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The checkered history of checkerboard distributions

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Abstract. To address the idea that the process of interspecific competition can be inferred from data on geographical distribution alone and that evidence from geographical distribution implies an important role for interspecific competition in shaping ecological communities, we reexamine the occurrence of "true checkerboard" distributions among the land and freshwater birds in three Melanesian archipelagoes: Vanuatu, the Bismarck Archipelago, and the Solomon Islands. We use the most recently published distributional records and explicitly include the geography of the distributions of species within each archipelago.

We use the overlap of convex hulls to estimate the overlap in the geographic range for each pair of species in each of these archipelagoes. We define a "true checkerboard" to consist of a pair of species with exclusive island-by-island distributions, but that have overlapping geographical ranges. To avoid the "dilution effect," we follow Diamond and Gilpin in focusing only on congeneric and within-guild species pairs as potential competitors.

Few, if any, "true checkerboards" exist in these archipelagoes that could possibly have been influenced by competitive interactions, and even "true checkerboards" can arise for reasons other than interspecific competition. The similarity between related species pairs (congeneric and within-guild pairs) and unrelated species pairs in their deviation from expectation of the number of islands shared and the overlap of their geographic ranges indicates that these are not distinct statistical populations, but rather a single population of species pairs. Our result, which is based on an examination of the distributional data alone, is consistent with the interpretation that, in these avifaunas, the distributions of congeneric, within-guild, and unrelated species pairs are shaped by a common set of biological and physical environmental processes.

Key words: avifauna; bird guilds; Bismarck Archipelago; checkerboard distribution; convex hull overlap; geographic range overlap; interspecific competition; Solomon Islands; species pairs; Vanuatu.

Introduction

The idea that interspecific competition leads to a lack of co-occurrence of species on islands was popularized by Diamond's (1975) examination of the distribution of birds in the Bismarck Archipelago. Diamond (1975) proposed, as a metaphor for the distribution of competing species, a "checkerboard"—a game board for draughts or checkers—composed of alternating squares of contrasting colors. In this metaphor, islands are squares with squares of each color containing only one member of a pair of species. In essence, Diamond's (1975) idea was that species pairs with exclusive island-by-island distributions, but that occur on islands that are geographically interspersed, are likely to maintain such a distribution by interspecific competition. Diamond (1975) contended that observation of such a "checkerboard distribution" was evidence that the distribution of these species is affected by interspecific competition.

In a critique of the idea that data on geographical distribution alone provide a strong basis to infer interspecific competition and imply an important role for interspecific competition in shaping ecological communities, Connor and Simberloff (1979) proposed a different metaphor for the distribution of species among islands: a binary matrix. They likened the columns of such a matrix to islands, the rows to species, and 1's and 0's in the matrix to presences and absences, respectively, of species on specific islands. Connor and Simberloff (1979) applied Monte Carlo techniques to ask if, conditional on the observed number of species on each island (column sums) and the observed breadth of species distributions (row sums), the observed level of species co-occurrence suggested pairwise independence in the island-by-island distribution of species or if other processes leading to nonindependence within species pairs were implied by the data (e.g., interspecific competition, differences in habitat, geographical speciation, historical limitations on dispersal).

While a controversy focusing on the ecological problem depicted by these metaphors ensued, much of the approach proposed by Connor and Simberloff (1979) continues to be employed today, but with

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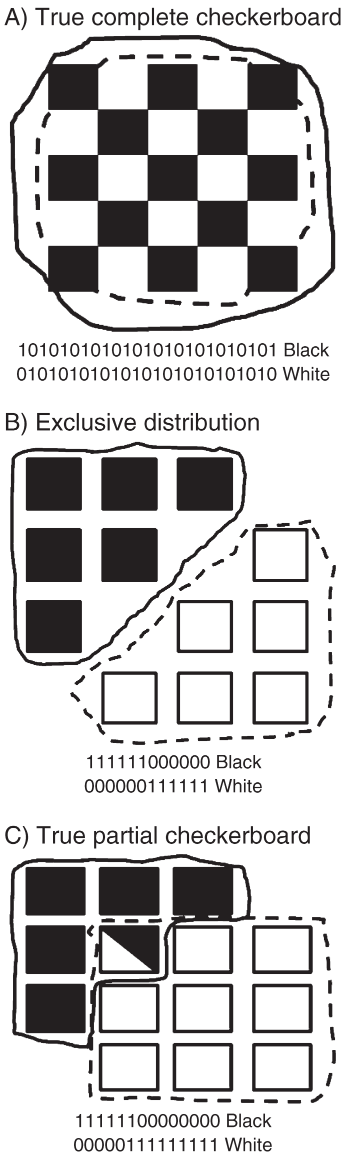

FIG. 1. Schematic map representation of a "true checkerboard," a regionally allopatric exclusive distribution, and a "partial" checkerboard and how they would be represented in a binary matrix. In each diagram the map shows the explicit geographical location of each island while the binary matrix representation cannot preserve the spatial relationships among islands. (A) A true "complete" checkerboard distribution (TCC) showing the exclusive distribution of two species represented by black and white squares with their geographic ranges shown by the solid and dashed lines broadly overlapping. (B) An exclusive distribution shown by two species represented by black and white squares with their geographic ranges not overlapping (regionally allopatric pair). (C) A true "partial" checkerboard (TPC) showing that the pair shares a single island as represented by a square that is both black and white. Although only a single white and black rectangle is depicted, multiple islands could contain both species.

modifications of the method in response to criticisms (Diamond and Gilpin 1982, Gilpin and Diamond 1982, 1984, Gotelli and Graves 1996, Gotelli 2000, Gotelli and Entsminger 2003, Sfenthourakis et al. 2006, Sanderson et al. 2009, Simberloff and Collins 2010, Collins et al. 2011). For example, the swap algorithm for generating a sample of binary matrices with fixed row and column sums proposed by Connor and Simberloff (1979) is widely used. Miklós and Podani's (2004) trial-swap method modifies the algorithm to ensure that all matrices in the universe $U(R, S)$ of binary matrices with the same vectors of row (R) and column sums (S) are sampled equiprobably. Restricting examination of nonindependence among species to only congeneric or within-guild pairs has also become standard in response to the criticism by Diamond and Gilpin (1982) and Gilpin and Diamond (1984) that examining noncongeneric or unrelated species dilutes the potential to detect competitive interactions, because competition is unlikely to occur between more distantly related species.

