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Pairwise co-existence of Bismarck and Solomon landbird species

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ABSTRACT

Questions: Can the difference between chance and pattern be determined by the composition of species across islands in an archipelago? In particular, will one find 'checkerboards' – a pattern of mutual exclusivity that is the simplest pattern that might occur under competitive exclusion?

Organisms: 150 and 141 species of land birds inhabiting 41 and 142 islands of the Bismarck and the Solomon Archipelagos, respectively. (See http://evolutionary-ecology.com/data/2447_Supplement.pdf)

Analytical methods: For each pair of species within each archipelago, the observed number of co-occurrences is compared to the distribution of the number of co-occurrences derived from a collection of 10^6 representative unique random, or null, communities. Those species pairs actually co-occurring less often than they do in 5% of those nulls are 'unusually negative' pairs; those co-occurring more often than they do in 95% of those nulls are 'unusually positive' pairs. Islands are ranked from those with the smallest number of species to the largest. A species incidence is the span from the smallest to the largest number of species on islands on which it is found.

Results: In each archipelago, proportionately more congeneric species pairs than non-congeneric species pairs are unusually negative pairs. This holds even for species pairs that overlap in their incidences. Among congeneric species pairs found in both archipelagos, a pair that is unusual in one archipelago generally proves to be unusual in the other archipelago as well and to belong to a genus segregating ecologically by means of spatial niche differences.

Conclusions: Diamond (1975) suggested that island bird communities were structured by assembly rules that could be deduced by observation of which species did or did not co-occur on particular islands. Critics countered with analyses arguing that co-occurrence patterns in several ecological communities did not differ from random expectations. We conclude that the difference between chance and pattern can be unequivocally determined.

Keywords: competition, co-occurrence, incidence function, null model, species pairs.

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INTRODUCTION

Diamond (1975) analysed four guilds of landbird species on islands of the Bismarck Archipelago in the tropical Southwest Pacific. He noted that species of each guild co-existed on islands only in certain combinations, and he proposed interpretations in terms of species interactions and other features of species' biology. The main criticism of Diamond's analysis was that the observed co-occurrence patterns had not been demonstrated to differ from those expected by chance, hence it was unnecessary to invoke species interactions to explain them (Connor and Simberloff, 1979).

The debate about pairwise co-existence patterns was fiercest around 25 years ago. Putman (1994) remarked that the debate was 'almost unprecedented in the apparent entrenchment and hostility of the opposing camps'. The debate remained unresolved in the minds of many ecologists. Today's computer power and improved methods for constructing and analysing millions of null matrices were unavailable at that time. There have also been important conceptual advances. Now that better technologies and insights are finally available, some ecologists may feel a sense of *déjà vu* and may wonder, 'Why resurrect this old debate? Hasn't the field moved on and by-passed the debate?'

In fact, the debate persists vigorously, as judged by a continuing stream of papers and books (e.g. Gilpin and Diamond, 1982; Colwell and Winkler, 1984; Gotelli, 2000, Gotelli *et al.*, 1997; Sanderson *et al.*, 1998; Weiher and Keddy, 1999; Miklós and Podani, 2004; Lehsten and Harmand, 2006; Sfenthourakis *et al.*, 2006). As we shall see below, application of new methods to pairwise co-existence patterns yields previously unexpected conclusions deserving further exploration. Those conclusions include the contribution of incidence differences to positive and negative associations between non-congeners, and the dominant contribution of spatially segregated genera to negative associations between congeners. We show below that re-analysis of pairwise co-existence patterns offers broader lessons for other studies of community-wide patterns now at the forefront of community ecology (e.g. of food webs, co-evolution, and species/abundance relations).

We analysed all pair-wise species combinations in two large avifaunas to extract all pairs whose individual co-occurrence patterns differed substantially from chance expectations (henceforth termed 'unusual pairs'). As suggested by Diamond's critics, we thereby detected many unusual species pairs that do not interact ecologically (e.g. ducks and flycatchers: Fig. 1b), but their unusual pairwise association still proves to have a biological explanation, most often in terms of differing 'incidences'. By *incidence*, we mean the range of island species richness on which a species occurs – species richness measured by the total number of bird species inhabiting each island. Thus, a species found on islands with a richness range of 4–20 species inevitably does not overlap in incidence and therefore cannot co-occur with another species found in islands with from 30 to 80 species.

In a novel analysis that we term 'taxonomic sieving', we show that the proportion of negatively associated species pairs increases with taxonomic relatedness. This proportion remains unusually high even in pairs of species that overlap substantially in their incidences.

METHODS

Our database

An archipelago with n species has $(n)\ (n-1)/2$ possible species pairs. We assembled the observed landbird species presence/absence matrices for two tropical Southwest Pacific

avifaunas (Mayr and Diamond, 2001): the Bismarck Archipelago (150 bird species on 41 islands, with $150 \times 149/2 = 11{,}175$ possible species pairs) and the Solomon Archipelago immediately to the east (141 species on 142 islands, with $141 \times 140/2 = 9870$ possible species pairs, many of those species being shared with the Bismarck Archipelago). Mayr and Diamond (2001) published complete records for all major islands and many small islands. To that database, we added unpublished lists for 10 small Bismarck islands and 98 small Solomon islands surveyed by Diamond and his field associates. The presence/absence matrices form the online appendix (See http://evolutionary-ecology.com/data/2447_Supplement.pdf).

