report total woodland bird abundance with kiskadees included for final analysis. None of our vegetation variables significantly affected total woodland bird abundance ($p > 0.05$ for all tests). White-eyed Vireo abundance also increased with woodland area ($R^2 = 0.23$, $t = 2.82$, $p = 0.009$;

Fig. 2), but our vegetation variables were not significantly related to the abundance of White-eyed Vireos ($p > 0.05$ for all tests). Species richness and abundance of non-resident woodland birds also increased as a function of woodland size (species richness: $R^2 = 0.46$, $t = 5.06$, $p < 0.0001$; abundance: $R^2 = 0.46$, $t = 4.71$, $p < 0.0001$; Fig. 2). Vegetation variables exhibited no significant effect on the species richness of non-resident woodland birds or on the abundance of non-resident woodland birds ($p > 0.05$ for all tests).

Vegetation Composition

We identified 15 species of trees across sampling sites (Fig. 3). Woodlands were dominated largely by introduced trees (paired $t_{24} = 6.99$, $p < 0.0001$). Twelve (80%) of the surveyed species of trees were introduced, whereas the remaining three species (20%) were native. Among introduced trees, 10 (83%) were invasive. Dominant tree species included allspice, fiddlewood, Brazilian pepper, and Chinese fan palm, all of which are invasive (Challinor and Wingate 1971). Saplings of introduced species largely outnumbered native saplings ($t_{19} = -6.38$, $p < 0.0001$). Sapling species also consisted of twelve (80%) introduced and three (20%) native species.

Comparison of Woodland Size and Vegetation Models

The model that best explained total species richness consisted of canopy cover, woodland area, and supercanopy cover (Table 2). Woodland area was present in all top ranking models, with a cumulative AIC_c weight of 1.00. Total species richness was positively related to woodland area ($\beta = 0.85 \pm 0.18$, 95% CI: 0.48–1.22) and supercanopy cover ($\beta = 2.02 \pm 1.06$, 95% CI: -0.16–4.20) and negatively related to canopy cover

($\beta = -3.16 \pm 1.61$, 95% CI: -6.46–0.14), although all parameter estimates for the vegetation variables overlapped zero, indicating low reliability. Similarly, woodland area appeared consistently among all top models explaining total woodland bird abundance, with a cumulative weight of 1.00. Total woodland bird abundance was positively related to woodland area ($\beta = 3.63 \pm 0.46$, 95% CI: 2.69–4.57). All vegetation parameter estimates overlapped zero.

The best model for predicting White-eyed Vireo abundance was that containing only the variable woodland area (Table 2), with a cumulative AIC_c weight of 0.99. White-eyed Vireo abundance was positively related to woodland area ($\beta = 0.52 \pm 0.18$, 95% CI: 0.15–1.04). Models containing vegetation variables had parameter estimates that overlapped zero, suggesting that they are much less important in explaining White-eyed Vireo abundance than woodland area.

Woodland area was the best variable for predicting both non-resident species richness and abundance, and for both variables the relationship was positive (species richness: $R^2 = 0.57 \pm 0.11$, 95% CI: 0.34–0.80; abundance: $R^2 = 0.82 \pm 0.17$, 95% CI: 0.47–1.17) (Table 2). The cumulative AIC_c weight for both non-resident species richness and abundance was 1.00. Non-resident abundance exhibited a negative relationship with herbaceous cover. However, for both non-resident models, all the parameter estimates for vegetation variables overlapped zero, indicating low reliability.

Discussion

Our analysis suggests that woodland area is an important predictor of the distribution of woodland bird communities in Bermuda. Total species richness and woodland bird abundance

