RESEARCH PAPER

Composition and structure of Caribbean bat (*Chiroptera*) assemblages: effects of inter-island distance, area, elevation and hurricane-induced disturbance

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ABSTRACT

Aim Although bats of the Caribbean have been studied extensively, previous work is largely restricted to zoogeography, phylogeography or the effects of island characteristics on species richness. Variation among islands in species composition that is related to geographical or environmental variation remains poorly understood for much of the Caribbean.

Location Caribbean islands, including the Bahamas, Greater Antilles and Lesser Antilles.

Methods Using presence–absence data, we assessed the extent to which island area, maximum island elevation, inter-island distance and hurricane-induced disturbance affected patterns of composition and nestedness for bats in the Bahamas, Greater Antilles and Lesser Antilles. Analyses were conducted for all species, as well as for two broadly defined guilds: carnivores and herbivores.

Results For the Bahamas, only inter-island distance accounted for variation in species composition between islands. For the Greater and Lesser Antilles, differences in island area and inter-island distance accounted for differences in species composition between islands. Variation in species composition was not related significantly to differences in elevation or hurricane-related disturbance. In general, results of analyses restricted to a particular broad guild (i.e. carnivores or herbivores) mirrored those for all bats. Bat species composition was nested significantly in each island group. Nestedness was stronger in the Greater Antilles and in the Lesser Antilles than in the Bahamas. Carnivore assemblages were nested significantly in the Greater and in the Lesser Antilles, but not in the Bahamas. In contrast, herbivore assemblages were nested significantly in each island group.

Main conclusions Inter-island distance had a greater effect on compositional similarity of Caribbean bat assemblages than did island area, elevation or disturbance related to hurricanes. Differential immigration and hierarchical habitat distributions associated with elevational relief are likely to be primary causes for nestedness of Caribbean bat assemblages.

Keywords
Bats, Caribbean islands, community structure, endemic species, island biogeography, nestedness, Phyllostomidae, species composition, species co-occurrence.

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INTRODUCTION

Understanding how variation in island characteristics affects the structure of assemblages and communities is a prominent theme in ecology (Brown, 1995) and biogeography (Lomolino *et al.*, 2006). The study of species richness and composition on islands is of interest in its own right (Williamson, 1981; Whittaker, 1998); however, insular studies also provide insights into mainland phenomena associated with human-induced loss and conversion of habitats. This aspect of island research is important, because such studies cannot be conducted on mainlands due to ethical, financial or logistical considerations associated with large-scale

manipulative experiments. Indeed, the importance of under-standing the effects of insularity on population-, community- and ecosystem-level characteristics has increased as human activities on continents continue to fragment landscapes, creating isolated patches of habitat dispersed within a sea of agricultural, urban or suburban development. In addition, studies of insular systems have important ramifications for conservation biology because they provide insights into mechanisms that lead to species persistence, loss or coexistence.

The Caribbean is a hotspot of biodiversity, with high species richness and high species endemism (Woods, 1989; Woods & Sergile, 2001), including 7000 endemic vascular plants and 779 endemic vertebrates (Myers, 2001). The biota of the Caribbean is a conservation concern because of accelerating rates of anthropogenic activity that threaten the persistence of species. Indeed, primary vegetation of the Caribbean islands covers only 10% of its original extent (Myers, 2001). Because the Caribbean comprises many small, densely populated nations, development of conservation strategies in the Caribbean is more challenging than on mainland North or South America.

Bats of the Caribbean have been studied extensively (e.g. Koopman, 1959; Baker & Genoways, 1978; Koopman, 1989; Ricklefs & Lovette, 1999; Morand, 2000; Rodríguez-Durán & Kunz, 2001; Willig et al., 2008); however, previous work focused on zoogeography, phylogeography or the effects of island characteristics on species richness. Geographical or environmental effects on species composition of Caribbean bats for which species identity is critical remain poorly understood. This paper uses the same incidence data (i.e. species occurrences on 65 Caribbean islands) as in Willig et al. (2008), who evaluated the effects of environmental and geographical characteristics of islands on species, genus and guild richness, largely addressing traditional questions related to the theory of island biogeography (MacArthur & Wilson, 1967).

In addition to predictions about species richness, the theory of island biogeography (MacArthur & Wilson, 1967) predicts that species turnover occurs on islands, and that species identity on any particular island at any given time will be random and not associated with island or species characteristics. We hypothesize that island characteristics such as area, elevation, geographical proximity and disturbance regime affect species composition as well as species richness.

Gradients of precipitation and temperature occur with changes in elevation, which affect the number and types of habitat that occur on an island. Moreover, the number and diversity of habitats may increase with island area as habitat type may change with distance from the coast. Because island size and topography affect the types of habitat and niches available to bats, we expect islands with similar area or elevational relief to support more similar assemblages of bats than islands that differ in either character. Islands that are geographically proximate are exposed to more similar environmental conditions and to more similar sources of colonization than are islands that are geographically more distant. Consequently, we expect islands that are proximate to have more similar species compositions than do islands that are distant. In consideration of all island characteristics as a group, we predict that islands that are geographically proximate or similar in size, elevational relief or disturbance regime maintain more similar assemblages of bat species than do islands that differ more greatly in these characters.

Factors that affect species number may not be the same as those that affect species identity. Moreover, responses to island characteristics may be species specific. As a result, analyses in which species identity is a defining characteristic will allow the identification of species that respond most strongly to variation in particular island characters. Moreover, these compositional analyses will address biogeographical questions that are complementary to those that focus on species number, thereby conferring greater understanding of Caribbean biogeography than would be possible using a single approach.