Like Mayr and Diamond (2001) and many other modern biogeographic studies of birds, we define the species unit for the purposes of our analyses as the so-called zoogeographic species: that is, a superspecies, or else an isolated species not belonging to a superspecies. The term *superspecies* refers to sets of two or more populations whose distributions are allopatric (i.e. occupying separate islands or geographic areas), and which are believed on morphological/molecular grounds to be recently derived from a common ancestor, but to have already achieved reproductive isolation (for discussion, see Mayr and Diamond, 2001, pp. 119–126). Thus, our analysis is unaffected by debates about whether certain closely related populations on different islands are or are not reproductively isolated: that is, whether they should be ranked as allospecies of the same superspecies or just as subspecies of the same species or allospecies – in either case, they would belong to the same superspecies. Hence our recognition of checkerboard distributions is conservative: taking the unit of analysis instead as the allospecies (or, for short, 'species' in the terminology used by most bird field guides) would inflate our results by adding 35 more checkerboard distributions of (mere) allospecies.

Comparisons with null matrices

From each of those two observed matrices, our computer algorithm generated randomized or 'null' matrices, each of which preserved the observed matrix's row and column sums (the numbers of islands occupied by each species and the numbers of species on each island, respectively). These are essential constraints. Some islands (e.g. larger ones) support more species than do other islands, and some species (e.g. more abundant or vagile ones) occur on more islands than do other species. Maintaining row and column sums of the null matrices identical to those of the observed matrix removes such influences from comparisons of observed and null co-occurrence patterns. Because the full null space of all possible matrices satisfying the row and column constraints is prohibitively large, a representative sample null space must be created; we did so by the method that we shall now describe, generating a sample space of 10^6 distinct random matrices for each archipelago. This large number of matrices suffices to sample the null space, because two separate sets of 10^6 matrices yielded virtually identical values of the following results.

Two methodologies can create the null matrices: construction methods and swap methods. Construction algorithms [e.g. the Knight's Tour method used by Sanderson *et al.* (1998)] start with an empty matrix and fill it. Swap algorithms (e.g. Miklós and Padani, 2004) start with the observed matrix and repeatedly swap 2×2 unitary sub-matrices to create different null matrices with the same row and column sums. Because the observed incidence matrices analysed here are so large that construction of 10^6 null matrices by the Knight's Tour method would be too slow, we used the modification of the swapping algorithm proposed by Miklós and Podani (2004) to populate the sample null space. Miklós and Podani

provided a proof that their swapping algorithm populated the null space uniform-randomly, but their algorithm was computationally too slow for observed matrices as large as ours. They provided a modification of their swapping suited for large matrices, although no proof was given that the modified algorithm sampled the full null space uniform randomly. We tested each sample null matrix and found that each was unique, presumably because the size of the full null space is huge in comparison with our sample of 10^6 null matrices (on the order of 10^{41} distinct nulls).

The modest computing power formerly available limited the number of null matrices that could feasibly be constructed. Under those circumstances, a key concern, and one difficult to resolve, was whether the sample null space adequately represented the full null space. However, the more powerful computers now available enable us to construct so many null matrices that this concern has become moot. To show that it is moot, in the present study we constructed two different sets of 10^6 distinct null matrices for the Bismarcks and compared the resulting lists of unusually negatively associated congeneric pairs, as defined in the text. The two lists proved to be identical, and the resulting two sets of probability values differed by a root mean square value of only 0.01%. In contrast, 10,000 distinct null matrices are insufficient, because two different sets yielded some differences in those lists.

By 'positively associated' or 'negatively associated' species pairs, tending to have coincident or complementary distributions, respectively, we mean pairs whose two component species co-exist on more or fewer islands, respectively, than the median values (50th percentiles) of number of islands of co-existence in our 10^6 null matrices. If species were distributed randomly and independently with respect to each other, we would expect to find 5% of all the possible species pairs (494 and 559 for the Solomons and Bismarcks, respectively) to be in the bottom and top 5% of the distribution. (By the same reasoning, in tossing a coin six times, we expect to get six heads – or six tails – in a row less than 2% of the time for each case.) If we tighten our cut-off from the 5% extremes to the 2% or 1% extremes, then the results that we shall describe below remain qualitatively the same, but the excess of negatively over positively associated pairs becomes even more marked.

Consider the pair of congeneric fruit-pigeon species *Ducula rubricera* and *Ducula spilorrhoa* (see Fig. 1c). They occur on islands having from 127 species (both pigeon species) down to islands having 15 or 5 species, respectively. They co-occur on only six islands. In this example, based on just 10,000 runs (for simplicity), such a pattern (or one more extreme) is found in only five null matrices. The most likely number of co-occurrences is on 11 islands.

