

# Nestedness of desert bat assemblages: species composition patterns in insular and terrestrial landscapes

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**Abstract** Nested patterns of community composition exist when species at depauperate sites are subsets of those occurring at sites with more species. Nested subset analysis provides a framework for analyzing species occurrences to determine non-random patterns in community composition and potentially identify mechanisms that may shape faunal assemblages. We examined nested subset structure of desert bat assemblages on 20 islands in the southern Gulf of California and at 27 sites along the Baja California peninsula coast, the presumable source pool for the insular faunas. Nested structure was analyzed using a conservative null model that accounts for expected variation in species richness and species incidence across sites (fixed row and column totals). Associations of nestedness and island traits,

such as size and isolation, as well as species traits related to mobility, were assessed to determine the potential role of differential extinction and immigration abilities as mechanisms of nestedness. Bat faunas were significantly nested in both the insular and terrestrial landscape and island size was significantly correlated with nested structure, such that species on smaller islands tended to be subsets of species on larger islands, suggesting that differential extinction vulnerabilities may be important in shaping insular bat faunas. The role of species mobility and immigration abilities is less clearly associated with nestedness in this system. Nestedness in the terrestrial landscape is likely due to stochastic processes related to random placement of individuals and this may also influence nested patterns on islands, but additional data on abundances will be necessary to distinguish among these potential mechanisms.

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## Introduction

Understanding processes that shape faunal assemblages is a central goal of community ecology. Whether composition patterns arise from stochastic processes or deterministic factors, such as interspecific interactions or species-specific extinction or colonization probabilities, is relevant to ecological theory and may also have important implications for conservation (Gotelli and Graves 1996; Lomolino 1996; Patterson 1987). Nested subset theory provides one framework for analyzing community composition patterns that may be useful for identifying potential mechanisms that influence local diversity (Patterson and Atmar 2000),

yet its applicability to conservation decision-making remains uncertain (Boecklen 1997; Doak and Mills 1994; Donlan et al. 2005).

Nested community patterns occur when species at species-poor sites are subsets of the suite of species that occur at more species-rich sites (Patterson and Atmar 1986). Numerous studies have investigated nestedness patterns for a variety of taxa over the past 15 years (Bascompte et al. 2003; Bolger et al. 1991; Conroy et al. 1999; Cook et al. 2004; Cook and Quinn 1995; Davidar et al. 2002; Fischer and Lindenmayer 2005; Greve et al. 2005; Hausdor and Hennig 2003; Kadmon 1995; Martínez-Morales 2005; McAbendroth et al. 2005; Meyer and Kalko 2008; Patterson and Atmar 1986; Sfenthourakis et al. 2004; Wethered and Lawes 2005; Wright et al. 1998; Wright and Reeves 1992). These studies and others suggest nestedness is quite common in faunal assemblages, causing some authors to suggest that absence of nestedness may be more interesting than its presence (Kadmon 1995; Simberloff and Martin 1991). However, recent reviews and re-analyses of the most popular null algorithms and metrics used in studies of nestedness, such as those employed by the Nestedness Temperature Calculator (Atmar and Patterson 1993, 1995) are prone to type I errors, which may over-emphasize the pervasiveness of nestedness as a non-random pattern of species occurrences in nature (Moore and Swihart 2007; Rodríguez-Gironés and Santamaría 2006; Ulrich and Gotelli 2007). For example, Ulrich and Gotelli (2007) re-analyzed 288 empirical matrices previously reported as significantly nested and found that only between 10% and 40% were nested based on more conservative null algorithms and metrics.

We investigated nested subset structure of bat assemblages in both insular and contiguous desert habitats in Baja California, Mexico to compare patterns of community composition of bats across two landscape types (insular and terrestrial) and explore potential mechanisms of nestedness. Relatively few studies have examined nested subset patterns for bats (Meyer and Kalko 2008; Wright et al. 1998), particularly in terrestrial or near-shore archipelago systems (Meyer and Kalko 2008). As the only volant mammals, bats are generally highly vagile and assumed to have high immigration rates in many insular systems (Carvajal and Adler 2005; Lawlor 1986; Lomolino 1984; Lomolino 1986; Ricklefs and Lovette 1999). However, patterns of bat community composition in different landscape types and their underlying mechanisms are not well understood for most bat assemblages and may be important for conservation of species in anthropogenically fragmented landscapes (Meyer and Kalko 2008; Moreno et al. 2006).

In insular and fragmented landscapes, differential immigration and persistence abilities among species are

likely drivers of nestedness (Cook and Quinn 1995; Cutler 1994; Lomolino 1996; Lomolino 2000; Patterson and Atmar 1986). While some systems may be dominantly extinction-driven (i.e., landbridge islands) and others colonization-driven (i.e., oceanic islands), these forces reinforce each other to produce nestedness when immigration and persistence abilities of species are correlated (Cutler 1994; Lomolino 2000). Both immigration and persistence are expected to contribute to nestedness in systems where the gradients of area and isolation are sufficient to influence the persistence and immigration of some, but not all, species (Lomolino 2000).

