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Bat metacommunity structure on Caribbean islands and the role of endemics

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ABSTRACT

Aim We evaluate characteristics of species ranges (i.e. coherence, species turnover and range boundary clumping) to determine the structure of bat metacommunities and metaensembles from Caribbean islands. We evaluate the effects of endemic species on that structure, and quantify associations between island characteristics and latent environmental gradients that structure these metacommunities and metaensembles.

Location Sixty-five Caribbean islands throughout the Bahamas, Greater Antilles and Lesser Antilles.

Methods Metacommunity structure is an emergent property of a set of ecological communities at different sites defined by species distributions across geographic or environmental gradients. We analysed elements of metacommunity structure (coherence, range turnover and range boundary clumping) to determine the best-fit pattern for metacommunities from all Caribbean islands, as well as from the Bahamas, the Greater Antilles and the Lesser Antilles separately. For each island group, analyses were conducted for all bats and for each of two broadly defined guilds (i.e. carnivores and herbivores). In addition, analyses were conducted for all species and for a subset in which endemic species were removed from the fauna. Spearman rank correlations identified island characteristics (area, elevation, latitude, longitude) that were associated significantly with island scores for ordination axes based on reciprocal averaging.

Results Metacommunity structure for all bats and for carnivores was similar for each island group, with Clementsian distributions (i.e. discrete communities with groups of species replacing other groups of species along the gradient) for all islands, the Bahamas and the Lesser Antilles, but with nested distributions for the Greater Antilles. Herbivore distributions were random for the Bahamas, but were Clementsian for all other island groups. Removal of endemic species affected the best-fit model of metacommunity structure in only 3 of 12 cases. In general, ordination scores for islands were correlated with longitude or latitude, but not with island area or elevation.

Main conclusions Characteristics of bat species ranges and associated metacommunity structure were primarily dependent on the number and geographic arrangement of primary sources of colonization, and not on interspecific interactions, species-specific levels of environmental tolerance, or the physical characteristics of islands. Endemic species did not greatly affect metacommunity structure in Caribbean bats.

Keywords

Caribbean, Chiroptera, coherence, endemic species, island biogeography, nestedness, species boundary clumping, species composition, species range turnover.

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INTRODUCTION

A metacommunity can be defined broadly as a set of ecological communities at different sites that are potentially, but not necessarily, linked by dispersal, with each community being a group of species at a given site (Leibold & Mikkelsen, 2002). The spatial extent of a site may differ among metacommunity studies; however, the crucial aspect of scale in a metacommunity context is that the definition of a site is consistent with the theoretical questions addressed in the analysis as well as with the explanatory characteristics and mechanisms invoked to account for empirical patterns. During the recent maturation of metacommunity concepts (e.g. Leibold & Miller, 2004; Leibold *et al.*, 2004; Holyoak *et al.*, 2005), many innovative analytical approaches were developed (e.g. Hoagland & Collins, 1997; Hofer *et al.*, 1999; Leibold & Mikkelsen, 2002; Hausdorf & Hennig, 2007) that facilitate the identification, exploration and evaluation of biotic structure in space. These approaches differ in the aspects of metacommunity structure that they consider, as well as in the spatial extent and focal scale to which they apply. The approach developed by Leibold & Mikkelsen (2002) is unique in that: (1) the focal units of analysis are the distributions of species rather than the species composition of sites, and (2) elements of metacommunity structure (EMS) uniquely combine to assess multiple competing hypotheses. Because this methodological approach simultaneously evaluates fit with multiple models of species distribution, it represents a more powerful tool than do analyses that are restricted to comparisons of one structural model with randomness (e.g. traditional analyses of nested subsets; Patterson & Atmar, 1986; Wright *et al.*, 1998; Ulrich *et al.*, 2009).

Analyses of EMS have a number of conceptual and methodological advantages over other approaches that explore metacommunity structure along gradients. For example, analyses of EMS ordinate matrices via reciprocal averaging, which is the best indirect ordination procedure for discerning empirical variation in response to environmental gradients (Gauch *et al.*, 1977; Pielou, 1984). This places analyses of EMS and associated structure of the metacommunity in an environmental context that can enhance ecological and biogeographic understanding compared with approaches that focus on gradients of richness or occurrence, as in traditional analyses of nestedness.

Leibold & Mikkelsen (2002) defined three EMS (i.e. coherence, species turnover and boundary clumping). In concert, analyses of these three elements identify which of six patterns of structure (checkerboard, nested, Clementsian, Gleasonian, evenly spaced and random distributions) best reflects the distribution of species along the primary axis of environmental variation as determined via reciprocal averaging (Fig. 1). Each of the non-random models assumes that distributions of species are moulded by biotic (e.g. competition, habitat associations) or abiotic (e.g. temperature, rainfall) factors that form a gradient. Importantly, the mechanisms and theoretical underpinnings consistent with each model are unique. Consequently, identification of the best-fit model of metacommunity structure provides insights about how the group of species responds to environmental variation. Although the nature of the responses may differ among species, as a group the biota must respond to the same latent environmental gradient(s) for a metacommunity to evince non-random structure (i.e. coherence). If species as a group do not respond to the same environmental gradient, their distributions will not form a coherent structure, indicating

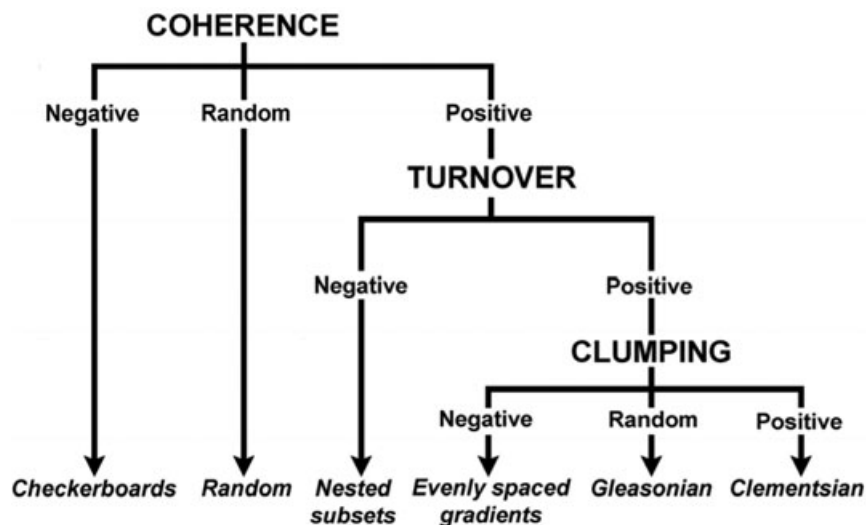


Figure 1 Analytical approach using three elements of metacommunity structure (coherence, range turnover and range boundary clumping) to identify the best-fit pattern (italics) for species distributions (modified from Willig *et al.*, in press a). Metacommunities that lack coherence have random structure. Negative coherence is unique to metacommunities that exhibit checkerboards. Positive coherence is characteristic of four patterns, which may be distinguished by analyses of range turnover and range boundary clumping. Coherent metacommunities with negative range turnover are indicative of nested subsets. Coherent metacommunities with positive range turnover may exhibit negative, random or positive clumping of range boundaries, which are consistent with evenly spaced, Gleasonian and Clementsian distributions, respectively.

that species occurrences with respect to the latent gradient are random (Leibold & Mikkelsen, 2002). Checkerboard distributions occur if pairs of species are mutually exclusive (Diamond, 1975), and if mutually exclusive responses are independent of each other along the gradient. Distributions are nested if ranges of species that occupy a smaller portion of the environmental gradient are contained within the ranges of those that occupy a larger portion of the gradient. Distributions that exhibit turnover and whose boundaries are clumped along the environmental gradient are termed Clementsian in reference to Clements' model of distinctive 'communities' in which the boundaries of species ranges are highly coincident (Clements, 1916). Distributions that exhibit turnover and whose boundaries occur idiosyncratically along the environmental gradient are termed Gleasonian in reference to Gleason's concept of individualistic responses of species (Gleason, 1926). Evenly spaced distributions exhibit turnover with boundaries that are hyperdispersed along the environmental gradient, indicating maximal differences in environmental tolerances among species.