Islands	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Nulls	0	0	0	0	0	0	5	56	323	1127	2497	3208	2138	592	54	0	0	0

Species co-occurrences are not independent, however: if species A and B occur on identical sets of islands, but if A and C do not co-occur on any island, then B and C also cannot co-occur. Through simulation, we can ask which species pairs occur in the lower 5% of the distribution (that is, equal to or less than 50,000 of 10^6 runs) and, likewise, in the upper 95% of the distribution. These pairs we call 'unusual' negative or positive pairs, respectively. But they are not 'statistically significant at the 5% level', as one might naively be tempted to state, because we do not know the underlying statistical distribution. (That is why we instead must simulate it!)

Sample statistics depend on the distribution created by the population. Since little *a priori* knowledge is available regarding the distribution of the number of co-occurrences of a pair of species in the sample null space, we must employ methods that make no assumptions regarding the distribution and the parameters of the population. For instance, we know that if species A is present m times and species B n times within an archipelago of K islands, then in each sample null community the number of co-occurrences of the species pair (A, B) lies somewhere in the closed interval [max $(0, (m+n)-K)$, min (m, n)] and varies between null communities (thus creating a distribution within the sample null space). But because the distribution of the number of co-occurrences is neither continuous nor known, statistics such as those used to analyse normal and other distributions cannot be employed – although it was routine in the earlier literature on pairwise co-existence patterns to calculate probability values based on that erroneous assumption of a normal distribution. Statistical analyses that do not depend on knowledge of the distribution and of population parameters are called *non-parametric* or *distribution-free* methods.

RESULTS

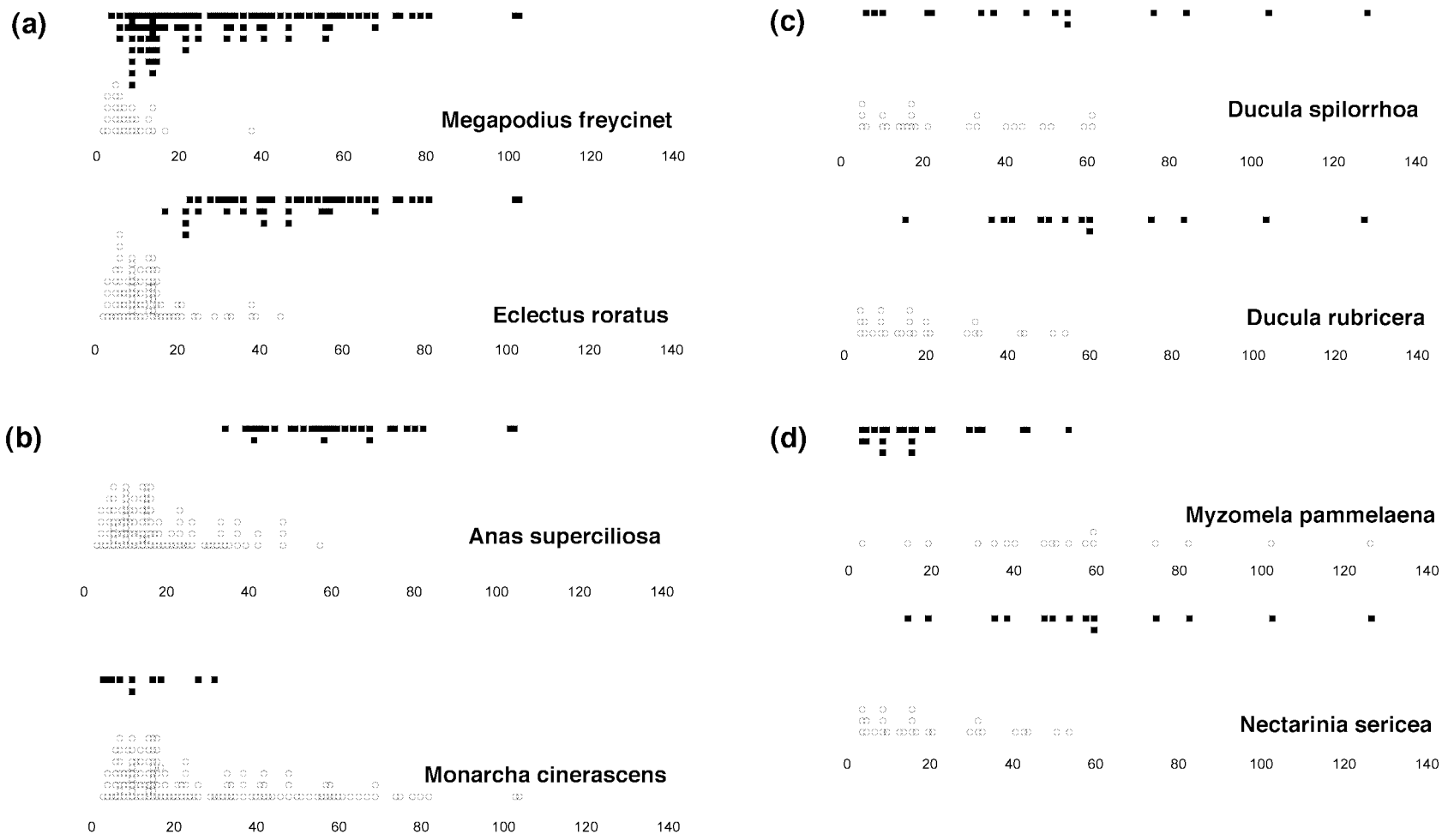
Positive and negative associations

We find 626 Solomon and 879 Bismarck negative pairs, but only 465 Solomon and 292 Bismarck positive pairs, compared with the 494 and 559 species pairs, respectively, that constitute 5% of all possible pairs in each archipelago. In addition, the degree of deviation from expectations is far more extreme for negative pairs than for positive pairs: even the most unusual Bismarck positive pair has a distribution found in 408 of the 10^6 null matrices, but there are 91 negative Bismarck pairs with distributions found in none of the 10^6 null matrices.

