Nestedness in insular floras: spatiotemporal variation and underlying mechanisms

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Abstract

Aims
Nestedness is a characteristic of insular metacommunity structure. Relatively few studies, however, have attempted to evaluate temporal changes in nestedness, or elucidate the mechanisms underlying nestedness. I evaluated both spatial and temporal patterns of nestedness in the insular floras of four archipelagoes of small islands in the Bahamas and the potential underlying environmental gradients.

Methods
The NODF (a nestedness metric based on overlap and decreasing fill) and the matrix temperature measure, T, were used to quantify nestedness in insular floras on small islands near Abaco, Andros, Great Exuma and the Exuma Cays, Bahamas. Two different null models were employed for each nestedness measure. Six environmental variables were evaluated in relation to nestedness by ordering islands according to gradients and recalculating NODF scores.

Important Findings
All archipelagoes were significantly nested. Nestedness among sites contributed more to overall nestedness than did nestedness among species. NODF scores varied among archipelagoes, but were surprisingly constant over time. Ordering islands by vegetated area yielded the highest nestedness scores for three archipelagoes; ordering islands by protection from exposure yielded the highest nestedness score for one archipelago. Nestedness scores varied little over time even though species compositions changed, indicating that extinctions occurred in a deterministic manner. The relative importance of area suggests extinction is an important mechanism in producing nestedness. Attempting to determine the relative importance of immigrations or extinctions requires some assumptions, however, and both processes are likely cumulative in most cases.

Keywords: Bahamas, environmental gradient, insular floras, nestedness, NODF metric

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INTRODUCTION

Nestedness is a concept applied to metacommunity structure. The most common concept of nestedness specifies that species present at species-poor sites represent subsets of the species present at species-rich sites. Nestedness, however, could also be defined as a situation in which the relatively more endemic species occupy a subset of the sites at which the more widespread species are found (Almeida-Neto et al. 2008).

A number of metrics have been developed to quantify nestedness (summarized by Ulrich et al. 2009), although they are all subject to some potential bias. Many metrics are dependent upon matrix size, shape or fill, and may have inflated type I error rates (Almeida-Neto et al. 2008; Ulrich et al. 2009; Wright et al. 1998). In a study of nestedness in parasite assemblages, Timi and Poulin (2008) determined that whether or not a community exhibited significant nestedness depended “entirely on the metric and null model chosen for analysis”.

A relatively new metric, NODF (nestedness metric based on overlap and decreasing fill), has been shown to avoid many of the biases of other metrics. It is unrelated to matrix size or shape, although it is positively correlated with matrix fill (Almeida-Neto et al. 2008). Because matrix fill corresponds to the degree of species occupancy, it has been argued that this relationship is not an analytical artifact but simply a consequence of the concept of nestedness (Almeida-Neto et al. 2008).

NODF scores may be calculated independently for rows and columns to evaluate how species and sites contribute to overall community nestedness. NODF (row) scores evaluate nestedness among sites (i.e., species composition), addressing the question of whether species assemblages in species-poor sites are subsets of those in more species-rich sites. NODF (column) scores evaluate nestedness among species (i.e.,...
species incidence), addressing the question of whether the relatively more endemic species occupy a subset of the sites at which the more widespread species are found (Almeida-Neto et al. 2008). Nestedness among sites best fits the concept that most ecologists have of nestedness, and is what most other metrics attempt to measure (Almeida-Neto et al. 2008).

Most metacommunities existing in fragmented habitats, when evaluated, do demonstrate relatively high degrees of nestedness (Almeida-Neto et al. 2008; Cook and Quinn 1995; Wright et al. 1998). While fragmentation is not a direct cause of nestedness, it is thought to result in a nested pattern because the fragmented patches differ in characteristics such as size, shape and quality (Ulrich et al. 2009). Thus the mere existence of nested patterns in a fragmented metacommunity could be considered as almost trivial, and the more interesting questions concern the underlying mechanism(s) that generated the nested pattern.

Nested patterns were originally attributed to differential immigration (Darlington 1957), although it was later proposed that nestedness in insular biotas resulted from an orderly sequence of extinctions (Patterson 1987; Patterson and Atmar 1986). Today explanations of nestedness are associated with either ordered colonization or extinctions along some environmental gradient (e.g., area, distance, habitat quality) or a nested structure in environmental conditions (Ulrich et al. 2009).