Nevertheless, mixing of the metaphors of checkerboards and binary matrices has led to an unfortunate stew of metrics and to arguments that fail to address Diamond's (1975) original contentions that interspecific competition is widespread in its effects on the geographical distribution of species, that competitively generated checkerboard distributions are common, and that one can readily infer competition from data on geographical distributions. Two of us (E. F. Connor and D. Simberloff) take responsibility for generating some of this confusion, because the metaphor of a binary matrix fails to maintain the explicit geography of islands within an archipelago.

Examination of binary matrices to search for species pairs whose geographical distributions might reflect some form of nonindependence (e.g., interspecific competition, allopatric speciation) has traditionally entailed searching for pairs of rows (species) that never have 1's in the same column. Pairs of species that mismatch in this way have exclusive geographical distributions: where species A is found, species B is not found, and vice versa. However, such mismatched species are not necessarily "checkerboards" sensu Diamond (1975). In Fig. 1A, we illustrate a checkerboard in which different-shaded squares represent the mapped geographical distributions of two species each on different islands. These two species have exclusive island-by-island distributions, so when represented in a binary matrix they would not have 1's in the same column. If one were to draw a line around the set of islands occupied by the black species and do the same for the white species to produce polygons encompassing each species' geographic range, the two polygons would broadly overlap. Such a pair of species would constitute a "true checkerboard" sensu Diamond (1975), because the pair never co-occurs on the same island and the islands occupied by these two species are geographically interspersed. In Fig. 1B, we illustrate a pair of species that also has exclusive island-by-island distributions, but this second pair of species does not have a true checkerboard distribution because their geographic ranges do not overlap. We have termed these distributions "regionally allopatric" (Collins et al. 2011). Diamond's (1975) requirement that pairs of species must occur on islands that are spatially interspersed was his attempt to separate competitively determined lack of co-occurrence from a lack of co-occurrence owing to what has subsequently been termed "spatial turnover" (Podani and Schmera 2011, Ulrich et al. 2012, Ulrich and Gotelli 2013).

Unfortunately, the bookkeeping procedures used to inspect binary matrices to count the number of checkerboard pairs do not and cannot parse competitively determined lack of co-occurrence from a lack of co-occurrence owing to spatial turnover, because the metaphor of the binary matrix has no explicit geography. Stone et al. (1996) pointed out that without explicitly incorporating species geographic ranges there is no way to distinguish the two classes of exclusive distributions. Therefore, methods outlined by Podani and Schmera (2011), Ulrich et al. (2012), and Ulrich and Gotelli (2013) that do not explicitly include the geography of species ranges cannot parse competitively determined lack of co-occurrence from a lack of co-occurrence owing to spatial turnover. Furthermore, the count of pairs of species that never co-occur on an island (CH as in Collins et al. 2011) is not a count of true checkerboard distributions, but merely a count of pairs of species with exclusive island-by-island distributions. The "checkerboard score" or "C-score" of Stone and Roberts (1990) is not a "true checkerboard" score and does not measure exclusiveness; rather, C-score measures deviation from randomness (see Stone and Roberts 1992). Although exclusive interspecific patterns of island occupancy can occur for many reasons, true checkerboards are more likely to represent interspecific competition, as suggested by Diamond (1975).

To address once again the idea that interspecific competition can be strongly implied by data on geographical distributions, we reexamine the occurrence of true checkerboard distributions among birds in three Melanesian archipelagoes. We use the most recently published distributional records and explicitly include the geography of the distributions of species within each archipelago.

Methods

Species and island data

We examine data on the distributions of the land and freshwater birds of Vanuatu, the Bismarck Archipelago, and the Solomon Islands (see Plate 1). Connor and Simberloff (1979) originally examined the data for Vanuatu, but publication of the distributional data on the birds of the Bismarck Archipelago and the Solomon Islands by Mayr and Diamond (2001) rekindled our interest in this problem (Simberloff and Collins 2010, Collins et al. 2011). Additional data published with a new study of the Bismarcks and Solomons by Sanderson et al. (2009) provide an opportunity for a more complete analysis of the underlying problem. For our analysis of Vanuatu, we use the data on bird distributions published by Diamond and Marshall (1976) that we examined previously (Connor and Simberloff 1979). For the analysis of the Bismarcks and Solomons, we use the data updated from Mayr and Diamond (2001) that are available as a table labeled "as analyzed" in the online supplement to Sanderson et al. (2009).

To integrate the explicit geography of these archipelagoes into our analysis, we obtained geographical coordinates of a sample of points to represent the perimeters of each island in decimal degrees. We selected locations on the perimeters of each island to outline each island roughly. The number of perimeter locations sampled for a specific island was a function of island size and shape. We used Google Earth as our source for these coordinates. We used a variety of web resources to locate many of the small islands within these archipelagoes. However, we could not locate all of the small islets in the Solomon Islands located in the Wana Wana and Roviana lagoons reported by Sanderson et al. (2009). After we contacted the authors, they indicated that some of the islands' names do not correspond to the names on existing maps, so that it was not possible to locate some islands (J. M. Diamond, *personal communication*). For these islands, we simply chose a location not occupied by another island within the Wana Wana or Roviana lagoon to serve as a surrogate location and assumed that the islands were small. The coordinates of these locations and their perimeters assuming small size were recorded.

Mayr and Diamond (2001) define island groups within the Bismarck Archipelago and the Solomon Islands. According to Mayr and Diamond (2001), these island groups are separated by significant barriers to dispersal and were separated even during past lower sea levels, and these barriers suffice to generate morphological differences within species or species groups and compositional differences in the bird communities on islands in different island groups. We use these island group definitions as provided in Mayr and Diamond (2001) and mapped in Simberloff and Collins (2010) and Collins et al. (2011). Because Diamond's (1975) idea of a checkerboard pair implies that the exclusive island-by-island distribution of a pair of species is maintained in ecological time by interspecific competition, pairs of species that are exclusive in their island-by-island distribution because they are found in different island groups would not constitute a "true checkerboard." See Supplement 1 for the data on species incidences, the coordinates of the island perimeters, and island group membership.