The extents of most metacommunity studies, including those that employ the methods of Leibold & Mikkelsen (2002), are at the local or landscape level (e.g. Kusch *et al.*, 2005; Zimmerman, 2006; Bloch *et al.*, 2007; Burns, 2007; Werner *et al.*, 2007; Willig *et al.*, 2007; Barone *et al.*, 2008; Presley *et al.*, 2009); however, these methods also can be applied in studies of biogeography. Caribbean islands long have been a focus of biogeographic investigation (e.g. Koopman, 1959, 1989; MacArthur & Wilson, 1967; Baker & Genoways, 1978; Woods, 1989; Ricklefs & Lovette, 1999; Morand, 2000; Woods & Sergile, 2001). As a result, sufficient data exist for many taxa on these islands to explore large-scale ecological and biogeographic questions, and to apply newly developed analytical techniques at geographic scales for which high-quality data are otherwise rare.

Islands of the Caribbean are numerous (> 7000 islands, islets, reefs and cays), cover a large geographic area (Fig. 2), and differ greatly in size, elevational relief, sources of colonization, degree of isolation, geological history and disturbance regime associated with exposure to hurricanes (Woods, 1989; Woods & Sergile, 2001). Consequently, Caribbean islands exhibit the environmental variation that is necessary to evaluate the relative importance of island-specific characteristics in delimiting the geographical distribution of vagile species. In addition, the Caribbean is a hotspot of terrestrial biodiversity with high species endemism (Woods, 1989; Woods & Sergile, 2001), including 7000 endemic vascular plants and 779 endemic vertebrates (Myers, 2001). Bats of the Caribbean are well studied (e.g. Koopman, 1959, 1989; Baker & Genoways, 1978; Ricklefs & Lovette, 1999; Morand, 2000; Rodríguez-Durán & Kunz, 2001; Presley & Willig, 2008) and the distributions of species on islands are well delimited (Willig *et al.*, in press b and citations therein). We used bats from Caribbean islands and the analytical methods of Leibold & Mikkelsen (2002) to evaluate patterns of species distribution with three primary goals: (1) to determine the primary environmental gradients (i.e. island characteristics) to which species of Caribbean bat respond, (2) to determine the best-fit model of species distributions for bat metacommunities

and metaensembles (groups of species in an area restricted by taxon and guild affiliation; Fauth *et al.*, 1996) along the primary environmental gradient, and (3) to determine the contribution of endemic species to the metacommunity and metaensemble structure.

MATERIALS AND METHODS

Islands and bats of the Caribbean

Caribbean islands range from 27.33° N to 10.05° N latitude and from 84.96° W to 59.42° W longitude (Fig. 2). They differ greatly in physical characteristics and span a gamut from small (< 1 km²), low (< 5 m above sea level) cays, with little more than sand and sparse scrub vegetation, to large (114,524.0 sq km²), high (3175.0 m) islands that are physiographically diverse, with many different habitat types (Myers, 2001). Each Caribbean island belongs to one of three major island groups (Bahamas, Greater Antilles or Lesser Antilles) based on geological and biogeographical considerations (Baker & Genoways, 1978). The Bahamas are low-lying islands (maximum elevation 63 m) formed from carbonate banks of the Bahamas Platform, a part of the North American tectonic plate. In contrast, andesitic volcanism in the Antilles created more physiographically and geologically diverse islands (Hedges, 2001). Because bats are highly vagile, and to avoid confounding effects related to continental proximity, we omitted Trinidad, Tobago and the Leeward Antilles from analyses. Consequently, the most southerly island in analyses was Grenada (12.11° N, 61.67° W).

Caribbean islands adjoin parts of North, Central and South America, resulting in multiple sources of colonization from the mainland. The three primary continental sources of colonization for Caribbean bats are subtropical North America, the Yucatán of Central America and northern South America (Baker & Genoways, 1978). The relative influence of each source of colonization on bat species composition on each island is primarily associated with geographic proximity; however, this relationship is contingent on island-specific characteristics such as topographic complexity, habitat diversity and area (Presley & Willig, 2008).

A species incidence matrix for Caribbean islands was constructed based on a comprehensive search of the literature, including the most recently published records (for details see Willig *et al.*, in press b). We eliminated records based on questionable identification of individuals as well as records based only on fossils. In addition, we removed islands for which data on species presences were based only on cursory observations. As a result, reliable data concerning bat species composition were available for 65 islands, including 23 in the Bahamas, 19 in the Greater Antilles and 23 in the Lesser Antilles (Appendix 1). Families of bats that occur on Caribbean islands include the Emballonuridae (1 species), Phyllostomidae (24 species), Noctilionidae (1 species), Mormoopidae (5 species), Natalidae (7 species), Molossididae (7 species) and Vespertilionidae (13 species). We followed the taxonomic treatment of Simmons (2005), except for recognizing *Eptesicus lynni* (Arnold *et al.*,