Passive sampling may also result in a nested pattern, due to the fact that rare species have a lower probability of being drawn at random than the more common species. Because of the passive sampling effect, significant nestedness may be found, but due to an artifact of underlying stochastic processes rather than mechanisms of ecological interest, such as selective immigration/extinction and nested habitats (Fischer and Lindenmayer 2002).

Most studies of nestedness do not elucidate the causes, because when sites are ordered by species richness, nestedness scores (regardless of how calculated) are neutral with respect to the underlying mechanisms (Simberloff and Martin 1991). The primary cause of nested patterns in insular florals and faunas is often thought to be extinction, supported by the observation that landbridge biotas are often more nested than the biotas of oceanic islands (Cutler 1991; Patterson 1990; Wright and Reeves 1992; Wright et al. 1998). For many taxa, however, landbridge islands could be influenced by immigration as well (Lomolino 1996). Differential colonization produced highly nested patterns in a short-term experimental study (Loo et al. 2002).

Most previous studies of nestedness seem to view the phenomenon as a static pattern, and relatively few have evaluated temporal changes on ecological time scales (Norton et al. 2004; Vidal-Martínez and Poulin 2003). Metacommunities that are frequently disturbed, however, may experience pronounced changes in nestedness, and an observation at a single time may not characterize a system in general. For example, Bloch et al. (2007) found that terrestrial gastropod assemblages were least nested following hurricane disturbances, and became more nested over time. Nestedness was found to increase over time in an experimental defaunation experiment (Loo et al. 2002).

In this paper I compare relative degrees of nestedness in insular florals, focusing on spatial and temporal variation as well as evaluating the important underlying gradients. I use data from comprehensive surveys of plants on four archipelagoes of small islands in the Bahamas, three of which have been surveyed multiple times (Morrison 2003, 2010; Morrison and Spiller 2008). A relatively large number of extinctions occurred in these archipelagos between the late 1990s and the last surveys in 2007, resulting in decreasing species richnesses compared to earlier time periods (Morrison 2010).

The following main questions are addressed: (i) How do patterns of nestedness vary among the four archipelagoes? (ii) How does nestedness among sites (i.e., species composition) compare to nestedness among species (i.e., species incidence)? (iii) Did nestedness change over time as species richnesses decreased? (iv) What are the important environmental gradients underlying the observed nestedness patterns?

MATERIALS AND METHODS

Study areas and survey methods

Plant species compositions were obtained from islands in four Bahamian archipelagoes at multiple time periods (Fig. 1). Species lists were generated from comprehensive surveys designed to detect immigrations, extinctions and turnover (Morrison 2003, 2010; Morrison and Spiller 2008). An archipelago at Abaco included 42 small islands in a tidal creek network between Snake Cay (26°27′ N, 77°03′ W) and Buckaroo Bay (26°23′ N, 77°02′ W) on the east coast of Great Abaco. An archipelago at Andros included 48 small islands between Nicholls Town (25°08′ N, 78°00′ W) and Staniard Creek (24°52′ N, 77°54′ W) between the northeast coast of Andros and the barrier reef. An archipelago in the Exuma Cays included 107 small islands within the 13.5-km island chain between O’Brien’s Cay (24°19′ N, 76°33′ W) and Bitter Guana Cay (24°08′ N, 76°25′ W). An archipelago at Great Exuma included 39 islands in the region near Georgetown. Eleven islands were located on the northeast side of Great Exuma in Elizabeth Harbour (23°32′ N, 75°48′ W to 23°28′ N, 75°42′ W), and the other 28 were located on the southwest side of Great Exuma (23°26′ N, 75°46′ W to 23°25′ N, 75°53′ W).

Surveys were conducted on all islands at Abaco in December of 2003 and again in November of 2007; on all islands at Andros in April–May of 1999 and again in July of 2007; and on all islands in the Exuma Cays in May of 1998 and again in May of 2007. Surveys were conducted at Great Exuma in October of 1998, except for six islands that were surveyed in 1999 (October) or 2000 (September). Surveys were restricted to islands that were small enough to ensure that no species would be overlooked (this varied by archipelago,
but was always <6000 m² vegetated area). Islands exposed to heavy wave action on the windward side of the main protective islands or reefs in the area were excluded, as were very low-lying islands that were normally submerged at low tide and only supported intertidal mangrove species. Fewer islands were included in the 2007 surveys from Andros and the Exuma Cays compared to earlier surveys, because all the vegetation went extinct on seven islands (three at Andros and four in the Exuma Cays) in the intervening period (Morrison 2010).