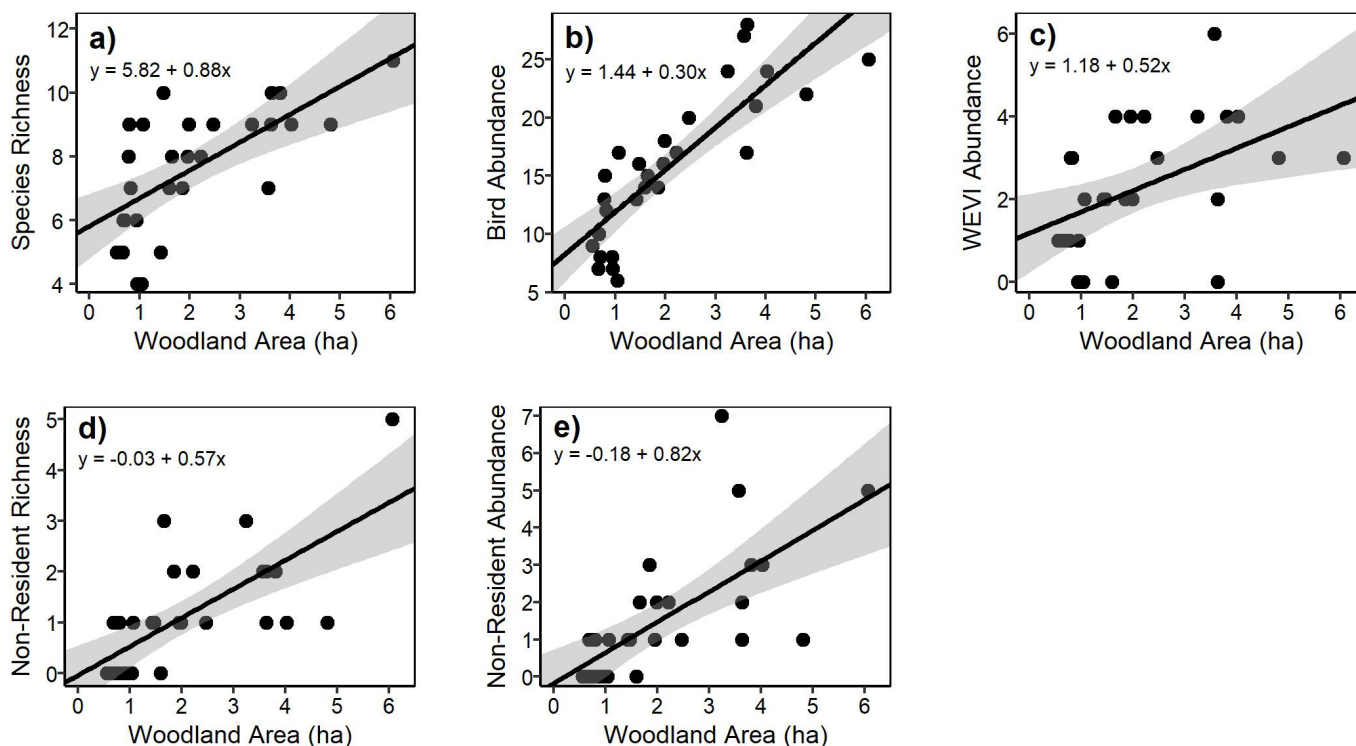


Fig. 2. The relationships between woodland area and (a) total species richness, (b) total woodland bird abundance, (c) White-eyed Vireo abundance, (d) non-resident species richness, and (e) non-resident abundance.

increased with woodland area. Smaller woodlands supported an average of six species. In contrast, larger woodlands supported an average of nine species, which included non-resident woodland birds that were mostly absent from small woodlands. Woodland size accounted for almost half ($R^2 = 0.44$) of the variation in total species richness. In comparison, more than half of the variation in total woodland bird abundance was explained by woodland area ($R^2 = 0.71$). Many of the woodland birds, particularly Mourning Doves, White-eyed Vireos, Gray Catbirds, and Northern Cardinals, consistently occurred in low numbers in small woodlands and their numbers increased only marginally in large woodlands. Great Kiskadee was by far the most abundant woodland bird encountered across all woodlands, occurring in consistently high numbers. This was not surprising as the species quickly established itself as one of the most invasive birds in Bermuda after its intentional introduction in 1957 (Crowell and Crowell 1976). Its prevalence among woodlands, regardless of their size, is further testament to its invasive nature.

Our results are consistent with most of the avian literature that finds a positive relationship between woodland area and species richness (van Dorp and Opdam 1987, Rudnický and Hunter 1993, Andren 1994). Likewise, evidence from previous work also acknowledges the positive effect patch size has on songbird abundance (Howell *et al.* 2000, Lee *et al.* 2002, Myczko *et al.* 2014). These findings, however, contrast with a few studies where no such relationship was found (Golet *et al.* 2001, Askins *et al.* 2007, Olechnowski and Debinski 2008). Discrepancies among these similar studies might be explained by differences in the nature

