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ORIGINAL ARTICLE

Binary matrices and checkerboard distributions of birds in the Bismarck Archipelago

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ABSTRACT

Aim We examine a presence–absence matrix of the avifauna of the Bismarck Archipelago, for which the concept of competitively driven community assembly rules was formulated, to determine whether data support widespread competitive determination of geographical distributions.

Location Bismarck Archipelago.

Methods We obtained occurrences of 154 land and freshwater bird species on 31 islands. We calculated the observed number of checkerboards for all species pairs, for congeneric species pairs and for pairs of species within guilds, and employed randomization techniques to detect unusual co-occurrence patterns.

Results Compared with random expectations, there are excesses of checkerboard pairs within both genera and defined guilds, but a detailed examination shows that competition is a cogent possible explanation in few instances. For many checkerboard pairs, species are not widely interspersed but are regionally allopatric, which probably reflects historical biogeography and dispersal limitation. Most congeneric and intraguild checkerboards include a species classified as a supertramp; when supertramps are omitted, there are 11 congeneric checkerboards and four intraguild but heterogeneric checkerboards.

Main conclusions In isolation, presence–absence matrices provide limited insight into the role of competition in structuring bird communities of the Bismarcks. A major problem is disentangling historical geography and colonization history of the archipelago from the present-day ecology of the species. Examination of observed checkerboards from a geographically explicit perspective and with knowledge of colonization routes suggests that many checkerboards are likely to result, at least in part, from historical biogeography and supertramps. Although species may be forced into supertramp status by competition, other factors (e.g. habitat preference) may be causal, and biogeographical distributions alone cannot distinguish between causes.

Keywords

Assembly rules, Bismarck Archipelago, checkerboard distribution, competition, historical biogeography, island biogeography, presence–absence matrix, supertramp.

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INTRODUCTION

Binary matrices of presence and absence of species on sites have been analysed for many years in biogeography and ecology, usually in comparisons of site similarity, but also in comparisons of the similarity of sets of sites occupied by pairs or larger groups of species (Simberloff & Connor, 1979). Inevitably, with the great interest in the role of interspecific competition in determining species' distributions, a burst of research on statistical analyses of such matrices began in the late 1970s and has continued to the present (Gilpin & Diamond, 1982, 1984; Colwell & Winkler, 1984; Gotelli &

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Graves, 1996; Gotelli *et al.*, 1997; Sanderson *et al.*, 1998, 2009; Gotelli, 2000; Gotelli & McCabe, 2002; Miklós & Podani, 2004; Lehsten & Harmand, 2006; Sfenthourakis *et al.*, 2006; Simberloff & Collins, 2010). Much of the research focused on Diamond's (1975) seven assembly rules, which implicitly discussed patterns in binary matrices, and tests of the rules as null hypotheses by Connor & Simberloff (1979). Although Diamond (1975) deduced the assembly rules from data on 147 species of land birds distributed among 50 islands in the Bismarck Archipelago near New Guinea, the subset of those data that we use for our analyses became available only with the publication of Mayr & Diamond (2001).

Our goal here was to use the data on avian distributions in the Bismarck Archipelago (Mayr & Diamond, 2001) to determine if they supported Diamond's (1975) claim of widespread competitive determination of geographical distributions. We focused on the assembly rule that has received the most attention, the fifth rule: 'Some pairs of species never coexist, either by themselves or as part of a larger combination' (Diamond, 1975, p. 344). These checkerboard distributions have been taken as strong evidence for interspecific competition (Diamond, 1975), although that inference is not always well founded (Gotelli & Graves, 1996). The gist of the controversy over checkerboard distributions stems from two observations. First, depending on the numbers of species and islands in the matrix, as well as the species richnesses of the islands and the number of occurrences of each species, one might have expected some checkerboard distributions even if species colonized islands independently of one another (Connor & Simberloff, 1979). Second, even if a particular checkerboard distribution is unlikely to have arisen by two species having colonized islands independently, other possible explanations exist for such an exclusive arrangement in addition to competition (Connor & Simberloff, 1979; Simberloff & Connor, 1981); for example, two species may have different habitat requirements, or they may simply be sister species that have recently speciated allopatrically. In the light of the new availability of data on the distributions of the Bismarck Archipelago birds, on which the original assembly rules were based, we explored the checkerboards and their interpretation in this avifauna.

MATERIALS AND METHODS

Excluding migratory, transient and non-breeding species, and species occurrences with questionable records, Mayr & Diamond (2001) tabulate 154 land and freshwater bird species on 31 islands in the Bismarcks (Fig. 1). If the pattern of ones and zeros in a given binary matrix is hypothesized to be affected by a particular force (in this instance, interspecific competition), then a test must compare this matrix with those constructed randomly, without this force operating, from the universe of all possible matrices for this particular biota and set of sites. With sites represented as columns in the matrix and species as rows, a 1 in row i and column j means species i is found in site j, and a 0 means it is absent. For a given matrix $\mathbf{M}$, the universe of matrices with which it is compared is usually taken to consist of all matrices with the same sets of row and column sums as $\mathbf{M}$. The column sum constraint ensures that each site maintains the same number of species that it actually has (so that such patterns as the species–area relationship continue to hold), while the row sum constraint ensures that each species continues to occupy the same number of sites as it does in nature (so that widespread species are still widespread, and narrowly distributed ones are still narrowly distributed). Gotelli & Graves (1996) explain the