All islands were composed primarily of marine limestone, with some islands consisting of small amounts of fossil sand deposits or loose sand. Because of their rocky composition, island size or shape does not vary over time as has been reported for sand islands (e.g., Flood and Heatwole 1986). The perimeter of most islands is characterized by a swash zone—an area regularly disturbed by high tides and waves—that is usually barren of vegetation. All plant species present on these small islands were long-lived perennials, representative of the beach/strand, coastal rock and coastal coppice vegetative communities (Correll and Correll 1982; Nickrent et al. 1988). Intertidal mangroves were common on small islands in the Andros archipelago, but rare on small islands in the Abaco, Exuma Cays and Great Exuma archipelagos.

Survey methods are described in detail by Morrison (2003, 2010) and Morrison and Spiller (2008). Observed extinction and immigration events were verified for accuracy to eliminate spurious turnover due to sampling error, or pseudoturnover (sensu Lynch and Johnson 1974). Species identifications followed Correll and Correll (1982). Lists of species present in each archipelago at each time period can be found in Morrison (2003, 2010) and Morrison and Spiller (2008). Voucher specimens were placed in the J. M. Tucker Herbarium at U. C. Davis, and the University of Florida Herbarium at Gainesville, FL, USA.

Environmental gradient analysis

Six environmental gradients were evaluated in relation to nestedness for each archipelago: (i) total island area, (ii) vegetated area, (iii) the ratio of vegetated area to island area (VA/A), (iv) elevation, (v) distance from nearest “mainland” island and (vi) protection. Total island area and vegetated area were both included because vegetated area may be a better measure of the habitable size of the island (Morrison 2002). VA/A represents an effect of both island size and disturbance; VA/A will generally increase as island size increases, particularly if the width of the swash zone remains relatively constant. This ratio will decrease as the swash zone increases in width, for islands of a similar size (Morrison 2002).

Elevation was measured as the vertical distance from the mean tide mark to the highest part of the island. Distance was measured from the nearest “mainland” island. In the Exuma Cays this was any island >46 580 m², which reflects a natural discontinuity in the distribution of island areas in the region (Schoener 1987). In the Great Exuma archipelago, distance was measured to the main island of Great Exuma. At Abaco and Andros, distance was measured either to the main island of Abaco or Andros, respectively, or to the nearest large island. (An exact size threshold was not used at Abaco or Andros, but “large islands” were always at least an order of magnitude larger than the largest island sampled.)

Protection was quantified by drawing a circle around each island 1 km from the island center and determining the sum of the arcs obstructed by neighboring islands. Protection from waves and wind conferred by nearby islands could range from 0° (in the case where no other islands were near and exposure was greatest) to 360° (when the island in question was completely surrounded by islands in all directions and exposure was least). Protection was determined to the nearest 5°. (See Morrison 2002 for a complete description of this technique.)

Quantification of nestedness

To quantify nestedness for a particular archipelago at a particular time, the NODF nestedness metric was used. NODF scores range from 0 to 100, and increase as nestedness increases. The matrix temperature measure, T (Atmar and Patterson 1993), was also calculated for the main comparisons because this has been the most used nestedness metric historically (Almeida-Neto et al. 2008), and presentation of T scores will allow for comparisons with previous studies. T decreases as nestedness increases. The Fortran program NODF (Almeida-Neto and Ulrich 2011) was used to calculate all NODF and T scores.