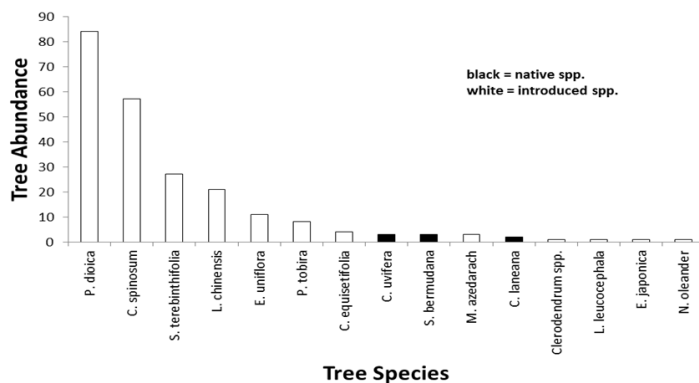


Fig. 3. The abundance of all mature (DBH > 2.5 cm) native and introduced tree species counted within 6 m x 6 m sub-plots across all woodlands ($n = 28$) in Bermuda from 24 March to 9 April 2014. Latin names, followed when possible by associated vernacular names (VN), of native and introduced trees are listed below. Invasive species are denoted with an asterisk (*). Native species: *Cassine lanceana* VN: Bermuda olivewood; *Coccoloba uvifera* VN: baygrape; and *Sabal bermudana* VN: Bermuda palmetto. Introduced species: *Casuarina equisetifolia* VN: Australian pine*; *Clerodendrum* spp.*; *Eriobotrya japonica* VN: loquat tree*; *Eugenia uniflora* VN: Surinam cherry*; *Leucaena leucocephala* VN: jumbie bean*; *Livistona chinensis* VN: Chinese fan palm*; *Melia azedarach* VN: white cedar*; *Nerium oleander* VN: oleander; *Pittosporum tobira* VN: Japanese pittosporum; *Pimenta dioica* VN: allspice*; *Citharexylum spinosum* VN: fiddlewood*; and *Schinus terebinthifolia* VN: Brazilian pepper*.

and resources of the habitat matrix surrounding fragmented woodlands (Estades 2001, Brotons *et al.* 2003). The habitat matrix of our sites commonly consisted of lawns, public parks, golf courses, and large commercial vegetable gardens. Obtaining food from these urban landscapes may be difficult for woodland birds because supplemental resources, such as bird feeders, are seldom provided in Bermuda. Furthermore, most commercial vegetable gardens and golf courses are treated heavily with insecticides. These vegetable gardens are also ploughed regularly before weeds that would otherwise attract insects for insectivorous birds can become established. Although the majority of Bermuda's habitat matrix appears sterile, there may be additional food resources for birds that we are not accounting for, such as hedges, small shrubs, and trees amongst green space. Nonetheless, the species we observed in Bermuda appear to depend largely on resources provided by woodlands, and with more area, more individuals could be supported.

The Bermudian White-eyed Vireo was the most abundant native woodland bird detected, and was especially prevalent in larger woodlands. Although woodland size was a significant factor influencing White-eyed Vireo abundance, our regression coefficient ($R^2 = 0.23$) suggests that it is not the primary variable influencing their numbers. This was somewhat surprising, as woodlands serve as their primary breeding habitat. There has yet to be a thorough study investigating the territory size of Bermudian White-eyed Vireos. Therefore, it is difficult to assess the minimum home range size for this species. Nonetheless, our findings do suggest that Bermudian White-eyed Vireos may be more tolerant of smaller woodlands than originally thought. Therefore, additional unexplored factors (e.g., the connectivity of focal study sites to adjacent woodland fragments, or number of available shrubs and trees for foraging vireos across the surrounding greenspace) may also account for variation in White-eyed Vireo abundance.

Woodland area was a positive predictor of non-resident species richness and abundance. In our study, these birds consisted largely of wood-warblers. Woodland area explained a relatively large portion of the variation in warbler abundance. The strong positive relationships between woodland area and non-resident species richness could be a consequence of warblers forming multispecies flocks during the non-breeding period (Hutto 1988, Gram 1998). Larger woodlands could contain higher amounts of prey items capable of attracting and supporting a diverse group of warblers more effectively than smaller woodlands. The greater abundance of warblers in large woodlands was mostly due to larger numbers of Ovenbirds, which we consistently heard or saw in the presence of other warblers, particularly Northern Parula and American Redstart. However, it is uncertain if these species were actively traveling together or simply using the same area independent of heterospecific presence. The high abundance of Ovenbirds in larger woodlands may also be a consequence of their preference for large forest stands during the breeding season (Flather and Sauer 1996, Howell *et al.* 2000, Lee *et al.* 2002). Wood-warblers can obtain resources well outside their usual forest niche (Greenberg 1992, Wunderle 1999). Nonetheless, it may be possible that wintering warblers and other Neotropical migrants actively avoid smaller woodlands, which are largely edge habitat in closer proximity to the urban landscape. By contrast,

Table 2. Model selection results for testing hypotheses about the effects of woodland area and vegetation characteristics on Bermuda songbird population metrics. Models with $w_i < 0.01$ are not presented.