Analytical procedures

The goal of our analysis was to determine whether the number of "true checkerboard" distributions in each archipelago was larger than expected under a hypothesis of pairwise independence among congeneric species or species within guilds, and to determine how common such true checkerboard distributions were. We defined a true checkerboard as a pair of species that (1) has exclusive island-by-island distributions, (2) co-occurs in at least one island group, and (3) has geographical ranges that overlap more or significantly more than expected under a hypothesis of pairwise independence. We use this definition in an effort to mirror more closely Diamond's (1975) original idea of a checkerboard distribution. That two species never co-occur is a necessary, but not a sufficient, condition to constitute a true checkerboard distribution. The sufficient condition for a true checkerboard is that two species never co-occur on any island, yet the islands they occupy are interspersed: that is, their geographical ranges overlap more than expected were they distributed independently of each other.

Generating a sample of matrices from $U(R, S)$.—We used a Markov chain Monte Carlo (MCMC) approach in which, conditional on the observed row and column sums of the species occurrence matrix, we selected a sample of 1000 matrices from $U(R, S)$. We used Miklós and Podani's (2004) trial-swap algorithm in which randomly chosen 2×2 sub-matrices with 1's and 0's on the opposing diagonals have their elements swapped within rows. We imposed the further restriction that species could occur only on islands within island groups where they are found in the data provided by Sanderson et al. (2009). This ensures that regionally allopatric species that are restricted to different island groups will not be viewed as "true checkerboards." To accomplish this restriction of the MCMC, we established a binary permissibility matrix so that candidate pairs of rows and columns were checked to determine if they were permissible swaps (i.e., resulted in swaps to other islands in the island groups where the species is found). We term this algorithm the "conditional trial-swap" algorithm, which we used previously (Collins et al. 2011). We show in Appendix A that the conditional trial-swap algorithm samples matrices equiprobably. To reduce autocorrelation between subsequent matrices sampled in the Markov chain, we used a burn-in of 10^6 selected sub-matrices and a thinning rate of 10^6 selected sub-matrices, which exceeds that recommended by Miklós and Podani (2004). Because no island groups were defined by Diamond and Marshall (1976) for Vanuatu, the data for Vanuatu were analyzed without the criterion that pairs must share at least one island group.

Estimating overlap in geographic ranges.—We estimated overlap in the geographical range of pairs of species by the overlap of their convex hulls. We estimated the geographical range for each species within each archipelago by fitting a convex hull to the geographical coordinates of the perimeters of each island on which the species occurred (e.g., the minimum convex polygon). We then defined the overlap in the geographical ranges between a pair of species to be the area of the intersection of their convex hulls divided by the area of the union of their convex hulls:

$$\text{overlap} = \text{Area}(A \cap B)/\text{Area}(A \cup B)$$

where A and B are the convex hulls of the two species. To make the overlap values more comparable between species pairs, we rescaled the estimated overlap by dividing by the maximum possible overlap for that pair [for $\text{Area}(A) < \text{Area}(B)$]:

$$\text{scaled overlap} = \text{overlap}/[\text{Area}(A)/\text{Area}(B)].$$

Because the bird species found on islands in the Wana Wana and Roviana lagoons have widespread distributions in the Solomons, none of their convex hulls involved the coordinates of islands located within these lagoons. Therefore, the lack of specific locality information on some islands in these lagoons has no effect on our estimates of the geographical ranges of any of the birds in the Solomon Islands.

Determining which and how many species pairs are true checkerboards.—To classify pairs with exclusive distributions as true checkerboards for both the observed data matrix and each matrix sampled from the Markov chain, we determined which and how many pairs of species had exclusive distributions and, of these, which had geographical ranges that overlapped more or significantly more than expected under a hypothesis of pairwise independence. Thus our approach requires that exclusivity and overlap of convex hulls be determined for all observed and simulated species pairs. To avoid the dilution effect (Diamond and Gilpin 1982, Gilpin and Diamond 1984), we examined the number of true checkerboards for congeneric species pairs and for species within four multi-generic guilds as defined by Diamond (1975). However, we also examined the number of true checkerboards among unrelated pairs to determine if the overall pattern for congeneric and within-guild pairs differed from that shown by unrelated pairs.

Previous algorithms to estimate the expected number of exclusive pairs were able to identify pairs with exclusive island-by-island distributions simply by inspection of the observed and simulated matrices. However, given our probabilistic definition of a true checkerboard as a congeneric or within-guild pair that has an exclusive distribution, co-occurs in at least one island group, and has geographic ranges that overlap *more* or *significantly more* than expected under a hypothesis of pairwise independence, we needed to use the simulated matrices both to detect in the observed data which pairs are true checkerboards, and to determine whether the observed number of true checkerboards was larger than expected under a hypothesis of pairwise independence at some specified α level. To do so we used the $n = 1000$ matrices generated by the MCMC approach described previously to determine for each congeneric or within-guild pair, and each unrelated pair that had an exclusive distribution and co-occurred in at least one island group, whether observed overlap in geographic range exceeded expected overlap. This enabled us to identify as true checkerboards those pairs that met all three criteria and whose overlap in geographic range exceeded expectation. We also used a probabilistic definition of a true checkerboard. For each species pair, we determined the proportion of the simulated matrices with overlap in geographic range equal to or greater than the observed overlap. This proportion was then compared to a nominal $\alpha = 0.2$ to determine which and how many pairs were true checkerboards at that α level. We chose $\alpha = 0.2$ to minimize the probability of failing to detect a true checkerboard that was actually present. This increases the power of our test at the risk of inflating our false discovery rate.

To determine if the observed number of true checkerboards for congeneric pairs, within-guild pairs, and unrelated pairs was greater than expected under a hypothesis of pairwise independence, we used the same 1000 simulated matrices to generate a jackknife-like estimate of the expected number of true checkerboards, their standard deviations, and the significance levels of all tests. The algorithm involved reserving a single matrix from the n simulated matrices and using the remaining $n - 1$ matrices to define in the reserved matrix which and how many pairs met our criteria to be classified as true checkerboards, including having overlap in geographic range significantly greater than expected under a hypothesis of pairwise independence at some specified α level. We then repeated this process, reserving the other $n - 1$ matrices individually. In essence, we were defining in each of the simulated matrices which and how many pairs were true checkerboards in the same way that we defined which and how many pairs were true checkerboards in the matrix of observed data. This approach allowed us to generate n values of a statistic of interest, such as the total number of true congeneric checkerboards, to which we could compare the observed statistic. If the proportion of simulated values that equaled or exceeded the observed value was less than some specified α level, the null hypothesis that the observed number of true checkerboards was no different from that expected under a hypothesis of pairwise independence was rejected. The details of our analytical algorithms are given in Appendix B.