The significance of both scores was determined with a Monte Carlo procedure (1000 iterations) based on two null models. A variety of null models have been used in nestedness analyses (reviewed by Ulrich and Gotelli 2007; Ulrich et al. 2009). Multiple null models are possible because, among other operations, one may either preserve (i.e., “fix”) row or column totals or allow them to vary (termed “equiprobable” if allowed to vary freely). Some null models, such as the EE
model that maintains equiprobable row and column totals, are liberal and prone to type I error (Ulrich and Gotelli 2007; Ulrich et al. 2009). In contrast, others, such as the FF model that fixes both observed row and column totals, are conservative and likely to result in type II error (Jonsson 2001; Ulrich and Gotelli 2007). In a study of the NODF metric on 287 empirical matrices, Almeida-Neto et al. (2008) found that 83% (237) of the matrices were significantly nested under the EE null model, whereas only 1% (3) were significantly nested under the FF null model. Here I employ two null models more intermediate with respect to the type I–type II error trade-off: (i) FE (fixed row totals, equiprobable column totals) and (ii) EF (equiprobable row totals, fixed column totals). Additionally, the FE model is thought to control for passive sampling (Fischer and Lindenmayer 2002).

Presence–absence matrices were created for each archipelago and time interval, and ordered by decreasing number of sites occupied (rows) from top to bottom and decreasing number of species present (columns) from left to right (Tables S1–S7, see online supplementary material). NODF and T scores were calculated for entire matrices, and NODF scores were calculated independently among rows and among columns. NODF scores for rows allow the evaluation of nestedness among sites (i.e., species composition), whereas NODF scores for columns allow the evaluation of nestedness among species (i.e., species incidence).

For the 2007 data, rows were also ordered by each of the six gradients. (Column ordering remained the same, based on decreasing number of species present.) Rows were ordered from top to bottom by decreasing area, vegetated area, VA/A, elevation and protection, but increasing distance, reflecting the hypotheses that species richness should be positively associated with the first five variables and negatively associated with distance. Separate analyses were run for each gradient in each archipelago. To evaluate correlations among the variables used in gradient analyses, correlation coefficients (Pearson) were calculated for all pairs of variables in each archipelago.

I also evaluated the associations between the environmental gradients and total species richness by simple linear regressions. Transformations were performed to normalize the distributions of variables, as in Morrison (2002). Area, vegetated area, distance and species richness were all log10-transformed. Elevation and protection from surrounding islands were square root-transformed, and the VA/A ratio was arcsine square root-transformed.

**RESULTS**

Nestedness scores calculated for all archipelagoes and time periods were significant \( (P < 0.001) \) for both nestedness metrics (NODF and \( T \)) and both null models (Table 1). Comparing among the four archipelagos, NODF (total) scores were highest for the Exuma Cays and lowest for Great Exuma (Table 1). For all archipelagoes, the NODF (row) scores were higher than the NODF (column) scores, indicating that nestedness among sites (i.e., species composition) contributed more to the overall nestedness pattern than did nestedness among species (i.e., species incidence). This suggests that differences in habitat variables of the islands are more important than differences in life history traits of the species in promoting nestedness. In other words, the quality of the insular habitat as determined by area, isolation, disturbance, etc., is relatively more important than variability in the species’ ability to disperse to or survive on these small islands. This difference between row and column scores was most pronounced for

**Table 1:** nestedness measures for the florals of four Bahamian archipelagoes

<table>
<thead>
<tr>
<th>Archipelago</th>
<th>NODF total</th>
<th>NODF rows</th>
<th>NODF columns</th>
<th>Number of islands</th>
<th>Number of species</th>
<th>Percentage fill</th>
<th>NODF (FE)</th>
<th>NODF (EF)</th>
<th>( T )</th>
<th>( T ) (FE)</th>
<th>( T ) (EF)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Great Exuma</td>
<td>52.33</td>
<td>70.48</td>
<td>41.35</td>
<td>39</td>
<td>50</td>
<td>16.3</td>
<td>34.38</td>
<td>22.34</td>
<td>7.77</td>
<td>19.53</td>
<td>34.97</td>
</tr>
<tr>
<td>Abaco</td>
<td>55.10</td>
<td>63.02</td>
<td>48.51</td>
<td>42</td>
<td>46</td>
<td>17.6</td>
<td>32.92</td>
<td>26.57</td>
<td>8.19</td>
<td>23.72</td>
<td>31.21</td>
</tr>
<tr>
<td>Andros</td>
<td>56.82</td>
<td>62.49</td>
<td>50.87</td>
<td>42</td>
<td>41</td>
<td>18.3</td>
<td>23.88</td>
<td>20.23</td>
<td>7.17</td>
<td>36.76</td>
<td>45.88</td>
</tr>
<tr>
<td>Exuma Cays</td>
<td>61.90</td>
<td>64.28</td>
<td>58.06</td>
<td>48</td>
<td>38</td>
<td>16.8</td>
<td>36.76</td>
<td>26.51</td>
<td>4.88</td>
<td>19.93</td>
<td>28.32</td>
</tr>
<tr>
<td></td>
<td>58.38</td>
<td>59.79</td>
<td>56.30</td>
<td>45</td>
<td>37</td>
<td>17.1</td>
<td>23.01</td>
<td>20.82</td>
<td>6.45</td>
<td>34.34</td>
<td>41.60</td>
</tr>
</tbody>
</table>