Correlations among area and isolation values and nestedness may be used to explore the role of selective immigration and extinctions as mechanisms of nestedness (Lomolino 1996; Rodríguez-Gironés and Santamaría 2006). Species traits may also be useful for assessing the contribution of differential abilities of species to nestedness, although this approach has received less attention (but see Meyer and Kalko 2008). For example, if immigration ability is a strong determinant of nested patterns (Kadmon 1995; Lomolino 1996; Loo et al. 2002), then ecomorphological characters representing relative mobility of species may indicate the role of immigration in structuring composition patterns. We explore the possible role of differential immigration and persistence abilities of bats in producing nested composition patterns by analyzing correlations of island area and isolation as well as the correlation of an ecomorphological trait related to bat mobility to nested subset structure.

Factors influencing species composition may operate at different spatial scales, such that species that are widespread across one scale (e.g., local sites within habitats) could be rare across another scale (e.g., a suite of discrete habitat patches or islands) (Cook et al. 2004; Sfenthourakis et al. 2004; Wiens 1989). Other studies have shown that nestedness may depend on spatial scale of the analysis (Cook et al. 2004; Sfenthourakis et al. 2004). If composition patterns are scale dependent, then the scale of investigation could strongly influence which species are identified as conservation priorities (Hartley and Kunin 2003). We examine nested subset structure of bats at the scale of individual islands in an insular landscape and compare these patterns to nestedness of bat communities across local sample sites within coastal habitats on the Baja peninsula, the presumed source pool for insular faunas, to determine how insular community patterns may differ from those in contiguous habitats as well as change across spatial scales.

Nestedness analysis may be useful for conservation in part because the data required are relatively easy to collect (i.e., presence–absence data). Certain taxa, including bats, present formidable challenges for obtaining demographic data (e.g., abundance estimates or

densities) (O’Shea et al. 2003). The ability to assess community patterns with simple presence–absence data is appealing for these groups, but depends on accurate information about species occurrences across sample sites (Cam et al. 2000). Recent attention has focused on the problem of imperfect detectability in determining species occurrence patterns (MacKenzie et al. 2006), which is likely for mobile, cryptic, nocturnal animals such as bats. We use MacKenzie et al.’s (2006) approach to estimate the probability that zeros in our species occurrence matrix reflect true absences to assess the accuracy of our presence–absence data prior to making inferences about community nestedness.

## Materials and methods

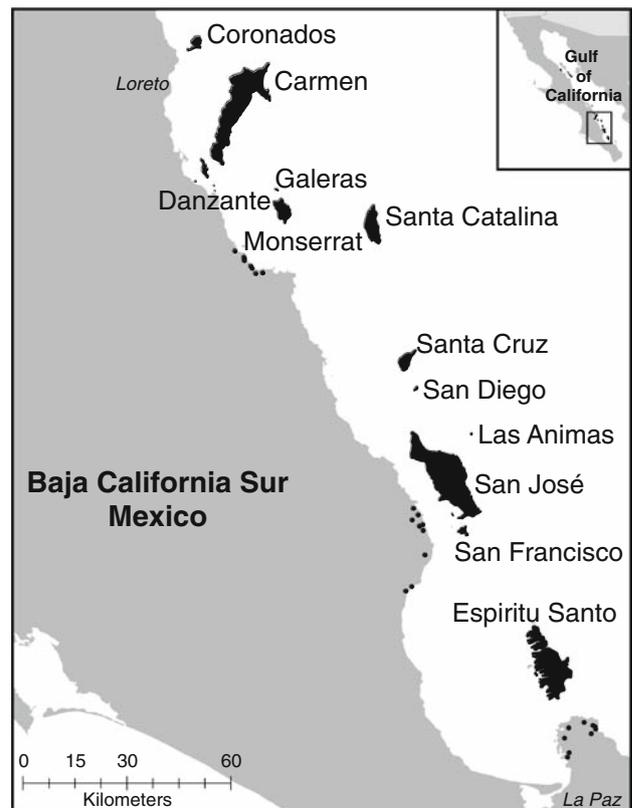
### Study system and data collection

This study takes place on 20 islands in the southern part of the Gulf of California in northwest Mexico and in coastal habitats on the Baja California peninsula (Fig. 1). Vegetation on islands and peninsular coastal habitats conform to Sonoran Desert sarcocaulous vegetation type (Shreve 1951; Wiggins 1980), dominated by columnar cacti (*Pachycereus pringlei* and *Stenocereus thurberias*) and desert trees (*Cercidium*, *Bursera*, and *Jatropha*). Rainfall in the region is unpredictable and averages between 100 and 150 mm per year (Cody et al. 2002).