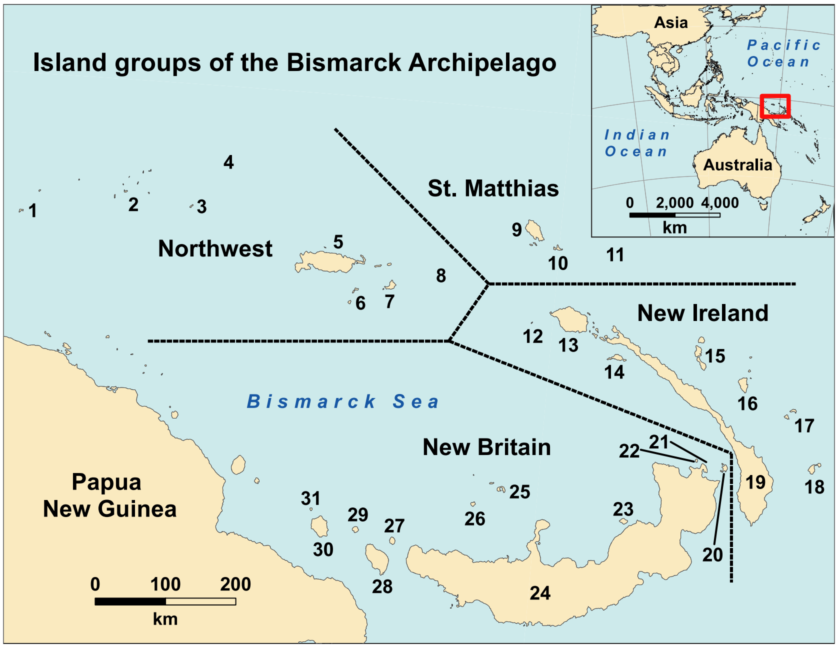

Figure 1 Island groups in the Bismarck Archipelago used in the study of binary matrices and checkerboard distributions of birds. Island groups are separated by dispersal barriers (dashed lines), which are determined by differences in avian species composition between island groups and by morphological differences in species occurring across barriers (from Mayr & Diamond, 2001). Islands: 1, Wuvulu; 2, Ninigo; 3, Hermits; 4, Anchorites; 5, Manus; 6, San Miguel; 7, Rambutyo; 8, Nauna; 9, St Matthias; 10, Emirau; 11, Tench; 12, Tingwon; 13, New Hanover; 14, Dyaul; 15, Tabar; 16, Lihir; 17, Tanga; 18, Feni; 19, New Ireland; 20, Duke of York; 21, Credner; 22, Vuatom; 23, Lolobau; 24, New Britain; 25, Witu, 26, Unea; 27, Sakar; 28, Umboi; 29, Tolokiwa; 30, Long; 31, Crown.

rationale for these conventions and discuss alternative views. We used the method of Miklós & Podani (2004) to sample matrices in this universe equiprobably, generating 1000 randomized matrices in each simulation with 500,000 attempted swaps between sampled matrices.

Several statistics have been used to quantify co-occurrence patterns (Gotelli, 2000 and references therein). Here we focus on the number of checkerboard distributions (CH, i.e. number of exclusively distributed species pairs). We do not evaluate the *C*-score [‘checkerboardedness’ index of the matrix as a whole (Stone & Roberts, 1990)], or the *T*-score [‘togetherness’ index, proposed as an index of congruence among species distributions in the matrix as a whole (Stone & Roberts, 1992)] because these metrics are counterintuitive and widely misunderstood (Stone & Roberts, 1992; Ulrich & Gotelli, 2007; Gotelli & Ulrich, 2010).

We first calculated the number of checkerboards by examining the avifauna as a whole. Diamond & Gilpin (1982) and Gilpin & Diamond (1984) criticize the idea of scanning entire binary matrices for checkerboards and comparing the number of checkerboards thus detected with the number expected, on the grounds that one would expect competition only between species within guilds, and that the number of checkerboards of pairs of species that are unlikely to compete cannot inform a search for competitive interactions. They called this shortcoming of dealing with entire matrices the ‘dilution effect’. Colwell & Winkler (1984, p. 357) describe the ‘J.P. Morgan effect’: ‘close relatives are more similar than distant ones, and are thus more likely to be incompatible when competition is intense. Including distantly related species in a re-sampling pool simply drowns out the signal with noise, progressively weakening the power of the design to detect competition’.

To avoid these difficulties, we then used genera as proxies for guilds and calculated the number of checkerboards for congeneric pairs of species. Taxonomic groups are not always congruent with guilds (Diamond & Gilpin, 1982; Simberloff & Dayan, 1991). However, many authors have suggested that congeneric species are ecologically more similar to each other than to species of other genera (e.g. Darwin, 1859; Elton, 1946; den Boer, 1980; Graves & Gotelli, 1983), and many studies have used taxonomy to partition biotas into guilds (e.g. MacArthur, 1958; Lambert & Reid, 1981; Schoener, 1984; Walter & Ikonen, 1989; Sfenthourakis *et al.*, 2006). In addition, all mapped examples of checkerboard distributions adduced by Diamond (1975) were of congeners in the Bismarck Archipelago.

Diamond (1975) listed the membership of four guilds in the Bismarcks. In three instances these included two genera, and one guild contained three genera (Table 1). In each case, all species in a genus were included in the guild. We repeated the entire analysis of checkerboards by randomizing the full matrix and looking at observed and expected numbers of checkerboards within these guilds.