All archipelagoes in all time periods were significantly nested \( (P < 0.001) \) by both the NODF and \( T \) metrics, for both null models evaluated. Percentage fill = the number of occupied cells divided by the total number of cells in the matrix; NODF (FE) = expected value of NODF for matrices generated by Monte Carlo simulations based on null model with fixed row totals and equiprobable column totals; NODF (EF) = expected value of NODF for matrices generated by Monte Carlo simulations based on null model with fixed row totals and equiprobable column totals; \( T \) (FE) = expected value of \( T \) for matrices generated by Monte Carlo simulations based on null model with fixed row totals and equiprobable column totals; \( T \) (EF) = expected value of \( T \) for matrices generated by Monte Carlo simulations based on null model with equiprobable row totals and fixed column totals.
Great Exuma and the Exuma Cays, and least pronounced for Andros. The matrix temperature measure, $T$ (which measures overall matrix nestedness), revealed similar patterns among archipelagoes as the NODF (total) scores. NODF scores varied relatively little between the two time periods for the three archipelagos surveyed at different times (Table 1).

The percentage of matrix fill was always low and within a very narrow range (10.94–18.29). Moreover, the association of NODF scores with matrix fill over this range (Table 1) was negative rather than positive. Thus there were no obvious biases due to matrix fill.

NODF scores were higher for all archipelagos when rows were ordered by 2007 marginal totals (i.e., decreasing number of islands occupied) (Table 1), compared to any of the gradients. The gradients associated with higher NODF scores varied by archipelago (Table 2). Ordering rows by vegetated area, total area and $VA/A$ varied by archipelago (Table 2). Ordering rows by vegetated area, total area and $VA/A$ yielded the highest three NODF scores for Abaco, Andros and the Exuma Cays. Many of the gradients evaluated were intercorrelated (Tables 3 and 4), and this was the case for vegetated area, total area and $VA/A$ for these three archipelagoes (Tables 3 and 4). In contrast, ordering rows by protection yielded the highest NODF score for Great Exuma, followed by vegetated area and area (Table 2).

NODF (column) scores were invariable in the gradient analyses, and were the same as in Table 1 (2007 values for archipelagoes evaluated at two time periods). Because only the rows were rearranged, this did not affect the NODF (column) scores. All NODF (total) scores presented in Table 2 were statistically significant ($P < 0.01$) by either null model. Because of the way NODF (total) scores are calculated, however, the ordering of the columns (species) accounts for much of the non-randomness. When rows are ordered by environmental gradients, statistically significant nestedness of the overall matrix is of secondary interest to the NODF (row) scores, which compare the relative contribution of each gradient to the degree of nestedness among sites (i.e., species composition).

The ratio of the largest value divided by the smallest value for each variable was generally positively associated with nestedness for Abaco, Andros and the Exumas, but this was not true for Great Exuma. The gradients associated with island size—primarily vegetated area—had the largest ratios (i.e., ranges between the smallest and largest observed values). Overall, elevation varied little and generally had the smallest ratios, and was always in the bottom three gradients examined for each archipelago. Islands at Abaco tended to be smaller and closer than in the other archipelagos. The low ranking of distance at Abaco may be due to the small range of distances there (no island was >300 m from the mainland or a large island), although distance ranked relatively low for the other archipelagos as well (Table 2).