Connor and Simberloff (1979) attempted to examine what could be called "partial" checkerboards by comparing the number of pairs of species that shared 0, 1, 2, 3, ... islands to the expected value under a hypothesis of pairwise independence. It is conceivable that a pair of species is not a true "complete" checkerboard (TCC), as initially described by Diamond (1975), but actually shares a small number of islands. However, if that pair co-occurs in at least one island group, shares *fewer* islands than expected, yet overlaps in geographic range more than expected under a hypothesis of pairwise independence, that also could be interpreted as evidence of interspecific competition (Fig. 1C). We also examine data for each of the three archipelagoes to determine if the number of true "partial" checkerboards (TPC) is statistically unusual.

Comparing congeneric and within-guild pairs to pairs of unrelated species.—To determine whether the related species pairs (congeneric and within-guild pairs) represent a distinct statistical population compared to unrelated species pairs with respect to their levels of exclusivity and overlap of geographic ranges, we performed an ANCOVA. We compared the regression of the number of islands shared on the overlap of geographic ranges for all pairs of species that share at least one island group for related and unrelated pairs. We fit an ANCOVA model that included overlap of geographic range as the covariate, a factor for group membership (e.g., related pairs or unrelated pairs), and a term for the factor-by-covariate interaction. We tested for coincidence of the regressions (e.g., equality of repression slopes and intercepts) for related and unrelated pairs by performing a partial F test comparing the saturated model with all three terms to the reduced model with only the covariate. Because of nonindependence among pairs, we generated the null distribution of our F test by fitting the same ANCOVA model and performing the same F test on each of the 1000 simulated matrices. We computed the significance of F as the proportion of the simulated matrices that have F values that equal or exceed the observed F value. See Supplement 2 for the MATLAB code to perform the simulations and the ANCOVA.

Calculating power of our tests.—As proof of concept of how one might calculate the power of the class of tests that we perform, we outline here a power calculation for the number of congeneric true complete checkerboards defined at the $\alpha = 0.2$ level for the Bismarck Archipelago. Because we use the number of congeneric TCC defined at $\alpha < 0.2$ in the observed data matrix as our test statistic, which we will call S_{TCC}, its distribution under the null hypothesis of pairwise independence will be a discrete distribution with support of the positive integers. For a set of n matrices sampled from $U(R, S)$, we examined the distribution of $S_{\mathrm{TCC}.}$ For the sample size we used in our tests ($n = 1000$ matrices), the distribution of S_{TCC} had a mean of 0.31 TCC and was overdispersed relative to the Poisson distribution, but was well fit by the negative binomial distribution. Therefore, we conjectured that the distribution of S_{TCC} under the alternative hypothesis followed a negative binomial distribution with mean equal to a specific effect size δ, and having the same dispersion as the distribution of S_{TCC} under the null hypothesis. Given our intent to define the region of rejection under the null hypothesis

TABLE 1. Breakdown for Vanuatu, the Bismarck Archipelago, and the Solomon Islands of the numbers of congeneric and noncongeneric pairs of bird species and within-guild pairs into those with exclusive distributions and those that are regionally allopatric.

Pair type, by islands	No. pairs	Exclusive distributions	Regionally allopatric	Different island groups
Vanuatu				
Congeners	12	0	0	0
Noncongeners	1 528	61	55	0
Total	1 540	61	55	0
Guilds	7	0	0	0
Bismarck Archipelago				
Congeners	102	27	17	11
Noncongeners	11 073	1484	984	553
Totals	11 175	1511	1001	564
Guilds	110	25	12	1
Solomon Islands				
Congeners	97	23	19	19
Noncongeners	9 773	1939	1678	1476
Totals	9 870	1962	1697	1495
Guilds	53	9	2	1

Notes: Values for within-guild pairs are for both congeneric and heterogeneric within-guild pairs. Pairs that are regionally allopatric have nonoverlapping geographical ranges based on convex hulls. Data from Diamond and Marshall (1976) and Sanderson et al. (2009) are based on 56 species on 28 islands for Vanuatu, 150 species on 41 islands for the Bismarck Archipelago, and 141 species on 142 islands for the Solomon Islands.

as $\alpha < 0.2$ and the discrete nature of the distribution of the test statistic, we defined the region of rejection as the observation of one or more TCC. Again because of the discrete nature of the distribution of S_{TCC}, the actual test was performed at $\alpha = 0.257$. The region of acceptance under the null hypothesis contained only the outcome of observing zero congeneric TCC. Therefore, we calculated power for a specific effect size as the probability of detecting no congeneric TCC when, in fact, δ were present.

RESULTS

A summary of the number of species pairs that are congeneric, within-guild, have exclusive island-by-island distributions, are regionally allopatric, and are restricted to different island groups for each of the three archipelagoes is presented in Table 1. Among all three archipelagoes, only ~1% of the species pairs are either congeneric or within-guild; among these pairs, many are regionally allopatric. Some pairs have convex hulls that overlap to some extent even though they are restricted to different islands groups (Appendix C). This arises because of the geography of the island groups, which in some instances themselves are not convex.

Our analysis was designed to determine whether levels of exclusivity and overlap of geographic ranges of pairs of related species (congeneric and within-guild pairs) represent a distinct statistical population when compared to those for unrelated species pairs. Examination of true partial checkerboards allows us to calculate the deviation from expectation of the number of islands shared and the overlap of geographic ranges for all species pairs, whether they are related or not. The observation that the values for congeneric and within-guild pairs fall within the cloud of points for unrelated species pairs in Figs. 2–4 indicates that these are not distinct statistical populations, but rather a single statistical population of species pairs. Furthermore, the ANCOVA performed to determine whether the regression of the number of islands shared on overlap of geographic ranges (for pairs that share at least one island group) differs between related and unrelated species shows that these regressions were coincident (e.g., have equal slopes and intercepts) in all three archipelagos (for Vanuatu, $F_{2,1536} = 0.5716$, $P = 0.979$; for the Bismarcks, $F_{2,\,10\,607} = 2.2828$, $P > 0.999$; for the Solomons, $F_{2,8371} = 2.926$, $P = 0.971$).