Thus, we first examined the observed and expected number of checkerboards for the entire avifauna. We also determined, by inspection of the same sample of 1000 matrices, the expected number of checkerboards for each genus with two or more species, and in each guild for comparison with observed numbers. Then we investigated the specific species involved in checkerboards to assess possible explanations.

Diamond (1975) noted that some species, termed ‘supertramps’, are found only on islands with few species. These absences could be due to competition, but they could also be due to other factors, such as preference for habitats found on small islands (e.g. see Simberloff & Martin, 1991). The presence of supertramps complicates analysis of co-occurrence, because the presence of such species only on islands with few species means that such species are automatically likely to produce checkerboards. Supertramp- and competitively-driven checkerboards are not mutually exclusive, but one supertramp can result in multiple checkerboards in a genus or guild. We therefore repeated the analysis of congeneric checkerboards with supertramps eliminated from the matrix. Diamond (1975) did not provide unambiguous quantitative criteria for classifying a species as a supertramp, and his list differs slightly from that of Mayr & Diamond (2001) by including *Turdus poliocephalus*. We defined supertramps statistically, in the belief that a supertramp should occupy species-poor islands more than expected, given the number of islands occupied. We sorted islands from richest to poorest and used a Mann–Whitney *U*-test at $P < 0.05$ to identify supertramps (see Simberloff & Levin, 1985). By this test, several species listed as supertramps by Mayr & Diamond (2001) do not qualify (Table 2).

Table 1 Guild memberships of bird genera in the Bismarck Archipelago for guilds specifically designated by Diamond (1975).

Guild	Genera	Number of species
Cuckoo-dove	*Macropygia*, *Reinwardtoena*	4
Gleaning flycatcher	*Monarcha*, *Myiagra*, *Pachycephala*	7
Myzomela-sunbird	*Myzomela*, *Nectarinia*	8
Fruit pigeon	*Ducula*, *Ptilinopus*	11

Table 2 Supertramp bird species of the Bismarck Archipelago determined statistically, and as tallied by Mayr & Diamond (2001, Table 12.2).

Statistical supertramps	Additional supertramps of Mayr & Diamond (2001)
Ptilinopus solomonensis	*Ducula pistrinaria*
Ducula pacifica	*Ducula spilorrhoa*
Monarcha cinerascens	*Macropygia mackinlayi*
Myzomela lafargei	*Myzomela sclateri*
Aplonis feadensis	*Caloenas nicobarica*
	Pachycephala melanura
	Zosterops griseotinctus

RESULTS

For the avifauna as a whole, 1516 pairs of species exhibited a checkerboard distribution, significantly more than the 1221 ± 97 (mean ± SD) present in randomized matrices ($P = 0.003$). The 27 observed congeneric checkerboards also exceeded random expectation (13.2 ± 3.6; $P < 0.001$; Table 3). Ten genera contained one or more checkerboards, and seven of them had significantly more observed than expected checkerboards (Table 3). When statistical supertramps were omitted, three genera (*Aplonis*, *Ducula* and *Myzomela*) became statistically non-significant (Table 3). When supertramps as defined by Mayr & Diamond (2001) were excluded, *Rhipidura* was the only genus with significantly more checkerboards than expected (Table 3). Patterns within guilds, as designated by Diamond (1975), were similar. When all species were included, all four guilds contained significantly more checkerboards than expected (Table 4). When statistical supertramps were omitted, the myzomelid-sunbird and fruit-pigeon guilds were statistically non-significant, and with Diamond's supertramps omitted, no guild remained significant (Table 4).

DISCUSSION AND CONCLUSIONS

Community-wide checkerboards

For the whole matrix, including supertramps, the number of checkerboards significantly exceeded expectation, consistent with the hypothesis of strong influence by interspecific competition, but also with other hypotheses. This result is equally consistent, for example with the notion that mutualism, or similar habitat preferences between species, or allopatric speciation, have helped shape the distributions (Connor & Simberloff, 1979; Stone & Roberts, 1992). The

Table 3 Observed and expected numbers of congeneric checkerboards (CH) for bird genera in the Bismarck Archipelago with all species included, with statistical supertramps omitted, and with Diamond's (Mayr & Diamond, 2001) supertramps excluded.

	All species				Excluding statistical supertramps				Excluding Diamond's supertramps			
Genus	*S*	Obs CH	Exp CH	*P*	*S*	Obs CH	Exp CH	*P*	*S*	Obs CH	Exp CH	*P*
Accipiter	6	5	5.53	0.622	6	5	5.53	0.622	6	5	5.53	0.622
Aplonis	3	1	0	<0.001	2	0	0	1	2	0	0	1
Ducula	6	4	0.26	0.001	5	0	0.14	1	3	0	0.12	1
Falco	3	1	0.84	0.533	3	1	0.84	0.533	3	1	0.84	0.533
Macropygia	3	1	0	<0.001	3	1	0	<0.001	2	0	0	1
Myzomela	6	10	3.61	0.002	5	6	3.35	0.153	4	2	2.7	0.812
Pachycephala	2	1	0	<0.001	2	1	0	<0.001	1	–	–	–
Rhipidura	4	2	0.22	0.021	4	2	0.22	0.021	4	2	0.22	0.021
Tyto	2	1	0.38	0.377	2	1	0.38	0.377	2	1	0.38	0.377
Zosterops	2	1	0.03	0.03	2	1	0.03	0.03	1	–	–	–
Total		27	13.25	<0.001		18	12.91	0.094		11	12.17	0.705

S, number of species; Obs CH, observed number of checkerboards; Exp CH, mean number of checkerboards from 1000 randomized matrices; *P* is the fraction of the 1000 randomly generated matrices in which the number of checkerboards equals or exceeds the observed number of checkerboards. Totals include all genera, including those with no observed checkerboards.