Ranking the environmental gradients as a function of decreasing explanation of the variability in plant species richness (Table 5) resulted in similar orderings as the nestedness results (Table 2). Orderings were exactly the same for Abaco and the Exuma Cays, and the same for the first four variables at Andros. While vegetated area and area explained the most variation at Great Exuma, protection did rank higher in the regression analyses at Great Exuma compared to the other archipelagoes.

**Table 2: nestedness (NODF) scores for matrices in which islands were ordered by each of six gradients**

<table>
<thead>
<tr>
<th>Variable</th>
<th>NODF rows</th>
<th>NODF total</th>
<th>Range</th>
<th>Ratio*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abaco</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vegetated area</td>
<td>56.66</td>
<td>53.84</td>
<td>0.08–134.49 m²</td>
<td>1681</td>
</tr>
<tr>
<td>Area</td>
<td>51.92</td>
<td>51.41</td>
<td>2.63–168.11 m²</td>
<td>64</td>
</tr>
<tr>
<td>$VA/A$</td>
<td>50.44</td>
<td>50.65</td>
<td>0.01–0.95</td>
<td>95</td>
</tr>
<tr>
<td>Elevation</td>
<td>45.49</td>
<td>48.12</td>
<td>0.15–1.73 m</td>
<td>12</td>
</tr>
<tr>
<td>Protection</td>
<td>25.56</td>
<td>37.91</td>
<td>30–330°</td>
<td>11</td>
</tr>
<tr>
<td>Distance</td>
<td>24.65</td>
<td>37.44</td>
<td>20–300 m</td>
<td>15</td>
</tr>
<tr>
<td>Andros</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vegetated area</td>
<td>53.09</td>
<td>54.38</td>
<td>0.5–2071 m²</td>
<td>4142</td>
</tr>
<tr>
<td>Area</td>
<td>50.85</td>
<td>53.04</td>
<td>1.8–4728 m²</td>
<td>2627</td>
</tr>
<tr>
<td>$VA/A$</td>
<td>50.14</td>
<td>52.62</td>
<td>0.004–1.0</td>
<td>250</td>
</tr>
<tr>
<td>Elevation</td>
<td>46.65</td>
<td>50.53</td>
<td>0.08–1.80 m</td>
<td>23</td>
</tr>
<tr>
<td>Distance</td>
<td>31.68</td>
<td>41.58</td>
<td>100–3197 m</td>
<td>32</td>
</tr>
<tr>
<td>Protection</td>
<td>25.52</td>
<td>37.90</td>
<td>0–240°</td>
<td>48</td>
</tr>
<tr>
<td>Exuma Cays</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vegetated area</td>
<td>61.39</td>
<td>59.25</td>
<td>0.06–5444 m²</td>
<td>90.733</td>
</tr>
<tr>
<td>$VA/A$</td>
<td>59.38</td>
<td>57.61</td>
<td>0.0004–0.91</td>
<td>2275</td>
</tr>
<tr>
<td>Area</td>
<td>53.55</td>
<td>52.85</td>
<td>21.0–16,875 m²</td>
<td>804</td>
</tr>
<tr>
<td>Elevation</td>
<td>43.96</td>
<td>45.01</td>
<td>0.55–5.44 m</td>
<td>10</td>
</tr>
<tr>
<td>Distance</td>
<td>43.83</td>
<td>44.90</td>
<td>3.05–2436 m</td>
<td>799</td>
</tr>
<tr>
<td>Protection</td>
<td>42.99</td>
<td>44.27</td>
<td>0–275°</td>
<td>55</td>
</tr>
<tr>
<td>Great Exuma</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protection</td>
<td>49.80</td>
<td>44.53</td>
<td>0–290°</td>
<td>58</td>
</tr>
<tr>
<td>Vegetated area</td>
<td>48.64</td>
<td>44.10</td>
<td>2.63–1488 mm²</td>
<td>566</td>
</tr>
<tr>
<td>Area</td>
<td>47.67</td>
<td>43.73</td>
<td>3.28–2470 m²</td>
<td>753</td>
</tr>
<tr>
<td>Distance</td>
<td>43.71</td>
<td>42.24</td>
<td>20–11,700 m</td>
<td>585</td>
</tr>
<tr>
<td>Elevation</td>
<td>42.05</td>
<td>41.61</td>
<td>0.41–3.66 m</td>
<td>9</td>
</tr>
<tr>
<td>$VA/A$</td>
<td>41.68</td>
<td>41.47</td>
<td>0.13–1.0</td>
<td>7</td>
</tr>
</tbody>
</table>

*Ratio is the largest value in the range divided by the smallest value. When the smallest value in the range for protection was 0°, 5° (the smallest possible non-zero value) was used to calculate the ratio.