MATERIALS AND METHODS

Caribbean islands, hurricanes and bats

Because there are many Caribbean islands (> 7000 islands, islets, reefs and cays) that differ greatly in size, elevational relief, sources of colonization, isolation, geological history and exposure to hurricane-induced disturbance, they represent a valuable opportunity to study the effects of environmental variation on species diversity, composition and community structure. The Caribbean islands (Fig. 1a) range from 27.33° N to 10.05° N and are classified into three major groups based on biogeographical considerations (Bahamas, Greater Antilles, Lesser Antilles; Baker & Genoways, 1978). The Bahamas (Fig. 1b) range from the Grand Bahama Bank in the north-west, to the Turks and Caicos in the south-east. They are low-lying islands (maximum elevation is 63 m), formed from carbonate banks of the Bahamas platform, which is part of the North American tectonic plate. In contrast, the Antilles were formed by andesitic volcanism, have mountainous terrain and possess a greater number of caves that are often used by bats for roosts (Hedges, 2001). The Greater Antilles (Fig. 1a,c) range from Cuba in the west to Anegada in the east. The Lesser Antilles (Fig. 1c) range from Sombrero in the north to Trinidad in the south, including the Leeward Islands along the northern coast of Venezuela. To avoid confounding effects related to continental proximity and island origin, we omitted Trinidad, Tobago and the Leeward Antilles from analyses. Consequently, the most southern island in analyses was Grenada (12.11° N).

Three likely sources of colonization for Caribbean bats are subtropical North America, the Yucatán of Central America and northern South America (Baker & Genoways, 1978). Effects of distance to mainland sources of colonization on species richness of bats are weak (Willig et al., 2008). Consequently, we used pair-wise inter-island distances to investigate effects of geographical separation on bat assemblage composition. Inter-island distances can affect many aspects of biodiversity, such as species richness, evenness, dominance, species composition and compositional similarity (Ricklefs & Lovette, 1999; Morand, 2000). Islands act as stepping stones for colonization from the mainland and can be
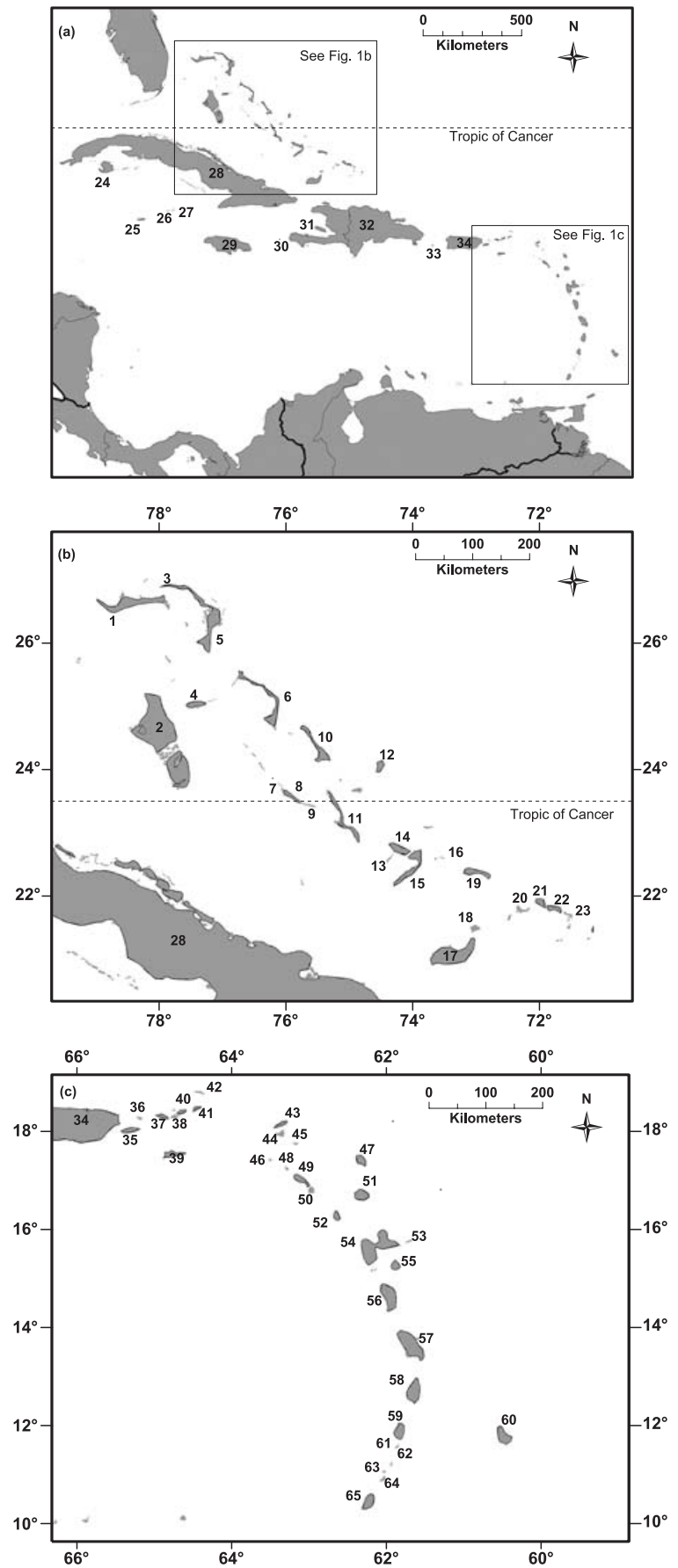
Figure 1 Maps of islands in the Caribbean (modified from Willig *et al.*, 2008). (a) Islands of the Greater Antilles (24–42) in relation to the Bahamas and Lesser Antilles. (b) Bahamian islands (1–23) in relation to Cuba (island 28). (c) Lesser Antilles (43–65) in relation to the eastern most Greater Antilles (34–42). Island characteristics are in Appendix S1.

sources of recolonization after local extinction events. Inter-island distances were calculated using the great circle distances calculator (Earth.exe for Windows) that is available online (http://www.chemical-ecology.net/moregen.htm). The area of each island was obtained from an equal-area projection map (National Geographic Society, 1985). The maximum elevation of islands was obtained from maps (National Geographic Society, 1985) and geographical gazetteers (e.g. National Oceanic and Atmosphere Administration, 1976; United States Department of Agriculture, 1998).

