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Avian Community Ecology: Patterns of Co-occurrence, Nestedness, and Morphology

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To the Graduate Council:

I am submitting herewith a dissertation written by Michael David Collins entitled "Avian Community Ecology: Patterns of Co-occurrence, Nestedness, and Morphology." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Daniel Simberloff, Christine R. B. Boake, Major Professor

We have read this dissertation and recommend its acceptance:

David Buehler, Sergey Gavrilets, Louis J. Gross

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Department Head

We have read this dissertation
and recommend its acceptance:

David Buehler

Sergey Gavrilets

Louis J. Gross

Accepted for the Council:

Anne Mayhew
Vice Chancellor and Dean of
Graduate Studies

(Original signatures are on file with official student records.)

**Avian Community Ecology:
Patterns of Co-occurrence, Nestedness, and Morphology**

A Dissertation

Presented for the

Doctor of Philosophy Degree

The University of Tennessee, Knoxville

Michael David Collins

December 2006

To my mom and dad. I miss you, Mom.

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ABSTRACT

A central tenet of the competition paradigm is that community structure is governed by deterministic rules. The competition paradigm pervades nearly all subdisciplines and extends to the broadest, deepest questions in ecology. To determine whether patterns of co-occurrence, nestedness, and morphology in avian communities are consistent with a competition hypothesis, I use null models to compare observed patterns to patterns expected in the absence of competition.

I use presence-absence matrices of birds in three archipelagoes to test whether species exhibit exclusive distributions. Congeneric birds co-occur significantly less frequently than predicted in two archipelagoes, consistent with a competition hypothesis. However, when examined separately, most genera do not exhibit patterns that differ from random expectations. Furthermore, species differences in habitat preference and barriers to dispersal within archipelagoes are two alternate hypotheses that can explain many exclusive patterns and are supported by available data. Distributional evidence alone does not implicate competition. I argue that the range of conditions under which competition is likely to generate exclusive distributions across islands is narrow.

Although nested patterns are viewed as the converse of competitive exclusion, meta-analyses of presence-absence matrices simultaneously support the ubiquity of exclusive distributions and indicate that most ecological systems are nested. I show why these apparently contradictory patterns are not mutually exclusive. Patterns of nestedness can result from multiple processes; without understanding mechanisms, nestedness analysis is unlikely to prove useful for conservation.

I study algorithms that randomize presence-absence matrices. Two commonly used algorithms generate biased statistical distributions and should be abandoned.

I test for community-wide character displacement in wing length and talon size among *Accipiter* hawks. I also assess whether subspecific variation in wing length is predictable from community composition. I find limited evidence of community-wide character displacement for wing length, but talon size, which relates directly to resource use, shows larger minimum and more equal size ratios than predicted. I find no evidence of competitively driven change in wing length. These findings demonstrate the importance of examining traits directly related to function. I cannot determine whether community-wide character displacement of talon size results from ecological character displacement, species assortment, or both.

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CHAPTER 1

A COMPARISON OF MATRIX RANDOMIZATION ALGORITHMS

Abstract. We compare algorithms that randomize presence-absence matrices while maintaining row and column sums and examine how the statistical distribution of the C-score varies with randomization algorithm, matrix size, matrix fill, and evenness of marginal sums (row and column totals) in a fully crossed four-way analysis of variance. We also compare the distribution of the C-score for the avifaunas of three archipelagoes: Bismarck Archipelago, Solomon Islands, and Vanuatu. The most popular “fill” algorithm, the random Knight’s Tour, produces distributional means that differ from all “swap” algorithms. Furthermore, the random Knight’s Tour produces distributions with higher variances. The Manly Swap and Gotelli Swap methods produce distributions with smaller variances than other swap algorithms. Both the random Knight’s Tour algorithm and Gotelli Swap method produce distributions that are more different from the initial matrix than the distributions generated by other swap algorithms. Statistical distributions generated by Connor and Simberloff’s original swap algorithm closely match those produced by Zaman and Simberloff’s weighted means and Miklós and Podani’s trial-swap methods. Examination of the avifaunas of the three archipelagoes generally corroborates the results the ANOVA. The random Knight’s Tour, Manly Swap, and Gotelli Swap do not produce uniform random samples.

Because the random Knight’s Tour algorithm produces biased distributions with inflated variances, we recommend its discontinuation. Manly’s Swap should also be avoided. We recommend that researchers employ Miklós and Podani’s trial-swap method, which produces uniformly random samples, requires computational time comparable to other algorithms, and is easily implemented.

Key words: *co-occurrence, fill algorithms, Knight’s tour, Monte Carlo, null models, presence-absence matrices, randomization methods, swap algorithms*

INTRODUCTION

The occurrence of species at sites (e.g., islands) can be represented in a two-dimensional, $r \times c$, presence-absence matrix. In such a matrix, also termed a co-occurrence or incidence matrix, each row, r_i , represents a species, and each column, c_j , a site. Each cell in the matrix (a_{ij}) contains a one or a zero, indicating the presence or absence, respectively, of species i at site j . The row sum, R_i , represents the number of occurrences of each species, and the column sum, C_j , represents

the number of species at each site. For example, a presence-absence matrix for 13 species of finches on 17 islands in the Galápagos Islands is presented in Table 1.1.¹

In community ecology, the number of sites shared between pairs of species has been used to draw inferences about interspecific interactions, especially competition. Typically, a researcher selects one or more statistics and compares the observed statistic(s) to a distribution obtained from Monte Carlo simulations in which the matrix is randomized subject to certain constraints. Although the use of these null models spurred considerable controversy and debate (see Gotelli and Graves 1996), it is now generally agreed that for a large number of ecological questions, one should employ a null model that maintains both row and column sums. Maintaining row sums retains differences in incidence among species, and maintaining column sums preserves differences in species richness across islands.

However, constructing a random matrix with fixed row and column sums is a nontrivial exercise. A fundamental problem in island biogeography is the difficulty that arises in generating null communities to compare to actual observations (Sanderson 2000). Many researchers have tried to generate random samples from the universe of possible matrices (see Zaman and Simberloff 2002). There are two major methods, swap algorithms and fill mechanisms, for creating a random co-occurrence matrix with fixed row and column totals. Gotelli and Entsminger (2001) prefer the swap algorithm, originally developed by Connor and Simberloff (1979), for generating null matrices with fixed row and column sums. With the swap algorithm, two rows and two columns are randomly selected (rows and columns need not be adjacent). If the 2 x 2 submatrix is of the form (a) $\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$ or (b) $\begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}$, swap the rows (or the columns); this swap is equivalent to switching between these two submatrices. A sufficiently large number of swaps will produce a randomized matrix while maintaining island richnesses and species' incidences.

Several contributions have modified Connor and Simberloff's (1979) swap algorithm. First, Manly (1995), citing Besag and Clifford (1989) and Brualdi (1980), introduced a sequential algorithm that is more efficient (i.e., faster) than the swap method. Whereas the original swap algorithm swaps circa 30,000 submatrices between samples, the Manly Swap interchanges only one submatrix between consecutive samples, reducing computation time substantially. Another sequential algorithm is the Gotelli Swap (Gotelli 2000).

A second development with the original swap algorithm is the finding that all possible matrices are not sampled equiprobably (Zaman and Simberloff 2002, Miklós and Podani 2004). Zaman and Simberloff (2002) showed that the original swap algorithm samples each matrix in proportion to its number of neighbors and provided a Monte Carlo method using random walks on graphs and weighted means that gives correct estimates for the distributions of statistics. Miklós and Podani (2004) presented the "trial-swap method," which also samples matrices equiprobably and gives correct estimates for the distributions of statistics.

Sanderson and colleagues (Sanderson et al. 1998, Sanderson 2000, Manly and Sanderson 2002) have criticized swap algorithms and have advocated using fill algorithms, in particular, the Knight's Tour. Fill algorithms begin with an empty matrix and fill it sequentially, one element at a time, until a solution is obtained (Sanderson et al. 1998). The Knight's Tour algorithm begins

¹ Tables and figures are in Appendices A and B, respectively.

with a matrix of zeros, randomly selects matrix elements, and changes the zeros to ones until a prescribed row or column sum has been exceeded. In that case, the Knight's Tour reverses the last change that caused the row or column violation and randomly chooses another matrix element. The algorithm continues filling the matrix until all row and column sums equal observed sums.

Gotelli and Entsminger (2001) introduced the random Knight's Tour, an unbiased version of the Knight's Tour that does not sample exhaustively and removes a cell at random (instead of the last cell changed) upon retreating. Gotelli and Entsminger compared the swap algorithm with their implementation of the fill algorithm of Sanderson et al. (1998) and concluded that the Knight's Tour is biased, does not sample all unique matrices with equal frequency, and produces greater variances of the S^2 statistic. This bias in sampling matrices arises because the original Knight's Tour algorithm samples exhaustively at each step before retreating.

Both classes of algorithms have their proponents, and over the past decade, a lengthy debate has ensued. A series of papers (Sanderson et al. 1998, Gotelli 2000, Gotelli 2001, Gotelli and Entsminger 2001, Manly and Sanderson 2002) has shown that the statistical distributions obtained from various algorithms differ, but none has compared the obtained distributions to a distribution known to arise from a random sample of possible matrices (i.e., to a distribution from a truly random algorithm). Gotelli and Entsminger (2001) found that the distribution of statistics from the Knight's Tour differs from that produced by the swap algorithm. However, their conclusion that the Knight's Tour is biased, does not sample matrices equiprobably, and produces greater variances is not warranted because the swap algorithm they implemented is also biased. These algorithms must be compared to a benchmark that produces unbiased distributions of statistics. Here, we examine the distributions obtained from one fill algorithm (Gotelli and Entsminger's [2001] randomized Knight's Tour) and from several swap methods including two (Zaman and Simberloff's [2002] weighted means algorithm and Miklós and Podani's [2004] trial-swap method) that are known to produce unbiased distributions of statistics. We also examine the original swap algorithm (Connor and Simberloff 1979) and two of its modifications, the Manly (1995) Swap and the Gotelli (2000) Swap. The relative advantages and disadvantages of the various swap methods and of the random Knight's Tour are unknown.

METHODS

Experimental Design

We compared a number of swap algorithms and one fill algorithm and examined how the statistical distribution of the C-score varies with randomization algorithm in matrices of different size, fill, and evenness of marginal sums (row and column totals) in a fully crossed four-way analysis of variance (ANOVA). We established presence-absence matrices with four sizes (10x8, 20x16, 40x32, and 80x64), four levels of fill (15, 30, 45, and 60%), and three levels of evenness of row and column sums (high, medium, and low). We specified the row and column sums and generated "observed" matrices with fixed rows sums and proportional column sums. Discrepancies between specified and observed column sums occurred in pairs, with one column having a surplus and the other a deficiency. Such column pairs were selected at random. A species was selected randomly, and, if possible, a presence from the surplus column was switched with an absence from the deficient column. If two columns could not be swapped with 100 attempts (randomly selected rows), we swapped 100 2 x 2 submatrices of the form (a) $\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$ or

(b) $\begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}$ and continued resolving column discrepancies until observed and specified column

sums were equal. The resulting matrices functioned as “observed” matrices. Because they were generated nearly randomly, these initial matrices should, on average, exhibit little or no structure.

For each initial matrix, we constructed 1000 randomized matrices (random iterations) for each of seven algorithms. We used the version of the rand function recommended in Press et al. (1992) to generate random integers. We chose to construct 1,000 iterations based on observations that statistics converge and change only minimally with larger samples. From this sample of 1000 randomized matrices, we measured the mean and variance for checkerboardedness (C-score, C), number of neighbors, number of checkerboards, S-squared (S^2), and Togetherness (T). For each of these co-occurrence metrics, Table 1.2 lists the original source and describes its calculation. We replicated each treatment three times for a total of 1008 (= 4 matrix sizes * 4 fill levels * 3 levels of evenness of marginal sums * 7 algorithms * 3) initial matrices.

We also compared the algorithms’ statistical distributions for three real island systems: the avifaunas of the Bismarck Archipelago (Appendix C), Solomon Archipelago (Appendix D), and Vanuatu (formerly New Hebrides; Appendix E). With nearly 200 expeditions to observe or collect birds (Dutson 2001), Melanesia is well explored ornithologically (Mayr and Diamond 2001). We obtained presence-absence data from Mayr and Diamond (2001). The Bismarck Archipelago consists of 31 islands, the Solomon Archipelago of 45, and Vanuatu of 28 islands. The Bismarcks, Solomons, and Vanuatu contain 155, 144, and 56 species of birds, respectively. For these analyses, we excluded migratory, transient, and nonbreeding species and species occurrences with questionable records. The avifaunas of these three archipelagoes are not independent; moving southeast from New Guinea (i.e., from the Bismarcks to the Solomons to Vanuatu), the avifauna of each archipelago is partially a subset of the previous archipelago (Mayr and Diamond 2001). As a result, the three archipelagoes have a total of about 200 species.

Description of Algorithms

We compared six “swap” algorithms and one “fill” method. Our version of Connor and Simberloff’s (1979) original swap algorithm used 50,000 initial swaps and sampled a randomized matrix every 50,000 swaps. The Manly (1995) Swap sequential swap algorithm is considerably faster than the original swap. In the Manly Swap, one chooses a random integer, m , in $[1, N]$, where N is the total number of randomized matrices to be sampled. Beginning with the original matrix, one applies a single swap to create V_m , samples the matrix, and decrements m . While $m > 1$, one continues to apply a single swap to V_m , to sample the matrix, and to decrement m . When $m = 1$, one returns to the observed matrix and applies a single swap to construct V_{m+1} . While $m < N$, one continues to apply a single swap to V_m , to sample the matrix, and to increment m . Gotelli (2000) developed the Gotelli Swap, an algorithm similar to Manly’s sequential swap. After a sequence of initial swaps, the Gotelli Swap samples each subsequent matrix after a single swap. We used 50,000 initial swaps in our implementation of the Gotelli Swap.

Zaman and Simberloff (2002) showed that the original swap algorithm (and, therefore, both the Manly Swap and the Gotelli Swap) does not sample matrices equiprobably, but proportionally to the number of “neighbors” of each (i.e., the number of submatrices that can be swapped). To obtain correct estimates for the distribution of statistics, Zaman and Simberloff calculated a weighted average, with each sampled matrix weighted inversely proportionally to its number of neighbors.

Instead of interchanging a predetermined number of submatrices, Miklós and Podani's (2004) trial-swap method modified the original swap algorithm to specify a number of swap attempts. This simple change generates a uniform random sample of matrices: while the probability of obtaining a particular matrix is proportional to that matrix's number of neighbors, the probability of retaining the matrix (by selecting a submatrix that cannot be swapped) is inversely proportional to its number of neighbors. Thus, the probability of obtaining a matrix after a large number of swap attempts is independent of its number of neighbors, and each matrix is sampled equiprobably. In our implementation of Miklós and Podani's trail-swap method, we specified 50,000 swap attempts. Because some matrices (e.g., strongly nested assemblages) might not be sufficiently randomized with 50,000 swap attempts, in Miklós and Podani (long), we required 500,000 swap attempts between samples.

We used the random Knight's Tour described by Gotelli (2000) and available with EcoSim 6.0 (Gotelli and Entsminger 2001). The random Knight's Tour starts with an empty matrix and sequentially fills randomly selected elements. If a cell cannot be filled with a small number of attempts without violating the row or column sums, the algorithm retreats and randomly removes a previously filled cell. The algorithm continues recursively until a matrix is completed. Table 1.3 lists each randomization algorithm and its salient features. Except for the random Knight's Tour, all algorithms were coded in C and are available from the author.

Statistics

To test for differences among algorithms, we examined the distribution of the C-score statistic for each algorithm. We also developed a series of a priori hypothesis tests. First, to determine whether the random Knight's Tour differs from all six swap methods, we compared means and variances generated by each algorithm. Second, we examined whether Connor and Simberloff's original swap, the Manly Swap, and the Gotelli Swap differ from Zaman and Simberloff's (2002) weighted means method and Miklós and Podani's (2004) trial-swap method. Third, because the Manly Swap and the Gotelli Swap sample matrices that differ by only a single swap, we tested whether these sequential algorithms produce distributions with smaller variances than other swap algorithms. Fourth, to examine whether the Manly Swap generates distributional means that are more similar to the observed value than other swap algorithms, we compared the difference between the distribution mean and the observed C-score across algorithms. Fifth, we examined interaction effects to determine whether differences among algorithms vary across matrices of different size, fill, or evenness of marginal totals. We also conducted these statistical comparisons on other measures of community-wide co-occurrence, including number of checkerboards, S^2 , number of neighbors, and Togetherness. Statistical analyses were performed using SAS 9.1.

RESULTS

ANOVA results of main effects of simulated communities

Randomization algorithms generate significantly different mean C-scores ($F_{6,672} = 78.39$; $p < 0.0001$; Table 1.4). Pairwise comparisons of mean C-score show that the random Knight's Tour differs significantly from all swap methods and that no swap algorithm differs from any other. Though statistically significant, the difference in means is small: the mean C-score from matrices generated with the randomized Knight's Tour algorithm is 23.57, and the mean C-score from all swap algorithms is 23.50.

Randomization algorithms generate distributions with different variances ($F_{6,672} = 387.65$; $p < 0.0001$; Table 1.5). Pairwise comparisons show that the random Knight's Tour produces larger variances (mean variance = 0.056) in C-score than all other algorithms and that the Manly Swap and Gotelli Swap generate smaller variances (mean variance = 0.020) than other swap algorithms (mean variance = 0.027). The original swap method, Zaman and Simberloff's weighted means algorithm, and Miklós and Podani's trial-swap algorithm do not differ in variance of C-score.

The difference between the mean C-score of randomized matrices and the observed C-score differs significantly across algorithms ($F_{6,672} = 2123.53$; $p < 0.0001$; Table 1.6). Pairwise comparisons show that the Manly Swap generates distributional means that are more similar to the observed C-score than other algorithms. Also, the random Knight's Tour and the Gotelli Swap generate distributional means that are more different from the observed C-score than other swap algorithms.

There are significant main effects for matrix size, matrix fill and evenness of the row and column sums for mean C-score, variance in C-score, and difference between observed C-score and distributional mean (Tables 1.4–1.6; $p < 0.0001$). Because C-score measures the mean number of checkerboard units per species pair (Table 1.2), one would expect its value to increase with matrix size, to peak near matrix fill of 50%, and to increase with evenness of the row and column sums. Our interest lies not in understanding how C-score varies with these matrix traits but in understanding whether differences in matrix randomization algorithms vary with matrix size, fill, and evenness. To address these patterns, we examine interactions involving algorithm type.

Interactions

Significant interaction effects exist for mean C-score, variance of C-score, and difference between the observed C-score and the distributional means of randomization algorithms (Tables 1.4–1.6). Algorithm type interacts with matrix size, matrix fill, and evenness of marginal sums (row and column totals). Algorithm type also interacts with matrix size x matrix fill, matrix size x evenness, matrix fill x evenness, and matrix size x fill x evenness (Tables 1.4–1.6; $p < 0.0001$). These interactions indicate that differences among matrix randomization algorithms are not consistent and vary in matrices of different size, fill, and evenness of row and column totals. As a result, algorithm methods generate similar distributions of statistics for some matrices but widely different distributions for others (Fig. 1.1). Qualitatively similar results are obtained for other community-wide measures of co-occurrence including number of checkerboards, S^2 , number of neighbors, and Togetherness.

Examination of empirical communities

For the avifauna of the Bismarck Archipelago, the Manly Swap produces a distribution that differs from all other randomization methods; most notably, the distribution includes a long tail that stretches to the observed C-score of 111812 (Fig. 1.2). The Gotelli Swap produces a distribution with less variance than those produced by other algorithms, and the randomized Knight's Tour generates a distribution with a lower mean C-score than other algorithms (Fig. 1.2).

For the Solomon Archipelago, the Manly Swap produces a statistical distribution with a long tail that abuts the observed C-score of 166678 (Fig. 1.3). Excluding the Manly Swap, the randomized Knight's Tour produces a distribution with a higher mean and larger variance than those produced by swap algorithms.

Randomization algorithms produce more similar statistical distributions for Vanuatu than for the other two archipelagoes (Fig. 1.4). Nevertheless, the Manly Swap continues to show a longer tail extending towards the observed C-score of 14888, and the Gotelli Swap shows smaller variance than other algorithms (Fig. 1.4).

DISCUSSION

Simulated communities

We compare algorithms that randomize presence-absence matrices while maintaining row and column sums and examine how the statistical distribution of the C-score and other community-wide measures of co-occurrence vary among seven randomization algorithms. We examine the distributions obtained from one “fill” algorithm (Gotelli and Entsminger’s [2001] randomized Knight’s Tour) and from several “swap” methods including two (Zaman and Simberloff’s [2002] weighted means algorithm and Miklós and Podani’s [2004] trial-swap method) that are known to produce unbiased distributions of statistics. We also examine the original swap algorithm (Connor and Simberloff 1979) and two of its modifications, the Manly (1995) Swap and the Gotelli (2000) Swap. Because these modified algorithms sample matrices sequentially (i.e., with only a single swap between sampled matrices), they are considerably faster than other swap methods.

We compare these randomization algorithms in matrices of different size, fill, and evenness of marginal sums (row and column totals) in a fully crossed four-way analysis of variance. The most popular fill algorithm, the random Knight’s Tour (Gotelli and Entsminger 2001), produces distributional means that differ from all swap algorithms ($F_{6,672} = 78.39$; $p < 0.0001$; Table 1.4). No distributional mean generated by a swap algorithm differs from the mean of any other swap algorithm.

Matrix randomization algorithms also generate statistical distributions with different variances in C-score ($F_{6,672} = 387.65$; $p < 0.0001$; Table 1.5). Connor and Simberloff’s (1979) original swap method, Zaman and Simberloff’s (2002) weighted means algorithm, and Miklós and Podani’s (2004) trial-swap algorithms do not differ significantly from each other in variance of C-score. Mean variance of these three algorithms is 0.027. Compared to these three swap algorithms, both sequential swap algorithms, the Manly (1995) Swap and Gotelli (2000) Swap, generate smaller variances (mean variance = 0.020). Because they interchange only one submatrix between samples, sequential swap algorithms sample only a small subsection of possible matrices and consequently produce distributions of statistics with artificially small variances. In short, matrices produced by sequential swap algorithms are not independent and are not representative of the entire universe of possible matrices. As a result, sample variance underestimates population variance and inflates Type I errors. In contrast to the artificially low variances generated by sequential swap algorithms, the random Knight’s Tour produces distributions with larger variances (mean variance = 0.056) in C-score than any swap algorithm.

The Manly (1995) Swap generates distributional means that are more similar to the observed C-score than other algorithms ($F_{6,672} = 2123.53$; $p < 0.0001$; Table 1.6). Because the Manly Swap does not interchange a large number of submatrices before sampling, this result is not surprising. Manly’s (1995) Swap generates biased estimates of means, and this bias reduces statistical power and increases Type II errors. In contrast to the Manly Swap, both the random Knight’s Tour algorithm and the Gotelli Swap produce distributions that are more different from the initial, observed matrix than the distributions generated by other swap algorithms. These

biased estimates increase the Type I error rate. The difference between the distribution mean and the observed C-score does not differ for Connor and Simberloff's (1979) original swap algorithm, Zaman and Simberloff's (2002) weighted means method, and Miklós and Podani's (2004) trial-swap algorithm.

Interaction effects

For mean C-score, variance of C-score, and difference between the observed C-score and the distributional means of randomization algorithms, significant interactions exist between algorithm type and every other factor or interaction (i.e., between algorithm type and matrix size, matrix fill, evenness of marginal sums (row and column totals), matrix size x matrix fill, matrix size x evenness, matrix fill x evenness, and matrix size x fill x evenness (Tables 1.4–1.6; $p < 0.0001$)). Because differences among matrix randomization algorithms are not consistent and vary in matrices of different size, fill, and evenness of row and column totals, algorithm methods generate similar distributions of statistics for some matrices but widely different distributions for others (Fig. 1.1). Therefore, the degree to which particular algorithms sample matrices nonrandomly, generate inflated or reduced variances, or produce biased estimates of means varies from one dataset to another further impugning the use of the random Knight's Tour (Gotelli and Entsminger 2001), Manly (1995) Swap, and Gotelli (2000) Swap algorithms.

Empirical communities

Examination of the avifaunas of three archipelagoes off Papua New Guinea generally supports the ANOVA results of the simulated communities. In the Bismarck and Solomon archipelagoes, the randomized Knight's Tour produces mean C-scores that differ from those of swap algorithms (Figs. 1.2–1.3). In the Solomons, the randomized Knight's Tour also produces a distribution with a larger variance than those produced by swap algorithms. The Gotelli Swap produces a distribution with a smaller variance than those produced by other algorithms for the Bismarck Archipelago and Vanuatu (Figs. 1.2, 1.4).

Despite these similar findings, an important difference exists between simulated matrices and empirical communities. In simulated communities, the Manly Swap produces distributions with similar means but smaller variances than other swap algorithms. In the empirical communities, however, the Manly Swap produces a distribution that differs greatly from all other randomization methods. In all three archipelagoes, the distributions produced by the Manly Swap include a long tail, and these tail distributions stretch to abut the observed C-scores (Figs. 1.2–1.4). Excluding the Manly Swap, swap algorithms begin with a series of shuffles before sampling begins, so observed C-score does not affect the statistical distribution of randomized matrices. In contrast to other swap algorithms, the Manly Swap begins sampling after only a single swap in the observed matrix and samples each matrix after only one swap. Consequently, when an observed matrix is unusual (as the avifaunas of all three archipelagoes are) the starting point for the random matrices will also be unusual. C-scores will tend to drift gradually toward the random C-score and variance is inflated. Thus, the Manly Swap produces distributions with inflated variances when the observed matrix is unusual and generates distributions with smaller variances when the observed matrix has no structure. Neither outcome is desirable, and use of the Manly Swap should be discontinued.

Conclusions

Because the random Knight's Tour algorithm produces biased distributions with inflated variances, we recommend its discontinuation. The Manly Swap and the Gotelli Swap generate

lower variances than other swap algorithms and should also be avoided. We recommend that researchers employ Miklós and Podani's (2004) trial-swap method to randomize presence-absence matrices while maintaining marginal sums. Miklós and Podani's algorithm produces uniformly random samples, requires computational time comparable to other swap algorithms, and is easily implemented.

CHAPTER 2

AN EXAMINATION OF SPECIES CO-OCCURRENCE PATTERNS

Abstract. Over the past three decades, co-occurrence matrices have been scoured for evidence that competitive interactions influence distributional patterns of species across islands. A number of metrics exist to quantify these co-occurrence matrices. Because these metrics examine all possible pairs of species and produce a single statistic, we term these metrics community-wide measures of co-occurrence. Because community-wide measures examine all possible pairs of species, some have suggested that they are unlikely to be able to detect competitive patterns, which are likely strongest between ecologically similar or evolutionarily related species. Furthermore, the most commonly used community-wide measure, the C-score, cannot distinguish between exclusive and congruent distributions when row and column sums are maintained in Monte Carlo randomizations. Restricting measures of co-occurrence to pairs of species within taxa or within guilds circumvents both problems.

We examine the avifaunas from three archipelagoes: Bismarck Archipelago, Solomon Islands, and Vanuatu. For each archipelago, we calculate two community-wide metrics: C-score and Togetherness. Then, we examine co-occurrence patterns within families and within genera by restricting our measures to pairs of species within taxa. We find statistically significant community-wide C-scores for the bird communities on all three archipelagoes. Bird communities in the Bismarck and Solomon archipelagoes show significantly less co-occurrence both within families and within genera: C-scores are significantly higher than those from randomized matrices, and Togetherness scores are lower or do not differ significantly from randomized matrices. In contrast, the avifauna of Vanuatu shows lower C-scores and higher Togetherness scores within taxa, but the differences are usually nonsignificant.

Although co-occurrence patterns within taxa in the Bismarck and Solomon Archipelagoes are consistent with a competition hypothesis, when genera are examined separately, most do not exhibit patterns that differ from random expectations. Furthermore, most observed exclusive distributions patterns are explained by the occurrence of single species that occur predominantly on species-poor islands and by the existence of barriers to dispersal within archipelagoes. The distributions of birds across these archipelagoes provide little evidence for competition. We argue that the range of conditions under which competition is likely to create significantly exclusive co-occurrence patterns at the island scale is limited and conclude that community-wide measures of co-occurrence are of limited utility in community ecology and biogeography. Their greatest contribution to ecology, biogeography, and conservation is to help direct future observations and experiments.

Key words: assembly rules, competition, co-occurrence, C-score, Monte Carlo, null models, presence-absence matrices

INTRODUCTION

A community is an assemblage or set of species populations at some defined place and time. A central theme in community ecology is that the species composition of a community is governed by deterministic rules. Many of these rules focus on the importance of interspecific interactions, especially competition, in determining community composition. The hypothesis that competition influences community structure is long-standing in ecology (Gause 1934). Gause formulated the competitive exclusion principle, which states that competing species can coexist in a stable environment only if their niches differ. Encouraged by Gause's work, Root (1967) developed the concept of a guild, a group of coexisting species that exploits a shared resource in a similar way. To test Gause's (1934) competitive exclusion principle, early research examined guilds for evidence of niche differentiation (MacArthur and Levins 1967, Schoener 1974), character displacement (Brown and Wilson 1956) and morphological size ratios (Hutchinson 1959, Schoener 1965).

With conceptual advances and empirical support (e.g., MacArthur 1972, Cody 1975), the competition hypothesis quickly established itself as the dominant paradigm (sensu Kuhn 1970) in ecology. This paradigm continues to guide much research today. Some major investigations into the effects of competition on community structure include Diamond's (1975) assembly rules, Tilman's (1982) competitive hierarchies, and Fox's assembly rules (Fox and Brown 1993). Each of these studies suggested that competition is an important factor in community assembly. Diamond's (1975) landmark paper on the birds of the Bismarck Archipelago argued that the species of a community are selected and coadjusted in their niches to coexist and to resist invaders. Diamond provided examples of pairs of species that he believed co-occurred on islands less than expected by chance alone.

Connor and Simberloff (1979) presented a pioneering approach, the null model, and rigorously tested Diamond's (1975) assembly rules. Connor and Simberloff argued that each of Diamond's assembly rules is either tautological, untestable, or not empirically supported. Because the data for the Bismarck Archipelago were not available, Connor and Simberloff tested Diamond's assembly rules with other biotas, including the avifauna of Vanuatu (formerly New Hebrides).

Connor and Simberloff's (1979) critique of Diamond's (1975) assembly rules sparked an unprecedented controversy in the ecological literature. According to Wiens (1989, p. 86), "The debate has been prolonged, repetitive, and often acrimonious, but it has served to sharpen our focus . . ." Besides sharpening the focus on some critical issues in community ecology, the historical exchange that began with Diamond (1975) and Connor and Simberloff (1979) also served to settle some points of contention. First, there is now widespread agreement that null models are necessary and useful tools in the study of community ecology (Gotelli and Graves 1996, Gotelli 2001) and that these null models should reflect, in some way, the fact that species differ in the number of islands they inhabit and that islands contain different numbers of species. Second, it is generally agreed that analyses designed to test for the effect of competition should not examine the entire fauna (all species pairs); instead they should examine pairs or groups of species within ecological guilds (Simberloff 1986), within genera, or within genera within ecological guilds (Graves and Gotelli 1993). A third point of agreement is that to compare

observed and simulated test statistics, one should employ classical randomization procedures (Edington 1987) and not assume any particular statistical distribution (e.g., a *t* or chi-squared distribution) (Gotelli and Graves 1996). Despite agreement on these points, the role of competition in structuring the assembly of ecological communities remains unresolved (Gotelli 1999).

The occurrence of species at sites (e.g., islands) can be represented in a two-dimensional, $r \times c$, presence-absence matrix. Presence-absence matrices are a frequently used unit of study in biogeography and community ecology (McCoy and Heck 1987). In a presence-absence matrix, also termed a co-occurrence or incidence matrix, each row, r_i , represents a species, and each column, c_j , a site. Each cell in the matrix (a_{ij}) contains a one or a zero, indicating the presence or absence, respectively, of species i at site j . The row sum, R_i , represents the number of occurrences of each species, and the column sum, C_j , represents the number of species at each site. Table 2.1 shows a presence-absence matrix for 13 species of finches on 17 islands in the Galápagos Islands.

Five common metrics quantify co-occurrence patterns: number of species combinations, number of checkerboard distributions (i.e., the number of species pairs that share no islands), “checkerboardedness” index (C-score), Togetherness index, and Schluter’s (1984) variance ratio (Table 2.2). These metrics measure slightly different aspects of species co-occurrence and can produce drastically different results (Gotelli 2000). The C-score is particularly useful because it is relatively insensitive to noise, is not prone to Type I errors (false positives), and has good statistical properties (Gotelli 2000).

Community-wide measures of co-occurrence, particularly the C-score, have been used to draw inferences about community structure and interspecific interactions (Stone and Roberts 1990, Sanderson et al. 1998, Gotelli and Rohde 2002, Gotelli and McCabe 2002, Sfenthourakis et al. 2005). In a meta-analysis of 96 assemblages that report the distribution of species across sites, Gotelli and McCabe (2002) concluded that observed co-occurrence in most communities is less than expected by chance, consistent with Diamond’s (1975) assembly rules.

Roberts and Stone (1990) showed that the mean number of islands shared among all species pairs is constant when row and column totals are constrained. And Stone and Roberts (1992) proved that the measures for exclusive (C-score) and congruent distributions (Togetherness) differ by only a constant when marginal sums are constrained. Paradoxically, this discovery proves that matrices with a large number of species pairs with exclusive distributions must also have a large number of species pairs with congruent distributions (Stone and Roberts 1992). Biologically, a community that has a significant community-wide C-score, consistent with a competition hypothesis, must also exhibit a significant community-wide Togetherness score, consistent with a hypothesis of shared habitat preferences. When all possible pairs of species are measured, both C-score and Togetherness measure deviation from randomness, but neither can assess the direction in which an observed community differs from random matrices. Therefore, studies that have used community-wide measures of co-occurrence (e.g., Gotelli and McCabe 2002) cannot distinguish patterns that are consistent with competition from patterns that are not.

Quantifying distributional patterns for only a subset of species pairs (e.g., pairs of species within an ecological guild or within a genus) while randomizing the entire presence-absence matrix can yield useful information (Stone and Roberts 1992) and provides two major advantages over calculating a community-wide measure of co-occurrence. First, this method examines the subset of interactions that is most interesting biologically. Examining pairs of species within a guild removes noise and allows one to focus on those patterns most likely to be shaped by interspecific interactions, including competition. In addition, restricting analyses to pairs of species within guilds reduces the ‘dilution effect’ (Diamond and Gilpin 1982), which posits that,

even if species within guilds or within taxa are competing, these biologically important patterns might go undetected because one is also measuring many pairs of species that are not likely to compete. A real biological signal is drowned in a sea of noise. Second, examining a subset of species pairs eliminates the linear dependence of C-score and Togetherness, thereby allowing separation of these opposing patterns and determination of whether species within guilds or within taxa exhibit more or less co-occurrence than expected by chance. Because different co-occurrence patterns within guilds can produce identical community-wide measures (Table 2.3), even significant community-wide measures are of limited use in testing assembly rules.

We use taxonomic groups (families and genera) as a proxy for guilds. Although taxonomic groups are not always congruent with guilds (Gilpin and Diamond 1982, Simberloff and Dayan 1991), we believe that, on average, congeneric species are ecologically more similar to each other than they are to species of other genera (Darwin 1859, Elton 1946, den Boer 1980, Graves and Gotelli 1983, Colwell and Winkler 1984). Many studies have used taxonomy as a proxy for guild (e.g., MacArthur 1958, Lambert and Reid 1981, Schoener 1984, Walter and Ikonen 1989, Sfenthourakis et al. 2005), and taxonomy can provide an imperfect but useful indication of guild.

Here, we examine the avifaunas of three archipelagoes: the Bismarck Archipelago, Solomon Islands, and Vanuatu. For each, we calculate community-wide C-score and Togetherness by summing over all possible pairs of species. Using taxon (family or genus) as a proxy for guilds, we calculate C-score and Togetherness only for pairs of species within a taxon to test whether congeneric or confamilial species co-occur less than expected by chance alone. We then examine each genus separately for significantly high exclusion or aggregation. For each genus that exhibits an unusual co-occurrence pattern, we assess whether competitive exclusion best explains the observed distribution.

METHODS

Study sites

Melanesia consists of three archipelagoes: the Bismarck Archipelago, the Solomon Archipelago, and Vanuatu (Fig. 2.1). The first two archipelagoes compose Northern Melanesia. For the purposes of this investigation, the Bismarck Archipelago consists of 31 islands, the Solomon Archipelago of 45, and Vanuatu of 28 islands. Melanesia is well explored ornithologically (Mayr and Diamond 2001), and there have been nearly 200 expeditions to observe or collect birds in Melanesia (Dutson 2001). The Bismarcks, Solomons, and Vanuatu contain 154, 142, and 56 bird species, respectively. For these analyses, we excluded migratory, transient, and nonbreeding species and species occurrences with questionable records. The avifaunas of these three archipelagoes are not independent; moving southeast from New Guinea (i.e., from the Bismarcks to the Solomons to Vanuatu), the avifauna of each archipelago is partially a subset of the previous archipelago (Mayr and Diamond 2001). As a result, the three archipelagoes have a total of about 200 species.

Statistics

For each archipelago, we constructed a presence-absence matrix (Appendices C–E) and calculated community-wide C-score and Togetherness. Instead of calculating the mean score per species pair (by dividing the score by the total number of species pairs), we measured the total score to examine the fraction of the community-wide measure that is contributed by pairs of

species within families or within genera. To test matrices for nonrandom co-occurrence patterns, we used Monte Carlo simulations and implemented Miklós and Podani's (2004) trial-swap algorithm to generate 1,000 randomized matrices with 500,000 attempted swaps between sampled matrices. With Connor and Simberloff's (1979) original swap algorithm, two rows and two columns are randomly selected (rows and columns need not be adjacent). If the 2 x 2 submatrix is of the form (a) $\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$ or (b) $\begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}$, swap the rows (or the columns); this swap is equivalent to switching between these two submatrices. A sufficiently large number of swaps will produce a randomized matrix while maintaining the marginal sums and species' incidence functions. Instead of interchanging a predetermined number of submatrices, Miklós and Podani's (2004) trial-swap method modified Connor and Simberloff's (1979) original swap algorithm to specify a number of swap attempts. This simple change generates a uniform random sample of matrices: while the probability of obtaining a particular matrix is proportional to that matrix's number of neighbors, the probability of retaining the matrix (by selecting a submatrix that cannot be swapped) is inversely proportional to its number of neighbors. Thus, the probability of obtaining a matrix after a large number of swap attempts is independent of its number of neighbors, and each matrix is sampled equiprobably. Miklós and Podani's (2004) trial-swap method, which produces uniformly random samples, requires computational time comparable to other algorithms, is easily implemented, and gives correct estimates for the distributions of statistics. Zaman and Simberloff's (2002) weighted means method also gives correct estimates for the distributions of statistics but is less intuitive than Miklós and Podani's (2004) trial-swap method (Chapter 1).

Swap methods maintain row and column sums so that each species retains its observed commonness and each island retains its observed species richness. Diamond (1975) noted that some species, termed supertramps, are present only on small islands with few species while other species are found only on large islands with many species. Diamond argued that these patterns result from competitive exclusion. We used the swap method to generate 1,000 randomized incidence matrices. In randomized incidence matrices, each species can occur only within its observed range of island richnesses. With these constraints, we conducted the same analyses as above.

For both randomization methods, we also examined each family and each genus separately for significantly high exclusion or aggregation with one-sided tests. We calculated p -values by counting the number of randomized matrices that had a measure equal to or more extreme than the observed matrix and dividing by the total number of randomized matrices (1,000). We also examined whether genera exhibit consistent co-occurrence patterns across archipelagoes. Lastly, we examined the specific genera that exhibited statistically significant distribution patterns ($p < 0.01$) and identified possible causes. We did not employ a Bonferroni correction for multiple tests because of its inherent conservatism and reduction of statistical power (Nakagawa 2004). Instead of excluding genera based on statistics alone, we wanted an inclusive sample of genera so that we could examine the possible role of competition and the details of biology, geography, and history in shaping the co-occurrence patterns of these genera. All computer code was written in C. We used the version of the rand function recommended in Press et al. (1992) to generate random integers.

RESULTS

Trial-swap method

Community-wide measures of co-occurrence show that the avifaunas of all three archipelagoes exhibit highly nonrandom species distributions consistent with a competition hypothesis (Bismarck Archipelago: obs $C = 111812$, exp $C = 97319.4$, $p < 0.001$, Table 2.4, Fig. 2.2; Solomon Archipelago: obs $C = 166678$, exp $C = 129813.0$, $p < 0.001$, Table 2.5, Fig. 2.3; Vanuatu: obs $C = 14888$, exp $C = 14238.7$, $p < 0.001$; Table 2.6, Fig. 2.4). The bird community of each archipelago also exhibits a Togetherness score that is higher than randomized communities (Bismarck Archipelago: obs $T = 468217$, exp $T = 466609.3$, $p < 0.001$, Table 2.4; Solomon Archipelago: obs $T = 818273$, exp $T = 796354.2$, $p < 0.001$, Table 2.5; Vanuatu: obs $T = 43283$, exp $T = 42610.9$, $p < 0.001$; Table 2.6).

Co-occurrence patterns of confamilial species exhibit differences among archipelagoes. The Bismarck and Solomon archipelagoes continue to exhibit a significantly higher C-score (Bismarcks: obs $C = 6575$ vs. exp $C = 5189.0$, $p < 0.001$; Table 2.4; Solomons: obs $C = 9045$ vs. 6290.7, $p < 0.001$; Table 2.5), but Vanuatu does not (obs $C = 283$ vs. 378.9, $p = 0.978$; Table 2.6). Togetherness within families is not significantly higher than in random communities in the Bismarck Archipelago (obs $T = 23805$ vs. 22984.7, $p = 0.083$; Table 2.4). But in the Solomon and Vanuatu archipelagoes, Togetherness is significantly higher than in random matrices (Solomons: obs $T = 41812$ vs. 39444.7, $p < 0.001$, Table 2.5; Vanuatu: obs $T = 1303$ vs. 1119.5, $p = 0.020$; Table 2.6). For all archipelagoes, pairs of species within families constitute only a small fraction of the community-wide C-score. Bird communities of the Bismarck, Solomon, and Vanuatu archipelagoes obtain only 5.9% (= 6575/111812), 5.4% (= 9045/166678), and 1.9% (= 283/14888), respectively, of their C-score from pairs of species within families (Tables 2.4–2.6). The bulk of the community-wide C-score for the avifaunas on these archipelagoes is derived from pairs of species from different families.

When C-score and Togetherness measures are restricted to congeneric pairs of species, birds in the Bismarck Archipelago have a significantly higher C-score than expected (1893 vs. 848.4; $p < 0.001$; Table 2.4). Bird species in the Solomon Archipelago also exhibit a significantly higher C-score (2528 vs. 1450.0; $p < 0.001$; Table 2.5), but birds in Vanuatu do not (53 vs. 98.6; $p = 0.96$; Table 2.6). Togetherness scores for species within genera are not higher than those from random communities in any archipelago ($p > 0.11$; Tables 2.4–2.6). Congeneric pairs of species account for only 1.7%, 1.5% and 0.4%, respectively, of the community-wide C-score in the Bismarck, Solomon, and Vanuatu archipelagoes.

Families and genera

Forty-six bird families occur in the Bismarck Archipelago, and 23 families have two or more species. Of these 23, five families (Columbidae, Monarchidae, Pachycephalidae, Meliphagidae, and Sturnidae) show exclusive co-occurrence patterns ($p < 0.001$; Table 2.7). In addition, two families (Psittacidae and Campephagidae) exhibit aggregated patterns ($p = 0.002$; Table 2.7). Of the 98 genera that occur in the Bismarck Archipelago, 30 genera contain at least two species. Seven of these genera (*Ptilinopus*, *Ducula*, *Macropygia*, *Monarcha*, *Pachycephala*, *Myzomela*, and *Aplonis*) exhibit exclusive co-occurrence patterns ($p \leq 0.002$; Table 2.8). No genus shows significantly congruent species distributions ($p > 0.20$; Table 2.8).

In the Solomon Archipelago, 21 of 42 families contain at least two species. Five families (Columbidae, Cuculidae, Monarchidae, Zosteropidae, and Sturnidae) show exclusive species distributions ($p < 0.001$; Table 2.7), and two (Accipitridae and Campephagidae) show congruent

distributions ($p < 0.001$; Table 2.7). Of the 93 genera present in the Solomon Archipelago, 21 genera contain at least two species. Five genera (*Ducula*, *Monarcha*, *Zosterops*, *Myzomela*, and *Aplonis*) have exclusive distributional patterns ($p \leq 0.002$; Table 2.8), and one genus (*Coracina*) shows aggregated co-occurrence patterns ($p < 0.001$; Table 2.8).

Sixteen of the 27 families represented in Vanuatu are represented by two or more species. None of these 16 families displays an exclusive distributional pattern, but one (Anatidae) shows an aggregated pattern ($p = 0.002$; Table 2.7). Ten of the 45 genera present in Vanuatu contain at least two species. No genus displays either a significantly aggregated or exclusive co-occurrence pattern ($p > 0.24$; Table 2.8).

Co-occurrence patterns within taxa exhibit some consistency across archipelagoes. Nineteen families are represented by at least two species in both the Bismarck and Solomon archipelagoes. Family effect size, calculated as ((observed score – randomized mean) / (randomized standard deviation)), is correlated between the Bismarck and Solomon archipelagoes for both C-score (Pearson's $r = 0.70$; $p < 0.001$) and Togetherness ($r = 0.49$; $p = 0.033$; Table 2.9). Patterns within genera across archipelagoes reveal a similar pattern. Twenty genera are represented by two or more species in both the Bismarck and Solomon archipelagoes. Genus effect size is correlated between archipelagoes for both C-score ($r = 0.86$; $p < 0.001$) and Togetherness ($r = 0.80$; $p < 0.001$; Table 2.9). Co-occurrence measures in Vanuatu are not correlated with measures in either the Bismarck or Solomon archipelagoes ($p > 0.10$ for all comparisons; Table 2.9).

Incidence

We obtain qualitatively similar results when community-wide measures of co-occurrence are compared to randomized matrices in which each species is constrained by the randomization algorithm to occur only within its observed range of island richnesses. Community-wide measures continue to show that the avifaunas of all three archipelagoes differ significantly from randomized matrices with higher observed C-scores and Togetherness than expected ($p < 0.05$; Tables 2.4–2.6).

When co-occurrence metrics are restricted to pairs of species within families, results for the Bismarck Archipelago differ from those obtained with the unconstrained trial-swap method. Within families, birds of the Bismarck Archipelago no longer exhibit a significantly exclusive pattern (obs C = 6575 vs. exp = 6312.6; $p = 0.146$; Table 2.4) but rather a congruent one (obs T = 23805 vs. exp = 23077.8; $p = 0.049$; Table 2.4). Species in the Solomon Archipelago continue to show evidence of both aggregated and congruent co-occurrence patterns (obs C = 9045 vs. exp = 7650.0; $p < 0.001$; obs T = 41812 vs. exp = 39153.8; $p < 0.001$; Table 2.5) at the family level. Birds of Vanuatu remain significantly aggregated (obs T = 1303 vs. exp = 1076.5; $p = 0.007$; Table 2.6).

When co-occurrence measures are restricted to pairs of species within genera, species in the Bismarcks continue to show significant exclusion (obs C = 1893 vs. exp = 1362.2; $p < 0.001$; Table 2.4), and so do birds in the Solomons (obs C = 2528 vs. exp = 2270.1; $p = 0.027$; Table 2.5). Avifaunas of the Solomons and of Vanuatu also exhibit significant aggregation in the co-occurrence patterns of congeneric species (Solomons: obs T = 8831 vs. exp = 8123.9; $p = 0.001$; Table 2.5; Vanuatu: obs T = 340 vs. exp = 272.3; $p = 0.027$; Table 2.6).

Families and genera

Of the 23 families with two or more species in the Bismarck Archipelago, one family (Monarchidae) has an exclusive co-occurrence pattern ($p = 0.002$; Table 2.10) and one family

(Psittacidae) shows an aggregated pattern ($p < 0.001$; Table 2.10). In the Bismarck Archipelago, four genera (*Ptilinopus*, *Macropygia*, *Monarcha*, and *Aplonis*) exhibit exclusive co-occurrence patterns ($p < 0.01$; Table 2.11), and none exhibits a significantly aggregated distribution ($p > 0.18$; Table 2.11).

In the Solomon Islands, three families (Columbidae, Cuculidae, and Zosteropidae) show an exclusive pattern ($p < 0.01$; Table 2.10), and three (Accipitridae, Campephagidae, and Monarchidae) have an aggregated distribution ($p \leq 0.005$; Table 2.10). Of the 21 genera represented by at least two species in the Solomons, two (*Ducula* and *Zosterops*) show an exclusive distributional pattern ($p < 0.001$; Table 2.11). Only one genus (*Coracina*) has an aggregated co-occurrence pattern ($p < 0.001$; Table 2.11).

None of the 16 families with at least two species in Vanuatu displays an exclusive distributional pattern, and only Anatidae shows a congruent distribution ($p = 0.006$; Table 2.10). No genus displays either a significantly aggregated or exclusive co-occurrence pattern in Vanuatu ($p \geq 0.15$; Table 2.11).

Co-occurrence patterns within families are not consistent across archipelagoes. Family effect size is not correlated between the Bismarck and Solomon archipelagoes for either C-score ($r = 0.24$; $p = 0.33$) or Togetherness ($r = 0.31$; $p = 0.20$). Genus effect size is correlated between archipelagoes for both C-score ($r = 0.46$; $p = 0.042$) and Togetherness ($r = 0.45$; $p = 0.046$).

DISCUSSION

Community-wide C-scores demonstrate that the avifaunas of the Bismarck Archipelago, Solomon Archipelago, and Vanuatu exhibit nonrandom distributions. Bird communities of all three archipelagoes exhibit significantly higher C-scores and Togetherness scores than randomized communities ($p < 0.001$; Tables 2.4–2.6). Our analyses of community-wide measures of co-occurrence agree with the findings of Gotelli and McCabe (2002). In a meta-analysis of 96 assemblages, Gotelli and McCabe (2002) conclude that observed co-occurrence in most communities is less than expected by chance and consistent with Diamond's (1975) assembly rules.

Although community-wide measures of co-occurrence such as the C-score have been used to draw inferences about community structure and interspecific interactions (Stone and Roberts 1990, Sanderson et al. 1998, Gotelli and Rohde 2002, Gotelli and McCabe 2002, Sfenthourakis et al. 2005), community-wide measures of co-occurrence are plagued by problems that severely restrict their usefulness in understanding or even quantifying distributional patterns. Because C-score and Togetherness are positively linearly related (Stone and Roberts 1992), significantly high community-wide C-scores are consistent with a competition hypothesis but also with many other hypotheses, including hypotheses that increase aggregation, such as shared habitat preferences or shared dispersal routes. Examination of only a subset of species interactions (e.g., pairs of species within an ecological guild or congeneric species pairs) avoids many of these problems, and the resulting metrics can yield biologically useful information (Stone and Roberts 1992; see Sfenthourakis et al. 2005).

For all three archipelagoes examined here, pairs of species within families constitute only a small fraction of the community-wide C-score. The Bismarck, Solomon, and Vanuatu archipelagoes respectively obtain only 5.9%, 5.4%, and 1.9% of their C-score from pairs of species within families (Tables 2.4–2.6). Only 1.7%, 0.7% and 0.4% of the community-wide C-score results from congeneric pairs of species in the Bismarck, Solomon, and Vanuatu

archipelagoes, respectively (Tables 2.4–2.6). The bulk of the community-wide C-score for these archipelagoes is derived from pairs of species from different families. This finding supports Diamond and Gilpin's (1982) 'dilution effect': community-wide measures of co-occurrence might not detect real biological patterns (e.g., exclusive distributions between pairs of congeneric species) because the inclusion of many pairs of species that are not likely to compete drowns the pattern in a sea of noise.

Examination of pairs of species within guilds removes noise, reduces the dilution effect (Diamond and Gilpin 1982), and allows one to focus on the patterns most likely to be shaped by interspecific interactions. In addition, examining only a subset of species pairs eliminates the linear dependence of C-score and Togetherness when marginal sums are constrained (Stone and Roberts 1992). The linear dependence of C-score and Togetherness implies that both metrics quantify deviation from randomness but that neither can assess whether species co-occur more or less than one would expect by chance. Because different co-occurrence patterns within guilds or taxa can produce identical community-wide measures (Table 2.3), even significant community-wide C-scores are of limited use in testing assembly rules or in understanding distribution patterns or community structure. One can distinguish between exclusive and congruent patterns by quantifying C-score and Togetherness for a subset of species pairs and ask whether species within guilds or within taxa exhibit more or less co-occurrence than expected by chance.

We use taxonomic groups (families and genera) as a proxy for guilds. Avian communities on all three archipelagoes exhibit significant community-wide C-scores, but different co-occurrence patterns emerge upon examination of pairs of species within families or genera. Birds of the Bismarck and Solomon archipelagoes exhibit significantly higher C-scores within families and within genera ($p < 0.001$; Tables 2.4–2.5). In the Bismarcks, Togetherness is not significantly higher than random communities at the family or genus level ($p > 0.08$; Table 2.4). In the Solomons, Togetherness is not significantly higher than random matrices within genera ($p > 0.16$; Table 2.5) but is significantly higher within families ($p < 0.001$; Table 2.5). In the Bismarck and Solomon archipelagoes, measures of co-occurrence within genera continue to show exclusive co-occurrence patterns consistent with Diamond's assembly rules.

In contrast to the Bismarck and Solomon archipelagoes, the birds of Vanuatu do not exhibit an unusually high C-score within families or within genera ($p \geq 0.96$; Table 2.6). On Vanuatu, Togetherness for confamilial species is significantly higher than that from random communities ($p = 0.02$; Table 2.6), but Togetherness for species within genera does not differ significantly from random communities ($p = 0.118$; Table 2.6). Thus, despite showing significant community-wide C-scores consistent with Diamond's (1975) assembly rules, deeper scrutiny of the birds on Vanuatu does not support Diamond's assembly rules or the competition hypothesis. These findings indicate that some of the data sets examined by Gotelli and McCabe (2002) might also fail to support the competition hypothesis. Examination of co-occurrence patterns of these data sets at the family and genus level would be enlightening.

When we modify Connor and Simberloff's (1979) original swap algorithm and add the restriction that each species can occur only within its observed range of island richnesses, we obtain qualitatively similar results for community-wide measures of co-occurrence. All three archipelagoes continue to exhibit significantly high community-wide C-scores and Togetherness scores ($p < 0.04$; Tables 2.4–2.6). Co-occurrence measures within taxa are generally, but not always, similar. At the genus level, birds in the Bismarck and Solomon archipelagoes continue to exhibit significantly higher C-scores ($p < 0.03$; Tables 2.4–2.5). The bird community on Vanuatu continues to show a lower C-score, and the higher Togetherness score becomes significant ($p <$

0.03; Table 2.6). Togetherness for species within genera in the Solomon Archipelago also becomes significantly higher than random ($p = 0.001$; Table 2.5).

Effect sizes for both C-score and Togetherness for families and genera display some consistency across archipelagoes. Effect sizes between the Bismarck and Solomon archipelagoes are correlated ($r > 0.48$; $p < 0.04$; Table 2.9), but co-occurrence measures from these archipelagoes are not correlated with those from Vanuatu ($p > 0.11$; Table 2.9). Positive correlations indicate that co-occurrence patterns within taxa are not merely idiosyncratic phenomena restricted to single archipelagoes and that peculiarities of these two archipelagoes are not responsible for the observed co-occurrence patterns in the Bismarck Archipelago and Solomon Islands. Similar forces likely govern the distribution of species in both the Bismarck and Solomon archipelagoes, but forces in Vanuatu might differ. Of the three archipelagoes, Vanuatu is the most isolated, has the fewest species, has fewer genera with at least two species, and has fewer species per genus (only one genus has more than two species in Vanuatu). Birds of Vanuatu tend to be more widely dispersed within the archipelago than birds of the other archipelagoes (mean island occupancy in Vanuatu = 57%; Bismarcks = 19%; Solomons = 33%). One hypothesis is that the birds of Vanuatu might be better dispersers than birds of the Bismarcks and Solomons (because of Vanuatu's isolation) and that superior dispersal ability and a depauperate avifauna might alter or weaken competitive interactions. Another hypothesis is that Vanuatu's low number of species per genus precludes sufficient statistical power to detect nonrandom co-occurrence patterns within genera.

As with community-wide measures, examination of co-occurrence patterns of species within taxa does not circumvent the problem of inferring causality. Communities that exhibit higher C-scores within guilds than randomized communities could arise through a myriad of mechanisms, including interspecific competition, allopatric speciation, different invasion routes with limited dispersal, or independently evolved habitat preferences with physical or biological differences among islands (including differences caused by natural or anthropogenic disturbances, food resources, predators, parasites, and mutualists). Unusually high Togetherness scores can reflect shared habitat preferences with physical or biological differences among islands, sympatric speciation, shared invasion routes with limited dispersal, mutualism, or insufficient sampling (different sampling intensities among islands).

Examination of Genera

Although presence-absence data alone cannot address why some taxa exhibit nonrandom distribution patterns, additional information can eliminate some hypotheses, suggest likely mechanisms, and direct future observations or experimental manipulations. In the Bismarck Archipelago, seven genera (*Ptilinopus*, *Ducula*, *Macropygia*, *Monarcha*, *Pachycephala*, *Myzomela*, and *Aplonis*) exhibit exclusive co-occurrence patterns ($p \leq 0.002$; Table 2.8). In the Solomons, five genera (*Ducula*, *Monarcha*, *Zosterops*, *Myzomela*, and *Aplonis*) exhibit exclusive distributional patterns ($p \leq 0.002$; Table 2.8), and one genus (*Coracina*) has an aggregated co-occurrence patterns ($p < 0.001$; Table 2.8). Table 2.12 lists these genera, their common name, archipelago, the number of species of each genus in the archipelago, the observed co-occurrence pattern (exclusive or congruent), and the likely proximate cause(s) of that pattern.

Before we examine each of these genera, we must discuss two important facts. The first relates to the distributions of a handful of birds, termed supertramps, and the second involves the geography of the Bismarck and Solomon archipelagoes. Supertramps occur disproportionately on small or depauperate islands, and many genera with exclusive distributions contain a supertramp. In the Bismarcks, five species are statistically identified as supertramps with a Mann–Whitney *U*-

test ($p < 0.05$; Chapter 3). All five supertramps, *Ptilinopus solomonensis*, *Ducula pacifica*, *Monarcha cinerascens*, *Myzomela lafargei*, and *Aplonis feadensis*, belong to genera that exhibit an exclusive co-occurrence pattern in the Bismarcks. Three of these supertramps, *Ducula pacifica*, *Monarcha cinerascens* and *Aplonis feadensis*, also exhibit supertramp distributions in the Solomon Archipelago, where each of their genera has an exclusive distribution. *Myzomela lafargei* also occurs in the Solomons but is not a supertramp there, inhabiting both large and small islands. No other supertramps exist in the Solomon Islands, and no supertramps occur in Vanuatu.

Because we believe that barriers to dispersal between island groups within the Bismarck and Solomon archipelagoes play a role in the distributional patterns of these genera, we first discuss the island groups for each archipelago before discussing some details of each genus. In both the Bismarck and Solomon archipelagoes, barriers to dispersal between island groups coincide with differences in species composition and with genetic differentiation across populations within species (Mayr and Diamond 2001).

Bismarck Archipelago

The Bismarck Archipelago consists of four island groups: (1) the New Britain group, consisting of New Britain and its Pleistocene land-bridge islands, Uboi, Lolobau and Duke of York, and several smaller islands (Vuatom, Witu, Unea, and Sakar) that were not connected during the Pleistocene, (2) the New Ireland group, which consists of New Ireland and New Hanover, which were connected in the Pleistocene, and several smaller islands that were not connected (Dyaul, Tabar, Lihir, Tanga, Feni, and Tingwon), (3) the St. Matthias group (St. Matthias and Emirau), and (4) the Northwest group, consisting of Manus and its associated islands (San Miguel, Rambutyo and Nauna) and several small, western outliers (Anchorite, Hermit, and Ninigo archipelagoes and Wuvulu) (Mayr and Diamond 2001; Fig. 2.5). These four island groups are separated by barriers to dispersal (Mayr and Diamond 2001) and can explain many of the distributional patterns observed within the Bismarcks, further weakening the case for competitive exclusion.

Five species of *Ptilinopus* inhabit the Bismarcks. One species, *P. solomonensis* is morphologically and ecologically similar to *P. rivoli* (Mayr and Diamond 2001). Morphologically and ecologically similar species are pairs of species that are closely related that show a minimal or no difference in morphology and niche use (habitat use, diet, foraging technique, vertical stratum, and elevational range) (see Mayr and Diamond 2001, p. 166). *P. solomonensis* is a supertramp and is found throughout the St. Matthias and Northwestern island groups, on some small islands west of New Britain, and in the Solomon Archipelago. *P. rivoli* is found only in the New Britain and New Ireland island groups. Diamond (1975, Mayr and Diamond 2001) argues that *P. solomonensis* and *P. rivoli* coexist by segregating by island size: *P. rivoli* excludes *P. solomonensis* from large islands, and *P. solomonensis* outcompetes *P. rivoli* on small, remote, or volcanically disturbed islands. However, *P. rivoli* is absent from the St. Matthias and Northwestern island groups and does not occur on even large islands such as St. Matthias and Manus, which harbor *P. solomonensis* and other congeners. When the supertramp *P. solomonensis* is excluded from the analysis, the genus does not exhibit a significant C-score ($p > 0.70$). Thus, it appears that dispersal limitation between island groups is at least partially responsible for the exclusive distribution of *Ptilinopus* in the Bismarcks.

In the Bismarcks, *Ducula* is represented by six species, including the supertramp *D. pacifica*, which occurs only in the St. Matthias and Northwest groups. Three congeners, *D. myristicivora*, *D. rufigaster*, and *D. pinon*, are absent from these island groups, which are typically the last island groups to be colonized by species spreading from Papua New Guinea (Mayr and Diamond 2001). Because *D. pacifica* also occurs in the Solomons and in Vanuatu,

from where it originated (Mayr and Diamond 2001), its range is probably not restricted by barriers within the Bismarck Archipelago. Holyoak and Thibault (1978) argue that *D. pacifica* is restricted to small islands near Fiji because small islands lack predatory *Accipiter* hawks. In the Bismarcks, *D. pacifica* occupies no islands that contain any species of *Accipiter*. Excluding *D. pacifica* from the analysis makes the C-score nonsignificant ($p > 0.70$). Thus, the key to understanding the distributional pattern for *Ducula* in the Bismarcks lies in determining what restricts the distribution of a single species, *D. pacifica*, to small or remote islands.

Macropygia has three species in the Bismarcks, *M. nigrirostris*, *M. mackinlayi*, and *M. amboinensis*. *M. nigrirostris* and *M. mackinlayi* are daughter species of a recent, largely allopatric speciation and overlap only in the Bismarck Archipelago (Mayr and Diamond 2001). They remain largely allopatric within the Bismarcks, with *M. nigrirostris* occurring on islands in the southeast and *M. mackinlayi* spread across islands in the north and west. *M. nigrirostris* and *M. mackinlayi* are morphologically and ecologically similar (Mayr and Diamond 2001). Though vagrants of *M. mackinlayi* frequently reach islands with resident populations of *M. nigrirostris*, but breeding populations co-occur on no island in the Bismarck archipelago. Diamond (1975, Mayr and Diamond 2001) attributes this pattern to competitive exclusion of *M. mackinlayi* from larger islands by *M. nigrirostris*. The pattern is compelling, but subtle habitat differences have not been eliminated as a possible explanation for the absence of *M. mackinlayi* from large islands in the Bismarck Archipelago.

Three species of *Monarcha* inhabit the Bismarcks: *M. cinerascens*, *M. manadensis*, and *M. chrysomela*. *M. cinerascens* is a supertramp and occurs on small, remote, or species-poor islands throughout the archipelago. *M. cinerascens* also exists in the Solomons and on islands off the coast of Papua New Guinea. In both places, *M. cinerascens* occurs predominantly on species-poor islands. Consequently, it is plausible that *M. cinerascens* is a small island specialist and that its distribution across the Bismarcks might more accurately reflect this habitat preference than competitive exclusion. Exclusion of *M. cinerascens* from the analysis makes the C-score nonsignificant ($p > 0.70$), so understanding the factors that prevent this supertramp from inhabiting larger, richer islands is essential to understanding the exclusive distributional patterns within the genus.

The Bismarcks harbor two species of *Pachycephala*, *P. pectoralis* and *P. melanura*. These two species are morphologically and ecologically similar, and Diamond (1975, Mayr and Diamond 2001) attributed their distributions to interspecific competition. However, *P. melanura* continues to occupy predominantly small islets in New Guinea, where *P. pectoralis* is absent. And in the Solomon Archipelago, where *P. melanura* is absent, *P. pectoralis* continues to occupy large islands. Without additional data, one could parsimoniously attribute the exclusive distributions to species-specific differences in habitat preference.

Six species of *Myzomela*, including the supertramp *M. lafargei*, occur in the Bismarck Archipelago. *M. lafargei* occurs on many islands in the St. Matthias and Northwestern island groups and on several small islands west of New Britain. No other species of *Myzomela* occurs in the St. Matthias or Northwestern island group. *M. lafargei* is the only supertramp that does not explain the exclusive co-occurrence pattern: when *M. lafargei* is excluded from the analysis, *Myzomela* continues to exhibit a significantly high C-score ($p = 0.002$). Of the remaining species, *M. cardinalis* survives only on New Britain, *M. sclateri* and *M. eques* are restricted to the New Britain island group, *M. pulchella* occurs only on New Ireland, and *M. cruentata* occurs in the New Ireland island group and on New Britain. Thus, of the five species, only *M. cruentata* occurs in both the New Britain and New Ireland island groups. As we have seen for several other genera, the exclusive co-occurrence pattern in this genus is largely driven by the presence of a supertramp

on small, remote islands and by the existence of largely allopatric ranges that likely result from barriers to dispersal that exist between island groups.

Three species of *Aplonis* occur in the Bismarcks: *A. feadensis*, *A. cantoroides*, and *A. metallica*. In the Bismarcks, the supertramp *A. feadensis* occurs only in the St. Matthias and Northwest groups. But because *A. feadensis* also exists in the Solomon Islands, it seems unlikely that its distribution in the Bismarcks is restricted by dispersal barriers within the archipelago. *A. feadensis* is endemic to the Bismarck and Solomon archipelagos and exists only on small, depauperate, or remote islands throughout its range. It is possible that the distribution of *A. feadensis* is limited by competition with *A. cantoroides*, a species that is morphologically and ecologically similar to *A. feadensis* (Mayr and Diamond 2001). However, *A. cantoroides* is absent from only one island greater than 15 km² (Rambutyo), from which *A. feadensis* is absent. It is possible that *A. feadensis* is a small island specialist, and that its distribution is governed by this specialization, rather than by interspecific competition. When *A. feadensis* is excluded from the genus, the C-score becomes nonsignificant ($p > 0.90$). Thus, understanding the co-occurrence pattern for *Aplonis* in the Bismarck Archipelago requires determining why *A. feadensis* inhabits on only small islands.

Solomon Archipelago

The Solomon Archipelago is separated into five island groups: (1) the Bukida group, consisting of the Pleistocene land-bridge island Greater Bukida, which included the chain of islands extending from Buka to Florida and Guadalcanal, (2) the New Georgia Group, consisting of three Pleistocene land-bridge islands with modern islands from Vella Lavella to Gatukai, and two islands that were not connected, Gizo and Simbo, (3) Malaita, (4) the San Cristobal group, consisting of San Cristobal, Ulawa, Ugi, Three Sisters, Santa Anna, and Santa Catalina, and (5) the Rennell group, including Rennell and Bellona (Mayr and Diamond 2001; Fig. 2.6). In addition to these five island groups, a number of small, remote islands occur north and east of the archipelago's main islands. These outlier islands include Nissan, Fead, Kilinailau, Tauu, Nukumanu, Ontong Java, Ramos, Gower, and Sikaina. As in the Bismarck Archipelago, island groups are separated by barriers to dispersal (Mayr and Diamond 2001). These barriers and the presence of supertramps explain many of the unusual distributional patterns observed within the Solomons.

In the Solomons, *Ducula* is represented by four species, including the supertramp *D. pacifica*, which occurs on some outlier islands and on some small islands in the eastern part of the archipelago. *D. myristicivora* and *D. rosacea* occur on nearly every island in the Bukida, New Georgia, Malaita, and San Cristobal island groups, but neither occurs in the Rennell island group, and only *D. rosacea* reaches any outlier, occurring on Nissan and Ramos. Like *D. pacifica*, *D. latrans* invaded from the east. Unlike *D. pacifica*, *D. latrans* is confined to the southeastern part of the archipelago, ranging only as far as Malaita and Guadalcanal. Thus, only *D. pacifica* exists in the Rennell island group or on most outlier islands. Again, species are frequently absent from particular island groups. Exclusion of the supertramp makes the C-score nonsignificant for *Ducula* ($p = 1.0$). Because *D. pacifica* also occurs in the Bismarcks and in Vanuatu, its distribution is likely not limited by barriers within the Solomons. And because *D. pacifica* occupies large and small islands in Vanuatu, its restriction to small islands in the Solomons is also unlikely to be a consequence of habitat preference. *D. pacifica* occurs on only three small islands in the Bukida group (Buena Vista, Savo, and Florida). On all three islands, *D. pacifica* coexists with *D. myristicivora* and *D. rosacea*. *D. pacifica* co-occurs with the similarly-sized *D. latrans* on only one island, Three Sisters, in the San Cristobal island group where four other small islands harbor only *D. latrans*. Competition with *D. latrans* or with a species of *Ptilinopus* might

play a role. *D. pacifica* co-occurs with three species of *Accipiter*, *A. novaehollandiae*, *A. rufitorques*, and *A. fasciatus*, in the Solomon Archipelago. Understanding why *D. pacifica* is restricted to small islands is the key to understanding the exclusive pattern in this genus.

Coracina is the only genus that exhibits significant Togetherness in any archipelago. Five species exist in the Solomons, but no species occurs on any outlier island (Nissan, Fead, Kilinailau, Tauu, Nukumanu, Ontong Java, Gower, and Sikaina). Another seven small, but not isolated, islands (Ramos, Simbo, Borokua, Ugi, Three Sisters, Santa Anna, and Santa Catalina) are also uninhabited by any species of *Coracina*, but at least two species occur on some small islands, such as Buena Vista, Wana Wana, and Bagga. Thus, species of *Coracina* are largely restricted to medium and large islands that are not isolated. Difficulty maintaining populations on small islands, perhaps due either to specific habitat or resource requirements or to minimum area requirements, and perhaps difficulty colonizing remote islands cause this genus to exhibit a congruent distribution.

The Solomon Islands contain three species of *Monarcha*: *M. cinerascens*, *M. melanopsis*, and *M. manadensis*. *M. cinerascens* is a supertramp, surviving on all nine outlier islands and on Borokua and coexisting with neither congener. *M. melanopsis*, and *M. manadensis* are widespread and coexist on many islands from the San Cristobal, Malaita, Bukida, and New Georgia island groups, but both are absent from the Rennell island group and from all outlier islands. Although *M. cinerascens* and *M. melanopsis* are morphologically and ecologically similar, *M. cinerascens* is a small island specialist wherever it occurs, and its distribution in the Solomons might result from habitat preference rather than from competition. Exclusion of *M. cinerascens* from the analysis makes the C-score nonsignificant ($p = 1.0$), so understanding the factors responsible for the absence of *M. cinerascens* from larger islands is essential to understanding the exclusive distributional patterns within the genus.

Five species of *Zosterops* occur in the Solomons, and four are restricted to one or two island groups. *Z. stresemanni* is endemic to Malaita, *Z. metcalfi* is endemic to the Bukida group, *Z. murphyi* occupies only one island (Kulambangra) in the New Georgia group, and *Z. ugiensis* is present in only the Bukida and San Cristobal island groups. In addition, twelve of the fourteen occurrences of *Z. griseotinctus* are in the New Georgia group. Thus, the exclusive co-occurrence pattern for this genus stems largely from the confinement of species to one or two island groups. Rather than a true checkerboard distribution in which two or more species are dispersed among islands, these species segregate spatially by island group. Without additional data, it seems likely that these exclusive patterns are maintained by barriers to dispersal between island groups and not by competitive exclusion.

Two species of *Myzomela* occur in the Solomon Archipelago: *M. cardinalis* and *M. lafargei*. *M. cardinalis* is restricted to southeastern islands in the San Cristobal and Rennell island groups. *M. lafargei* occurs in the San Cristobal group and on many islands in the Bukida, New Georgia, and Malaita groups. Neither species has colonized any outlier island. Thus, the species co-occur only in the San Cristobal island group, where they coexist on San Cristobal. The exclusive distribution of *Myzomela* does not seem to result from competitive exclusion. Rather, each species is confined to different parts of the archipelago and overlap only in the San Cristobal island group.

The pattern for five species of *Aplonis* in the Solomons mirrors the pattern for *Aplonis* in the Bismarck Archipelago. The supertramp *A. feadensis* occurs on several small, outlying islands (Fead, Nissan, Kilinailau, Tauu, and Ontong Java). *A. metallica* and *A. cantoroides* occur widely throughout larger islands of the Solomon Archipelago, but neither occupies many outlier islands. *A. metallica* and *A. cantoroides* reach two outliers (Nissan and Kilinailau), and *A. cantoroides*

also occurs on a third, Gower. *A. grandis* and *A. brunneicapilla* do not reach any outlier island or the Rennell island group, and *A. metallica* is also absent from the Rennell group. Exclusion of *A. feadensis* from the analysis makes the C-score nonsignificant ($p > 0.90$). Consequently, determining why *A. feadensis* exists only on small, depauperate, or remote islands throughout its range is essential to understanding why this genus exhibits an exclusive distribution in the Solomons.

Two patterns emerge from examination of genera with exclusive distributional patterns. First, to understand why some genera exhibit exclusive co-occurrence patterns, one must understand why particular species are supertramps. Supertramps, for example, might occur predominantly on small, depauperate islands because they are competitively excluded from islands by superior competitors as Diamond (1975, Mayr and Diamond 2001) claims. However, it is also possible that supertramps exist on species-poor islands because supertramps are adapted to particular features of these islands (e.g., specific habitats, frequent disturbance, lack of predators). For example, *Monarcha cinerascens* and *Aplonis feadensis*, inhabit only small, remote, or volcanically disturbed islands throughout their range, independently of the suite of potential competitors. Predation by *Accipiter* hawks might confine another supertramp, *Ducula pacifica*, to small islands in at least part of its geographic range (Holyoak and Thibault 1978).

Future work focused on supertramps might provide insight into the causes of exclusive co-occurrence patterns within genera. For example, if the distributions of supertramps are limited by interspecific competition (i.e., if supertramps are inferior competitors), competition theory predicts that supertramps should exhibit either superior dispersal abilities or wider niche breadths (i.e., ecological tradeoffs). Superior dispersal or wider niche tolerances would permit an inferior competitor to survive on islands that are inaccessible or inhospitable to better competitors, which would competitively exclude them from the islands on which they occur. We examine measures of dispersal ability and habitat use provided by Mayr and Diamond (2001), and find no evidence that supertramps are better dispersers or use more habitat types than congeners (Table 2.13). These data are crude measures of dispersal ability and habitat use (or niche breadth) and provide only a weak test of the pattern expected if competition drives the distributions of supertramps. In addition, subtle habitat differences between large and small islands could reverse a competitive advantage. Determining the mechanisms responsible for the distributions of these supertramps will likely require experimental manipulations and detailed understanding of the natural history and biology of these species.

A second recurring pattern among these genera that have unusual co-occurrence patterns is that most species do not occur across the entire archipelago. In fact, many species are common in some island groups and completely absent from other groups. Barriers to dispersal exist within archipelagoes and act to segregate species across island groups. Consequently, although exclusive patterns exist, these patterns differ substantially from Diamond's (1975) concept of assembly rules in which two or more species are dispersed throughout a set of islands in an exclusive pattern resulting from competitive exclusion. Simberloff et al. (unpublished manuscript) have examined checkerboard distributions within four guilds defined by Diamond (1975) and found qualitatively similar results to our results for C-scores within genera.

Our work has reframed the question of how competition structures communities. Instead of asking, "Does competition govern the distribution of birds across these islands", we can now ask, "Does interspecific competition limit the distributions of particular species (e.g., supertramps)?" Alternatively, we can ask "Why doesn't interspecific competition produce exclusive distributions within most genera?" We suggest that even when interspecific competition is strong, only under a narrow range of conditions is this process likely to generate exclusive

distributional patterns at the island scale. For an exclusive pattern to arise from competitive interactions, interspecific competition must be sufficiently strong to allow for competitive exclusion. But, when species compete for limited resources, ecological and evolutionary processes can operate to reduce interspecific competition. These ecological and evolutionary processes can result in differences among species in morphology (i.e., character displacement) or in niche use (e.g., microhabitat, diet, foraging technique, or elevational range or habitat use). The development of such differences reduces the intensity of interspecific competition, facilitates coexistence, and reduces the likelihood of competitive exclusion. Thus, congeneric pairs are likely to exhibit exclusive distributions due to competition under narrow conditions: competition must be sufficiently strong to cause competitive exclusion but this competitive pressure must be recent enough that morphological or niche differences that permit coexistence have not evolved. Interspecific competition can also result in changes in population density, but analyses of population densities, instead of only presence-absence, has not been explored. Investigations of population densities have been restrained by a paucity of data and developed statistical methods.

That most genera do not exhibit an exclusive distribution supports our contention that the range of conditions under which competition is likely to produce exclusive distributions at the island scale is narrow. While interspecific competition might influence many aspects of community structure (e.g., morphology, habitat partitioning, elevational range, population density, behavior) and might influence the distribution of some species, most genera do not show a significant pattern. For genera that exhibit an exclusive distribution, alternate hypotheses, notably differences in habitat preference and dispersal barriers within the archipelago, exist and are supported by available data. We conclude that, in general, the distributions of species across islands are not governed by competitive interactions.

Conclusions

Community-wide measures of co-occurrence such as the C-score are of limited utility in community ecology and biogeography. Because the C-score incorporates all possible pairs of species, the vast majority of this statistic is derived from species belonging to different genera or different families. In addition, the C-score cannot distinguish between exclusive and congruent distribution patterns when row and column sums are maintained in Monte Carlo randomizations. Restricting measures of co-occurrence to pairs of species within taxa or within guilds can circumvent these problems.

The avifaunas of three archipelagoes (Bismarck Archipelago, Solomon Islands, and Vanuatu) exhibit significant community-wide C-score and Togetherness metrics. When co-occurrence measures are restricted to pairs of species within families or within genera, birds of the Bismarck and Solomon archipelagoes continue to exhibit significantly higher C-scores consistent with Diamond's (1975) assembly rules. In contrast, the avifauna of Vanuatu shows higher Togetherness scores within taxa, but these differences are usually not significant.

Although co-occurrence patterns within genera in the Bismarck and Solomon archipelagoes are consistent with a competition hypothesis, when genera are examined separately, most do not exhibit patterns that differ from random expectations. For many genera that exhibit an exclusive distribution, differences in habitat preference and barriers to dispersal within the archipelago are two alternate hypotheses that are supported by available data. Because selective pressure can produce morphological or niche differences that facilitate coexistence, competition is likely to generate exclusive co-occurrence patterns at the island scale for only a narrow range of conditions. Because of their observational nature, co-occurrence matrices are unlikely to provide a mechanistic understanding of the factors that structure communities. Their greatest

contribution to ecology, biogeography, and conservation is to help direct future observations and experiments.

CHAPTER 3

PATTERNS AND CAUSES OF NESTEDNESS

Abstract. Although studies of nestedness can be viewed as a subset of the study of co-occurrence patterns, the two subdisciplines have progressed with surprisingly little interchange. While co-occurrence studies examine the importance of interspecific interactions, especially competition, in governing community composition, nestedness focuses on autecological factors such as differences among species in extinction risk, dispersal ability, habitat or area requirements, or sensitivity to environmental factors. Although nested patterns are often viewed as the converse of competitive exclusion, meta-analyses of presence-absence matrices simultaneously support Diamond's assembly rules, which are consistent with a hypothesis that competitive interactions govern community composition, and indicate that most ecological systems are nested.

These apparently contradictory outcomes arise because most co-occurrence and nestedness analyses employ different randomization algorithms. In analyses of co-occurrence, randomization algorithms retain differences in incidence among species and preserve differences in species richness across islands. In contrast, most studies of nestedness do not maintain differences in species richness across islands; some also do not preserve species sums. When marginal sums are maintained, measures of exclusive distributions (e.g., C-score) and of aggregated distributions (e.g., Togetherness) are directly positively related, indicating that exclusive distributions are not incompatible with nestedness.

We examine a series of matrix randomization models for the avifaunas of three archipelagoes: Bismarck Archipelago, Solomon Islands, and Vanuatu. We find that the Bismarck and Solomon archipelagoes are significantly nested for all algorithms and that Vanuatu is nested for all algorithms except when both marginal sums are maintained. Different algorithms produce different levels of statistical significance.

We examine causes of nestedness, but because island area and island isolation are correlated within archipelagoes, we are unable to separate among possible mechanisms. We examine the distributions of individual species and identify five species that exhibit a significantly anti-nested distribution. Species nestedness is associated with variation in life history variables (e.g., level of endemism, population density, dispersal ability) within archipelagoes, but these relationships are not consistent across archipelagoes.

Patterns of nestedness can result from a number of mechanisms, and different mechanisms suggest different strategies for conservation. We contend that without understanding the mechanisms responsible for nested patterns, studies of nestedness are unlikely to be a useful tool for conservation biology.

Key words: area, Bismarck Archipelago, conservation, co-occurrence, dispersal, extinction, island, isolation, nestedness, Solomon Islands, Vanuatu

INTRODUCTION

Three primary characteristics of communities are species richness, relative abundance of species, and species composition (Worthen et al. 1998). A central theme in community ecology is that the species composition of a community is governed by deterministic rules. In nested biotas, the species comprising a depauperate fauna constitute a proper subset of those in richer faunas. Nestedness implies that individual species have a tendency to occur in all assemblages larger than the smallest in which they occur (Cook and Quinn 1998).

Studies of nestedness can be viewed as a subset of the study of co-occurrence patterns (Brualdi and Sanderson 1999). Co-occurrence matrices are depicted as a two-dimensional, $r \times c$, presence-absence matrix. In such a matrix, each row, r_i , represents a species, and each column, c_j , a site. Each cell in the matrix (a_{ij}) contains a one or a zero, indicating the presence or absence, respectively, of species i at site j . The row sum, R_i , represents the number of occurrences of each species, and the column sum, C_j , represents the number of species at each site. A nested matrix is constructed by ordering species (rows) from most to least ubiquitous and by sorting sites (columns) from richest to poorest. Creating a nested matrix changes only the appearance of the matrix, but it does not change which species occur at which sites. In a nested matrix (Table 3.1), most presences are located in the upper left and most absences in the lower right.

Since the recognition that most ecological communities are nested (Simberloff and Martin 1991, Wright and Reeves 1992, Cook and Quinn 1995, Wright et al. 1998), many studies of nestedness have focused on either investigating the causes of nestedness (Cutler 1994, Lomolino 1996, Worthen 1996, Loo et al. 2002) or exploring whether nested patterns can be a useful tool in conservation biology (Doak and Mills 1994, Boecklen 1997, Kerr et al. 2000, Patterson and Atmar 2000, Fleishman and Mac Nally 2002, Maron et al. 2004, Fischer and Lindenmayer 2005, Martínez-Morales 2005).

Nested patterns can result from myriad mechanisms, including selective extinction (Patterson and Atmar 1986, Patterson 1987, Brown 1995), differential colonization (Darlington 1957, Simberloff and Martin 1991, Lomolino 1996), nested habitats (Calmé and Desrochers 1999, Honnay et al. 1999), hierarchical niche relationships (Worthen et al. 1998), and passive sampling (Andrén 1994, Cutler 1994). The selective extinction hypothesis maintains that in archipelagoes experiencing relaxation (cf. Patterson and Atmar 1986), species disappear in a deterministic order. Species with large minimum viable population sizes, large area requirements, Allee effects, or sensitivity to environmental or demographic stochasticity are expected to have higher extinction rates (Connor and McCoy 1979, Simberloff and Levin 1985). Differences in extinction risk across species can create a predictable sequence of population extinctions that results in a nested system (Patterson and Atmar 1986, Blake 1991, Bolger et al. 1991, Cutler 1991, Newmark 1991, Patterson and Brown 1991, Soulé et al. 1992, Atmar and Patterson 1993, Yiming et al. 1998)

The differential colonization hypothesis maintains that differences in dispersal ability among species produce nested patterns (Darlington 1957, Patterson 1990, Patterson and Brown 1991, Cook and Quinn 1995, Kadmon 1995, Conroy et al. 1999). Differential colonization can produce nested patterns in two ways. First, colonization ability can interact with among-island

variation in isolation such that only species with strong dispersal ability are able to colonize distant sites. Species with poorer dispersal abilities are restricted to sites that are more easily colonized, and these sites contain most species. Second, differences in dispersal ability can create nestedness even if all species can colonize all sites. If better dispersers are able to recolonize sites more quickly than poorer dispersing species following local extinctions and local extinction rates are similar to colonization rates, sites with low extinction rates will harbor many species, but sites with higher extinction rates will often lack species with poorer dispersal abilities. Patterson and colleagues (Patterson and Atmar 1986, Patterson 1990) argued that communities governed by colonization are likely to be less nested than extinction-driven systems because colonization is more strongly influenced by unpredictable events than is extinction. But, despite these arguments, strongly nested patterns may result from colonization patterns in which species are added to assemblages in a relatively deterministic order based on dispersal ability (Darlington 1957, Patterson and Atmar 1986, Cook and Quinn 1995).

The nested habitat hypothesis argues that a taxon's nested pattern is a consequence of its close association with particular habitats, which themselves are nested (Cutler 1991, 1994; Cook and Quinn 1995). For example, if islands vary in maximum elevation, and habitats are associated closely with elevation, habitats might be distributed approximately as concentric bands. Islands with high peaks will contain many bands of habitat and will contain the species associated with each of those habitats. In contrast, lower islands will contain only low elevation habitats and will not contain species that occur only in high elevation habitats. Honnay et al. (1999) found that certain nested plant assemblages arise from nested habitats.

The hypothesis of hierarchical niche relationships posits that species vary in their sensitivity to environmental conditions. Examples include resistance to environmental stress (e.g., temperature fluctuations, water stress, fire frequency), physiological tolerance (e.g., to pollutants, salt, carbon dioxide, nitrogen oxides), aversion to edge habitat (e.g., forest interior nesting birds), and niche breadth (e.g., size range of seeds consumed). Variation among sites in environmental factors will selectively eliminate species based on their sensitivity to that factor. For example, one would predict that sites with low salinity will contain many plant species, but sites with higher levels will contain only those species most tolerant of high salt concentrations. Worthen et al. (1998) showed that species of mycophagous flies were differentially susceptible to desiccation stress and that nestedness increased with desiccation stress, which was mediated by mushroom size.

Passive sampling, which describes the phenomenon in which rare species are less likely to occur in a given area than common species (Connor and McCoy 1979), can also produce nested patterns. Cutler (1994) found that significant nestedness can result from the random placement of species with skewed relative abundance distributions, and Andr n (1994) found that random samples of species with different densities can produce nested patterns and that tests of nestedness are sensitive to the occurrence of rare species. Because most communities consist of a few common species and many rare species (Preston 1948, Hubbell 2001), some nested patterns might represent a mere sampling phenomenon that is a direct consequence of the relative abundance distribution.

Lomolino (1996) set out to test the selective extinction and differential colonization hypotheses for nested patterns. Citing the equilibrium theory of island biogeography (MacArthur and Wilson 1967), he assumed that extinction rates are a function of area and that immigration rates are a function of distance. This approach assumes that island area and isolation are not correlated, that extinction is not correlated with island isolation, and that colonization is not correlated with island area. Instead of sorting sites in the co-occurrence matrix by species

richness, Lomolino's (1996) method sorts sites by another variable, such as island area or island isolation. If nestedness results from selective extinctions, one should obtain high measures of nestedness when islands are ranked and sorted by area. In contrast, if nestedness is caused by differential immigration, one expects to obtain high nestedness scores when islands are ranked by isolation. If nested habitats underlie the pattern, one would expect to maintain the same degree of nestedness when islands are sorted by number of habitats as when islands are sorted by species richness (Calmé and Desrochers 1999). Lomolino's method cannot be used to evaluate directly the importance of passive sampling in generating nested patterns, but his method has been used extensively to examine other hypotheses for causes of nestedness.

Many studies have employed Lomolino's (1996) method to test hypotheses for nestedness. Collectively, these studies demonstrate that the likely cause of nestedness varies across systems and includes selective extinctions (Bruun and Moen 2003, Azeria 2004), differential colonization abilities (Kadmon 1995, Conroy et al. 1999, Loo et al. 2002), and nested habitats (Worthen et al. 1998, Honnay et al. 1999, Calmé and Desrochers 1999, Fleishman and Mac Nally 2002, Azeria 2004). Because Lomolino's (1996) method relies on correlations and is not experimental, caution in interpretation is warranted. In some archipelagoes, island area and isolation might be correlated with each other or with other potentially important variables. In addition, extinction events might be influenced by both area and isolation (rescue effect) and colonization probabilities might be affected by both area and isolation.

Although significant nestedness scores are often attributed to extinction events, most purported extinction events are undocumented. Because other mechanisms can also create nested patterns, significant nestedness scores need not imply that faunal relaxation has occurred. Processes influencing distribution patterns can differ among taxa and the relative importance of these factors may vary spatially within the group (Fleishman et al. 2002). Hansson (1998) found that degree of nestedness varies among taxa and that variables correlated with nestedness vary across taxa. In addition, factors that can generate patterns of nestedness (e.g., extinction and immigration) can act antagonistically to reduce nestedness (Wright et al. 1998). For example, although differential colonization can create nested patterns, colonization might decrease nestedness in extinction-driven systems by saving small or locally extirpated populations through the rescue effect (Brown and Kodric-Brown 1977).

Nestedness analyses can also examine whether particular environmental variables or certain life history traits are likely to affect local species composition (Cook and Quinn 1995, Kadmon 1995, Hecnar and M'Closkey 1997, Fleishman and Murphy 1999, Jonsson and Jonsell 1999, Mac Nally et al. 2002, Fleishman et al. 2002).

In this paper, we test for nestedness in three Melanesian archipelagoes. For each, we calculate nestedness scores and use Lomolino's (1996) method to examine how nestedness varies when islands are sorted by area or by isolation. We also use a series of null models to examine how patterns of nestedness are influenced by passive sampling, by variation among islands in species richness, and by differences among species in commonness (i.e., the number of islands a species inhabits). For each archipelago, we examine the extent to which each species exhibits a nested pattern, and we investigate whether life history or ecological traits relate to degree of nestedness. We identify idiosyncratic species (species with distributions that do not conform to a nested pattern). We also examine whether idiosyncratic islands (i.e., islands that contain a disproportionate number of idiosyncratic species) are correlated with island traits such as size, elevation, and isolation.

METHODS

Study sites

Melanesia consists of three archipelagoes: the Bismarck Archipelago, the Solomon Archipelago, and Vanuatu (formerly New Hebrides). The first two archipelagoes compose Northern Melanesia. For the purposes of this investigation, the Bismarcks consist of 31 islands, the Solomons of 45, and Vanuatu of 28 islands. Figs. 3.1, 3.2, and 3.3 are maps of the Bismarck, Solomon, and Vanuatu archipelagoes, respectively. Melanesia is well explored ornithologically (Mayr and Diamond 2001), and there have been nearly 200 expeditions to observe or collect birds in Melanesia (Dutson 2001). The Bismarcks, Solomons, and Vanuatu contain 154, 142, and 56 species of birds, respectively. We excluded migratory, transient, and nonbreeding species and species occurrences with questionable records. The avifaunas of these three archipelagoes are not independent: as one moves southeast from New Guinea (i.e., from the Bismarcks to the Solomons to Vanuatu), one finds that the avifauna of each archipelago is partially a subset of the previous archipelago (Mayr and Diamond 2001). As a result, the three archipelagoes combined have a total of about 200 species.

Data sets

We constructed presence-absence matrices for the Bismarck and Solomon archipelagoes from data obtained in Mayr and Diamond (2001) and for Vanuatu from data obtained in Diamond and Marshall (1976). Presence-absence matrices for the Bismarcks, Solomons, and Vanuatu are presented in Appendices C, D, and E, respectively. In such a matrix, also termed a co-occurrence or incidence matrix, each row, r_i , represents a species, and each column, c_j , a site. Most studies of nestedness transpose rows and columns, but we will employ the structure above, which is used in studies of co-occurrence patterns. Each cell in the matrix (a_{ij}) contains a one or a zero, indicating the presence or absence, respectively, of species i at site j . The row sum, R_i , represents the number of occurrences of each species, and the column sum, C_j , represents the number of species at each site (i.e., island richness). To create a nested matrix, we sorted each presence-absence matrix by ranking species (rows) from most ubiquitous to least and by ranking islands (columns) from richest to poorest.

Measures of nestedness

For each observed nested matrix, we calculated several measures of nestedness including N_0 , N_I , N_C , Ua , Up , and Ut . Table 3.2 summarizes these metrics. Except for N_C , all decrease with increasing nestedness. We did not calculate matrix temperature, T , because the Temperature Calculator (Atmar and Patterson 1995, Patterson and Atmar 2000) does not contain options to specify particular null models (see below). We concentrate our analyses on Ut , the minimum number of changes needed to transform an existing matrix into a perfectly nested one. A change can represent either the filling of an unexpected absence, Ua , (i.e., colonizing an unoccupied island, termed a hole) or the removal of an unexpected presence, Up , (i.e., extinction of an outlier population from an island). We focused on Ut because this measure of nestedness counts both unexpected absences and presences, allows for different randomization models, and is not uniquely determined by row and column sums.

Matrix randomization algorithms

We developed a series of six matrix randomization algorithms to examine how different assumptions affect the statistical significance of observed nestedness scores (Table 3.3). These

algorithms differ in how they constrain species (row) and site (column) totals. We constrain marginal totals in three ways. Fixed sampling constrains randomized matrices to maintain the observed totals. With fixed sampling, each species occurs on the same number of islands as observed, and each island contains the same number of species as observed. Proportional sampling draws species in proportion to the number of islands on which they occur and draws islands in proportion to its observed species richness. Equiprobable sampling selects species or sites equiprobably (i.e., all species or sites are sampled completely randomly). These sampling constraints can be combined in various combinations (e.g., fixed species and equiprobable islands) to create different algorithms. We name each algorithm by the constraints it places on species and site totals. For example, the “Fixed/Proportional” algorithm places each species on the number of islands on which it was observed to occur (Fixed) and draws islands in proportion to their observed species richnesses (Proportional).

The Equiprobable/Equiprobable algorithm (Atmar and Patterson 1993) incorporates neither differences among species in commonness nor differences among sites in species richness and generates randomized matrices without either row or column constraints. The only constraint is that the total number of presences must equal the observed value. Species (rows) and sites (columns) are sampled randomly. The resulting cell is filled and the process repeated until the proper number of presences is obtained. Degenerate matrices, those that have empty rows (species that are absent from all islands) or empty columns (islands with no species) are retained. Equiprobable/Equiprobable is identical to Atmar and Patterson’s (1993) RANDOM00 algorithm and to the NESTCALC algorithm, which the Temperature Calculator (Atmar and Patterson 1995, Patterson and Atmar 2000) employs to assess statistical significance of nested scores. When the relative abundance distribution is uneven, Equiprobable/Equiprobable overestimates nestedness and its statistical significance and is prone to Type I errors (Cook and Quinn 1998, Fischer and Lindenmayer 2002).

For each island in an archipelago, the Equiprobable/Fixed algorithm adds randomly selected species until that island’s species richness equals its observed richness (Patterson and Atmar 1986, Wright and Reeves 1992). Equiprobable/Fixed includes differences in species richness among islands, but does not introduce incidence differences across species and is identical to Patterson and Atmar’s (1986) RANDOM0 algorithm. Cook and Quinn (1998) have suggested that Equiprobable/Fixed is the best null model to examine nestedness.

Called RANDOM1 by Patterson and Atmar (1986), Proportional/Fixed samples species in proportion to observed incidence values and fixes island sums (Patterson and Atmar 1986). In so doing, Proportional/Fixed oversamples rare species and undersamples ubiquitous species. This bias overestimates the number of holes in random matrices and inflates statistical significance (Simberloff and Martin 1991, Andrén 1994). Andrén (1994) showed that the difference between Equiprobable/Fixed and Proportional/Fixed may have a profound effect on statistical tests.

Jonsson (2001) proposed that the basic biological question for nested analyses is: Is the distribution of species across sites random, given that some species are common and some rare? Andrén (1994) and Cutler (1994) found that when some species are ubiquitous and some are rare, random placement of species can produce significant nestedness. Jonsson (2001) argues that for tests of nestedness, all sites should be regarded as equal: the extent to which island area, isolation, or habitat quality influences species distributions is a secondary question, if nestedness exists. To examine how observed relative abundance distributions affect nested patterns, we developed an algorithm, Fixed/Equiprobable. For each species, Fixed/Equiprobable fills randomly selected sites until that species’ incidence equals its observed incidence. Because sites are sampled randomly,

Fixed/Equiprobable does not include differences among islands in species richness. Fixed/Equiprobable is identical to Gotelli's (2000) SIM2 model.

The Fixed/Proportional algorithm (Gotelli's [2000] SIM4) maintains species incidence and randomly samples islands in proportion to their observed species richnesses. Because this algorithm samples islands proportionately to observed incidence values, Fixed/Proportional suffers from the same type of problem as Proportional/Fixed. Fixed/Proportional oversamples depauperate islands and undersamples rich islands, which inflates statistical significance.

We used Miklós and Podani's (2004) trial-swap algorithm to generate randomized matrices with fixed row and columns sums (Fixed/Fixed). Instead of interchanging a predetermined number of submatrices, Miklós and Podani's (2004) trial-swap method modifies the original swap algorithm (Connor and Simberloff's 1979) to specify a number of swap attempts. This simple change generates a uniform random sample of matrices: while the probability of obtaining a particular matrix is proportional to that matrix's number of neighbors, the probability of retaining the matrix (by selecting a submatrix that cannot be swapped) is inversely proportional to its number of neighbors. Thus, the probability of obtaining a matrix after a large number of swap attempts is independent of its number of neighbors, and all matrices are sampled equiprobably.

We specified 500,000 attempted swaps between sampled matrices. In each attempt, two rows and two columns are randomly selected (rows and columns need not be adjacent). If the 2 x 2 submatrix is of the form (a) $\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$ or (b) $\begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}$, swap the rows (or the columns); this swap is equivalent to switching between these two submatrices. A sufficiently large number of swaps produces a randomized matrix while maintaining species incidence and island richness. This algorithm can reach every matrix in the universe of possible matrices with those row and column sums. If a system is perfectly nested, only one arrangement that maintains both row and column sums exists, but, if gaps exist, there are generally many matrices that satisfy row and column constraints (Wang 1988). Wright et al. (1998) found only two of 163 data sets exhibited perfect nestedness (i.e., had no gaps); both data sets contained only three sites. These matrix randomization algorithms are summarized in Table 3.3. All computer code was written in C. We used the version of the rand function recommended in Press et al. (1992) to generate random integers.

Statistics

To test matrices for significant nestedness, we used Monte Carlo simulations to generate 1,000 matrices for each randomization algorithm. We calculated measures of nestedness for randomized matrices and calculated *p*-values by dividing the number of randomized matrices that had a measure equal to or more extreme than the observed matrix by the total number of randomized matrices (1,000). We did not employ a Bonferroni correction for multiple tests because of its inherent conservatism and reduction of statistical power (Nakagawa 2004). To reduce Type I error, we set $\alpha = 0.01$.

Effect of area and isolation

For the Bismarck and Solomon archipelagoes, we obtained island areas from Mayr and Diamond (2001). If an island's area was not provided, we measured its area from the East Asia Geographic Map Series, Sheet 7 (U.S. Geological Survey, 2000). Areas for islands of Vanuatu were obtained from Diamond and Marshall (1977). We measured island isolation as the distance

to the richest island in the archipelago. Island characteristics for the Bismarcks, Solomons, and Vanuatu are listed in Appendices F, G, and H, respectively.

Following the procedure of Lomolino (1996), we sorted each presence-absence matrix to obtain two matrices: the first sorted sites by increasing island isolation and the second ranked sorted sites by decreasing area. We then calculated deviation from complete nestedness by recording the number of departures, D (i.e., the number times the absence of a species is followed by its presence on the next more isolated (or smaller) island). We generated 1000 matrices in which islands were ordered randomly. We compared the observed number of departures from nestedness to the distribution produced from randomized matrices. We calculated p -values as above using one-sided tests with $\alpha = 0.05$.

For each departure from perfect nestedness, we assessed whether changes in the island variable not used to sort columns (island area or isolation) could explain the deviation. For example, an unexpected absence can be explained by decreasing area or increasing isolation and an unexpected presence by increasing area or decreasing isolation. We used a binomial test to determine whether the other island variable explained more than half of the observed departures.

Species

To quantify nestedness for each species, we calculated a Mann–Whitney U -test on each species in each archipelago with islands sorted by species richness. Following the advice of Simberloff and Martin (1991), we searched for species that do not conform to nestedness and set $\alpha = 0.05$. We also examined whether species' nestedness scores are predictable from life history variables such as dispersal ability, level of endemism, population density, and habitat. We obtained information on species' traits from Mayr and Diamond (2001). When different habitats were listed for different subtaxa (e.g., species within superspecies), we used the habitat associated with the largest number of islands. If one habitat was not associated with more islands than all other habitats, we used the first habitat listed. If more than one habitat type was listed for a species, we used the first habitat listed. Because of small sample sizes, we lumped some levels of endemism: species listed as "0,1" were classified as "0" and species listed as "1,2" were grouped as "2". Species characteristics for the Bismarcks, Solomons, and Vanuatu are listed in Appendices I, J, and K, respectively.

Islands

We calculated a Mann–Whitney score for each island after sorting species from most ubiquitous to most rare. Using the same procedure as we did to examine species, we looked for idiosyncratic islands (i.e., islands that harbored an unusually high number of rare species). We examined whether the tendency of islands to harbor rare species is predictable from island area and isolation.

Species grouped by dispersal ability

We examined whether community nestedness varies with dispersal ability. For each archipelago, we separated species into groups based on dispersal ability (four levels). For each group, we constructed a presence-absence matrix, measured community nestedness, and calculated its standard effect size. Because of small sample sizes in Vanuatu, the two best dispersing groups were combined into a single group and the two poorest dispersing groups were combined into another group.

RESULTS

Nestedness

The Bismarck Archipelago requires 440 transformations ($U_t = 440$) to produce a perfectly nested matrix and is significantly nested for all randomization algorithms ($p < 0.001$; Table 3.4). The Bismarck Archipelago is relatively outlier-rich with 281 unexpected presences compared to 159 unexpected absences. The Solomon Archipelago needs 503 transformations to create a perfectly nested matrix and is significantly nested for all randomization algorithms ($p < 0.001$; Table 3.5). The Solomons are outlier-rich with 336.5 unexpected presences and 166.5 unexpected absences. With 108 unexpected presences and 82 unexpected absences, Vanuatu is slightly outlier-rich. Except for the Fixed/Fixed model, Vanuatu's 190 required transformations for perfect nestedness show significant nestedness for all randomization algorithms ($p < 0.001$; Table 3.6).

In general, other measures of nestedness produce qualitatively similar results to U_t , but some exceptions exist. In the Bismarck Archipelago, the number of unexpected absences, U_a , is not statistically significant for the Equiprobable/Equiprobable, Equiprobable/Fixed and Fixed/Fixed algorithms ($p > 0.15$; Table 3.4). In the Solomon Archipelago, number of absences, N_o , and unexpected presences, U_p , are not statistically significant for the Fixed/Fixed algorithm ($p \geq 0.095$; Table 3.5).

In all three archipelagoes, assuming a normal distribution and calculating effect sizes and p -values produces a higher degree of statistical significance than conventional Monte Carlo techniques (Tables 3.4–3.6). In all three archipelagoes, the distributions of statistics produced by the Equiprobable/Equiprobable algorithm are left-skewed and leptokurtotic (Table 3.7).

Effect of area and isolation

The Bismarck Archipelago remains significantly nested when sites are ordered by either island area or island isolation ($p < 0.001$; Table 3.8). When sorted by island area, 436 unexpected deviations exist and the matrix has 35.5% perfect nestedness. Of these deviations, 269 are explained by decreasing island isolation, and this number is significantly more than half (partial nestedness = 0.62; $p < 0.0001$; Table 3.8). When sorted by island isolation, percent perfect nestedness is 29.4 and 474 deviations exist. Of these 474 deviations, 333 are explained by increasing island area.

The Solomon Archipelago is significantly nested and has 549 deviations when islands are ranked by area ($p < 0.001$; Table 3.8). Of these 549 deviations, 268 are explained by increasing isolation, which is not statistically different from random (partial nestedness = 0.49; $p > 0.70$; Table 3.8). Percent perfect nestedness for island area is 38.4%. When islands are ranked by isolation, the Solomon Archipelago has 807 deviations, 9.4% perfect nestedness, and is not significantly nested ($p = 0.07$; Table 3.8). A significant number of these deviations (711) are explained by increasing island area ($p < 0.0001$; Table 3.8)

When sorted by island area, Vanuatu is significantly nested ($p < 0.001$; Table 3.8) and shows 176 discrepancies. Fewer than half of these discrepancies are explained by decreasing island isolation (partial nestedness = 0.41; $p > 0.99$; Table 3.8). Percent perfect nestedness is 24.0. When sites are ranked by island isolation, Vanuatu is significantly nested (26.2% of perfect nestedness, and contains 171 discrepancies ($p < 0.001$; Table 3.8). Of these 171 discrepancies, 124 are explained by increasing island area ($p < 0.0001$; Table 3.8).

Species

In the Bismarck Archipelago, five species (*Ptilinopus solomonensis*, *Ducula pacifica*, *Monarcha cinerascens*, *Myzomela lafargei*, and *Aplonis feadensis*) exhibit a statistically significant anti-nested distribution ($z > 2.0$; $p < 0.05$; Appendix I). Three of these species, *D. pacifica*, *M. cinerascens*, and *A. feadensis*, also exhibit a significantly anti-nested distribution in the Solomon Archipelago ($z > 3.0$; $p < 0.01$; Appendix J). No other species in the Solomons or in Vanuatu is significantly anti-nested ($z < 1.25$; $p > 0.10$; Appendices J–K).

Species traits

A nonparametric analysis of variance reveals that median species nestedness varies by level of endemism and population density in the Bismarck Archipelago ($F_{10,134} = 4.70$; $p < 0.0001$; Table 3.9). Post hoc tests indicate that species with the highest degree of endemism (endemism level 3) are significantly more nested than species of intermediate endemism (endemism levels 1 and 2) ($p < 0.01$; Fig. 3.4) and that species of intermediate density (abundance level 2, 0.1–1 pairs/km²) are significantly more nested than species with higher densities (abundance levels 3 and 4, 1–10 and 10–100 pairs/km²) ($p < 0.01$; Fig. 3.5).

In the Solomon Archipelago, median species nestedness varies across species with different dispersal habits ($F_{11,120} = 8.91$; $p < 0.0001$; Table 3.10). Post hoc tests reveal that better dispersing species (dispersal levels 1 and 2) are more nested than more poorly dispersing species (dispersal levels 3 and 4) ($p < 0.01$; Fig. 3.6).

In Vanuatu, median species nestedness varies with species density ($F_{9,26} = 2.83$; $p = 0.0185$; Table 3.11). Post hoc tests show that species with the highest density (abundance level 5, ≥ 100 pairs/km²) are more nested than species with abundance levels 2 or 4 ($p < 0.01$; Fig. 3.7).

Species grouped by dispersal ability

In the Bismarck Archipelago, all dispersal groups are significantly nested ($p < 0.001$; Fig. 3.8), but there is no clear pattern relating nestedness to dispersal ability. In the Solomon Archipelago, nestedness is strongest in the group comprised of the best dispersing species (level 1) (Fig. 3.8). Nestedness decreases monotonically as dispersal ability decreases, and the two most weakly dispersing groups (levels 3 and 4) are not significantly nested (Fig. 3.8). In Vanuatu, the poorly dispersing group (level 2.5) is significantly nested ($p < 0.001$) but the better dispersing group (level 1.5) is not significantly nested (Fig. 3.8).

Island area and isolation and island nestedness

In the Bismarck Archipelago, island area and island isolation significantly predict island nestedness ($F_{2,25} = 33.8$; $p < 0.0001$; Table 3.12), explaining 71% of the variation in island nestedness. Island nestedness increases with island area and decreases with island isolation. In the Solomons, island nestedness increases with island area, explaining 51% of the variation in island nestedness, but does not decrease with island isolation ($F_{2,39} = 22.6$; $p < 0.0001$; Table 3.13). In Vanuatu, neither island area nor island isolation significantly predicts island nestedness ($F_{2,24} = 1.90$; $p = 0.17$; Table 3.14).

DISCUSSION

In a nested community, species comprising a depauperate fauna constitute a proper subset of those in richer faunas, and individual species have a tendency to occur in all assemblages

larger than the smallest in which they occur (Cook and Quinn 1998). As a result, species pairs in nested communities tend to exhibit a large number of co-occurrences (both species are present on islands with many species) and joint absences (both species are absent from depauperate islands). Avifaunas of the Bismarck and Solomon archipelagoes are significantly nested for all randomization algorithms (Tables 3.4–3.5), and birds of Vanuatu are significantly nested for all algorithms except for the Fixed/Fixed model, which fixes both species and island sums (Table 3.6).

Each of these three archipelagoes also has a statistically significant large C-score (Chapter 2). C-score counts the number of “checkerboard units” per species pair for community. A “checkerboard unit” consists of two species and two islands, with each species present on only one island and each island harboring only one species. Each “checkerboard unit” is a 2 x 2 submatrix from the nested matrix of the form (a) $\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$ or (b) $\begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}$. C-score is a measure of species co-occurrence, and a significantly high C-score is commonly interpreted as evidence that species co-occur less than expected by chance, perhaps due to interspecific competition.

Our results demonstrate that some communities (e.g., the avifaunas of the Bismarck and Solomon archipelagoes) exhibit both significant C-scores and significant nestedness, even when the same randomization algorithm (e.g., Fixed/Fixed) is employed in both analyses. That some communities exhibit both a significant C-score and significant nestedness initially seems implausible because C-score measures the tendency of species pairs to exist on different islands and nestedness measures the tendency of species pairs to coexist on the same islands. This apparent inconsistency is resolved when one understands the limitations of the C-score. Roberts and Stone (1990) demonstrated that the mean number of islands shared among all species pairs is constant when the Fixed/Fixed model is used. And Stone and Roberts (1992) proved that the measures for exclusive (C-score) and congruent distributions (Togetherness) differ by only a constant when the Fixed/Fixed model is used. Togetherness measures the tendency for species pairs to co-occur and counts the number of 2 x 2 submatrices with mutual co-occurrence and absence (i.e., 2 x 2 submatrices of the form (a) $\begin{bmatrix} 1 & 0 \\ 1 & 0 \end{bmatrix}$ or (b) $\begin{bmatrix} 0 & 1 \\ 0 & 1 \end{bmatrix}$). Communities with a large number of species pairs that co-occur less than expected also have a large number of species pairs that co-occur more than expected (Stone and Roberts 1992). Paradoxically, a community that has a significant community-wide C-score must also exhibit a significant community-wide Togetherness score. Togetherness measures the tendency for species pairs to co-occur, and nestedness predicts a high degree of co-occurrence. Consequently, a community with a significantly high C-score can also show significant nestedness.

Null models for nestedness

We concentrate our analyses on U_t because this metric is the only measure that counts both unexpected absences and presences and is not uniquely determined by row and column sums. With U_t , the Bismarck and Solomon archipelagoes are significantly nested regardless of the randomization algorithm and Vanuatu is significantly nested for all algorithms except Fixed/Fixed (Tables 3.4–3.6; Fig. 3.9F).

Across all randomization algorithms and all metrics, the Solomon Archipelago tends to exhibit the highest nestedness, followed by the Bismarck Archipelago and then Vanuatu, but some measures of nestedness rank archipelagoes differently (Fig. 3.10). For number of

unexpected absences, Ua , Vanuatu is more nested than the Bismarck Archipelago for four of six randomization algorithms and is more nested than the Solomon Archipelago for two algorithms (Fig. 3.9D). Also, the number of unexpected presences, Up , and N_0 generally show that the Solomon Archipelago is less nested than the Bismarck Archipelago for most randomization algorithms (Fig. 3.9A,B). Up and N_0 ordinate archipelagoes differently than other metrics because Up and N_0 count only matrix absences. In contrast, N_1 and Ua count only presences and N_C and Ut measure both absences and presences. Our results largely agree with those of Wright et al. (1998), who found similarities between N_0 and Up , between N_1 and Ua , and between N_C and Ut , but we do not find similarity between N_1 and Ua .

Although all randomization algorithms and most metrics rank archipelagoes similarly, degree of nestedness, measured as standard effect size, varies widely across algorithms (Fig. 3.9). For example, the Solomon Archipelago is significantly nested for all metrics for any algorithm except for Fixed/Fixed. With the Fixed/Fixed algorithm, the Solomons are not significantly nested using N_0 and Up . In contrast, Vanuatu is not significantly nested with any metric in the Fixed/Fixed model but is significantly nested for all metrics with every other algorithm. Our results support the contention that whether a null model is rejected depends as much on the model as it does on the data (Worthen 1996, Cook and Quinn 1998, Brualdi and Sanderson 1999).

The Temperature Calculator (Atmar and Patterson 1995, Patterson and Atmar 2000) uses the Equiprobable/Equiprobable (NESTCALC) algorithm to assess statistical significance of nested scores. Because this model incorporates neither differences among species in commonness nor differences among sites in species richness, the Temperature Calculator overestimates nestedness and statistical significance and is prone to Type I errors (Cook and Quinn 1998, Fischer and Lindenmayer 2002). Instead of using standard Monte Carlo techniques to measure statistical significance, the Temperature Calculator uses a normal distribution of nestedness measures and calculates an effect size and p -value. In all three archipelagoes, assuming a normal distribution and calculating effect sizes and p -values produces a higher degree of statistical significance than conventional Monte Carlo techniques (Tables 3.4–3.6) regardless of the null model employed. Compared to other randomization algorithms, Equiprobable/Equiprobable produces a higher degree of statistical significance (Tables 3.4–3.6). In addition, the distributions of statistics produced by the Equiprobable/Equiprobable algorithm are left-skewed and leptokurtotic in all three archipelagoes (Table 3.7). Left skewness and leptokurtosis are likely to inflate Type I errors further. Consequently, the Temperature Calculator is biased towards finding significant results. This bias comes from two sources: (1) use of a null model (Equiprobable/Equiprobable) that does not account for differences among species in commonness, and (2) an assumption of a normal distribution. We suggest the use standard Monte Carlo techniques to estimate statistical significance and the adoption of an algorithm that incorporates differences among species.

We agree with Jonsson (2001) that the basic biological question for nested analyses is: Is the distribution of species across sites random, given that some species are common and some rare? Jonsson (2001) argues that for tests of nestedness, all sites should be regarded as equal, and that the extent to which island area, isolation, or habitat quality influences species distributions is a secondary question. Our Fixed/Equiprobable algorithm maintains species' relative abundance distributions but samples sites randomly. Because sites are sampled randomly, Fixed/Equiprobable does not include differences among islands in species richness. If nestedness is observed, one can design a series of null models to assess the influence of differences among islands in species richness by comparing the observed nestedness score to a sample of matrices generated using a Fixed/Fixed algorithm. Because Fixed/Fixed maintains both row and column sums, one can assess whether observed patterns of nestedness are explained by differences among

islands in species richness. In Vanuatu, nestedness is not significant when species' incidences and island richnesses are maintained. The Bismarcks and Solomons remain significantly nested, indicating that additional forces are operating in these archipelagoes.

Causes of nestedness

Nested patterns can result from many mechanisms, including selective extinction (Patterson and Atmar 1986, Patterson 1987, Brown 1995), differential colonization (Darlington 1957, Simberloff and Martin 1991, Lomolino 1996), nested habitats (Calmé and Desrochers 1999, Honnay et al. 1999), hierarchical niche relationships (Worthen et al. 1998), and passive sampling (Andrén 1994, Cutler 1994). We use Lomolino's (1996) method to examine the roles of extinction and of immigration in producing nested patterns.

The Bismarck Archipelago remains significantly nested when sites are ordered by either island area or island isolation ($p < 0.001$; Table 3.8). When islands are sorted by either area or isolation, significantly more than half of the discrepancies are explained by the other variable ($p < 0.0001$; Table 3.8). These findings indicate that both island area and island isolation influence nested patterns in the Bismarck Islands. The Solomon Archipelago is significantly nested when islands are ranked by area ($p < 0.001$; Table 3.8) but not when islands are sorted by isolation ($p = 0.07$; Table 3.8). Vanuatu is significantly nested when sites are ordered by either island area or island isolation ($p < 0.001$; Table 3.8). When sites are ranked by island isolation, a significant fraction of the deviations are explained by island area ($p < 0.0001$; Table 3.8), but island isolation does not explain a significant fraction of the deviations when islands are first ranked by island area.

While these results might suggest that both deterministic extinctions and different colonization rates are important in at least some archipelagoes, one must be careful not to overinterpret these results and assign causal relationships for nested patterns. Lomolino's (1996) method assumes that (1) extinction rates are a function of area, (2) immigration rates are a function of distance, (3) island area and isolation are not correlated, (4) extinction is not correlated with island isolation, and (5) colonization is not correlated with island area. Although it is likely that extinction rates are a function of area and immigration rates are a function of distance, other assumptions might not hold. For example, island area and isolation are significantly negatively correlated in Vanuatu ($r = -0.44$; $p = 0.02$) and are marginally negatively correlated in the Bismarcks ($r = -0.32$; $p = 0.08$) and in the Solomons ($r = -0.29$; $p = 0.06$). In addition, it is plausible that extinction is correlated with island isolation (e.g., because of the rescue effect (Brown and Kodric-Brown 1977)) and that colonization is correlated with island area. Thus, despite finding significant nestedness in these archipelagoes when islands are sorted by area or by isolation, we cannot conclude to what extent selective extinctions, differential colonization, nested habitats, hierarchical niche relationships, and passive sampling are responsible for observed patterns of nestedness. Understanding the processes responsible for patterns of nestedness will require detailed natural history studies of the existing community and, perhaps, of past communities (e.g., documented extinction events).

Life history traits and nestedness

For each archipelago, we examine whether species nestedness varies with dispersal ability, degree of endemism, or population density. In the Bismarcks, species nestedness varies among species with different levels of endemism and population density ($F_{10,134} = 4.70$; $p < 0.0001$; Table 3.9). Endemic species exhibit significantly higher nestedness than species that are endemic at only the allospecies or subspecies level (Fig. 3.4). Additionally, species of

intermediate population density (0.1–1 pair/km²) are more nested than species with densities of 1–100 pairs/km² (Fig. 3.5). In the Solomon Archipelago, median species nestedness varies with dispersal ability, with better dispersing species exhibiting higher nestedness than poorly dispersing species (Fig. 3.6). In Vanuatu, species with population densities greater than 100 pairs/km² have higher nestedness than species with population densities of 0.1–1 or 10–100 pairs/km² (Fig. 3.7). Habitat preference is not significant for any archipelago. Including habitat does not affect significance of other variables nor does removing other life history variables affect the significance of habitat preference. Despite obtaining significant results within each archipelago, no clear relationship exists across archipelagoes. Hansson (1998) found that variables correlated with nestedness vary across taxa. Our results demonstrate that variables correlated with nestedness also vary across space and agree with the findings of Fleishman et al. (2002).

We find that dispersal ability affects a species' nestedness only in the Solomon Archipelago, with better dispersing species exhibiting higher nestedness than poorly dispersing ones (Fig. 3.6). While these findings agree with those of Schoener and Schoener (1983), Ryti and Gilpin (1987), and Cook and Quinn (1995), Kadmon (1995) found that species having no adaptations for dispersal were most nested. To explain their finding that species with poor dispersal abilities are less nested than other species, Ryti and Gilpin hypothesized that (1) taxa with limited dispersal might be more sensitive to biotic and abiotic factors that affect the probability of colonization, or (2) taxa with poor dispersal ability might have a larger random component in colonization patterns and processes than better dispersing species. However, it should not be surprising that different studies have found opposing influences of dispersal on nestedness. The differential colonization hypothesis asserts that patterns of nestedness result from differences in dispersal ability among species. Because dispersal ability must interact with the geographic configuration of islands (Kadmon 1995), the influence of dispersal ability should vary among taxa and across archipelagoes (see Hansson 1998).

Each archipelago exhibits a different pattern when we grouped species by dispersal ability and measured community nestedness for each group (Fig. 3.8). In the Bismarck Archipelago, all dispersal groups are significantly nested, but no clear pattern relates nestedness to dispersal ability. In the Solomon Archipelago, nestedness decreases monotonically with increasing dispersal ability, and the two most weakly dispersing groups are not significantly nested. In Vanuatu, only the poorly dispersing group is significantly nested. These contrasting patterns are not unexpected if nestedness in these archipelagoes is driven by differential colonization among species. In all three archipelagoes, the entire community is more nested than any single dispersal group (Fig. 3.8). That dispersal groups also exhibit nested patterns indicates that variation in colonization ability exists within dispersal groups or that another mechanism is contributing to nestedness.

Species with anti-nested distributions

Following Simberloff and Martin (1991), we search for species that do not conform to a nested pattern. These species have anti-nested distributions and occur predominantly on species-poor islands. We refer to these species as “supertramps.” In the Bismarck Archipelago, five species (*Ptilinopus solomonensis*, *Ducula pacifica*, *Monarcha cinerascens*, *Myzomela lafargei*, and *Aplonis feadensis*) exhibit a statistically significant anti-nested distribution (Appendix I). Three of these species, *D. pacifica*, *M. cinerascens*, and *A. feadensis* also exhibit a significantly anti-nested distribution in the Solomon Archipelago (Appendix J). No other supertramps exist in the Solomons or in Vanuatu (Appendices J–K). We seek to understand why these supertramps are

found predominantly on depauperate islands and why they are not present on richer, larger islands.

One hypothesis for the distribution of supertramps on predominantly small, depauperate islands is that they are competitively excluded from islands with more species (Diamond 1975, Mayr and Diamond 2001). If the distributions of supertramps are caused by interspecific competition (i.e., if supertramps are inferior competitors), competition theory predicts that supertramps should exhibit either superior dispersal abilities or wider niche breadths than their competitors (i.e., ecological tradeoffs). Superior dispersal or wider niche tolerances would permit an inferior competitor to survive on islands that are inaccessible or inhospitable to better competitors, which would competitively exclude them from the islands on which they occur. We examine measures of dispersal ability and habitat use provided by Mayr and Diamond (2001) and find no evidence that supertramps are better dispersers or use more habitat types than congeners (Table 3.15). These data are crude measures of dispersal ability and habitat use (or niche breadth) and provide only a weak test of the pattern expected if competition drives the distributions of supertramps.

A second hypothesis is that supertramps exist on species-poor islands because supertramps are adapted to particular features of these islands (e.g., specific habitats, frequent disturbance, lack of predators). For example, *Monarcha cinerascens* and *Aplonis feadensis*, are found on small, remote, or volcanically disturbed islands throughout their range, independently of the suite of potential competitors. Predation by *Accipiter* hawks might confine another supertramp, *Ducula pacifica*, to small islands in at least part of its geographic range (Holyoak and Thibault 1978). Determining the mechanisms responsible for the distributions of these supertramps will likely require experimental manipulations and detailed understanding of the natural history and biology of these species.

Island traits and nestedness

In the Bismarck Archipelago, larger, less isolated islands exhibit a higher degree of nestedness, and these two island traits explain 71% of the variation among islands in nestedness score (Table 3.12). In the Solomons, larger islands have higher nestedness scores (Table 3.13). Neither island size nor isolation predicts island nestedness in Vanuatu (Table 3.14). To test whether these patterns are driven by the presence of supertramps on small, isolated islands, we omitted supertramps and reran the analyses. All previous patterns hold.

Nestedness and conservation

Considerable effort has been expended to examine the utility of nestedness in conservation biology (Doak and Mills 1994, Boecklen 1997, Kerr et al. 2000, Patterson and Atmar 2000, Fleishman and Mac Nally 2002, Fischer and Lindenmayer 2005, Maron et al. 2004, Donlan et al. 2005, Martínez-Morales 2005). Because studies of nestedness require only presence-absence data, nestedness analyses could potentially improve conservation efforts by collecting quicker, less expensive data. By omitting data such as population sizes and trajectories, nestedness studies attain high “data economy” (Patterson and Atmar 2000). The usefulness of studies of nestedness for conservation biology should not be dismissed prematurely simply because only presence-absence data are used. All biological models make simplifying assumptions and omit information. Nevertheless, some of these models are commonly used in conservation. Examples include species diversity measures (e.g., Shannon–Weaver Index, rarefaction), which omit species composition, models of population dynamics (e.g., Lotka–Volterra, Beverton–Holt), which ignore age and sex data, and life history models, which ignore

spatial patterns and genetic variation among individuals. The applicability of nestedness analyses to conservation biology should not be rejected out of hand simply because they omit abundance data.

In a perfectly nested community, the largest site contains the entire species pool: any species found in any site will also exist in the richest site. Consequently, the prevalence of nestedness in ecological systems has created a misconception that conservation of a single large site is superior to preservation of several small sites (Brown 1986, Patterson 1987). Wright and Reeves (1992) even recommended that conservation managers should seek to minimize nestedness and the development of nested structure in systems of nature reserves. However, Fischer and Lindenmayer (2005) demonstrated that the implications for conservation differ between significantly but imperfectly nested assemblages and theoretical, perfectly nested ones. In addition, empirical evidence demonstrates that several small sites generally contain more species than a single large reserve (Simberloff and Gotelli 1984, Quinn and Harrison 1988, Wright and Reeves 1992, Beckon 1993, Cook 1995, Skaggs and Boecklen 1996, Boecklen 1997, Honnay et al. 1999). Boecklen (1997), for example, found that 90% of archipelagoes support a strategy of several small reserves even though almost all were significantly nested.

The debate about the usefulness nestedness studies to conservation biology has paralleled the debate over the utility of MacArthur and Wilson's (1967) equilibrium theory of island biogeography to optimize refuge design. Despite early criticism (Sauer, 1969; Lack 1970, 1976), the theory of island biogeography was readily accepted. The theory was quickly employed to address the design of nature reserves (Diamond and May 1976; but see Simberloff and Abele 1976) until its eventual fall from favor two decades later (Williamson 1989). Nestedness likely will face a similar end, and we agree with Worthen (1996) and Boecklen (1997) that nestedness is a poor tool for reserve design. Without understanding the mechanisms responsible for nested patterns, studies of nestedness provide little information about optimal reserve design. Attempts to use nestedness to guide the design of nature reserves appear as unjustified and ill-fated as earlier efforts to use MacArthur and Wilson's (1967) equilibrium theory of island biogeography to optimize reserve designs.

Some researchers (Patterson and Atmar 2000, Fleishman and Mac Nally 2002) have argued that nestedness patterns can be an effective conservation tool by identifying species and populations that are most vulnerable to extinction and extirpation and by identifying sites that maximize probability of successful reintroductions of locally extirpated populations. Although significant nestedness scores are often attributed to extinction events, most purported extinction events are undocumented. Equally troubling are the findings of Donlan et al. (2005), who found that nested analyses were unable to predict extinction risk of nonvolant mammals on islands off the Pacific coast of North America. A large number of factors may act simultaneously to shape the distributional patterns of species on islands (Boecklen 1997), and these processes can differ among taxa (Hansson 1998) and across space (Fleishman et al. 2002). In addition, the historic factors responsible for an observed nested pattern might differ from current threats to populations and species.

Recall that nested patterns can result from selective extinction (Patterson and Atmar 1986, Patterson 1987, Brown 1995), differential colonization (Darlington 1957, Simberloff and Martin 1991, Lomolino 1996), nested habitats (Calmé and Desrochers 1999, Honnay et al. 1999), hierarchical niche relationships (Worthen et al. 1998), and passive sampling (Andrén 1994, Cutler 1994). These mechanisms suggest different conservation strategies. For example, a program to conserve a biota that is nested because of nested habitats would need to protect or enhance rare habitats. In contrast, if a biota shows the exact same pattern of nestedness, but that pattern occurs

because species vary in sensitivity to disturbance (i.e., species exhibit hierarchical niche relationships), effective conservation strategies must act to mediate the impact of disturbance events. If selective extinctions are responsible for a nested pattern, conservation biologists might opt to monitor rare species or populations on small islands and perhaps take measures to reduce the impact of genetic or environmental stochasticity on these populations. To the extent that patterns of nestedness result from passive sampling, nestedness would offer no recommendations for conservation. In each of these cases, the pattern might be identical, but, if the causal processes vary, so too must effective conservation strategies.

Consequently, merely documenting the existence of a nested pattern without understanding the mechanism producing that pattern provides little insight to aid conservation. More importantly, conservation does not usually aim to maximize species richness. If it did, island biotas – whether nested or not – could be enhanced, at least temporarily, by facilitating colonization. Actually, humans are already engaged in such a phenomenon in our transport of exotic species. Were maximizing species richness the primary goal of conservationists, most exotic species would be welcomed as only a small fraction become invasive or cause extinctions. In reality, conservation efforts are directed to protect particular species, specifically uncommon native species. Species that do not exhibit a nested pattern (e.g., supertramps) will require specific strategies for their protection. In fact, successful conservation of any focal species likely requires careful consideration of many ecological factors and substantial knowledge of the natural history of the focal species to be successful (Bennett and Owens 1997, Owens and Bennett 2000, Donlan et al. 2005). We conclude that studies of nestedness are of limited direct use in conservation and that their greatest contribution to conservation biology is to help direct future observations and experiments.

Conclusions

Exclusive co-occurrence distribution patterns and nestedness are not mutually exclusive. These superficially contradictory patterns coexist, in part, because most co-occurrence and nestedness analyses employ different randomization algorithms. In analyses of co-occurrence, randomization algorithms retain differences in incidence among species and preserve differences in species richness across islands. In contrast, most studies of nestedness do not preserve differences in species richness across islands, and some do not maintain species sums either. Additionally, when marginal sums are maintained, measures of exclusive distributions (e.g., C-score) and of aggregated distributions (e.g., Togetherness) differ by only a constant (Stone and Roberts 1992). This fact demonstrates that exclusive distributions are not incompatible with nestedness. Patterns of nestedness can result from a number of mechanisms, and without understanding the mechanisms, studies of nestedness are unlikely to prove useful for conservation biology.

CHAPTER 4

MORPHOLOGICAL PATTERNS IN THE GENUS *ACCIPITER*

Abstract. We test for ecological and community-wide character displacement in two groups, *Accipiter* hawks and bird-eating hawks. We use published data on geographic distributions and elevational ranges and a geographic information system (GIS) to identify real communities. We obtain morphological data on wing length and talon size from the literature and use Barton–David statistics and minimum size ratios as measures of community-wide character displacement. We compare observed data to Monte Carlo simulations in which morphological traits are randomly assigned to species. To test for ecological character displacement, we examine subspecific variation in wing length and assess whether community composition predicts size variation among subspecies. We find limited evidence for community-wide character displacement of wing length in either accipiters or bird-eating hawks, but accipiters exhibit overdispersion of talon sizes. We find no support for ecological character displacement of wing length in accipiters. Our findings demonstrate that sympatric accipiters exhibit morphological segregation for talon size among species and sexes of sympatric *Accipiter* hawks. These results accord with a hypothesis of resource partitioning and illustrate the importance of measuring traits that relate directly to functional morphology and resource use.

Key words: *Accipiter*, *character displacement*, *competition*, *geographic variation*, *morphology*, *reverse size dimorphism*, *sexual dimorphism*, *subspecies*

INTRODUCTION

Hutchinson (1959) argued that if coexisting species reduce competition by using different resources and if resource use is reflected in certain morphological characters, then real communities should exhibit greater differences in these morphological characters than random communities. While Hutchinson’s “rule of 1.3” has long since been discounted on both empirical (Simberloff and Boecklen 1981) and theoretical grounds (Roth 1981), community-wide character displacement, a pattern in which coexisting species are more dissimilar morphologically than one would expect by chance, has survived. Schluter (1988) postulated that community-wide character displacement may be common.

Community-wide character displacement is a pattern, not a process. Even if driven by competition, community-wide character displacement can result from two distinct processes, species assortment and ecological character displacement (Grant 1969, 1970; Roughgarden 1983; Sinclair et al. 1985a,b; Fig. 4.1). Species assortment results from selective extinctions or colonizations such that morphologically similar species cannot coexist, and one species is competitively excluded. With species assortment, community-wide character displacement is an

ecological product of community assembly. Few studies provide compelling evidence of species assortment (Dayan and Simberloff 2005).

Community-wide character displacement can also result from evolutionary processes. If interspecific competition confers an advantage on individuals that are morphologically dissimilar from a competitor, then natural selection can act to cause similar-sized species to diverge in size or shape. Ecological character displacement is the evolution of morphological differences to reduce resource overlap in response to interspecific competition (Grant 1972).

Both community-wide character displacement (Strong et al. 1979) and ecological character displacement (Brown and Wilson 1956, Grant 1972) lie at the center of the debate regarding the role of competition in structuring communities (Dayan and Simberloff 2005). Empirical investigations of community-wide character displacement (Dayan et al. 1989, 1990; Dayan and Simberloff 1994a,b; Jones 1997; Foitzik and Heinze 1999; Millien-Parra and Loreau 2000; Ben-Moshe et al. 2001; Marchinko et al. 2004), empirical studies of ecological character displacement (Schluter 1988, 1994, 1996, 2003; Losos 1990, 2000; Miles and Dunham 1996; Sidorovich et al. 1999; Adams and Rohlf 2000; Simberloff et al. 2000; Schneider et al. 2001; Melville 2002; Benkman 2003; Forseth et al. 2003; Knouft 2003; Grant and Grant 2006), and theoretical studies of ecological character displacement (Slatkin 1980; Abrams 1986, 1987, 1989, 1990, 1996; Taper and Case 1985, 1992; Doebeli 1996; Drossel and McKane 1999) remain active areas of research. Here, we investigate all species of the genus *Accipiter* and assess whether this taxon shows evidence of ecological or community-wide character displacement.

Accipiter is a genus of medium-sized, bird-eating hawks that inhabit well-vegetated zones nearly worldwide (Ferguson-Lees and Christie 2001). Brown and Amadon (1968) recognized 47 species of *Accipiter* but there may be up to 54 (Ferguson-Lees and Christie 2001). Accipiters are characterized as having short, rounded wings and long tails, two traits that improve maneuverability, especially in wooded habitats (Wattel 1973). Accipiters are more likely than most taxa to be structured by competition because most accipiters have few predators, feed primarily on birds, and hunt in similar habitats (Schoener 1974, Menge and Sutherland 1976). Previous studies have suggested that size differences allow accipiter species to coexist (Storer 1966, Reynolds and Meslow 1984, Schoener 1984), and Burton and Olsen (1997) claim that coexisting accipiters generally show low dietary overlap and pronounced morphological segregation.

Schoener (1984) examined morphological patterns among species of sympatric accipiters and found evidence of limiting similarity: sympatric pairs, trios, quartets, and quintets had significantly larger minimum size ratios than expected from a null model. Schoener examined only one morphological trait, wing length. When studying the effects of competition on community structure, it is preferable to use the trophic appendage, the morphological trait that determines the type and rate of prey acquisition (Simberloff and Dayan 1991). Accipiters characteristically use a kneading action with the talons to kill their prey (Goslow 1971), so claw length or other foot measures might be a more suitable measure than wing length.

In a study of forest accipiters of Gabon, Brosset (1973) concluded that selective pressure plays a role both intra- and interspecifically and that differences in morphology, especially of the feet, reflect adaptation to different predatory behavior. Brosset (1973) found that digits of bird-eating accipiters are relatively long and thin, and Whaley and White (1994) showed that geographic variation in foot morphology of accipiters in North America reflects the percentage of mammals in the diet. In addition, Wattel (1973) proposed that shape differences, especially in foot and wing measures, might reduce competition among sympatric species of *Accipiter*. Thus,

much available evidence suggests that differences in foot morphology may be important in permitting coexistence.

Accipiters show the greatest reversed size dimorphism (RSD: females larger than males) among diurnal birds of prey (Ferguson-Lees and Christie 2001). RSD has apparently evolved at least five times (Paton et al. 1994) and is prevalent among diurnal raptors (Falconiformes), owls (Strigiformes), jacanas (Jacanidae), phalaropes (*Phalaropus*), frigatebirds (Fregatidae), boobies (Sulidae), and skuas (Stercorariidae). Mueller (1990) reviews RSD in monogamous birds.

Several hypotheses exist to explain RSD, especially in birds of prey, and the cause of RSD may vary across taxa (Andersson and Norberg 1981). One hypothesis is that RSD is an adaptation allowing the two members of a breeding pair to exploit different niches and to reduce resource competition between the sexes (Storer 1966, Newton 1979; Meiri et al. 2005). Studies that have tested for intersexual differences in prey size selection have been equivocal (Storer 1966, Opdam 1975, Newton 1979, Kennedy and Johnson, 1986, Boal and Mannan 1996). Regardless of the cause of RSD in raptors, RSD increases with the proportion of birds in the diet (Andersson and Norberg 1981) and is predominant in taxa such as *Accipiter* that require aerial maneuvers to capture prey (Paton et al. 1994). Schoener (1984) averaged sexes to obtain a single measure for each species. Because accipiters display strong RSD, and RSD may be linked to feeding niche, we treat each sex of each species as a separate morphospecies.

Most *Accipiter* species have subspecies, and many subspecies vary morphologically. Morphological variation within species is potentially influenced by multiple factors, including clinal variation, ecological character displacement, other natural selective pressures, gene flow, founder effects, and chance. Although many studies have examined character displacement between two or a handful of species (see Dayan and Simberloff [2005] for a review), we are aware of no study that tests for ecological character displacement within an entire large genus. We examine the extent to which changes in community composition (species additions and deletions) can explain subspecific variation in morphology. Specifically, we ask (1) Do sympatric species differ more in morphology than expected were local communities assembled at random? (2) Is variation in subspecific morphology predictable based on changes in community composition?

METHODS

Species

Following Schoener, we analyze two species pools. The first consists of all 47 species in the genus *Accipiter* recognized by Ferguson-Lees and Christie (2001). The second comprises the first group excluding five non-bird-eating accipiters and including 14 heterogeneric but ecologically similar species (Appendix L). To identify groups of syntopic species, we classify species by habitat use and elevational range.

We analyze communities of open and closed habitats separately. We classify species into one of three broad habitat categories (open habitats only, closed habitats only, or both). “Open” habitats include thornbush, desert, savannah, and wooded savannah. “Closed” habitats include primary and secondary forest, tropical forest, dense woodland, rainforest, riverine strips, and mangrove. Species that occupy broken forest, open woodland, or edge habitats are classified as “both” and are included in both open and closed analyses. We do not consider habitat use described as “recent” or habitats that result from anthropogenic habitat alteration, such as plantations and gardens.

We demarcate elevational limits as the range over which a species mostly occurs. We do not include unusual, rare, or local records. When a species occurs at different elevations in different regions, we record the range as the lowest and highest elevations at which the species usually occurs. By grouping species based on broad habitat categories and by elevational range, we aim to identify species groupings that coexist in a shared habitat and at a common elevation. We obtained habitat and elevational data and species maps from Ferguson-Lees and Christie (2001).

To obtain syntopic communities, we digitized the breeding distribution of each species and imported range maps into ArcGIS 9.0 (ESRI, Redlands, CA) with the sinusoidal projection to measure areas accurately. For each combination of habitat category and species group (open accipiters, closed accipiters, open bird-eating hawks, and closed bird-eating hawks), we identified and calculated the area of each geographic region that harbored a unique species composition (Fig. 4.2). Then, each unique association was separated into communities based on elevational boundaries, and the elevational range of each resulting community was calculated (Fig. 4.3). Separating groups of species by elevation can generate a community that does not contain all species in the geographic association, and these communities can have the same species composition as those from other geographic associations. Therefore, after splitting geographic associations by elevation to obtain communities of syntopic species, we searched for and combined the areas of identical communities across geographic regions.

Morphological data for accipiters were obtained from Kemp and Crowe (1994). Data unavailable in Kemp and Crowe (some accipiters and most non-accipiters) were obtained from Ferguson-Lees and Christie (2001). Data for male and female *A. collaris* were obtained from Ferguson-Lees and Christie (2001). Each sex is treated as a morphospecies (Dayan et al. 1989, 1990). When only a range of sizes is provided, we calculate size as the mean of the range. When data are combined for males and females, we calculate average size and then adjust the size of the sexes to obtain the mean size dimorphism observed across all accipiters. Traits for each species are listed in Appendix L.

We analyzed wing length for all species, and we also examined talon size for accipiters. Our measure of talon size is calculated as the sum of the lengths of the hind toe and hind claw and the average length of the inner, center, and outer toes and claws. When data on talon size were available for only one sex, we obtained the size of the other sex by multiplying the measured sex by the average size ratio between sexes across all species. When data were unavailable for both sexes, we used linear regression of talon size on wing length to estimate the talon size of each sex. Separate regressions were used for males and females.

Statistics

To test for nonrandom morphological patterns, we calculated minimum size ratios and Barton–David statistics (Barton and David 1956, Simberloff and Boecklen 1981) for each observed community. Barton–David statistics are ratios of size ratios, such as the ratio of the smallest size ratio to the largest size ratio, and test for constancy of size ratios. Here, we examine three Barton–David Statistics: the ratio of the smallest size ratio to the largest, $G_{1,n}$, the ratio of the smallest size ratio to the second smallest, $G_{1,n-1}$, and the ratio of the second smallest size ratio to the largest, $G_{2,n}$. In contrast to Barton–David statistics, minimum size ratios test for unusually large (but not necessarily equal) ratios. We calculated two minimum size ratios: the minimum size ratio between any two morphospecies, and the minimum interspecific size ratio. We calculated minimum interspecific size ratios to ensure that treating each sex as a separate morphospecies does not cause intraspecific patterns of size dimorphism to swamp interspecific patterns.

Because the two morphospecies of each species are not independent and because communities share species, we used Monte Carlo simulations (Manly 1997) to assess whether Barton–David statistics show evidence of unusual size ratios. For each of 1,000 iterations, we shuffled the species’ morphological traits while maintaining the geographic range of each species. That is, each species in each randomization had its observed geographic distribution with the morphology of a species selected at random without replacement. If interspecific competition has influenced observed size ratios, then real communities should have higher Barton–David measures than randomized ones. Our null hypothesis is that communities of sympatric species are structured no differently than communities assembled at random: minimum size ratios and Barton–David statistics will not differ between observed and randomized communities (Strong et al. 1979). Because minimum size ratios and Barton–David measures vary with the number of species in a community, we separated communities by number of species (two, three, four, etc.) and examined each level of richness separately. Lastly, to avoid analyzing communities that actually do not exist, we examined only communities that occur over an elevational range of at least 150 m and over an area of 10,000 km² and examined how patterns change when minimum area increases to 40,000 km² and 250,000 km².

Subspecies

As with the species-level analyses, we examined two groups of species (accipiters and bird-eating hawks) and separated species by broad habitat affiliation (open vs. closed) and by elevational range. Wing length data were obtained from Brown and Amadon (1968) and Ferguson-Lees and Christie (2001). When data were unavailable for only one sex of a subspecies, we estimated wing length by regressing wing length of that sex against wing length of the other sex (within species). When data for both sexes were absent, we substituted the mean wing length of subspecies in that species. Estimated data were used only to order morphospecies by size and were excluded from analyses. Subspecific wing lengths are presented in Appendix M.

Distributional maps for subspecies of *Accipiter* were obtained from Brown and Amadon (1968) and were digitized and imported into ArcGIS 9.0. We obtained unique communities of subspecies using the same procedure that we used to obtain species communities. Then, we identified unique communities that differ by the presence of a single species, the “invader”. We examined wing lengths of smaller and larger morphospecies in uninvaded and invaded communities. If subspecific morphological variation is influenced by the presence of congeners, one would expect the morphospecies smaller than the male invader to have diverged from that invader; that is, to be smaller in the invaded community than it is in the uninvaded community. Similarly, one would expect the morphospecies larger than the female invader to have increased in size in the presence of the invader. For each invasion, we scored whether the adjacent morphospecies in the recipient community exhibits a change in wing length and, if so, whether the change is in the predicted direction. We tested for significance with a binomial test. To test for robustness to imprecision in the maps of species distributions and in published elevational ranges, we varied the thresholds for geographic area or elevational range as described above.

RESULTS

Species

Wing length

Accipiters in closed forest tend towards morphological segregation by wing length, but this trend is not consistent among measures nor is it robust to changes in the threshold for geographic area. With a minimal area of 10,000 km², minimum size ratios are significantly larger than random ratios only for communities of four species ($p < 0.04$; Table 4.1; Fig. 4.4). At this minimum threshold for area, minimum size ratios, which examine minimum size ratios between any two morphospecies, and minimum interspecific size ratios, which exclude size ratios between conspecific morphospecies (male/female pairs), give qualitatively similar results for most comparisons (Tables 4.1–4.2). Therefore, we focus our analyses on minimum size ratios. For accipiters in closed forest, only one Barton–David measure, $G_{2,n}$, for communities with five species, differs significantly from expected ($p < 0.01$; Table 4.1). When the threshold for area is increased to 40,000 km², minimum size ratios for wing length are significantly large for communities of three, four, and five species ($p < 0.05$; see Appendix N for results for larger minimum area thresholds). For areas over 250,000 km², communities of two, three, and four species have significantly larger minimum size ratios of wing length ($p < 0.05$). At these higher area thresholds, a few other Barton–David statistics become significant, but no clear pattern for wing length emerges for any particular size community or for any Barton–David measure.

Minimum size ratios of wing length of accipiters in open habitats are significantly large for communities of two species ($p = 0.022$; Table 4.1; Fig. 4.5), but interspecific size ratios are only marginally significant ($p = 0.095$; Table 4.1; Fig. 4.5). Significantly larger than random minimum wing length ratios remain when minimum area increases to 40,000 km² ($p < 0.04$), but the result is only marginally significant for the largest area threshold ($p = 0.077$). No minimum interspecific size ratios differ significantly for larger area thresholds ($p > 0.07$). As with closed forest accipiters, some Barton–David statistics show evidence for constant size ratios of wing lengths among sympatric open habitat accipiters, but these significant statistics are uncommon and produce no consistent pattern across minimum area thresholds.

Wing lengths of bird-eating hawks of closed forest show no evidence of morphological overdispersion. Minimum size ratios are not significantly large for any sized community ($p > 0.10$; Table 4.1), and Barton–David measures do not indicate constant size ratios of wing length for any sized community ($p > 0.09$). These nonsignificant patterns for bird-eating hawks in closed forests do not change qualitatively with increases in minimum area ($p > 0.09$ for all communities).

Bird-eating hawks of open habitats show little evidence of overdispersed size ratios for wing length. Communities of two or three species show significantly or marginally significantly large minimum size ratios for the two lower area thresholds ($p < 0.06$; Table 4.1), but the pattern weakens for the largest area requirement and does not exist at any area threshold for minimum interspecific size ratios. With a minimum area threshold of 10,000 km², no Barton–David measure is significant ($p > 0.08$; Table 4.1). Qualitative results are robust to changes in the threshold for geographic area and do not change for minimum areas of 40,000 or 250,000 km².

Talon size

For closed forest accipiters, talon size exhibits strong morphological segregation. Minimum size ratios of talons in observed communities are significantly larger than random expectations for communities of two through five species ($p \leq 0.40$; Table 4.2; Fig. 4.4).

Observed minimum size ratios are larger than predicted, but most communities exhibit small minimum size ratios. Minimum size ratios for communities with three or more species are generally lower than 1.05 (Table 4.2; Fig. 4.4). Observed and predicted minimum size ratios decrease predictably with the number of sympatric accipiters (Fig. 4.4). Barton–David statistics also indicate significant overdispersion for communities of closed forest accipiters with three or four species (Table 4.2), and these results are fairly consistent across area thresholds (Appendix N).

In open habitats, communities with two species of *Accipiter* show larger minimum size ratios than expected ($p < 0.001$; Table 4.2; Fig. 4.5), but communities with more species do not ($p > 0.07$). The two Barton–David statistics that examine ratios with the smallest size ratio as numerator are also significantly larger than expected for communities with two species ($p < 0.01$; Table 4.2) but not for communities with three or more species ($p > 0.20$; Table 4.2). Qualitative results for talon size for both open and closed habitat accipiters are robust to changes in the threshold for geographic area and generally do not change for minimum areas of 40,000 km² or 250,000 km².

Subspecies

When all communities with a minimum area of 10,000 km² and an elevational range of at least 150 m are examined, wing lengths of subspecies of accipiters closest in size to invading species of accipiters or bird-eating hawks show no evidence of size shifts between invaded and uninvaded communities (one-tailed binomial test: $p > 0.40$ for all tests; Table 4.3). Contrary to predictions from competition theory, wing lengths of smaller species in closed-forest communities of both accipiters and bird-eating hawks show a significant tendency to increase in size towards the size of the invading species (two-tailed Binomial test: $p < 0.001$ for both groups; Table 4.3).

When the threshold for elevational range is increased to 500 m, these qualitative patterns remain. When minimum area for sampling is increased to 100,000 km², smaller morphospecies in closed forests no longer show a tendency to increase in size. No group exhibits a significant size response to invasion ($p > 0.05$ for all tests), but one group, accipiters in closed forests, shows a marginally significant trend for smaller and larger morphospecies to increase in the invaded community size ($p < 0.07$ for both tests).

DISCUSSION

If interspecific competition results in specialization of resource use, and if resource use is related to morphology, then sympatric pairs or groups of species should exhibit overdispersion in size spacing. Consequently, both ecological and community-wide character displacement are at the center of the debate regarding the role of competition in structuring communities (Dayan and Simberloff 2005). Community-wide character displacement is the overdispersion of morphological traits among groups of potentially competing species (Strong et al. 1979). In contrast, autecological processes, such as habitat and prey requirements and physiological tolerances, and historic factors (phylogenetic relationships, biogeography, and chance colonization) might govern the distributions and size ratios of potentially competing species, and species might adapt to the specifics of their environment independently of the suite of potential competitors (Grinnell 1917).

Our results with respect to community-wide character displacement for *Accipiter* hawks demonstrate that *Accipiter* hawks of closed forests exhibit morphological segregation for talon

size (Table 4.2; Fig. 4.4) but weak or no segregation for wing length (Table 4.1). In open habitats, communities with two species of accipiters, but not more, also exhibit larger minimum size ratios for talons than expected (Table 4.2; Fig. 4.5). Bird-eating hawks in both open and closed habitats show minimal evidence for morphological segregation by wing length (Table 4.1). Larger minimum size ratios for talon size in communities of five or fewer species of accipiters in closed forest and in communities of two species in open forest are statistical, not absolute (Fig. 4.4). That is, an absolute minimum size ratio (e.g., 1.3) does not exist, and many communities, especially those with three or more species, have morphospecies with similar sized talons with minimum size ratios of less than 1.05 (Figs. 4.4–4.5). But, on average, size ratios of talons of sympatric accipiters are larger than expected by chance alone.

These findings demonstrate the importance of measuring biologically appropriate traits that relate directly to functional morphology (see Simberloff and Boecklen 1981). Accipiters characteristically use a kneading action with the talons to kill their prey (Brown and Amadon 1968; Goslow 1971), and foot size has been shown to relate to resource partitioning and dietary differences (Brosset 1973, Whaley and White 1994). Consequently, a measure of foot morphology, such as talon size, relates directly to resource use and partitioning. These findings suggest that morphological segregation of talon size and resource partitioning among species and sexes of sympatric accipiters facilitates coexistence.

In contrast to talon size, wing length does not relate directly to resource use. Consequently, our finding that sympatric accipiters and bird-eating hawks exhibit little or no overdispersion in wing length is not entirely surprising. However, Schoener (1984) analyzed wing length and found a statistical pattern of larger than expected minimum size ratios in communities of two, three, and four species. Curiously, Schoener calculated a mean wing length for each species by lumping males and females. By combining sexes, Schoener examined sizes that do not correspond to any entity that exists in nature. In contrast, our analysis treats each sex as a separate morphospecies and examines real size ratios found in nature. We find some larger than expected minimum size ratios of wing lengths for closed forest accipiters (Table 4.1; Fig. 4.4) but little or no such evidence for open forest accipiters or for bird-eating hawks of either open or closed habitats.

Subspecific variation in wing length shows no evidence of ecological character displacement for wing length (Table 4.3). Neither accipiters in open habitats nor those in closed forest show a significant pattern towards character divergence. In fact, contrary to the predictions from competition theory, wing lengths of smaller species in closed-forest accipiters show a significant trend towards character convergence. Our finding that subspecies in some groups tend to converge towards the size of an invader is puzzling. We can speculate that, in some cases, a species might invade an area in response to prey availability. Because accipiter size is related to prey size (Storer 1966), presence of an invader could indicate the availability of a resource that is absent in the uninvaded community. If accipiter invasions are driven by availability of new resources, one might expect species in that area to adapt morphologically to exploit that resource. If so, natural selection could cause species in invaded communities to evolve and to converge upon the size of the invading accipiter. This speculation is tempered by a lack of data on underlying resource availability and by the fact that larger accipiters in forests do not show morphological convergence. Alternatively, smaller morphospecies might evolve increased sizes in response to interference competition from the invading species and to “alpha selection” (Jaeger et al. 2002, Adams 2004, but see Melville 2002).

Because communities of accipiters show community-wide character displacement for talon size but only limited morphological segregation for wing length, our analysis of subspecific

variation in wing length cannot address directly whether observed patterns of talon size result from species assortment or from ecological character displacement of talon size. It is plausible that wing length does not respond to the suite of potential competitors but that subspecific variation in talon size does. Thus, community-wide character displacement of talon size in *Accipiter* hawks could result from ecological character displacement or from species assortment through selective extinctions or colonizations. These mechanisms might vary among habitats or across communities within a habitat.

Conclusions

We examine *Accipiter* hawks and bird-eating hawks of open and closed habitats, test for community-wide character displacement in wing length and talon size, and assess whether subspecific variation in wing length is predictable from the suite of potential competitors. We find limited evidence of community-wide character displacement for wing length. In contrast, talon size, which is directly related to resource use, shows larger minimum and more equal size ratios than expected by chance alone. We find no evidence of competitively driven morphological change in wing length. Our results demonstrate the importance of examining traits directly related to functional morphology. We cannot determine whether community-wide character displacement of talon size results from ecological character displacement, species assortment, or both.

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APPENDICES

APPENDIX A. Tables.

Table 1.1. Presence-absence matrix for finches in the Galápagos Islands.

	Sey	Bal	Isa	Fern	San	Rab	Pin	SC	SFe	SCr	Esp	Flor	Gen	Mar	Pta	Dar	Wolf
<i>Geospiza magnirostris</i> ¹	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
<i>G. fortis</i> ²	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0
<i>G. fuliginosa</i> ³	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0
<i>G. difficilis</i> ⁴	0	0	1	1	1	0	0	1	0	1	0	1	1	0	1	1	1
<i>G. scandens</i> ⁵	1	1	1	0	1	1	1	1	1	1	0	1	0	1	1	0	0
<i>G. conirostris</i> ⁶	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
<i>Camarhynchus psittacula</i> ⁷	0	0	1	1	1	1	1	1	1	0	0	1	0	1	1	0	0
<i>C. pauper</i> ⁸	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>C. parvulus</i> ⁹	0	0	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0
<i>Platyspiza crassirostris</i> ¹⁰	0	0	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0
<i>Cactospiza pallidus</i> ¹¹	0	0	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0
<i>Cactospiza heliobates</i> ¹²	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Certhidea olivacea</i> ¹³	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

1 = presence, 0 = absence.

Islands: Sey=Seymour, Bal=Baltra, Isa=Isabella, Fern=Fernandina, San=Santiago, Rab=Rabida, Pin=Pinzon, SC=Santa Cruz, SFe=Santa Fe, SCr=San Cristobal, Esp=Espanola, Flor=Floreana, Gen=Genovesa, Mar=Marchena, Pta=Pinta, Dar=Darwin, Wolf=Wolf.

Species: ¹ large ground finch, ² medium ground finch, ³ small ground finch, ⁴ sharp-beaked ground finch, ⁵ cactus ground finch, ⁶ large cactus ground finch, ⁷ large tree finch, ⁸ medium tree finch, ⁹ small tree finch, ¹⁰ vegetarian finch, ¹¹ woodpecker finch, ¹² mangrove finch, ¹³ warbler finch.

Table 1.2. Co-occurrence metrics.

Metric	Source	Description	Comments	Value expected under competition
Number of checkerboards	Diamond (1975)	The number of species pairs that form perfect checkerboards (do not share any islands)	Related to Diamond's (1975) assembly rule (5). Sensitive to slight variation in co-occurrence patterns; susceptible to Type II error	Observed > Simulated
S-squared, S^2	Roberts and Stone (1990)	The sum, over all species pairs, of the square of the number of islands shared by each species pair	Criticized by Sanderson et al. (1998)	Observed > Simulated
C-score, C , Checkerboardedness	Stone and Roberts (1990)	Mean number of "checkerboard units" per species pair for the community.	Measures the overall tendency for species pairs to co-occur. Recommended by Gotelli and Entsminger (2001)	Observed > Simulated
Number of neighbors	Zaman and Simberloff (2002)	Total number of "checkerboard units" in the community.	Equals the C-score multiplied by $(\text{species} * (\text{species} - 1) / 2)$	Observed > Simulated
Togetherness, T	Stone and Roberts (1992)	Mean number of submatrices with mutual co-occurrence and absence	Measures the tendency for species pairs to co-occur; positive and negative values are possible. With marginal constraints, $T = C + \text{constant}$	Observed > Simulated

Table 1.3. Characteristics of matrix randomization algorithms.

Algorithm^a	Randomization Method	Initial swaps	Subsequent Swaps	Reference
Gotelli Swap	Swap	50,000	1	Gotelli 2000
Random Knight's Tour	Fill	N/A	N/A	Gotelli and Entsminger 2001, Sanderson et al. 1998
Manly Swap	Swap	0	1	Manly 1995, Manly and Sanderson 1998
Miklós and Podani's trial-swap	Swap	50,000 ^b	50,000	Miklós and Podani 2004
Miklós and Podani's trial-swap (long)	Swap	500,000 ^b	500,000	Miklós and Podani 2004
Original Swap	Swap	50,000	50,000	Simberloff 1986
Zaman and Simberloff's weighted means	Swap	50,000	50,000	Zaman and Simberloff 2002

^a Each listed algorithm maintains row and column sums.

^b Miklós and Podani's trial-swap algorithm specifies the number of swap attempts, not the number of actual swaps.

Table 1.4. ANOVA: Mean C-score.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	335	953069.9	2844.985	2170732	< 0.0001
Error	672	0.8807	0.0013		
Corrected Total	1007	953070.8			
	R²	Coefficient of Variation	Root MSE	Mean C-Score	
	0.9999	0.154004	0.036202	23.50737	

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Algorithm	6	0.6164	0.1027	78.39	< 0.0001
Size	3	704474.8	234824.9	1.79E+08	< 0.0001
Algorithm*Size	18	4.003	0.2224	169.68	< 0.0001
Fill	3	70220.75	23406.92	1.79E+07	< 0.0001
Algorithm*Fill	18	13.8715	0.7706	588	< 0.0001
Size*Fill	9	109845.6	12205.06	9312498	< 0.0001
Algorithm*Size*Fill	54	23.1421	0.4286	326.99	< 0.0001
Evenness	2	35399.76	17699.88	1.35E+07	< 0.0001
Algorithm*Evenness	12	1.1268	0.0939	71.65	< 0.0001
Size*Evenness	6	27000.61	4500.101	3433590	< 0.0001
Algorithm*Size*Evenness	36	2.6427	0.0734	56.01	< 0.0001
Fill*Evenness	6	3911.412	651.9019	497403	< 0.0001
Algorithm*Fill*Evenness	36	3.4228	0.0951	72.54	< 0.0001
Size*Fill*Evenness	18	2161.519	120.0844	91624.7	< 0.0001
Algorithm*Size*Fill*Evenness	108	6.721	0.0622	47.48	< 0.0001

Table 1.5. ANOVA: Variance in C-score.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	335	2.780416	0.008300	146.53	< 0.0001
Error	672	0.038064	0.000057		
Corrected Total	1007	2.818480			
	R²	Coefficient of Variation	Root MSE	Variance of C-score	
	0.986	25.909	0.008	0.029	

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Algorithm	6	0.131747	0.021958	387.65	< 0.0001
Size	3	0.752463	0.250821	4428.08	< 0.0001
Algorithm*Size	18	0.396102	0.022006	388.5	< 0.0001
Fill	3	0.023266	0.007755	136.91	< 0.0001
Algorithm*Fill	18	0.292706	0.016261	287.09	< 0.0001
Size*Fill	9	0.034612	0.003846	67.9	< 0.0001
Algorithm*Size*Fill	54	0.672386	0.012452	219.82	< 0.0001
Evenness	2	0.009053	0.004527	79.91	< 0.0001
Algorithm*Evenness	12	0.043774	0.003648	64.4	< 0.0001
Size*Evenness	6	0.019080	0.003180	56.14	< 0.0001
Algorithm*Size*Evenness	36	0.103557	0.002877	50.78	< 0.0001
Fill*Evenness	6	0.014553	0.002425	42.82	< 0.0001
Algorithm*Fill*Evenness	36	0.074489	0.002069	36.53	< 0.0001
Size*Fill*Evenness	18	0.016982	0.000943	16.66	< 0.0001
Algorithm*Size*Fill*Evenness	108	0.195646	0.001812	31.98	< 0.0001

Table 1.6. ANOVA: Difference between observed C-score and mean C-score.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	335	65.676	0.196	276.75	< 0.0001
Error	672	0.476	0.001		
Corrected Total	1007	66.152			
	R²	Coefficient of Variation	Root MSE	Difference in C-score	
	0.993	18.249	0.027	0.146	

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Algorithm	6	9.0256	1.5043	2123.53	< 0.0001
Size	3	9.7899	3.2633	4606.69	< 0.0001
Algorithm*Size	18	17.0654	0.9481	1338.37	< 0.0001
Fill	3	0.3077	0.1026	144.79	< 0.0001
Algorithm*Fill	18	2.2385	0.1244	175.56	< 0.0001
Size*Fill	9	2.1197	0.2355	332.48	< 0.0001
Algorithm*Size*Fill	54	7.2790	0.1348	190.29	< 0.0001
Evenness	2	0.1467	0.0734	103.57	< 0.0001
Algorithm*Evenness	12	2.9800	0.2483	350.56	< 0.0001
Size*Evenness	6	2.3553	0.3926	554.15	< 0.0001
Algorithm*Size*Evenness	36	5.1045	0.1418	200.16	< 0.0001
Fill*Evenness	6	0.7237	0.1206	170.27	< 0.0001
Algorithm*Fill*Evenness	36	1.0735	0.0298	42.09	< 0.0001
Size*Fill*Evenness	18	2.2399	0.1244	175.66	< 0.0001
Algorithm*Size*Fill*Evenness	108	3.2263	0.0299	42.17	< 0.0001

Table 2.1. Presence-absence matrix for finch species in the Galápagos Islands.

	Sey	Bal	Isa	Fern	San	Rab	Pin	SC	SFe	SCr	Esp	Flor	Gen	Mar	Pta	Dar	Wolf
<i>Geospiza magnirostris</i> ¹	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
<i>G. fortis</i> ²	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0
<i>G. fuliginosa</i> ³	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0
<i>G. difficilis</i> ⁴	0	0	1	1	1	0	0	1	0	1	0	1	1	0	1	1	1
<i>G. scandens</i> ⁵	1	1	1	0	1	1	1	1	1	1	0	1	0	1	1	0	0
<i>G. conirostris</i> ⁶	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
<i>Camarhynchus psittacula</i> ⁷	0	0	1	1	1	1	1	1	1	0	0	1	0	1	1	0	0
<i>C. pauper</i> ⁸	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>C. parvulus</i> ⁹	0	0	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0
<i>Platyspiza crassirostris</i> ¹⁰	0	0	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0
<i>Cactospiza pallidus</i> ¹¹	0	0	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0
<i>Cactospiza heliobates</i> ¹²	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Certhidea olivacea</i> ¹³	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

1 = presence, 0 = absence.

Islands: Sey=Seymour, Bal=Baltra, Isa=Isabella, Fern=Fernandina, San=Santiago, Rab=Rabida, Pin=Pinzon, SC=Santa Cruz, SFe=Santa Fe, SCr=San Cristobal, Esp=Espanola, Flor=Floreana, Gen=Genovesa, Mar=Marchena, Pta=Pinta, Dar=Darwin, Wolf=Wolf.

Species: ¹ large ground finch, ² medium ground finch, ³ small ground finch, ⁴ sharp-beaked ground finch, ⁵ cactus ground finch, ⁶ large cactus ground finch, ⁷ large tree finch, ⁸ medium tree finch, ⁹ small tree finch, ¹⁰ vegetarian finch, ¹¹ woodpecker finch, ¹² mangrove finch, ¹³ warbler finch.

Table 2.2. Co-occurrence measures.

Metric	Source	Description	Comments	Value expected under competition
Number of checkerboards	Diamond (1975)	The number of species pairs that form perfect checkerboards (do not share any islands)	Related to Diamond's (1975) assembly rule (5). Sensitive to slight variation in co-occurrence patterns; susceptible to Type II error	Observed > Simulated
S-squared, S^2	Roberts and Stone (1990)	The sum, over all species pairs, of the square of the number of islands shared by each species pair	Criticized by Sanderson et al. (1998)	Observed > Simulated
C-score, C , Checkerboardedness	Stone and Roberts (1990)	Mean number of "checkerboard units" per species pair for the community.	Measures the overall tendency for species pairs to co-occur. Recommended by Gotelli and Entsminger (2001)	Observed > Simulated
Shared islands, S	Stone and Roberts (1992)	Mean number of islands shared by a species pair	Is constant when row and column sums are fixed.	Observed > Simulated

Table 2.2. Continued.

Metric	Source	Description	Comments	Value expected under competition
Togetherhness, T	Stone and Roberts (1992)	Mean number of submatrices with mutual co-occurrence and absence	Measures the tendency for species pairs to co-occur; positive and negative values are possible. With marginal constraints, $T = C + \text{constant}$	Observed > Simulated
Schluter's variance ratio, V ratio	Schluter (1984)	Sum of species' co-variances	Determined solely by the row and column sums. Is constant when row and column sums are fixed. Similar to C , but does not maintain column sums Measures the variability in the number of species per site	Observed < Simulated
Number of species combinations	Pielou and Pielou (1968)	Number of unique species combinations occurring over all sites	Related to Diamond's (1975) assembly rules (1) and (2) Sensitive to slight variation in co-occurrence patterns; susceptible to Type II error	Observed < Simulated

Table 2.3. Measures of co-occurrence within taxa.

Data set A		Sites						Community-wide	Within genera
A. species 1	1	1	1	1	0	0	0	0	
A. species 2	0	0	0	0	1	1	1	1	
B. species 1	1	1	1	1	0	0	0	0	Obs <i>C</i>
B. species 2	0	0	0	0	1	1	1	1	Mean <i>C</i>
C. species 1	1	1	1	1	0	0	0	0	St. dev.
C. species 2	0	0	0	0	1	1	1	1	<i>p</i> -value
D. species 1	1	1	1	1	0	0	0	0	
D. species 2	0	0	0	0	1	1	1	1	Obs <i>T</i>
E. species 1	1	1	1	1	0	0	0	0	Mean <i>T</i>
E. species 2	0	0	0	0	1	1	1	1	St. dev.
F. species 1	1	1	1	1	0	0	0	0	<i>p</i> -value
F. species 2	0	0	0	0	1	1	1	1	

Data set B		Sites						Community-wide	Within genera
A. species 1	1	1	1	1	0	0	0	0	
A. species 2	1	1	1	1	0	0	0	0	
B. species 1	1	1	1	1	0	0	0	0	Obs <i>C</i>
B. species 2	1	1	1	1	0	0	0	0	Mean <i>C</i>
C. species 1	1	1	1	1	0	0	0	0	St. dev.
C. species 2	1	1	1	1	0	0	0	0	<i>p</i> -value
D. species 1	0	0	0	0	1	1	1	1	
D. species 2	0	0	0	0	1	1	1	1	Obs <i>T</i>
E. species 1	0	0	0	0	1	1	1	1	Mean <i>T</i>
E. species 2	0	0	0	0	1	1	1	1	St. dev.
F. species 1	0	0	0	0	1	1	1	1	<i>p</i> -value
F. species 2	0	0	0	0	1	1	1	1	

Each data set consists of six genera (A–F) with two species each. In data set A, congeners show a completely exclusive distribution. In data set B, congeners have completely congruent distributions. The two data sets have identical community-wide measures of co-occurrence, and both C-score and Togetherness are significantly higher than expected. When co-occurrence measures are restricted to pairs of species within genera, data set A shows significantly exclusive distributions, and data set B shows significantly congruent distributions.

Table 2.4. Co-occurrence measures: birds of the Bismarck Archipelago.

	Random		Incidence	
	<i>C</i>	<i>T</i>	<i>C</i>	<i>T</i>
Community-wide				
Observed ^a	111812	468217	111812	468217
Random mean ^b	97319.4	453724.4	110204.3	466609.3
Random SD ^c	837.7	837.7	864.2	864.2
<i>p</i> -value ^d	< 0.001	< 0.001	0.042	0.042
Within Families				
Observed	6575	23805	6575	23805
Random mean	5189.0	22984.7	6312.6	23077.8
Random SD	325.8	575.7	260.0	426.3
<i>p</i> -value	< 0.001	0.083	0.146	0.049
Within Genera				
Observed	1893	3230	1893	3230
Random mean	848.4	3957.9	1362.2	3539.2
Random SD	92.1	172.6	90.6	125.5
<i>p</i> -value	< 0.001	1.000	< 0.001	0.998

Measures are reported for all possible pairs of species (Community-wide), for pairs of species within families, and for pairs of species within genera. Co-occurrence measures are reported for each of two matrix randomization algorithms, Random and Incidence.

^a Observed is the value of the metric in the observed matrix.

^b Mean of 1,000 randomly generated matrices.

^c Standard deviation of 1,000 randomly generated matrices.

^d *p*-value is the fraction of randomized matrices with an equal or more extreme co-occurrence metric than the observed presence-absence matrix.

Table 2.5. Co-occurrence measures: birds of the Solomon Archipelago.

	Random		Incidence	
	<i>C</i>	<i>T</i>	<i>C</i>	<i>T</i>
Community-wide				
Observed ^a	166678	818273	166678	818273
Random mean ^b	129813.0	781408.0	144759.2	796354.2
Random SD ^c	918.9	918.9	1033.1	1033.1
<i>p</i> -value ^d	< 0.001	< 0.001	< 0.001	< 0.001
Within Families				
Observed	9045	41812	9045	41812
Random mean	6290.7	39444.7	7650.0	39153.8
Random SD	361.9	664.8	334.1	512.6
<i>p</i> -value	< 0.001	< 0.001	< 0.001	< 0.001
Within Genera				
Observed	2528	8831	2528	8831
Random mean	1450.1	8565.6	2270.1	8123.9
Random SD	145.5	272.4	141.8	227.4
<i>p</i> -value	< 0.001	0.162	0.027	0.001

Measures are reported for all possible pairs of species (Community-wide), for pairs of species within families, and for pairs of species within genera. Co-occurrence measures are reported for each of two matrix randomization algorithms, Random and Incidence.

^a Observed is the value of the metric in the observed matrix.

^b Mean of 1,000 randomly generated matrices.

^c Standard deviation of 1,000 randomly generated matrices.

^d *p*-value is the fraction of randomized matrices with an equal or more extreme co-occurrence metric than the observed presence-absence matrix.

Table 2.6. Co-occurrence measures: birds of Vanuatu.

	Random		Incidence	
	<i>C</i>	<i>T</i>	<i>C</i>	<i>T</i>
Community-wide				
Observed ^a	14888	43283	14888	43283
Random mean ^b	14238.7	42633.7	14215.9	42610.9
Random SD ^c	133.4	133.4	106.0	106.0
<i>p</i> -value ^d	< 0.001	< 0.001	< 0.001	< 0.001
Within Families				
Observed	283	1303	283	1303
Random mean	378.9	1119.5	388.1	1076.5
Random SD	53.6	86.6	48.9	76.4
<i>p</i> -value	0.978	0.020	0.981	0.007
Within Genera				
Observed	53	340	53	340
Random mean	98.6	292.4	104.1	272.3
Random SD	28.0	38.4	25.7	35.4
<i>p</i> -value	0.960	0.118	0.986	0.027

Measures are reported for all possible pairs of species (Community-wide), for pairs of species within families, and for pairs of species within genera. Co-occurrence measures are reported for each of two matrix randomization algorithms, Random and Incidence.

^a Observed is the value of the metric in the observed matrix.

^b Mean of 1,000 randomly generated matrices.

^c Standard deviation of 1,000 randomly generated matrices.

^d *p*-value is the fraction of randomized matrices with an equal or more extreme co-occurrence metric than the observed presence-absence matrix.

Table 2.7. Co-occurrence measures: bird families by archipelago.^a

Family	Common Name	Measure	Bismarcks		Solomons		Vanuatu	
			≥ Obs ^b	Effect ^c	≥ Obs	Effect	≥ Obs	Effect
Ardeidae	Hérons	<i>C</i>	353	0.27	651	-0.47	1000	-0.40
Ardeidae	Hérons	<i>T</i>	252	0.67	40	1.81	860	0.40
Threskiornithidae	Ibises, spoonbills	<i>C</i>	-	-	1000	-2.06	-	-
Threskiornithidae	Ibises, spoonbills	<i>T</i>	-	-	191	2.06	-	-
Anatidae	Ducks	<i>C</i>	1000	-1.35	-	-	1000	-2.43
Anatidae	Ducks	<i>T</i>	52	2.14	-	-	2	3.26
Accipitridae	Hawks	<i>C</i>	925	-1.35	668	-0.48	1000	-0.20
Accipitridae	Hawks	<i>T</i>	37	1.84	0	3.18	960	0.20
Falconidae	Falcons	<i>C</i>	432	0.41	1000	-0.92	-	-
Falconidae	Falcons	<i>T</i>	821	-0.64	541	0.92	-	-
Rallidae	Rails	<i>C</i>	212	0.83	510	-0.06	812	-0.91
Rallidae	Rails	<i>T</i>	857	-1.09	59	1.63	21	2.29
Columbidae	Pigeons	<i>C</i>	0	3.82	0	5.04	418	0.15
Columbidae	Pigeons	<i>T</i>	624	-0.39	497	-0.01	645	-0.38

^a Randomized matrices were generated with Miklós and Podani's (2004) trial-swap algorithm, which maintains both row (species) and column (island) sums.

^b Number of randomized matrices of 1,000 that had a measure greater than or equal to the observed measure.

^c Effect size, calculated as ((observed value – mean of random matrices) / (standard deviation of randomized matrices)).

Table 2.7. Continued.

Family	Common Name	Measure	Bismarcks		Solomons		Vanuatu	
			≥ Obs	Effect	≥ Obs	Effect	≥ Obs	Effect
Psittacidae	Parrots	<i>C</i>	1000	-2.92	446	0.08	335	1.28
Psittacidae	Parrots	<i>T</i>	2	3.17	31	1.93	1000	-1.15
Cuculidae	Cuckoos	<i>C</i>	968	-1.76	0	3.82	984	-1.35
Cuculidae	Cuckoos	<i>T</i>	36	1.90	1000	-2.85	149	1.57
Tytonidae	Barn owls	<i>C</i>	377	1.27	-	-	-	-
Tytonidae	Barn owls	<i>T</i>	1000	-1.16	-	-	-	-
Strigidae	Owls	<i>C</i>	-	-	1000	-1.35	-	-
Strigidae	Owls	<i>T</i>	-	-	204	1.49	-	-
Apodidae	Swifts	<i>C</i>	777	-0.73	925	-1.30	844	-0.85
Apodidae	Swifts	<i>T</i>	281	0.67	107	1.29	372	0.57
Alcedinidae	Kingfishers	<i>C</i>	845	-1.04	895	-1.26	1000	0.00
Alcedinidae	Kingfishers	<i>T</i>	33	1.81	70	1.48	1000	0.00
Pittidae	Pittas	<i>C</i>	100	2.00	-	-	-	-
Pittidae	Pittas	<i>T</i>	993	-1.74	-	-	-	-
Campephagidae	Cuckoo-shrikes	<i>C</i>	993	-2.20	964	-1.72	962	-1.03
Campephagidae	Cuckoo-shrikes	<i>T</i>	2	2.79	0	3.37	281	1.03
Turdidae	Thrushes	<i>C</i>	721	-0.34	960	-1.08	-	-
Turdidae	Thrushes	<i>T</i>	518	0.17	310	1.09	-	-

Table 2.7. Continued.

Family	Common Name	Measure	Bismarcks		Solomons		Vanuatu	
			≥ Obs	Effect	≥ Obs	Effect	≥ Obs	Effect
Sylviidae	Old World warblers	<i>C</i>	980	-1.86	950	-1.69	-	-
Sylviidae	Old World warblers	<i>T</i>	19	2.05	110	1.37	-	-
Rhipiduridae	Fantails	<i>C</i>	78	1.50	840	-1.03	1000	-1.27
Rhipiduridae	Fantails	<i>T</i>	918	-1.40	26	1.85	245	1.42
Monarchidae	Monarch flycatchers	<i>C</i>	0	6.91	0	10.85	847	-0.82
Monarchidae	Monarch flycatchers	<i>T</i>	942	-1.50	856	-1.03	372	0.56
Pachycephalidae	Whistlers	<i>C</i>	0	5.46	165	0.94	-	-
Pachycephalidae	Whistlers	<i>T</i>	1000	-3.36	748	-0.87	-	-
Nectariniidae	Sunbirds	<i>C</i>	909	-0.78	-	-	-	-
Nectariniidae	Sunbirds	<i>T</i>	402	0.77	-	-	-	-
Zosteropidae	White-eyes	<i>C</i>	30	2.87	0	3.95	1000	-0.64
Zosteropidae	White-eyes	<i>T</i>	1000	-2.12	1000	-2.79	709	0.64
Meliphagidae	Honey-eaters	<i>C</i>	0	6.42	36	2.27	79	2.10
Meliphagidae	Honey-eaters	<i>T</i>	985	-2.14	905	-1.05	994	-1.69
Estrildidae	Waxbills, grassfinches	<i>C</i>	989	-1.58	695	0.66	704	0.65
Estrildidae	Waxbills, grassfinches	<i>T</i>	89	1.71	1000	-0.66	1000	-0.62
Sturnidae	Starlings	<i>C</i>	0	4.84	0	6.91	463	0.39
Sturnidae	Starlings	<i>T</i>	952	-1.61	652	-0.44	820	-0.54

Table 2.8. Co-occurrence measures: bird genera by archipelago.^a

Genus	Common Name	Measure	Bismarcks		Solomons		Vanuatu	
			≥ Obs ^b	Effect ^c	≥ Obs	Effect	≥ Obs	Effect
<i>Ardea</i>	Hérons	<i>C</i>	847	-0.38	1000	-1.80	-	-
<i>Ardea</i>	Hérons	<i>T</i>	725	0.17	62	2.42	-	-
<i>Ixobrychus</i>	Bitterns	<i>C</i>	1000	-0.34	1000	-0.67	-	-
<i>Ixobrychus</i>	Bitterns	<i>T</i>	894	0.34	692	0.67	-	-
<i>Dendrocygna</i>	Wood-ducks	<i>C</i>	1000	-1.35	-	-	-	-
<i>Dendrocygna</i>	Wood-ducks	<i>T</i>	71	2.26	-	-	-	-
<i>Anas</i>	Ducks	<i>C</i>	-	-	-	-	1000	-1.29
<i>Anas</i>	Ducks	<i>T</i>	-	-	-	-	264	1.41
<i>Accipiter</i>	Accipiters	<i>C</i>	628	-0.35	381	0.27	-	-
<i>Accipiter</i>	Accipiters	<i>T</i>	195	0.78	389	0.23	-	-
<i>Falco</i>	Falcons	<i>C</i>	432	0.41	1000	-0.92	-	-
<i>Falco</i>	Falcons	<i>T</i>	821	-0.64	541	0.92	-	-
<i>Gallirallus</i>	Rails	<i>C</i>	1000	-0.38	-	-	-	-
<i>Gallirallus</i>	Rails	<i>T</i>	876	0.38	-	-	-	-
<i>Ptilinopus</i>	Fruit-doves	<i>C</i>	0	5.39	12	2.73	1000	0.00
<i>Ptilinopus</i>	Fruit-doves	<i>T</i>	985	-2.00	811	-0.86	1000	0.00
<i>Ducula</i>	Imperial pigeons	<i>C</i>	2	3.40	0	7.42	1000	-0.77
<i>Ducula</i>	Imperial pigeons	<i>T</i>	969	-1.79	981	-1.95	585	0.80
<i>Columba</i>	Pigeons	<i>C</i>	1000	-1.09	948	-1.06	-	-
<i>Columba</i>	Pigeons	<i>T</i>	455	1.09	238	1.12	-	-

^a Randomized matrices were generated with Miklós and Podani's (2004) trial-swap algorithm, which maintains both row (species) and column (island) sums.

^b Number of randomized matrices of 1,000 that had a measure greater than or equal to the observed measure.

^c Effect size, calculated as ((observed value – mean of random matrices) / (standard deviation of randomized matrices)).

Table 2.8. Continued.

Genus	Common Name	Measure	Bismarcks		Solomons		Vanuatu	
			≥ Obs	Effect	≥ Obs	Effect	≥ Obs	Effect
<i>Macropygia</i>	Cuckoo-doves	<i>C</i>	0	3.89	-	-	-	-
<i>Macropygia</i>	Cuckoo-doves	<i>T</i>	1000	-2.56	-	-	-	-
<i>Gallicolumba</i>	Ground-doves	<i>C</i>	333	0.74	622	-0.15	-	-
<i>Gallicolumba</i>	Ground-doves	<i>T</i>	891	-0.84	421	0.29	-	-
<i>Lorius</i>	Lories	<i>C</i>	1000	-0.47	-	-	-	-
<i>Lorius</i>	Lories	<i>T</i>	819	0.47	-	-	-	-
<i>Charmosyna</i>	Lorikeets	<i>C</i>	1000	-0.54	669	-0.46	-	-
<i>Charmosyna</i>	Lorikeets	<i>T</i>	767	0.54	193	0.70	-	-
<i>Micropsitta</i>	Pygmy-parrots	<i>C</i>	1000	-0.51	1000	-0.72	-	-
<i>Micropsitta</i>	Pygmy-parrots	<i>T</i>	784	0.52	621	0.73	-	-
<i>Centropus</i>	Coucals	<i>C</i>	1000	-1.26	-	-	-	-
<i>Centropus</i>	Coucals	<i>T</i>	253	1.46	-	-	-	-
<i>Tyto</i>	Barn owls	<i>C</i>	377	1.27	-	-	-	-
<i>Tyto</i>	Barn owls	<i>T</i>	1000	-1.16	-	-	-	-
<i>Aerodramus</i>	Swiftlets	<i>C</i>	1000	-1.25	1000	-1.40	-	-
<i>Aerodramus</i>	Swiftlets	<i>T</i>	200	1.38	107	1.69	-	-
<i>Collocalia</i>	Swiftlets	<i>C</i>	-	-	-	-	844	-0.85
<i>Collocalia</i>	Swiftlets	<i>T</i>	-	-	-	-	372	0.57
<i>Alcedo</i>	Kingfishers	<i>C</i>	999	-1.80	999	-1.91	-	-
<i>Alcedo</i>	Kingfishers	<i>T</i>	21	2.34	14	2.65	-	-
<i>Halcyon</i>	Kingfishers	<i>C</i>	136	1.28	288	0.50	1000	0.00
<i>Halcyon</i>	Kingfishers	<i>T</i>	976	-1.65	860	-1.07	1000	0.00
<i>Pitta</i>	Pittas	<i>C</i>	100	2.00	-	-	-	-
<i>Pitta</i>	Pittas	<i>T</i>	993	-1.74	-	-	-	-
<i>Coracina</i>	Cuckoo-shrikes	<i>C</i>	926	-1.18	1000	-3.47	-	-
<i>Coracina</i>	Cuckoo-shrike	<i>T</i>	74	1.62	0	4.80	-	-

Table 2.8. Continued.

Genus	Common Name	Measure	Bismarcks		Solomons		Vanuatu	
			≥ Obs	Effect	≥ Obs	Effect	≥ Obs	Effect
<i>Lalage</i>	Trillers	<i>C</i>	-	-	-	-	1000	-0.73
<i>Lalage</i>	Trillers	<i>T</i>	-	-	-	-	599	0.76
<i>Phylloscopus</i>	Old-world warblers	<i>C</i>	-	-	1000	-1.09	-	-
<i>Phylloscopus</i>	Old-world warblers	<i>T</i>	-	-	457	1.09	-	-
<i>Rhipidura</i>	Fantails	<i>C</i>	78	1.50	840	-1.03	1000	-1.27
<i>Rhipidura</i>	Fantails	<i>T</i>	918	-1.40	26	1.85	245	1.42
<i>Monarcha</i>	Monarch flycatchers	<i>C</i>	0	8.93	0	11.79	-	-
<i>Monarcha</i>	Monarch flycatchers	<i>T</i>	1000	-2.98	999	-2.87	-	-
<i>Myiagra</i>	Myiagra flycatchers	<i>C</i>	808	-0.37	-	-	-	-
<i>Myiagra</i>	Myiagra flycatchers	<i>T</i>	625	0.28	-	-	-	-
<i>Pachycephala</i>	Whistlers	<i>C</i>	0	5.46	165	0.94	-	-
<i>Pachycephala</i>	Whistlers	<i>T</i>	1000	-3.36	748	-0.87	-	-
<i>Nectarina</i>	Sunbirds	<i>C</i>	909	-0.78	-	-	-	-
<i>Nectarina</i>	Sunbirds	<i>T</i>	402	0.77	-	-	-	-
<i>Zosterops</i>	White-eyes	<i>C</i>	30	2.87	0	4.27	704	0.65
<i>Zosterops</i>	White-eyes	<i>T</i>	1000	-2.12	1000	-2.95	1000	-0.62
<i>Myzomela</i>	Myzomela honey-eaters	<i>C</i>	0	6.51	2	3.94	-	-
<i>Myzomela</i>	Myzomela honey-eaters	<i>T</i>	1000	-3.29	1000	-3.37	-	-
<i>Erythrura</i>	Parrot-finches	<i>C</i>	-	-	-	-	463	0.39
<i>Erythrura</i>	Parrot-finches	<i>T</i>	-	-	-	-	820	-0.54
<i>Lonchura</i>	Munias	<i>C</i>	1000	-1.04	-	-	-	-
<i>Lonchura</i>	Munias	<i>T</i>	399	1.12	-	-	-	-
<i>Aplonis</i>	Starlings	<i>C</i>	0	7.84	0	7.31	1000	-0.64
<i>Aplonis</i>	Starlings	<i>T</i>	732	-0.73	984	-1.99	709	0.64

Table 2.9. Correlation in co-occurrence measures in bird taxa across archipelagoes.

Taxon		Bismarcks	Solomons	Vanuatu
			0.801	0.577
	Bismarcks	-	< 0.0001 (20)	0.231 (6)
Genera		0.864		0.706
	Solomons	< 0.0001 (20)	-	0.117 (6)
		-0.016	0.072	
	Vanuatu	0.976 (6)	0.892 (6)	-
			0.490	0.117
	Bismarcks	-	0.033 (19)	0.667 (16)
Families		0.701		0.107
	Solomons	0.0008 (19)	-	0.703 (15)
		0.280	0.040	
	Vanuatu	0.293 (16)	0.888 (15)	-

C-scores are in the lower left; Togetherness in the upper right. From top to bottom, reported values reflect Pearson Product-Moment correlation, *p*-value, and sample size.

Table 2.10. Co-occurrence measures for bird families by archipelago: Incidence algorithm.^a

Family	Common Name	Measure	Bismarcks		Solomons		Vanuatu	
			≥ Obs ^b	Effect ^c	≥ Obs	Effect	≥ Obs	Effect
Ardeidae	Hérons	<i>C</i>	337	0.42	202	0.83	1000	-0.49
Ardeidae	Hérons	<i>T</i>	770	-0.72	492	0.02	798	0.50
Threskiornithidae	Ibises, spoonbills	<i>C</i>	-	-	1000	-1.27	-	-
Threskiornithidae	Ibises, spoonbills	<i>T</i>	-	-	382	1.27	-	-
Anatidae	Ducks	<i>C</i>	1000	-0.56	-	-	1000	-2.62
Anatidae	Ducks	<i>T</i>	446	1.02	-	-	6	3.27
Accipitridae	Hawks	<i>C</i>	919	-1.33	639	-0.33	1000	-0.39
Accipitridae	Hawks	<i>T</i>	99	1.29	0	3.14	870	0.39
Falconidae	Falcons	<i>C</i>	772	-0.11	1000	-0.37	-	-
Falconidae	Falcons	<i>T</i>	752	-0.03	882	0.37	-	-
Rallidae	Rails	<i>C</i>	546	-0.12	498	-0.03	810	-0.92
Rallidae	Rails	<i>T</i>	468	0.04	13	2.22	25	2.26
Columbidae	Pigeons	<i>C</i>	55	1.63	0	4.12	473	0.09
Columbidae	Pigeons	<i>T</i>	401	0.24	186	0.93	402	0.13

^a Randomized matrices were generated with the Incidence algorithm, which maintains both row (species) and column (island) sums and restricts each species to occur only within its observed range of island richnesses.

^b Number of randomized matrices of 1,000 that had a measure greater than or equal to the observed measure.

^c Effect size, calculated as ((observed value – mean of random matrices) / (standard deviation of randomized matrices)).

Table 2.10. Continued.

Family	Common Name	Measure	Bismarcks		Solomons		Vanuatu	
			≥ Obs	Effect	≥ Obs	Effect	≥ Obs	Effect
Psittacidae	Parrots	<i>C</i>	1000	-2.95	110	1.27	550	0.86
Psittacidae	Parrots	<i>T</i>	0	3.67	123	1.19	1000	-0.81
Cuculidae	Cuckoos	<i>C</i>	911	-1.25	7	2.37	989	-1.44
Cuculidae	Cuckoos	<i>T</i>	135	1.19	926	-1.44	119	1.73
Tytonidae	Barn owls	<i>C</i>	965	0.19	-	-	-	-
Tytonidae	Barn owls	<i>T</i>	1000	-0.19	-	-	-	-
Strigidae	Owls	<i>C</i>	-	-	1000	-0.85	-	-
Strigidae	Owls	<i>T</i>	-	-	529	0.88	-	-
Apodidae	Swifts	<i>C</i>	878	-1.14	818	-0.82	943	-1.23
Apodidae	Swifts	<i>T</i>	138	1.18	259	0.75	155	1.36
Alcedinidae	Kingfishers	<i>C</i>	338	0.38	961	-1.73	1000	0.00
Alcedinidae	Kingfishers	<i>T</i>	697	-0.50	16	2.22	1000	0.00
Pittidae	Pittas	<i>C</i>	602	0.32	-	-	-	-
Pittidae	Pittas	<i>T</i>	842	-0.42	-	-	-	-
Campephagidae	Cuckoo-shrikes	<i>C</i>	993	-2.20	964	-1.72	962	-1.03
Campephagidae	Cuckoo-shrikes	<i>T</i>	2	2.79	0	3.37	281	1.03
Turdidae	Thrushes	<i>C</i>	721	-0.34	960	-1.08	-	-
Turdidae	Thrushes	<i>T</i>	518	0.17	310	1.09	-	-

Table 2.10. Continued.

Family	Common Name	Measure	Bismarcks		Solomons		Vanuatu	
			≥ Obs	Effect	≥ Obs	Effect	≥ Obs	Effect
Sylviidae	Old World warblers	<i>C</i>	980	-1.86	950	-1.69	-	-
Sylviidae	Old World warblers	<i>T</i>	19	2.05	110	1.37	-	-
Rhipiduridae	Fantails	<i>C</i>	78	1.50	840	-1.03	1000	-1.27
Rhipiduridae	Fantails	<i>T</i>	918	-1.40	26	1.85	245	1.42
Monarchidae	Monarch flycatchers	<i>C</i>	0	6.91	0	10.85	847	-0.82
Monarchidae	Monarch flycatchers	<i>T</i>	942	-1.50	856	-1.03	372	0.56
Pachycephalidae	Whistlers	<i>C</i>	0	5.46	165	0.94	-	-
Pachycephalidae	Whistlers	<i>T</i>	1000	-3.36	748	-0.87	-	-
Nectariniidae	Sunbirds	<i>C</i>	909	-0.78	-	-	-	-
Nectariniidae	Sunbirds	<i>T</i>	402	0.77	-	-	-	-
Zosteropidae	White-eyes	<i>C</i>	30	2.87	0	3.95	1000	-0.64
Zosteropidae	White-eyes	<i>T</i>	1000	-2.12	1000	-2.79	709	0.64
Meliphagidae	Honey-eaters	<i>C</i>	0	6.42	36	2.27	79	2.10
Meliphagidae	Honey-eaters	<i>T</i>	985	-2.14	905	-1.05	994	-1.69
Estrildidae	Waxbills, grassfinches	<i>C</i>	989	-1.58	695	0.66	704	0.65
Estrildidae	Waxbills, grassfinches	<i>T</i>	89	1.71	1000	-0.66	1000	-0.62
Sturnidae	Starlings	<i>C</i>	0	4.84	0	6.91	463	0.39
Sturnidae	Starlings	<i>T</i>	952	-1.61	652	-0.44	820	-0.54

Table 2.11. Co-occurrence measures for bird genera by archipelago: Incidence algorithm.^a

Genus	Common Name	Measure	Bismarcks		Solomons		Vanuatu	
			≥ Obs ^b	Effect ^c	≥ Obs	Effect	≥ Obs	Effect
<i>Ardea</i>	Hérons	<i>C</i>	739	0.59	1000	-1.27	-	-
<i>Ardea</i>	Hérons	<i>T</i>	1000	-0.59	383	1.27	-	-
<i>Ixobrychus</i>	Bitterns	<i>C</i>	1000	0.00	1000	0.00	-	-
<i>Ixobrychus</i>	Bitterns	<i>T</i>	1000	0.00	1000	0.00	-	-
<i>Dendrocygna</i>	Wood-ducks	<i>C</i>	1000	-0.98	-	-	-	-
<i>Dendrocygna</i>	Wood-ducks	<i>T</i>	511	0.98	-	-	-	-
<i>Anas</i>	Ducks	<i>C</i>	-	-	-	-	1000	-1.54
<i>Anas</i>	Ducks	<i>T</i>	-	-	-	-	173	1.72
<i>Accipiter</i>	Accipiters	<i>C</i>	341	0.51	798	-0.83	-	-
<i>Accipiter</i>	Accipiters	<i>T</i>	920	-0.90	68	1.48	-	-
<i>Falco</i>	Falcons	<i>C</i>	772	-0.11	1000	-0.37	-	-
<i>Falco</i>	Falcons	<i>T</i>	752	-0.03	882	0.37	-	-
<i>Gallirallus</i>	Rails	<i>C</i>	1000	0.00	-	-	-	-
<i>Gallirallus</i>	Rails	<i>T</i>	1000	0.00	-	-	-	-
<i>Ptilinopus</i>	Fruit-doves	<i>C</i>	0	4.01	38	1.82	1000	0.00
<i>Ptilinopus</i>	Fruit-doves	<i>T</i>	941	-1.52	948	-1.62	1000	0.00
<i>Ducula</i>	Imperial pigeons	<i>C</i>	262	0.67	0	4.00	1000	-0.73
<i>Ducula</i>	Imperial pigeons	<i>T</i>	500	0.01	696	-0.49	613	0.76
<i>Columba</i>	Pigeons	<i>C</i>	1000	0.00	850	-0.63	-	-
<i>Columba</i>	Pigeons	<i>T</i>	1000	0.00	457	0.53	-	-

^a Randomized matrices were generated with the Incidence algorithm, which maintains both row (species) and column (island) sums and restricts each species to occur only within its observed range of island richnesses.

^b Number of randomized matrices of 1,000 that had a measure greater than or equal to the observed measure.

^c Effect size, calculated as ((observed value – mean of random matrices) / (standard deviation of randomized matrices)).

Table 2.11. Continued.

Genus	Common Name	Measure	Bismarcks		Solomons		Vanuatu	
			≥ Obs	Effect	≥ Obs	Effect	≥ Obs	Effect
<i>Macropygia</i>	Cuckoo-doves	<i>C</i>	2	3.28	-	-	-	-
<i>Macropygia</i>	Cuckoo-doves	<i>T</i>	994	-2.37	-	-	-	-
<i>Gallicolumba</i>	Ground-doves	<i>C</i>	215	1.29	770	-0.62	-	-
<i>Gallicolumba</i>	Ground-doves	<i>T</i>	962	-1.25	132	1.07	-	-
<i>Lorius</i>	Lories	<i>C</i>	1000	-0.31	-	-	-	-
<i>Lorius</i>	Lories	<i>T</i>	914	0.31	-	-	-	-
<i>Charmosyna</i>	Lorikeets	<i>C</i>	1000	-0.19	279	0.68	-	-
<i>Charmosyna</i>	Lorikeets	<i>T</i>	966	0.19	599	-0.41	-	-
<i>Micropsitta</i>	Pygmy-parrots	<i>C</i>	1000	-0.16	1000	-0.27	-	-
<i>Micropsitta</i>	Pygmy-parrots	<i>T</i>	975	0.16	930	0.27	-	-
<i>Centropus</i>	Coucals	<i>C</i>	1000	-0.52	-	-	-	-
<i>Centropus</i>	Coucals	<i>T</i>	787	0.52	-	-	-	-
<i>Tyto</i>	Barn owls	<i>C</i>	965	0.19	-	-	-	-
<i>Tyto</i>	Barn owls	<i>T</i>	1000	-0.19	-	-	-	-
<i>Aerodramus</i>	Swiftlets	<i>C</i>	1000	-1.31	1000	-0.91	-	-
<i>Aerodramus</i>	Swiftlets	<i>T</i>	182	1.42	427	0.94	-	-
<i>Collocalia</i>	Swiftlets	<i>C</i>	-	-	-	-	943	-1.23
<i>Collocalia</i>	Swiftlets	<i>T</i>	-	-	-	-	155	1.36
<i>Alcedo</i>	Kingfishers	<i>C</i>	911	-0.88	998	-1.89	-	-
<i>Alcedo</i>	Kingfishers	<i>T</i>	365	0.77	19	2.62	-	-
<i>Halcyon</i>	Kingfishers	<i>C</i>	343	0.66	782	-0.80	1000	0.00
<i>Halcyon</i>	Kingfishers	<i>T</i>	891	-0.90	202	0.83	1000	0.00
<i>Pitta</i>	Pittas	<i>C</i>	602	0.32	-	-	-	-
<i>Pitta</i>	Pittas	<i>T</i>	842	-0.42	-	-	-	-
<i>Coracina</i>	Cuckoo-shrikes	<i>C</i>	607	-0.18	1000	-2.79	-	-
<i>Coracina</i>	Cuckoo-shrike	<i>T</i>	400	0.46	0	3.91	-	-

Table 2.11. Continued.

Genus	Common Name	Measure	Bismarcks		Solomons		Vanuatu	
			≥ Obs	Effect	≥ Obs	Effect	≥ Obs	Effect
<i>Lalage</i>	Trillers	<i>C</i>	-	-	-	-	1000	-0.66
<i>Lalage</i>	Trillers	<i>T</i>	-	-	-	-	674	0.67
<i>Phylloscopus</i>	Old-world warblers	<i>C</i>	-	-	1000	0.00	-	-
<i>Phylloscopus</i>	Old-world warblers	<i>T</i>	-	-	1000	0.00	-	-
<i>Rhipidura</i>	Fantails	<i>C</i>	268	0.59	340	0.31	1000	-1.29
<i>Rhipidura</i>	Fantails	<i>T</i>	643	-0.43	204	0.81	272	1.39
<i>Monarcha</i>	Monarch flycatchers	<i>C</i>	0	3.53	73	1.35	-	-
<i>Monarcha</i>	Monarch flycatchers	<i>T</i>	886	-1.17	23	2.16	-	-
<i>Myiagra</i>	Myiagra flycatchers	<i>C</i>	771	-0.24	-	-	-	-
<i>Myiagra</i>	Myiagra flycatchers	<i>T</i>	686	0.14	-	-	-	-
<i>Pachycephala</i>	Whistlers	<i>C</i>	43	2.36	776	0.44	-	-
<i>Pachycephala</i>	Whistlers	<i>T</i>	1000	-1.88	969	-0.43	-	-
<i>Nectarina</i>	Sunbirds	<i>C</i>	966	-1.13	-	-	-	-
<i>Nectarina</i>	Sunbirds	<i>T</i>	240	1.23	-	-	-	-
<i>Zosterops</i>	White-eyes	<i>C</i>	669	0.68	0	3.59	1000	0.00
<i>Zosterops</i>	White-eyes	<i>T</i>	1000	-0.67	1000	-3.40	1000	0.00
<i>Myzomela</i>	Myzomela honey-eaters	<i>C</i>	35	1.85	30	2.86	-	-
<i>Myzomela</i>	Myzomela honey-eaters	<i>T</i>	993	-2.17	1000	-2.53	-	-
<i>Erythrura</i>	Parrot-finches	<i>C</i>	-	-	-	-	751	0.57
<i>Erythrura</i>	Parrot-finches	<i>T</i>	-	-	-	-	1000	-0.56
<i>Lonchura</i>	Munias	<i>C</i>	1000	-0.41	-	-	-	-
<i>Lonchura</i>	Munias	<i>T</i>	855	0.41	-	-	-	-
<i>Aplonis</i>	Starlings	<i>C</i>	9	2.74	335	0.46	643	-0.06
<i>Aplonis</i>	Starlings	<i>T</i>	467	0.15	56	1.62	688	-0.11

Table 2.12. Hypotheses for nonrandom distribution patterns within genera.

Genus	Common Name	Archipelago	Number of Species	Pattern	Potential Proximate Cause(s)
<i>Ptilinopus</i>	Fruit-doves	Bismarcks	5	Exclusive	Dispersal barriers or competitive exclusion Supertramp, <i>P. solomonensis</i> Similar species ^a : <i>P. solomonensis</i> and <i>P. rivoli</i>
<i>Ducula</i>	Imperial pigeons	Bismarcks	6	Exclusive	Dispersal barriers, predation, or competitive exclusion Supertramp, <i>D. pacifica</i>
<i>Macropygia</i>	Cuckoo-doves	Bismarcks	3	Exclusive	Competitive exclusion, subtle habitat differences, or dispersal barriers <i>M. mackinlayi</i> and <i>M. nigrirostris</i>
<i>Monarcha</i>	Monarch flycatchers	Bismarcks	3	Exclusive	Different habitat preferences or competitive exclusion Supertramp, <i>M. cinerascens</i>
<i>Pachycephala</i>	Whistlers	Bismarcks	2	Exclusive	Different habitat preferences or competitive exclusion Similar species: <i>P. pectoralis</i> and <i>P. melanura</i>
<i>Myzomela</i>	Honey-eaters	Bismarcks	6	Exclusive	Dispersal barriers or competitive exclusion Supertramp, <i>M. lafargei</i>
<i>Aplonis</i>	Starlings	Bismarcks	3	Exclusive	Different habitat preferences or competitive exclusion Supertramp, <i>A. feadensis</i>

^a indicates a pair of closely related species that show minimal or no difference in morphology and niche use (habitat use, diet, foraging technique, vertical stratum, and elevational range) and that met in Northern Melanesia and achieved partly or wholly sympatric ranges there (Mayr and Diamond [2001, Table 22.1]).

Table 2.12. Continued.

Genus	Common Name	Archipelago	Number of Species	Pattern	Potential Proximate Cause(s)
<i>Ducula</i>	Imperial pigeons	Solomons	4	Exclusive	Dispersal barriers or competitive exclusion Supertramp, <i>D. pacifica</i>
<i>Coracina</i>	Cuckoo-shrikes	Solomons	5	Congruent	Shared island requirements and possible dispersal barriers
<i>Monarcha</i>	Monarch flycatchers	Solomons	3	Exclusive	Different habitat preferences or competitive exclusion Supertramp, <i>M. cinerascens</i> Similar species: <i>M. melanopsis</i> and <i>M. cinerascens</i>
<i>Zosterops</i>	White-eyes	Solomons	5	Exclusive	Dispersal barriers
<i>Myzomela</i>	Honey-eaters	Solomons	2	Exclusive	Dispersal barriers
<i>Aplonis</i>	Starlings	Solomons	5	Exclusive	Different habitat preferences or competitive exclusion Supertramp, <i>A. feadensis</i>

Table 2.13. Dispersal and niche breadth of supertramps versus congeners.

Archipelago	Genus	Dispersal of Supertramp ^a	Dispersal of Congeners	Supports Dispersal Hypothesis ^b	Number of Habitats Used by Supertramp	Number of Habitats Used by Congeners ^c	Supports Niche Breadth Hypothesis ^d
Bismarcks	<i>Ptilinopus</i>	1	2.0	Yes	2	1	Yes
Bismarcks	<i>Ducula</i>	1	1.2	Yes	1	1	No
Bismarcks	<i>Monarcha</i>	1	3.0	Yes	1	1	No
Bismarcks	<i>Myzomela</i>	1	3.7	Yes	1	1.2	No
Bismarcks	<i>Aplonis</i>	1	1.0	No	1	1	No
Solomons	<i>Ducula</i>	2	1.7	No	1	1	No
Solomons	<i>Monarcha</i>	2	1.0	No	1	1	No
Solomons	<i>Aplonis</i>	3 ^e	1.5	No	1	1	No

^a Lower numbers indicate superior dispersal ability. See Appendices I and J. Data are from Mayr and Diamond (2001).

^b If supertramps are competitively inferior to congeners, they might exist by being superior dispersers.

^c See Appendices I and J. Data are from Mayr and Diamond (2001).

^d If supertramps are competitively inferior to congeners, they might survive by having a wider niche breadth or using more habitats.

^e *Aplonis feadensis* barely extends into the Solomons, so little data on dispersal ability exist for this species in the Solomons.

Table 3.1. Nested matrix for finches in the Galápagos Islands.

	Isa	Fern	San	SC	Flor	Pin	SCr	Pta	Rab	SFe	Mar	Sey	Bal	Gen	Esp	Dar	Wolf
<i>Certhidea olivacea</i> ¹	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Geospiza magnirostris</i> ²	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1	1
<i>Geospiza fuliginosa</i> ³	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0
<i>Geospiza fortis</i> ⁴	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
<i>Geospiza scandens</i> ⁵	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
<i>Platyspiza crassirostris</i> ⁶	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
<i>Geospiza difficilis</i> ⁷	1	1	1	1	1	0	1	1	0	0	0	0	0	1	0	1	1
<i>Camarhynchus psittacula</i> ⁸	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0	0	0
<i>Certhidea parvulus</i> ⁹	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
<i>Cactospiza pallidus</i> ¹⁰	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Geospiza conirostris</i> ¹¹	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>Cactospiza heliobates</i> ¹²	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Certhidea pauper</i> ¹³	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0

1 = presence, 0 = absence.

Islands: Isa=Isabella, Fern=Fernandina, San=Santiago, SC=Santa Cruz, Flor=Floreana, Pin=Pinzon, SCr=San Cristobal, Pta=Pinta,

Rab=Rabida, SFe=Santa Fe, Mar=Marchena, Sey=Seymour, Bal=Baltra, Gen=Genovesa, Esp=Espanola, Dar=Darwin, Wolf=Wolf.

Species: ¹ warbler finch, ² large ground finch, ³ small ground finch, ⁴ medium ground finch, ⁵ cactus ground finch, ⁶ vegetarian finch, ⁷ sharp-beaked ground finch, ⁸ large tree finch, ⁹ small tree finch, ¹⁰ woodpecker finch, ¹¹ large cactus ground finch, ¹² mangrove finch, ¹³ medium tree finch.

Table 3.2. Measures of nestedness.

Nestedness Metric	Symbol	Source	Comments
Number of absences	N_0	Patterson and Atmar (1986)	Counts the number of absences from sites richer than the poorest site on which a species occurs and sums across all species Proposed as N by Patterson and Atmar (1986)
Number of presences	N_1	Cutler (1991) Wright and Reeves (1992)	Counts the number of presences at sites poorer than the richest from which a species is absent and sums across all species Complement of N_0
Nestedness index	N_C	Wright and Reeves (1992)	Counts the number of times a species' presence correctly predicts its presence at richer sites and sums these counts across species and sites Equals the sum of the number of species shared over all pairs of sites Is constant when island richnesses are maintained
Standardized nestedness metric	C	Wright and Reeves (1992)	Standardized measure of N_C that is not affected by matrix size A value of 1 indicates perfect nestedness A value of 0 indicates no difference from random expectation
Number of unexpected absences	U_a	Cutler (1991)	Number of absences that must be filled (holes filled) to transform an existing matrix into a perfectly nested one
Number of unexpected presences	U_p	Cutler (1991)	Number of presences that must be removed to transform an existing matrix into a perfectly nested one
Number of transformations	U_t	Cutler (1991)	Minimum number of changes needed to transform an existing matrix into a perfectly nested one. $U_t = U_a + U_p$
Number of departures	D	Lomolino (1996)	Counts the number of times the absence of a species is followed by its presence on the next island (smaller, poorer, or more isolated)

Table 3.3. Matrix randomization algorithms for studies of nestedness.

Randomization algorithm	Source	Species (rows)^a	Sites (columns)^b	Comments
Equiprobable/ Equiprobable	Atmar and Patterson (1993)	Equiprobable	Equiprobable	Same as NESTCALC algorithm, which is used by the Temperature Calculator Identical to RANDOM00 (Atmar and Patterson 1993) and to SIM1 (Gotelli 2000) See Sokal and Rohlf (1995)
Equiprobable/ Fixed	Patterson and Atmar (1986)	Equiprobable	Fixed	Identical to Patterson and Atmar's (1986) RANDOM0 and to Abele and Patton's (1976) algorithm
Proportional/ Fixed	Patterson and Atmar (1986)	Proportional	Fixed	Identical to Patterson and Atmar's (1986) RANDOM1 Samples species proportionately Inflates statistical significance (Simberloff and Martin 1991)
Fixed/ Equiprobable	Sale (1974) Gotelli (2000)	Fixed	Equiprobable	Identical to SIM2 (Gotelli 2000)
Fixed/ Proportional	Coleman et al. (1982) Gotelli (2000)	Fixed	Proportional	Samples sites proportionately Inflates statistical significance (Simberloff and Martin 1991)
Fixed/ Fixed	Miklós and Podani (2004)	Fixed	Fixed	Randomly samples matrices with fixed row and column sums

^a Species are selected randomly (Equiprobable), proportionally to observed species occurrence (Proportional), or have species occurrence totals equal to observed number of islands inhabited (Fixed).

^b Islands are drawn randomly (Equiprobable), proportionally to observed species richness (Proportional), or have species richness totals equal to observed species richness (Fixed).

Table 3.4. Measures of nestedness by randomization algorithm for birds of the Bismarcks.

Algorithm	Metric	N_0	N_I	N_c	Ut	Ua	Up
	Observed ^a	1060	674	9841	440	159	281
Equiprobable/ Equiprobable	Mean ^b	2854.1	1254.1	5739.4	1182.7	125.6	1057.1
	SD ^c	40.6	19.1	53.6	17.0	20.7	27.6
	p -value ^d	0	0	0	0	946	0
	Effect size ^e	-44.20	-30.42	76.57	-43.65	1.61	-28.10
Equiprobable/ Fixed	Mean	2266.5	1036.3	5667.4	915.7	162.7	753.0
	SD	35.5	10.2	44.9	9.3	14.2	18.4
	p -value	0	0	0	0	404	0
	Effect size	-34.01	-35.44	92.99	-51.16	-0.26	-25.65
Proportional/ Fixed	Mean	1807.7	885.5	7862.1	686.9	188.3	498.5
	SD	61.2	19.6	124.1	16.1	15.9	21.2
	p -value	0	0	0	0	32	0
	Effect size	-12.22	-10.78	15.95	-15.34	-1.84	-10.24
Fixed/ Equiprobable	Mean	2354.8	1156.2	9841.0	824.5	252.8	571.7
	SD	60.9	25.6	0.0	12.8	19.3	21.6
	p -value	0	0	1000	0	0	0
	Effect size	-21.26	-18.83	-	-30.06	-4.86	-13.44
Fixed/ Proportional	Mean	1930.1	935.2	9841.0	675.4	197.4	478.0
	SD	69.1	28.0	0.0	15.7	16.3	19.8
	p -value	0	0	1000	0	8	0
	Effect size	-12.60	-9.32	-	-14.97	-2.36	-9.94
Fixed/ Fixed	Mean	1232.14	756.19	9841.00	494.66	172.62	322.04
	SD	44.73	25.00	0.00	9.10	12.85	14.62
	p -value	0	0	1000	0	154	3
	Effect size	-3.85	-3.29	-	-6.01	-1.06	-2.81

^a Value of the metric in the observed matrix.

^b Mean value of 1,000 randomized matrices.

^c Standard deviation of the randomized matrices.

^d Number of randomized matrices that have a measure equal to or more extreme than the observed value.

^e Effect size equals ((observed score – randomized mean) / (randomized standard deviation))

Table 3.5. Measures of nestedness by randomization algorithm for birds of the Solomons.

Algorithm	Metric	N_0	N_I	N_c	U_t	U_a	U_p
	Observed ^a	1591	950	26548	503	166.5	336.5
Equiprobable/ Equiprobable	Mean ^b	3822.3	1998.8	15437.9	1866.5	238.9	1627.6
	SD ^c	36.9	23.7	84.6	20.5	33.1	40.2
	p -value ^d	0	0	0	0	11	0
	Effect size ^e	-60.50	-44.18	131.27	-66.58	-2.19	-32.15
Equiprobable/ Fixed	Mean	2930.5	1836.1	15340.9	1530.0	406.5	1123.4
	SD	29.8	12.9	72.9	14.0	27.5	32.3
	p -value	0	0	0	0	0	0
	Effect size	-44.99	-68.72	153.78	-73.12	-8.73	-24.40
Proportional/ Fixed	Mean	2285.3	1494.5	22181.8	940.0	363.4	576.6
	SD	73.2	32.3	233.1	21.5	21.4	26.4
	p -value	0	0	0	0	0	0
	Effect size	-9.48	-16.85	18.73	-20.35	-9.18	-9.09
Fixed/ Equiprobable	Mean	3014.7	1880.4	26548.0	1117.3	512.9	604.5
	SD	82.6	28.2	0.0	14.1	25.9	26.8
	p -value	0	0	1000	0	0	0
	Effect size	-17.24	-32.95	-	-43.47	-13.38	-9.99
Fixed/ Proportional	Mean	2381.2	1492.5	26548.0	846.0	330.5	515.5
	SD	81.2	44.7	0.0	17.6	20.5	22.1
	p -value	0	0	1000	0	0	0
	Effect size	-9.73	-12.13	-	-19.53	-8.00	-8.11
Fixed/ Fixed	Mean	1500.7	1195.7	26548.0	616.0	257.0	359.0
	SD	55.6	41.6	0.0	10.3	15.4	16.8
	p -value	942	0	1000	0	0	95
	Effect size	1.62	-5.90	-	-11.02	-5.86	-1.34

^a Value of the metric in the observed matrix.

^b Mean value of 1,000 randomized matrices.

^c Standard deviation of the randomized matrices.

^d Number of randomized matrices that have a measure equal to or more extreme than the observed value.

^e Effect size equals ((observed score – randomized mean) / (randomized standard deviation))

Table 3.6. Measures of nestedness by randomization algorithm for the birds of Vanuatu.

Algorithm	Metric	N_0	N_1	N_c	U_t	U_a	U_p
	Observed ^a	333	359	8747	190	82	108
Equiprobable/ Equiprobable	Mean ^b	596.9	751.9	6787.7	478.3	269.5	208.8
	SD ^c	12.9	16.7	35.4	12.8	21.8	22.0
	p -value ^d	0	0	0	0	0	0
	Effect size ^e	-20.48	-23.57	55.32	-22.51	-8.59	-4.59
Equiprobable/ Fixed	Mean	558.1	687.6	6768.9	409.9	218.3	191.7
	SD	10.2	12.8	31.6	7.0	13.4	14.8
	p -value	0	0	0	0	0	0
	Effect size	-22.18	-25.59	62.61	-31.61	-10.14	-5.65
Proportional/ Fixed	Mean	476.9	543.3	7844.0	288.8	144.9	144.0
	SD	23.3	24.5	83.6	10.8	12.3	13.4
	p -value	0	0	0	0	0	1
	Effect size	-6.16	-7.52	10.81	-9.17	-5.12	-2.68
Fixed/ Equiprobable	Mean	483.3	564.6	8747.0	264.0	130.2	133.8
	SD	23.2	25.9	0.0	8.0	11.0	12.2
	p -value	0	0	1000	0	0	21
	Effect size	-6.48	-7.95	-	-9.24	-4.40	-2.11
Fixed/ Proportional	Mean	468.0	495.6	8747.0	249.4	115.9	133.4
	SD	24.6	27.9	0.0	8.9	10.8	11.9
	p -value	0	0	1000	0	0	13
	Effect size	-5.49	-4.90	-	-6.69	-3.15	-2.15
Fixed/ Fixed	Mean	342.6	384.9	8747.0	188.2	90.9	97.3
	SD	20.2	22.9	0.0	5.4	8.4	9.3
	p -value	341	133	1000	659	158	877
	Effect size	-0.47	-1.13	-	0.33	-1.06	1.15

^a Value of the metric in the observed matrix.

^b Mean value of 1,000 randomized matrices.

^c Standard deviation of the randomized matrices.

^d Number of randomized matrices that have a measure equal to or more extreme than the observed value.

^e Effect size equals ((observed score – randomized mean) / (randomized standard deviation))

Table 3.7. Skewness and kurtosis for measures of nestedness.

	Measure	N_0	N_I	N_c	Ut	Ua	Up
Bismarcks							
Equiprobable/Equiprobable	Skewness ^a	-0.47	-2.67	0.14	-1.32	0.19	-0.96
	Kurtosis ^b	1.11	14.07	-0.34	4.29	1.94	3.79
Equiprobable/Fixed	Skewness	-0.17	-0.18	0.25	-0.03	0.14	-0.10
	Kurtosis	0.02	0.12	0.20	0.13	0.08	-0.14
Proportional/Fixed	Skewness	0.11	-0.08	0.03	0.06	0.02	0.02
	Kurtosis	-0.09	-0.08	0.01	0.06	-0.05	0.02
Fixed/Equiprobable	Skewness	0.07	-0.25	-	-0.26	0.10	0.01
	Kurtosis	0.23	0.42	-	0.53	-0.11	-0.12
Fixed/Proportional	Skewness	-0.03	0.03	-	-0.19	0.06	0.09
	Kurtosis	-0.15	-0.12	-	0.03	-0.06	-0.16
Fixed/Fixed	Skewness	0.28	-0.09	-	-0.07	0.17	-0.10
	Kurtosis	0.18	-0.12	-	-0.05	0.18	-0.28
Solomons							
Equiprobable/Equiprobable	Skewness	-0.74	-2.80	0.20	-1.06	0.16	-0.56
	Kurtosis	1.43	18.10	0.03	3.57	2.20	1.78
Equiprobable/Fixed	Skewness	-0.05	-0.24	0.11	-0.08	-0.07	0.00
	Kurtosis	-0.26	0.12	-0.02	-0.19	0.00	0.05
Proportional/Fixed	Skewness	-0.02	-0.14	0.04	-0.07	-0.06	0.06
	Kurtosis	0.17	0.16	-0.04	-0.21	-0.13	-0.26
Fixed/Equiprobable	Skewness	-0.11	-0.36	-	-0.42	-0.10	0.07
	Kurtosis	0.20	0.79	-	1.25	-0.18	-0.01
Fixed/Proportional	Skewness	0.10	-0.01	-	-0.03	0.17	0.03
	Kurtosis	-0.10	-0.04	-	-0.04	-0.18	-0.09
Fixed/Fixed	Skewness	0.03	-0.03	-	-0.10	0.15	0.01
	Kurtosis	-0.23	-0.14	-	0.30	0.11	0.05
Vanuatu							
Equiprobable/Equiprobable	Skewness	-1.08	-0.56	0.38	-0.74	-0.22	-0.03
	Kurtosis	3.23	0.95	0.10	2.56	0.15	0.41
Equiprobable/Fixed	Skewness	-0.19	-0.22	0.42	-0.10	0.10	-0.05
	Kurtosis	-0.02	-0.10	0.50	-0.14	-0.16	-0.12
Proportional/Fixed	Skewness	-0.08	-0.04	0.05	-0.02	0.22	0.14
	Kurtosis	0.02	0.03	-0.15	-0.26	0.13	-0.08
Fixed/Equiprobable	Skewness	-0.10	-0.09	-	-0.42	0.02	0.00
	Kurtosis	0.30	0.00	-	0.50	0.14	0.09
Fixed/Proportional	Skewness	-0.02	-0.07	-	-0.25	0.05	-0.03
	Kurtosis	-0.17	-0.06	-	0.26	-0.20	-0.12
Fixed/Fixed	Skewness	0.17	0.09	-	0.05	-0.05	0.09
	Kurtosis	-0.07	0.07	-	-0.18	-0.23	-0.27

^a Negative skewness values indicate left-skewed distributions.

^b Positive kurtosis values indicate leptokurtotic distributions. See Sokal and Rohlf (1995; p. 115).

Table 3.8. Nestedness results when islands are sorted by area or by isolation.

	Bismarcks			Solomons			Vanuatu		
Number of species	154			142			56		
Number of islands	31			45			28		
Correlations	<i>r</i> ^a	<i>p</i> -value		<i>r</i>	<i>p</i> -value		<i>r</i>	<i>p</i> -value	
Species vs. Area	0.87	< 0.0001		0.88	< 0.0001		0.84	< 0.0001	
Species vs. Isolation	-0.56	0.0011		-0.27	0.0682		-0.47	0.0114	
Area vs. Isolation	-0.32	0.0808		-0.29	0.0562		-0.44	0.0192	
Nestedness	%PN ^b	D ^c	<i>p</i> -value ^d	%PN	D	<i>p</i> -value ^d	%PN	D	<i>p</i> -value ^d
By Area	35.5	436	< 0.001	38.4	549	< 0.001	24.0	176	< 0.001
By Isolation^e	29.4	474	< 0.001	9.4	807	0.07	26.2	171	< 0.001
Partial Nestedness	D2/D ^f		<i>p</i> -value	D2/D		<i>p</i> -value	D2/D		<i>p</i> -value
(I A)^g	0.62	269/436	< 0.0001	0.49	268/549	> 0.70	0.41	72/176	> 0.99
(A I)	0.70	333/474	< 0.0001	0.85	684/807	< 0.0001	0.73	124/171	< 0.0001

^a Pearson Product-Moment correlation.

^b Percent perfect nestedness = $100 * ((R - D)/R)$, where R = mean number of departures for 1,000 randomly ordered matrices, and D = number of departures from perfect nestedness for matrices ordered by area or isolation.

^c Number of departures from perfect nestedness for matrices ordered by area or isolation.

^d *p*-value = fraction of randomized matrices that have an equal or fewer number of departures from perfect nestedness than the observed matrix. Other *p*-values are calculated by SAS.

^e Island isolation is measured as the distance to the island with the largest number of species in the archipelago.

^f D2 is the number of departures from perfect nestedness explained by the second variable (area or isolation).

^g Partial nestedness is the fraction of observed departures from perfect nestedness explained by the other variable (D2/D). (I | A) is the partial nestedness of isolation (I) given that the matrix was sorted by area (A).

Table 3.9. ANOVA: Species rank nestedness and life history traits in the Bismarcks.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	68919.1	6891.9	4.7	< 0.0001
Error	134	196526.6	1466.6		
Corrected Total	144	265445.7			
	R²	Coefficient of Variation	Root MSE	Nestedness Mean Rank	
	0.260	50.708	38.296	75.524	

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Dispersal	3	10178	3392.66	2.31	0.079
Endemism	3	16228.2	5409.38	3.69	0.014
Density	4	15677.7	3919.43	2.67	0.035

Table 3.10. ANOVA: Species rank nestedness and life history traits in the Solomons.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	11	93220.5	8474.6	8.91	< 0.0001
Error	120	114088	950.7		
Corrected Total	131	207308			
	R²	Coefficient of Variation	Root MSE	Nestedness Mean Rank	
	0.450	44.404	30.834	69.439	
Source	DF	Type III SS	Mean Square	F Value	Pr > F
Dispersal	3	64422.4	21474.1	22.59	< 0.0001
Endemism	4	1083.2	270.8	0.28	0.887
Density	4	7669.9	1917.5	2.02	0.096

Table 3.11. ANOVA: Species rank nestedness and life history traits in Vanuatu.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	9	4663.3	518.1	2.83	0.019
Error	26	4768.5	183.4		
Corrected Total	35	9431.8			
	R²	Coefficient of Variation	Root MSE	Nestedness Mean Rank	
	0.494	51.921	13.543	26.083	
Source	DF	Type III SS	Mean Square	F Value	Pr > F
Dispersal	3	503.4	167.8	0.92	0.447
Endemism	2	595.8	297.9	1.62	0.216
Density	4	2326.4	581.6	3.17	0.030

Table 3.12. Linear Regression: Island nestedness and island traits in the Bismarcks.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	47.460	23.730	33.84	< 0.0001
Error	25	17.529	0.701		
Corrected Total	27	64.989			
	R²	Coefficient of Variation	Root MSE	Variance	Adj R²
	0.730	12.064	0.837	6.941	0.709
Variable	DF	Estimate	Error	t Value	Pr > t
Intercept	1	6.181	0.483	12.81	< 0.0001
Log (Area)	1	1.067	0.156	6.85	< 0.0001
Sqrt (Isolation)	1	-0.061	0.024	-2.5	0.019

Table 3.13. Linear Regression: Island nestedness and island traits in the Solomons.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	173.87	86.94	22.6	< 0.0001
Error	39	150.00	3.85		
Corrected Total	41	323.87			
	R²	Coefficient of Variation	Root MSE	Variance	Adj R²
	0.5369	26.5366	1.96117	7.39043	0.5131
Variable	DF	Estimate	Error	t Value	Pr > t
Intercept	1	4.436	1.055	4.21	0.0001
Log (Area)	1	1.795	0.279	6.43	< 0.0001
Sqrt (Isolation)	1	0.046	-0.180	0.860	0.0192

Table 3.14. Linear Regression: Island nestedness and island traits in Vanuatu.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	1.392	0.696	1.9	0.171
Error	24	8.785	0.366		
Corrected Total	26	10.177			
	R²	Coefficient of Variation	Root MSE	Variance	Adj R²
	0.137	12.176	0.605	4.969	0.065
Variable	DF	Estimate	Error	t Value	Pr > t
Intercept	1	5.929	0.517	11.46	< 0.0001
Ln (Area)	1	-0.086	0.068	-1.26	0.219
Sqrt (Isolation)	1	-0.260	0.144	-1.8	0.084

Table 3.15. Dispersal ability and niche breadth of supertramps versus congeners.

Archipelago	Genus	Dispersal of Supertramp ^a	Dispersal of Congeners	Supports Dispersal Hypothesis ^b	Number of Habitats Used by Supertramp	Number of Habitats Used by Congeners ^c	Supports Niche Breadth Hypothesis ^d
Bismarcks	<i>Ptilinopus</i>	1	2.0	Yes	2	1	Yes
Bismarcks	<i>Ducula</i>	1	1.2	Yes	1	1	No
Bismarcks	<i>Monarcha</i>	1	3.0	Yes	1	1	No
Bismarcks	<i>Myzomela</i>	1	3.7	Yes	1	1.2	No
Bismarcks	<i>Aplonis</i>	1	1.0	No	1	1	No
Solomons	<i>Ducula</i>	2	1.7	No	1	1	No
Solomons	<i>Monarcha</i>	2	1.0	No	1	1	No
Solomons	<i>Aplonis</i>	3 ^e	1.5	No	1	1	No

^a Lower numbers indicate superior dispersal ability. See Appendices I and J. Data are from Mayr and Diamond (2001).

^b If supertramps are competitively inferior to congeners, they might exist by being superior dispersers.

^c See Appendices I and J. Data are from Mayr and Diamond (2001).

^d If supertramps are competitively inferior to congeners, they might survive by having a wider niche breadth or using more habitats.

^e *Aplonis feadensis* barely extends into the Solomons, so little data on dispersal ability exist for this species in the Solomons.

Table 4.1. Community-wide character displacement: wing length. Values show number of 1,000 iterations that equaled or exceeded the observed value.

Species Group	Habitat	Species ^a	Minimum Size Ratio ^b	Minimum Interspecific Size Ratio ^c	Barton–David 1 ^d	Barton–David 2 ^e	Barton–David 3 ^f
Accipiters	Closed	2	144	90	675	627	418
Accipiters	Closed	3	59	113	211	217	229
Accipiters	Closed	4	25	34	94	87	95
Accipiters	Closed	5	93	93	174	139	8
Accipiters	Closed	6	120	120	212	269	171
Accipiters	Open	2	22	95	300	247	350
Accipiters	Open	3	109	411	136	91	399
Accipiters	Open	4	102	114	223	31	675
Accipiters	Open	5	84	84	120	16	288
Bird-eating hawks	Closed	2	221	112	720	421	694
Bird-eating hawks	Closed	3	122	210	445	487	293
Bird-eating hawks	Closed	4	557	709	677	764	264
Bird-eating hawks	Closed	5	707	854	721	855	96
Bird-eating hawks	Closed	6	550	729	539	640	508
Bird-eating hawks	Closed	7	427	587	404	527	167
Bird-eating hawks	Open	2	58	101	361	109	686
Bird-eating hawks	Open	3	31	76	337	175	737
Bird-eating hawks	Open	4	102	141	292	351	450
Bird-eating hawks	Open	5	384	571	389	574	520
Bird-eating hawks	Open	6	64	106	88	134	227

^a Number of species in the community.

^b Minimum size ratio between any two morphospecies.

^c Minimum interspecific size ratio (excludes conspecific male/female pairs).

^d Barton–David statistic, $G_{1,n}$: ratio of the smallest size ratio to the largest size ratio.

^e Barton–David statistic, $G_{1,n-1}$: ratio of the smallest size ratio to the second largest size ratio.

^f Barton–David statistic, $G_{2,n}$: ratio of the second smallest size ratio to the largest size ratio.

Table 4.2. Community-wide character displacement: talon size. Values show number of 1,000 iterations that equaled or exceeded the observed value.

Habitat	Species ^a	Minimum Size Ratio ^b	Minimum Interspecific Size Ratio ^c	Barton–David 1 ^d	Barton–David 2 ^e	Barton–David 3 ^f
Closed	2	9	20	102	51	539
Closed	3	7	36	12	31	115
Closed	4	0	1	1	6	32
Closed	5	40	50	102	121	73
Closed	6	562	562	637	702	499
Open	2	0	6	8	6	292
Open	3	71	79	267	254	299
Open	4	331	338	517	414	718
Open	5	519	519	591	545	514

^a Number of species in the community.

^b Minimum size ratio between any two morphospecies.

^c Minimum interspecific size ratio (excludes conspecific male/female pairs).

^d Barton–David statistic, $G_{1,n}$: ratio of the smallest size ratio to the largest size ratio.

^e Barton–David statistic, $G_{1,n-1}$: ratio of the smallest size ratio to the second largest size ratio.

^f Barton–David statistic, $G_{2,n}$: ratio of the second smallest size ratio to the largest size ratio.

Table 4.3. Size response of *Accipiter* subspecies to invasion by congeners or by bird-eating hawks.

Species Group	Response	Closed ^a		Open	
		Smaller ^b	Larger ^c	Smaller	Larger
Accipiters	None ^d	403	484	457	165
	Predicted ^e	177	242	86	117
	Opposite ^f	266	236	95	131
	<i>p</i> -value ^g	< 0.001 ^h	0.41	0.77	0.80
Bird-eating hawks	None	1020	1126	515	543
	Predicted	443	357	251	175
	Opposite	552	401	268	185
	<i>p</i> -value	< 0.001 ^h	0.102 ^h	0.79	0.72

^a Habitat type.

^b Smaller resident morphospecies.

^c Larger resident morphospecies.

^d Subspecies is the same size in the invaded (richer) and uninvaded community.

^e Nearest smaller or larger morphospecies in the recipient community is morphologically more different from the invader in the invaded community than is the corresponding morphospecies in the uninvaded community.

^f Subspecies in the recipient community is more similar in size to the invader than is the subspecies in the uninvaded community.

^g *p*-values are one-tailed binomial tests unless otherwise marked.

^h Two-tailed binomial test (fewer size shifts in predicted direction than expected).

APPENDIX B. Figures.

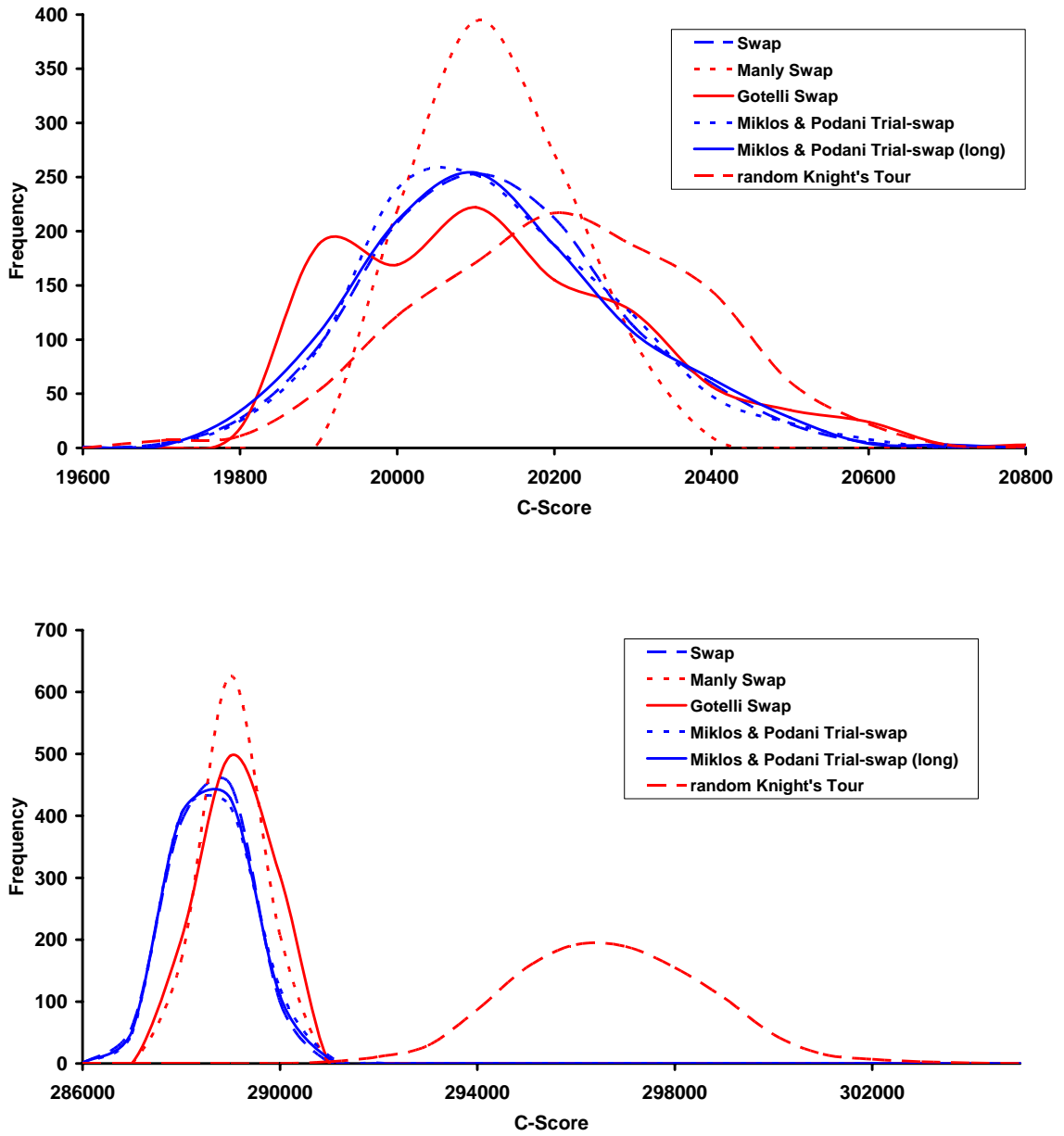


Figure 1.1. Frequency distribution of the C-score for two co-occurrence matrices. Randomization algorithms generate similar distributions for some matrices but dissimilar distributions for others.

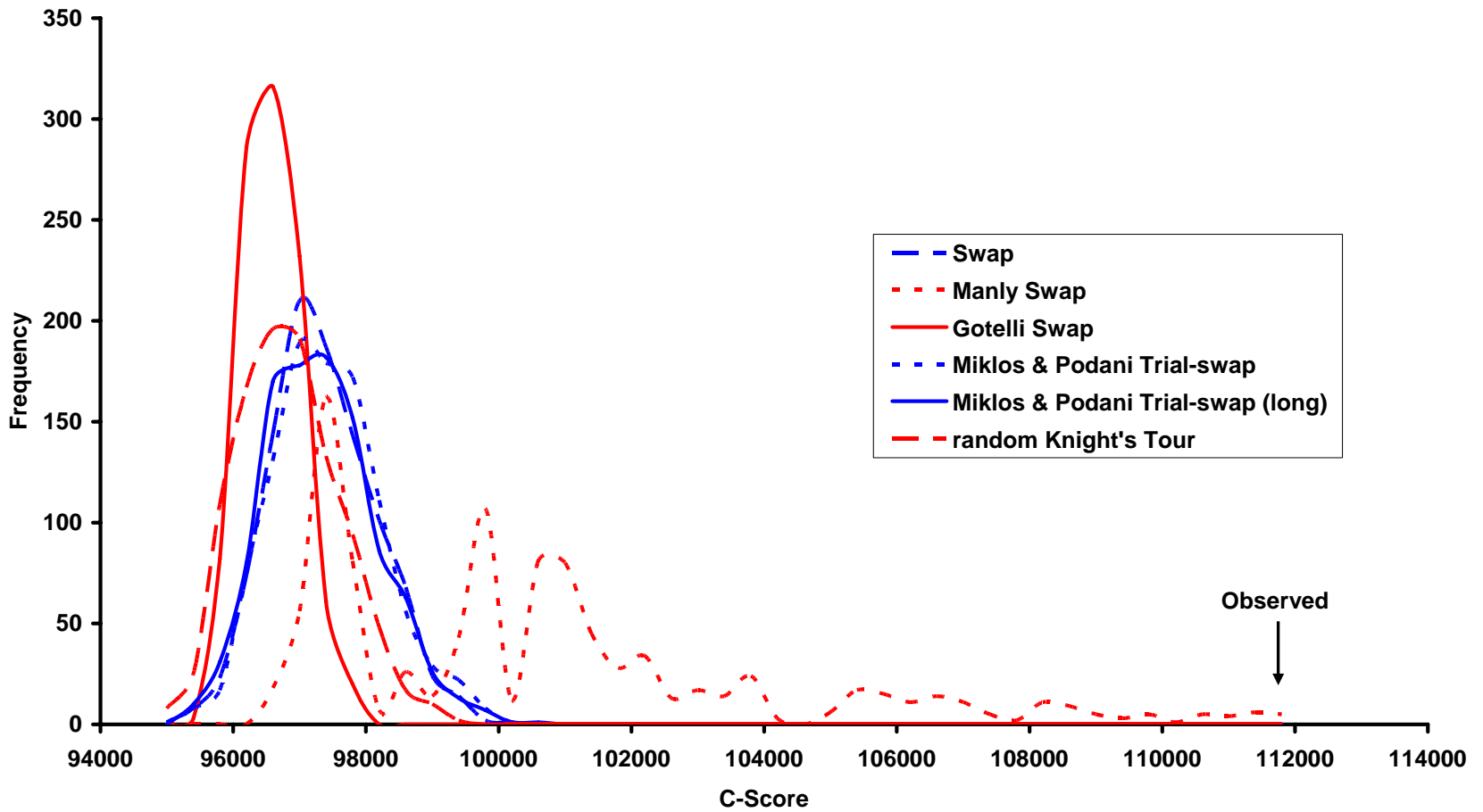


Figure 1.2. Frequency distribution of the C-score by randomization algorithm for birds of the Bismarck Archipelago.

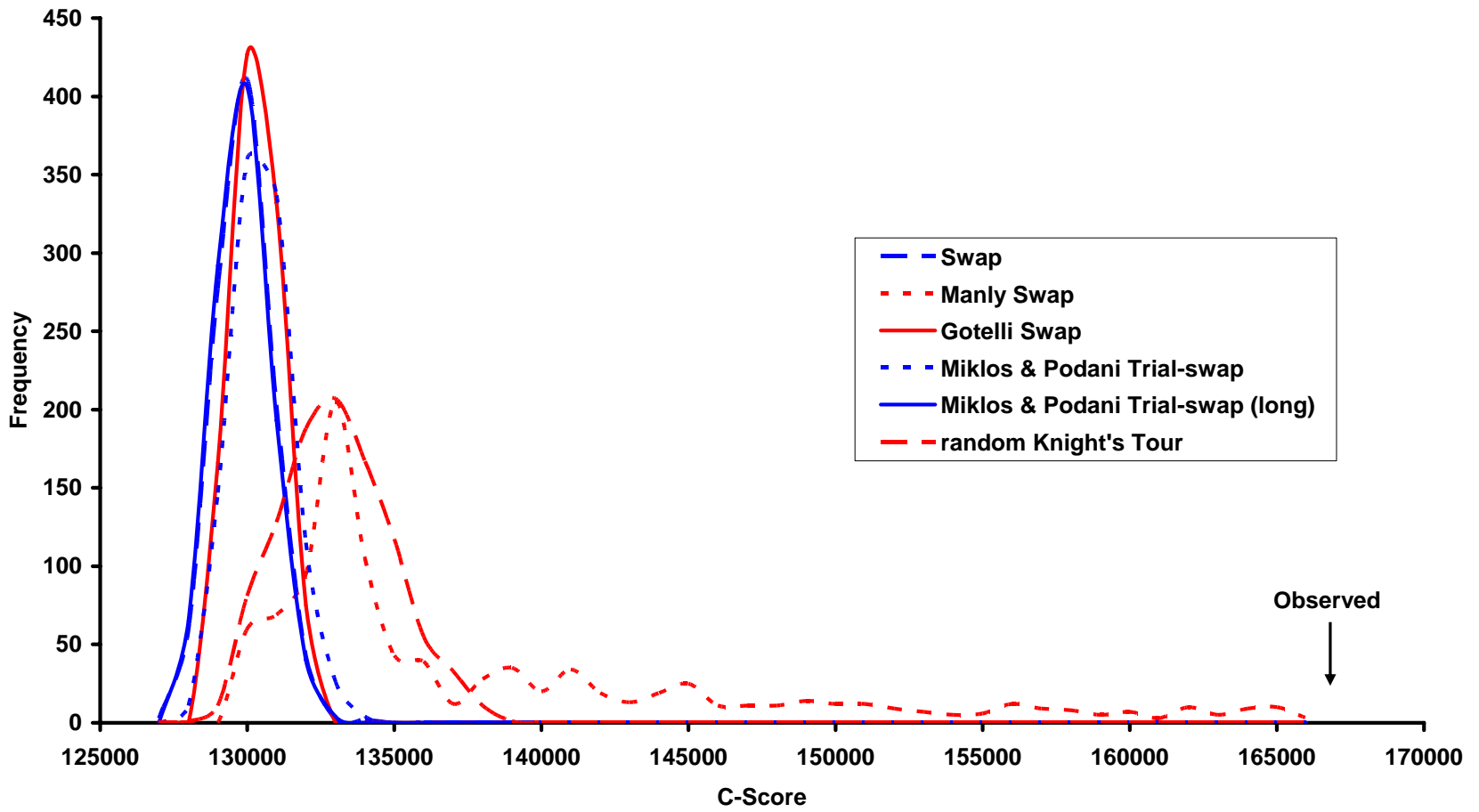


Figure 1.3. Frequency distribution of the C-score by randomization algorithm for birds of the Solomon Archipelago.

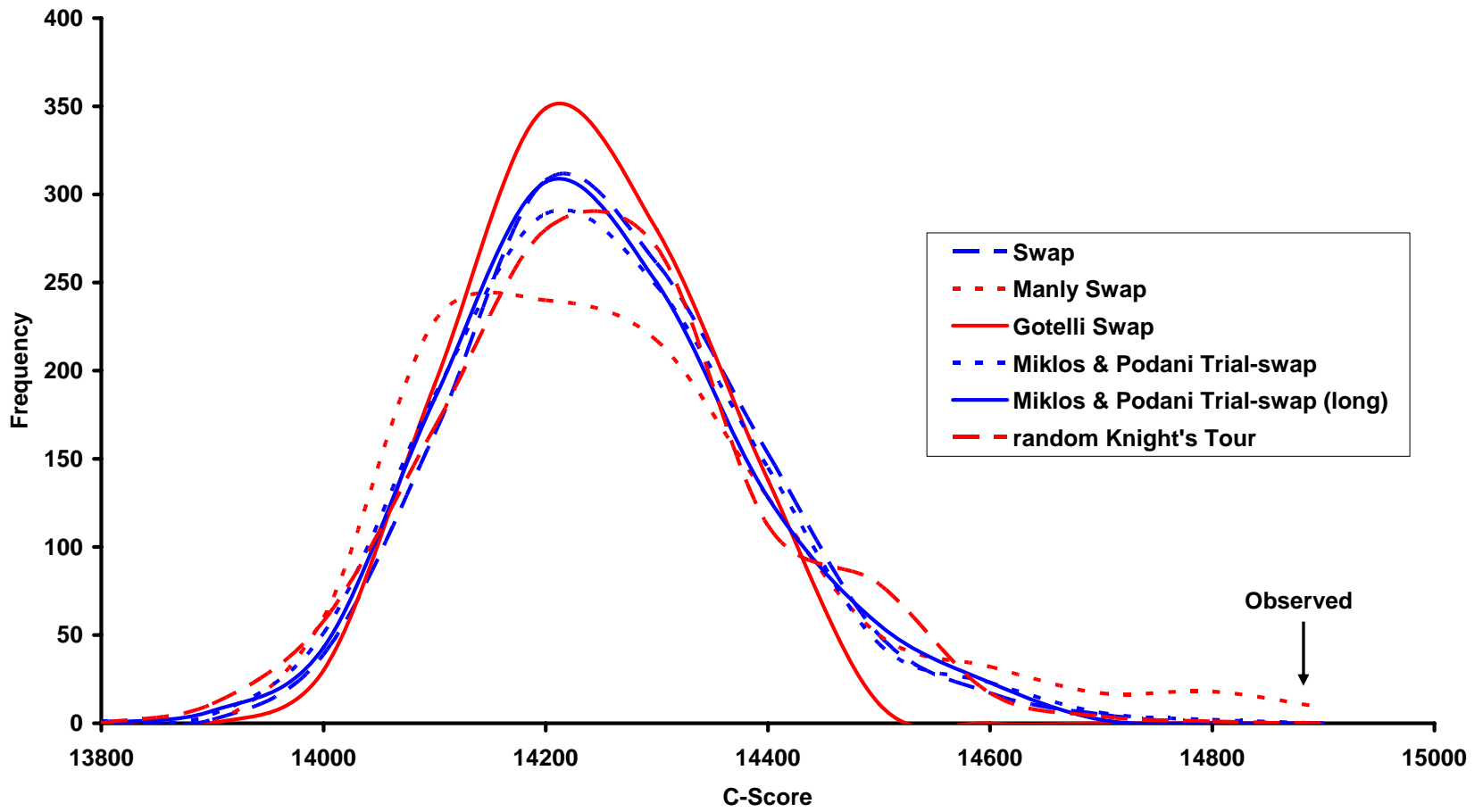


Figure 1.4. Frequency distribution of the C-score by randomization algorithm for birds of Vanuatu.

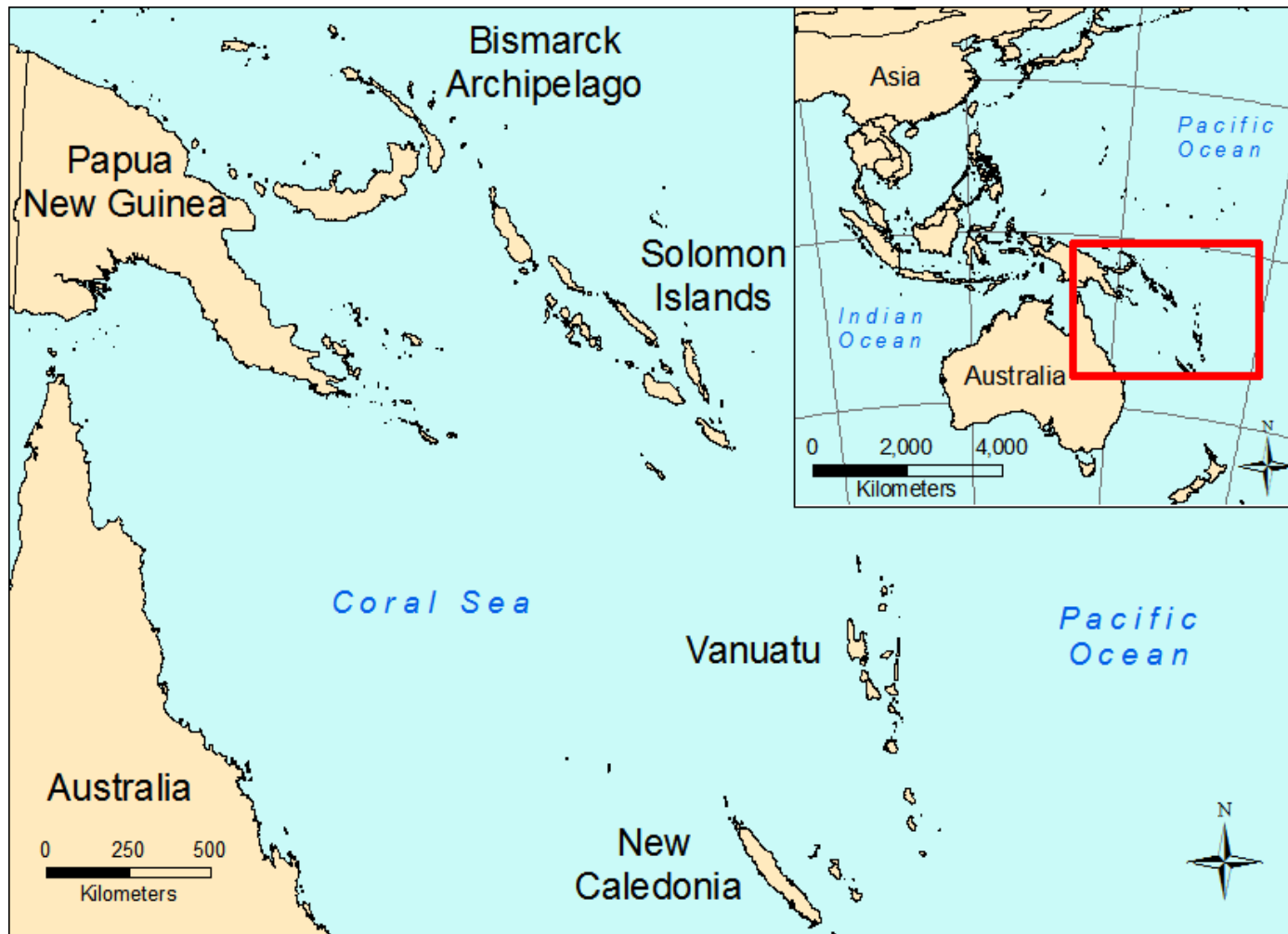


Figure 2.1. Map of the Bismarck Archipelago, Solomon Archipelago, and Vanuatu.

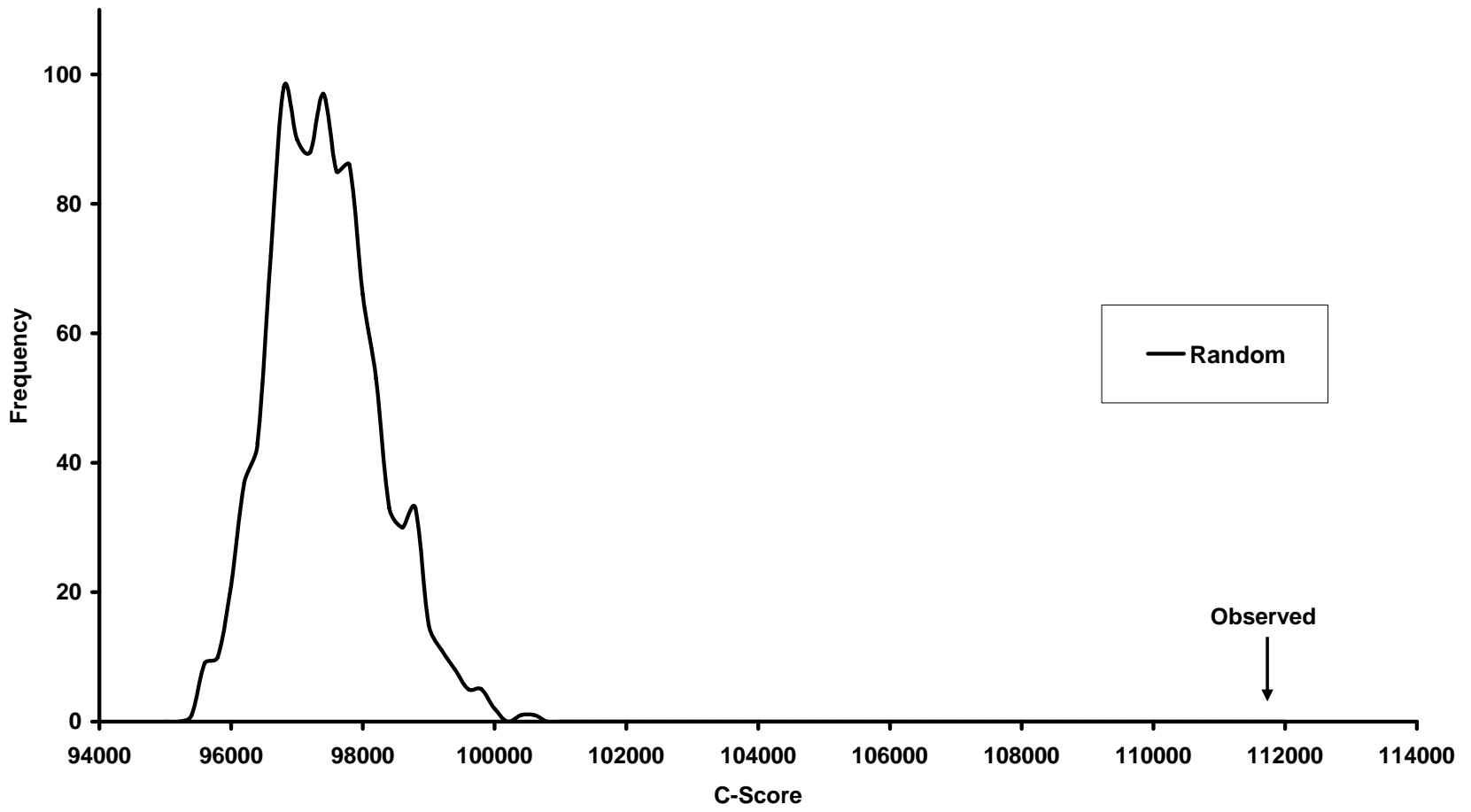


Figure 2.2. C-score: birds of the Bismarck Archipelago.

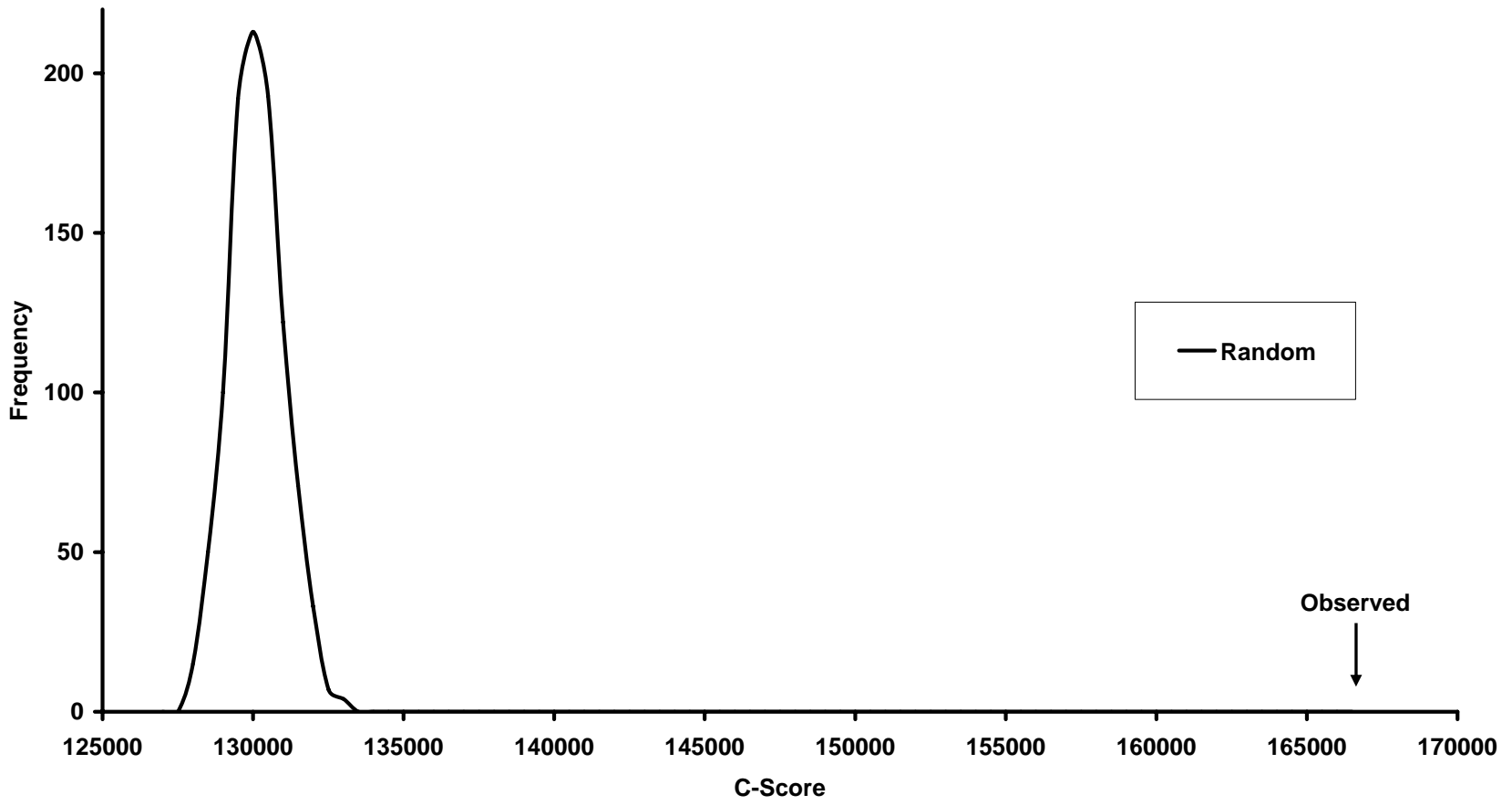


Figure 2.3. C-score: birds of the Solomon Archipelago.

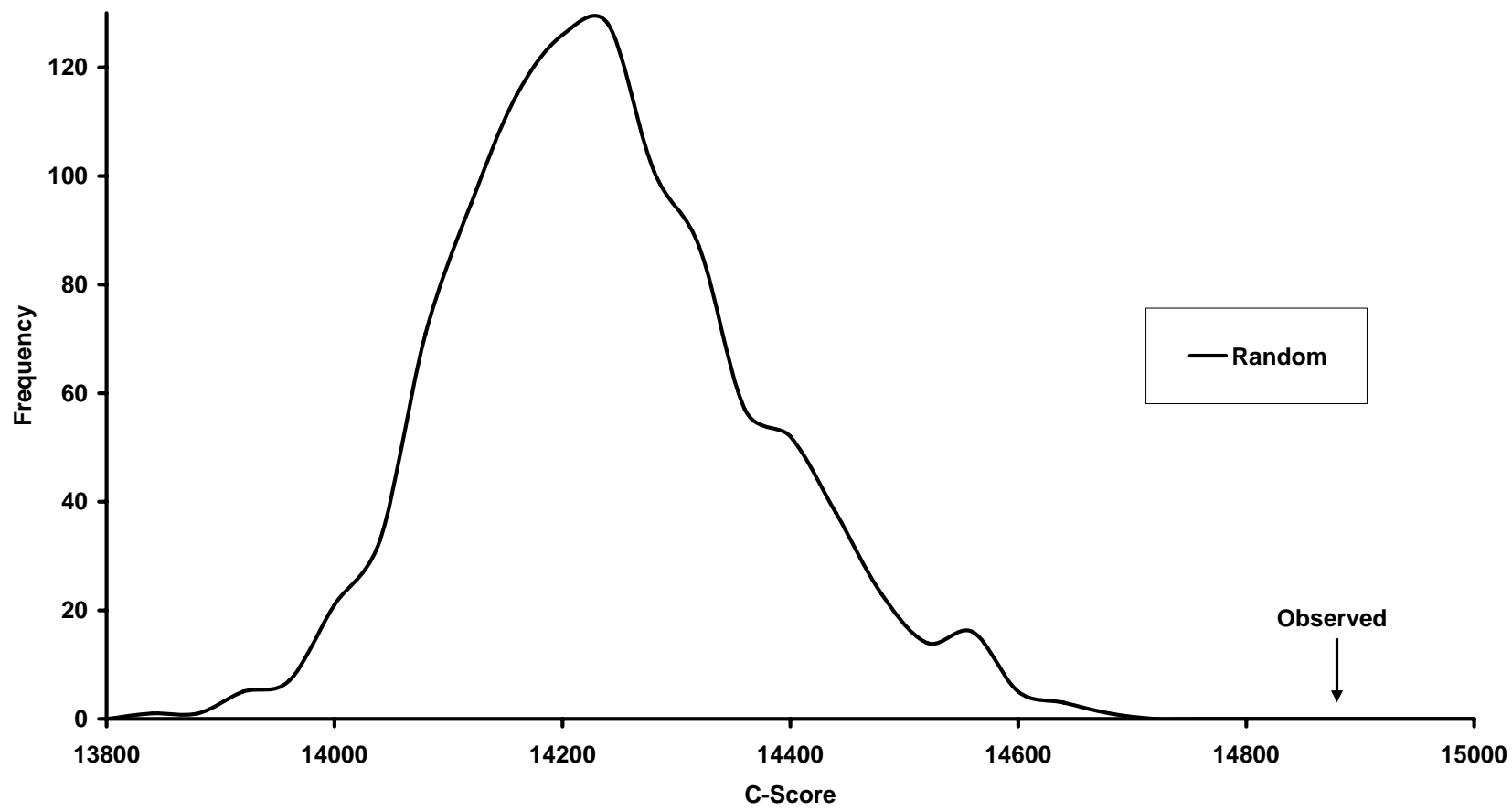


Figure 2.4. C-score: birds of Vanuatu.



Figure 2.5. Map of the Bismarck Archipelago.



Figure 2.6. Map of the Solomon Archipelago.



Figure 3.1. Islands of the Bismarck Archipelago.



Figure 3.2. Islands of the Solomon Archipelago.



Figure 3.3. Islands of Vanuatu.

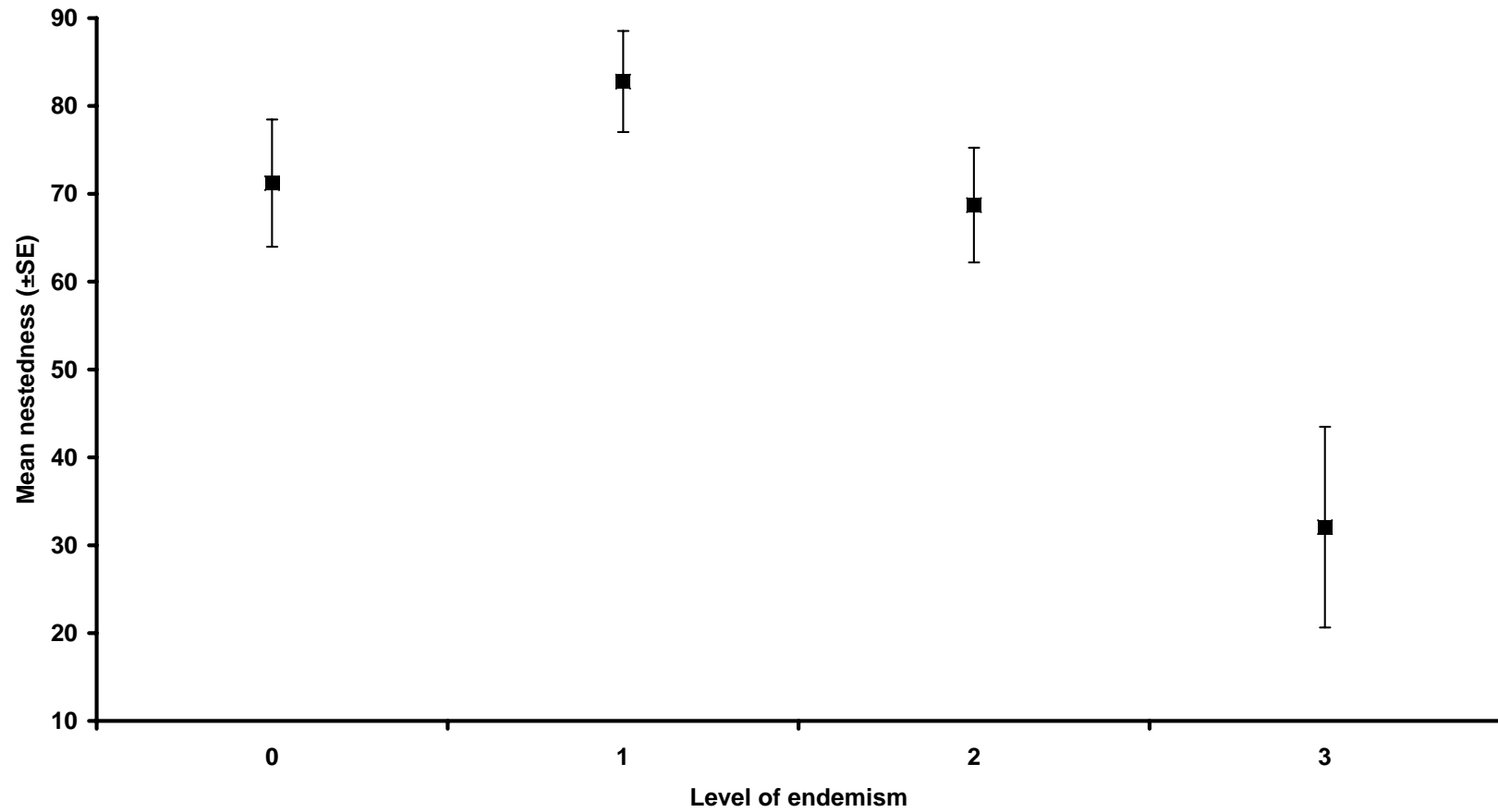


Figure 3.4. Nestedness by level of endemism for birds in the Bismarcks. Levels of endemism indicate not endemic (0), or endemic at the subspecies (1), allospecies (2), full species (3), or genus level (4).

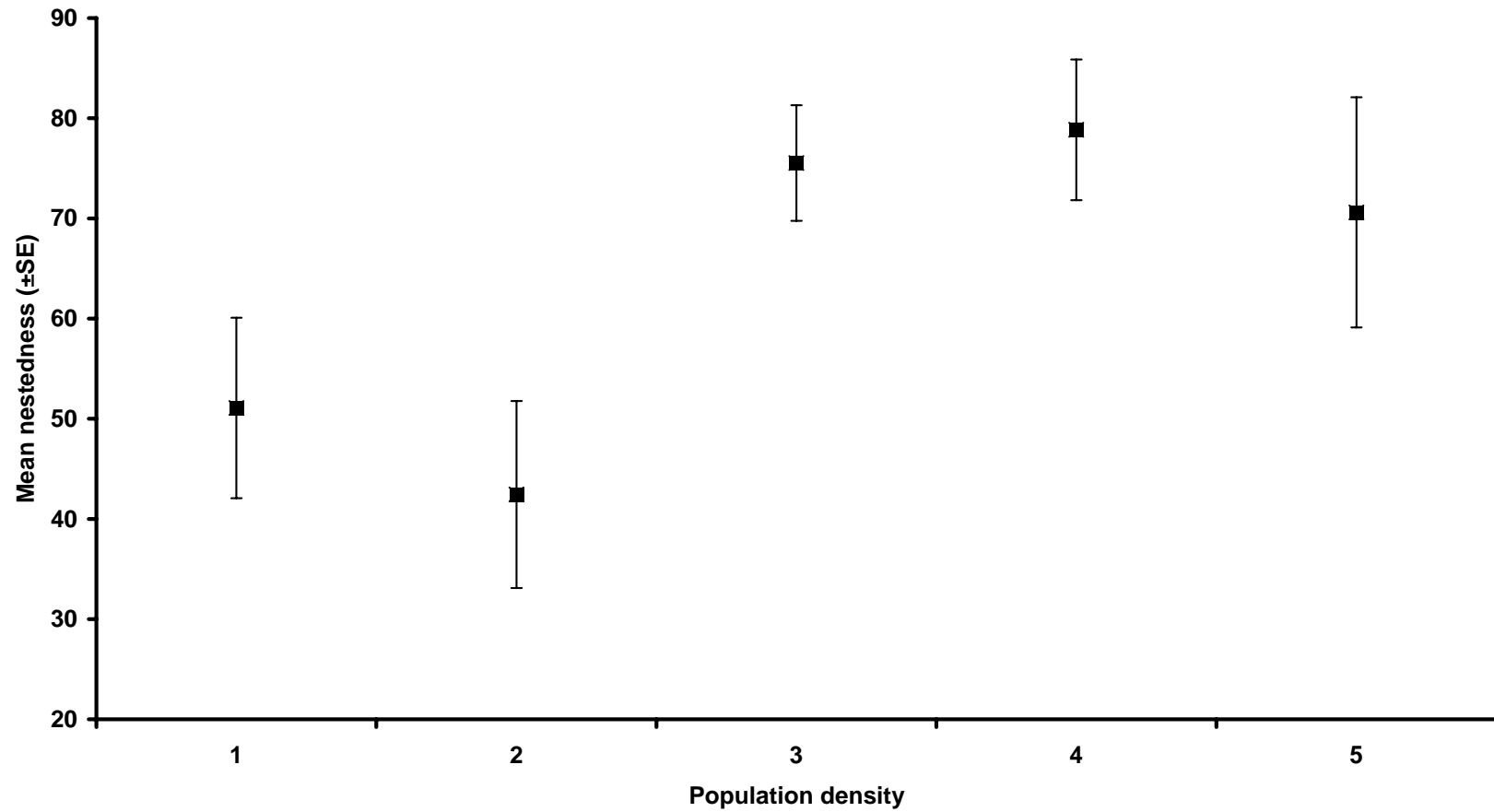


Figure 3.5. Nestedness by population density for birds in the Bismarcks. Population density groups are: (1) < 0.1 pairs/km²; (2) 0.1–1 pair/km²; (3) 1–10 pairs/km²; (4) 10–100 pairs/km²; and (5) ≥ 100 pairs/km².

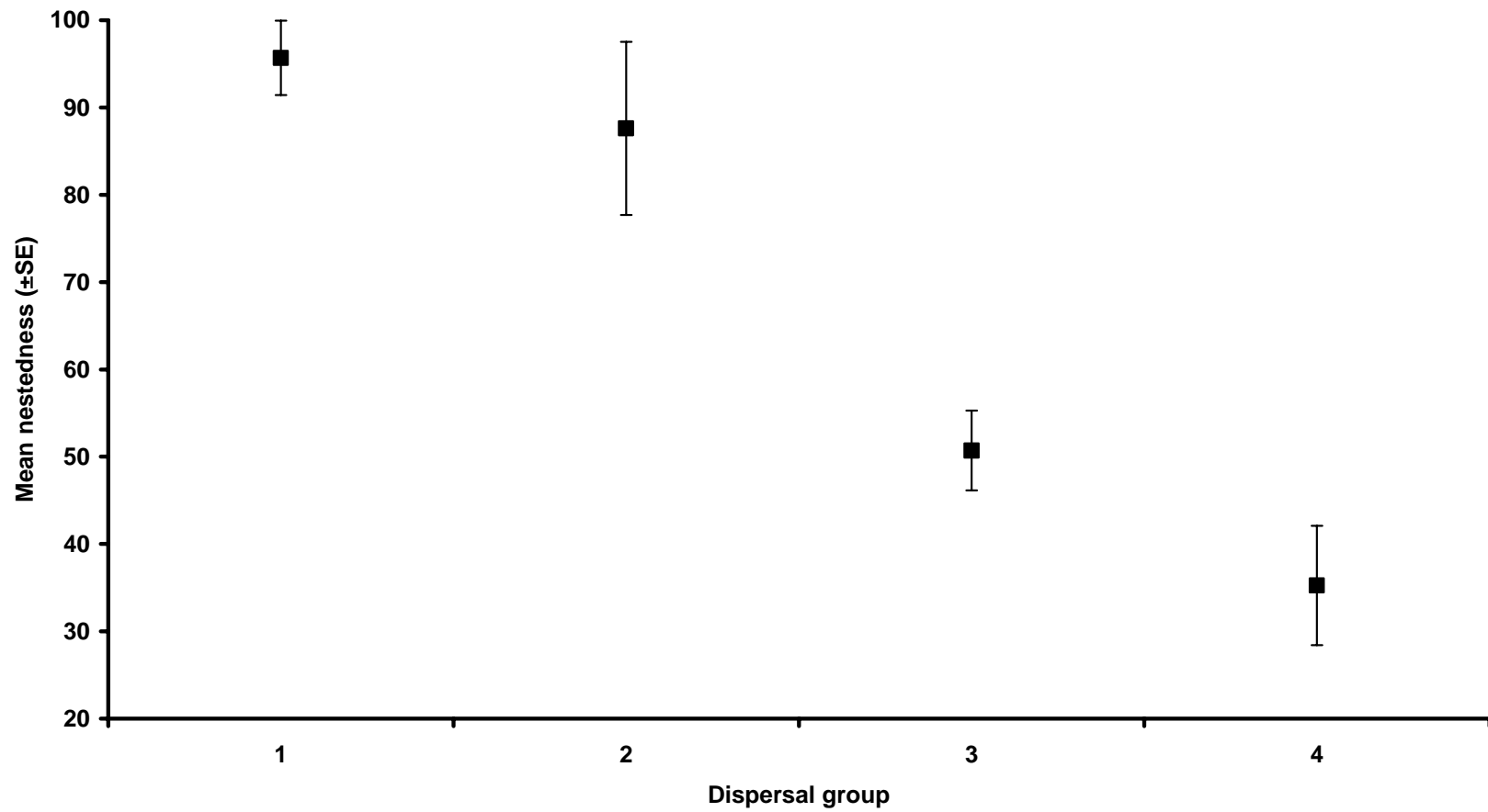


Figure 3.6. Nestedness by dispersal group for birds in the Solomons. Group 1 is comprised of the best dispersing species, and group 4 of the poorest dispersing species.

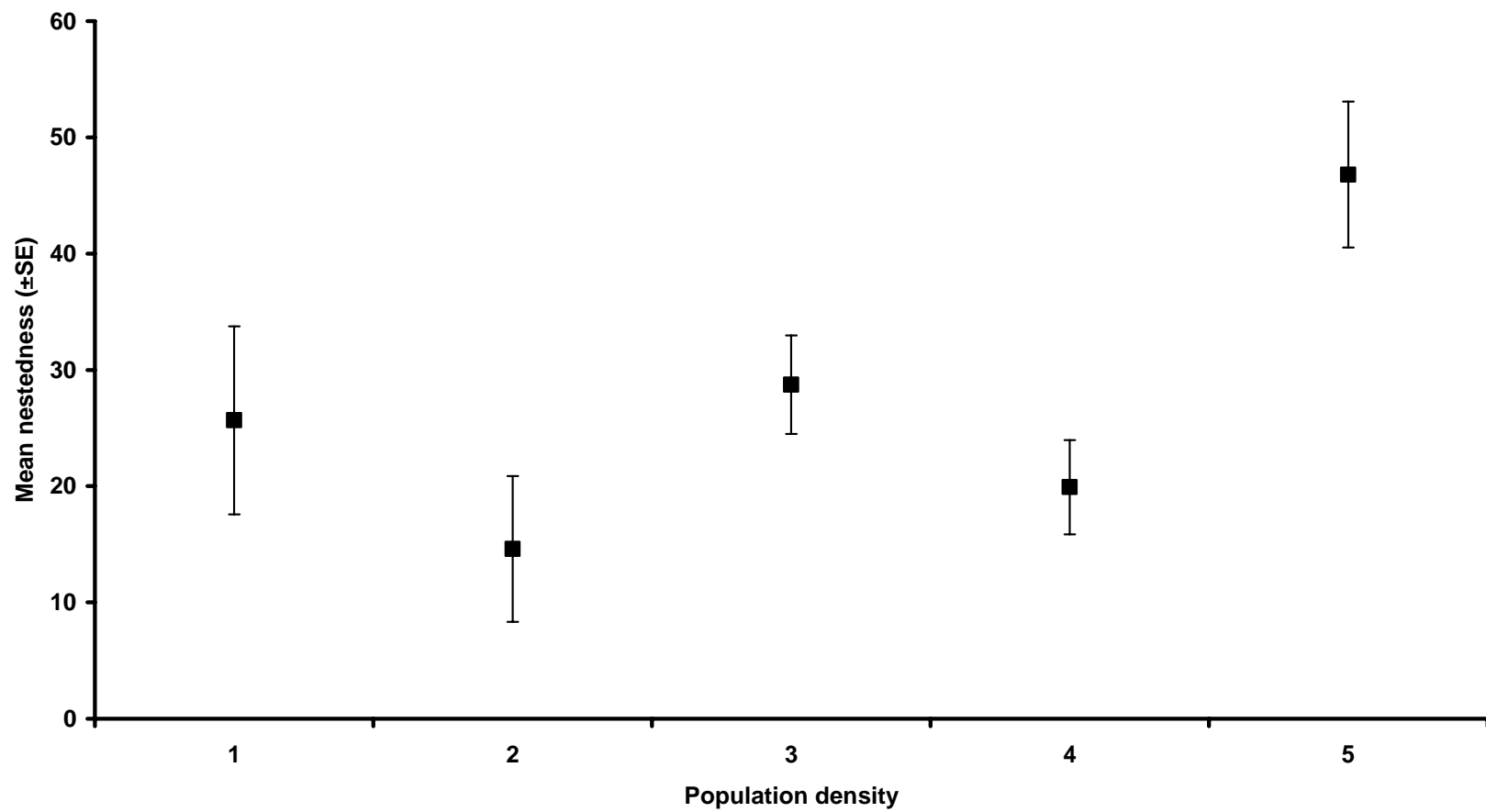


Figure 3.7. Nestedness by population density for birds in Vanuatu. Population density groups are: (1) < 0.1 pairs/km²; (2) 0.1–1 pair/km²; (3) 1–10 pairs/km²; (4) 10–100 pairs/km²; and (5) ≥ 100 pairs/km².

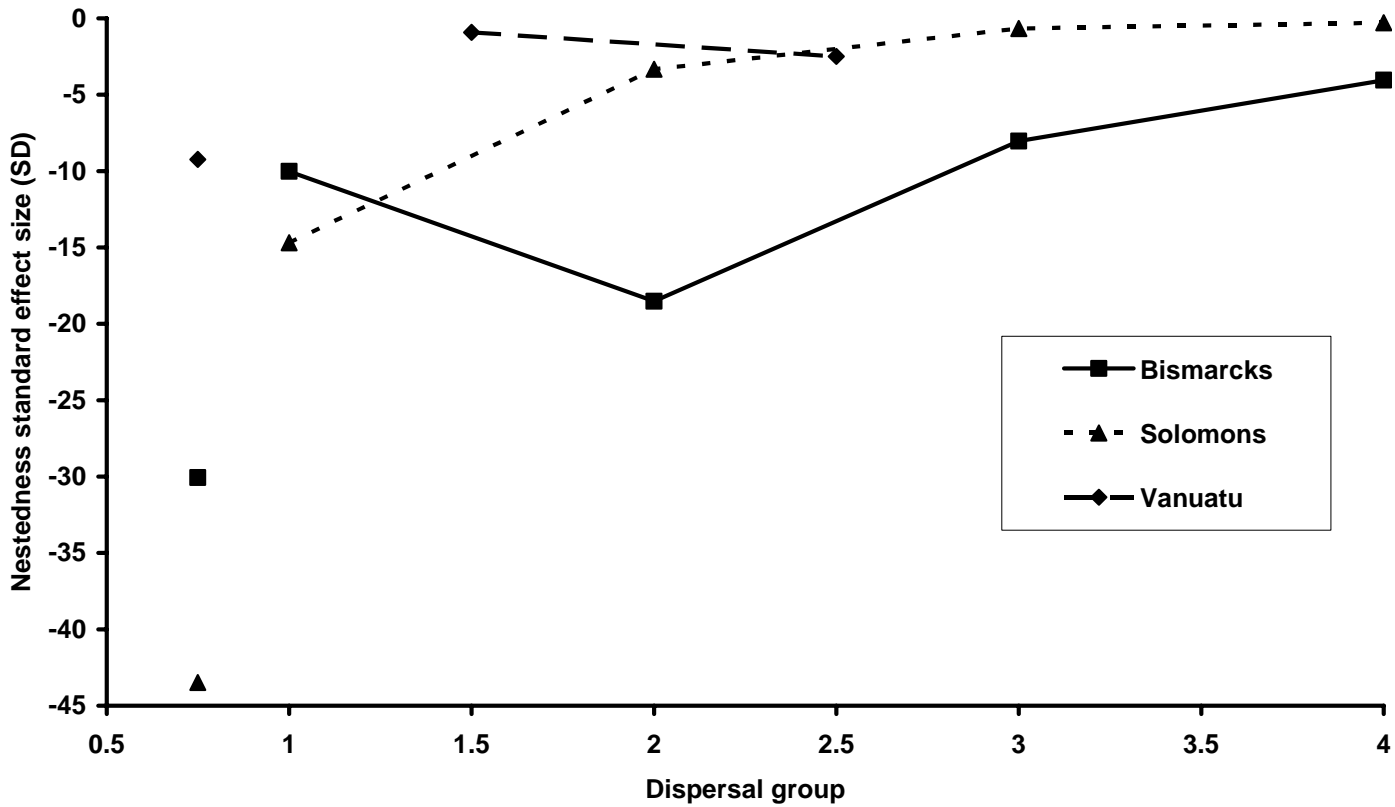


Figure 3.8. Nestedness effect size of dispersal groups by archipelago. For each archipelago, effect size for all dispersal groups combined is graphed on the left. Lower dispersal groups consists of better dispersing species. In Vanuatu, groups 1 and 2 and groups 3 and 4 were merged to form groups 1.5 and 2.5, respectively. Effect size equals $((\text{observed nestedness} - \text{randomized mean}) / (\text{randomized standard deviation}))$.

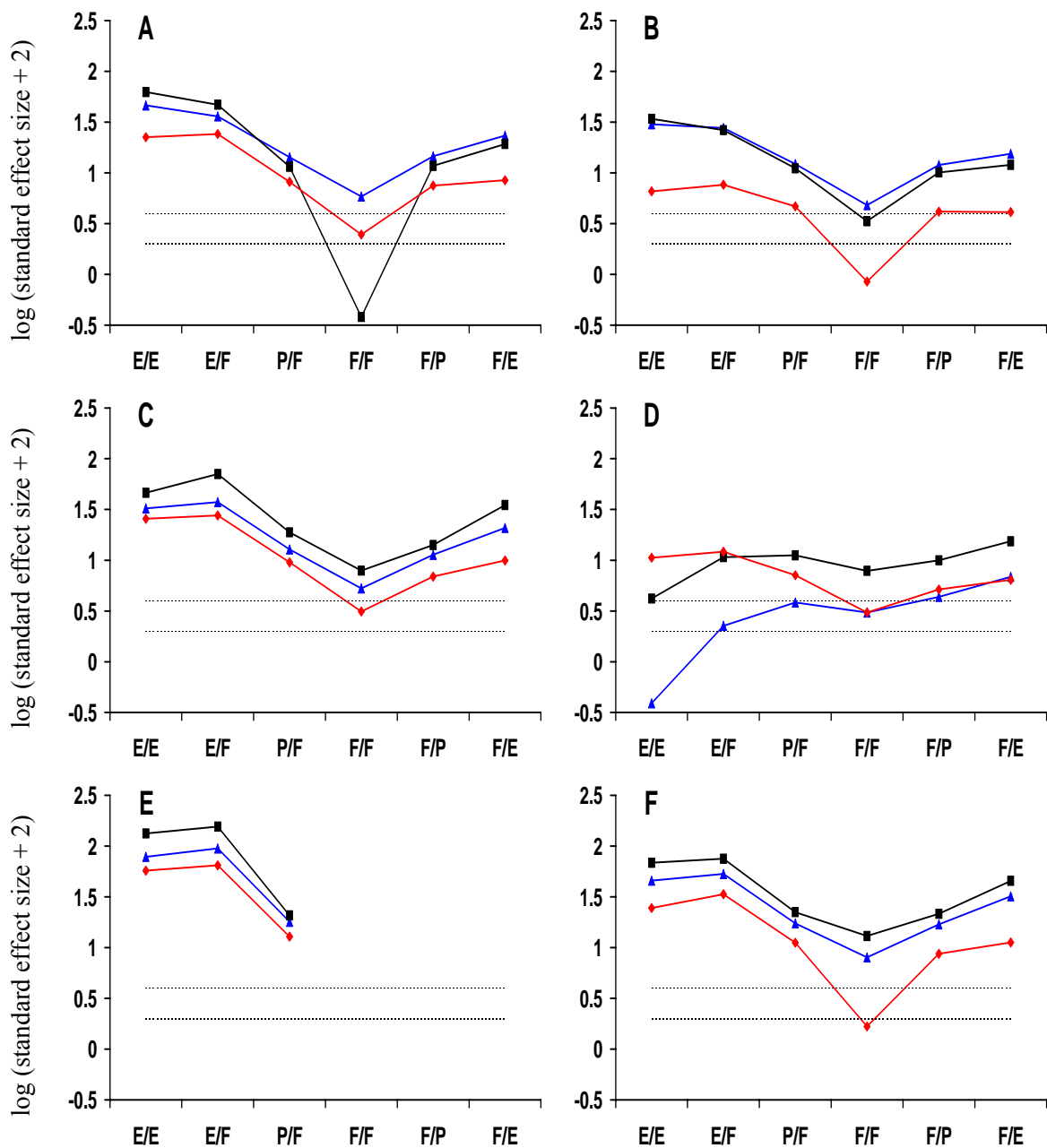


Figure 3.9. Standard effect sizes by randomization algorithm for nestedness metrics. Randomization algorithms are designated by species constraint / island constraint, where E = Equiprobable, P = Proportional, and F = Fixed. The Bismarck Archipelago is represented by blue triangles, the Solomon Archipelago by black squares, and Vanuatu by a red line with red diamonds. The upper dashed line indicates statistical significance ($p = 0.05$), and the lower dashed line indicates random expectation. Note that the y-axis is log transformed. A = N_0 ; B = Up ; C = N_I ; D = Ua ; E = N_C ; F = Ut . Figure E does not include measures for three randomization algorithms because N_C is constant for these algorithms.

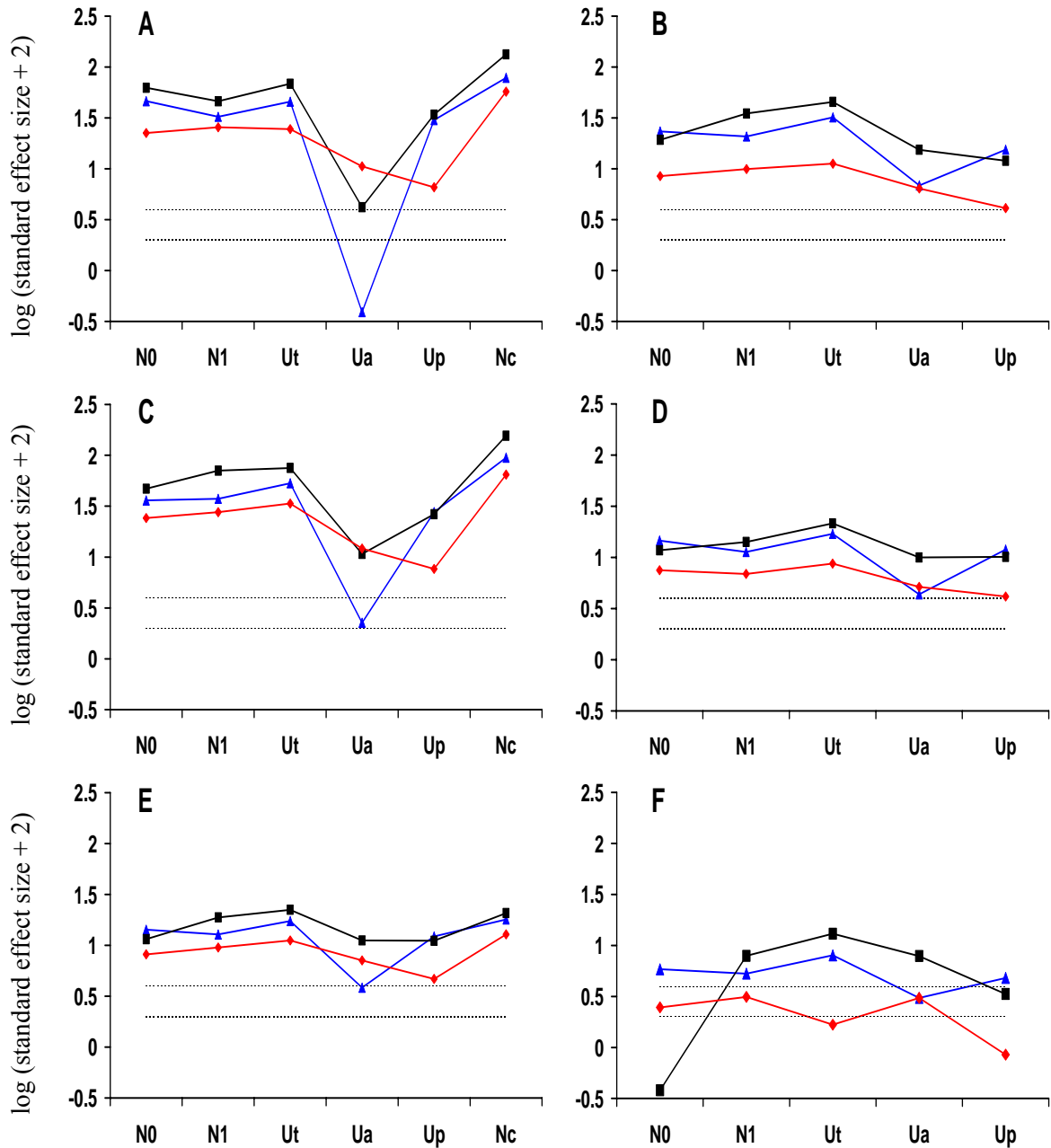


Figure 3.10. Standard effect sizes of nestedness metrics by randomization algorithm. The Bismarck Archipelago is represented by a blue line with blue triangles, the Solomon Archipelago by black lines with black squares, and Vanuatu by a red line with red diamonds. The upper dashed line indicates statistical significance ($p = 0.05$), and the lower dashed line indicates random expectation. Note that the y-axis is log transformed. A = Equiprobable/Equiprobable randomization algorithm; B = Fixed/Equiprobable; C = Equiprobable/Fixed; D = Fixed/Proportional; E = Proportional/Fixed; F = Fixed/Fixed. Figures B, D, and F do not include N_C because this metric is constant for these algorithms.

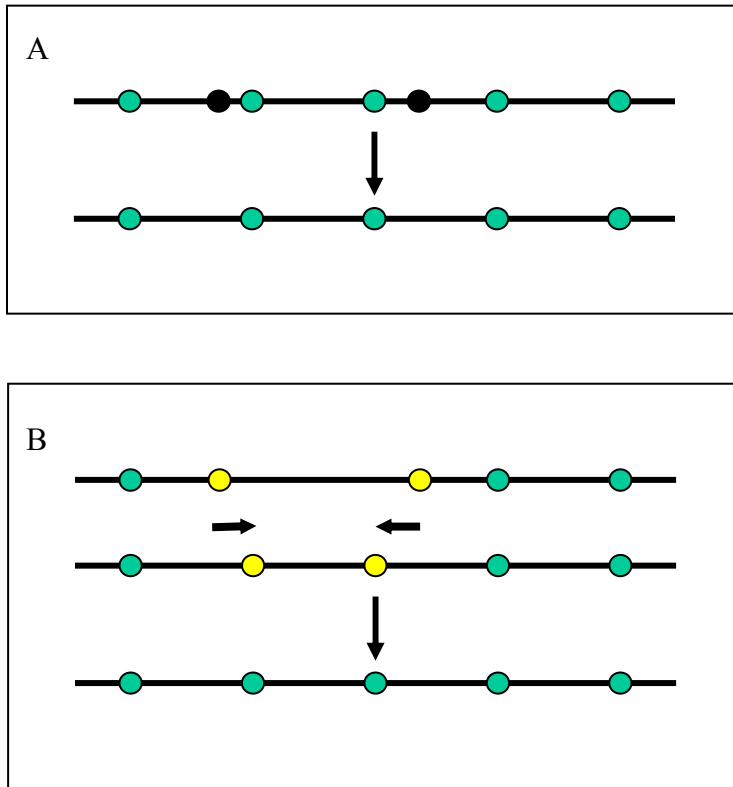


Figure 4.1. Two mechanisms of community-wide character displacement. Species assortment (A) is a product of community assembly and results from selective extinctions (shown here) or from nonrandom colonizations. Ecological character displacement (B) is an evolutionary response to interspecific competition (shown by yellow dots) and is driven by natural selection.

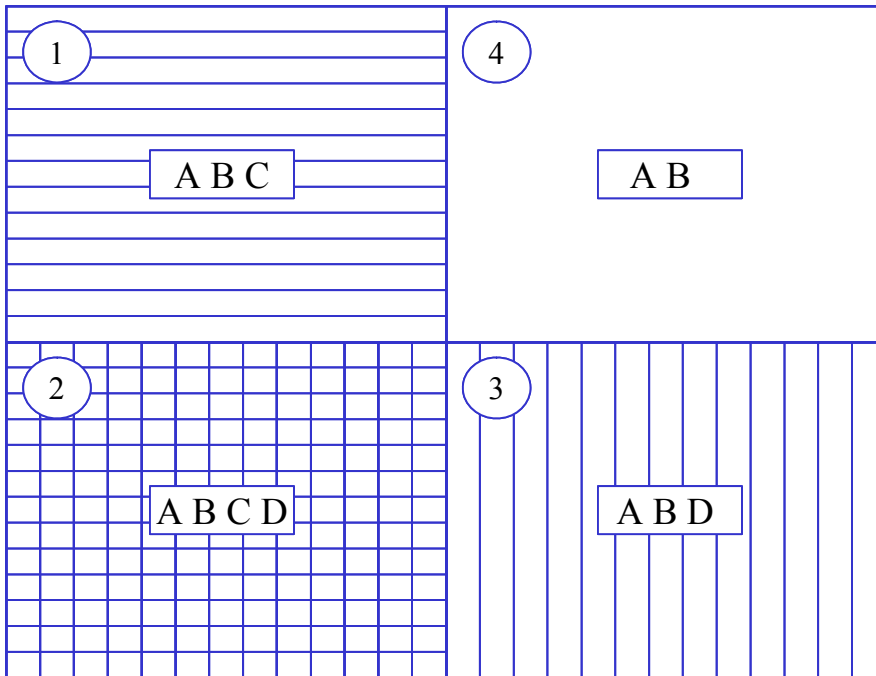
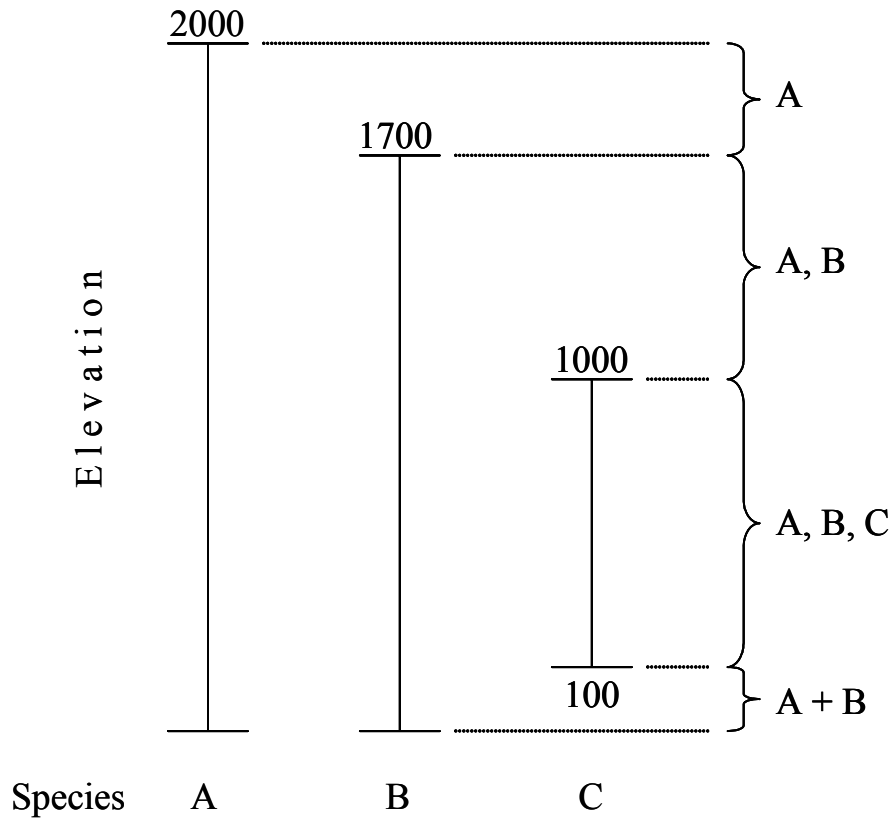


Figure 4.2. Representation of four geographic regions. Species A and B occur throughout the area depicted, species C occurs only in the West, and species D only in the South. The geographic ranges of these four species result in four geographic regions, each of which harbors a unique species composition.



Community	Species Composition	Elevation (m)
1	A, B	800
2	A, B, C	900
3	A	300

Figure 4.3. Separation of a geographic region into communities by elevation. Community 1, comprised of species A and B, occurs in two elevational bands, one at sea level to 100 m and another between 1000 m and 1700 m. Elevational bands are summed within geographic regions, and community 1 spans 800 m in elevation (100 + 700).

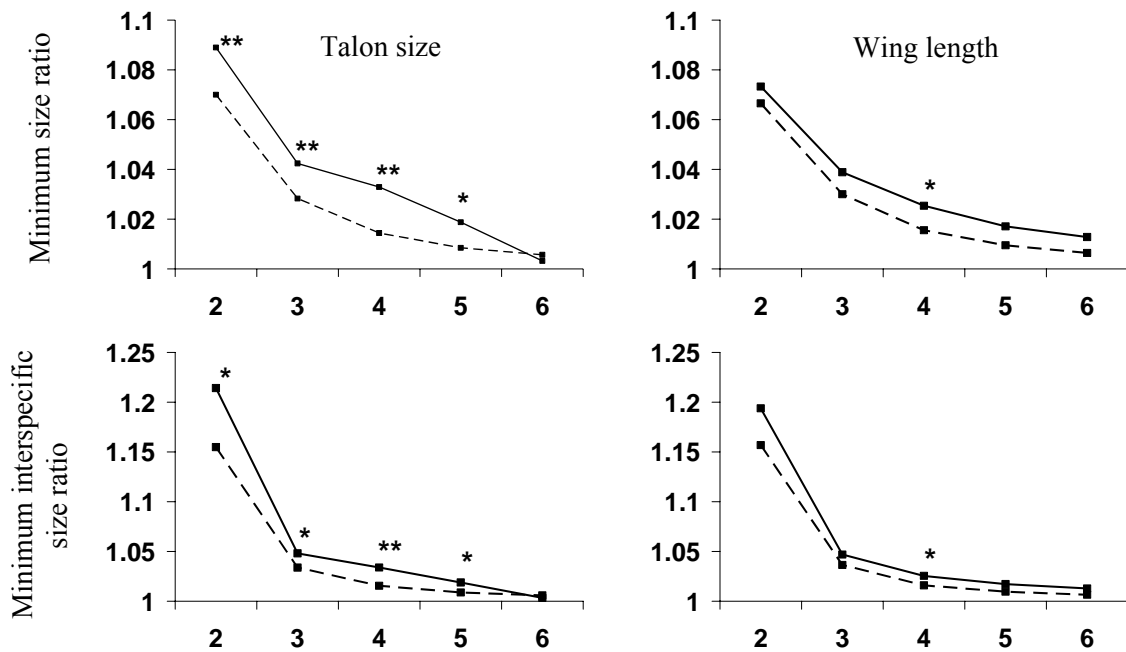


Figure 4.4. Minimum size ratios of *Accipiter* hawks in closed habitats. Two morphological traits, talon size and wing length, and two size ratios, minimum size ratio between any two morphospecies and minimum interspecific size ratio, are examined. Solid line shows observed minimum size ratio. Dashed line shows predicted minimum size ratio. ** indicates $p < 0.01$; * indicates $p < 0.05$.

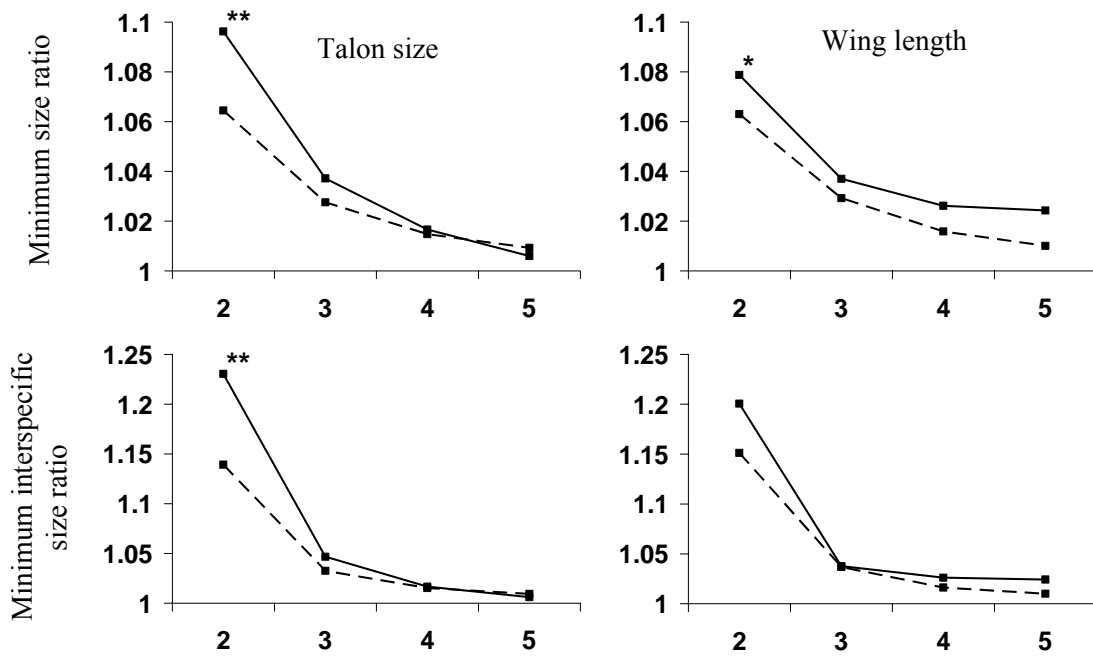


Figure 4.5. Minimum size ratios of *Accipiter* hawks in open habitats. Two morphological traits, talon size and wing length, and two size ratios, minimum size ratio between any two morphospecies and minimum interspecific size ratio, are examined. Solid line shows observed minimum size ratio. Dashed line shows predicted minimum size ratio. * indicates $p < 0.05$.

APPENDIX C. Presence-absence matrix for the Bismarck Archipelago.

Species	A*	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
<i>Casuaris bennetti</i>	1																
<i>Tachybaptus ruficollis</i>	1	1											1	1			
<i>Pelecanus conspicillatus</i>	1																
<i>Phalacrocorax melanoleucos</i>	1																
<i>Butorides striatus</i>	1	1															
<i>Egretta sacra</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Ardea intermedia</i>	1				1									1			
<i>Ardea alba</i>	1																
<i>Nycticorax nycticorax</i>	1	1	1		1	1		1	1		1	1	1	1	1	1	
<i>Ixobrychus minutus</i>	1																
<i>Ixobrychus flavicollis</i>	1	1	1	1	1					1	1			1	1	1	
<i>Dendrocygna bicolor</i>	1													1			
<i>Dendrocygna guttata</i>	1													1			
<i>Anas platyrhynchos</i>	1	1	1		1	1							1	1			
<i>Aviceda cuculoides</i>	1	1	1		1			1									
<i>Henicopernis lognicauda</i>	1																
<i>Haliastur indus</i>	1	1	1	1	1	1	1	1			1	1	1	1	1	1	
<i>Accipiter gentilis</i>	1													1			
<i>Accipiter novaehollandiae</i>	1	1	1	1	1	1	1	1						1		1	
<i>Accipiter rufitorques</i>	1																
<i>Accipiter luteoschistaceus</i>	1													1			
<i>Accipiter poliocephalus</i>	1																
<i>Accipiter cirrhocephalus</i>	1	1															
<i>Haliaeetus leucogaaster</i>	1	1	1	1	1		1	1				1	1	1	1	1	
<i>Pandion haliaetus</i>	1	1	1	1	1	1	1				1	1	1	1	1	1	
<i>Falco peregrinus</i>	1												1				
<i>Falco subbuteo</i>	1																1
<i>Falco berigora</i>	1												1				
<i>Megapodius freycinet</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Coturnix chinensis</i>	1	1	1												1	1	
<i>Turnix sylvatica</i>	1																1
<i>Gallirallus philippensis</i>	1	1	1						1	1	1	1	1		1	1	
<i>Gallirallus insignis</i>	1																
<i>Rallina eurizonoides</i>		1	1	1													
<i>Porzana tabuensis</i>												1			1		
<i>Poliolimnas cinereus</i>	1	1	1	1										1			
<i>Amauornis akool</i>	1	1	1										1	1	1	1	
<i>Porphyrio porphyrio</i>	1		1		1	1								1	1		
<i>Irediparra gallinacea</i>	1																
<i>Charadrius dubius</i>	1	1															

* Island abbreviations are defined in Appendix F.

APPENDIX C. Continued.

Species	R	S	T	U	V	W	X	Y	Z	AA	AB	AC	AD	AE
<i>Casuarius bennetti</i>														
<i>Tachybaptus ruficollis</i>								1				1		
<i>Pelecanus conspicillatus</i>					1									
<i>Phalacrocorax melanoleucos</i>														
<i>Butorides striatus</i>														
<i>Egretta sacra</i>	1	1		1	1	1	1	1	1	1	1	1	1	1
<i>Ardea intermedia</i>														
<i>Ardea alba</i>													1	
<i>Nycticorax nycticorax</i>		1		1	1	1	1	1	1	1	1			
<i>Ixobrychus minutus</i>														
<i>Ixobrychus flavicollis</i>	1	1		1	1	1						1		
<i>Dendrocygna bicolor</i>														
<i>Dendrocygna guttata</i>														
<i>Anas platyrhynchos</i>				1	1	1								
<i>Aviceda cuculoides</i>		1				1		1						
<i>Henicopernis lognicauda</i>								1						
<i>Haliastur indus</i>	1	1	1	1	1	1	1	1	1	1	1			
<i>Accipiter gentilis</i>														
<i>Accipiter novaehollandiae</i>		1		1		1	1	1						
<i>Accipiter rufitorques</i>					1									
<i>Accipiter luteoschistaceus</i>														
<i>Accipiter poliocephalus</i>														
<i>Accipiter cirrhocephalus</i>														
<i>Haliaeetus leucogaaster</i>	1			1	1	1	1	1	1		1	1		
<i>Pandion haliaetus</i>	1	1		1	1	1	1		1		1	1		1
<i>Falco peregrinus</i>				1	1							1		
<i>Falco subbuteo</i>								1						
<i>Falco berigora</i>														
<i>Megapodius freycinet</i>	1	1	1	1	1	1	1	1	1	1	1	1		1
<i>Coturnix chinensis</i>				1		1	1							
<i>Turnix sylvatica</i>														
<i>Gallirallus philippensis</i>				1		1	1					1		
<i>Gallirallus insignis</i>														
<i>Rallina eurizonoides</i>														
<i>Porzana tabuensis</i>														
<i>Poliolimnas cinereus</i>	1			1										
<i>Amauornis akool</i>				1		1	1		1	1		1		
<i>Porphyrio porphyrio</i>						1								
<i>Irediparra gallinacea</i>														
<i>Charadrius dubius</i>														

APPENDIX C. Continued.

Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
<i>Himantopus himantopus</i>	1												1	1			
<i>Esacus magnirostris</i>	1	1	1	1	1								1			1	1
<i>Ptilinopus superbus</i>	1	1	1		1	1								1			
<i>Ptilinopus hyogaster</i>	1	1	1	1									1	1	1	1	
<i>Ptilinopus rivoli</i>	1	1	1											1			
<i>Ptilinopus solomonensis</i>			1	1	1	1	1	1	1	1	1	1	1	1	1		
<i>Ptilinopus viridis</i>					1												
<i>Ducula pacifica</i>									1	1	1	1					
<i>Ducula myristicivora</i>	1	1	1											1	1	1	1
<i>Ducula rufigaster</i>	1	1												1			
<i>Ducula rosacea</i>	1	1	1	1	1	1	1	1		1		1	1	1	1	1	1
<i>Ducula pinon</i>	1	1												1			
<i>Ducula bicolor</i>	1	1	1		1		1						1	1			
<i>Gymnophaps albertisii</i>	1	1															
<i>Columba leucomela</i>		1															
<i>Columba pallidiceps</i>	1	1															
<i>Macropygia amboinensis</i>	1	1	1		1								1	1	1	1	
<i>Macropygia nigrirostris</i>	1	1	1													1	
<i>Macropygia mackinlayi</i>				1	1	1	1	1					1	1	1		
<i>Reinwardtoena reinwardtii</i>	1	1	1		1	1	1							1		1	
<i>Chalcophaps stephani</i>	1	1	1	1	1	1	1						1	1	1	1	
<i>Henicophaps albifrons</i>	1													1			
<i>Gallucolumba canifrons</i>	1	1	1	1	1								1	1		1	
<i>Gallucolumba erythroptera</i>	1	1								1				1	1		
<i>Caloenas nicobarica</i>	1	1	1	1	1	1	1			1		1	1	1	1	1	1
<i>Chalcopsitta cardinalis</i>																	
<i>Trichoglossus ornatus</i>	1	1	1	1	1	1	1	1		1	1		1	1	1	1	
<i>Lorius albidinucha</i>		1															
<i>Lorius chlorocercus</i>	1	1	1										1	1			
<i>Charmosyna palmarum</i>	1	1															
<i>Charmosyna placentas</i>	1	1	1										1	1	1	1	1
<i>Micropsitta bruijnii</i>	1	1															
<i>Micropsitta pusio</i>	1	1	1	1	1	1								1	1	1	
<i>Cacatua alba</i>	1																
<i>Eclectus roratus</i>	1	1	1		1	1								1	1	1	
<i>Geoffroyus heteroclitus</i>	1	1	1											1		1	
<i>Loriculus aurantiifrons</i>	1	1	1													1	
<i>Cacomantis variolosus</i>	1	1	1		1	1					1		1	1	1	1	
<i>Eudynamys scolopacea</i>	1	1											1	1	1	1	
<i>Scythrops novaehollandiae</i>	1	1		1	1			1					1	1	1	1	

APPENDIX C. Continued.

Species	R	S	T	U	V	W	X	Y	Z	AA	AB	AC	AD	AE
<i>Himantopus himantopus</i>														
<i>Esacus magnirostris</i>	1			1					1	1	1			
<i>Ptilinopus superbus</i>				1	1	1	1	1	1					
<i>Ptilinopus hyogaster</i>	1	1		1	1	1		1	1	1	1			
<i>Ptilinopus rivoli</i>		1		1		1	1	1						
<i>Ptilinopus solomonensis</i>	1		1						1	1	1	1		1
<i>Ptilinopus viridis</i>				1			1							
<i>Ducula pacifica</i>														1
<i>Ducula myristicivora</i>		1		1	1	1	1	1		1				
<i>Ducula rufigaster</i>		1												
<i>Ducula rosacea</i>	1	1		1	1	1	1	1	1		1	1	1	
<i>Ducula pinon</i>														
<i>Ducula bicolor</i>								1	1	1	1			
<i>Gymnophaps albertisii</i>														
<i>Columba leucomela</i>														
<i>Columba pallidiceps</i>														
<i>Macropygia amboinensis</i>		1		1	1	1	1	1	1	1				
<i>Macropygia nigrirostris</i>						1								
<i>Macropygia mackinlayi</i>	1			1					1	1	1	1		1
<i>Reinwardtoena reinwardtii</i>		1		1		1		1						
<i>Chalcophaps stephani</i>	1	1		1	1	1	1	1	1	1	1	1	1	
<i>Henicophaps albifrons</i>								1						
<i>Gallucolumba canifrons</i>	1			1	1		1	1	1	1	1	1		
<i>Gallucolumba erythroptera</i>				1		1		1		1				
<i>Caloenas nicobarica</i>	1	1		1	1	1	1	1	1	1	1		1	1
<i>Chalcopsitta cardinalis</i>				1	1	1	1							
<i>Trichoglossus ornatus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Lorius albidinucha</i>														
<i>Lorius chlorocercus</i>		1		1		1		1		1		1		
<i>Charmosyna palmarum</i>														
<i>Charmosyna placentas</i>		1		1	1	1	1	1	1	1	1	1		
<i>Micropsitta bruijnii</i>														
<i>Micropsitta pusio</i>	1	1		1		1		1	1	1		1	1	
<i>Cacatua alba</i>														
<i>Eclectus roratus</i>		1		1	1	1	1	1				1	1	
<i>Geoffroyus heteroclitus</i>		1		1		1		1				1		
<i>Loriculus aurantiifrons</i>														
<i>Cacomantis variolosus</i>		1		1		1	1	1					1	
<i>Eudynamys scolopacea</i>								1	1	1	1			
<i>Scythrops novaehollandiae</i>		1		1	1	1	1	1		1				

APPENDIX C. Continued.

Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
<i>Centropus ateralbus</i>	1	1												1			
<i>Centropus violaceus</i>	1	1															
<i>Tyto alba</i>													1				
<i>Tyto novaehollandiae</i>	1				1												
<i>Ninox novaeseelandiae</i>	1	1	1		1										1		
<i>Caprimulgus macrurus</i>	1	1	1										1	1	1		
<i>Aerodramus orientalis</i>		1															
<i>Aerodramus vanikorensis</i>	1	1	1	1	1	1							1	1	1	1	
<i>Aerodramus spodiopygius</i>	1	1		1	1										1		
<i>Collocalia esculenta</i>	1	1	1		1	1	1						1				
<i>Hemiprocne mystacea</i>	1	1	1	1	1	1							1	1	1	1	
<i>Alcedo atthis</i>	1	1	1	1	1								1	1	1	1	
<i>Alcedo azurea</i>	1	1	1											1			
<i>Alcedo pusilla</i>	1	1	1											1			
<i>Ceyx lepidus</i>	1	1	1		1									1	1		
<i>Halcyon diops</i>	1																
<i>Halcyon australasia</i>	1	1	1	1	1	1	1			1		1	1	1	1	1	1
<i>Halcyon chloris</i>	1	1	1	1									1	1	1		
<i>Halcyon saurophaga</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Tanyiptera sylvia</i>	1													1		1	
<i>Merops superciliosus</i>	1												1	1			
<i>Eurystomus orientalis</i>	1	1	1	1										1		1	
<i>Rhyticeros plicatus</i>	1	1	1														
<i>Pitta sordida</i>					1								1				
<i>Pitta erythrogaster</i>	1	1	1											1	1		
<i>Hirundo rustica</i>	1	1	1		1								1	1	1	1	
<i>Coracina lineata</i>	1	1															
<i>Coracina papuensis</i>	1	1	1											1	1		
<i>Coracina tenuirostris</i>	1	1	1	1	1								1	1			
<i>Lalage aurea</i>	1	1	1	1										1	1	1	
<i>Saxicola caprata</i>	1	1											1		1		
<i>Zoothera dauma</i>	1			1										1			
<i>Turdus poliocephalus</i>	1	1		1													
<i>Ortygocichla rubiginosa</i>	1																
<i>Cichlornis whitneyi</i>	1																
<i>Acrocephalus arundinaceus</i>	1	1											1	1			
<i>Cisticola exilis</i>	1	1	1										1	1	1	1	
<i>Megalurus timoriensis</i>	1	1	1												1		
<i>Phylloscopus trivirgatus</i>	1	1		1										1			
<i>Rhipidura leucophrys</i>	1	1	1	1									1	1	1	1	1

APPENDIX C. Continued.

Species	R	S	T	U	V	W	X	Y	Z	AA	AB	AC	AD	AE
<i>Centropus ateralbus</i>		1						1						
<i>Centropus violaceus</i>														
<i>Tyto alba</i>							1							
<i>Tyto novaehollandiae</i>														
<i>Ninox novaeseelandiae</i>														
<i>Caprimulgus macrurus</i>				1		1		1	1					
<i>Aerodramus orientalis</i>														
<i>Aerodramus vanikorensis</i>	1	1	1	1	1	1	1		1		1	1	1	
<i>Aerodramus spodiopygius</i>	1			1		1								
<i>Collocalia esculenta</i>		1		1	1	1	1		1		1	1		1
<i>Hemiprocne mystacea</i>	1	1		1	1	1	1	1						
<i>Alcedo atthis</i>	1	1		1	1	1	1		1	1				
<i>Alcedo azurea</i>				1										
<i>Alcedo pusilla</i>		1				1								
<i>Ceyx lepidus</i>		1		1		1		1						
<i>Halcyon diops</i>														
<i>Halcyon australasia</i>	1			1	1	1			1	1	1	1	1	1
<i>Halcyon chloris</i>	1	1	1	1	1	1	1	1	1		1	1	1	
<i>Halcyon saurophaga</i>	1	1	1	1	1	1	1	1	1		1	1		1
<i>Tanyiptera sylvia</i>								1						
<i>Merops superciliosus</i>										1				
<i>Eurystomus orientalis</i>				1	1	1		1	1	1		1	1	
<i>Rhyticeros plicatus</i>														
<i>Pitta sordida</i>									1		1			
<i>Pitta erythrogaster</i>		1				1		1	1					
<i>Hirundo rustica</i>				1	1	1	1		1	1	1			
<i>Coracina lineata</i>								1						
<i>Coracina papuensis</i>								1						
<i>Coracina tenuirostris</i>	1	1		1	1	1	1	1		1				
<i>Lalage aurea</i>		1		1		1		1		1				
<i>Saxicola caprata</i>														
<i>Zoothera dauma</i>	1													
<i>Turdus poliocephalus</i>									1					
<i>Ortygocichla rubiginosa</i>														
<i>Cichlornis whitneyi</i>														
<i>Acrocephalus arundinaceus</i>														
<i>Cisticola exilis</i>				1		1				1				
<i>Megalurus timoriensis</i>									1					
<i>Phylloscopus trivirgatus</i>														
<i>Rhipidura leucophrys</i>	1	1	1	1		1		1	1	1		1	1	

APPENDIX C. Continued.

Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
<i>Rhipidura rufiventris</i>	1	1	1	1	1	1									1	1	
<i>Rhipidura rufifrons</i>					1			1									
<i>Rhipidura rufidorsa</i>	1	1		1										1			
<i>Monarcha cinerascens</i>				1		1	1	1	1	1	1	1	1		1		1
<i>Monarcha manadensis</i>	1	1	1	1	1	1								1		1	
<i>Monarcha chrysomela</i>		1	1														
<i>Myiagra alecto</i>	1	1	1		1	1								1	1	1	1
<i>Myiagra hebetior</i>	1	1	1	1											1		
<i>Monachella muelleriana</i>	1																
<i>Pachycephala pectoralis</i>	1	1	1	1	1									1			
<i>Pachycephala melanura</i>													1		1		1
<i>Dicaeum erythrothorax</i>	1	1	1												1		
<i>Nectarinia sperata</i>	1	1	1											1	1	1	1
<i>Nectarinia jugularis</i>	1	1	1	1	1	1				1	1		1	1	1	1	
<i>Zosterops atriceps</i>	1	1	1		1									1	1		
<i>Zosterops griseotinctus</i>							1						1				
<i>Myzomela eques</i>	1													1			
<i>Myzomela cruentata</i>	1	1	1														
<i>Myzomela pulchella</i>		1															
<i>Myzomela cardinalis</i>	1																
<i>Myzomela sclateri</i>													1		1		1
<i>Myzomela lafargei</i>				1	1	1	1	1	1	1	1	1	1				
<i>Philemon moluccensis</i>	1	1			1									1			
<i>Melidectes whitemanensis</i>	1																
<i>Erythrura trichroa</i>	1	1		1									1	1			
<i>Lonchura spectabilis</i>	1	1	1										1	1	1		
<i>Lonchura castaneothorax</i>	1	1															
<i>Aplonis cantoroides</i>	1	1	1	1	1		1	1		1		1	1	1	1	1	
<i>Aplonis feadensis</i>										1	1	1					
<i>Aplonis metallica</i>	1	1	1	1	1	1							1	1	1	1	1
<i>Mino dumontii</i>	1	1	1											1			
<i>Dicrurus hottentottus</i>	1	1												1			
<i>Artamus maximus</i>	1	1															
<i>Corvus orru</i>	1	1	1											1	1		

APPENDIX C. Continued.

Species	R	S	T	U	V	W	X	Y	Z	AA	AB	AC	AD	AE
<i>Rhipidura rufiventris</i>		1		1		1	1	1						
<i>Rhipidura rufifrons</i>														
<i>Rhipidura rufidorsa</i>														
<i>Monarcha cinerascens</i>	1		1	1	1	1	1		1	1	1	1	1	1
<i>Monarcha manadensis</i>		1												
<i>Monarcha chrysomela</i>		1		1		1								
<i>Myiagra alecto</i>		1			1	1	1	1		1			1	
<i>Myiagra hebetior</i>		1												
<i>Monachella muelleriana</i>														
<i>Pachycephala pectoralis</i>		1		1	1	1			1					
<i>Pachycephala melanura</i>			1								1	1		
<i>Dicaeum erythrothorax</i>		1		1				1						
<i>Nectarinia sperata</i>		1		1	1	1		1		1			1	
<i>Nectarinia jugularis</i>	1	1		1	1	1	1	1		1	1		1	1
<i>Zosterops atriceps</i>														
<i>Zosterops griseotinctus</i>									1		1			
<i>Myzomela eques</i>														
<i>Myzomela cruentata</i>		1				1								
<i>Myzomela pulchella</i>														
<i>Myzomela cardinalis</i>														
<i>Myzomela sclateri</i>									1		1	1	1	
<i>Myzomela lafargei</i>	1		1						1		1			1
<i>Philemon moluccensis</i>														
<i>Melidectes whitemanensis</i>														
<i>Erythrura trichroa</i>	1				1				1		1			
<i>Lonchura spectabilis</i>									1					
<i>Lonchura castaneothorax</i>														
<i>Aplonis cantoroides</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Aplonis feadensis</i>														1
<i>Aplonis metallica</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Mino dumontii</i>							1	1						
<i>Dicrurus hottentottus</i>								1						
<i>Artamus maximus</i>														
<i>Corvus orru</i>		1						1		1		1		

APPENDIX D. Presence-absence matrix for the Solomon Archipelago.

Species	A*	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
<i>Tachybaptus ruficollis</i>		1																								
<i>Pelecanus conspicillatus</i>	1	1								1	1		1		1		1		1	1	1		1		1	1
<i>Phalacrocorax melanoleucos</i>		1			1					1							1		1	1	1		1		1	
<i>Butorides striatus</i>	1	1	1	1	1	1	1		1	1	1	1	1		1		1	1	1	1	1	1	1	1	1	1
<i>Egretta sacra</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Ardea intermedia</i>	1	1																								
<i>Ardea alba</i>	1	1																								
<i>Nycticorax nycticorax</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Ixobrychus minutus</i>		1																								
<i>Ixobrychus flavicollis</i>		1			1	1				1					1	1					1	1	1	1	1	
<i>Threskiornis aethiopicus</i>																										
<i>Platalea leucorodia</i>																										
<i>Anas platyrhynchos</i>	1	1		1	1	1	1	1		1	1	1	1		1		1	1	1	1	1	1	1	1	1	1
<i>Aviceda cuculoides</i>	1	1	1	1	1	1	1			1	1		1	1	1	1	1	1	1	1	1	1	1		1	1
<i>Haliastur indus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Accipiter gentiles</i>										1					1						1					
<i>Accipiter novaehollandiae</i>	1	1	1	1	1	1	1			1			1		1	1		1	1	1	1	1	1	1	1	1
<i>Accipiter fasciatus</i>																										
<i>Accipiter imitator</i>		1			1	1																				
<i>Accipiter rufitorques</i>	1	1	1	1	1	1	1			1			1	1	1			1	1	1	1	1	1	1	1	1
<i>Haliaeetus leucogaaster</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Pandion haliaetus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Falco peregrinus</i>										1																
<i>Falco subbuteo</i>	1	1			1	1				1										1	1					
<i>Megapodius freycinet</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Turnix sylvatica</i>										1																

* Island abbreviations are defined in Appendix G.

APPENDIX D. Continued.

Species	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS
<i>Tachybaptus ruficollis</i>											1								
<i>Pelecanus conspicillatus</i>		1			1		1				1		1						
<i>Phalacrocorax melanoleucos</i>		1		1	1						1								
<i>Butorides striatus</i>	1	1	1	1	1		1		1										
<i>Egretta sacra</i>	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1			
<i>Ardea intermedia</i>		1																	
<i>Ardea alba</i>																			
<i>Nycticorax nycticorax</i>	1	1	1	1	1	1	1		1	1			1	1					
<i>Ixobrychus minutus</i>																			
<i>Ixobrychus flavicollis</i>	1										1								
<i>Threskiornis aethiopicus</i>											1	1							
<i>Platalea leucorodia</i>											1								
<i>Anas platyrhynchos</i>	1	1	1	1	1		1				1								
<i>Aviceda cuculoides</i>	1	1	1		1	1	1												
<i>Haliaastur indus</i>	1	1	1	1	1	1	1	1	1	1			1						
<i>Accipiter gentilis</i>																			
<i>Accipiter novaehollandiae</i>	1						1												
<i>Accipiter fasciatus</i>											1	1							
<i>Accipiter imitator</i>																			
<i>Accipiter rufitorques</i>	1	1	1		1	1	1			1									
<i>Haliaeetus leucogaaster</i>	1	1	1	1	1	1	1						1						
<i>Pandion haliaetus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1						
<i>Falco peregrinus</i>																			
<i>Falco subbuteo</i>		1																	
<i>Megapodius freycinet</i>	1	1	1	1	1	1	1	1	1	1			1	1	1	1			1
<i>Turnix sylvatica</i>																			

APPENDIX D. Continued.

Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
<i>Gallirallus philippensis</i>										1	1	1								1	1	1	1			1
<i>Nesoclopeus poecilopterus</i>		1				1				1																
<i>Porzana tabuensis</i>										1																
<i>Poliolimnas cinereus</i>	1	1								1																
<i>Amaurornis akool</i>	1	1	1	1	1	1	1	1		1	1	1	1		1		1	1	1	1	1	1	1	1	1	1
<i>Pareudiastes sylvestris</i>																										
<i>Porphyrio porphyrio</i>	1	1	1	1	1	1	1	1	1	1	1	1	1		1		1	1	1	1	1	1	1	1	1	1
<i>Esacus magnirostris</i>		1	1	1	1	1	1	1		1	1	1	1		1		1	1	1	1	1	1	1	1	1	1
<i>Ptilinopus superbus</i>	1	1	1	1	1	1	1			1	1	1	1		1		1	1	1	1	1	1	1	1	1	1
<i>Ptilinopus purpuratus</i>																										
<i>Ptilinopus solomonensis</i>		1	1				1	1	1	1	1		1		1		1			1		1	1	1	1	1
<i>Ptilinopus viridis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Ducula pacifica</i>							1	1	1																	
<i>Ducula myristicivora</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Ducula rosacea</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Ducula latrans</i>										1			1	1												
<i>Gymnophaps albertisii</i>		1								1			1								1				1	
<i>Columba leucomela</i>		1				1	1			1			1		1						1				1	1
<i>Columba pallidiceps</i>		1			1		1			1					1											
<i>Macropygia mackinlayi</i>	1	1	1	1	1	1	1	1	1	1	1	1	1		1		1	1	1	1	1	1	1	1	1	1
<i>Reinwardtoena reinwardtii</i>		1			1	1	1			1			1		1					1		1	1	1	1	1
<i>Chalcophaps stephani</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Gallicolumba canifrons</i>		1								1										1	1			1		
<i>Gallicolumba salamonis</i>																										
<i>Gallicolumba erythroptera</i>										1					1											
<i>Caloenas nicobarica</i>		1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Chalcopsitta cardinalis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Trichoglossus ornatus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Lorius chlorocerus</i>										1	1			1	1											

APPENDIX D. Continued.

Species	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS
<i>Gallirallus philippensis</i>		1	1	1	1	1													
<i>Nesoclopeus poecilopterus</i>																			
<i>Porzana tabuensis</i>		1									1								
<i>Poliolimnas cinereus</i>		1		1															
<i>Amaurornis akool</i>		1	1		1	1	1		1										
<i>Pareudiastes sylvestris</i>		1																	
<i>Porphyrio porphyrio</i>	1	1	1		1	1	1		1		1	1			1				
<i>Esacus magnirostris</i>	1		1	1	1	1	1	1		1									
<i>Ptilinopus superbus</i>	1		1	1	1	1	1												
<i>Ptilinopus purpuratus</i>			1	1	1	1			1		1	1							
<i>Ptilinopus solomonensis</i>		1	1	1				1					1						
<i>Ptilinopus viridis</i>	1	1	1	1	1	1	1		1				1						
<i>Ducula pacifica</i>				1				1	1		1	1			1	1			1
<i>Ducula myristicivora</i>	1	1	1	1	1	1	1												
<i>Ducula rosacea</i>	1	1	1	1	1	1	1	1		1			1						
<i>Ducula latrans</i>		1	1	1	1	1													
<i>Gymnophaps albertisii</i>																			
<i>Columba leucomela</i>		1																	
<i>Columba pallidiceps</i>		1						1	1										
<i>Macropygia mackinlayi</i>		1	1	1	1	1	1		1		1	1	1						
<i>Reinwardtoena reinwardtii</i>		1	1	1	1	1													
<i>Chalcophaps stephani</i>	1	1	1	1	1	1	1	1	1				1						
<i>Gallicolumba canifrons</i>		1		1	1				1		1	1	1						
<i>Gallicolumba salamonis</i>		1						1											
<i>Gallicolumba erythroptera</i>		1																	
<i>Caloenas nicobarica</i>	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1			1
<i>Chalcopsitta cardinalis</i>	1	1	1	1		1	1			1			1		1				
<i>Trichoglossus ornatus</i>	1	1	1				1		1				1	1					
<i>Lorius chlorocercus</i>		1	1			1					1								

APPENDIX D. Continued.

Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	
<i>Charmosyna palmarum</i>		1				1				1			1								1						
<i>Charmosyna placentis</i>	1	1																									
<i>Charmosyna margarethae</i>		1				1				1			1							1	1					1	
<i>Micropsitta bruijnii</i>		1								1											1						
<i>Micropsitta pusio</i>	1	1			1	1	1			1	1	1	1		1		1	1	1	1	1	1	1	1	1	1	1
<i>Cacatua tenuirostris</i>	1	1	1	1	1	1	1	1	1	1	1	1	1		1					1	1	1	1	1	1	1	1
<i>Eclectus roratus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1
<i>Geoffroyus heteroclitus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1					1	1	1	1	1	1	1	1
<i>Cacomantis variolosus</i>		1				1				1			1	1							1	1	1	1			
<i>Chrysococcyx lucidus</i>																											
<i>Eudynamis scolopacea</i>	1	1	1	1	1	1	1	1	1	1	1	1	1		1		1	1	1	1	1	1	1	1	1	1	1
<i>Scythrops novaehollandiae</i>										1										1							
<i>Centropus ateralbus</i>							1	1		1					1	1	1	1	1	1		1	1	1	1	1	1
<i>Tyto alba</i>	1	1				1				1			1		1									1			
<i>Ninox novaeseelandiae</i>	1	1	1		1	1	1			1			1														
<i>Nesasio solomonensis</i>		1			1	1																					
<i>Podargus ocellatus</i>		1			1	1																					
<i>Eurostopodus mystacalis</i>		1		1		1									1					1	1	1		1	1	1	1
<i>Aerodramus orientalis</i>		1								1																	
<i>Aerodramus vanikorensis</i>	1	1	1		1	1	1		1	1	1	1	1		1					1	1	1	1	1	1	1	1
<i>Aerodramus spodiopygius</i>	1	1			1	1				1			1								1	1					
<i>Collocalia esculenta</i>	1	1	1	1	1	1	1			1	1	1	1		1		1		1	1			1	1	1	1	1
<i>Hemiprocne mystacea</i>	1	1	1	1	1	1				1	1	1	1		1		1	1	1	1	1	1	1	1	1	1	1
<i>Alcedo atthis</i>	1	1			1	1				1			1		1	1	1		1	1	1	1	1	1	1	1	1
<i>Alcedo pusilla</i>	1	1	1		1	1	1			1	1		1		1	1	1		1	1	1	1	1	1	1	1	1
<i>Ceyx lepidus</i>	1	1			1	1				1			1		1		1				1			1	1	1	1
<i>Halcyon diops</i>	1	1		1	1	1	1	1		1																	
<i>Halcyon australasia</i>	1	1	1	1	1	1	1	1	1	1	1	1	1		1					1	1	1	1	1	1	1	1
<i>Halcyon chloris</i>	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1

APPENDIX D. Continued.

Species	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS
<i>Charmosyna palmarum</i>																			
<i>Charmosyna placentis</i>													1	1					
<i>Charmosyna margarethae</i>		1			1														
<i>Micropsitta bruijnii</i>																			
<i>Micropsitta pusio</i>	1	1	1		1						1								
<i>Cacatua tenuirostris</i>	1		1	1	1	1	1		1										
<i>Eclectus roratus</i>	1	1	1				1			1									
<i>Geoffroyus heteroclitus</i>	1	1									1								
<i>Cacomantis variolosus</i>		1	1																
<i>Chrysococcyx lucidus</i>											1	1							
<i>Eudynamys scolopacea</i>	1	1		1	1	1	1												
<i>Scythrops novaehollandiae</i>											1								
<i>Centropus ateralbus</i>	1																		
<i>Tyto alba</i>		1	1	1	1	1					1	1	1						
<i>Ninox novaeseelandiae</i>		1	1			1	1												
<i>Nesasio solomonensis</i>																			
<i>Podargus ocellatus</i>																			
<i>Eurostopodus mystacalis</i>	1																		
<i>Aerodramus orientalis</i>																			
<i>Aerodramus vanikorensis</i>		1	1	1	1	1	1				1	1	1	1					
<i>Aerodramus spodiopygius</i>		1	1																
<i>Collocalia esculenta</i>	1	1	1	1						1	1	1	1						
<i>Hemiprocne mystacea</i>	1	1			1	1					1								
<i>Alcedo atthis</i>	1	1					1						1						
<i>Alcedo pusilla</i>	1																		
<i>Ceyx lepidus</i>	1	1																	
<i>Halcyon diops</i>																			
<i>Halcyon australasia</i>	1	1	1	1			1	1	1		1	1	1	1				1	1
<i>Halcyon chloris</i>	1	1	1	1	1	1			1		1	1	1		1	1			

APPENDIX D. Continued.

Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
<i>Halcyon saurophaga</i>	1	1	1	1	1	1	1			1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Halcyon bougainvillei</i>		1								1																
<i>Eurystomus orientalis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Rhyticeros plicatus</i>	1	1	1	1	1	1				1			1		1		1		1	1		1	1	1	1	1
<i>Pitta brachyura</i>		1			1	1																				
<i>Hirundo rustica</i>	1	1	1	1	1	1	1	1		1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Coracina caledonica</i>		1				1				1											1		1	1		
<i>Coracina lineata</i>	1	1	1	1	1	1				1			1		1					1	1	1	1	1	1	1
<i>Coracina papuensis</i>	1	1	1	1	1	1	1	1		1	1		1	1	1	1	1			1	1	1	1	1	1	1
<i>Coracina tenuirostris</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			1	1	1	1	1	1	1
<i>Coracina holopolia</i>	1	1			1	1				1			1								1		1	1	1	
<i>Lalage leucopyga</i>																										
<i>Zoothera dauma</i>		1			1					1																
<i>Turdus poliocephalus</i>		1								1											1					
<i>Gerygone flavolateralis</i>																										
<i>Cichlornis whitmey</i>		1								1																
<i>Cettia parens</i>																										
<i>Acrocephalus arundinaceus</i>	1	1				1				1		1														
<i>Phylloscopus trivirgatus</i>		1				1				1			1								1					
<i>Phylloscopus amoenus</i>																					1					
<i>Rhipidura leucophrys</i>	1	1	1	1	1	1	1	1		1		1	1	1	1		1	1	1	1	1	1	1	1	1	1
<i>Rhipidura rufiventris</i>	1	1	1		1	1	1			1			1		1		1				1		1	1	1	1
<i>Rhipidura spilodera</i>		1								1																
<i>Rhipidura fuliginosa</i>																										
<i>Rhipidura rufifrons</i>	1	1	1	1	1	1				1			1		1	1	1	1	1	1	1	1	1	1	1	1
<i>Rhipidura rufidorsa</i>													1													
<i>Clytorhynchus nigrogularis</i>																										
<i>Monarcha cinerascens</i>																										
<i>Monarcha melanopsis</i>	1	1	1	1	1	1	1	1	1	1	1		1		1	1	1	1	1	1	1	1	1	1	1	1

APPENDIX D. Continued.

Species	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS
<i>Halcyon saurophaga</i>	1	1	1	1	1	1	1		1				1	1					
<i>Halcyon bougainvillei</i>																			
<i>Eurystomus orientalis</i>	1	1	1	1	1	1	1		1										
<i>Rhyticeros plicatus</i>	1						1			1									
<i>Pitta brachyura</i>																			
<i>Hirundo rustica</i>	1	1	1	1	1	1	1						1						
<i>Coracina caledonica</i>																			
<i>Coracina lineata</i>	1	1									1	1							
<i>Coracina papuensis</i>	1																		
<i>Coracina tenuirostris</i>	1						1												
<i>Coracina holopolia</i>																			
<i>Lalage leucopyga</i>		1	1																
<i>Zoothera dauma</i>		1																	
<i>Turdus poliocephalus</i>											1								
<i>Gerygone flavolateralis</i>											1								
<i>Cichlornis whitneyi</i>																			
<i>Cettia parens</i>		1																	
<i>Acrocephalus arundinaceus</i>																			
<i>Phylloscopus trivirgatus</i>		1																	
<i>Phylloscopus amoenus</i>																			
<i>Rhipidura leucophrys</i>	1	1	1	1	1	1	1												
<i>Rhipidura rufiventris</i>	1																		
<i>Rhipidura spilodera</i>		1									1								
<i>Rhipidura fuliginosa</i>		1																	
<i>Rhipidura rufifrons</i>	1	1	1		1	1													
<i>Rhipidura rufidorsa</i>																			
<i>Clytorhynchus nigrogularis</i>											1								
<i>Monarcha cinerascens</i>								1	1	1			1	1	1	1	1	1	1
<i>Monarcha melanopsis</i>	1	1	1	1	1	1													

APPENDIX D. Continued.

Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	
<i>Monarcha manadensis</i>	1	1	1	1	1	1	1	1		1			1		1	1	1			1	1	1	1	1		1	
<i>Myiagra rubecula</i>	1	1	1	1	1	1	1	1		1			1		1	1	1		1	1	1	1	1	1	1	1	1
<i>Petroica multicolor</i>		1								1										1							
<i>Pachycephala pectoralis</i>	1	1	1		1	1	1			1	1		1		1	1	1			1		1	1	1	1	1	
<i>Pachycephala melanura</i>																											
<i>Pachycephala implicata</i>		1								1																	
<i>Dicaeum erythrorhox</i>	1	1	1	1	1	1	1	1		1			1														
<i>Nectarinia jugularis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	
<i>Zosterops metcalfei</i>	1	1	1		1	1	1																				
<i>Zosterops griseotinctus</i>																1	1	1		1	1	1	1	1	1	1	
<i>Zosterops murphyi</i>																					1						
<i>Zosterops ugiensis</i>		1								1																	
<i>Zosterops stresemanni</i>													1														
<i>Woodfordia superciliosa</i>																											
<i>Myzomela cardinalis</i>																											
<i>Myzomela lafargei</i>	1	1	1	1	1	1	1		1	1			1		1	1	1		1	1	1	1	1	1	1	1	
" <i>Stresemannia</i> " <i>bougainvillei</i>		1																									
<i>Meliarchus sclateri</i>																											
" <i>Guadalcanaria</i> " <i>inexpectata</i>											1																
<i>Erythrura trichroa</i>		1								1											1						
<i>Lonchura castaneothorax</i>	1																										
<i>Aplonis cantoroides</i>	1	1	1		1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	
<i>Aplonis feadensis</i>																											
<i>Aplonis grandis</i>	1	1	1	1	1	1	1			1			1		1	1	1	1	1	1	1	1	1	1	1	1	
<i>Aplonis metallica</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Aplonis brunneicapilla</i>		1			1					1																1	
<i>Mino dumontii</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	
<i>Dicrurus hottentottus</i>											1																
<i>Corvus woodfordi</i>	1	1	1		1	1				1																	

APPENDIX D. Continued.

Species	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS
<i>Monarcha manadensis</i>	1	1	1		1														
<i>Myiagra rubecula</i>	1	1	1		1		1				1								
<i>Petroica multicolor</i>			1																
<i>Pachycephala pectoralis</i>	1	1			1						1								
<i>Pachycephala melanura</i>														1					
<i>Pachycephala implicata</i>																			
<i>Dicaeum erythrorhox</i>			1																
<i>Nectarinia jugularis</i>	1		1	1	1	1	1	1	1	1					1				
<i>Zosterops metcalfei</i>																			
<i>Zosterops griseotinctus</i>	1										1		1						
<i>Zosterops murphyi</i>																			
<i>Zosterops stresemanni</i>			1																
<i>Woodfordia superciliosa</i>																			1
<i>Myzomela cardinalis</i>			1	1							1								1
<i>Myzomela lafargei</i>	1	1			1	1													
" <i>Stresemannia</i> " <i>bougainvillei</i>																			
<i>Meliarchus sclateri</i>			1																
" <i>Guadalcánaria</i> " <i>inexpectata</i>																			
<i>Erythrura trichroa</i>																			
<i>Lonchura castaneothorax</i>																			
<i>Aplonis cantoroides</i>	1	1	1	1	1		1	1	1		1	1							
<i>Aplonis feadensis</i>													1	1	1		1	1	
<i>Aplonis grandis</i>	1	1					1												
<i>Aplonis metallica</i>	1	1	1	1	1	1	1	1					1				1		
<i>Aplonis brunneicapilla</i>																			
<i>Mino dumontii</i>	1		1	1	1	1	1												
<i>Dicrurus hottentottus</i>			1																
<i>Corvus woodfordi</i>																			

APPENDIX E. Presence-absence matrix for Vanuatu.

Species	Am [*]	An	Aw	Ef	Em	Ep	Er	F	G	L	M	Mau	Mk	ML
<i>Tachybaptus novaehollandiae</i>				1					1					
<i>Butorides striatus</i>			1				1				1			
<i>Egretta sacra</i>	1	1	1	1	1	1	1	1	1		1	1	1	1
<i>Anas superciliosa</i>		1		1			1		1		1			
<i>Anas gibberifrons</i>				1										
<i>Aythya australis</i>				1			1		1					
<i>Accipiter fasciatus</i>		1												
<i>Circus approximans</i>	1	1	1	1	1	1	1	1		1	1	1	1	
<i>Falco peregrinus</i>		1	1	1			1	1	1		1			
<i>Megapodius freycinet</i>	1			1	1	1			1	1	1	1		
<i>Gallirallus philippensis</i>	1	1		1	1	1	1				1	1		
<i>Porzana tabuensis</i>		1					1							
<i>Poliolimnas cinereus</i>							1		1					
<i>Porphyrio porphyrio</i>		1		1	1	1	1	1			1	1	1	
<i>Ptilinopus greyii</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Ptilinopus tannensis</i>	1	1		1	1	1	1		1	1	1	1		1
<i>Ducula bakeri</i>	1								1					
<i>Ducula pacifica</i>	1	1	1	1	1	1	1	1	1		1	1		1
<i>Columba vitiensis</i>	1	1	1	1	1	1	1	1		1	1	1	1	1
<i>Macropygia mackinlayi</i>	1	1		1	1	1	1	1	1	1	1	1	1	1
<i>Chalcophaps indica</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Gallicolumba sanctaecrucis</i>														
<i>Trichoglossus haematodus</i>	1	1	1	1	1	1	1		1		1	1	1	1
<i>Vini palmarum</i>	1	1		1	1	1	1	1	1	1	1			1
<i>Chrysococcyx lucidus</i>	1		1			1	1	1	1	1	1	1		
<i>Cacomantis pyrrhophanus</i>	1		1	1	1	1	1	1	1	1	1			
<i>Tyto alba</i>	1	1	1	1	1	1	1	1			1	1		1

* Island abbreviations are defined in Appendix H.

APPENDIX E. Continued.

Species	Mlo	Mw	Ng	O	P	Pa	S	T	Tg	Tk	Tor	U	VL	VI
<i>Tachybaptus novaehollandiae</i>	1			1			1							
<i>Butorides striatus</i>							1				1		1	
<i>Egretta sacra</i>	1	1	1	1	1		1	1	1	1	1	1	1	1
<i>Anas superciliosa</i>				1			1	1						
<i>Anas gibberifrons</i>								1						
<i>Aythya australis</i>	1			1			1	1						
<i>Accipiter fasciatus</i>														
<i>Circus approximans</i>	1	1	1	1	1	1	1	1	1		1	1	1	
<i>Falco peregrinus</i>	1		1				1	1	1					
<i>Megapodius freycinet</i>	1	1	1	1	1	1	1		1	1		1	1	1
<i>Gallirallus philippensis</i>	1	1	1	1	1		1	1	1				1	
<i>Porzana tabuensis</i>								1						
<i>Poliolimnas cinereus</i>								1						
<i>Porphyrio porphyrio</i>	1	1	1	1	1		1	1	1	1				
<i>Ptilinopus greyii</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Ptilinopus tannensis</i>	1	1	1	1	1	1	1	1	1	1			1	1
<i>Ducula bakeri</i>		1		1	1		1					1	1	
<i>Ducula pacifica</i>	1	1	1	1	1		1	1	1		1	1	1	1
<i>Columba vitiensis</i>	1	1	1	1	1	1	1	1	1		1	1	1	
<i>Macropygia mackinlayi</i>	1	1	1	1	1	1	1	1	1	1		1	1	1
<i>Chalcophaps indica</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Gallicolumba sanctaecrucis</i>							1							
<i>Trichoglossus haematodus</i>	1	1	1	1	1	1	1	1	1		1	1	1	1
<i>Vini palmarum</i>	1	1	1	1	1	1	1	1	1	1		1	1	1
<i>Chrysococcyx lucidus</i>			1				1						1	
<i>Cacomantis pyrrhophanus</i>	1		1			1	1	1				1	1	1
<i>Tyto alba</i>	1	1	1	1	1		1	1	1			1	1	

APPENDIX E. Continued.

Species	Am	An	Aw	Ef	Em	Ep	Er	F	G	L	M	Mau	Mk	ML
<i>Collocalia vanikorensis</i>	1	1		1	1	1	1		1		1	1	1	
<i>Collocalia spodiopygia</i>	1	1		1	1	1	1				1			
<i>Collocalia esculenta</i>	1	1	1	1	1	1	1	1	1	1	1	1		1
<i>Halcyon chloris</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Halcyon farquhari</i>											1			
<i>Hirundo tahitica</i>		1	1	1		1	1				1			
<i>Lalage maculosa</i>				1	1	1					1	1		
<i>Lalage leucopyga</i>	1	1	1	1	1	1	1		1	1	1	1		1
<i>Coracina caledonica</i>							1				1			
<i>Turdus poliocephalus</i>	1			1	1	1	1	1	1	1	1	1		1
<i>Cichlornis whitneyi</i>														
<i>Gerygone flavolateralis</i>	1				1	1			1	1	1			
<i>Rhipidura spilodera</i>	1			1	1	1			1		1	1		
<i>Rhipidura fuliginosa</i>	1	1		1	1	1	1	1	1	1	1	1		1
<i>Myiagra caledonica</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Neolalage banksiana</i>	1			1		1					1			
<i>Clytorhynchus pachycephaloides</i>				1	1	1	1		1	1	1			1
<i>Petroica multicolor</i>	1	1		1	1	1	1		1	1	1	1		1
<i>Pachycephala pectoralis</i>	1	1		1	1	1	1		1	1	1	1		
<i>Artamus leucorhynchus</i>	1	1		1	1	1	1		1	1	1	1	1	
<i>Aplonis zelandicus</i>	1			1					1	1	1			1
<i>Aplonis santovestris</i>														
<i>Phylidonyris notabilis</i>	1					1					1			
<i>Lichmera incana</i>	1			1	1	1	1			1	1	1	1	
<i>Myzomela cardinalis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Zosterops flavifrons</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Zosterops laterlais</i>	1		1	1	1	1	1		1	1	1	1	1	1
<i>Erythrura trichroa</i>	1	1		1			1		1	1		1		
<i>Erythrura cyaneovirens</i>	1	1		1	1	1			1	1	1			

APPENDIX E. Continued.

Species	Mlo	Mw	Ng	O	P	Pa	S	T	Tg	Tk	Tor	U	VL	VI
<i>Collocalia vanikorensis</i>	1	1	1	1	1		1	1	1		1		1	
<i>Collocalia spodiopygia</i>	1						1	1				1		
<i>Collocalia esculenta</i>	1	1	1	1	1	1	1	1	1		1	1	1	1
<i>Halcyon chloris</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Halcyon farquhari</i>	1						1							
<i>Hirundo tahitica</i>	1	1		1	1	1	1	1	1		1			
<i>Lalage maculosa</i>	1		1			1	1		1					
<i>Lalage leucopyga</i>	1	1	1	1	1	1	1	1	1		1	1	1	1
<i>Coracina caledonica</i>	1						1							
<i>Turdus poliocephalus</i>	1	1	1	1	1	1	1	1				1	1	
<i>Cichlornis whitneyi</i>							1							
<i>Gerygone flavolateralis</i>	1	1		1	1		1						1	
<i>Rhipidura spilodera</i>	1	1	1	1	1	1	1		1	1			1	
<i>Rhipidura fuliginosa</i>	1	1	1	1	1	1	1		1	1	1	1	1	1
<i>Myiagra caledonica</i>	1	1	1	1	1		1	1	1		1	1	1	1
<i>Neolalage banksiana</i>	1	1		1	1		1						1	
<i>Clytorhynchus pachycephaloides</i>	1	1		1	1	1	1		1		1	1	1	1
<i>Petroica multicolor</i>	1	1	1	1		1	1	1	1	1			1	
<i>Pachycephala pectoralis</i>	1	1	1	1	1	1	1		1	1		1	1	
<i>Artamus leucorhynchus</i>	1	1	1	1	1		1	1	1					
<i>Aplonis zelandicus</i>	1			1	1	1	1					1		
<i>Aplonis santovestris</i>							1							
<i>Phylidonyris notabilis</i>		1		1	1	1	1					1	1	
<i>Lichmera incana</i>			1			1			1	1				
<i>Myzomela cardinalis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Zosterops flavifrons</i>	1	1	1	1	1	1	1	1	1	1	1		1	
<i>Zosterops laterlais</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Erythrura trichroa</i>			1	1				1						
<i>Erythrura cyaneovirens</i>				1	1	1	1		1	1				

APPENDIX F. Island characteristics for the Bismarck Archipelago.

Island	ID ^a	Species	<i>t</i> ^c	Area (km ²)	Isolation ^b (km)	Elevation (m)
New Britain (Neu Pommern)	A	131	2.39	35742	0	2439
New Ireland (Neu Mecklenburg)	B	105	6.54	7174	28.75	2399
New Hanover (<i>Lavongai</i>)	C	76	9.33	1186	202	960
St. Matthias (<i>Mussau</i>)	D	45	7.67	414	386.25	651
Manus	E	53	7.64	1834	382.5	718
Rambutyo	F	31	7.50	88	352.5	308
Nauna (La Vandola)	G	21	6.23	1	353	129
San Miguel	H	17	5.20	0.26	355	0
Anchorites (Kanit, Kaniet)	I	9	3.76	0.52	588.75	0
Hermits	J	17	5.16	10	552.5	244
Ninigos (Schachbrett, Echiquier)	K	16	4.97	13	620	0
Wuvulu (Matty, Mary)	L	18	5.08	15	713.75	37
Long (Ahrup)	M	56	7.59	329	118.75	1304
Umboi (Rooke)	N	85	7.73	816	26.25	1655
Vuatom	O	60	8.64	14	6.25	350
Duke of York (Neu Lauenburg)	P	50	8.28	52	15	0
Credner (Palakuuro, Pigeon)	Q	16	5.05	1	12.5	0
Emirau (Squally, Storm, Kerue)	R	33	7.83	41	317.5	0
Dyaul (Djaul, Sandwich)	S	51	8.10	110	143.75	180
Tingwon (Portland)	T	14	5.14	1.5	253.75	0
Lihir (Gardenijs)	U	62	9.39	205	120	854
Feni (Ambitle, Anir, St. Jan)	V	42	7.86	110	131.25	521
Tabar	W	62	9.43	218	130	621
Tanga (Anthony, Caens, Kaan)	X	42	7.56	98	138.75	500
Lolobau	Y	55	7.35	61	5	932
Tolokiwa (Lottin)	Z	45	7.94	46	77.5	1396
Sakar (Tupinier)	AA	38	7.62	40	23.75	998
Crown	AB	34	7.40	14	150	566
Witu (Garowe)	AC	33	7.09	57	60	351
Unea (Merite)	AD	21	5.85	31	66.25	591
Tench	AE	14	4.59	0.26	293.75	0

^a Island abbreviations are used in the presence-absence matrix in Appendix C.

^b Isolation is measured as the distance to New Britain, the island with the largest number of species in the archipelago.

^c *t*-value from Mann–Whitney *U*-test. Positive values indicate a tendency harbor common species.

APPENDIX G. Island characteristics for the Solomon Archipelago.

Island	ID ^a	Species	<i>t</i> ^c	Area (km ²)	Isolation ^b (km)	Elevation (m)
Buka	A	70	8.47	611	1.3	402
Bougainville	B	105	6.94	8591	0.0	2591
Shortland (Alu)	C	57	9.59	232	10.0	206
Fauro	D	51	9.31	71	12.0	587
Choiseul	E	74	9.00	2966	51.3	970
Ysabel (Bogotu)	F	80	8.91	4095	270.0	1250
Florida (<i>Nggela</i>)	G	60	9.49	368	482.5	400
Buena Vista (Vatilau)	H	41	8.44	14	468.8	302
Savo	I	35	7.78	31	462.5	484
Guadalcanal	J	104	7.29	5281	457.0	2448
Pavuvu	K	45	9.31	176	396.3	543
Banika	L	41	8.90	60	407.5	
Malaita	M	75	9.32	4307	502.5	1280
Ulawa	N	31	6.99	70	680.0	
Vella Lavella	O	68	9.89	640	105.0	793
Bagga	P	18	3.55	28	126.3	
Ganonga (<i>Ranonga</i> , Ronongo)	Q	55	9.37	142	140.0	854
Simbo (Narovo, Eddystone)	R	41	8.59	13	172.0	335
Gizo (<i>Ghizo</i>)	S	60	9.79	35	161.3	199
Kulambangra (<i>Kolombangara</i>)	T	83	8.92	704	158.8	1768
Wana Wana	U	59	9.75	69	187.5	80
Kohinggo (Arundel)	V	61	10.02	95	176.3	124
New Georgia	W	70	10.21	2044	198.8	1006
Vangunu	X	65	9.83	544	275.0	1124
Gatukai (<i>Nggatokae</i>)	Y	59	9.61	109	307.5	888
Rendova (Hammond)	Z	64	10.10	381	225.0	1063

^a Island abbreviations are used in the presence-absence matrix in Appendix D.

^b Isolation is measured as the distance to Bougainville, the island with the largest number of species in the archipelago.

^c *t*-value from Mann–Whitney *U*-test. Positive values indicate a tendency harbor common species.

APPENDIX G. Continued.

Island	ID	Species	<i>t</i>	Area (km²)	Isolation (km)	Elevation (m)
Tetipari (<i>Tetepare</i> , Montgomery)	AA	57	9.56	122	257.0	405
San Cristobal (<i>Makira</i> , Bauro)	AB	78	5.68	3090	650.0	1040
Ugi (Golfe)	AC	53	8.47	42	687.0	204
Three Sisters	AD	43	7.68	11	701.3	76
Santa Anna (Awa Raha)	AE	49	8.42	15	780.0	159
Santa Catalina (Awa Kaba)	AF	41	7.87	4.9	782.5	98
Mono (Treasury, Stirling)	AG	43	8.89	73	53.8	355
Ramos	AH	17	4.50	0.25	455.0	
Gower (<i>Ndai</i> , Inattendue)	AI	26	6.21	14.5	496.3	
Borokua (Murray)	AJ	14	4.91	4	370.0	360
Rennell (Mu Nggava)	AK	40	1.09	684	670.0	154
Bellona	AL	18	2.89	20	616.3	76
Nissan (Green, Sir Charles Hardy)	AM	31	5.99	37	103.8	34
Fead (Nuguria, Abgarris)	AN	10	2.96	25	218.8	
Ontong Java (Lord Howe, Liuanuia)	AO	9	3.14	9.6	403.8	0
Sikaiana (Stewart)	AP	6	2.79	1.3	712.5	0
Kilinailau (Carteret)	AQ	4	1.36	0.1	98.8	
Tauu (Taku, Mortlock, Marcken)	AR	3	0.65	0.2	236.3	
Nukumanu (Tasman)	AS	4	1.70	1.25	468.8	

APPENDIX H. Island characteristics for Vanuatu.

Island	Island ID	Number of Species	t^c	Area (km ²)	Isolation ^a (km)	Elevation (m)
Ambrym	Am	38	5.21	663	102	1402
Aneityum	An	32	4.25	154	569	852
Aniwa	Aw	20	4.40	7.7	473	42
Efate (Vate)	Ef	43	4.79	877	245	647
Emae	Em	35	5.99	33.1	207	644
Epi	Ep	39	5.71	439	149	833
Erromanga	Er	40	4.22	898	382	886
Futuna	F	20	4.84	11	507	643
Gaua (Santa Maria)	G	36	3.83	332	80	914
Lopevi	L	28	4.72	29	156	1413
Malekula	M	45	4.80	2034	29	945
Mau	Mau	31	5.58	8.3	251	448
Makura	Mk	16	4.69	2.4	216	297
Meralava (Star Peak)	ML	22	5.87	8.9	113	914
Malo	Mlo	41	4.76	176	4	366
Maewo (Aurora)	Mw	34	5.72	263	95	823
Nguna	Ng	34	5.79	27.4	236	593
Aoba	O	40	4.87	410	47	1496
Pentecost	P	35	5.46	448	91	934
Paama	Pa	28	4.56	32.3	142	544
Santo	S	50	2.89	3937	0	1890
Taana	T	34	3.87	550	465	1084
Tongoa	Tg	33	5.86	38.7	185	486
Tongariki	Tk	18	4.22	7.7	215	521
Torres group	Tor	19	4.96	112.1	155	366
Ureparapara (Bligh)	U	26	4.94	49.2	151	762
Vanua Lava	VL	34	5.30	298	116	975
Valua (Saddle)	VI	17	4.94	29.8	153	457

^a Island abbreviations are used in the presence-absence matrix in Appendix E.

^b Isolation is measured as the distance to Santo, the island with the largest number of species in the archipelago.

^c t -value from Mann–Whitney U -test. Positive values indicate a tendency harbor common species.

APPENDIX I. Species characteristics for the Bismarck Archipelago.

Species	Number of Islands ^a	U ^b	t ^c	Dispersal ^d	Endemism ^e	Population Density ^f	Incidence ^g	Habitat ^h
<i>Casuaris bennetti</i>	1	30	1.68		0		HS	F
<i>Tachybaptus ruficollis</i>	6	128.5	2.68	2	1	2		
<i>Pelecanus conspicillatus</i>	2	44.5	1.25		0		N	C
<i>Phalacrocorax melanoleucos</i>	1	30	1.68	2	0.5	2	HS	W
<i>Butorides striatus</i>	2	58	2.33	3	1	3	HS	Man
<i>Egretta sacra</i>	30	28.5	1.51	1	0	2	D	C
<i>Ardea intermedia</i>	3	76	2.27	3	0	2	HS	O
<i>Ardea alba</i>	2	37.5	0.68	2	0	2	HS	O
<i>Nycticorax nycticorax</i>	22	164.5	2.85	1	1	3	C	F
<i>Ixobrychus minutus</i>	1	30	1.68	2	0	2	HS	S
<i>Ixobrychus flavicollis</i>	16	194	2.93	2	0.5	3	C	F
<i>Dendrocygna bicolor</i>	2	57	2.25	3	1	2	HS	W
<i>Dendrocygna guttata</i>	2	57	2.25	3	0	2	HS	W

^a Number of islands on which the species occurs.

^b Mann–Whitney U -test for species nestedness. Islands are ranked from poorest to richest, and island ranks are summed across a species' occurrences.

^c t -value from Mann–Whitney U -test. Positive values indicate a tendency to occur on richer islands; negative values indicate a tendency to occur on islands with few species.

^d Lower values correspond to better dispersal ability.

^e Levels of endemism indicate not endemic (0), or endemic at the subspecies (1), allospecies (2), full species (3), or genus level (4). 0.5 indicates that some populations are not endemic and some are endemic at the subspecies level; 1.5 indicates that some populations are endemic at the subspecies level and some are endemic at the allospecies level.

^f 1 = < 0.1 pairs/km²; 2 = 0.1–1 pair/km²; 3 = 1–10 pairs/km²; 4 = 10–100 pairs/km²; 5 = ≥ 100 pairs/km².

^g HS = high-S species; ST = supertramp; A, B, C, or D = A tramp, B tramp, C tramp, or D tramp, respectively; N = confined to one or a few geographically peripheral islands and therefore not classified.

^h F = lowland forest; C = seacoast; A = lowland aerial; W = fresh water; Man = mangrove; O = open country, secondary growth, and forest edge; S = swamps and marshes; Mt = mountains.

APPENDIX I. Continued.

Species	Number of Islands	<i>U</i>	<i>t</i>	Dispersal	Endemism	Population Density	Incidence	Habitat
<i>Anas platyrhynchos</i>	10	189.5	3.57	2	0	3	B	W
<i>Aviceda cuculoides</i>	8	152	2.71	3	1	3	A	F
<i>Henicopernis lognicauda</i>	2	51	1.77	4	2	1	HS	F
<i>Haliastur indus</i>	25	134.5	2.98	2	0.5	3	D	O
<i>Accipiter gentiles</i>	2	57	2.25	1	0	1	HS	F
<i>Accipiter novaehollandiae</i>	15	199	3.13	1	1	3	C	F
<i>Accipiter rufitorques</i>	1	15.5	0.06	3	2	3	N	F
<i>Accipiter luteoschistaceus</i>	2	57	2.25	4	3	1	HS	F
<i>Accipiter poliocephalus</i>	1	30	1.68	4	2	1	HS	Mt
<i>Accipiter cirrhocephalus</i>	2	58	2.33	3	2	1	HS	F
<i>Haliaeetus leucogaaster</i>	21	187	3.47	1	2	1		
<i>Pandion haliaetus</i>	23	151.5	2.69	1	0	2	D	C
<i>Falco peregrinus</i>	5	95.5	1.64	2	0	1	A	A
<i>Falco subbuteo</i>	3	61.5	1.30	1	0	1	A	A
<i>Falco berigora</i>	1	23	0.90	2	0	1	N	O
<i>Megapodius freycinet</i>	30	21.5	0.73	1	1	3	D	F
<i>Coturnix chinensis</i>	8	167.5	3.41	2	1	2	A	O
<i>Turnix sylvatica</i>	2	48	1.53	2	1	2	HS	O
<i>Gallirallus philippensis</i>	14	131	0.48	2	2	3		
<i>Gallirallus insignis</i>	1	30	1.68	4	3	3	HS	F
<i>Rallina eurizonoides</i>	3	70.5	1.91	3	1	2	HS	F
<i>Porzana tabuensis</i>	2	30	0.08	2	0	2	N	S
<i>Poliolimnas cinereus</i>	7	147.5	3.00	3	0.5	2	A	S
<i>Amaurornis akool</i>	13	211.5	3.79	2	1	3	B	O
<i>Porphyrio porphyrio</i>	7	144.5	2.86	2	0	3	A	O

APPENDIX I. Continued.

Species	Number of Islands	U	t	Dispersal	Endemism	Population Density	Incidence	Habitat
<i>Irediparra gallinacea</i>	1	30	1.68	3	0	2	HS	W
<i>Charadrius dubius</i>	2	58	2.33	3	0	2	HS	W
<i>Himantopus himantopus</i>	3	78	2.41	3	0	2	HS	W
<i>Esacus magnirostris</i>	13	173.5	2.26	1	0	2	C	C
<i>Ptilinopus superbus</i>	12	200.5	3.51	1	0	3	C	F
<i>Ptilinopus hyogaster</i>	17	226	4.25	2	2	4	C	F
<i>Ptilinopus rivoli</i>	9	186.5	3.81	3	1	4	A	Mt
<i>Ptilinopus solomonensis</i>	20	159	-2.02	1	2	4	ST	F,Mt
<i>Ptilinopus viridis</i>	3	59	1.14	2	1	4	N	F
<i>Ducula pacifica</i>	5	122.5	-3.09	1	0.5	4	ST	F
<i>Ducula myristicivora</i>	14	207.5	3.52	1	2	4	B	F
<i>Ducula rufigaster</i>	4	101	2.77	2	2	3	HS	F
<i>Ducula rosacea</i>	26	119.5	2.93	1	2	4	ST	F
<i>Ducula pinon</i>	3	84	2.81	1	2	3	HS	Mt
<i>Ducula bicolor</i>	11	178	2.81	1	1	3	ST	F
<i>Gymnophaps albertisii</i>	2	58	2.33	3	2	3		
<i>Columba leucomela</i>	1	29	1.57	3	0	1	HS	F,Mt
<i>Columba pallidiceps</i>	2	58	2.33	3	3	1	HS	F,Mt
<i>Macropygia amboinensis</i>	16	236.5	4.61	2	1	4	C	F
<i>Macropygia nigrirostris</i>	5	120.5	2.98	1	1	4	A	F
<i>Macropygia mackinlayi</i>	15	127	0.28	1	1	4	ST	F
<i>Reinwardtoena reinwardtii</i>	12	199.5	3.47	1	2	1	B	F,Mt
<i>Chalcophaps stephani</i>	23	184	4.16	1	0.5	4	D	F
<i>Henicophaps albifrons</i>	3	77	2.34	4	2	1	HS	F
<i>Gallucolumba canifrons</i>	17	204.5	3.40	2	1	4	C	F

APPENDIX I. Continued.

Species	Number of Islands	U	t	Dispersal	Endemism	Population Density	Incidence	Habitat
<i>Gallicolumba erythroptera</i>	9	167.5	2.98	2	0.5	3	B	F
<i>Caloenas nicobarica</i>	26	118	2.85	1	0	3	ST	F
<i>Chalcopsitta cardinalis</i>	4	76	1.30	2	3	4	N	F
<i>Trichoglossus ornatus</i>	27	102	2.83	1	1	4	D	F
<i>Lorius albidinucha</i>	1	29	1.57	3	2	4	HS	Mt
<i>Lorius chlorocercus</i>	11	200.5	3.74	1	1	4	B	F
<i>Charmosyna palmarum</i>	2	58	2.33	3	2	3		
<i>Charmosyna placentis</i>	18	210.5	3.75	1	1	3	C	F
<i>Micropsitta bruijnii</i>	2	58	2.33	3	1	3	HS	Mt
<i>Micropsitta pusio</i>	18	208.5	3.67	2	2	4		
<i>Cacatua alba</i>	1	30	1.68	3	1	3	HS	F
<i>Eclectus roratus</i>	16	212	3.64	1	1	3	C	F
<i>Geoffroyus heteroclitus</i>	10	192.5	3.70	2	2	3	A	F
<i>Loriculus aurantiifrons</i>	4	99	2.65	2	2	1	HS	F
<i>Cacomantis variolosus</i>	16	211.5	3.62	2	1	3	B	F
<i>Eudynamys scolopacea</i>	10	174.5	2.94	2	1	3	B	F
<i>Scythrops novaehollandiae</i>	16	215	3.76		0		B	F
<i>Centropus ateralbus</i>	5	119	2.90	3	2	3	HS	F
<i>Centropus violaceus</i>	2	58	2.33	3	3	1	HS	F
<i>Tyto alba</i>	2	37.5	0.68	2	1	1	N	O
<i>Tyto novaehollandiae</i>	2	50	1.69	4	2	1		
<i>Ninox novaeseelandiae</i>	5	121	3.01	4	2	3	HS	F
<i>Caprimulgus macrurus</i>	10	206.5	4.29	2	0	3	B	A
<i>Aerodramus orientalis</i>	1	29	1.57	3	3	1	HS	Mt
<i>Aerodramus vanikorensis</i>	21	184	3.34	1	1	4	D	A

APPENDIX I. Continued.

Species	Number of Islands	<i>U</i>	<i>t</i>	Dispersal	Endemism	Population Density	Incidence	Habitat
<i>Aerodramus spodiopygius</i>	8	156	2.89	2	1	3	A	A
<i>Collocalia esculenta</i>	16	174	2.14	1	1	4	C	A
<i>Hemiprocne mystacea</i>	17	228	4.33	2	1	3	C	A
<i>Alcedo atthis</i>	17	227.5	4.31	2	0.5	2	C	W
<i>Alcedo azurea</i>	5	129.5	3.47	2	2	3	HS	W
<i>Alcedo pusilla</i>	6	144.5	3.48	3	1	3	HS	Man
<i>Ceyx lepidus</i>	10	207	4.31	2	1	4	A	F
<i>Halcyon diops</i>	1	30	1.68	4	2	3	HS	F
<i>Halcyon australasia</i>	24	121	1.75		0			O
<i>Halcyon chloris</i>	19	195	3.29	1	1	4	D	F
<i>Halcyon saurophaga</i>	29	36.5	0.60	1	0.5	2	D	C
<i>Tanyptera sylvia</i>	4	93	2.30	1	1	4	A	F
<i>Merops superciliosus</i>	4	89	2.06	2	0	3	A	A
<i>Eurystomus orientalis</i>	14	199.5	3.20	1	1	3	C	A
<i>Rhyticeros plicatus</i>	3	83	2.74	3	1	1	HS	F
<i>Pitta sordida</i>	4	68.5	0.86	2	2	4		
<i>Pitta erythrogaster</i>	9	187	3.83	2	1	4	B	F
<i>Hirundo rustica</i>	15	222.5	4.05	1	1	3	C	A
<i>Coracina lineate</i>	3	78	2.41	3	1	3	HS	F
<i>Coracina papuensis</i>	6	145	3.50	2	1	3	A	O
<i>Coracina tenuirostris</i>	15	220	3.96	2	1.5	3	C	F
<i>Lalage aurea</i>	12	215.5	4.12	2	1	5	B	F
<i>Saxicola caprata</i>	4	100	2.71	2	0	2	A	O
<i>Zoothera dauma</i>	4	81	1.59	3	2	3		
<i>Turdus poliocephalus</i>	4	88	2.01	2	1	5	A	Mt

APPENDIX I. Continued.

Species	Number of Islands	<i>U</i>	<i>t</i>	Dispersal	Endemism	Population Density	Incidence	Habitat
<i>Ortygocichla rubiginosa</i>	1	30	1.68	4	3	3	HS	F
<i>Cichlornis whitneyi</i>	1	30	1.68		1.5	3	HS	Mt
<i>Acrocephalus arundinaceus</i>	4	104	2.95	2	0	3	HS	S
<i>Cisticola exilis</i>	10	200	4.02	2	1	3	B	O
<i>Megalurus timoriensis</i>	5	117.5	2.82	2	1	3	A	O
<i>Phylloscopus trivirgatus</i>	4	98.5	2.62	3	1.5	5	HS	Mt
<i>Rhipidura leucophrys</i>	19	187.5	2.98	1	0	4	D	O
<i>Rhipidura rufiventris</i>	13	208	3.65	2	2	5		
<i>Rhipidura rufifrons</i>	2	32.5	-0.28	2	1	5	N	F
<i>Rhipidura rufidorsa</i>	4	98.5	2.62	3	2	4	HS	Mt,F
<i>Monarcha cinerascens</i>	23	168	-3.43	1	1	3	ST	F
<i>Monarcha manadensis</i>	9	165.5	2.90	3	2	4	A	F
<i>Monarcha chrysomela</i>	5	117	2.80	3	1	4	A	F
<i>Myiagra alecto</i>	16	192.5	2.87	2	0	4	C	F
<i>Myiagra hebetior</i>	6	132.5	2.88	2	3	4	A	F
<i>Monachella muelleriana</i>	1	30	1.68	3	1	2	HS	Mt
<i>Pachycephala pectoralis</i>	11	201.5	3.78	2	1	5	B	F,Mt
<i>Pachycephala melanura</i>	6	88.5	-0.68	1	0	3	ST	F
<i>Dicaeum erythrothorax</i>	7	156.5	3.43	2	2	5	A	F
<i>Nectarinia sperata</i>	14	200.5	3.24	1	1	3	C	F
<i>Nectarinia jugularis</i>	23	157	2.94	1	1	3	D	O
<i>Zosterops atriceps</i>	6	144	3.45	2	1	5	A	F
<i>Zosterops griseotinctus</i>	4	56	0.12	2	3	5	ST	F
<i>Myzomela eques</i>	2	57	2.25	4	2	4	HS	F
<i>Myzomela cruentata</i>	5	121.5	3.04	3	1	5	A	F,Mt

APPENDIX I. Continued.

Species	Number of Islands	<i>U</i>	<i>t</i>	Dispersal	Endemism	Population Density	Incidence	Habitat
<i>Myzomela pulchella</i>	1	29	1.57	4	3	5	HS	Mt
<i>Myzomela cardinalis</i>	1	30	1.68		1.5	5	HS	F
<i>Myzomela sclateri</i>	7	88	-0.19	1	3	3	ST	F
<i>Myzomela lafargei</i>	15	198.5	-3.11	1	3	5	ST	F
<i>Philemon moluccensis</i>	4	102	2.83	4	2	4	HS	F
<i>Melidectes whitemanensis</i>	1	30	1.68	4	3	4	HS	Mt
<i>Erythrura trichroa</i>	9	149	2.18	2	0.5	4	A	Mt
<i>Lonchura spectabilis</i>	7	157.5	3.48	2	1.5	3	A	O
<i>Lonchura castaneothorax</i>	2	58	2.33	3	2	2	HS	O
<i>Aplonis cantoroides</i>	26	121.5	3.04	1	0	3	D	O
<i>Aplonis feadensis</i>	4	96.5	-2.51	1	3	3	ST	F
<i>Aplonis metallica</i>	24	157.5	3.48	1	1	4	D	F
<i>Mino dumontii</i>	6	136.5	3.08	3	1	4	A	F
<i>Dicrurus hottentottus</i>	4	103	2.89		1.5	4	HS	F
<i>Artamus maximus</i>	2	58	2.33	2	2	3	HS	A
<i>Corvus orru</i>	9	169.5	3.07	1	1	3	HS	F

APPENDIX J. Species characteristics for the Solomon Archipelago.

Species	Number of Islands ^a	U ^b	t ^c	Dispersal ^d	Endemism ^e	Population Density ^f	Incidence ^g	Habitat ^h
<i>Tachybaptus ruficollis</i>	2	57	0.77	3	1	2		
<i>Pelecanus conspicillatus</i>	18	396.5	3.56		0		N	C
<i>Phalacrocorax melanoleucos</i>	13	333.5	3.14	1	0.5	2	A	W
<i>Butorides striatus</i>	30	440	5.18	1	1	3	D	Man
<i>Egretta sacra</i>	41	162	3.19	1	0	2	D	C
<i>Ardea intermedia</i>	3	117.5	2.48	3	0	2	HS	O
<i>Ardea alba</i>	2	79.5	2.01	1	0	2	HS	O
<i>Nycticorax nycticorax</i>	36	312	4.26	1	1	3	D	F
<i>Ixobrychus minutus</i>	1	44	1.69	3	0	2	HS	S
<i>Ixobrychus flavicollis</i>	13	348	3.51	1	0.5	3	A	F
<i>Threskiornis aethiopicus</i>	2	64.5	-1.18	1	1	3	N	O
<i>Platalea leucorodia</i>	1	30	-0.62	1	0	2	N	W
<i>Anas platyrhynchos</i>	29	450	5.17	1	0	3	D	W

^a Number of islands on which the species occurs.

^b Mann–Whitney U -test for species nestedness. Islands are ranked from poorest to richest, and island ranks are summed across a species' occurrences.

^c t -value from Mann–Whitney U -test. Positive values indicate a tendency to occur on richer islands; negative values indicate a tendency to occur on islands with few species.

^d Lower values correspond to better dispersal ability. 3* = species barely extends into the Solomons, so little data on dispersal ability exist for this species in the Solomons

^e Levels of endemism indicate not endemic (0), or endemic at the subspecies (1), allospecies (2), full species (3), or genus level (4). 0.5 indicates that some populations are not endemic and some are endemic at the subspecies level; 1.5 indicates that some populations are endemic at the subspecies level and some are endemic at the allospecies level.

^f 1 = < 0.1 pairs/km²; 2 = 0.1–1 pair/km²; 3 = 1–10 pairs/km²; 4 = 10–100 pairs/km²; 5 = ≥ 100 pairs/km².

^g HS = high-S species; ST = supertramp; A, B, C, or D = A tramp, B tramp, C tramp, or D tramp, respectively; N = confined to one or a few geographically peripheral islands and therefore not classified.

^h F = lowland forest; C = seacoast; A = lowland aerial; W = fresh water; Man = mangrove; O = open country, secondary growth, and forest edge; S = swamps and marshes; Mt = mountains.

APPENDIX J. Continued.

Species	Number of Islands	<i>U</i>	<i>t</i>	Dispersal	Endemism	Population Density	Incidence	Habitat
<i>Aviceda cuculoides</i>	28	440.5	4.74	1	1	3	D	F
<i>Haliastur indus</i>	36	314	4.32	1	0.5	3	D	O
<i>Accipiter gentilis</i>	3	117	2.46	3	0	1	HS	F
<i>Accipiter novaehollandiae</i>	21	454	4.60	1	1	3	C	F
<i>Accipiter fasciatus</i>	2	64.5	-1.18	3	0	3	N	O
<i>Accipiter imitator</i>	3	120	2.60	4	3	1	HS	F
<i>Accipiter rufitorques</i>	26	450.5	4.68	1	2	3	D	F
<i>Haliaeetus leucogaaster</i>	33	393	5.01	3*	2	1		
<i>Pandion haliaetus</i>	38	263.5	4.09	1	0	2	D	C
<i>Falco peregrinus</i>	1	43	1.62	3	0	1	HS	A
<i>Falco subbuteo</i>	8	287	4.13	3	0	1	A	A
<i>Megapodius freycinet</i>	40	177.5	2.80	1	1	3	D	F
<i>Turnix sylvatica</i>	1	43	1.62	3	1	2	HS	O
<i>Gallirallus philippensis</i>	13	314.5	2.67	1	2	3		
<i>Nesoclopeus poecilopterus</i>	3	125	2.82	4	2	3	HS	F
<i>Porzana tabuensis</i>	3	94	1.41	3	0	2	N	S
<i>Poliolimnas cinereus</i>	5	173	2.64	3	0.5	2	A	S
<i>Amaurornis akool</i>	29	443	5.01	2	1	3	D	O
<i>Pareudiastes sylvestris</i>	1	40	1.39	4	3	1	N	Mt
<i>Porphyrio porphyrio</i>	34	354	4.41	1	0	3	D	O
<i>Esacus magnirostris</i>	30	386.5	3.89	1	0	2	D	C
<i>Ptilinopus superbus</i>	28	450.5	4.98	1	0	3	C	F
<i>Ptilinopus purpuratus</i>	7	172.5	-1.24	3	2	4		
<i>Ptilinopus solomonensis</i>	21	391.5	3.18	2	2	4	C	F, Mt
<i>Ptilinopus viridis</i>	34	370	4.84	1	1	4	D	F
<i>Ducula pacifica</i>	11	301.5	-3.03	2	0.5	4	ST	F

APPENDIX J. Continued.

Species	Number of Islands	<i>U</i>	<i>t</i>	Dispersal	Endemism	Population Density	Incidence	Habitat
<i>Ducula myristicivora</i>	32	413.5	5.15	1	2	4	D	F
<i>Ducula rosacea</i>	35	339	4.48	1	2	4	D	F
<i>Ducula latrans</i>	8	187.5	1.17	3	2	4	A	F
<i>Gymnophaps albertisii</i>	5	192	3.32		2	3		
<i>Columba leucomela</i>	10	332	4.29	3	0	1	B	F,Mt
<i>Columba pallidiceps</i>	8	219.5	2.12	3	3	1	A	F,Mt
<i>Macropygia mackinlayi</i>	34	354.5	4.43	2	1	4	D	F
<i>Reinwardtoena reinwardtii</i>	19	452.5	4.73		2	1	C	F,Mt
<i>Chalcophaps stephani</i>	35	343	4.59	1	0.5	4	D	F
<i>Galllicolumba canifrons</i>	12	255.5	1.48	3	1	4	B	F
<i>Galllicolumba salamonis</i>	2	46	0.17	3	3	3	N	F
<i>Galllicolumba erythroptera</i>	3	115	2.37	3	0.5	3	HS	F
<i>Caloenas nicobarica</i>	40	123.5	0.85	1	0	3	ST	F
<i>Chalcopsitta cardinalis</i>	34	348	4.25	1	3	4	D	F
<i>Trichoglossus ornatus</i>	32	382	4.36	1	1	4	D	F
<i>Lorius chlorocercus</i>	8	173	0.74	1	2	4	A	F
<i>Charmosyna palmarum</i>	5	199	3.58		2	3		
<i>Charmosyna placentis</i>	4	91	0.36	3*	1	3	HS	F
<i>Charmosyna margarethae</i>	9	294	3.75	2	3	3	B	F
<i>Micropsitta bruijnii</i>	3	126	2.87	3	1	3	HS	Mt
<i>Micropsitta pusio</i>	24	473	5.03		2	4		
<i>Cacatua tenuirostris</i>	29	420.5	4.47	1	2	3	C	F
<i>Electus roratus</i>	30	422.5	4.76	1	1	3	D	F
<i>Geoffroyus heteroclitus</i>	26	455.5	4.79	1	2	3	C	F
<i>Cacomantis variolosus</i>	11	326.5	3.69	3	1	3	B	F
<i>Chrysococyx lucidus</i>	2	64.5	-1.18	3	1	4	N	F

APPENDIX J. Continued.

Species	Number of Islands	<i>U</i>	<i>t</i>	Dispersal	Endemism	Population Density	Incidence	Habitat
<i>Eudynamys scolopacea</i>	30	439	5.16	1	1	3	D	F
<i>Scythrops novaehollandiae</i>	3	85.5	-1.02		0			F
<i>Centropus ateralbus</i>	15	333	2.60		2	3	B	F
<i>Tyto alba</i>	15	326	2.43	2	1	1	C	O
<i>Ninox novaeseelandiae</i>	12	332.5	3.45		2	3	B	F
<i>Nesasio solomonensis</i>	3	120	2.60	4	4	1	HS	F
<i>Podargus ocellatus</i>	3	120	2.60	3	1	1	HS	F
<i>Eurostopodus mystacalis</i>	12	336.5	3.56	1	1	2	B	A
<i>Aerodramus orientalis</i>	2	86	2.37	3	3	1	HS	Mt
<i>Aerodramus vanikorensis</i>	30	394.5	4.08	1	1	4	D	A
<i>Aerodramus spodiopygius</i>	10	331	4.26	3	1	3	A	A
<i>Collocalia esculenta</i>	27	426.5	4.25	2	1	4	C	A
<i>Hemiprocne mystacea</i>	26	464	4.99	1	1	3	C	A
<i>Alcedo atthis</i>	21	462.5	4.79	1	0.5	2	C	W
<i>Alcedo pusilla</i>	20	461	4.82	1	1	3	C	Man
<i>Ceyx lepidus</i>	15	437	5.11	3	1	4	C	F
<i>Halcyon diops</i>	8	244.5	2.87		2	3	A	F
<i>Halcyon australasia</i>	35	280.5	2.88		0		D	O
<i>Halcyon chloris</i>	37	272	3.68	1	1	4	D	F
<i>Halcyon saurophaga</i>	33	378.5	4.64	1	0.5	2	D	C
<i>Halcyon bougainvillei</i>	2	86	2.37	4	3	1	HS	F
<i>Eurystomus orientalis</i>	33	391.5	4.97	1	1	3	D	A
<i>Rhyticeros plicatus</i>	20	449.5	4.56	1	1	1	C	F
<i>Pitta brachyura</i>	3	120	2.60	4	2	4	HS	F
<i>Hirundo rustica</i>	32	412	5.11	1	1	3	D	A
<i>Coracina caledonica</i>	6	225.5	3.62	3	1	3	A	Mt

APPENDIX J. Continued.

Species	Number of Islands	U	t	Dispersal	Endemism	Population Density	Incidence	Habitat
<i>Coracina lineata</i>	21	470	4.96	1	1	3	C	F
<i>Coracina papuensis</i>	24	454.5	4.61	1	1	3	C	O
<i>Coracina tenuirostris</i>	27	428.5	4.30	1	1.5	3	D	F
<i>Coracina holopolia</i>	10	337.5	4.44	3	3	3	B	F
<i>Lalage leucopyga</i>	2	63	1.10	3	1	5	N	F
<i>Zoothera dauma</i>	4	159	3.07	3	2	3		
<i>Turdus poliocephalus</i>	4	137	2.19	3	1	5	HS	Mt
<i>Gerygone flavolateralis</i>	1	30	-0.62	3	1	5	N	F
<i>Cichlornis whitneyi</i>	2	86	2.37	3	1.5	3	HS	Mt
<i>Cettia parens</i>	1	40	1.39	4	3	3	N	Mt
<i>Acrocephalus arundinaceus</i>	5	171	2.57	3	0	3	A	S
<i>Phylloscopus trivirgatus</i>	6	234	3.91	3	1.5	5	HS	Mt
<i>Phylloscopus amoenus</i>	1	42	1.54	4	3	3	HS	Mt
<i>Rhipidura leucophrys</i>	30	440.5	5.19	1	0	4	D	O
<i>Rhipidura rufiventris</i>	16	442.5	4.99		2	5		
<i>Rhipidura spilodera</i>	4	135	2.12	4	2	5	HS	Mt
<i>Rhipidura fuliginosa</i>	1	40	1.39	3	0	3	N	Mt
<i>Rhipidura rufifrons</i>	25	470	5.03	1	1	5	D	F
<i>Rhipidura rufidorsa</i>	1	39	1.31		2	4	HS	Mt,F
<i>Clytorhynchus nigrogularis</i>	1	30	-0.62	4	2	4	N	F
<i>Monarcha cinerascens</i>	10	345.5	-4.66	2	1	3	ST	F
<i>Monarcha melanopsis</i>	30	435.5	5.07	1	2	5	D	F
<i>Monarcha manadensis</i>	23	472	4.98		2	4	C	F
<i>Myiagra rubecula</i>	27	466.5	5.18	1	1.5	4	D	F
<i>Petroica multicolor</i>	4	163	3.23	3	1	4	HS	Mt
<i>Pachycephala pectoralis</i>	22	465.5	4.83	3	1	5	C	F,Mt

APPENDIX J. Continued.

Species	Number of Islands	U	t	Dispersal	Endemism	Population Density	Incidence	Habitat
<i>Pachycephala melanura</i>	1	32.5	-0.81	1	0	3	ST	F
<i>Pachycephala implicata</i>	2	86	2.37	4	3	3	HS	Mt
<i>Dicaeum erythrothorax</i>	11	323	3.59		2	5	B	F
<i>Nectarinia jugularis</i>	35	309	3.66	1	1	3	D	O
<i>Zosterops metcalfei</i>	6	201.5	2.82	4	3	5	A	F
<i>Zosterops griseotinctus</i>	14	294.5	1.90	3*	3	5	B	F
<i>Zosterops murphyi</i>	1	42	1.54	4	3	5	HS	Mt
<i>Zosterops ugiensis</i>	3	124	2.78	3	3	5	HS	Mt
<i>Zosterops stresemanni</i>	1	39	1.31	4	3	5	HS	F
<i>Woodfordia superciliosa</i>	1	30	-0.62	4	2	5	N	F
<i>Myzomela cardinalis</i>	4	91.5	0.38	3	1.5	5	N	F
<i>Myzomela lafargei</i>	24	468.5	4.93		3	5	C	F
" <i>Stresemannia</i> " <i>bougainvillei</i>	1	44	1.69	4	4	3	HS	Mt
<i>Meliarchus sclateri</i>	1	40	1.39	4	4	4	N	F
" <i>Guadalcanaria</i> " <i>inexpectata</i>	1	43	1.62	4	4	3	HS	Mt
<i>Erythrura trichroa</i>	3	126	2.87	3	0.5	4	HS	Mt
<i>Lonchura castaneothorax</i>	1	36.5	1.12	3	2	2	N	O
<i>Aplonis cantoroides</i>	34	348.5	4.27	1	0	3	D	O
<i>Aplonis feadensis</i>	6	213	-3.21	3*	3	3	ST	F
<i>Aplonis grandis</i>	24	481.5	5.22	1	3	4	C	F
<i>Aplonis metallica</i>	36	308	4.15	1	1	4	D	F
<i>Aplonis brunneicapilla</i>	4	152	2.79	3	3	3	HS	Mt
<i>Mino dumontii</i>	31	404.5	4.60	1	1	4	D	F
<i>Dicrurus hottentottus</i>	2	82	2.15		1.5	4	HS	F
<i>Corvus woodfordi</i>	6	214	3.24	4	3	3	A	F,Mt

APPENDIX K. Species characteristics for Vanuatu.

Species	Number of Islands ^a	<i>U</i> ^b	<i>t</i> ^c	Dispersal ^d	Endemism ^e	Population Density ^f	Incidence ^g	Habitat ^h
<i>Tachybaptus novaehollandiae</i>	5	107.5	3.01	3	1	2		
<i>Butorides striatus</i>	6	82.5	0.93	1	1	3	D	Man
<i>Egretta sacra</i>	26	36	0.89	1	0	2	D	C
<i>Anas superciliosa</i>	8	139.5	3.03	1	0	3	D	W
<i>Anas gibberifrons</i>	2	38.5	1.12	3	1	2	N	W
<i>Aythya australis</i>	7	133.5	3.19					
<i>Accipiter fasciatus</i>	1	16	-0.31	3	0	3	N	O
<i>Circus approximans</i>	24	74	1.71					
<i>Falco peregrinus</i>	12	138.5	1.98	3	0	1	HS	A
<i>Megapodius freycinet</i>	20	122	2.14	1	1	3	D	F
<i>Gallirallus philippensis</i>	17	178	3.98	1	2	3		
<i>Porzana tabuensis</i>	3	45	0.56	3	0	2	N	S
<i>Poliolimnas cinereus</i>	3	53	1.15	3	0.5	2	A	S

^a Number of islands on which the species occurs.

^b Mann–Whitney *U*-test for species nestedness. Islands are ranked from poorest to richest, and island ranks are summed across a species' occurrences.

^c *t*-value from Mann–Whitney *U*-test. Positive values indicate a tendency to occur on richer islands; negative values indicate a tendency to occur on islands with few species.

^d Lower values correspond to better dispersal ability.

^e Levels of endemism indicate not endemic (0), or endemic at the subspecies (1), allospecies (2), full species (3), or genus level (4). 0.5 indicates that some populations are not endemic and some are endemic at the subspecies level; 1.5 indicates that some populations are endemic at the subspecies level and some are endemic at the allospecies level.

^f 1 = < 0.1 pairs/km²; 2 = 0.1–1 pair/km²; 3 = 1–10 pairs/km²; 4 = 10–100 pairs/km²; 5 = ≥ 100 pairs/km².

^g HS = high-S species; ST = supertramp; A, B, C, or D = A tramp, B tramp, C tramp, or D tramp, respectively; N = confined to one or a few geographically peripheral islands and therefore not classified.

^h F = lowland forest; C = seacoast; A = lowland aerial; W = fresh water; Man = mangrove; O = open country, secondary growth, and forest edge; S = swamps and marshes; Mt = mountains.

APPENDIX K. Continued.

Species	Number of Islands	<i>U</i>	<i>t</i>	Dispersal	Endemism	Population Density	Incidence	Habitat
<i>Porphyrio porphrio</i>	18	133	2.07	1	0	3	D	O
<i>Ptilinopus greyii</i>	28	0	0.00		0	4	ST	F
<i>Ptilinopus tannensis</i>	23	106	2.91					
<i>Ducula bakeri</i>	8	114	1.73	3	2	4	A	F
<i>Ducula pacifica</i>	24	83	2.30	2	0.5	4	ST	F
<i>Columba vitiensis</i>	25	56	1.38	3	0	1	B	F,Mt
<i>Macropygia mackinlayi</i>	26	45.5	1.74	2	1	4	D	F
<i>Chalcophaps indica</i>	27	26	1.55	1	0.5	4	D	F
<i>Gallicolumba sanctaecrucis</i>	1	27	1.67					
<i>Trichoglossus haematodus</i>	25	63	1.90	1	1	4	D	F
<i>Vini palmarum</i>	24	84.5	2.40					
<i>Chrysococcyx lucidus</i>	12	126	1.40	3	1	4	N	F
<i>Cacomantis pyrrhophanus</i>	18	126.5	1.75					
<i>Tyto alba</i>	21	126	2.79	2	1	1	C	O
<i>Collocalia vanikorensis</i>	20	146	3.36					
<i>Collocalia spodiopygia</i>	11	160.5	3.16					
<i>Collocalia esculenta</i>	26	51	2.23	2	1	4	C	A
<i>Halcyon chloris</i>	28	0	0.00	1	1	4	D	F
<i>Halcyon farquhari</i>	3	74	2.72		2	3	A	F
<i>Hirundo tahitica</i>	15	148.5	2.35	1	1	3	D	A
<i>Lalage maculosa</i>	10	140.5	2.43					
<i>Lalage leucopyga</i>	25	71.5	2.53	3	1	5	N	F

APPENDIX K. Continued.

Species	Number of Islands	<i>U</i>	<i>t</i>	Dispersal	Endemism	Population Density	Incidence	Habitat
<i>Coracina caledonica</i>	4	93.5	2.99	3	1	3	A	Mt
<i>Turdus poliocephalus</i>	21	134.5	3.24	3	1	5	HS	Mt
<i>Cichlornis whitneyi</i>	1	27	1.67	3	1.5	3	HS	Mt
<i>Gerygone flavolateralis</i>	12	166	3.26	3	1	5	N	F
<i>Rhipidura spilodera</i>	17	159.5	3.11	4	2	5	HS	Mt
<i>Rhipidura fuliginosa</i>	25	59	1.60	3	0	3	N	Mt
<i>Myiagra caledonica</i>	26	42.5	1.47	1	1.5	4	D	F
<i>Neolalage banksiana</i>	10	167	3.70					
<i>Clytorhynchus pachycephaloides</i>	19	126	2.00					
<i>Petroica multicolor</i>	21	130.5	3.03	3	1	4	HS	Mt
<i>Pachycephala pectoralis</i>	21	134.5	3.24	3	1	5	C	F,Mt
<i>Artamus leucorhynchus</i>	19	156	3.47					
<i>Aplonis zelandicus</i>	12	145	2.28					
<i>Aplonis santovestris</i>	1	27	1.67					
<i>Phylidonyris notabilis</i>	10	133.5	2.09					
<i>Lichmera incana</i>	13	109.5	0.55					
<i>Myzomela cardinalis</i>	28	0	0.00	3	1.5	5	N	F
<i>Zosterops flavifrons</i>	26	45	1.70					
<i>Zosterops lateralis</i>	26	37.5	1.03					
<i>Erythrura trichroa</i>	10	122.5	1.56	3	0.5	4	HS	Mt
<i>Erythrura cyaneovirens</i>	14	146.5	2.23					

APPENDIX L. Wing length and talon size of accipiters and bird-eating hawks.

Species	ID ^a	Minimum Elevation	Maximum Elevation	Species Group	Habitat	Wing Male	Wing Female	Talon Male	Talon Female
<i>Micronisus gabar</i>	107	0	2000	B	Open	189.5	200.5		
<i>Accipiter poliogaster</i>	108	0	500	A, B	Closed	227	273	75.8	98.5
<i>Accipiter trivirgatus</i>	109	0	1800	A, B	Both	229	264	91.2	105.8
<i>Accipiter griseiceps</i>	110	0	2000	A, B	Both	181	197	74.1	82.7
<i>Accipiter tachiro</i>	111	0	3000	A, B	Closed	222	239	77.5	96.0
<i>Accipiter castanilius</i>	112	0	750	A, B	Closed	156	182	56.6	72.5
<i>Accipiter badius</i>	113	0	1500	A, B	Both	187	208	66.7	72.7
<i>Accipiter brevipes</i>	114	0	500	A, B	Both	217	235	63.3	67.3
<i>Accipiter soloensis</i>	115	0	1000	A	Both	186	198	53.9	56.5
<i>Accipiter butleri</i>	116	0	100	A	Closed	169	183	61.0	67.8
<i>Accipiter francesii</i>	117	0	2000	A	Both	159	171	56.5	64.2
<i>Accipiter trinotatus</i>	118	250	1300	A	Closed	155	164	56.6	61.3
<i>Accipiter fasciatus</i>	119	0	2000	A, B	Both	288	304	97.3	101.8
<i>Accipiter novaehollandiae</i>	120	0	1500	A, B	Closed	261	311	99.8	121.2
<i>Accipiter hiogaster</i>	121	0	500	A, B	Both	184	214	65.8	78.4
<i>Accipiter griseogularis</i>	122	0	1200	A, B	Closed	222	261	82.7	98.9
<i>Accipiter melanochlamys</i>	123	1800	3300	A, B	Both	220	251	75.2	87.9
<i>Accipiter albogularis</i>	124	0	1200	A, B	Closed	217	246	84.7	93.1
<i>Accipiter rufitorques</i>	125	0	1200	A, B	Both	201	234	71.1	84.4
<i>Accipiter haplochrous</i>	126	0	1100	A, B	Both	205	237	72.9	82.2

^a ID corresponds to the species number used in Ferguson-Lees and Christie (2001).

Appendix L. Continued.

Species	ID	Minimum Elevation	Maximum Elevation	Species Group	Habitat	Wing Male	Wing Female	Talon Male	Talon Female
<i>Accipiter henicogrammus</i>	127	200	1300	A, B	Both	215	247	68.6	76.7
<i>Accipiter luteoschistaceus</i>	128	200	700	A, B	Both	193	211.5	63.5	77.7
<i>Accipiter imitator</i>	129	400	1000	A, B	Closed	182	209	65.2	66.2
<i>Accipiter poliocephalus</i>	130	0	1500	A	Both	198	228	69.5	78.0
<i>Accipiter princes</i>	131	750	1450	A, B	Closed	255	285	91.3	106.4
<i>Accipiter superciliosus</i>	132	0	800	A, B	Both	134	160	56.9	73.0
<i>Accipiter collaris</i>	133	600	2200	A, B	Both	155	174	75.7	89.3
<i>Accipiter erythropus</i>	134	0	1500	A, B	Both	147	171	55.4	62.1
<i>Accipiter minullus</i>	135	0	1800	A, B	Both	140	158	51.4	61.2
<i>Accipiter gularis</i>	136	0	1000	A, B	Both	168	194	55.9	65.9
<i>Accipiter virgatus</i>	137	300	2200	A, B	Closed	154	207	62.6	81.3
<i>Accipiter nanus</i>	138	900	2250	A, B	Closed	156	173	55.9	62.6
<i>Accipiter cirrocephalus</i>	139	0	1500	A, B	Both	206	238	62.6	76.4
<i>Accipiter brachyurus</i>	140	0	1800	A, B	Both	173	203.5	62.0	74.5
<i>Accipiter erythrauchen</i>	141	0	1400	A, B	Both	200	207	80.3	86.0
<i>Accipiter rhodogaster</i>	142	0	2000	A, B	Both	166	195	65.5	85.1
<i>Accipiter ovampensis</i>	143	0	1800	A, B	Both	221	254	69.8	83.2
<i>Accipiter madagascariensis</i>	144	0	1000	A, B	Closed	173	218	62.2	82.5
<i>Accipiter nisus</i>	145	0	4500	A, B	Both	202	230	62.0	78.7
<i>Accipiter rufiventris</i>	146	2000	3000	A, B	Both	202	234	67.5	75.9

Appendix L. Continued.

Species	ID	Minimum Elevation	Maximum Elevation	Species Group	Habitat	Wing Male	Wing Female	Talon Male	Talon Female
<i>Accipiter striatus</i>	147	0	3700	A, B	Both	178	208	55.2	67.5
<i>Accipiter bicolor</i>	148	0	2000	A, B	Both	212	241	78.7	96.5
<i>Accipiter cooperi</i>	149	0	3000	A, B	Both	235	263	82.5	97.7
<i>Accipiter gundlachi</i>	150	0	800	A, B	Both	237	280	91.4	124.9
<i>Accipiter melanoleucus</i>	151	0	3700	A, B	Closed	280	337	104.3	127.4
<i>Accipiter henstii</i>	152	0	1800	A, B	Closed	282	322	110.0	135.6
<i>Accipiter gentiles</i>	153	0	3000	A, B	Both	318	357	109.9	130.5
<i>Accipiter meyerianus</i>	154	0	2700	A, B	Both	295	326	110.3	125.0
<i>Erythrotriorchis buergersii</i>	155	450	1600	B	Both	295	324		
<i>Erythrotriorchis radiatus</i>	156	0	1000	B	Closed	362	420		
<i>Megatriorchis doriae</i>	157	0	1100	B	Both	296	330		
<i>Urotriorchis macrourus</i>	158	0	900	B	Closed	284.5	301.5		
<i>Parabuteo unicinctus</i>	180	0	1500	B	Open	323.5	348.75		
<i>Hieraaetus fasciatus</i>	227	0	3000	B	Both	474	506		
<i>Hieraaetus ayresii</i>	232	0	3000	B	Both	335.5	390		
<i>Hieraaetus kienerii</i>	233	300	1200	B	Both	359.5	392.5		
<i>Micrastur ruficollis</i>	261	500	1800	B	Closed	176	179.2		
<i>Micrastur plumbeus</i>	263	300	1450	B	Closed	176	176.5		
<i>Micrastur mirandollei</i>	264	0	200	B	Closed	226.5	227.5		
<i>Micrastur semitorquatus</i>	265	0	1000	B	Both	257.25	269.75		
<i>Micrastur buckleyi</i>	266	100	700	B	Closed	214	217		

APPENDIX M. Wing lengths for subspecies of *Accipiter* hawks.

Species	Subspecies	Wing length	
		Male	Female
<i>Micronisus gabar</i>		189.5	200.5
<i>Accipiter poliogaster</i>		244.5	274.5
<i>Accipiter trivirgatus</i>	<i>trivirgatus</i>	201	221
	<i>indicus</i>	226	247
	<i>layardi</i>	186.5	202
	<i>peninsulae</i>	203.5	225.5
	<i>javanicus</i>	196	219
	<i>niasensis</i>	184	212
	<i>microstictus</i>	195.5	216.5
	<i>palawanus</i>	192	220
	<i>extimus</i>	187.5	211
	<i>castroi</i>	187	210
<i>Accipiter griseiceps</i>		175.5	196
<i>Accipiter tachiro</i>	<i>tachiro</i>	198.5	243
	<i>sparsinfasciatus</i>	194.7	226.8
	<i>unduliventer</i>	194.7	226.8
	<i>canescens</i>	194.7	226.8
	<i>toussenelii</i>	193.5	226.5
	<i>macroscelides</i>	192	211
	<i>lopezi</i>	194.7	226.8
<i>Accipiter castanilius</i>	<i>castanilius</i>	152.5	179
	<i>beniensis</i>	164	189
<i>Accipiter badius</i>	<i>badius</i>	176	196
	<i>dussumieri</i>	192	211
	<i>cenchroides</i>	188	217.5
	<i>poliopsis</i>	198	218
	<i>sphenurus</i>	179.5	193
	<i>polyzonoides</i>	174.5	192
<i>Accipiter brevipes</i>		219	235.5
<i>Accipiter soloensis</i>		185.5	197.5
<i>Accipiter butleri</i>	<i>butleri</i>	172.5	180.5
	<i>obsoletus</i>	183.5	192
<i>Accipiter francesii</i>	<i>francesii</i>	157	177
	<i>griveaudi</i>	142	169
	<i>pusillus</i>	142	159
	<i>brutus</i>	140	156
<i>Accipiter trinotatus</i>		150.5	165

Appendix M. Continued.

Species	Subspecies	Wing length	
		Male	Female
<i>Accipiter fasciatus</i>	<i>fasciatus</i>	257	299
	<i>didimus</i>	254.5	285.5
	<i>vigilax</i>	241.8	275.9
	<i>polycryptus</i>	226.9	258.9
	<i>dogwa</i>	228.3	260.5
	<i>buruensis</i>	227.8	259.9
	<i>hellmayri</i>	213.4	243.4
	<i>savu</i>	237.2	270.6
	<i>wallacei</i>	208.7	238.1
	<i>tjendanae</i>	215.7	246.1
	<i>Accipiter novaehollandiae</i>	<i>novaehollandiae</i>	256
<i>pallidimas</i>		225	273
<i>polionotus</i>		196.5	234
<i>leucosomus</i>		214.5	246
<i>misulae</i>		239	279
<i>lihirensis</i>		222	260
<i>dampieri</i>		193.5	224.5
<i>sylvestris</i>		183.5	210
<i>rubianae</i>		197.5	212
<i>rufoschistaceus</i>		207	239
<i>bougainvillei</i>		194	237
<i>malaitae</i>		193	216
<i>pulchellus</i>		224.5	257
<i>lavongai</i>		205.5	237
<i>manusi</i>		200.5	234
<i>matthiae</i>		194	228
<i>pallidiceps</i>		192.5	220.5
<i>albiventris</i>		180.5	205.6
<i>misoriensis</i>		197	215.5
<i>hiogaster</i>		185	215.5
<i>Accipiter hiogaster</i>			
<i>Accipiter griseogularis</i>	<i>griseogularis</i>	229	265.5
	<i>mortyi</i>	214.5	243.5
	<i>obiensis</i>	195.5	236
<i>Accipiter melanochlamys</i>		220.5	254
<i>Accipiter albogularis</i>	<i>albogularis</i>	217	246
	<i>woodfordi</i>	217	246
	<i>gilvus</i>	217	246
	<i>eichorni</i>	217	246
	<i>sharpei</i>	217	246
<i>Accipiter rufitorques</i>		200.5	236.5
<i>Accipiter haplochrous</i>		202	236
<i>Accipiter henicogrammus</i>		224.5	248.5
<i>Accipiter luteoschistaceus</i>		190	211.5
<i>Accipiter imitator</i>		182	203
<i>Accipiter poliocephalus</i>		195	210.5

Appendix M. Continued.

Species	Subspecies	Wing length	
		Male	Female
<i>Accipiter princeps</i>		255	285
<i>Accipiter superciliosus</i>	<i>superciliosus</i>	140.5	162.5
	<i>fontanieri</i>	130.5	151
<i>Accipiter collaris</i>		155	174
<i>Accipiter erythropus</i>	<i>erythropus</i>	149	169.5
	<i>zenkeri</i>	151	172
<i>Accipiter minullus</i>		140	160
<i>Accipiter gularis</i>		165	189
<i>Accipiter virgatus</i>	<i>virgatus</i>	153	177.5
	<i>confusus</i>	153	177.5
	<i>rufotibialis</i>	153	177.5
	<i>vanbemmeli</i>	153	177.5
	<i>besra</i>	155.5	184.5
	<i>affinis</i>	167.5	207
<i>Accipiter nanus</i>		156	173
<i>Accipiter cirrocephalus</i>	<i>cirrocephalus</i>	207	243
	<i>quaesitandus</i>	201.5	237
	<i>rosselianus</i>	198.2	230.8
	<i>papuanus</i>	186	212.5
<i>Accipiter brachyurus</i>		173	203.5
<i>Accipiter erythrauchen</i>	<i>erythrauchen</i>	166.5	200.5
	<i>ceramensis</i>	177	212.5
<i>Accipiter rhodogaster</i>	<i>rhodogaster</i>	166.5	204
	<i>butonensis</i>	166.5	204
	<i>sulaensis</i>	160	180
<i>Accipiter ovampensis</i>		221.5	253
<i>Accipiter madagascariensis</i>		183	226.5
<i>Accipiter nisus</i>	<i>nisus</i>	199	239.5
	<i>punicus</i>	208.5	244
	<i>granti</i>	193	225.5
	<i>wolterstorffi</i>	188.5	219
	<i>nisosimilis</i>	209.5	246.5
	<i>melaschistos</i>	209	250.5
<i>Accipiter rufiventris</i>	<i>rufiventris</i>	202	234.5
	<i>perspicillaris</i>	196	228.5
<i>Accipiter striatus</i>	<i>striatus</i>	142	183.5
	<i>velox</i>	169.5	198.5
	<i>perobscurus</i>	174	206
	<i>suttoni</i>	181	222.5
	<i>madrensis</i>	164.7	198
	<i>chionogaster</i>	170.5	203.5
	<i>ventralis</i>	165	203.5
	<i>erythronemius</i>	166.5	192.5
	<i>fringilloides</i>	157	181.5
	<i>venator</i>	157	190.7

Appendix M. Continued.

Species	Subspecies	Wing length	Wing length
		Male	Female
<i>Accipiter bicolor</i>	<i>bicolor</i>	206.5	242
	<i>fidens</i>	219	255.5
	<i>pileatus</i>	203	254.5
	<i>guttifer</i>	213	255.5
	<i>chilensis</i>	211	256.5
<i>Accipiter cooperi</i>		226	262.5
<i>Accipiter gundlachi</i>		248.5	271.5
<i>Accipiter melanoleucus</i>	<i>melanoleucus</i>	295.5	338.5
	<i>temminckii</i>	262	300
<i>Accipiter henstii</i>		279.5	324
<i>Accipiter gentilis</i>	<i>gentilis</i>	321	360.5
	<i>buteoides</i>	326.5	364
	<i>albidus</i>	331	379
	<i>arrigonii</i>	300.5	341
	<i>schvedowi</i>	310.5	346
	<i>fujiyamae</i>	293	326
	<i>atricapillus</i>	322.5	341.5
	<i>laingi</i>	312	332
	<i>apache</i>	349	377.5
<i>Accipiter meyerianus</i>		303	330.5
<i>Erythrotriorchis buergersii</i>		294.5	325.5
<i>Erythrotriorchis radiatus</i>		353.5	404.5
<i>Megatriorchis doriae</i>		286	330
<i>Urotriorchis macrourus</i>		284.5	301.5
<i>Parabuteo unicinctus</i>		323.5	348.8
<i>Hieraaetus fasciatus</i>		474	506
<i>Hieraaetus ayresii</i>		335.5	390
<i>Hieraaetus kienerii</i>		359.5	392.5
<i>Micrastur ruficollis</i>		176	179.2
<i>Micrastur plumbeus</i>		176	176.5
<i>Micrastur mirandollei</i>		226.5	227.5
<i>Micrastur semitorquatus</i>		257.3	269.8
<i>Micrastur buckleyi</i>		214	217

APPENDIX N. Minimum size ratios and Barton–David statistics.

Species Group	Habitat	Trait	Species ^a	Area ^b	Minimum Size Ratio ^c	Minimum Interspecific Size Ratio ^d	Barton–David 1 ^e	Barton–David 2 ^f	Barton–David 3 ^g
Accipiters	Closed	Wing	2	4	222	247	560	324	707
Accipiters	Closed	Wing	3	4	32	52	100	162	79
Accipiters	Closed	Wing	4	4	24	34	88	84	50
Accipiters	Closed	Wing	5	4	49	49	162	58	19
Accipiters	Closed	Wing	6	4	-	-	-	-	-
Accipiters	Closed	Wing	2	25	44	123	194	101	492
Accipiters	Closed	Wing	3	25	14	17	162	147	132
Accipiters	Closed	Wing	4	25	3	8	16	51	64
Accipiters	Closed	Wing	5	25	726	726	762	818	37
Accipiters	Closed	Wing	6	25	-	-	-	-	-
Accipiters	Closed	Talon	2	4	10	106	33	14	487
Accipiters	Closed	Talon	3	4	3	46	5	28	70
Accipiters	Closed	Talon	4	4	0	4	2	16	55
Accipiters	Closed	Talon	5	4	66	73	159	217	230
Accipiters	Closed	Talon	6	4	-	-	-	-	-
Accipiters	Closed	Talon	2	25	19	65	65	19	633
Accipiters	Closed	Talon	3	25	1	21	3	13	56
Accipiters	Closed	Talon	4	25	0	2	1	10	26
Accipiters	Closed	Talon	5	25	4	4	24	48	101
Accipiters	Closed	Talon	6	25	-	-	-	-	-

^a Number of species in the community.

^b Minimum geographic area threshold. ($\times 10^4 \text{ km}^2$)

^c Minimum size ratio between any two morphospecies.

^d Minimum interspecific size ratio (excludes conspecific male/female pairs).

^e Barton–David statistic, $G_{1,n}$: ratio of the smallest size ratio to the largest size ratio.

^f Barton–David statistic $G_{1,n-1}$: ratio of the smallest size ratio to the second largest size ratio.

^g Barton–David statistic $G_{2,n}$: ratio of the second smallest size ratio to the largest size ratio.

Appendix N. Continued.

Species Group	Habitat	Trait	Species	Area	Minimum Size Ratio	Minimum Interspecific Size Ratio	Barton–David 1	Barton–David 2	Barton–David 3
Accipiters	Open	Wing	2	4	39	259	210	114	320
Accipiters	Open	Wing	3	4	89	311	62	105	156
Accipiters	Open	Wing	4	4	71	82	130	18	566
Accipiters	Open	Wing	5	4	-	-	-	-	-
Accipiters	Open	Wing	6	4	-	-	-	-	-
Accipiters	Open	Wing	2	25	77	297	224	255	305
Accipiters	Open	Wing	3	25	88	229	147	189	145
Accipiters	Open	Wing	4	25	301	301	283	408	579
Accipiters	Open	Wing	5	25	-	-	-	-	-
Accipiters	Open	Talon	2	4	3	117	1	3	133
Accipiters	Open	Talon	3	4	78	173	186	217	158
Accipiters	Open	Talon	4	4	371	376	493	400	679
Accipiters	Open	Talon	5	4	-	-	-	-	-
Accipiters	Open	Talon	2	25	12	145	6	22	234
Accipiters	Open	Talon	3	25	16	103	69	123	128
Accipiters	Open	Talon	4	25	116	116	139	150	328
Accipiters	Open	Talon	5	25	-	-	-	-	-

Appendix N. Continued.

Species Group	Habitat	Trait	Species	Area	Minimum Size Ratio	Minimum Interspecific Size Ratio	Barton–David 1	Barton–David 2	Barton–David 3
Bird-eating hawks	Closed	Wing	2	4	196	117	637	328	812
Bird-eating hawks	Closed	Wing	3	4	95	244	356	413	232
Bird-eating hawks	Closed	Wing	4	4	585	638	632	812	164
Bird-eating hawks	Closed	Wing	5	4	839	911	834	924	248
Bird-eating hawks	Closed	Wing	6	4	472	662	453	561	502
Bird-eating hawks	Closed	Wing	7	4	427	587	404	527	167
Bird-eating hawks	Closed	Wing	2	25	446	147	743	579	687
Bird-eating hawks	Closed	Wing	3	25	328	249	435	583	134
Bird-eating hawks	Closed	Wing	4	25	874	774	853	931	316
Bird-eating hawks	Closed	Wing	5	25	689	852	720	826	429
Bird-eating hawks	Closed	Wing	6	25	492	662	564	702	862
Bird-eating hawks	Closed	Wing	7	25	-	-	-	-	-
Bird-eating hawks	Open	Wing	2	4	34	143	208	39	651
Bird-eating hawks	Open	Wing	3	4	21	111	196	161	610
Bird-eating hawks	Open	Wing	4	4	219	236	415	533	513
Bird-eating hawks	Open	Wing	5	4	311	463	335	483	421
Bird-eating hawks	Open	Wing	6	4	64	106	88	134	227
Bird-eating hawks	Open	Wing	2	25	121	89	528	273	643
Bird-eating hawks	Open	Wing	3	25	58	94	309	278	510
Bird-eating hawks	Open	Wing	4	25	112	110	244	306	189
Bird-eating hawks	Open	Wing	5	25	215	324	255	383	134
Bird-eating hawks	Open	Wing	6	25	-	-	-	-	-

VITA

I was born in 1970 in California and spent most of my childhood in Chandler, Arizona. Growing up in Arizona, I was exposed to a tremendous variety of plant and animal life. I noticed the vegetational changes that occur as one drives from Phoenix to Flagstaff, and I wondered why the desert plants were replaced by grasses and juniper trees and then they, in turn, were replaced by pine forest. While attending Chandler High School, I developed an interest in math, biology, and chemistry, but I did not realize that “ecology” is a science and can constitute a profession, not just an interest.

After graduating from high school in 1988, I attended the University of Arizona in Tucson. As an undergraduate, I gained an appreciation for the complexity of natural systems, realized the severity of the biodiversity crisis, and found a passion for birds. The lure of solving practical problems with science spawned my interest in ecology. My undergraduate education was enhanced through participation in the Hughes Undergraduate Biology Research Program at the University of Arizona. In this program, I studied the coloration of juvenile Cortez damselfish (*Eupomacentrus rectifraenum*) in the Sea of Cortez, Mexico.

My biological training also benefited from two summer employment opportunities. In 1991, I worked on a desert revegetation site, searched for nesting eyries of the peregrine falcon, and conducted surveys for the threatened desert tortoise as a research technician for the Bureau of Reclamation, U.S. Department of the Interior. In 1992, I worked for the Department of Wildlife Ecology, University of Arizona. From an observation blind, I identified prey items brought into the nest by breeding pairs of northern goshawks (*Accipiter gentilis*). I also learned identify prey remains from pellet castings and to trap, band, and radio track adults.

After earning a Bachelor’s of Science degree in Ecology and Evolutionary Biology from the University of Arizona in 1992, I worked for the Arizona Game and Fish Department for two years studying nest productivity of the northern goshawk and working on the Arizona Breeding Bird Atlas. In 1994, I entered the Department of Biological Science at Florida State University to study with Dr. Daniel Simberloff. Under his tutelage, my interest in biogeography and in population and community ecology continued to grow. I completed my Master’s thesis in 1998 on “The effect of spatial autocorrelation on rarefaction.” I followed Dr. Simberloff to the University of Tennessee to pursue a Doctor of Philosophy degree in the Department of Ecology and Evolutionary Biology. I graduated in 2006 with a dissertation on avian community ecology. In the fall of 2006, I will begin a one-year appointment as a Visiting Assistant Professor at The College of Wooster (OH).