Figure 1 provides some examples. In the Solomons, the mound-builder *Megapodius freycinet* occurs on 110 of the 142 islands, the parrot *Eclectus roratus* occurs on 55 islands, and the two species co-occur on 55 islands. (All islands supporting the parrot also support the mound-builder.) This positive association is unusual because the two species co-occur on 55 islands or more in only 16,118 matrices of the 10^6 nulls (discussed further in Fig. 1a). Conversely, in the Bismarcks, the nectarivorous black honeyeater *Myzomela pammelaena* occurs on 23 of the 41 islands, the nectarivorous black sunbird *Nectarinia sericea* on 14 islands, and the two species never co-occur – an outcome not found in any of the 10^6 null matrices (discussed further in Fig. 1d).

Differences between the two archipelagoes

The two principal inter-archipelagal differences involve the archipelagoes' numbers of islands surveyed and their avifaunas. While all major islands in both the Solomons and the Bismarcks have been surveyed, many more small islands have been surveyed in the Solomons than in the Bismarcks. To eliminate the effect of number of islands surveyed, we selected, from our 142 surveyed Solomon islands, a set of 41 islands matched in total numbers of species to the surveyed 41 Bismarck islands. That 41-island Solomon subset yields qualitatively the same generalizations about species co-existences as the whole 142-island set, but (as one would expect) reduced numbers of species pairs with significant positive or negative associations. The 41-island Solomon subset still differs from the


(a)
Megapodius freycinet
0 20 40 60 80 100 120 140
Eclectus roratus
0 20 40 60 80 100 120 140
(b)
Anas superciliosa
0 20 40 60 80 100 120 140
Monarcha cinerascens
0 20 40 60 80 100 120 140
(c)
Ducula spilorrhoa
0 20 40 60 80 100 120 140
Ducula rubricera
0 20 40 60 80 100 120 140
(d)
Myzomela pammelaena
0 20 40 60 80 100 120 140
Nectarinia sericea
0 20 40 60 80 100 120 140

41-Bismarck set in harbouring fewer positive and fewer negative pairs. Biologically, this result is to be expected, because the Bismarcks have a somewhat richer avifauna than the Solomons, with more differences among species in their incidences, and with twice as many supertramp species (8 vs. 4, respectively). As will be explained below in the Discussion, supertramps are species confined to species-poor islands and absent from species-rich islands. Most negatively associated species pairs consist of one supertramp, paired with a species concentrated on species-rich islands (e.g. Figs. 1b and 1d).

Taxonomic sieving and incidence effects

Among all randomly drawn pairs of species, by far the most are taxonomically unrelated and ecologically probably non-interacting members of different families and genera. By the same token, while taxonomically closely related pairs of congeneric species do appear among the negatively associated pairs, they are still far outnumbered by the taxonomically unrelated negative pairs. Taxonomically and ecologically close pairs are the ones expected to be most likely to exhibit negative associations or checkerboard distribution patterns because of competition. However, if taxonomically unrelated pairs proved equally likely to exhibit negative associations anyway (merely because of the incidence considerations depicted in Fig. 1b), there would then be no grounds for invoking competition to explain negative associations of congeneric pairs. Hence we carried out two further sets of analyses to resolve this question.

First, we carried out taxonomic 'sieving': we compared three sets of Bismarck pairs differing in taxonomic closeness, with respect to their proportions of negatively associated

Fig. 1. Examples of species pairs illustrating their presence (solid squares) or absence (open circles) on islands with varying total numbers of species (S). Stacks of circles or squares indicate that there is more than one island with that number of species. (a) An unusual positive association due to almost completely overlapping incidences: the ecologically dissimilar mound-builder *Megapodius freycinet* (a forest-floor omnivore) and parrot *Eclectus roratus* (a canopy-edge frugivore) in the Solomons. By 'unusual', we mean that an association this extreme or more so is found in fewer than 5% (in this case, only 1.6%) of the 10^6 nulls produced by simulation (see text). The former species shares all 55 islands occupied by the latter. The latter species is confined to islands with $S \geq 14$, but the former occupies every island with $S \geq 38$, and 92% of islands with $S = 14$–38, making their sharing of all or almost all individual islands virtually inevitable. But because our and other null models do not incorporate these incidences, the strong positive association of this species pair appears unusual compared with the null matrices. (b) Unusual negative association (matched in <0.0001% of nulls) due to mutually exclusive S ranges: the ecologically dissimilar omnivorous aquatic duck *Anas superciliosa* and the insectivorous forest flycatcher *Monarcha cinerascens* in the Solomons. They co-exist on no island. The former is confined to islands with $S \geq 33$, the latter to islands with $S \leq 29$, so that their non-co-occurrence and strongly negative association compared with null matrices not incorporating incidence constraints are inevitable, despite their dissimilar habitats and diets. (c, d) Unusual negative associations of ecologically similar species despite overlapping incidences and broadly coincident geographic ranges, and presumably due to competition. (c) The ecologically very similar forest canopy fruit pigeons *Ducula spilorrhoa* and *Ducula rubricera* in the Bismarcks. Despite almost complete overlap (92%) of their incidences, they share only 6 islands, and they occupy 8 and 9 islands, respectively, without the other species. This outcome is duplicated in only 2.4% of the null matrices. (d) The nectarivorous black honey-eater *Myzomela pammelaena* and the ecologically very similar black sunbird *Nectarinia sericea* in the Bismarcks. Despite 32% overlap of their incidences, they co-exist on no island. This outcome is duplicated in none of the 10^6 null matrices.