Hurricanes are common in the Caribbean Basin (Landsea *et al.*, 1999) and are the basis of a disturbance regime dominated by high-intensity storms that can affect the structure and composition of the regional biota. In addition, the number and intensity of such storms is likely to increase in the region in response to global warming (Goldenberg *et al.*, 2001; Webster *et al.*, 2005). Using historical storm track data collected by the NOAA Coastal Services Center (http://hurricane.csc.noaa.gov/hurricanes/), we characterized the history of major hurricanes (category 3 and above on the Saffir–Simpson scale; Saffir, 1973; Simpson, 1974) for each island. Six metrics (number of hurricanes, cumulative hurricane intensity, mean intensity, average intensity, mean return time and standard error of return time) that measured variation in hurricane frequency, intensity or extent were quantified for each island (for details see Willig *et al.*, 2008). These metrics are incomplete characterizations of hurricane-related disturbance regimes of the region because they do not include estimates of severity of habitat destruction and resulting habitat heterogeneity or changes in resource availability on particular islands. We used principal components analysis (PCA) based on the correlation matrix with a varimax rotation of factors to distil the six disturbance metrics into fewer synthetic orthogonal variables. Varimax rotation enhances the interpretability of principal components by maximizing the correlation of the original variables on one factor and minimizing it on all others. Moreover, this rotation predisposes correlated variables to have maximal loadings on the same factor, and equalizes variation among factors. The first principal component accounted for 87.5% of the variation in hurricane metrics among islands.

The distribution of bats on islands of the Caribbean was determined via a comprehensive literature search to populate a species occurrence matrix for the islands (see Appendix 9.2 in Willig *et al.*, 2008). Reliable data concerning bat species composition and selected environmental characteristics were available for 65 islands throughout the Caribbean, including 19 in the Greater Antilles, 23 in the Bahamas and 23 in the Lesser Antilles (see Appendix S1 in Supporting Information). Analyses were based on records for 58 species, 34 genera and 7 families of bats from Caribbean islands, including 13 species, 13 genera and 5 families of bats from the Bahamas, 38 species, 25 genera and 6 families of bats from the Greater Antilles, and 24 species, 17 genera and 7 families of bats from the Lesser Antilles. Families of bats that occur on Caribbean islands include the Emballonuridae (1 species), Phyllostomidae (24), Noctilionidae (1), Mormoopidae (5), Natalidae (7), Molossidae (7) and Vespertilionidae (13). We

followed the taxonomic treatment of Simmons (2005), except for recognizing *Eptesicus lynni* (Arnold *et al.*, 1980; Genoways *et al.*, 2005) as an endemic of Jamaica, distinct from *Eptesicus fuscus*.

Bats occupy many narrowly defined trophic guilds, such as piscivore, carnivore, insectivore, sanguinivore, nectarivore and frugivore. Moreover, responses by bats to particular island characteristics may be guild specific. Nonetheless, many islands harbour few species of bat and many narrowly defined guilds are absent from a majority of islands; therefore, analyses based on delineations such as aerial insectivore or gleaning animalivore likely would not bear fruit. As a compromise, we categorized species into two broadly defined guilds based on their primary food sources. Broad guilds were carnivores (i.e. insectivores, piscivores, carnivores, animalivores and omnivores) and herbivores (i.e. nectarivores and frugivores).

Statistical analyses

We evaluated the effect of inter-island distance and variation in environmental characteristics (i.e. area, elevation, hurricane-induced disturbance) on differences in bat composition among islands. Island area was log_{10}-transformed to enhance correspondence to assumptions of parametric tests and to linearize relationships with dependent variables. Analyses were executed in the program Permute 3.4 (Legendre *et al.*, 1995) and were conducted for each island group separately. In addition, analyses restricted to each of two broad feeding guilds were conducted for each island group. Use of inter-island distances violates the assumption of independence associated with least-squares techniques; consequently, a permutation approach is preferred over classical regression models for such analyses (Manly, 1991; Morand *et al.*, 1996). For each environmental characteristic, we produced an island-by-island matrix of differences in character values. For inter-island distance, we produced an island-by-island matrix of inter-island geographical distances. Ochiai's index was applied to the species occurrence matrix to estimate pair-wise similarities in species composition between islands (Ludwig & Reynolds, 1988). Multiple regressions assessed the extent to which the matrix based on species composition was a function of a suite of environmental matrices (i.e. island-by-island differences in area, maximum elevation and hurricane-induced disturbance) as well as a matrix of inter-island distances. A step-down procedure was used for each multiple regression, one for the empirical data, as well as for each of 999 simulations in which the arrangement of cells in the dependent variable matrix was randomized to create null matrices. Partial regression coefficients based on the empirical data were compared with the distribution of partial regression coefficients from regressions involving the randomized null matrices. Significance was estimated as the proportion of regression coefficients from null matrices that were greater than or equal to the corresponding empirical coefficient.

For each island group, nestedness was estimated for each of three groups: all bats, carnivores and herbivores. In general, indices of nestedness differ in how unexpected absences (holes)

or unexpected presences (outliers) effect a metric's magnitude. The metric N_C is the number of times a species presence correctly predicts its occurrence at equally rich or richer sites (Wright & Reeves, 1992). We used PN_C, a standardized version of N_C, which removes correlations between rank of the data matrix and magnitude of the index (Wright *et al.*, 1998). Several null models evaluate significance of nestedness indices (Gotelli, 2000). These models differ in the constraints on randomization and their susceptibility to Type I or Type II errors. We used the RANDOM1 null model (Coleman *et al.*, 1982; Patterson & Atmar, 1986), which constrains row totals to equal observed species richnesses and probabilities of species placement to be proportional to observed incidence values. RANDOM1 is not prone to Type I or Type II errors (Gotelli, 2000) and has been used extensively in the literature. The empirical value of PN_C was z-transformed by subtracting the mean and dividing by the SD of 1000 simulated values of that metric obtained by randomization based on RANDOM1. The level of significance (P) was equal to the likelihood of obtaining a normalized random variate greater than or equal to the transformed empirical value. Simulations were performed with algorithms written in MATLAB 6.0. Results were considered significant at an α-level of 0.05.