**DISCUSSION**

**Temporal dynamics of nestedness**

Insular species compositions may change over time (MacArthur and Wilson 1967; Morrison 2013), which in turn may affect degrees of nestedness. A multi-year study of a coral cay on the Great Barrier Reef provided a detailed analysis of many facets of the insular dynamics of tropical island biotas in relation to cyclones and drought (Heatwole et al. 1981).

In the Bahamas, extinction rates were higher than immigration rates in the Exuma Cays and Andros, by up to an order of magnitude, from 1998 (Exuma Cays) or 1999 (Andros) to 2007.
Extinction rates were four times higher than immigration rates at Abaco from 2003 to 2007 (Morrison 2010). (Great Exuma was not sampled at multiple intervals.) Average species richnesses in the Exuma Cays and Andros declined by 9–11% over the 8- or 9-year interval, while average species richness at Abaco declined by 7% over the 4-year interval. Three islands at Andros and four in the Exuma Cays lost all plant species (Morrison 2010). In the preceding decade, however, immigration rates were higher than extinction rates for both the Exuma Cays and Andros, but the difference was much less pronounced (Morrison 2010). (No data are available from Abaco from this period.)

Four hurricanes impacted the Bahamian archipelagoes from 1999 to 2004: Hurricane Floyd in September 1999, Hurricane Michelle in November 2001, and Hurricanes Frances and Jeanne, both in September 2004. The available evidence suggests the hurricanes were not directly responsible for the extinctions, although indirect effects of hurricanes, such as increased herbivory and possible decreased nutrient availability, may have been important. A long-term (quarter century) increase in temperature and possible decreased nutrient availability, may have been important. A long-term (quarter century) increase in temperature and decline in rainfall were also observed (Morrison 2010).

Thus it is of interest to compare nestedness surrounding this interval of unusually high extinction rates and declining species richness and characterized by major storm events. The finding that NODF scores varied only slightly for all three archipelagoes over the 4- to 9-year intervals indicates that the loss of species had relatively little effect on nestedness, and suggests that extinctions occurred in a deterministic manner.
Mechanisms of nestedness

Lomolino (1996) proposed that ordering matrices by island area and isolation (rather than species richness) would allow a test of the relative importance of immigration and extinction. This follows from two of the main tenets of classical island biogeography theory (MacArthur and Wilson 1967): the probability of immigration increases as island area decreases, and the probability of extinction increases as island area decreases. Thus, a high degree of nestedness in a matrix in which fragments are sorted by area suggests the importance of extinction, whereas a high degree of nestedness in a matrix sorted by isolation should indicate the importance of immigration (Bruun and Moen 2003). It is possible, however, that immigration may increase with area (i.e., the target effect; Buckley and Knedlhaus 1986; Lomolino 1990) and extinction may increase with isolation (i.e., the rescue effect; Brown and Kodric-Brown 1977; Wright 1985). Thus attempting to infer the mechanism from comparing nestedness based on sorting by different gradients requires some assumptions.

Gradients other than area and distance may also be important in producing nested patterns. Disturbance or environmental stress has been found to affect nestedness (Bloch et al. 2007; Fernández-Juricic 2002; Fleishman and Murphy 1999; Worthen et al. 1998), as has habitat quality (Hylander et al. 2005).

At Abaco, Andros and the Exuma Cays, vegetated area produced the highest nestedness scores, with area and VA/A ranked either second or third, suggesting extinction is a relatively important mechanism (discounting the target effect). At Great Exuma, by contrast, ranking the sites by protection resulted in the highest nestedness scores. Protection, as quantified here, was designed to measure susceptibility to disturbance from storm winds and waves (Morrison 2002).

Less protected islands may be washed over more frequently by storm-driven waves, which could result directly in extinctions. Less protected islands that are frequently washed over by waves are likely to have less soil and organic matter present, and thus potential colonists may be less likely to successfully immigrate. This latter effect may be more appropriately interpreted as one of habitat quality (Ulrich et al. 2009; Wright et al. 1998). Unfortunately, the data to evaluate directly such a habitat quality effect are not available.