Table 4 Observed and expected number of intraguild checkerboards (CH) of birds in the Bismarck Archipelago with all species included, with statistical supertramps omitted, and with Diamond's (Mayr & Diamond, 2001) supertramps omitted from the analysis.

	Guild	*S*	Obs CH	Exp CH	*P*
All species included	Cuckoo-dove	4	1	0.002	0.002
	Gleaning flycatcher	7	3	0.031	<0.001
	Myzomelid-sunbird	8	11	3.95	0.006
	Fruit-pigeon	11	10	0.67	<0.001
With statistical supertramps omitted	Cuckoo-dove	4	1	0.002	0.002
	Gleaning flycatcher	6	3	0.031	<0.001
	Myzomelid-sunbird	7	6	3.686	0.217
	Fruit-pigeon	9	2	0.48	0.128
With Diamond's supertramps omitted	Cuckoo-dove	3	0	0.002	1.000
	Gleaning flycatcher	5	0	0.017	1.000
	Myzomelid-sunbird	6	2	3.036	0.814
	Fruit-pigeon	7	2	0.457	0.122

S, number of species; Obs CH, observed number of checkerboards; Exp CH, mean number of checkerboards from 1000 randomized matrices.

bulk of community-wide checkerboards (98%) came from heterogeneric species pairs. So, if competition is unlikely between distantly related species, we are unable to get much insight into it by looking at statistics based on this entire matrix, because community-wide measures of co-occurrence were dominated by pairs of unrelated species. We next turned to congeneric checkerboard pairs and literature descriptions to attempt to learn why these species pairs were distributed exclusively.

Congeneric checkerboards

Ten genera contained 27 congeneric checkerboards (Table 3). A first observation is that for almost all of these pairs, one or both species were found on very few of the 31 islands. In fact, each pair had at least one species on six or fewer islands (Table 5). Seven genera had significantly more checkerboards than expected under a hypothesis of independent colonization (Table 3). However, of five statistical supertramps in the Bismarcks, three were members of these congeneric checkerboard pairs: *Aplonis feadensis*, *Ducula pacifica* and *Myzomela lafargei*. Mayr & Diamond (2001) also list as supertramps four other species that are part of congeneric checkerboards: *Macropygia mackinlayi*, *Pachycephala melanura*, *Myzomela sclateri* and *Zosterops griseotinctus*. When the analysis was rerun with all supertramps omitted, the difference between observed and expected number of checkerboards for all these genera was not significant (Table 3).

The historical geography of the Bismarck Archipelago suggests a partial explanation for some of these patterns independent of species interactions. The Bismarck Archipelago contains four main island groups (Fig. 1): (1) the New Britain group, consisting of New Britain and its Pleistocene land-bridge islands, plus Umboi, Lolobau and Duke of York, and several smaller islands (Vuatom, Witu, Unea and Sakar) not connected during the Pleistocene; (2) the New Ireland group, consisting of New Ireland and New Hanover, which were connected in the Pleistocene, and several smaller islands and island groups 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

Table 5 Possible factors contributing to congeneric checkerboard distributions among Bismarck birds.

Species 1	Islands 1	Species 2	Islands 2	ST	DST	His	Hab	Inc
Accipiter rufitorques	1	*Accipiter gentilis*	2	N	N	Y	N	Y
Accipiter rufitorques	1	*Accipiter novaehollandiae*	15	N	N	N	N	Y
Accipiter rufitorques	1	*Accipiter luteoschistaceus*	2	N	N	Y	N	Y
Accipiter rufitorques	1	*Accipiter poliocephalus*	1	N	N	Y	N	Y
Accipiter rufitorques	1	*Accipiter cirrhocephalus*	2	N	N	Y	N	Y
Aplonis feadensis	4	*Aplonis metallica*	24	Y	Y	N	Y	N
Ducula pacifica	5	*Ducula myristicivora*	14	Y	Y	Y	N	N
Ducula pacifica	5	*Ducula rufigaster*	4	Y	Y	Y	N	N
Ducula pacifica	5	*Ducula pinon*	3	Y	Y	Y	N	Y
Ducula pacifica	5	*Ducula bicolor*	11	Y	Y	Y	N	N
Falco subbuteo	3	*Falco berigora*	1	N	N	Y	N	Y
Macropygia nigrirostris	5	*Macropygia mackinlayi*	15	N	Y	Y	Y	N
Myzomela pulchella	1	*Myzomela eques*	2	N	N	Y	Y	Y
Myzomela pulchella	1	*Myzomela cardinalis*	1	N	N	Y	Y	Y
Myzomela pulchella	1	*Myzomela sclateri*	7	N	Y	Y	Y	Y
Myzomela pulchella	1	*Myzomela lafargei*	15	Y	Y	Y	Y	Y
Myzomela cardinalis	1	*Myzomela sclateri*	7	N	Y	N	N	Y
Myzomela cardinalis	1	*Myzomela lafargei*	15	Y	Y	Y	N	Y
Myzomela eques	2	*Myzomela sclateri*	7	N	Y	N	N	Y
Myzomela eques	2	*Myzomela lafargei*	15	Y	Y	Y	N	N
Myzomela cruentata	5	*Myzomela sclateri*	7	N	Y	N	N	N
Myzomela cruentata	5	*Myzomela lafargei*	15	Y	Y	Y	N	N
Pachycephala pectoralis	11	*Pachycephala melanura*	6	N	Y	N	Y	N
Rhipidura rufifrons	2	*Rhipidura leucophrys*	19	N	N	Y	N	N
Rhipidura rufifrons	2	*Rhipidura rufidorsa*	4	N	N	Y	N	Y
Tyto alba	2	*Tyto novaehollandiae*	2	N	N	Y	N	Y
Zosterops atriceps	6	*Zosterops griseotinctus*	4	N	Y	Y	N	Y
Total				9	16	21	7	17