pairs. The proportions vary with taxonomic closeness: 7.7% (824 of a possible 10,631 pairs) for species pairs from different families, and 7.5% (33 of 442) for pairs from the same family but different genera, but 21.6% (22 of 102) congeneric pairs (Fig. 2). Solomon proportions increase in the same direction: 6.2, 6.8, and 14.4%, respectively. These high percentages of unusual pairs among congeners are highly significant statistically ($P < 0.001$, χ^2 test, for both archipelagoes).

Second, we wondered whether the high proportion of negative associations among congeners arose mainly just from the incidence considerations underlying most negative associations among non-related pairs (see Discussion below). That is, perhaps the disproportionately high frequency of complementary distributions among congeners is just because for some reason (e.g. historic effects of competition) their incidences are especially likely to be non-overlapping. Hence we calculated, for the two species of a species pair, their proportional incidence overlaps measured in terms of numbers of species present on the islands they occupy.

For example, the fruit dove *Ptilinopus superbus* occupies 12 Bismarck islands, of which the poorest and richest support 30 and 127 species, respectively; its congener *Ptilinopus solomonensis* occupies 22 islands, of which the poorest and richest support 4 and 83 species, respectively. Thus, the total range of island species numbers S occupied by the two species is $127 - 4 = 123$; their shared range of island species numbers is $83 - 30 = 53$; and their percentage overlap in incidence is $53/123 = 43\%$. Yet they co-exist on only five islands. If their ranges of incidences had been nearly mutually exclusive – for example, if one species had been largely confined to species-poor islands and the other to species-rich islands – that would immediately explain the rareness of their co-existence. Instead, their incidences overlap extensively.

We compared incidence overlaps for all negatively unusual Bismarck and Solomon pairs, divided into three taxonomic sets (non-confamilial, confamilial but non-congeneric, and congeneric pairs), and also divided by their patterns of incidence overlap. As Fig. 2 shows, the high proportion of unusual congeneric pairs remains high even when the species overlap substantially (> 30%) in their incidences.

Thus, differing incidences fail to account for the high frequency of complementary distributions among congeners. They tend to have complementary distributions *despite* having similar incidences, and not because of having differing incidences. Instead, this tendency of close relatives to choose different individual islands within the same range of island species richness is as one would expect for a role of ongoing competitive exclusion, which would be strongest for the most closely related species. For instance, in the Bismarcks, the fruit pigeons *Ducula rubricera* and *Ducula spilorrhoa* have almost complete (92%) overlap in incidences, occupying islands with from 127 species (both pigeon species) down to 15 or 5 species (*D. rubricera* and *D. spilorrhoa*), respectively. Nevertheless, their occupancies of individual islands within this broadly overlapping range of islands are unusually exclusive, being found together on only six islands; on only 24,000 of 10^6 nulls do the species occur on six or fewer islands (Fig. 1c).

Which genera develop checkerboards?

Diamond (1975) noted a second-order assembly rule, whereby the presence or absence of other species modifies such patterns as checkerboards. In particular, larger islands than those considered here – such as New Guinea and Borneo – often have many co-existing