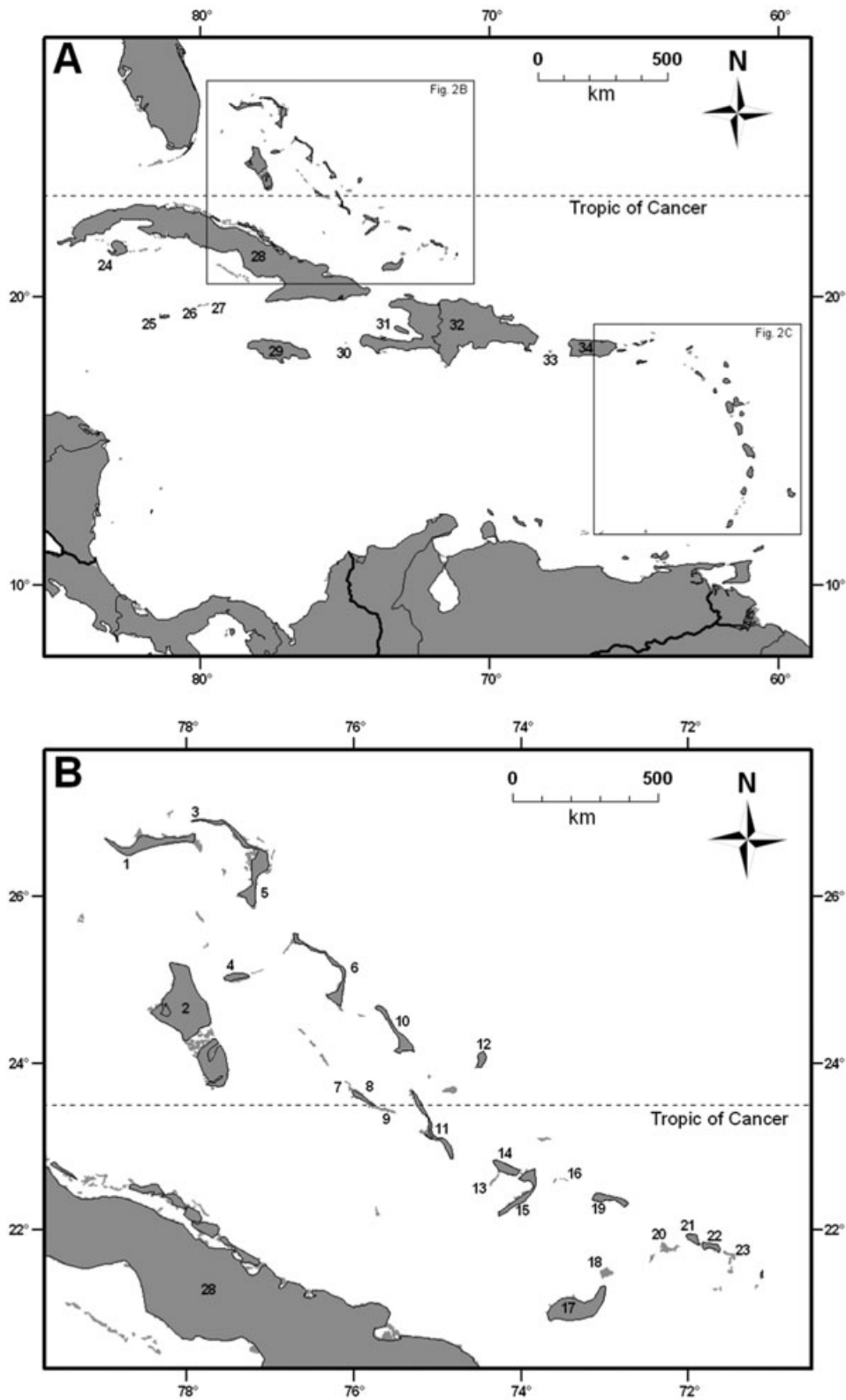


Figure 2 Maps of islands in the Caribbean (modified from Presley & Willig, 2008). (a) Islands of the Greater Antilles (24–42) in relation to the Bahamas and Lesser Antilles. (b) Bahamian islands (1–23) in relation to Cuba (island 28). (c) Lesser Antilles (43–65) in relation to the easternmost Greater Antilles (34–42). Solid lines in (c) mark the transitions between discrete ensembles of carnivores or discrete ensembles of herbivores in the Lesser Antilles. In addition, these lines mark transitions between discrete communities of bats. For the Bahamas and Greater Antilles, islands are numbered from west to east; for the Lesser Antilles, islands are numbered from north to south. Island names are in Appendix 1.

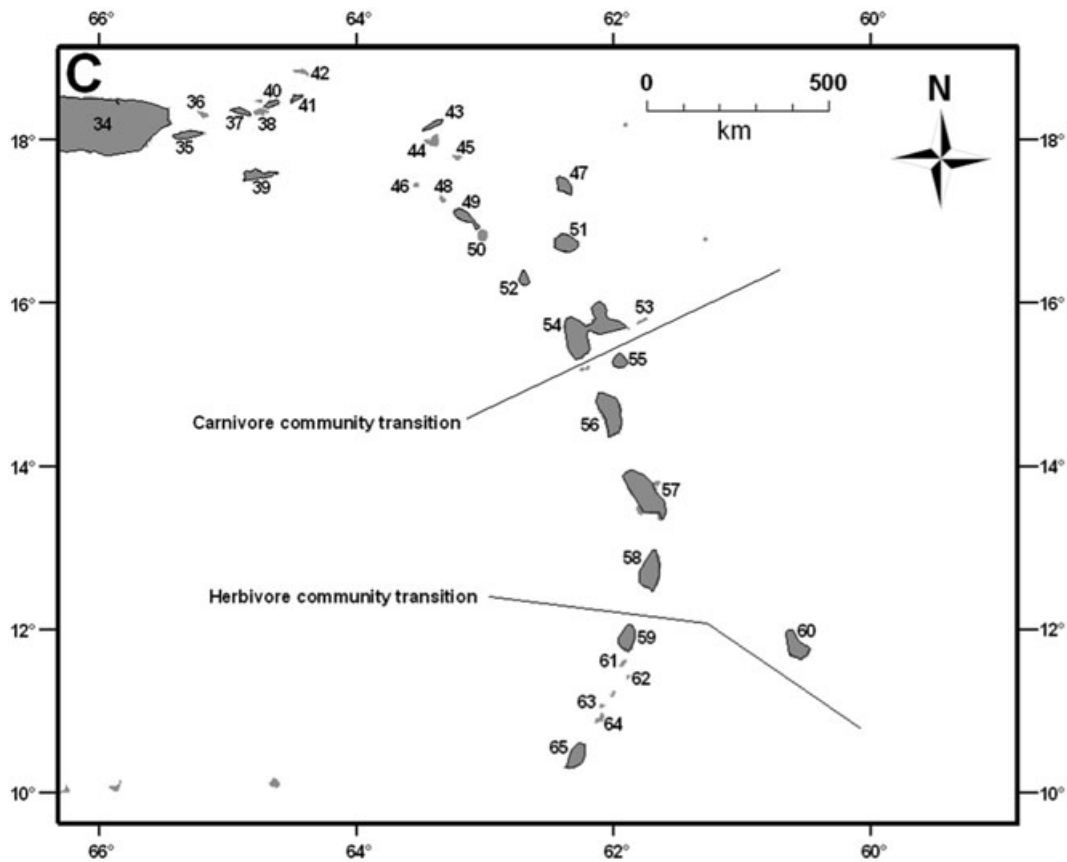


Figure 2 *Continued*.

1980; Genoways *et al.*, 2005) as an endemic of Jamaica, distinct from *Eptesicus fuscus*.

Caribbean bats are functionally diverse and occupy many trophic groups, including piscivore, carnivore, insectivore, sanguivore, nectarivore and frugivore guilds. The way in which particular species respond to environmental gradients is probably contingent on guild affiliation. Many Caribbean islands harbour few species of bat, and some guilds are absent from a majority of islands; therefore, analyses based on assignment of species to narrowly defined guilds such as aerial insectivore or gleaning animalivore would be problematic. As a consequence, we categorized species based on primary dietary components into two broadly defined guilds (Appendix 2): carnivores (i.e. insectivores, piscivores, carnivores, animalivores and omnivores) and herbivores (i.e. nectarivores and frugivores).

Statistical analyses

Because bat species composition is quite different for each island group (Koopman, 1959; Baker & Genoways, 1978; Presley & Willig, 2008; Willig *et al.*, in press b), analyses were conducted for all islands and separately for each of three island groups (Bahamas, Greater Antilles and Lesser Antilles). In addition, for each group of islands, analyses were conducted separately for all bats (metacommunity), for the carnivore metaensemble and for the herbivore metaensemble.

To evaluate metacommunity and metaensemble structure, we used the analytical methods and terminology of Leibold & Mikkelsen (2002), except that we employed a null model with a more desirable combination of type I and type II error properties for analyses of coherence. Prior to calculation of metrics, sites and species in an incidence matrix were ordinated via reciprocal averaging; a correspondence algorithm that maximizes the degree to which sites with the most similar species composition and species that have comparable distributions are adjacent in the matrix (and in correspondence space). As a result, reciprocal averaging allows the composition of sites and the occurrences of species to define a latent environmental gradient, and orders sites and species along that gradient. Moreover, when subjected to reciprocal averaging, a metacommunity or metaensemble may be ordered along a gradient that integrates multiple environmental factors that are important to the distributions of species.

Coherence was evaluated by counting the number of embedded absences in the ordinated matrix, and comparing the empirical value to a null distribution of embedded absences. An embedded absence is defined as 'an interruption in a range or community' and is identified in the incidence matrix as an absence that is bounded on either side in a range or community by a presence. A by-product of reciprocal averaging is that it minimizes the number of embedded absences in the ordinated matrix. This standardization of embedded absences helps to ensure that the null distribution of values derived from

randomly generated matrices is appropriate for determining the significance of empirical values. For each analysis, the null model generated 1000 random matrices that were ordinated via reciprocal averaging and whose numbers of embedded absences were tallied to create a null distribution of such values. The empirical value was compared with the null distribution to determine significance based on a two-tailed test with an α of 0.05. Significantly positive coherence indicates that the incidence of each species was associated strongly with a latent environmental gradient and that the biota, as a group, responded to the same gradient. Positive coherence is consistent with nested, Gleasonian, Clementsian or evenly spaced distributions (Fig. 1). Significantly negative coherence (i.e. more embedded absences than expected by chance) indicates checkerboard distributions (Fig. 1). Non-coherent matrices indicate that occurrences of species are not strongly affected by environmental factors associated with the ordination axis (i.e. a random metacommunity structure).