We conducted presence–absence surveys for bats from 1 April to 1 June 2004–2006 using passive Anabat acoustic stations (Titley Electronics, Ballina, Australia) for 5-day sampling periods on each island and in peninsular habitats. Mist-net surveys and active monitoring of bat acoustic activity were conducted on nine islands and in all peninsular regions to verify identification of species detected with passive acoustic stations. A species was considered present if it was detected at least once, without determination of breeding or residency status.

Number of passive acoustic stations deployed on an island increased with island size (range 1–13 detectors per island) and were placed at randomly determined distances between 100 and 1,000 m from safe boat landings, usually in arroyo habitats. On the peninsula, passive acoustic stations were placed in accessible arroyos within 3 km of the shore. Passive acoustic stations that ran for 5 consecutive nights ( $n = 27$ ) on the peninsula were used in analyses of probability of site use ( $\Psi$ ) and peninsular nestedness.

A detailed description of field methods and analyses of echolocation signatures to determine presence of species on islands and in peninsular coastal habitats is provided by Frick et al. (2008a).



**Fig. 1** Map of islands (in black) in the archipelago landscape in the Gulf of California and acoustic sample sites (dots) in coastal habitats on the Baja peninsula, Mexico

### Probability of use of peninsular sites

Comparing community composition patterns may be misleading if sites where species were never detected were in fact occupied (or used) by the species (Cam et al. 2000). We used program Presence (MacKenzie et al. 2006) to estimate probabilities of detector site occupancy ( $\Psi$ ) and detection ( $p$ ) for species using 27 detector sites sampled for 5 consecutive nights in coastal peninsular habitats to determine whether probabilities of detection were sufficient for community analyses. Key assumptions of the site occupancy model are: (1) closure to changes in occupancy during repeat sample visits, which means that the true presence/absence status of a species at the sample site does not change between repeat visits; and (2) no misclassification of species.

The assumption of closure may be relaxed if a species moves randomly in and out of a sample site, but apparent occupancy should accurately be interpreted as site use, not true occupancy (MacKenzie et al. 2006). Given the high mobility of bats and our sampling methodology, we interpret our data to be indicative of use rather than occupancy as the area sampled by an acoustic detector is not constantly occupied by a species. In this case,  $p$  is a

function of the probabilities that the species is available to be detected and that the species is detected and identified correctly. These two components are not separately estimable, but jointly account for both sources of imperfect detectability to allow an unbiased estimate of site use (MacKenzie et al. 2006).

Violation of the misclassification assumption could lead to positively biased estimates of site use if a species that is not present is recorded as present (Royle and Link 2006). For the majority of the species investigated, distinct echolocation calls make misclassification unlikely. However, echolocation calls from *Macrotus californicus* and *Myotis californicus* are similar and estimates of site use for these two species may be confounded.

To determine if sampling at the detector-site scale was exhaustive, we used MacKenzie et al.'s (2006) approach for calculating the probability that a site was used by a species, given it was never detected during the 5-night sampling period ( $\Psi_{\text{condl}}$ ), using the following equation:

$$\Psi_{\text{condl}} = \frac{\Psi \sum_{j=1}^5 (1 - p_j)}{(1 - \Psi) + \Psi \sum_{j=1}^5 (1 - p_j)}$$

where  $p_j$  is the probability of detection. Associated SE estimates were calculated using the approximate asymptotic variance from the delta method (MacKenzie et al. 2006, p. 98). This allowed us to determine the probability that non-detections in the presence–absence matrix used in the nestedness analysis in the terrestrial landscape represented true absences of species. For the insular landscape, examination of species accumulation curves determined that sampling on islands was exhaustive (Frick 2007).

#### Nested subset analysis

We estimated nestedness using the program BinMatNest (Rodríguez-Gironés and Santamaría 2006), which uses a genetic algorithm to maximally pack the binary presence–absence matrix and calculates a uniquely defined isocline that minimizes nestedness temperature. Temperatures of 0° represent perfectly ordered or nested matrices and temperatures of 100° represent perfectly disordered matrices (Atmar and Patterson 1993; Rodríguez-Gironés and Santamaría 2006). In the archipelago analysis, rows represent islands and presence–absence data from detector sites within islands are aggregated. For the peninsular analysis, rows represent individual detector sampling sites.