Attempting to infer the processes underlying the relative importance of such gradients is difficult in practice. All gradients may reflect underlying processes that contribute to nestedness to some degree (although many gradients evaluated here were intercorrelated and may reflect the same process) and likely have a cumulative effect, influencing both immigrations and extinctions.

Spatial variability in underlying mechanisms of nestedness

In this study, the variable “protection” is likely to represent differing degrees of susceptibility to disturbance, depending upon the archipelago. At Abaco, all islands were located in a tidal creek, protected from the open ocean, and exposure would be to the surrounding calm, shallow waters. At Andros, all islands were located along the northeastern coast of the main island of Andros, and exposure was primarily to the open ocean, with winds and swells coming from the nearby deepwater Tongue of the Ocean. All islands at Abaco were relatively protected from strong waves and winds, whereas most islands at Andros were relatively exposed to these forces. Thus the gradient protection may represent a relatively narrow range of conditions within each of these two archipelagoes, one at the high end and the other at the low end of the scale. In the absence of enough variability, this mechanism may operate only weakly, and area assumes the role as the key underlying gradient.

In the Exuma Cays and Great Exuma, in contrast, small islands of this study were located in a greater diversity of positions relative to larger islands, open ocean and protected/calmer waters. Protection, as measured here, may cover a wider range of conditions in such cases, and have a relatively greater effect on metacommunity structure. Thus protection may be a more important underlying gradient for archipelagos with islands spanning a relatively wide range of susceptibility to disturbance. This was found to be true for Great Exuma, but not for the Exuma Cays. The difference between the two archipelagoes in the relative importance of underlying mechanisms is that the range of variation in vegetated area was much greater (by two orders of magnitude) in the Exuma Cays than at Great Exuma (a ratio of 90733 compared to 566). Thus it appears that protection may play a small role when the range of vegetated areas is relatively great, but a larger role when islands are of similar size.

In a comparative analysis of 279 metacommunities, Wright et al. (1998) found that archipelagoes with a wide range of island sizes exhibited stronger nestedness. In general, an environmental gradient that is represented by a relatively broad range may contribute to higher nestedness scores for matrices ordered by such gradients. In the extreme case, for example, a gradient that spans a very narrow range of observed values (e.g., distance at Abaco, elevation for all archipelagoes) would not be expected to have much effect on metacommunity structure. In contrast, a gradient that encompasses a wide range of variation (e.g., most area measures) is more likely to have an effect.

The results for Abaco, Andros and the Exuma Cays in Table 2 are consistent with the idea that the apparent relative importance of gradients in producing a nested pattern could be dependent on variation in the range of conditions (i.e., the ratio) encountered for that gradient. This was not clearly true for Great Exuma, as protection ranked higher than the area measures, although the ratios for that archipelago were more similar among gradients.

CONCLUSIONS

A number of islands in the archipelagoes studied, particularly in the Exuma Cays, contain no terrestrial vegetation. The finding that island area and protection are important in producing nested patterns complements a recent finding that
area and exposure (the inverse of protection as used here) were the two most important predictors of whether terrestrial vegetation was present or not on islands in the Exuma Cays (Morrison 2011). Thus, whether an island supports terrestrial vegetation—and, if it does, which species are present—appears to be a deterministic process, affected at least in part by insular area and exposure.

The available evidence indicates that extinction is the more important mechanism in producing nestedness, given the relationship between area and extinction in classic island biogeographic theory and the fact that more exposed islands represent harsher environments where extinction may be more likely. Extinction as a process in this system is probably not analogous to the relaxation of biotas on land bridge islands, however. Most islands are not too distant to be colonized, and extinction, operating through the area and exposure of an island, determines which species survive. In fact, extinction per se may not be the mechanism, but many species may simply not be able to become established on an island even if their reproductive propagules are able to reach the island (Morrison 2011). The habitat quality of the island may simply be too poor (i.e., too small, too exposed) for the species to survive.

SUPPLEMENTARY MATERIAL

Supplementary Tables S1–S7 are available at Journal of Plant Ecology online.

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