ST, supertramp by Mann–Whitney *U*-test; DST, classified as supertramp by Mayr & Diamond (2001); His, potential historical explanation (e.g. regional allopatry, differing colonization routes); Hab, habitat differences; Inc, low incidence (number of islands occupied) by one or both species; Islands 1 and Islands 2, the number of islands on which species 1 and species 2 occur, respectively. Total, number of checkerboard pairs likely to be influenced by each factor.

and Nauna) and several small, western outliers (Anchorite, Hermit and Ninigo archipelagos and Wuvulu) (Mayr & Diamond, 2001). According to Mayr & Diamond (2001), these four island groups are separated by dispersal barriers that existed even during lower sea levels during the Pleistocene, reflected by morphological differences in species occupying more than one group as well as compositional differences between avifaunas of different island groups. Several islands west of the New Britain group – Long, Crown, and possibly Tolokiwa – are viewed by Mayr & Diamond (2001) as being in a different category ornithologically because they were defaunated by a massive volcanic eruption in the mid-17th century and their avifaunas were therefore assembled only in the past three centuries (Diamond *et al.*, 1989).

To examine how dispersal barriers influence checkerboard distributions, we generated another 1000 matrices with the restriction that each species can occur only on islands within island groups in which it actually occurs. With this restriction, the expected number of congeneric checkerboards increased to 19.5 ± 2.0 (from 13.2) but remained significantly fewer than the 27 observed checkerboards ($P = 0.008$; Table 6). Of the 10 genera with at least one checkerboard, four had significantly more checkerboards than expected (Table 6). Excluding statistical supertramps reduced the number of significant genera to three, and omitting Diamond's supertramps resulted in no genus having significantly more checkerboards than expected (Table 6).

Examination of congeneric checkerboards (see Appendix S1 in Supporting Information) showed that dispersal barriers, Pleistocene geography and colonization history could plausibly explain 20 of the 27 congeneric checkerboards, while differing habitat preferences may have played a role in two others (Table 5; Fig. 2). When we excluded supertramps listed by Mayr & Diamond (2001), 11 congeneric checkerboards remained, for 10 of which a plausible explanation would entail historical factors. When we omitted the supertramps that qualified by our criterion, of 18 congeneric checkerboards, history may be implicated in 12 and habitat differences in one.

Two patterns recur among genera with checkerboard pairs. The first is that most members of such pairs do not occupy the entire archipelago. The pairs can be termed 'regionally allopatric'. Boundaries delineating the regions of allopatry often coincide with barriers to dispersal hypothesized by Mayr & Diamond (2001) based on the late Pleistocene geography of the archipelago, species' range limits, and morphological differences between conspecific populations of those species that occupy more than one of the four island groups. Consequently, although exclusive patterns exist, these patterns differ substantially from Diamond's (1975) concept of checkerboards, in which two or more species are scattered throughout an entire archipelago in an exclusive pattern resulting from competitive exclusion (Fig. 2). Sanderson *et al.* (2009) also investigated the influence of spatial patterns on negative co-occurrence patterns of birds in the Bismarck and Solomon archipelagos but concluded that their contribution is minor. One explanation for the differing conclusions is that Sanderson *et al.* (2009) searched for species confined to single island groups to examine allopatry, whereas we (Simberloff & Collins, 2010) mapped species distributions and could identify species pairs that exhibited regional allopatry even if species occurred in more than one island group. We also included species pairs that showed substantial but not perfect allopatry (e.g. *Macropygia nigrirostris* and *M. mackinlayi*). Another possible factor is that we examined only a subset of the islands analysed by Sanderson *et al.* (45 vs. 142 islands in the Solomons; 31 vs. 41 in the Bismarcks), who examined many more small islands. If some species that are absent from some regions occur there when smaller islands are examined, some

Table 6 Observed and expected numbers of congeneric checkerboards (CH) for bird genera in the Bismarck Archipelago with all species included, with statistical supertramps omitted, and with Diamond's (Mayr & Diamond, 2001) supertramps excluded when matrix randomizations restrict species to occur only in island groups in which they actually occur.

	All species				Excluding statistical supertramps				Excluding Diamond's supertramps			
Genus	*S*	Obs CH	Exp CH	*P*	*S*	Obs CH	Exp CH	*P*	*S*	Obs CH	Exp CH	*P*
Accipiter	6	5	4.527	0.349	6	5	4.527	0.349	6	5	4.527	0.349
Aplonis	3	1	0	<0.001	2	0	0	1	2	0	0	1
Ducula	6	4	3.111	0.111	5	0	0.016	1	3	0	0.016	1
Falco	3	1	1.507	1	3	1	1.507	1	3	1	1.507	1
Macropygia	3	1	0	<0.001	3	1	0	<0.001	2	0	0	1
Myzomela	6	10	5.562	<0.001	5	6	3.506	0.049	4	2	2.46	1
Pachycephala	2	1	0	<0.001	2	1	0	<0.001	1	–	–	–
Rhipidura	4	2	2.106	1	4	2	2.106	1	4	2	2.106	1
Tyto	2	1	1	1	2	1	1	1	2	1	1	1
Zosterops	2	1	0.325	0.325	2	1	0.325	0.325	1	–	–	–
Totals		27	19.51	0.008		18	14.36	0.066		11	12.99	0.920

S, number of species; Obs CH, Observed number of checkerboards; Exp CH, mean number of checkerboards from 1000 randomized matrices; *P* is the fraction of the 1000 randomly generated matrices in which the number of checkerboards equals or exceeds the observed number of checkerboards. Totals include all genera, including those with no observed checkerboards.