We estimate that the power of our test to detect an effect size of $\delta = 1$, 2, or 3 congeneric TCC defined at $\alpha < 0.2$ in the Bismarcks was 0.54 ± 0.029 (standard error), 0.69 ± 0.039, and 0.75 ± 0.046, respectively. These estimates are based on using the method of nonoverlapping batch means (e.g., based on 10 batches of 1000 matrices) to estimate the Monte Carlo error of the simulation (Flegal and Jones 2010).

Vanuatu

Among the congeneric and within-guild pairs in Vanuatu, none have exclusive distributions, and none are true complete checkerboards (TCC; see Tables 1 and 2).

For true partial checkerboards (TPC), overlap of convex hulls identifies two congeneric and two within-guild pairs with geographic ranges that are more interspersed than expected and share fewer islands than expected (Table 2; Appendices D and E). However, when TPC are defined probabilistically, there are no TPC at $\alpha < 0.2$ (Table 2, Fig. 2; Appendix D and E).

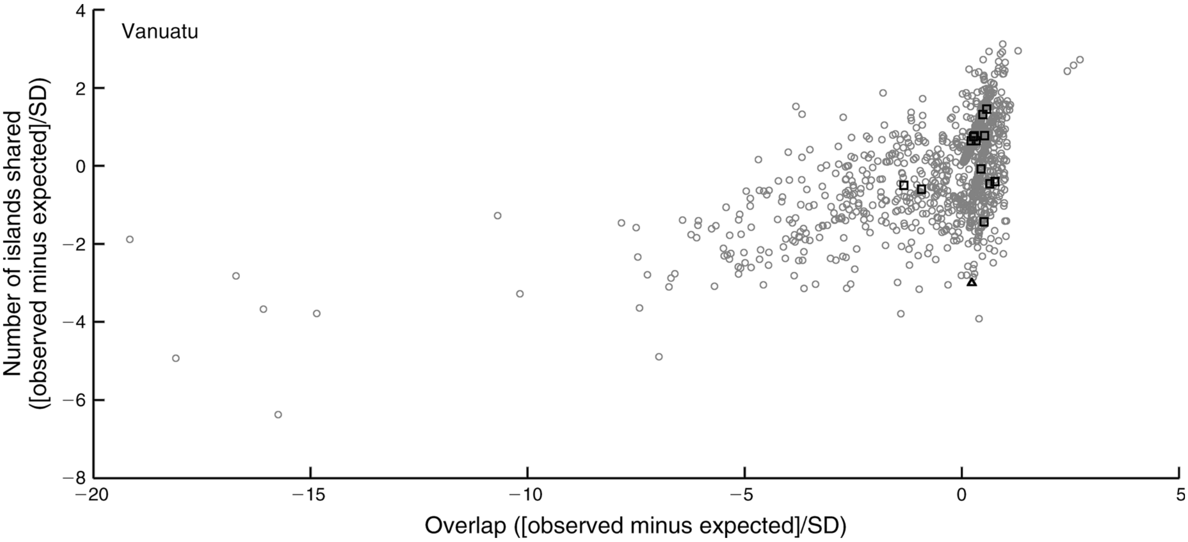

FIG. 2. Plot of the *z* scores of number of islands shared (level of exclusivity in island-by-island distribution) vs. the *z* scores of island interspersion (overlap of convex hulls) for pairs of birds in Vanuatu. Black open squares ($n \approx 15$) are congeneric and within-guild pairs that would *not* be classified as true partial checkerboards at $\alpha < 0.20$. No congeneric and within-guild pairs that would be classified as true partial checkerboards at $\alpha < 0.20$ were detected. The black open triangle ($n = 14$) is an unrelated species pair that would be classified as true partial checkerboard at $\alpha < 0.10$. Gray open circles ($n > 1500$) are unrelated pairs that would not be classified as true partial checkerboards at $\alpha < 0.10$. Only pairs that share at least one island group are shown. Under a hypothesis of pairwise independence, one would expect most pairs to occur in the upper right (+,+) and lower left (–,–) quadrants of the plot. Only pairs in the lower right quadrant (+,–) would potentially be true partial checkerboards (TPC). The coincidence of plots of the population of congeneric and within-guild pairs with the population of unrelated pairs suggests that, for these two traits of their geographic distribution, these two groups comprise a single statistical population. By coincidence we mean that the values for congeneric and within-guild pairs plot within the cloud of points for unrelated pairs and that the regression lines for these two groups do not differ significantly in slope and intercept. A color version of this figure is available in Appendix F.

For Vanuatu overall, the total numbers of TCC and TPC and the numbers in each genus and guild are no greater than expected under a hypothesis of pairwise independence when defined either probabilistically or as those that have observed values exceeding expectation ($\alpha > 0.05$; Appendix D).

Bismarcks

In the Bismarcks, 17 of the 27 congeneric and 3 of the 9 heterogeneric, within-guild exclusive pairs are regionally allopatric, and of these 11 and 1, respectively, are restricted to different island groups (Table 1; Appendix C). Of the congeneric and within-guild exclusive pairs that are not restricted to different island groups, only two pairs would be considered TCC when TCC are defined as having geographic ranges that overlap more than expected. However, when overlap of geographic range is defined probabilistically at $\alpha < 0.2$, there are no TCC in the Bismarck Archipelago (Table 2; Appendices D and E).

If TCC are defined as having overlap of geographic ranges that is greater than expected, then neither the total numbers of congeneric nor within-guild TCC is statistically significantly greater than expected (Appendix D). The numbers of TCC in the genera *Pachycephala* and *Tyto* and the gleaning-flycatcher guild are statistically high. However, if TCC are defined probabilistically at $\alpha < 0.2$, no genera or guilds have more TCC than expected ($P > 0.999$; Fig. 3; Appendix D).

If true partial checkerboards in the Bismarcks are defined by the criteria that they have geographic ranges that overlap more than expected and share fewer islands than expected, then there are several congeneric and within-guild TPC (Table 2; Appendices D and E). However, if we define TPC probabilistically at $\alpha < 0.2$, only a single congeneric pair, *Ducula rosacea*–*D. bicolor*, would be defined as TPC (Appendix E).