In the original methodology (Leibold & Mikkelsen, 2002), two null model options were used for demonstration purposes to represent ends of a spectrum from highly liberal (Random 0) to highly conservative (Random 4). Random 0 assigns equiprobable occurrences throughout the matrix. Because null models such as this have no structure, they are highly prone to type I errors (Gotelli, 2000). In contrast, Random 4 fixes row and column totals to equal empirical values. Highly constrained null models such as this may incorporate the ecological mechanisms under examination, which can create an unrealistically small null space and an analysis with little statistical power, resulting in a high likelihood of type II errors (Gotelli & Graves, 1996). The magnitude of these problems with fixed–fixed null models is contingent on matrix size, with power decreasing and type II error rates increasing with decreasing matrix size. Indeed, a recently developed method (Hausdorf & Hennig, 2007) to evaluate clustering of species (i.e. species aggregation) and nested subsets in metacommunities that employed a fixed–fixed null model concluded that ‘Just as for clustering, it is also difficult to detect nestedness in species-poor metacommunities (with less than about 30 species)’. This may arise because the null model does not allow sufficient randomization of matrix aspects associated with the structure under evaluation, resulting in exceedingly low statistical power and a high susceptibility to type II errors. This problem can also occur with the application of a fixed–fixed null model in analyses of coherence (Leibold & Mikkelsen, 2002).

An ecological concern when selecting a null model is that it only allows the factor of interest to occur at random, while constraining all other parameters. The range of a species is defined by the number and identity of sites at which the species occurs, and occurrences are determined by species-specific characteristics that combine to define the ranges of species. Consequently, these factors (number and location of species occurrences) should be allowed to occur at random in the null model when assessing the degree of range coherence in a metacommunity. Importantly, the number of species occurrences in all of these null model approaches is constrained to equal the

total number of occurrences in the empirical metacommunity. Island characteristics (area, number of habitats) and passive sampling affect the number of bat species (though not the identity of those species) that occur on Caribbean islands (Willig *et al.*, in press b). For these reasons, we used a null model that constrained simulated species richness of each island to equal empirical richness, with equiprobable occurrences for each species. This null model has a more desirable combination of type I and type II error properties than does Random 0 or Random 4 (Gotelli & Graves, 1996; Gotelli, 2000) and has been applied successfully to analyses of coherence (Presley *et al.*, 2009).

If a metacommunity exhibited positive coherence, species turnover was evaluated (Fig. 1). Species turnover was measured as the number of times one species replaced another between two sites in an ordinated matrix (i.e. the number of replacements). The observed number of replacements was compared to a distribution of randomly generated values based on a null model that randomly shifts entire ranges of species. Significantly low species turnover is consistent with nested subsets. Significantly high species turnover is consistent with Gleasonian, Clementsian or evenly spaced distributions, and requires analysis of boundary clumping to distinguish among them (Fig. 1). Boundary clumping was evaluated via Morisita’s index (Morisita, 1971) and a chi-square test comparing observed and expected distributions of range boundary locations (Hoagland & Collins, 1997; Leibold & Mikkelsen, 2002). Values of Morisita’s index not significantly different from 1.0 indicate randomly distributed range boundaries and are consistent with Gleasonian distributions; values significantly greater than 1.0 indicate clumped range boundaries and are consistent with Clementsian distributions; and values significantly less than 1.0 indicate hyperdispersed range boundaries and are consistent with evenly spaced distributions (Fig. 1).

Caribbean islands harbour many endemic species of bat that may play a critical role in affecting patterns of species composition (Presley & Willig, 2008). In addition, each island group has a number of species that only occur on a single island within that group. Because species that occur at a single site in a metacommunity (hereafter endemics) affect measures of coherence and boundary clumping, such species may have a disproportionate effect on metacommunity structure. Nonetheless, effects of endemic species on metacommunity or metaensemble structure remain uninvestigated and poorly understood. To evaluate such effects, we removed all endemics from each metacommunity or metaensemble, and accordingly reanalysed EMS. For all analyses, we used an α of 0.05 to assign significance based on the range perspective as described by Leibold & Mikkelsen (2002). Analyses of coherence, turnover and boundary clumping were conducted with algorithms written in MATLAB 6, release 12 (script files and documentation are available at <http://www.tarleton.edu/~higgins/EMS.htm>).

In general, visual inspection of ordinated matrices is required to identify details associated with the best-fit model of metacommunity structure and to understand the role of particular biotic or abiotic factors in structuring the metacommunity. For

example, visual inspection is required to identify the locations of boundary clumps that delimit aggregations of species, and to determine the number of aggregations for metacommunities that evince Clementsian structure.

For each metacommunity, component scores for each island were quantified for the primary ordination axis derived via reciprocal averaging using the simple correspondence analysis option of MINI-TAB 15.1.20.0. To determine if island scores for the ordination axis were correlated significantly with the island characteristics (i.e. island area, maximum elevation, latitude, longitude), Spearman rank correlations were conducted using the R programming environment (R Development Core Team, 2009). The area of each island was obtained from an equal-area projection map (National Geographic Society, 1985). Maximum elevation of islands was obtained from maps (National Geographic Society, 1985) and geographic gazetteers (National Oceanic and Atmospheric Administration, 1976; United States Department of Agriculture, 1998).

RESULTS

Each metacommunity and seven of eight metaensembles exhibited positive coherence (Table 1). Results for all bats and for carnivores were similar for each island group, with species distributions for all islands, for the Bahamas and for the Lesser Antilles being best described by the Clementsian model and species distributions for the Greater Antilles being best described by nested subsets (Figs 3–5). Herbivore distributions were random in the Bahamas, and were best described by the Clementsian model for all islands, for the Greater Antilles and for the Lesser Antilles.

In general, removal of endemic species had little effect on analyses of EMS (Table 1). More specifically, coherence was not affected by the removal of endemics in 11 of 12 cases. In the lone exception of carnivores in the Bahamas, distributions were coherent with endemics and non-coherent without them. Removal of endemics did not affect qualitative results for species turnover in any metacommunity or metaensemble. Boundary clumping was affected by the removal of endemics in 2 of 12 cases. In each case, species boundaries were less clumped after the removal of endemics. As a result, Bahamian carnivores exhibited Clementsian distributions for all bats and random distributions without endemics, whereas the Bahamian metacommunity and Lesser Antillean carnivores each exhibited Clementsian distributions for all bats and Gleasonian distributions without endemics.

With the exception of analyses that included all islands, scores for islands on the primary ordination axis exhibited little correlation with physical attributes (i.e. area, elevation) of islands regardless of island group (Table 2). In contrast, geographical location (i.e. latitude, longitude) was significantly correlated with island scores for the majority of metacommunities and metaensembles. In general, removal of endemics did not affect correlations between island scores and physical attributes or geographic location of islands. Island scores were correlated with island area only for carnivores (Table 2).

DISCUSSION

Species distributions in the Caribbean were generally coherent, indicating that occurrences were determined by responses to latent environmental gradients, and that the preponderance of species in each metacommunity or metaensemble responded to the same gradient. When the domain included islands throughout the Caribbean (i.e. all three island groups), bats showed clumped range boundaries and high species turnover, consistent with a Clementsian pattern, and did so from metacommunity and metaensemble perspectives as well as with and without the removal of endemics. Results for analyses restricted to particular domains were quite different, with structure contingent on island group, inclusion of endemics, or trophic affiliation (Table 1; Figs 3–5). Ordination scores were correlated with island location regardless of domain (i.e. for all islands as well as for the Bahamas, Greater Antilles and Lesser Antilles), indicating that geographic location is a contributing factor to bat species composition on Caribbean islands at multiple scales. In contrast, ordination scores generally were correlated with the geophysical characteristics of islands only for analyses that included all islands (Table 2), indicating that geophysical characteristics within particular groups of islands are not related to mechanisms that structure metacommunities or metaensembles at that scale. Because the Bahamas, Greater Antilles and Lesser Antilles each have distinct bat species compositions (Baker & Genoways, 1978; Presley & Willig, 2008; Willig *et al.*, in press b), we expected a Clementsian structure in analyses that included all islands. The continental sources of colonization are unique for each of these three groups of islands (Koopman, 1959, 1989; Baker & Genoways, 1978), resulting in more-or-less distinctive assemblages inhabiting each group of islands. Consequently, we focus the discussion of metacommunity and metaensemble structure on more careful consideration of patterns and mechanisms operating within each of the three island groups (Figs 3–5).

Clementsian distributions

Metacommunities and metaensembles best characterized by a Clementsian model exhibited one, two or three discrete groups of islands, each of which was characterized by a distinct bat species composition. Consistent with correlations between island scores and island location or physical attributes (Table 2), the number of discrete groups of islands was primarily related to the number of primary colonization sources associated with the island group and to the relative proximity of islands to each source. Species with similar evolutionary origins may have similar levels of environmental tolerance or resource requirements, which may contribute to those species having similar distributions in geographic or environmental space. In addition, priority effects (Paine, 1977) may determine the location of boundaries between distinct communities or ensembles. Because bats are highly vagile, it is likely that most species capable of dispersal from continental sources to newly formed or inhabitable islands colonized those areas during the same

Table 1 Results of analyses of coherence, species turnover and boundary clumping for Caribbean bats.

	Coherence			Species turnover			Boundary clumping			Metacommunity pattern	
	Number of absences	<i>P</i>	Mean	SD	Number of replacements	<i>P</i>	Mean	SD	Morisita's index		<i>P</i>
All species											
All islands											
All bats	827	<0.001	1907	107.9	78,275	0.015	64,681	6238.6	6.483	<0.001	Clementsian
Carnivores	503	<0.001	895	76.4	23,979	0.045	19,046	2906.0	8.705	<0.001	Clementsian
Herbivores	136	<0.001	467	35.8	11,142	0.170	9775	1434.0	2.819	<0.001	Clementsian
Bahamas											
All bats	61	0.004	90	11.1	860	0.081	592	191.1	1.750	0.011	Clementsian
Carnivores	21	0.006	38	6.7	347	0.033	193	84.2	2.418	0.007	Clementsian
Herbivores	12	0.553	12	3.5							Random
Greater Antilles											
All bats	113	<0.001	251	31.4	3254	0.021	4281	505.6			Nested
Carnivores	62	<0.001	134	21.7	141	<0.001	1636	236.8			Nested
Herbivores	26	0.018	42	7.6	563	0.088	427	99.9	3.462	<0.001	Clementsian
Lesser Antilles											
All bats	92	<0.001	231	15.6	2967	<0.001	1354	285.8	5.895	<0.001	Clementsian
Carnivores	59	0.005	84	9.5	413	<0.001	181	57.2	4.146	<0.001	Clementsian
Herbivores	16	<0.001	79	9.4	798	<0.001	279	100.3	8.250	<0.001	Clementsian
Endemics removed											
All islands											
All bats	530	<0.001	1305	57.7	78,233	0.007	61,214	6872.7	3.688	<0.001	Clementsian
Carnivores	293	<0.001	581	39.2	21,967	0.027	16,359	2905.3	5.050	<0.001	Clementsian
Herbivores	121	<0.001	401	29.1	10,057	0.145	8,614	1362.3	3.040	<0.001	Clementsian
Bahamas											
All bats	43	0.009	60	7.2	688	0.052	411	170.1	1.750	0.052	Gleasonian
Carnivores	20	0.578	19	3.7							Random
Herbivores	11	0.737	9	3.2							Random
Greater Antilles											
All bats	81	<0.001	158	18.1	2323	0.046	3156	493.2			Nested
Carnivores	42	0.004	76	12.8	141	<0.001	1077	215.7			Nested
Herbivores	24	0.023	36	6.2	494	0.059	352	91.1	5.000	<0.001	Clementsian
Lesser Antilles											
All bats	70	<0.001	146	10.0	1575	0.004	886	259.8	3.000	<0.001	Clementsian
Carnivores	30	0.001	46	5.5	249	0.003	98	53.8	2.111	0.081	Gleasonian
Herbivores	16	<0.001	63	6.4	600	<0.001	218	89.3	6.417	<0.001	Clementsian

Analyses were performed for all islands and separately for each of three island groups: Bahamas, Greater Antilles and Lesser Antilles. For each group of islands, analyses were performed separately for all bats and for each of two broad foraging guilds: carnivores and herbivores. Each analysis was performed for all species as well as with endemic species (i.e. species that occurred on a single island in an island group) removed. Significant results ($P \leq 0.05$) are bold. SD, standard deviation.

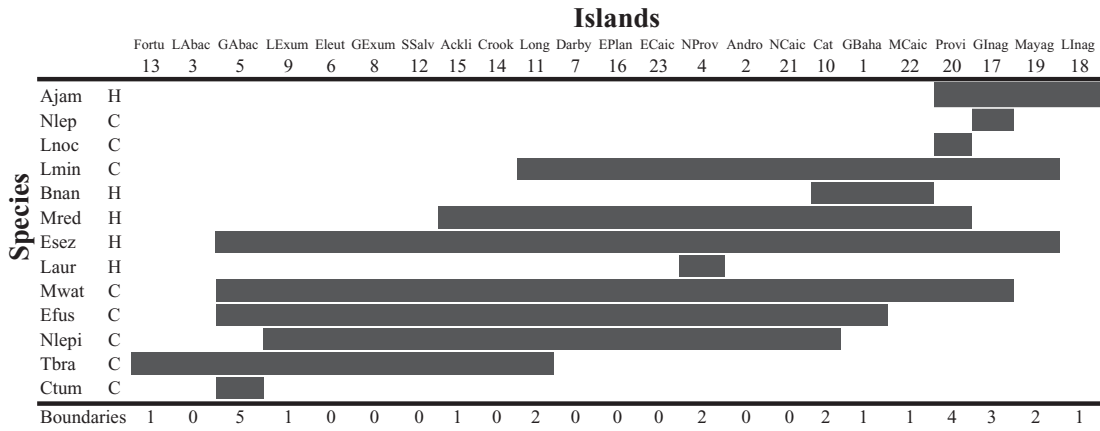


Figure 3 Bahamian bat distributions with species and sites ordinated according to the primary axis extracted via reciprocal averaging. Shaded bars represent the distributions of species along a latent environmental gradient. Abbreviations for islands and species are in Appendices 1 and 2, respectively. Bahamian island codes were assigned from west (1) to east (23). Guild affiliations are indicated by H and C for herbivores and carnivores, respectively. The number of range boundaries that occur at each island is listed along the bottom.

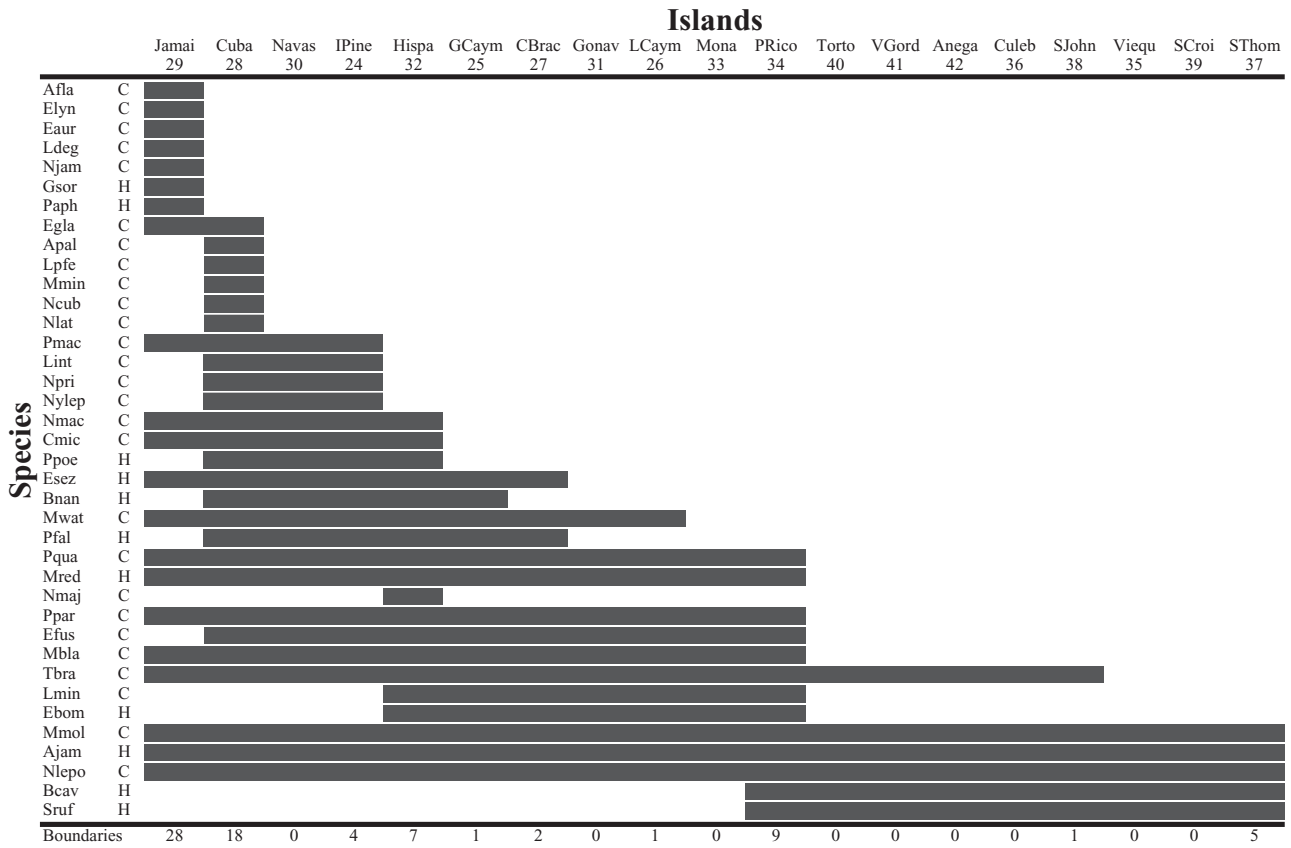


Figure 4 Greater Antillean bat distributions with species and sites ordinated according to the primary axis extracted via reciprocal averaging. Shaded bars represent the distributions of species along a latent environmental gradient. Abbreviations for islands and species are in Appendices 1 and 2, respectively. Greater Antillean island codes were assigned from west (24) to east (42). Guild affiliations are indicated by H and C for herbivores and carnivores, respectively. The number of range boundaries that occur at each island is listed along the bottom.

geological time frame. As a result, distinct communities (or ensembles) of bats from opposite ends of an archipelago would systematically colonize islands until they met. In this transition area, priority effects may allow species to prevent farther dis-

persal of ecologically similar species. If enough such interspecific boundaries form, discrete communities would emerge. Therefore, a combination of priority effects, environmental tolerance and resource or habitat specialization related to the

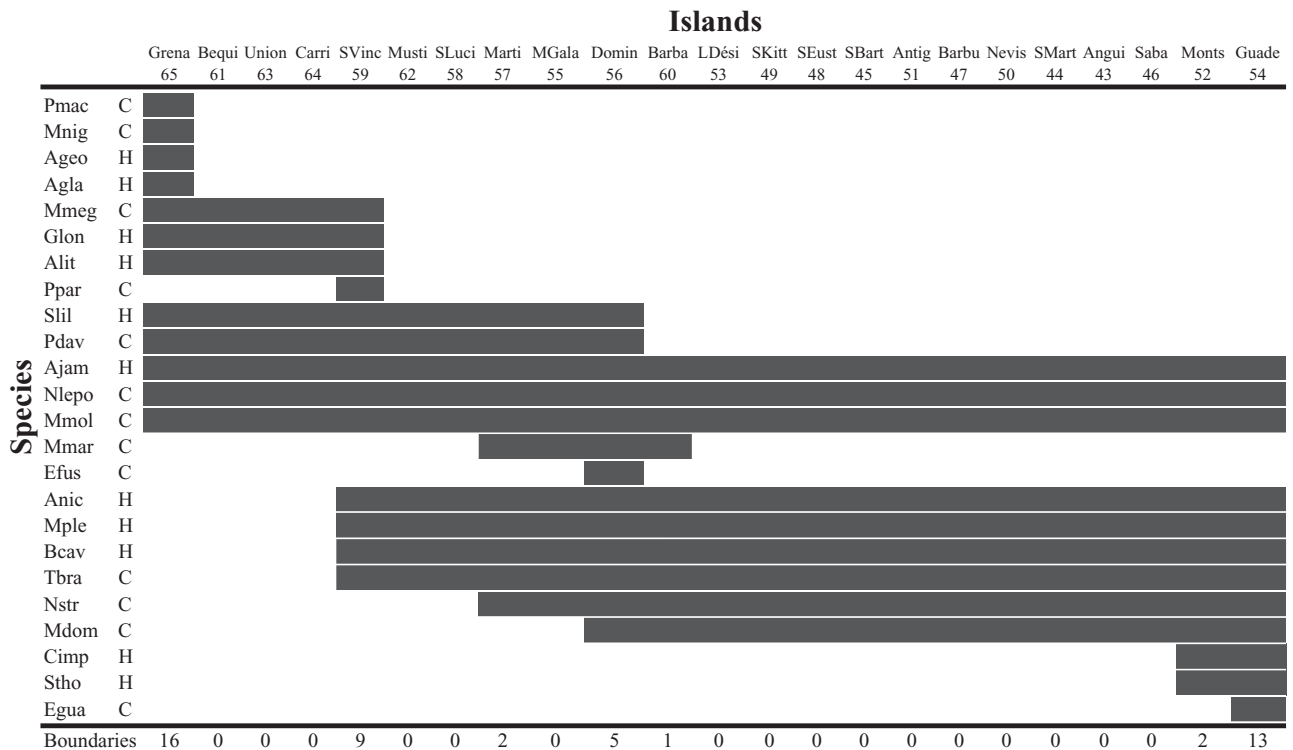


Figure 5 Lesser Antillean bat distributions with species and sites ordinated according to the primary axis extracted via reciprocal averaging. Shaded bars represent the distributions of species along a latent environmental gradient. Abbreviations for islands and species are in Appendices 1 and 2, respectively. Greater Antillean island codes were assigned from north (47) to south (65). Guild affiliations are indicated by H and C for herbivores and carnivores, respectively. The number of range boundaries that occur at each island is listed along the bottom.

common evolutionary origins probably contributed to species having more-or-less coincident range boundaries on Caribbean island systems.

Bahamian bats have a single continental source of colonization (subtropical North America). Although a number of species originated in the Bahamas, each of these species is distributed throughout the island system. Moreover, Bahamian islands are physiognomically similar (i.e. low lying with similar habitat types). The geophysical similarity of Bahamian islands coupled with the high vagility of bats is likely to homogenize species composition of assemblages throughout these islands, resulting in a single community and a single carnivore ensemble (Fig. 3).

Lesser Antillean bat metacommunities and metaensembles exhibited Clementsian structure with two or more distinct communities (Fig. 5). The Lesser Antillean bat fauna has two primary sources of colonization (Greater Antilles and northern South America); however, the relative influence of each source was ensemble specific. Two distinct carnivore ensembles occurred in the Lesser Antilles (Fig. 2c). One ensemble spanned the northern half of the Lesser Antilles, south to Guadeloupe, and was influenced primarily by species of Greater Antillean origin. The other ensemble comprised islands south of Guadeloupe and was influenced primarily by species of South American origin. Similarly, two distinct herbivore ensembles occurred in the Lesser Antilles; however, the geographical delineation of

these ensembles was not coincident with that of carnivores (Fig. 2c). One herbivore ensemble was restricted to Grenada, St Vincent and the Grenadines, and the other comprised the remainder of the Lesser Antilles. The unique geographical patterns associated with each ensemble created three distinct bat communities in the Lesser Antilles: (1) Grenada, St Vincent and the Grenadines, (2) northern islands south to and including Guadeloupe, and (3) islands between and including Marie Galante and St Lucia (Fig. 2c). Thus, metacommunity structure for an assemblage may obscure structure at the ensemble level or structure may differ for assemblages and component ensembles.

Nested subsets

Species distributions of the bat metacommunity and carnivore metaensemble from the Greater Antilles were nested (Table 1, Fig. 4). The majority of Greater Antillean bat species (26 of 38) is of Caribbean origin (Baker & Genoways, 1978), and evolved on the larger islands (i.e. Cuba, Hispaniola or Jamaica). However, dispersal of these species to other islands has been idiosyncratic; many species occur only on Jamaica (i.e. *Phyllo-nycteris aphylla*, *Ariteus flavescens*, *Natalus jamaicensis*, *Eptesicus lynni*, *Lasiurus degelidus*), on Cuba (i.e. *Mormopterus minutus*, *Nyctinomops laticaudatus*, *Lasiurus pfeifferi*, *Nycticeius cubanus*) or on Cuba and the nearby Isle of Pines (i.e. *Natalus primus*,

Table 2 Spearman rank correlations (ρ) and corresponding P-values for associations between island area, maximum elevation, latitude, and longitude and the island scores for the primary axis of correspondence extracted via reciprocal averaging.

	Island area		Elevation		Latitude		Longitude	
	ρ	P-value	ρ	P-value	ρ	P-value	ρ	P-value
All species								
All islands								
All bats	0.319	< 0.001	-0.471	< 0.001	0.817	< 0.001	0.747	< 0.001
Carnivores	0.349	0.005	-0.494	< 0.001	0.710	< 0.001	0.656	< 0.001
Herbivores	0.295	< 0.001	-0.498	< 0.001	0.885	< 0.001	0.807	< 0.001
Bahamas								
All bats	-0.008	0.970	0.040	0.855	0.524	0.010	0.457	0.028
Carnivores	0.011	0.960	0.115	0.611	0.392	0.071	0.324	0.141
Herbivores	-0.054	0.827	-0.259	0.285	-0.630	0.004	-0.463	0.046
Greater Antilles								
All bats	0.355	0.136	0.191	0.435	0.550	0.015	0.765	< 0.001
Carnivores	0.518	0.028	0.153	0.545	0.467	0.051	0.823	< 0.001
Herbivores	0.413	0.099	0.169	0.516	0.655	0.004	0.667	0.003
Lesser Antilles								
All bats	0.032	0.886	0.132	0.548	0.828	< 0.001	0.632	0.001
Carnivores	-0.396	0.075	-0.144	0.533	0.760	< 0.001	0.624	0.003
Herbivores	0.124	0.573	0.169	0.441	0.717	< 0.001	0.493	0.017
Endemics removed								
All islands								
All bats	0.320	0.009	-0.475	< 0.001	0.821	< 0.001	0.756	< 0.001
Carnivores	0.348	0.005	-0.494	< 0.001	0.708	< 0.001	0.657	< 0.001
Herbivores	0.290	0.026	-0.495	< 0.001	0.888	< 0.001	0.814	< 0.001
Bahamas								
All bats	-0.047	0.834	0.034	0.878	0.474	0.023	0.411	0.052
Carnivores	-0.010	0.966	0.124	0.579	0.375	0.086	0.311	0.158
Herbivores	-0.050	0.840	0.381	0.108	0.275	0.253	0.017	0.943
Greater Antilles								
All bats	0.284	0.236	0.106	0.662	0.596	0.008	0.782	< 0.001
Carnivores	0.252	0.308	-0.040	0.876	0.637	0.005	0.813	< 0.001
Herbivores	0.371	0.143	0.087	0.737	0.764	< 0.001	0.689	0.003
Lesser Antilles								
All bats	0.104	0.633	0.181	0.405	0.818	< 0.001	0.661	< 0.001
Carnivores	-0.489	0.026	-0.209	0.360	0.789	< 0.001	0.682	< 0.001
Herbivores	0.148	0.498	0.180	0.409	0.714	< 0.001	0.498	0.017

For all islands as well as for each of three island groups, analyses were performed for all bats as well as for each of two foraging guilds. Analyses were conducted for all species as well as with endemic species (i.e. species occurring on a single island) removed. Significant results ($P \leq 0.05$) are in bold.

Nyctiellus lepidus, *Lasiurus intermedius*). As a result, ranges of Greater Antillean bats form nested subsets, with a core group of widespread species that occur throughout the Greater Antilles that is augmented by restricted-range species that occur on larger islands and on small islands near them. Indeed, populations of restricted-range species on smaller islands (e.g. Caymans, Isle of Pines, Gonâve) may not be self-sustaining. Rather, they may persist because of their proximity to larger islands via source–sink dynamics (Presley & Willig, 2008).

For the carnivore metaensemble on the Greater Antilles, island scores along the ordination axis were correlated with island area and longitude (Table 2), with western, larger islands having more species-rich ensembles than the smaller, eastern islands. The geographic configuration of the Greater Antilles may predispose the creation of nested subsets via speciation and

the subsequent dispersal of those species. Larger islands can support more species via two mechanisms (Rosenzweig, 1995). First, larger areas support more individuals; therefore, more species maintain large population sizes and avoid stochastic extinction. Second, larger areas harbour more habitat types, and greater habitat heterogeneity can increase species richness. Arguably, speciation rates increase with the number of individuals (VanderMeulen *et al.*, 2001), such that large islands with more individuals provide greater opportunity for chance mutations that enhance speciation rates. Because larger islands of the Greater Antilles harbour more habitat types (Arecos-Mallea *et al.*, 1999) and more individuals, larger islands are more likely to be the site of species origination than are smaller islands. Moreover, larger islands in the Greater Antilles are closer to continental sources of colonization compared to smaller islands.

Consequently, populations on larger, western islands probably replaced continental populations as the primary sources of colonization for smaller, eastern islands of the Greater Antilles and for islands of the northern Lesser Antilles. Differential dispersal of species, specialization on locally abundant resources and size-mediated hierarchical habitat distributions on islands are probable mechanisms that enhance nestedness for the bat metacommunity and carnivore metaensemble in the Greater Antilles (Presley & Willig, 2008).

Endemics and metacommunity structure

Endemics account for relatively few occurrences in any metacommunity. Nonetheless, their effects on metacommunity structure may be disproportionate to their occurrence such that overall structure does not reflect patterns exhibited by more widely distributed species. For an embedded absence to occur in a particular row or column of a matrix, a species must occur in at least two communities, or a community must comprise at least two species. By occurring at a single site, endemic species cannot create an embedded absence in the species row, whereas randomly generated matrices using null models without fixed row totals can form such embedded absences. The overall effect is that endemics enhance coherence. Both range boundaries for an endemic occur at the same site; therefore, endemic species may increase boundary clumping in a metacommunity. Because EMS evaluate species distributions along latent environmental gradients, and because endemic species span little (nearly none) of such gradients, understanding how their presence affects conclusions from analyses of metacommunity structure is critical.

Four (three carnivores and one herbivore) of 13 species (31%) were endemics in the Bahamas, 13 (11 carnivores and two herbivores) of 38 species (34%) were endemics in the Greater Antilles and 7 (five carnivores and two herbivores) of 24 (29%) species were endemics in the Lesser Antilles. Nonetheless, removal of these species only changed qualitative conclusions in 3 of 36 analyses of EMS (Table 1). Despite representing a third of Caribbean bat species, endemics were not a primary factor affecting overall metacommunity structure. Assessment of metacommunity structure may be robust to the number of range-restricted or endemic species, but this hypothesis should be evaluated for more combinations of taxa and gradients.

CONCLUSIONS

Metacommunity approaches are powerful and promising methods for advancing the understanding of the structure of island biotas. Bats are highly vagile and easily move between islands in the Caribbean, making it likely that isolation (geographic distance from any potential source of colonization) per se does not greatly affect community composition on islands (Costa *et al.*, 2006). In the Caribbean, bat species richness is a function of geophysical island characteristics (Willig *et al.*, in press b); however, these characteristics do not determine which species occur on an island or the structure of metacommunities. Rather, the locale of origination and associated specialization of

faunal elements, the number of colonization sources and the proximity of islands to each source of colonization combine to shape bat metacommunity structure in the Caribbean. A single continental colonization source, many species of Bahamian origin and high bat vagility combined to create a Clementsian structure with a single aggregation of species in the Bahamas. In contrast, the Lesser Antilles have two sources of colonization, resulting in Clementsian structure with multiple aggregations of species whose boundaries are probably determined by environmental tolerance, resource availability or priority effects. In the Greater Antilles, a significant radiation of bats occurred on the larger islands, which are closest to mainland sources of colonization. As a result, the recently evolved taxa on larger islands are the primary sources of colonization for smaller, more isolated islands, and successful dispersal of bats combines with hierarchical distribution of habitats to promote the formation of nested species distributions.

ACKNOWLEDGEMENTS

This research was supported by a grant from NSF (DEB-0218039) to the Institute for Tropical Ecosystem Studies, University of Puerto Rico and to the International Institute of Tropical Forestry, USDA Forest Service, as part of the Long-term Ecological Research Program in the Luquillo Experimental Forest. Additional financial support was provided by the Center for Environmental Sciences and Engineering, University of Connecticut. Advice from H. Genoways improved the quality of data for bats on Caribbean islands. Matlab script files were written by R. Strauss and C. Higgins; we appreciate the assistance of both.

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Editor: Brian McGill

APPENDIX 1 NAMES, ABBREVIATIONS, AND NUMERIC CODES (FIG. 2) FOR EACH OF 65 ISLANDS THROUGHOUT THE CARIBBEAN: BAHAMAS, GREATER ANTILLES AND LESSER ANTILLES

Code	Bahamas		Greater Antilles			Lesser Antilles		
	Island name	Abbreviation	Code	Island name	Abbreviation	Code	Island name	Abbreviation
1	Grand Bahama	Gbaha	24	Isle of Pines	IPine	43	Anguilla	Angui
2	Andros	Andro	25	Grand Cayman	GCaym	44	St Martin	SMart
3	Little Abaco	LABac	26	Little Cayman	LCaym	45	St Barthelemy	SBart
4	New Providence	NProv	27	Cayman Brac	CBrac	46	Saba	Saba
5	Great Abaco	GABac	28	Cuba	Cuba	47	Barbuda	Barbu
6	Eleuthera	Eleut	29	Jamaica	Jamai	48	St Eustatius	SEust
7	Darby	Darby	30	Navassa	Navas	49	St Kitts	SKitt
8	Great Exuma	GExum	31	Gonave	Gonav	50	Nevis	Nevis
9	Little Exuma	LExum	32	Hispanola	Hispa	51	Antigua	Antig
10	Cat	Cat	33	Mona	Mona	52	Montserrat	Monts
11	Long	Long	34	Puerto Rico	PRico	53	La Désirade	LDesi
12	San Salvador	SSalv	35	Vieques	Viequ	54	Guadeloupe	Guade
13	Fortune	Fortu	36	Culebra	Culeb	55	Marie Galante	MGala
14	Crooked	Crook	37	St Thomas	SThom	56	Dominica	Domin
15	Acklins	Ackli	38	St John	SJohn	57	Martinique	Martin

APPENDIX 1 *Continued*

Code	Bahamas		Greater Antilles			Lesser Antilles		
	Island name	Abbreviation	Code	Island name	Abbreviation	Code	Island name	Abbreviation
16	East Plana Cay	EPlan	39	St Croix	SCroi	58	St Lucia	SLuci
17	Great Inagua	GInag	40	Tortola	Torto	59	St Vincent	SVinc
18	Little Inagua	LInag	41	Virgin Gorda	VGord	60	Barbados	Barba
19	Mayauana	Mayag	42	Anegada	Anega	61	Bequia	Bequi
20	Providenciales	Provi				62	Mustique	Musti
21	North Caicos	NCaic				63	Union	Union
22	Middle Caicos	MCaic				64	Carriacou	Carri
23	East Caicos	ECaic				65	Grenada	Grena

APPENDIX 2 SPECIES NAMES, ABBREVIATIONS, AND GUILD AFFILIATIONS (C, CARNIVORE; H, HERBIVORE) FOR EACH OF 58 SPECIES OF BAT RECORDED FROM THE CARIBBEAN

Family	Species	Species abbreviation	Guild	Family	Species	Species abbreviation	Guild
Emballonuridae	<i>Peropteryx macrotis</i>	Pmac	C	Natalidae	<i>Chilonatalus micropus</i>	Cmic	C
Phyllostomidae	<i>Brachyphylla cavernarum</i>	Bcav	H		<i>Chilonatalus tumidifrons</i>	Ctum	C
	<i>Brachyphylla nana</i>	Bnan	H		<i>Natalus jamaicensis</i>	Njam	C
	<i>Erophylla bombifrons</i>	Ebom	H		<i>Natalus major</i>	Nmaj	C
	<i>Erophylla sezekorni</i>	Esez	H		<i>Natalus stramineus</i>	Nstr	C
	<i>Phyllonycteris aphylla</i>	Paph	H		<i>Natalus primus</i>	Npri	C
	<i>Phyllonycteris poeyi</i>	Ppoe	H		<i>Nyctiellus lepidus</i>	Nylep	C
	<i>Anoura geoffroyi</i>	Ageo	H	Molossidae	<i>Eumops auripendulus</i>	Eaur	C
	<i>Glossophaga longirostris</i>	Glon	H		<i>Eumops glaucinus</i>	Egla	C
	<i>Glossophaga soricina</i>	Gsor	H		<i>Molossus molossus</i>	Mmol	C
	<i>Monophyllus plethodon</i>	Mple	H		<i>Mormopterus minutus</i>	Mmin	C
	<i>Monophyllus redmani</i>	Mred	H		<i>Nyctinomops laticaudatus</i>	Nlat	C
	<i>Lonchorhina aurita</i>	Laur	H		<i>Nyctinomops macrotis</i>	Nmac	C
	<i>Macrotus waterhousii</i>	Mwat	C		<i>Tadarida brasiliensis</i>	Tbra	C
	<i>Micronycteris megalotis</i>	Mmeg	C	Vespertilionidae	<i>Antrozous pallidus</i>	Apal	C
	<i>Ardops nichollsi</i>	Anic	H		<i>Eptesicus fuscus</i>	Efus	C
	<i>Ariteus flavescens</i>	Afla	C		<i>Eptesicus guadeloupensis</i>	Egua	C
	<i>Artibeus glaucus</i>	Agla	H		<i>Eptesicus lynni</i>	Elyn	C
	<i>Artibeus jamaicensis</i>	Ajam	H		<i>Lasiurus degelidus</i>	Ldeg	C
	<i>Artibeus lituratus</i>	Alit	H		<i>Lasiurus intermedius</i>	Lint	C
	<i>Chiroderma improvisum</i>	Cimp	H		<i>Lasiurus minor</i>	Lmin	C
	<i>Phyllops falcatus</i>	Pfal	H		<i>Lasiurus pfeifferi</i>	Lpfe	C
	<i>Stenoderma rufum</i>	Sruf	H		<i>Lasiurus noctivagans</i>	Lnoc	C
	<i>Sturnira lilium</i>	Slil	H		<i>Myotis dominicensis</i>	Mdom	C
	<i>Sturnira thomasi</i>	Stho	H		<i>Myotis martiniquensis</i>	Mmar	C
Noctilionidae	<i>Noctilio leporinus</i>	Nlepo	C		<i>Myotis nigricans</i>	Mnig	C
Mormoopidae	<i>Mormoops blainvillii</i>	Mbla	C		<i>Nycticeius cubanus</i>	Ncub	C
	<i>Pteronotus davyi</i>	Pdav	C				
	<i>Pteronotus macleayii</i>	Pmac	C				
	<i>Pteronotus parnelli</i>	Ppar	C				
	<i>Pteronotus quadridens</i>	Pqua	C				