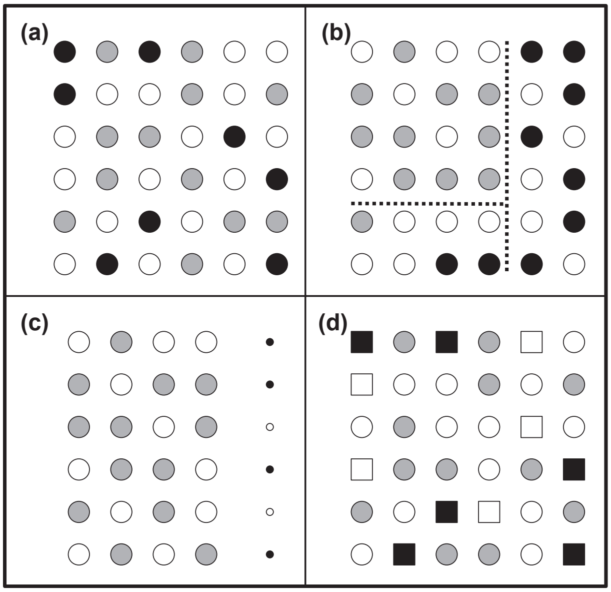

Figure 2 A representation of (a) Diamond's (1975) conceptualization of assembly rules contrasted with three observed patterns: (b) regional allopatry, (c) supertramp distributions, and (d) differences in habitat preference. In Diamond's conceptualization, islands are sufficiently similar and species are interspersed throughout the archipelago. With regional allopatry, checkerboard distributions result from historical biogeography and dispersal limitation. Supertramp species are restricted to small, isolated or volcanically disturbed islands. Circles represent islands; squares represent islands with a different habitat type from circles. Small circles represent small, isolated or volcanically disturbed islands. Black and grey represent islands occupied by different species; open circles symbolize unoccupied islands. Dashed lines indicate regional barriers to dispersal.

species pairs that show regional allopatry in our study would not do so when smaller islands are included. The larger number of islands in Sanderson *et al.* (2009) increases statistical power to detect unusual *C*-scores but could only reduce the number of checkerboard distributions.

The other pattern surfacing repeatedly in genera containing checkerboards is that at least one species in the checkerboard is a supertramp, whether we adopt a statistical criterion for supertramp or use the list of Mayr & Diamond (2001). Supertramps could certainly occupy predominantly small, depauperate islands because they are competitively excluded from other islands, as argued by Diamond and colleagues (Diamond, 1975; Mayr & Diamond, 2001; Sanderson *et al.*, 2009). Sanderson *et al.* (2009) provide several lines of evidence to support their claim that supertramps result from competitive exclusion from species-rich islands: (1) habitats of small islands also exist on the coasts of larger islands; (2) not only small islands, but islands that are species-poor for any reason (isolation, volcanic activity), contain supertramps; (3) a species might exhibit a supertramp distribution in a species-rich archipelago but not in a species-poor one; (4) where they occur, supertramps occupy a wide range of habitats; and (5) the absence of a supertramp can usually be plausibly related to the presence of specific congeners or competitors.

We agree that competition might play a role in restricting at least some species to supertramp status. However, some supertramp distributions may result from forces other than competition. 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, and predation by *Accipiter* hawks might confine another supertramp, *Ducula pacifica*, to small islands (Holyoak & Thibault, 1978).

Intraguild checkerboards

It can be argued, as noted earlier, that systematics does not track ecology sufficiently for genera to stand for guilds, although they are often used as such (e.g. Diamond & Gilpin, 1982). For the same analysis but with designated guilds, the results do not differ greatly from those with genera (Table 7; Appendix S2). Each guild contains congeneric checkerboards. Also, when all species considered as supertramps by Mayr & Diamond (2001) were omitted from the analysis, the matrix randomization showed no significant results (Table 4).

Partitioning into guilds yields nine heterogeneric checkerboards in addition to 16 congeneric checkerboards discussed above (Table 7); of these nine, habitat differences may contribute to two. Historical biogeography and dispersal difficulties may be an element of five of these nine, which may be seen as regionally allopatric rather than scattered exclusively among a group of nearby islands. The other striking point is that, as with congeneric checkerboards, supertramps are part of the great majority of intraguild checkerboards: 13 of 25 for statistical supertramps and 21 of 25 for the supertramp list of Mayr & Diamond (2001) (Table 7). As noted above, competitive exclusion is certainly a possible reason why a species may be a supertramp, but there are others, and the geographical distributions alone cannot distinguish among them.