We compared estimated nestedness temperature of our matrix to 1,000 Monte Carlo simulations generated with a constrained null model (null model 3) that accounts for the incidences of species (column totals) and richnesses of islands (row totals) while sampling the null space uniformly (Bascompte et al. 2003; Rodríguez-Gironés and

Santamaría 2006). There is little agreement on which null model is most appropriate for estimating significance of nested subset patterns (Brualdi and Sanderson 1999; Fischer and Lindenmayer 2002; Gotelli and Graves 1996; Jonsson 2001; Moore and Swihart 2007; Rodríguez-Gironés and Santamaría 2006; Ulrich and Gotelli 2007; Wright et al. 1998). We chose a doubly constrained null model because we believe building more biological realism into the null model provides a more meaningful test of the significance of nestedness by minimizing type I errors (Brualdi and Sanderson 1999; Moore and Swihart 2007; Rodríguez-Gironés and Santamaría 2006; Ulrich and Gotelli 2007). In addition, null model 3 is less prone to type I and II errors than null model 1 (unconstrained row and column totals) (Atmar and Patterson 1993) and null model 2 (constrained species column totals) (Fischer and Lindenmayer 2002), even when the generating constraints correspond to a different null algorithm (i.e., null 1 and 2) (Rodríguez-Gironés and Santamaría 2006). However, null model 3 is prone to type II errors if the generating constraints of the system under investigation correspond to null algorithm 1, making it a conservative test of nestedness (Patterson and Atmar 1986; Rodríguez-Gironés and Santamaría 2006).

Nested temperature is dependent on size and fill of the matrix, but the probability of observing the calculated nestedness metric from chance is not (Rodríguez-Gironés and Santamaría 2006). Therefore, we restrict our comparison of matrices to interpretation of the  $P$  values from the Monte Carlo simulations and do not directly compare nestedness temperatures (Rodríguez-Gironés and Santamaría 2006).

#### Correlates of nestedness

To determine correlates of nestedness, we used Spearman rank and partial Spearman rank correlation tests of the order of island rows in the maximally packed matrix to island area and isolation ranks (Table 1). Partial Spearman rank correlation tests were used to assess the correlation of area or isolation after accounting for the effect of the other variable (Shipley 2000). Islands with equivalent compositions were given tied ranks.

To evaluate the contribution of vagility of bats to nestedness, we performed a Spearman rank correlation of the rank of species order in the maximally packed matrix to wing aspect ratios, an ecomorphological trait that strongly relates to cost of transport during flight (Norberg and Rayner 1987). Wing aspect ratios were taken from published sources (Milner et al. 1990; Norberg and Rayner 1987; Sahley et al. 1993) (Table 2). Average values for Lasiurines in Norberg and Rayner (1987) were used in lieu of available estimates for *Lasiurus xanthinus*. Aspect ratio

**Table 1** Characteristics of 20 islands sampled for presence of bat species in the southern Gulf of California, Baja California Sur, Mexico. Islands are presented in order of descending size

Island	Area (ha)	Isolation (km)	Species richness	Nested matrix rank
San José	18,494.5	4.75	12	1
Carmen	14,801.4	5.50	9	2
Espiritu Santo/Partida Sur	10,367.1	6.21	8	4
Santa Catalina	3,995.6	25.06	5	11
Montserrat	1,902.8	13.66	6	8
Santa Cruz	1,315.1	19.81	5	7
Coronados	715.8	2.60	7	6
Danzante	423.7	2.67	8	5
San Francisco	419.0	7.16	8	3
San Ildefonso	104.2	10.01	4	12
San Diego	62.9	19.06	3	18
Las Animas Sur	9.1	16.49	3	19
Cayo	6.7	6.22	4	13
Galeras East	5.4	16.40	4	16
Pardo	4.3	0.36	5	10
Tijeras	4.0	1.90	4	14
Islitas	3.3	0.41	4	15
Galeras West	3.2	16.77	3	20
Gallina	2.0	7.18	6	9
Blanco	1.3	0.84	4	17

of the ecomorphologically similar *Tadarida brasiliensis* was used for *Nyctinomops femorosaccus*, which gave these two species equivalent ranks.

#### Comparison of peninsular and archipelago species composition

To determine whether species detected frequently across peninsular sites are also detected frequently across the archipelago, we compared the rank order of species in nested matrices for the peninsula and archipelago with a Spearman rank correlation test. Species that were detected on the peninsula and never detected on islands were given a tied rank of last place on the archipelago. Spearman rank and partial rank correlation analyses were conducted with PROC CORR in SAS version 9.1.

#### Sampling artifacts on the archipelago

Because the nestedness analysis for the archipelago aggregates presence–absence data across multiple detector sites for larger islands ( $n = 9$ ), we assessed whether nestedness of the archipelago could arise as a sampling artifact. We randomly sampled single detectors that ran for 5 nights from islands with multiple detectors and re-ran the nestedness analysis on 20 randomly compiled matrices using only the presence–absence information from single detectors for each island. Each matrix consisted of 20 rows representing the same islands as in the archipelago

analysis, but each row represented a randomly selected detector from that island rather than the aggregate of presence–absence information from all detector sites within an island. Rows representing small islands that only had one detector site ( $n = 11$ ) were repeated in each run. This approach does not rule out passive sampling as a mechanism of nestedness, but does provides information about the potential bias from greater sampling effort on larger islands to produce nested patterns.