	K ^a	AIC _c ^b	ΔAIC _c ^c	w _i ^d
<i>Total species richness</i>				
Canopy + Area + Supercanopy	5	101.73	0.00	0.21
Canopy + Area + Herbaceous Cover + Supercanopy	6	100.76	0.37	0.17
Area + Herbaceous Cover + Supercanopy	5	102.37	0.64	0.15
Canopy + Area	4	103.65	0.88	0.13
Area + Supercanopy	4	103.89	1.13	0.12
Area	3	105.01	1.46	0.10
Area + Herbaceous Cover	4	105.38	2.61	0.06
Canopy + Area + Herbaceous Cover	5	104.49	2.76	0.05
<i>Total woodland bird abundance</i>				
Area	3	153.39	0.00	0.47
Canopy + Area	4	154.21	1.60	0.21
Area + Herbaceous Cover	4	154.88	2.27	0.15
Area + Supercanopy	4	155.37	2.75	0.12
Area + Herbaceous Cover + Supercanopy	5	156.85	5.27	0.03
Canopy + Area + Herbaceous Cover + Supercanopy	6	157.86	7.63	0.01
<i>White-eyed Vireo abundance</i>				
Area	3	101.67	0.00	0.37
Canopy + Area	4	101.98	1.08	0.22
Area + Herbaceous Cover	4	103.22	2.32	0.12
Area + Supercanopy	4	103.30	2.41	0.11
Canopy + Area + Herbaceous Cover	5	105.90	3.30	0.07
Canopy + Area + Supercanopy	5	106.20	3.64	0.06
Area + Herbaceous Cover + Supercanopy	5	105.00	5.15	0.03
Canopy + Area + Herbaceous Cover + Supercanopy	6	104.91	6.40	0.02
Supercanopy	3	108.24	6.57	0.01
<i>Non-resident species richness</i>				
Area	2	77.18	0.00	0.35
Area + Supercanopy	3	77.94	1.30	0.18
Area + Herbaceous Cover	3	78.43	1.79	0.14
Canopy + Area	3	78.93	2.29	0.11
Area + Herbaceous Cover + Supercanopy	4	78.34	2.48	0.10
Canopy + Area + Supercanopy	4	79.45	3.59	0.06
Canopy + Area + Herbaceous Cover	4	80.28	4.42	0.04
Canopy + Area + Herbaceous Cover + Supercanopy	5	80.15	5.33	0.02
<i>Non-resident abundance</i>				
Area	2	77.18	0.00	0.35
Area + Supercanopy	3	101.14	2.42	0.14
Area + Herbaceous Cover	3	101.14	2.42	0.14
Canopy + Area	3	101.13	2.42	0.14
Canopy + Area + Herbaceous Cover	4	102.97	5.03	0.04
Area + Canopy + Supercanopy	4	103.00	5.06	0.04
Herbaceous Cover + Area + Supercanopy	4	103.06	5.12	0.04
Canopy + Area + Herbaceous Cover + Supercanopy	5	104.89	7.99	0.01

^aNumber of parameters^bAkaike's information criterion corrected for small sample sizes^cDifference in AIC_c values between the current and top-ranked model^dWeight of evidence supporting models

the presence of resident woodland birds in smaller woodlands suggests that they may be more tolerant of fragmentation.

There are numerous explanations in the literature as to why larger woodlands appear to be the favored habitat for resident and non-resident woodland birds. First, larger forest patches are thought to be comprised of more habitat niches that thereby can support larger, more diverse guilds of songbirds (Burke and Nol 2000, Suk *et al.* 2014). Second, arthropod abundance is also positively correlated with woodland area, which is important for supporting a large variety of insectivorous songbirds (Shure and Phillips 1991). However, intense competition for resources in larger woodlands may prompt some species to inhabit smaller woodlands to avoid both intraspecific and interspecific conflict (Suk *et al.* 2014). Density-dependence within woodlands on Bermuda may be more extreme than elsewhere due to lack of resources in the surrounding habitat matrix, which is relatively sterile. Lastly, there is evidence that songbirds living in woodland habitat near roads are indirectly threatened by traffic-induced noise (Reijnen *et al.* 1995, Reijnen and Foppen 2006). Persistent traffic noise can disrupt communication and change behavior of songbirds, potentially prompting large numbers of individuals to avoid otherwise suitable habitat (Francis *et al.* 2009). In the context of our study, smaller woodlands may not be as efficient at filtering traffic noise as larger woodlands.

None of the three forest structure variables we recorded for each woodland explained any of our bird metrics. We would have expected higher percent cover, among our three canopy layers, to correspond to more fruit and insects for woodland birds. Nonetheless, our very narrow sampling period (i.e., 17 days) in early Spring undoubtedly excluded peak fruiting periods of many of the diverse plants comprising woodlands in Bermuda, thus, likely reducing explanatory power among our vegetation variables.

A significant portion of Bermuda's flora is dominated by exotic trees. Approximately 22 introduced species are aggressively invading the landscape, with allspice, fiddlewood, Brazilian pepper, and Chinese fan palm creating complete stands (D.B. Wingate pers. comm., Challinor and Wingate 1971). The spread of these exotic trees is assisted through seed dispersal by invasive avifauna residing on the island, which includes the Great Kiskadee, European Starling, and House Sparrow (D.B. Wingate pers. comm.). We suspect that the role of native avifauna in dispersing exotic trees is less extreme; Bermudian White-eyed Vireos are largely insectivorous, although the frugivorous Gray Catbird may assist in the dispersal of Surinam cherry (*Eugenia uniflora*). The impact of exotic vegetation on native biodiversity is well documented but results of those studies are often mixed. On the one hand, invasive vegetation can reduce nest success of songbirds as well as facilitate reduction of biodiversity through homogenization of the landscape (Schmidt and Whelan 1999, Borgmann and Rodewald 2004, Olden 2006, Gan *et al.* 2009). On the other hand, exotic vegetation can be beneficial to avian nest success and supporting biodiversity, specifically passerines (Hobbs *et al.* 2006, Foster and Robinson 2007, Rogers and Chown 2014).

The present-day terrestrial avifauna of Bermuda appears to be highly adaptable. The occurrence of resident woodland birds across exotic woodlands suggests individuals are not overly selective, a likely beneficial trait since suitable woodland breeding

sites are scarce. Exotic vegetation can also serve as an important alternative supplier of resources (i.e., food and habitat). The occurrence of resident woodland birds, especially the Bermudian White-eyed Vireo, across exotic woodlands suggests they have adapted to the changing environment. The White-eyed Vireo evolved with the original pre-settlement forest of Bermuda, where it would have fed on Bermuda cedar berries and insects among native foliage. Presently, it is surviving on insects and berries largely associated with alien foliage. Numerous migrant passerines also appear to persist through consumption of the fruits and insects associated with exotic vegetation, and appear to tolerate the novel Bermuda island ecosystem.

Conservation Implications

A significant threat to woodland birds in Bermuda is large-scale removal of woodlands for development. If the native woodland birds on the island are to persist, remaining woodlands need to be preserved even if these woodlands are largely comprised of non-native vegetation. This conservation action can be accomplished through continued establishment of nature reserves. Removal and control of invasive vegetation is important for preserving native biodiversity, especially from a conservation and heritage standpoint. However, despite its intrusive nature, exotic vegetation provides habitat structure and food for resident and non-resident woodland birds in Bermuda. Complete eradication of all exotic vegetation from the island, although unlikely, could potentially hinder rather than assist avian assemblages. How these birds would respond to complete restoration of native flora throughout Bermuda is difficult to predict, as the vegetation at our study sites was comprised largely of exotic species. Therefore, it may be beneficial to gradually restore certain forested areas to their native form and compare bird assemblages in these restored pockets to birds residing in introduced vegetation. Understanding specific habitat requirements of resident and migratory passerines is crucial for avian conservation on remote oceanic islands.

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Title Page Illustration

White-eyed Vireo (*Vireo griseus*); photograph taken at Paget

Marsh Nature Reserve, Bermuda, on 12 January 2020 by LeShun Smith (Macaulay Library ML198911241).

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