The total number of congeneric and within-guild TPC, defined as those that have geographic ranges that are more interspersed than expected and share fewer islands than expected, is not significantly greater than expected ($P > 0.9$; Appendix D). However, some individual genera have more TPC than expected under this criterion. The genera *Ardea*, *Pachycephala*, and *Tyto* have significantly more TPC than expected ($P < 0.04$; Appendix D). However, if TPC are defined probabilistically at $\alpha < 0.2$, neither the total numbers of congeneric or within-guild TPC nor the numbers in individual genera or guilds significantly exceeds expectation ($P > 0.99$; Appendix D).

Solomon Islands

In the Solomons, 19 of the 23 congeneric and 1 of the 9 within-guild exclusive pairs are regionally allopatric, and all of these regionally allopatric pairs are composed

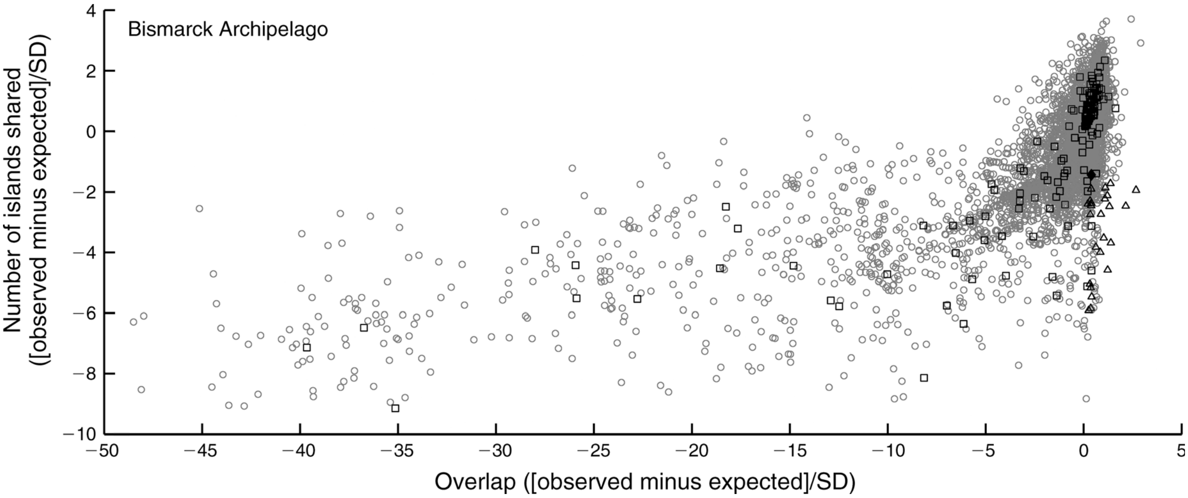

FIG. 3. Plot of the *z* scores of number of islands shared (level of exclusivity in island-by-island distribution) vs. the *z* scores of island interspersion (overlap of convex hulls) for pairs of birds in the Bismarck Archipelago. Black open squares ($n \approx 100$) are congeneric and within-guild pairs that would not be classified as true partial checkerboards at $\alpha < 0.20$. The large black solid diamond represents congeneric and within-guild pairs that would be classified as true partial checkerboards at $\alpha < 0.20$ (only one detected). Black open triangles ($n = 46$) are unrelated species pairs that would be classified as true partial checkerboards at $\alpha < 0.10$. Gray open circles ($n \approx 11\,000$) are unrelated pairs that would not be classified as true partial checkerboards at $\alpha < 0.10$. Only pairs that share at least one island group are shown. Some pairs of species are not plotted because their *z* values fall in extreme regions of the lower left quadrant. Under a hypothesis of pairwise independence, one would expect most pairs to occur in the upper right (+,+) and lower left (–,–) quadrants of the plot. Only pairs in the lower right quadrant (+,–) would potentially be true partial checkerboards (TPC). The coincidence of plots of the population of congeneric and within-guild pairs with the population of unrelated pairs suggests that, for these two traits of their geographic distribution, these two groups comprise a single statistical population. By coincidence we mean that the values for congeneric and within-guild pairs plot within the cloud of points for unrelated pairs and that the regression lines for these two groups do not differ significantly in slope and intercept. A color version of this figure is available in Appendix F.

of species restricted to different island groups (Table 2; Appendix C). Of the congeneric and within-guild exclusive pairs that are not restricted to different island groups, none would be identified as a TCC by the criterion that ranges overlap either more or significantly more than expected, $\alpha < 0.2$ (Table 2; Appendix E). If TCC are defined as having overlap of geographic ranges that is greater or significantly greater than expected ($\alpha < 0.2$), then neither the total number of congeneric or within-guild TCC nor the number of TCC in any individual genus or guild is statistically significantly greater than expected (Appendix D).

If true partial checkerboards in the Solomons are defined by the criteria that they have geographic ranges that are more interspersed than expected and share fewer island than expected, then there are several congeneric and within-guild TPC (Table 2; Appendices D and E). However, if we define TPC probabilistically at $\alpha < 0.2$, there are no TPC in the Solomon Islands (Fig. 4; Appendix E).

The total number of congeneric and within-guild TPC, defined as those that have geographic ranges that are more interspersed than expected and share fewer islands than expected, is not significantly greater than expected ($P > 0.99$; Appendix D). The genus *Myzomela* has significantly more TPC than expected by this criterion ($P = 0.023$; Appendix D). However, if TPC are defined probabilistically at $\alpha < 0.2$, neither the total number of congeneric or within-guild TPC pairs nor the numbers of TPC pairs in individual genera or guilds is significantly greater than expected ($P > 0.99$; Appendix D).

DISCUSSION

Our deconstruction of the metaphor of the checkerboard places equal emphasis on both exclusivity among species pairs in island distribution and overlap in geographical range. We believe that the approach we develop here to define true checkerboards accurately mirrors Diamond's (1975:388) initial meaning of "...two or more ecologically similar species have mutually exclusive but interdigitating distributions in an archipelago." Therefore the fact that we observed few if any true complete checkerboards in these archipelagoes provides stronger evidence than do metrics based solely on a lack of co-occurrence (such as C-scores or the number of exclusive pairs) that, if interspecific competition is operating in these avifaunas, the island-by-island distributions do not indicate it.