Neither Diamond (1975) nor other literature presents quantitative data justifying these guild assignments, and, in the absence of detailed publication of the criteria for guild membership and quantitative data supporting the assignments, this list of intraguild checkerboards should be viewed with caution. For instance, Crome (1975, 1978) studied diet and habitat use by all seven fruit pigeons in the lowland rain forest of Queensland and depicted a situation far more complex than a neat partition with species a–c in guild 1, species d and e in guild 2, etc. Rather, he determined that all species differed from one another to differing extents with respect to different variables, and that at least six other frugivorous birds might be grouped in guilds with all or some of these pigeons.

Finally, we emphasize that results should be viewed with caution because of massive anthropogenic extinction since humans colonized this archipelago (Steadman, 2006). Humans arrived as early as 32,000 years ago in New Ireland. Most bird fossil data are from New Ireland, where Steadman (2006)

Table 7 Possible factors contributing to intraguild checkerboard distributions among Bismarck birds.

Guild	Species 1	Islands 1	Species 2	Islands 2	ST	DST	His	Hab	Inc
CD	*Macropygia nigrirostris*	5	*Macropygia mackinlayi*	15	N	Y	Y	Y	N
GF	*Pachycephala melanura*	6	*Monarcha manadensis*	9	N	Y	N	N	N
GF	*Pachycephala melanura*	6	*Monarcha chrysomela*	5	N	Y	N	N	N
GF	*Pachycephala melanura*	6	*Pachycephala pectoralis*	11	N	Y	N	Y	N
MS	*Myzomela lafargei*	15	*Nectarinia sperata*	14	Y	Y	Y	N	N
MS	*Myzomela lafargei*	15	*Myzomela eques*	2	Y	Y	Y	N	N
MS	*Myzomela lafargei*	15	*Myzomela cruentata*	5	Y	Y	Y	N	N
MS	*Myzomela lafargei*	15	*Myzomela pulchella*	1	Y	Y	Y	Y	Y
MS	*Myzomela lafargei*	15	*Myzomela cardinalis*	1	Y	Y	Y	N	Y
MS	*Myzomela sclateri*	7	*Myzomela eques*	2	N	Y	N	N	Y
MS	*Myzomela sclateri*	7	*Myzomela cruentata*	5	N	Y	N	N	N
MS	*Myzomela sclateri*	7	*Myzomela pulchella*	1	N	Y	Y	Y	Y
MS	*Myzomela sclateri*	7	*Myzomela cardinalis*	1	N	Y	N	N	Y
MS	*Myzomela pulchella*	1	*Myzomela eques*	2	N	N	Y	Y	Y
MS	*Myzomela pulchella*	1	*Myzomela cardinalis*	1	N	N	Y	Y	Y
FP	*Ducula pacifica*	5	*Ptilinopus superbus*	12	Y	Y	Y	N	N
FP	*Ducula pacifica*	5	*Ptilinopus hyogaster*	17	Y	Y	Y	N	N
FP	*Ducula pacifica*	5	*Ptilinopus rivoli*	9	Y	Y	Y	Y	N
FP	*Ducula pacifica*	5	*Ptilinopus viridis*	3	Y	Y	Y	N	Y
FP	*Ducula pacifica*	5	*Ducula myristicivora*	14	Y	Y	Y	N	N
FP	*Ducula pacifica*	5	*Ducula rufigaster*	4	Y	Y	Y	N	N
FP	*Ducula pacifica*	5	*Ducula pinon*	3	Y	Y	Y	N	Y
FP	*Ducula pacifica*	5	*Ducula bicolor*	11	Y	Y	Y	N	N
FP	*Ptilinopus viridis*	3	*Ducula rufigaster*	4	N	N	N	N	Y
FP	*Ptilinopus viridis*	3	*Ducula pinon*	3	N	N	N	Y	Y
	Totals				13	21	17	8	11

ST, supertramp by Mann–Whitney *U*-test; DST, classified as supertramp by Mayr & Diamond (2001); His, potential historical explanation (e.g. regional allopatry, differing colonization routes); Hab, habitat differences; Inc, low incidence (number of islands occupied) by one or both species; Islands 1 and Islands 2, the number of islands on which species 1 and species 2 occur, respectively. CD, cuckoo-dove guild; GF, gleaning flycatcher guild; MS, myzomelid-sunbird guild; FP, fruit-pigeon guild. Totals, number of checkerboard pairs likely to be influenced by each factor.

estimates that *c.* 20% of late Pleistocene/early Holocene land birds became extinct owing to human activity by both early residents and the Lapita people who arrived *c.* 3000 years ago. Extinction rates on smaller islands (at least those inhabited by humans, the great majority of those tallied by Mayr & Diamond, 2001) are probably higher. Mayr & Diamond (2001) as well as Steadman (2006) suggest that extinction rates on the large Bismarck islands are lower than those reported for islands in remote Oceania because of the presence of an indigenous murid rodent, to which birds evolved adaptations. However, the prehistoric introduction of seven mammal species, including dogs, pigs, rats and marsupials, must surely have wreaked havoc with native bird communities, as has substantial habitat destruction beginning with the Lapita people (Steadman, 2006), and today including massive logging on certain islands (cf. BirdLife International, 2000). In any event, some fraction of the current checkerboards may well be artefacts of human activities.

The upshot of this analysis is that the vast majority of checkerboards occur among heterogeneric species pairs. Species that are only distantly related are comparatively unlikely to be close competitors, and it follows that alternative hypotheses (to competition) should be examined for such pairs. When the analysis was restricted to checkerboards within genera or within guilds, so as to avoid the dilution effect, it was difficult to pinpoint the probable reason for most checkerboards. In some cases, competitive exclusion is a plausible cause, but it is other evidence relating to the biology and/or history of the species that most strongly implicates it, rather than simply the checkerboard pattern itself.