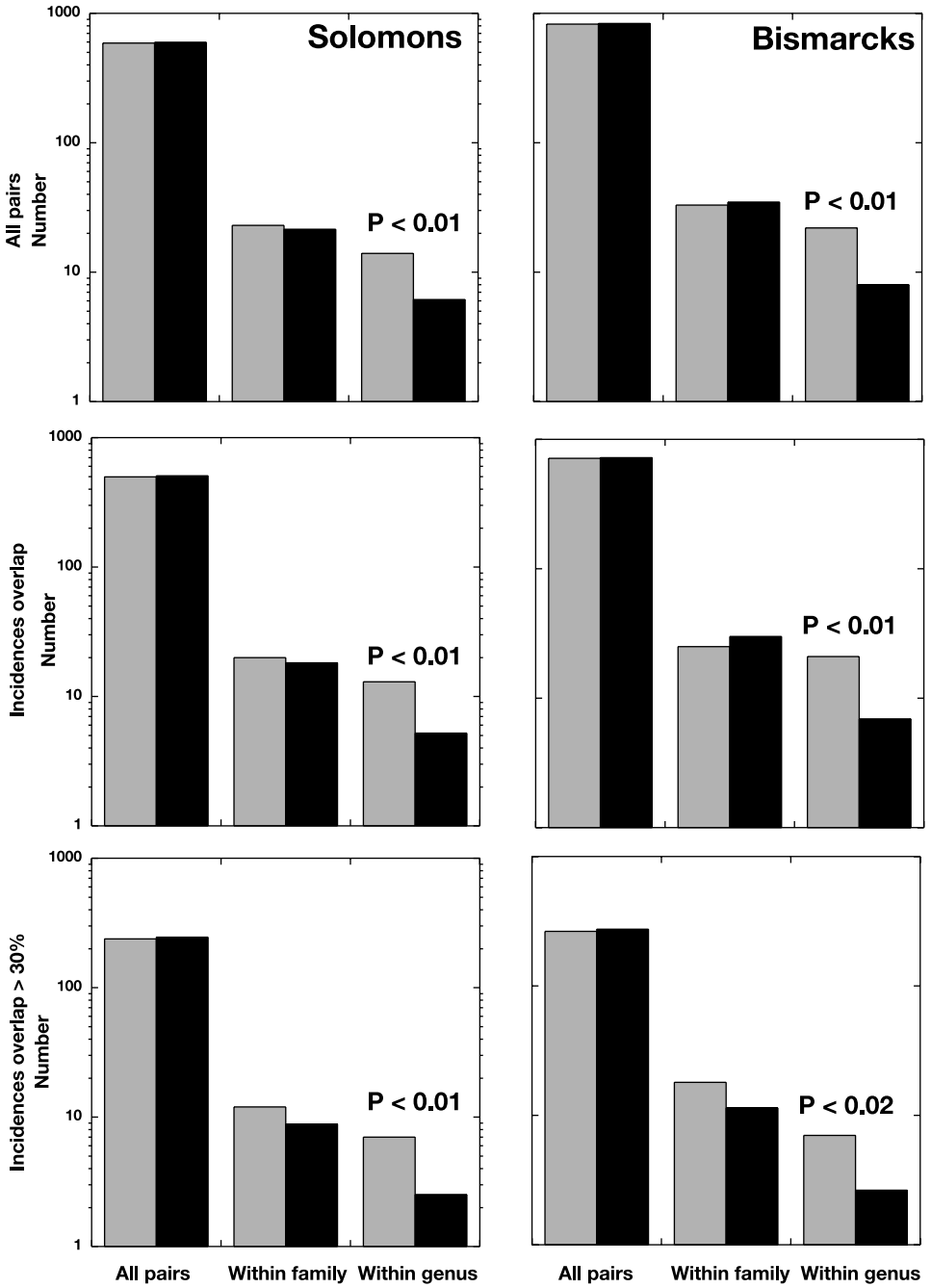


Fig. 2. Observed (grey) and expected (black) numbers of species pairs found fewer than 50,000 times out of 10^6 nulls. Note the logarithmic scale. There are highly significant excesses of such unusual pairs among species that are *within* the same *genus* (right-most pairs of bars), compared with species *within* the same *family* but different genera (middle pairs of bars), or *all pairs* excluding the other two groups, and so in different families (left-most pairs of bars). The top, middle, and bottom sets of data are, respectively, for all pairs regardless of incidence overlap, pairs that overlap at all in their incidences, and pairs whose incidence overlap is 30% or more of their combined incidence range (hence a higher percentage of each individual species' incidence range). Cut-offs higher or lower than 30% differ only in the number of cases passing the cut-off and so yield similar conclusions.

species of the genera that form checkerboards on smaller islands. So the rule roughly stated is 'A and B do not co-occur, unless species P, Q, R, S are also present, and P to S are found only on very large islands'.

Might the patterns of checkerboards be so sensitive to the presence or absence of other species that the patterns of co-existence differ between the two archipelagoes? Within the islands considered here, the answer is 'no' – only certain genera tend to develop checkerboards. Other genera do not. Which genera do and which do not does not depend on the archipelago and thus on the unique species found there.

In all, there are 20 genera represented by two or more congeneric species in both the Bismarcks and Solomons. Seven of those genera (*Ptilinopus*, *Ducula*, *Monarcha*, *Pachycephala*, *Zosterops*, *Myzomela*, and *Aplonis*) generate unusual negatively associated pairs in both archipelagoes; one (*Accipiter*) does so only in the Solomons, one (*Rhipidura*) only in the Bismarcks; and 11 (*Ardea*, *Ixobrychus*, *Falco*, *Columba*, *Gallicolumba*, *Charmosyna*, *Micropsitta*, *Aerodramus*, *Alcedo*, *Halcyon*, and *Coracina*) do so in neither. The first set of seven genera has 48 possible pairs in the Bismarcks and 39 in the Solomons, of which 19 and 13, respectively, are unusually negatively associated. The other sets of 13 genera have 42 possible pairs in the Bismarcks and 56 in the Solomons, of which only 1 and 1, respectively, are unusually negatively associated. The differences between the two sets are highly significant (χ^2 test) for both the Bismarcks ($P < 0.0001$) and Solomons ($P < 0.001$).

DISCUSSION

We start this discussion by considering five caveats that expand on concerns about the data and our analyses of them, and that might conceivably alter the conclusions that we draw from our results. Following these caveats, we discuss the results themselves and their extensions to other ecological questions.