Among the land and freshwater birds of the three Melanesian archipelagoes, no more than 1% of the possible pairs of interacting species in each archipelago are congeneric. Given Diamond and Gilpin's (1982) view that competition should be expected only among

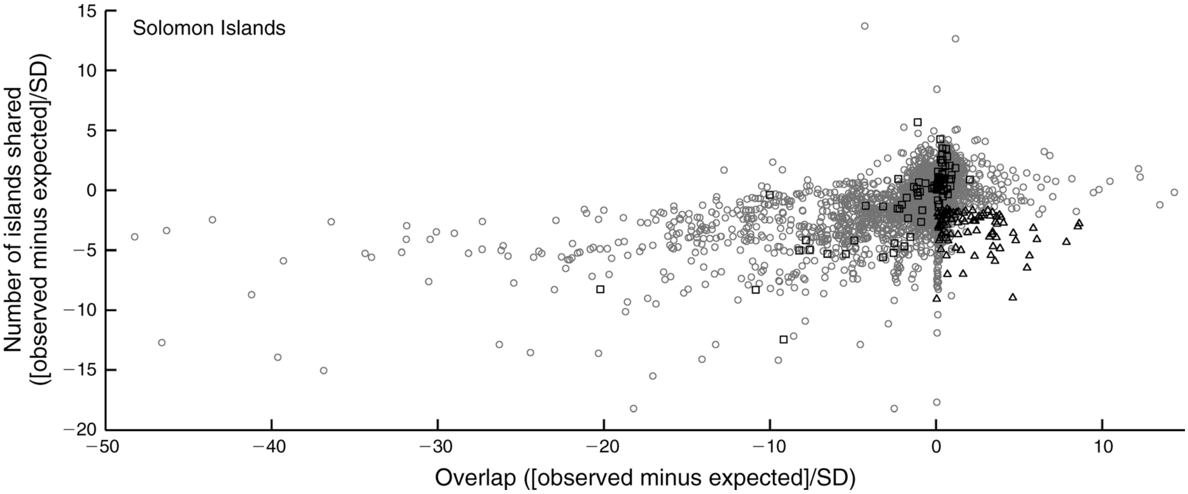

FIG. 4. Plot of the *z* scores of number of islands shared (level of exclusivity in island-by-island distribution) vs. the *z* scores of island interspersion (overlap of convex hulls) for pairs of birds in the Solomon Islands. Black open squares ($n \approx 100$) are congeneric and within-guild pairs that would *not* be classified as true partial checkerboards at $\alpha < 0.20$. No congeneric and within-guild pairs that would be classified as true partial checkerboards at $\alpha < 0.20$ were detected. Black open triangles ($n = 136$) are unrelated species pairs that would be classified as true partial checkerboards at $\alpha < 0.10$. Gray open circles ($n > 9600$) are unrelated pairs that would not be classified as true partial checkerboards at $\alpha < 0.10$. Only pairs that share at least one island group are shown. Some pairs of species are not plotted because their *z* values fall in extreme regions of the lower left quadrant. Under a hypothesis of pairwise independence one would expect most pairs to occur in the upper right (+,+) and lower left (–,–) quadrants of the plot. Only pairs in the lower right quadrant (+,–) would potentially be true partial checkerboards (TPC). The coincidence of plots of the population of congeneric and within-guild pairs with the population of unrelated pairs suggests that, for these two traits of their geographic distribution, these two groups comprise a single statistical population. By coincidence we mean that the values for congeneric and within-guild pairs plot within the cloud of points for unrelated pairs and that the regression lines for these two groups do not differ significantly in slope and intercept. A color version of this figure is available in Appendix F.

closely related species, <1% of the possible pairwise interactions could be competitive. If we focus on the exclusive pairs among the congeneric and within-guild species as evidence for competition as suggested by Diamond (1975), no more than 0.2% of the possible pairs of species are exclusive. If we also include Diamond's (1975) second criterion that species occur on islands that are geographically interspersed, then because the majority of exclusive pairs are regionally allopatric, no more than 0.08% of species pairs in each archipelago could even *potentially* be true checkerboards (Table 1). However, our results suggest that true checkerboards are virtually or completely absent from these three archipelagoes.

In our examination of the distributional data for the birds of three Melanesian archipelagoes, we used three

TABLE 2. Breakdown for Vanuatu, Bismarck Archipelago, and the Solomon Islands of the numbers of congeneric and within-guild pairs into those that constitute true complete checkerboards (TCC) and true partial checkerboards (TPC) based on various criteria.

	Vanuatu		Bismarck Archipelago		Solomon Islands	
Species pair type	O > E	O > E, $\alpha < 0.2$	O > E	O > E, $\alpha < 0.2$	O > E	O > E, $\alpha < 0.2$
True complete checkerboards (TCC)						
Congeners	0	0	2	0	0	0
Noncongeners	0	0	11	0	60	20
Guilds	0	0	2	0	0	0
True partial checkerboards (TPC)						
Congeners	2	0	8	1	8	0
Noncongeners	230	14	1057	46	1054	136
Guilds	2	0	7	1	4	0

Notes: Overlap of geographic ranges is measured as the scaled overlap of the convex hulls of each pair of species. We provide two definitions of the level of overlap in geographical range required to classify a pair as a true checkerboard; observed overlap > expected (O > E) overlap under a hypothesis of pairwise independence, and observed overlap significantly > expected (O > E) at $\alpha < 0.2$ under a hypothesis of pairwise independence. Guilds are as defined in Diamond (1975): cuckoo-dove (*Macropygia* and *Reinwardtoena*), gleaning flycatcher (*Monarcha*, *Myiagra*, and *Pachycephala*), myzomelid–sunbird (*Myzomela* and *Nectarinia*), and fruit pigeon (*Ptilinopus* and *Ducula*).

PLATE 1. *Monarcha castaneiventris ugiensis*, a melanic subspecies of the Chestnut-bellied Monarch (a member of the *Monarcha melanopsis* superspecies group), on Malaulalo Island (of the Three Sisters/Olu Malau Island group) in the Solomon Islands. *Monarcha* is one of the genera in Diamond's (1975) proposed gleaning-flycatcher guild along with *Myiagra* and *Pachycephala*. Photo credit: J. Albert C. Uy.

criteria to define true checkerboards. The minimum criteria for defining true checkerboards are that pairs are exclusive, they share at least one island group, and they are more interspersed than expected. Exclusive pairs that share at least one island group merely have to exceed the interspersion expected under a hypothesis of pairwise independence to be classified as a true checkerboard. Even our more stringent probabilistic criterion that pairs must be more interspersed than expected at $\alpha < 0.2$ was chosen to insure that we have adequate power to detect true checkerboards. However, even with these relatively weak criteria, we detected few if any true checkerboards in these archipelagoes. Furthermore, because identification of individual checkerboard pairs involves a hypothesis test at $\alpha = 0.20$, the probability that those pairs identified as true checkerboards actually represent Type I errors is high, and even more so because we have applied no correction for performing multiple-hypothesis tests.

The power of our test for the number of congeneric TCC defined at $\alpha < 0.2$ in the Bismarcks suggests that it is possible that 1–2 congeneric TCC exist that we were unable to detect. However, for Vanuatu there are no congeneric pairs with exclusive distributions. For the Solomon Islands and the Bismarcks after removing regionally allopatric pairs, there are only 4 and 10 exclusive congeneric pairs remaining, respectively, that could potentially be TCC. Therefore, it is unlikely that we have missed evidence of any widespread tendency for congeneric pairs to form TCC-exclusive distributions on islands that are spatially interspersed.

Expanding the analysis to include species pairs that are not completely exclusive, but share fewer islands than expected, still results in only a few pairs of species being classified as true partial checkerboards (TPC) and only by our most minimal criterion for defining a true checkerboard. True checkerboards (TCC) are generally a subset of true partial checkerboards (TPC) because presumably they share fewer islands than expected and occur on islands that are more interspersed than expected. Thus our analysis of true partial checkerboards contains within it true complete checkerboards as well.

Our examination of true partial checkerboards allows us to calculate the deviation from expectation of the number of islands shared and the overlap of geographic ranges for all species pairs whether they are related or not. The coincidence of the data points for congeneric and within-guild pairs with those for pairs of unrelated species shown in Figs. 2–4 and the statistically nonsignificant tests for the coincidence of the regressions of the number of islands shared on the overlap of geographic ranges clearly indicate that these are not distinct statistical populations, but rather a single statistical population of species pairs. This result, which is based on an examination of the distributional data alone, is consistent with the interpretation that the geographical distributions of congeneric, within-guild, and unrelated species pairs in these Melanesian archipelagoes are shaped by a common set of biological and physical environmental processes.

Although Diamond and Gilpin (1982) and Gilpin and Diamond (1984) suggest that examining pairs that are not closely related or members of the same guild should not be pertinent to a search for the effects of interspecific competition on the geographic distribution of species, Sanderson et al. (2009) resurrect such analyses. However, our examination of noncongeneric pairs also indicates that the observed number of true checkerboards among unrelated species defined as having observed overlap either greater or significantly greater than expected is no more than expected under a hypothesis of pairwise independence among species.

As to the idea that a true checkerboard distribution is clear and strong evidence for interspecific competition (Diamond 1975), we point out that the bulk of the true checkerboards we detected are between unrelated species (Table 2). If unrelated species are unlikely to compete (Diamond and Gilpin 1982, Gilpin and Diamond 1984), then true checkerboards would appear to arise for reasons other than interspecific competition. If true checkerboards can occur among unrelated pairs for reasons other than competition, why must we be compelled to believe that those detected among related pairs are due to competition? Although we agree that interspecific competition is more likely to account for true checkerboards than other potential causes, it remains conceivable that true checkerboard distributions among congeneric and within-guild pairs of species might arise because of differential habitat preferences among species, geographical speciation and limited range expansion, historical constraints on dispersal, differential responses to predators, parasites, or pathogens, or any of a number of other processes that might affect dispersal or establishment of species on islands (Connor and Simberloff 1979, 1983, 1984, 1986, Simberloff and Collins 2010, Collins et al. 2011).

Coda

Our paper is the latest installment in a controversy that has lasted more than 30 years. We doubt that it will be the last word. While we claim that there is little evidence that the geographic distribution of birds in these three Melanesian archipelagoes reflects the effects of interspecific competition, one should not conclude that bird species do not compete. Rather, in echoing what we said many years ago, one can only conclude that, if they do compete, competition does not strongly affect their patterns of distribution among islands. Furthermore, only careful field observations and experiments will yield the necessary information to determine which species do compete.

It is possible that more data will be brought to bear on this question in future years. For these Melanesian archipelagoes, data on more islands can only reduce or leave unaffected the number of pairs with exclusive distributions, but for pairs that share some islands, it can either leave unaffected or increase the number of islands shared. Additional data could either leave unaffected, increase, or decrease the estimated overlap in their geographic ranges. More study of the phylogeny and taxonomy of the Melanesian avifauna could lead to an increase or decrease in the number of congeneric pairs, or potentially an increase or decrease in the number of species. However, given the small percentage of related pairs that share fewer islands than expected and have ranges that are more interspersed than expected, it is unlikely that such taxonomic revisions would lead to substantial differences in these distributional attributes between related and unrelated species.

It is interesting to reflect on the longevity of this controversy and on how the discourse might have proceeded had we included the issue of interspersion of islands when we initially addressed Diamond's (1975) ideas. While we can only speculate, it is remarkable that it has taken so long for us and apparently everyone else to realize how crucial interspersion of geographic ranges is to the concept of checkerboard distributions, in spite of Diamond's (1975) initial definition of a checkerboard and Stone et al.'s (1996) recognition of its importance. Future attempts to delineate checkerboard distributions must explicitly integrate the geographic ranges of species.

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SUPPLEMENTAL MATERIAL

Appendix A

Demonstration that the conditional trial-swap algorithm is unbiased (*Ecological Archives* E094-221-A1).

Appendix B

Detailed description of analytical algorithms (*Ecological Archives* E094-221-A2).

Appendix C

Observed and expected range overlap of exclusive congeneric and within-guild pairs (*Ecological Archives* E094-221-A3).

Appendix D

Observed numbers of TCC, TPC, and significance tests (*Ecological Archives* E094-221-A4).

Appendix E

Congeneric and within-guild pairs of species identified as true complete checkerboards (TCC) or true partial checkerboards (*Ecological Archives* E094-221-A5).

Appendix F

Color versions of manuscript Figs. 2–4 (*Ecological Archives* E094-221-A6).

Supplement 1

Data on species incidences, island group membership, and coordinates of island perimeters (*Ecological Archives* E094-221-S1).

Supplement 2

MATLAB function files to perform MCMC analysis and the analysis of covariance (*Ecological Archives* E094-221-S2).