#### Results

Bat community composition was significantly nested in both the archipelago and terrestrial landscape. The maximally packed incidence matrix for the archipelago had an estimated nestedness temperature ( $T$ ) of 10.04, which was significantly lower ( $P < 0.001$ ) than the mean  $T$  of 1,000 randomly generated matrices ( $T = 35.3$ ;  $SE = 0.17$ ) using null model 3 (Table 3). The maximally packed matrix of detections at peninsular sites had an estimated nestedness  $T$  of 16.64, significantly lower ( $P < 0.001$ ) than the mean  $T$  of 1,000 randomly generated matrices ( $T = 38.47$ ;  $SE = 0.14$ ) using null model 3 (Table 4). On the archipelago, nestedness does not appear to be a sampling artifact from greater sampling effort on larger islands as 20 runs of matrices compiled from randomly selected single detectors from each island were still significantly nested (mean  $T = 15.68$ ,  $SE = 0.57$ ; mean  $P$  value  $< 0.03$ ,  $SE = 0.001$ ) (Table 5).

**Table 2** Bat species detected during sampling on southern islands in the Gulf of California and coastal habitats of the Baja peninsula. Foraging guild classifications follow Schnitzler and Kalko (2001)

Species	Species code	No. islands occupied	No. coastal sites used	Wing aspect ratio	Foraging guild	Roosting guild
Family: Mormoopidae						
<i>Mormoops megalophylla</i>	MOME	3	16	7.1	Edge and gap insectivore	Cave obligate
Family: Phyllostomidae						
<i>Macrotus californicus</i>	MACA	6	23	6.4	Narrow-space insectivore	Cave obligate
<i>Leptonycteris curasoae</i>	LECU	17	13	6.6	Nectarivore	Cave obligate
Family: Vespertilionidae						
<i>Antrozous pallidus</i>	ANPA	5	19	6.1	Narrow-space insectivore	Cave and crevice
<i>Eptesicus fuscus</i> <sup>a</sup>	EPFU	0	11		Edge and gap insectivore	Crevice
<i>Lasiurus blossevillii</i> <sup>a</sup>	LABL	0	4		Edge and gap insectivore	Foliage
<i>Lasiurus xanthinus</i>	LAXA	2	1	7.5	Edge and gap insectivore	Foliage
<i>Myotis californicus</i>	MYCA	7	26	5.6	Edge and gap insectivore	Crevice
<i>Myotis volans</i> <sup>a</sup>	MYVO	0	1		Edge and gap insectivore	Crevice
<i>Myotis yumanensis</i> <sup>a</sup>	MYYU	0	1		Edge and gap insectivore	Crevice
<i>Myotis vivesi</i>	MYVI	20	7	7.4	Piscivore	Crevice
<i>Pipistrellus hesperus</i>	PIHE	14	25	5.7	Edge and gap insectivore	Crevice
Family: Molossidae						
<i>Eumops</i> sp.	EUSP	1	0	9.5	Open-space insectivore	Crevice
<i>Nyctinomops femorosaccus</i>	NYFE	19	23	8.2	Open-space insectivore	Crevice
<i>Nyctinomops macrotis</i>	NYMA	7	4	9.7	Open-space insectivore	Crevice
<i>Tadarida brasiliensis</i>	TABR	11	6	8.2	Open-space insectivore	Cave and crevice

<sup>a</sup> Not included in correlation test on wing aspect ratios, because did not occur on islands

Area and nestedness order of islands in the maximally packed matrix were correlated (Spearman rank correlation  $\rho = 0.72$ ,  $P < 0.0003$ ). When the correlation of isolation was accounted for, area and order of islands were more strongly correlated (partial Spearman rank correlation  $\rho = 0.82$ ,  $P < 0.0001$ ). Nested order of islands was also significantly and inversely correlated with isolation rank when the effects of area were accounted for (partial Spearman rank correlation  $\rho = -0.61$ ,  $P < 0.006$ ), but not significant otherwise (Spearman rank correlation  $\rho = -0.26$ ,  $P < 0.27$ ). Species order in the maximally packed matrix was not significantly correlated with wing aspect ratios of bats (Spearman rank correlation  $\rho = 0.13$ ,  $P < 0.69$ ) (Table 2).

At detector sites on the peninsula, the probability that a species was present at a site where it was never detected was extremely low for seven species (Table 6), providing confidence in the interpretation that failure to detect these species at a site represents a true absence. For these species, the estimated  $\Psi$  was the same as the naive estimate (Table 6), which is the proportion of sites surveyed where a species was detected (MacKenzie et al. 2006). For four species, detection probabilities were sufficiently low to negatively bias naive estimates of use (Table 6). At the

scale of the detector site, occurrences may be more common than represented in our analysis for those species.

The rank orders of the species occurring across peninsular sites and the archipelago were significantly correlated (Spearman rank correlation  $\rho = 0.61$ ,  $P < 0.01$ ), indicating species that contributed to nestedness on the peninsula also contributed to nestedness across the archipelago. Substantial correspondence between insular and peninsular incidence occurred for species that were rarely detected (occur at <20% sites or islands) and two ubiquitous species (Fig. 2).

## Discussion

Desert bat assemblages in both the insular and terrestrial landscapes displayed significantly nested subset patterns even after accounting for potential structure due to ecological variation in species richness and incidence. Correlation of island size and nested community composition indicated that bat assemblages on smaller islands were predictable subsets of richer faunas occurring on larger islands. This correlation may suggest that differential extinction vulnerabilities exist among species such that

**Table 3** Maximally packed nested matrix of insular bat species on 20 islands in the Gulf of California, Baja California Sur, Mexico. For species codes see Table 2

	MYVI	NYFE	LECU	PIHE	TABR	MYCA	NYMA	MACA	ANPA	MOME	LAXA	EUSP
San José	1	1	1	1	1	1	1	1	1	1	1	1
Carmen	1	1	1	1	0	1	1	1	1	1	0	0
San Francisco	1	1	1	1	1	1	1	1	0	0	0	0
Espiritu Santo <sup>a</sup>	1	1	1	1	1	1	1	1	0	0	0	0
Danzante	1	1	1	1	0	1	1	1	0	1	0	0
Coronados	1	1	1	1	1	1	0	1	0	0	0	0
Santa Cruz	1	1	0	1	0	0	0	0	1	0	1	0
Montserrat	1	1	1	1	0	0	1	0	1	0	0	0
Gallina	1	1	1	1	1	1	0	0	0	0	0	0
Pardo	1	1	1	1	1	0	0	0	0	0	0	0
Santa Catalina	1	0	1	1	0	0	1	0	1	0	0	0
San Idefonso	1	1	1	0	1	0	0	0	0	0	0	0
Cayo	1	1	1	0	1	0	0	0	0	0	0	0
Tijeras	1	1	1	0	1	0	0	0	0	0	0	0
Las Islitas	1	1	0	1	1	0	0	0	0	0	0	0
Galeras East	1	1	1	0	1	0	0	0	0	0	0	0
Blanco	1	1	1	1	0	0	0	0	0	0	0	0
San Diego	1	1	0	1	0	0	0	0	0	0	0	0
Las Animas Sur	1	1	1	0	0	0	0	0	0	0	0	0
Galeras West	1	1	1	0	0	0	0	0	0	0	0	0

<sup>a</sup> Espiritu Santo includes Partida Sur

smaller areas of habitat support species with higher persistence capabilities (Lomolino 1996; Patterson and Atmar 1986; Wright and Reeves 1992). Our results are consistent with other studies of nestedness in systems that may be shaped by extinction processes (Patterson and Atmar 1986; Watling and Donnelly 2006; Wright et al. 1998), yet differ from patterns of bat distributions on landbridge islands in Lake Gatún in Panama where there was no relationship between nestedness and island size (Meyer and Kalko 2008).

Differential immigration rates may also produce nested subset structure when mobility of species varies across the scale of isolation values of islands or fragments in a landscape (Cook and Quinn 1995; Darlington 1957; Kadmon 1995; Loo et al. 2002). There was some evidence for correlation between isolation and nestedness in our insular landscape, such that bat species that occurred on far islands were subsets of larger faunas on near islands, but only after accounting for the association between island size and nested rank order. These results are consistent with analyses of richness and incidence patterns for insular bats on Baja islands, where area consistently had the strongest association with richness and probability of occurrence of individual species and isolation had some association after accounting for area (Frick et al. 2008a, b).

Our prediction that wing aspect ratio, as a measure of mobility, would correlate with nestedness was not supported. Our results suggest that island size may be a stronger determinant of community composition than isolation and thus differential mobility among the 12 bat species in this assemblage may not have a strong influence on nested patterns in this system. In contrast, Meyer and Kalko (2008) found that differences in mobility among phytophagous and animalivorous Phyllostomid bats on landbridge islands in Panama was likely a key driver of nested subset structure. Interpreting nestedness patterns is often context-specific and understanding causal mechanisms may depend on both the scale and history of the archipelago as well as the faunal assemblage. Our desert ecosystem had fewer species (12 vs. 20, respectively) and less variability in foraging strategies and mobilities, which may partially explain why mobility was less correlated with nestedness in our system compared to tropical bat faunas in Panama.

Differential extinction and colonization abilities among species are not the only potential mechanisms underlying nested community patterns. Other potential mechanisms include gradients in species tolerance for habitat variables (Cook et al. 2004; Patterson et al. 1996) or nested structure of habitat diversity (Calmé and Desrochers 1999; Cutler

**Table 4** Maximally packed matrix of 15 bat species on 27 sites in coastal peninsula habitat, Baja California Sur, Mexico. For species codes see Table 2

	MYCA	PIHE	NYFE	MACA	ANPA	LECU	MOME	EPFU	MYVI	TABR	NYMA	LABL	LAXA	MYVO	MYYU
SE1_AC06	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0
SE9_AC08	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0
AV4A_AC11	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0
AV3_AC09	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0
TE11_AC11	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0
AV2B_AC10	1	1	1	1	1	0	1	1	1	0	1	1	0	0	0
SE3_AC01	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
AV2A_AC04	1	1	1	1	0	0	1	1	1	0	0	0	1	0	0
SE2_AC05	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
SE5_AC10	1	1	1	1	1	0	1	1	0	1	0	0	0	0	0
SE10_AC07	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0
AV2R_AC02	1	1	1	1	0	0	1	0	1	0	0	1	0	0	0
SE1_ACH9	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0
AV6_AC06	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0
AV8_ACH9	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1
SE6_AC09	1	1	1	1	0	0	1	0	0	1	0	0	0	0	0
TE8_AC07	1	1	1	0	1	1	0	0	1	0	0	0	0	0	0
SE4_AC11	1	1	0	0	1	0	1	1	0	0	0	0	0	0	0
TE5_AC12	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0
TE1_AC09	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
TE3_AC08	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0
AV1_AC01	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
TE9_AC05	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
TE2_AC04	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0
AV8_ACH7	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
TE4_AC02	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0
TE6_AC01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

1994). Habitat heterogeneity was typically low on islands and we consider it unlikely that habitat nestedness was an important factor shaping bat community structure, as bats were not tightly associated with specific habitat types in this system. However, stepwise changes in drainage morphology and its relationship to increasing habitat diversity has been suggested as a likely cause of nested bird distributions on Baja islands (Cody 1983; Cody and Velarde 2002). Similar to the islands, habitat heterogeneity across sites in coastal habitats on the Baja peninsula was fairly low and not a likely cause of nestedness in the terrestrial landscape.

Random placement of individuals from species with different abundance distributions also produces nested composition patterns in interactive systems where immigration rates can be expected to influence local abundance (Higgins et al. 2006). This seems the most parsimonious explanation for the strong nestedness observed at local sites in coastal habitats on the Baja peninsula where there was no a priori expectation of colonization and extinction

differences because sites occurred in contiguous habitat. Six species were detected at greater than 50% of peninsular sites (Fig. 2) and the similarity in site use among these species had a strong influence on nestedness.

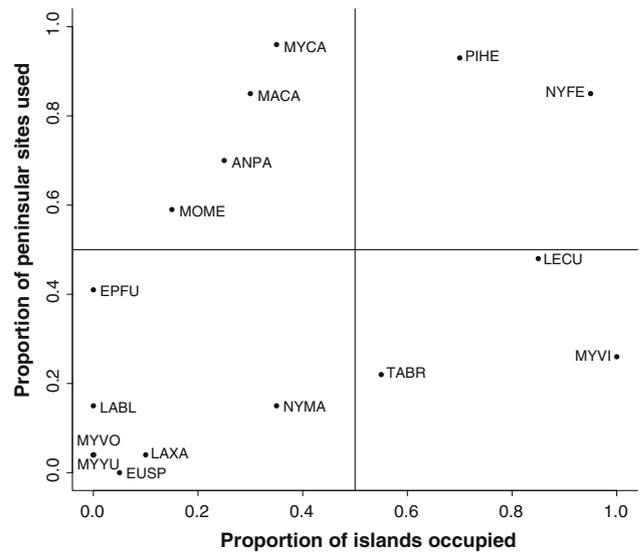
The importance of individual-based processes in determining nested subset structure is dependent on individual scales of movement and behavior that influence abundance distributions across sites (Higgins et al. 2006). If the near-shore islands in our study are an interactive system, meaning that individuals move among islands regularly enough to influence abundances on islands, then stochastic processes related to random placement of individuals may also help produce nested patterns on islands. We suspect that nestedness on islands is due to a combination of these stochastic processes as well as differential abilities of species to persist or use smaller islands. Unfortunately, due to the logistical limitations of collecting accurate abundance data for most bat species, determining the relative importance of these two factors may prove challenging.

**Table 5** Nested temperatures and associated *P* values for 20 matrices compiled using randomly selected detectors from each island

Run	Nested temperature	<i>P</i> value
1	17.93	0.002
2	10.74	0.000
3	14.21	0.001
4	15.89	0.001
5	16.65	0.002
6	12.53	0.000
7	12.71	0.000
8	16.97	0.002
9	15.47	0.003
10	19.63	0.011
11	13.53	0.002
12	16.63	0.002
13	20.12	0.007
14	19.74	0.019
15	17.12	0.002
16	15.16	0.002
17	14.01	0.000
18	16.92	0.001
19	14.43	0.001
20	13.23	0.000

*P* values generated from 1,000 Monte Carlo simulations using null algorithm 3

The nested order of species in both landscapes was significantly correlated, suggesting that propensity for commonness or rarity among species was similar in the



**Fig. 2** Frequency of occurrences across peninsular sites and islands. *Top left quadrant* contains species that were frequently found at sites on the peninsula, but detected on few islands. *Top right quadrant* contains species frequently detected on both the peninsula and islands. *Bottom right quadrant* contains species found at few sites on the peninsula, but frequently detected on islands. *Bottom left quadrant* contains species detected at few sites on the peninsula and on few islands. For species codes, see Table 2

archipelago and its presumable source pool (Fig. 2) (Frick et al. 2008a). Other studies have shown that nestedness is scale- and context-dependent and species that may be widespread across one scale (e.g., local sites within

**Table 6** Estimates of proportion of site use at 27 coastal sites on the peninsula, Baja California Sur, Mexico. *Naive*  $\Psi$  Proportion of sites where a species was detected

Species	Naive $\Psi$	Probability of site use		Probability of detection		Probability of use, given not detected	
		$\Psi$	SE	<i>p</i>	SE	$\Psi_{condl}$	SE
<i>Macrotus californicus</i>	0.96	0.96	0.04	0.83	0.03	0.00	0.005
<i>P. hesperus</i>	0.93	0.93	0.05	0.90	0.03	0.00	0.000
<i>Myotis californicus</i>	0.85	0.85	0.06	0.71	0.04	0.01	0.011
<i>N. femorosaccus</i>	0.85	0.85	0.07	0.72	0.03	0.01	0.008
<i>A. pallidus</i>	0.70	0.70	0.09	0.67	0.05	0.01	0.008
<i>M. megalophylla</i>	0.59	0.66	0.11	0.37	0.06	0.17	0.106
<i>L. curasoeae</i>	0.48	0.53	0.11	0.38	0.07	0.10	0.070
<i>E. fuscus</i>	0.41	0.42	0.10	0.53	0.07	0.02	0.014
<i>M. vivesi</i>	0.26	0.53	0.29	0.13	0.08	0.28	0.356
<i>T. brasiliensis</i>	0.22	0.33	0.15	0.20	0.10	0.11	0.132
<i>N. macrotis</i>	0.15	0.16	0.07	0.42	0.12	0.01	0.015
<i>N. blossevillii</i> <sup>a</sup>	0.15	–	–	–	–	–	–
<i>L. xanthinus</i> <sup>a</sup>	0.04	–	–	–	–	–	–
<i>M. volans</i> <sup>a</sup>	0.04	–	–	–	–	–	–
<i>M. yumanensis</i> <sup>a</sup>	0.04	–	–	–	–	–	–

<sup>a</sup> Estimation of  $\Psi$  and the probability that a site was used by a species given it was never detected during the 5-night sampling period ( $\Psi_{condl}$ ) was not possible due to sparse data

habitats) could be rare across another scale (e.g., islands) (Cook et al. 2004; Sfenthourakis et al. 2004; Wiens 1989). Although the nested-order ranks were correlated in the insular and terrestrial landscapes, our data seem to support this idea as species that were common in one landscape were not always equally common in the other (Fig. 2). Most species tended to occur across more sites on the Baja peninsula than on islands (Fig. 2). The few species that were more frequently detected on islands were associated with high vagility or unique natural histories (i.e., piscivory), which could suggest that mobility plays a role in insular occurrences even if not strongly associated with nestedness.

## Conclusion

Desert bat communities displayed strong nested subset structure both across islands and across local sites in contiguous habitats, demonstrating that non-random structure in community composition may be expected in both insular and terrestrial landscapes for bats. A recent similar analysis of community structure for Neotropical bat faunas in Panama (Meyer and Kalko 2008) provides an opportunity to make comparisons about the generality of the patterns we observed here. Although nestedness was common in both studies, the potential mechanisms may be different based on both the autecological details of species in each community as well as the habitat and historical context of each landscape. The scale and context-dependent nature of nestedness and its mechanisms may limit its utility as a predictive conservation tool. However, nested subset analysis proved useful for demonstrating non-random patterns of bat community composition and helped identify potential mechanisms important in shaping these faunal assemblages using data that are feasible to collect.

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