Advancing an understanding of co-occurrence patterns

Diamond's (1975) seminal paper on the distribution of birds of the Bismarck Archipelago initiated a continuing debate about the role of competition in assembling ecological communities (Connor & Simberloff, 1979; Simberloff & Connor, 1981; Gilpin & Diamond, 1982, 1984; Colwell & Winkler, 1984; Gotelli & Graves, 1996; Gotelli *et al.*, 1997; Sanderson *et al.*, 1998, 2009; Gotelli, 2000; Gotelli & McCabe, 2002; Miklós & Podani, 2004; Lehsten & Harmand, 2006; Sfenthourakis *et al.*, 2006; Simberloff & Collins, 2010). Earlier studies established the necessity of examining alternative hypotheses. Diamond (1975), for instance, discussed the possible role of chance in the biogeographical distributions of Bismarck Archipelago birds but concluded that competition is far more important. The use of null models to assess whether observed measures of co-occurrence are statistically unusual became a feature of the discussion about determinants of the ranges of birds of the Bismarcks and other archipelagos. Although the use of these null models spurred debate (see Gotelli & Graves, 1996), it is now generally agreed that for many ecological questions one should employ a null model that maintains row sums (to retain differences in incidence among species) and column sums (to preserve differences in species richness across islands).

Recent work further indicates that some agreement exists among researchers. Several papers (Sfenthourakis *et al.*, 2006; Sanderson *et al.*, 2009; Simberloff & Collins, 2010) have examined co-occurrence patterns among pairs of closely related species (e.g. within genera) or within guilds. This approach, termed ‘taxonomic sieving’ by Sanderson *et al.* (2009), minimizes the dilution effect and generates *C*-scores that truly measure exclusive co-occurrence patterns. *C*-scores calculated using all possible pairs of species measure departure from randomness in either direction and cannot distinguish between aggregated and exclusive distributions (Stone & Roberts, 1992). Because causal factors may differ across pairs of species, recent work (Sanderson *et al.*, 2009; Simberloff & Collins, 2010) has examined unusually distributed pairs on a case-by-case basis. Simple summary statistics such as the *C*-score can mask interesting biological phenomena. Combining simple presence–absence data with spatially explicit (GIS) models, colonization histories or phylogenies can provide insights into causal mechanisms that are not possible with presence–absence matrices alone.

This research, and that by Sanderson *et al.* (2009) and Simberloff & Collins (2010), points to the importance of supertramps in generating exclusive co-occurrence patterns. Future work focused on supertramps should provide considerable insight into the causes of exclusive co-occurrence patterns within genera. For example, if supertramps are inferior competitors, competition theory predicts they should exhibit either superior dispersal abilities or wider niche breadths (ecological trade-offs) that would permit them to survive on islands that are inaccessible or inhospitable to better competitors. Collins (2006) examined measures of dispersal ability and habitat use provided by Mayr & Diamond (2001), and found no evidence that supertramps are better dispersers or use more habitat types than congeners. 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. Thus, while we concur with Sanderson *et al.* (2009) that supertramps produce negative co-occurrence patterns, we see the contention that supertramps are confined by competition as a hypothesis still to be tested. The Bismarcks harbour 12 supertramps (Table 2); five of these, plus one species not found in the Bismarcks, are supertramps in the Solomons (Mayr & Diamond, 2001; Simberloff & Collins, 2010). Determining the mechanisms responsible for the distributions of these supertramps will require detailed understanding of the natural history and biology of these species, and possibly experimental manipulations.

Despite some agreement, substantial differences remain, particularly pertaining to the strength of the evidence that competition drives exclusive distributions. Our findings demonstrate that checkerboard distributions of birds in the Bismarck Archipelago are consistent with the hypothesis that they are driven largely by historical biogeography, dispersal difficulties and supertramps. Interspecific competition can also result in changes in population density even when it does not produce checkerboards, but analyses of population densities have been restrained by a paucity of data and well developed statistical methods.

Our analyses here of the Bismarck birds, and elsewhere (Simberloff & Collins, 2010) of the Solomons birds, demonstrate that at least three factors complicate interpretation of these presence–absence matrices. One is that these archipelagos do not have many censused islands, and most species are not present on many of them, so an observed checkerboard, although it may be generated by competition, would not have been too surprising, even if the species colonized islands independently. A second problem arises because many exclusive patterns result from a small number of supertramps, which are absent from species-rich islands. A third problem is the difficulty in disentangling the historical geography and colonization history of the archipelago from the present-day ecology of the species, making it difficult to know whether all species really could have occupied all sites, on historical grounds alone. Combining presence–absence matrices with other sorts of data might allow much stronger inferences about causality. For example, a resolved phylogeny for a taxon might help to sort out the extent to which checkerboards are caused by allopatric speciation. Losos (1990, 1992) has combined distributional with phylogenetic data in an attempt to understand the size structure of West Indian *Anolis* communities, and it seems possible that a combination of such data and historical biogeographical information would inform an exploration of checkerboards among the Bismarck birds. Mayr & Diamond (2001) call for greatly expanded molecular study of these birds, specifically to elucidate their historical biogeography. Additional data on abundances at each site, or variation in morphology or habitat or resource use among sites, could allow strong inference where simple presence or absence cannot.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Congeneric checkerboards of birds in the Bismarcks and possible explanations.

Appendix S2 Intraguild checkerboards of birds in the Bismarcks and possible explanations.

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