Caveats

How fully known are the modern avifaunas of our islands?

The first collections of Solomon and Bismarck birds were made in 1823, and systematic collections began in 1875. Tring Museum collectors A.S. Meek and A. Eichhorn and the Whitney South Seas Expedition made the largest collections in 1900–1925 and 1927–1935, respectively. The unpublished diaries of the latter expedition also contained abundant records and observations. The last major island previously unexplored ornithologically, the Bismarck island of Dyaul, was explored in 1962. From 1969 to 1976, Diamond visited more than 100 islands and obtained not only his own observations but also those of island residents intimately familiar with birds. In recent decades, observations have accumulated from resident Europeans and from visiting bird tours. All of these records and observations were evaluated critically by Mayr and Diamond (2001). As a result, while undoubtedly some further distributional records will emerge, the Bismarck and Solomon Archipelagos are ornithologically the best explored archipelagoes in the tropical Southwest Pacific Ocean. The only significant new distributional records that have emerged since the publication of Mayr and Diamond (2001) are the description of the warbler *Cettia haddeni* (LeCroy and Barker, 2006) previously observed but not identified in the mountains of Bougainville, and reports of

an unidentified *Microeca* flycatcher on New Britain and New Ireland. Instead, the main recent new types of information about Bismarck and Solomon birds have involved behaviour in life, descriptions of taxa that became extinct following human arrival over 30,000 years ago (Steadman, 2001), and molecular evidence of relationships (Filardi and Moyle, 2005; Smith and Filardi, 2007' Moyle *et al.*, 2009).

Steadman (2001, pp. 139, 294, 495) claimed that species totals for Solomon islands are suspect because of inadequate modern surveys. However, the examples that he cites as evidence are invalid, and reflect unfamiliarity with the published literature on Solomon birds. He reported that his own visits to Ysabel in 1997 and 1998 added four species, previously thought confined to Ysabel's mountains, to Ysabel's lowland avifauna, and added three species to the whole island's avifauna. In fact, lowland records of three of the four former species had already been published as early as the 1890s, and a published record was already available for one of the latter three species. Conversely, he reported that the megapode *Megapodius freycinet* is absent on the Solomon islands of Vangunu, Gatukai, and Florida because of human impact, but there are published recent records of that species on all three islands.

To what extent are our results affected by spatial patterns of species distributions?

Does each island in a cluster of *m* islands, all occupied by species A and none occupied by a congeneric species B, count as one of *m* independent events, or must the degrees of freedom somehow be discounted? That is, if certain species occupy certain geographically localized subsets of Bismarck or Solomon islands while other species occupy other geographically localized subsets, that spatial autocorrelation by itself would tend to produce positive associations in some species pairs and negative associations in other species pairs. Occupations of different islands within such a subset would tend to be coupled by migration between nearby islands. To count them as independent events would effectively inflate our sample sizes and hence our identifications of species pairs as unusual.

We assessed this effect by examining the contributions that the four most marked types of geographically localized distributions within the Bismarcks and Solomons make to our 1505 unusual negative pairs. Note that the more islands that each member of a pair actually occupies, the more unusual (compared with null matrices) will it appear if the pair's two species actually fail to co-occur. For instance, if species A and species B each occur on 37 islands without any overlap, that outcome will be duplicated in far fewer null matrices than if species A and species B each occur on only one island without any overlaps. From that perspective, by far the most marked geographic clumping within the Solomons or Bismarcks involves the Solomons' New Georgia group, which contains 98 of the 142 ornithologically surveyed Solomon islands. The group lacks 14 species otherwise geographically widespread in the Solomons, but contains two species confined to the New Georgia group plus two other species whose Solomon distributions are concentrated in, but not restricted to, the New Georgia group (Mayr and Diamond, 2001, p. 243). (Recall that our species unit for analysis is the superspecies or else the isolated species; the New Georgia group also contains some famous endemic allospecies that do not figure separately in our analyses because they belong to more widespread superspecies.) Those New Georgia group absentees and specialties prove to account for 5 of the Solomons' 626 unusual negative pairs.

The second most marked geographic clumping involves the Northwest Bismarcks. These contain 8 of the 41 ornithologically surveyed Bismarck islands and lack 52 species otherwise geographically widespread within the Bismarcks, but they contain one

species (the flycatcher *Rhipidura rufifrons*) confined in the Bismarcks to the Northwest Bismarcks (Mayr and Diamond, 2001, pp. 231–237). The Northwest Bismarcks prove to account for one of the Bismarcks' 879 unusual negative pairs: that flycatcher *Rhipidura rufrifrons* present on two surveyed Northwest Bismarck islands, paired with its congener *Rhipidura leucophrys* occupying 27 of the 33 Bismarck islands outside the Northwest Bismarcks.

The third most marked geographic clumping involves the Solomons' San Cristobal group, which contains five of the 142 ornithologically surveyed Solomon islands, and which lacks nine species otherwise geographically widespread in the Solomons, but which contains five species confined to the San Cristobal group plus three other species whose Solomon distributions are concentrated in, but not restricted to, the San Cristobal group. The group contributes none of the Solomons' 626 unusual negative pairs.

Finally, several unusual negative species pairs of the Bismarcks appear at first sight to have geographically complementary distributions (e.g. Figures 20 and 22 of Diamond, 1975), with one of the two species in each case seemingly confined to large central Bismarck islands and the other confined to outlying Bismarck islands. However, examination of these pairs shows that their segregation is not geographic: the former species in each case also occurs on one or several outlying islands, and the latter species is a supertramp that also occurs on small islands within a few kilometres of large central islands.

Thus, spatial patterns do make some contribution to our results, but that contribution is a minor one. The explanation for this finding is that mutually exclusive pairwise distributions are much more likely to appear unusual (by comparison with null matrices) for geographically widespread species present on many islands than for geographically restricted species present on fewer islands.

Does the inclusion of 98 small islands in our 142-island Solomon database, and of 10 small islands in our 41-island Bismarck database, skew the results?

For instance, if many of the islands were so small that only one viable population of a species pair could survive on an island, such islands might give rise to checkerboards unrelated to competition. In fact, 32 of our 41 Bismarck islands, and 105 of our 142 Solomon islands, support ≥ 10 species. As a more direct test, we separately analysed the New Georgia group of the Solomons, which contains 90 of our 98 small islands, as well as 13 larger islands. The New Georgia group proved to exhibit proportionately many fewer, not more, pairs with unusually negative pairwise associations than did the entire Solomon Archipelago. Thus, those associations are not an artifact of including many small islands for analysis.

Congeners or guilds?

Our 'sieving' procedure documents the number of unusual pairs according to taxonomic criteria. We examined the taxonomic category of congeners because it is traditionally assumed that congeners are more likely to compete with each other than are non-congeners. The fact underlying this widespread assumption is that congeners are in general more recently diverged, hence more similar morphologically and ecologically, than are non-congeners. Of course, to state this obvious fact does not deny the existence of any competition between non-congeners or deny any non-competition between congeners. Some non-congeners are convergently similar and probably do compete today, a striking example being the black sunbird *Nectarinia sericea* and black honey-eater *Myzomela*

pammelaena illustrated in Fig. 1d. Our sieving could have chosen to focus on guilds rather than on congeners, but we did not do so because there are more uncertainties and arbitrary judgements about guild limits than about genus limits. If we had added clear examples of ecological convergence to form guilds, such as 'sunbirds plus honeyeaters', that would have enhanced our results. In any case, considerations of guilds do not overturn the average expectation that congeners are more likely to compete than non-congeners, and that this tends to lead to checkerboard distributions.

Pairs or triplets, etc.?

We have analysed non-random pairwise co-occurrences of species within an entire avifauna. In addition, we have analysed all congeneric species triplets, and we find that unusual ones belong without exception to the same genera responsible for unusual congeneric pairs. Trial analyses of half of these genera revealed unusual species quartets, quintets, and singletons (i.e. islands occupied only by a single species of a multi-species genus). Much more effort and much higher computing power will be required to provide a complete analysis for singletons, triplets, quartets, and quintets, comparable to the analysis provided in this paper for species pairs.

The causes of negative and positive associations

What biological features could explain the positively associated pairs with unusually coincident distributions? We find few cases attributable to coincident narrow habitat requirements, and none attributable to a mutualistic interaction, although these *a priori* plausible explanations for positive associations are often mentioned in the literature. Most positively associated pairs consist of two species from different families and with different diets and habitat requirements, as in the case of the above-cited mound-builder/parrot pair (Fig. 1a). Instead, as illustrated in Fig. 1a and explained in its legend, the biological explanation is broad overlap in species incidences, making co-existence on many islands very likely unless some other consideration interfered. Almost all of our unusual positive pairs have broadly overlapping incidences similar to the example of Fig. 1a.

What biological features not incorporated into our null model could explain the negatively associated pairs with unusually complementary distributions? Five Solomon pairs are complementary because of geographic considerations not incorporated in the null model: each consists of one species geographically confined within the Solomons to the New Georgia group, paired with another Solomon species absent from that group. For the remainder, the species involved in the pairs occur throughout all or most of the archipelago involved.

Instead, most of the unusual negative pairs prove to have the converse explanation from that just mentioned for most unusual positive pairs: that is, non-overlapping rather than overlapping incidences, such that one species occupies many islands with few other species present, while the other species occupies islands with many other species present (see Fig. 1b for illustration and explanation). In particular, most of the most unusual 'checkerboard distributions' (meaning that the two species of the pair actually share no island) involve a 'supertramp' species (Diamond, 1974) (a species confined to species-poor islands and absent from species-rich islands) paired with a species concentrated on species-rich islands (Figs. 1b and 1d). There are, however, previously unappreciated patterns in the taxonomic affiliations of these pairs as well as in the overlap of their incidences.

Six lines of evidence make clear that this confinement of supertramps to species-poor islands is mainly because of competitive exclusion from species-rich islands, rather than because of a postulated preference for habitats of small species-poor islands. First, the habitats of small islands are also widespread on the coasts of large islands, from which the supertramps are nevertheless absent. Second, supertramps are associated with islands that are species-poor for any reason, rather than with small islands *per se*: supertramps also occur on an archipelago's large islands that are species-poor because of remoteness, and that support a wide range of habitats. