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

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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 &

Graves, 1996; Gotelli ., 1997; Sanderson ., 1998, 2009; Gotelli, 2000; Gotelli & McCabe, 2002; Miklós & Podani, 2004; Lehsten & Harmand, 2006; Sfenthourakis ., 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

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 -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;

RESULTS

For the avifauna as a whole, 1516 pairs of species exhibited a checkerboard distribution, significantly more than the 1221 ± 97 (mean $\pm$ SD) present in randomized matrices ($= 0.003$). The 27 observed congeneric checkerboards also exceeded random expectation (13.2 ± 3.6; < 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 (A , D and) became statistically non-significant (Table 3). When supertramps as defined by Mayr & Diamond (2001) were excluded, 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.

Genus	All species				Excluding statistical supertramps				Excluding Diamond's supertramps			
		Obs CH	Exp CH			Obs CH	Exp CH			Obs CH	Exp CH	
A	6	5	5.53	0.622	6	5	5.53	0.622	6	5	5.53	0.622
A	3	1	0	<0.001	2	0	0	1	2	0	0	1
D	6	4	0.26	0.001	5	0	0.14	1	3	0	0.12	1
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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: *A   , D   and   .*

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 ., 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 (= 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 875257.7(4.4(28(two)-P0a0-1.3341

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,   and *A   are found on small, remote or volcanically disturbed islands throughout their range, independently of the suite of potential competitors, and predation by

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   . (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   ., 2009). Sanderson   . (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)

estimates that . 20% of late Pleistocene/early Holocene land birds became extinct owing to human activity by both early residents and the Lapita people who arrived . 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.

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