For each analysis, we calculated an index of effect (I_E) to evaluate the relative contribution of a particular island or species to nestedness (Bloch *et al.*, 2007). The difference between the metric without a particular island or species and the metric based on all data estimated the contribution of that island or species to nestedness. Negative values of I_{Ei} indicate that nestedness is diminished when island or species i is removed from analysis; positive values of I_{Ei} indicate that nestedness is enhanced when island or species i is removed from analysis. Unless otherwise stated, analyses were conducted using SPSS for Windows 9.0.0.

RESULTS

Aspects of biodiversity and environmental characteristics were quite variable among islands (see Appendix S1). Island area spanned about five orders of magnitude (5.0 km² on East Plana Cay to 114,524.0 km² on Cuba), elevation spanned about three orders of magnitude (5 m on Grand Bahama to 3175.0 m on Hispaniola) and inter-island distances spanned about two orders of magnitude (14 km between St John and Tortola to 2636 km between Isle of Pines and Barbados). Bat species richness ranged from 1 on nine different islands to 26 on Cuba. Details about variation in environmental characteristics and species richness of islands are available elsewhere (Willig *et al.*, 2008).

Species composition

Results of multiple regression analyses based on matrix permutations were similar for the Greater and Lesser Antilles, but distinctive for the Bahamas. For each island group, compositional similarity was correlated negatively with distance between islands; islands in close proximity harboured more similar bat

assemblages than did more distantly separated islands (Bahamas, $b = -0.183$, $P = 0.048$; Greater Antilles, $b = -0.416$, $P = 0.001$; Lesser Antilles, $b = -0.478$, $P = 0.001$). For the Greater Antilles and the Lesser Antilles compositional similarity was correlated negatively with differences in island area; islands of similar area possessed similar bat species (Greater Antilles, $b = -0.246$, $P = 0.017$; Lesser Antilles, $b = -0.325$, $P = 0.002$). Differences in elevation (Bahamas, $b = 0.022$, $P = 0.416$; Greater Antilles, $b = 0.055$, $P = 0.425$; Lesser Antilles, $b = -0.007$, $P = 0.432$) or hurricane-related disturbance (Bahamas, $b = 0.052$, $P = 0.408$; Greater Antilles, $b = 0.076$, $P = 0.250$; Lesser Antilles, $b = 0.044$, $P = 0.340$) were not related significantly to variation in bat species composition.

In general, results of analyses restricted to a particular guild mirrored those for all bats. For the Bahamas, differences in inter-island distance accounted for differences in carnivore composition between islands ($b = -0.158$, $P = 0.041$), whereas differences in island area accounted for differences in herbivore composition ($b = 0.263$, $P = 0.002$). This similarity of herbivore composition between islands of the Bahamas with different areas reflects the influence of *Erophylla sezekorni*, which occurs on Bahamian islands of many disparate sizes. If *E. sezekorni* is removed from the analysis, herbivore composition does not respond to any environmental variable. For each guild in the Greater Antilles or Lesser Antilles, differences in inter-island distance (Greater Antilles, carnivores, $b = -0.507$, $P = 0.002$; Greater Antilles, herbivores, $b = -0.418$, $P = 0.001$; Lesser Antilles, carnivores, $b = -0.494$, $P = 0.001$; Lesser Antilles, herbivores, $b = -0.445$, $P = 0.001$) and island area (Greater Antilles, carnivores, $b = -0.177$, $P = 0.041$; Greater Antilles, herbivores, $b = -0.420$, $P = 0.001$; Lesser Antilles, carnivores, $b = -0.246$, $P = 0.008$; Lesser Antilles, herbivores, $b = -0.214$, $P = 0.010$) accounted for differences in species composition between islands.

Nestedness

Bat species composition was nested significantly in each island group. Nestedness was stronger in the Greater Antilles ($PN_C = 41.56$, $P < 0.001$) and Lesser Antilles ($PN_C = 52.76$, $P < 0.001$) than in the Bahamas ($PN_C = 17.96$, $P = 0.034$). Carnivore assemblages were significantly nested in the Greater Antilles ($PN_C = 49.65$, $P < 0.001$) and Lesser Antilles ($PN_C = 54.06$, $P < 0.001$), but not in the Bahamas ($PN_C = 12.87$, $P = 0.150$). Herbivore assemblages were significantly nested in each island group: Greater Antilles ($PN_C = 35.94$, $P < 0.001$), Lesser Antilles ($PN_C = 55.75$, $P < 0.001$) and Bahamas ($PN_C = 51.23$, $P = 0.011$).

In the Bahamas, the location or richness of an island was unrelated to the extent to which an island enhanced or diminished nestedness (Table 1). *Erophylla sezekorni* and *Macrotus waterhousii* were the only species that appreciably enhanced nestedness in the Bahamas. Each of these species was absent from only the most species-poor islands. Species that occurred on about half of Bahamian islands (i.e. *Eptesicus fuscus*, *Lasiurus minor*, *Tadarida brasiliensis*) diminished nestedness

Table 1 Species richness (all species, carnivores only, herbivores only) and index of effect (I_{Ei}) for islands in the Caribbean. Values of I_{Ei} quantify the contribution to nestedness of each island for analyses restricted to each island group. Islands with positive values of I_{Ei} enhanced nestedness. Islands with negative values of I_{Ei} diminished nestedness. Those islands within each island group with the largest effects (positive or negative) on nestedness (upper 50th percentile) are in bold. Dashes (–) indicate islands with no species of a particular guild.

Island group / Island	Species richness	Index of effect (I_{Ei}) All species	Carnivores	Herbivores	Island group / Island	Species richness	Index of effect (I_{Ei}) All species	Carnivores	Herbivores
Bahamas					Saint Thomas	5, 2, 3	0.35	**1.87**	−1.51
Long	6, 5, 1	**1.18**	**2.21**	**3.13**	Saint Croix	5, 2, 3	0.31	**1.97**	−1.55
Providenciales	6, 3, 3	0.67	0.77	1.11	Vieques	4, 2, 2	**1.85**	**1.97**	1.37
New Providence	5, 3, 2	**1.08**	0.61	−1.77	Culebra	3, 2, 1	**3.30**	**1.84**	**4.47**
Acklins	5, 3, 2	0.68	0.43	−0.73	Virgin Gorda	2, 1, 1	**2.85**	1.49	**4.49**
Crooked	5, 3, 2	0.64	0.95	−0.80	Tortola	2, 1, 1	**2.81**	1.51	**4.40**
Little Exuma	5, 4, 1	0.61	0.35	**3.10**	Little Cayman	2, 1, 1	0.63	**−2.51**	**4.49**
Great Inagua	5, 3, 2	0.59	0.67	−1.61	Mona	2, 2, 0	**−2.63**	**−4.35**	–
Cat	5, 3, 2	0.15	−0.67	−2.09	Anegada	1, 0, 1	**1.54**	–	**4.50**
Great Abaco	5, 4, 1	**1.25**	**2.22**	**3.38**	Navassa	1, 1, 0	−1.36	**−2.47**	–
Andros	4, 3, 1	**1.21**	0.57	**3.15**	**Lesser Antilles**				
Great Exuma	4, 3, 1	0.96	0.60	2.98	Guadeloupe	12, 6, 6	**1.09**	1.50	0.68
San Salvador	4, 3, 1	0.63	−0.12	**3.15**	Dominica	12, 7, 5	0.96	**3.03**	0.55
Eleuthera	4, 3, 1	0.35	−0.80	**3.03**	Saint Vincent	12, 5, 7	−0.12	**−1.75**	**2.21**
Middle Caicos	4, 1, 3	**−2.44**	**−2.35**	0.97	Grenada	12, 6, 6	**−10.09**	**−7.79**	**−14.25**
North Caicos	3, 1, 2	**1.00**	**2.12**	−0.91	Martinique	11, 6, 5	0.76	1.22	0.38
Grand Bahama	3, 2, 1	−0.93	**−3.50**	**3.00**	Montserrat	10, 4, 6	0.75	**1.70**	0.52
Mayauana	3, 1, 2	−1.63	**−2.52**	−1.42	Saint Martin	8, 4, 4	**1.47**	**1.63**	1.45
East Caicos	2, 1, 1	**2.58**	**2.08**	**3.06**	Nevis	8, 4, 4	**1.41**	1.60	**1.51**
East Plana Cay	1, 1, 0	0.68	**2.12**	–	Saint Lucia	8, 3, 5	0.39	**1.73**	0.54
Darby Island	1, 1, 0	0.63	**2.18**	–	Marie Galante	8, 4, 4	−0.86	**−4.04**	1.40
Little Abaco	1, 1, 0	−1.76	**−2.56**	–	Saint Kitts	7, 3, 4	**1.42**	1.56	1.43
Fortune	1, 1, 0	−1.78	**−2.47**	–	Antigua	7, 4, 3	**1.19**	**1.63**	1.56
Little Inagua	1, 0, 1	**−2.11**	–	**−14.60**	Barbuda	7, 4, 3	**1.18**	1.60	**1.51**
Greater Antilles					Saba	7, 3, 4	0.39	−0.48	1.49
Cuba	26, 20, 6	**3.00**	**6.33**	−1.84	Anguilla	6, 3, 3	0.76	−0.49	1.46
Jamaica	21, 16, 5	−0.97	0.50	**−2.59**	Barbados	6, 3, 3	−0.70	**−4.08**	1.52
Hispaniola	18, 12, 6	−0.68	**2.25**	**−2.77**	Saint Barthelemy	5, 2, 3	**1.56**	1.26	1.58
Isle of Pines	15, 10, 5	**−1.72**	−1.43	−2.47	Saint Eustatius	5, 3, 2	0.60	1.21	−0.47
Puerto Rico	13, 8, 5	**−1.82**	−1.01	**−2.72**	La Désirade	4, 2, 2	**1.43**	1.27	**1.51**
Grand Cayman	8, 4, 4	−1.51	−0.30	−1.48	Carriacou	4, 2, 2	**−1.58**	0.71	**−4.06**
Saint John	6, 3, 3	0.13	1.45	−1.42	Union Island	3, 1, 2	−1.08	**1.68**	**−4.10**
Gonave	6, 4, 2	−0.48	−1.69	1.91	Mustique	1, 0, 1	0.95	–	**1.64**
Cayman Brac	6, 3, 3	−1.06	−0.61	−1.48	Bequia	1, 0, 1	0.94	–	**1.53**

(Table 2) because occurrences were idiosyncratic and unrelated to bat richness.

Cuba contributed appreciably to nestedness because it harbours five endemic species and was the most species-rich island of the Greater Antilles (Table 1). In contrast, Jamaica did not enhance nestedness despite having 14 species in common with Cuba, because it was not the most species-rich island in the Greater Antilles but harboured seven endemic species. In a perfectly nested system, island endemics would only occur on the most species-rich island. A number of the Virgin Islands enhanced nestedness, whereas many smaller islands of the western Greater Antilles diminished nestedness. The two ubiquitous species of the Greater Antilles (*Artibeus jamaicensis* and *Molossus molossus*) were the only species that appreciably enhanced nestedness. In

contrast, many species that occurred on 25–60% of Greater Antillean islands diminished nestedness (Table 2).

Islands of the northern Lesser Antilles appreciably enhanced nestedness. In contrast, species with ranges restricted to the southern Lesser Antillean islands of Grenada and the Grenadines diminished nestedness (Table 1). Because *A. jamaicensis* and *M. molossus* were ubiquitous, they enhanced nestedness; other species (e.g. *Monophyllus plethodon*, *T. brasiliensis*, *Natalus stramineus*) that occurred on a large proportion of Lesser Antillean islands diminished nestedness (Table 2).

In general, islands or species that enhanced nestedness in analyses that included all species, enhanced nestedness in analyses restricted to carnivores or to herbivores (Tables 1 & 2). Similarly, islands or species that diminished nestedness in analyses that

Table 2 Frequency of occurrence and index of effect (I_{Ei}) for islands in the Caribbean. Values of I_{Ei} quantify the contribution to nestedness of each species for analyses restricted to each island group that included all species as well as for analyses restricted to carnivores or herbivores. Species with positive values of I_{Ei} enhanced nestedness. Species with negative values of I_{Ei} diminished nestedness. Those species within each island group with the largest effects (positive or negative) to nestedness (upper 50th percentile) are in bold. Dashes (–) indicate species that were excluded from particular analyses because of guild affiliation.

Island group Species	Frequency	Index of effect (I_{Ei}) All species	Carnivores	Herbivores	Island group Species	Frequency	Index of effect (I_{Ei}) All species	Carnivores	Herbivores
Bahamas					*Erophylla bombifrons*	2	**–0.69**	–	–0.16
Erophylla sezekorni	18	**9.17**	–	**62.36**	*Lasiurus minor*	2	**–0.70**	**–1.83**	–
Macrotus waterhousii	17	**4.86**	**20.34**	–	*Antrozous pallidus*	1	**0.44**	**0.72**	–
Eptesicus fuscus	10	**–3.46**	2.95	–	*Mormopterus minutus*	1	**0.43**	**0.74**	–
Lasiurus minor	9	**–4.10**	**–9.48**	–	*Nycticeius cubanus*	1	**0.43**	0.74	–
Tadarida brasiliensis	9	**–6.90**	–2.17	–	*Lasiurus pfeifferi*	1	0.37	**0.72**	–
Nyctiellus lepidus	5	–1.60	**6.01**	–	*Nyctinomops laticaudatus*	1	0.37	**0.75**	–
Monophyllus redmani	5	–2.23	–	–4.83	*Glossophaga soricina*	1	0.14	–	–0.53
Artibeus jamaicensis	4	**–2.82**	–	**–28.92**	*Lasiurus degelidus*	1	0.14	0.09	–
Brachyphylla nana	2	–0.56	–	–2.71	*Phyllonycteris aphylla*	1	0.14	–	–0.49
Lasionycteris noctivagans	1	0.66	5.91	–	*Ariteus flavescens*	1	0.10	0.12	–
Chilonatalus tumidifrons	1	0.23	**7.29**	–	*Eptesicus lynni*	1	0.10	0.10	–
Noctilio leporinus	1	0.10	5.85	–	*Eumops auripendulus*	1	0.10	0.16	–
Lonchorhina aurita	1	0.08	–	–4.61	**Lesser Antilles**				
Greater Antilles					*Artibeus jamaicensis*	23	**6.94**	–	14.78
Artibeus jamaicensis	17	**12.53**	–	**45.88**	*Molossus molossus*	21	**4.72**	**14.71**	–
Molossus molossus	15	**7.43**	**14.20**	–	*Brachyphylla cavernarum*	18	**–0.79**	–	–2.68
Noctilio leporinus	11	**–1.40**	**–2.52**	–	*Monophyllus plethodon*	16	**–1.44**	–	–4.80
Macrotus waterhousii	9	**–3.53**	**–7.11**	–	*Tadarida brasiliensis*	16	**–3.72**	**–11.26**	–
Tadarida brasiliensis	7	–0.10	–0.59	–	*Noctilio leporinus*	15	**–0.44**	**–0.90**	–
Monophyllus redmani	6	–0.38	–	–1.77	*Ardops nichollsi*	12	**–0.90**	–	–4.39
Eptesicus fuscus	6	**–1.28**	**–3.35**	–	*Natalus stramineus*	11	**–5.04**	**–8.40**	–
Mormoops blainvillii	6	**–2.74**	**–4.05**	–	*Sturnira lilium*	5	0.11	–	0.24
Pteronotus parnelli	5	**–0.75**	**–1.05**	–	*Pteronotus davyi*	4	–0.37	0.17	–
Erophylla sezekorni	5	**–1.35**	–	**–4.10**	*Glossophaga longirostris*	4	**–4.63**	–	–9.96
Stenoderma rufum	5	**–6.80**	–	**–13.10**	*Artibeus lituratus*	2	**0.70**	–	2.17
Chilonatalus micropus	4	0.31	0.45	–	*Myotis dominicensis*	2	**0.62**	**2.16**	–
Natalus major	4	0.30	0.50	–	*Micronycteris megalotis*	2	**0.61**	–0.06	–
Pteronotus quadridens	4	0.05	–0.04	–	*Chiroderma improvisum*	2	0.08	–	1.08
Brachyphylla nana	4	**–0.67**	–	–0.45	*Sturnira thomasi*	2	0.00	–	1.11
Phyllops falcatus	4	**–1.65**	–	**–2.74**	*Myotis martiniquensis*	2	**–1.71**	**–4.12**	–
Brachyphylla cavernarum	4	**–5.15**	–	**–8.75**	*Pteronotus parnelli*	1	0.41	–0.23	–
Nyctinomops macrotis	3	0.42	0.58	–	*Artibeus glaucus*	1	0.40	–	0.48
Pteronotus macleayii	3	0.17	0.14	–	*Eptesicus guadeloupensis*	1	0.39	0.37	–
Phyllonycteris poeyi	3	–0.03	–	0.65	*Anoura geoffroyi*	1	0.38	–	0.61
Eumops glaucinus	2	**0.54**	**0.72**	–	*Eptesicus fuscus*	1	0.38	**1.55**	–
Lasiurus intermedius	2	0.06	–0.30	–	*Myotis nigricans*	1	0.37	0.55	–
Nyctiellus lepidus	2	0.03	–0.23	–	*Peropteryx macrotis*	1	0.36	0.37	–

included all species, diminished nestedness in analyses restricted to carnivores or to herbivores.

DISCUSSION

MacArthur and Wilson's (1967) theory of island biogeography predicted species richness based on the effects of island characteristics on rates of immigration and extinction. A secondary prediction related to the equilibrium of immigration and extinction rates was that turnover would occur on islands with the identity of species going extinct or immigrating to islands determined by chance (i.e. at random). However, species composition on Caribbean islands was not random. Consistent with our predictions, islands that were more similar in area and islands that were geographically proximate exhibited more similar species composition than did islands that differed in area or were geographically remote. In addition, the structure of bat assemblages was significantly nested on each island group,

indicating that ecological or evolutionary factors beyond those considered in the equilibrium model are likely to structure these assemblages.

Species composition

In general, each group of Caribbean islands harbours a distinct combination of bat species (Rodríguez-Durán & Kunz, 2001; Willig *et al.*, 2008). The distinctiveness of each group of species is probably related to the primary source(s) of colonization for each island group (Baker & Genoways, 1978), with the Bahamas most influenced by colonization from subtropical North America, the Greater Antilles influenced by colonization from subtropical North America and Central America, and the Lesser Antilles influenced by colonization from Central America and northern South America. Island area, but not inter-island distance, was the most important characteristic influencing patterns of species richness on these same islands (Willig *et al.*, 2008). However, when species identity rather than number was considered in analyses, inter-island distance was the dominant factor influencing inter-island variation, with island area of secondary import. Island area and elevation are related to habitat diversity and the number of available niches for bats, which may account for the positive relationships between bat species richness and island area or elevation. Alternatively, geographical distance between islands (or perhaps geographical location) is associated with the relative influence of sources of colonization, which is reflected in the species composition of each island.

Effects of area *per se* may be confounded by its positive association with habitat diversity (Ricklefs & Lovette, 1999; Morand, 2000; Willig *et al.*, 2008). Habitat diversity on islands often arises as a consequence of variation in elevation and underlying environmental gradients of temperature and precipitation. Moreover, maximum elevation is correlated with island area in the Greater and Lesser Antilles, thus the effects of area *per se* and elevation *per se* are confounded by their positive association (Willig *et al.*, 2008). Despite the failure of species composition to respond to maximum elevation, two things suggest that elevational relief may contribute to the similarity of assemblages of Caribbean bats. First, species composition only responded to area in the Greater Antilles and Lesser Antilles, within which elevational variation is considerable. In contrast, species composition did not respond to area for the Bahamas, whose islands differ little in elevation. Second, elevation and log(area) are correlated highly in the Greater Antilles ($r = 0.866$, $P < 0.001$) and in the Lesser Antilles ($r = 0.625$, $P = 0.001$), but are not correlated in the Bahamas ($r = -0.08$, $P = 0.748$). Considering that maximum elevation is a crude measure of the elevational heterogeneity of an island, it is unsurprising that similarity of species composition failed to respond to this estimate of elevational heterogeneity. Nonetheless, the magnitude of effects statistically ascribed to island area probably represent the cumulative influences of area, as well as the effects of other aspects of islands (e.g. elevational relief, habitat diversity) that are correlated with it.

Predictions about the manner in which some island characters affect composition are biologically intuitive. For example, islands of similar area or elevational relief should have more similar bat assemblages than would islands with dissimilar areas or elevational relief, and geographical proximity should be correlated positively with compositional similarity. In contrast, predictions concerning the effects of hurricane-related disturbance on bat composition are less clear, for multifarious reasons. First, the potential effects of hurricane-induced disturbance are likely to be contingent on island size. When hurricanes strike smaller islands, it is likely that the entire island is devastated, resulting in decreased habitat diversity and a dramatic reduction in resource abundance. In addition, because average population size is positively associated with area (Rosenzweig, 1995), the probability of hurricanes causing extinctions on islands is probably negatively correlated with island size. Because hurricanes are less likely to have a severe impact on the entirety of larger islands, disturbances created by hurricanes may increase habitat heterogeneity on such islands, thereby promoting or maintaining species richness. Second, subsequent to any hurricane event, rescue effects may be contingent on distances to source populations (mainland or other islands). Species extirpated from an island as a result of a hurricane may re-establish more quickly on islands close to multiple source populations. Similarly, populations threatened with extinction may persist on islands close to source populations via source–sink dynamics (Pulliam, 1988). In contrast, the lasting effect of hurricanes on islands far from source populations may be much greater. Third, bats represent many foraging guilds, and food resources (e.g. fruit, flowers, insects, fish) for each guild may be affected differently by hurricanes. Therefore, effects of disturbance on bat assemblage composition may depend on the susceptibility of food resources to hurricanes (which may depend on island size) and the ability of bats in each guild to persevere until those resources are replenished (Gannon & Willig, 2008). Because effects of hurricanes on island biota are probably contingent on island area, inter-island distances and distance to the mainland, effects of hurricane-induced disturbance on bat species richness or composition may be difficult to predict or detect from a statistical perspective.

Nestedness

Nestedness in land-bridge island systems is primarily ascribed to differential extinction because such islands were once connected to the mainland. When created, all such islands should have had the same or similar biotas. In contrast, nestedness in oceanic island systems (e.g. Caribbean islands) is primarily ascribed to differential immigration because islands were originally devoid of species. Because nestedness is more frequently detected on land-bridge islands than on oceanic islands, differential extinction is considered the primary mechanism that contributes to nestedness (Wright & Reeves, 1992; Lomolino, 1996). Nonetheless, it is more likely that multiple mechanisms (e.g. differential extinction, differential immigration, hierarchical habitat distributions) contribute to nestedness in most cases, with the degree of contribution of each mechanism contingent on idiosyncratic characteristics of particular island systems. Although differential immigration capabilities of bat species may be a

primary mechanism contributing to nestedness in each group of islands in the Caribbean, circumstantial evidence suggests that hierarchical habitat distributions also may contribute to nestedness in the Greater Antilles and Lesser Antilles. Two conditions must be met for a species to establish successfully on an island: the species must be capable of dispersing to the island and the island must have suitable habitat for species persistence. Island area is correlated positively with elevation in the Greater Antilles and Lesser Antilles, and elevational relief is associated positively with habitat diversity. Consequently, the likelihood that a dispersing species encounters suitable habitat is associated positively with island area.

Many (e.g. Wright *et al.*, 1998; Higgins *et al.*, 2006) who study community composition evaluate patterns of nestedness and speculate about their mechanistic bases. In those discussions, the degree to which each island or species contributes to overall nestedness is ignored. In contrast, Bloch *et al.* (2007) evaluated the degree to which each sampling site contributed to nestedness. Our extension of their methodology to evaluate contributions to nestedness of species (Table 2) as well as islands (Table 1) is novel. By determining the relative contributions of particular islands or species, patterns in the species–island matrix may emerge that give insight into the relative contribution of mechanisms that affect nestedness. For each island group in the Caribbean, the more ubiquitous species of bats generally enhance nestedness. In contrast, species with restricted ranges, in particular species endemic to one or only a few islands, often diminish nestedness, with the obvious exception of species endemic to the most species-rich island.

Consideration of I_E for the Bahamas suggests that a species from Central America (*M. waterhousii*) and the Caribbean endemic *E. sezekorni* strongly enhance nestedness. These two species occur on species-rich islands and are often the only residents of species-poor islands. In contrast, establishment of species from North America is idiosyncratic on these islands, with some species (*E. fuscus*, *L. minor*, *T. brasiliensis*) often absent from species-rich islands but present on islands with intermediate richness. Because the ranges of many Bahamian bat species encompass all of the Bahamas, differential immigration related to dispersal abilities is an unsatisfactory explanation for nestedness. Rather, differential establishment on islands, possibly related to the availability of adequate roosts or forage, is a more likely explanation, with some islands providing a greater diversity of habitats than others.

Bat assemblages on islands of the Greater Antilles are nested strongly, despite the fact that 21 of the 36 species of bat in the Greater Antilles are endemic to the Caribbean and that 17 of those endemic species occur on four or fewer islands. However, most endemic species are restricted to larger and more species-rich islands (i.e. Cuba, Hispaniola, Jamaica, Puerto Rico) and are not found in the Virgin Islands. The observed distribution of bat species in the Greater Antilles is consistent with predictions of multiple mechanisms: differential immigration related to species-specific dispersal abilities and hierarchical habitat distributions related to variation in island size. The Virgin Islands are the most distant islands from the centres of endemism (i.e. Cuba,

Jamaica) in the Greater Antilles and are among the smallest islands of the Greater Antilles. Consequently, differential dispersal abilities or lack of appropriate habitat related to island size may explain the absence of species endemic to the Greater Antilles on many of the Virgin Islands.

Lesser Antillean bat assemblages exhibited the highest degree of nestedness of the three island groups, regardless of whether analyses included all species or were restricted to carnivores or to herbivores. A core of eight species (*Ardops nichollsi*, *A. jamaicensis*, *Brachyphylla cavernarum*, *M. molossus*, *M. plethodon*, *N. stramineus*, *Noctilio leporinus*, *T. brasiliensis*) is chiefly responsible for the high degree of nestedness in the Lesser Antilles. With the exception of Grenada, at least seven core species are recorded from the 13 other Lesser Antillean islands with at least seven species. In addition, core species are the only bat taxa recorded from most species-poor islands. Grenada and the Grenadines harbour distinctive bat assemblages that more strongly reflect colonization by species of South American origin (e.g. *Artibeus lituratus*, *Glossophaga soricina*, *Micronycteris megalotis*, *Sturnira lilium*) and lack Antillean endemics (e.g. *B. cavernarum*, *M. plethodon*, *A. nichollsi*) that are frequent on more northern representatives of the Lesser Antilles. In the Lesser Antilles, island area influences bat species richness and composition, as larger islands harbour more species than do smaller islands (Willig *et al.*, 2008), and islands of similar size harbour more similar assemblages than do islands of different sizes. Because of the geographical arrangement of islands in the Lesser Antilles, evaluation of the relative importance of hierarchical habitat distributions and differential immigration on species composition is difficult. The largest islands of the Lesser Antilles occur in the middle of the archipelago and these islands harbour a combination of Antillean endemics common in more northern islands as well as many species of South American origin. Consequently, species composition of these islands may be a result of geographical proximity to multiple species pools and increased habitat diversity associated with island area. Lesser Antillean islands north of Guadeloupe harbour fewer species of South American origin compared with the larger, more centrally located islands. Whether this is related to differential immigration of species of South American origin, hierarchical habitat heterogeneity or both is difficult to determine.

The role of endemics

Complex patterns of composition and nestedness characterize island systems in the Caribbean for a number of ecological and evolutionary reasons. In particular, speciation events in the Caribbean often produced local endemics that are restricted to one or a few islands in close proximity to each other (e.g. *Stenoderma rufum* on Puerto Rico, St Croix, St John, St Thomas and Vieques). Generally, local endemic species diminish nestedness via the creation of 'holes' (unexpected absences) and 'outliers' (unexpected presences) in the species–island incidence matrix. If a broad-ranging ancestral species evolved to become a local endemic, occupying one or a few islands, it would create holes with respect to the ancestral species, but only to the extent that the ancestral species persisted on other islands throughout the

system. At the same time, the local endemic species would represent an 'outlier' in the incidence matrix. If separate speciation events involving a single ancestral species occurred on multiple islands, the effect would be multiplied throughout the system. Thus it is remarkable that these islands were nested at the scale of each island group as well as at the scale of the entire system. Concomitantly, the existence of local endemics enhanced the correlation between inter-island proximity and compositional similarity, especially when the distribution of the endemic species occurred on a larger island and a number of smaller associated satellite islands (the latter potentially maintained by source–sink dynamics). Endemics also decreased the correlation between compositional similarity and measures of environmental similarity, especially if intra-generic competition between derived species prevented them from occupying a broader range of islands that otherwise share ecological conditions with the island on which the species originated.

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SUPPORTING INFORMATION

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

Appendix S1 Environmental characteristics and bat richness of 65 Caribbean islands.

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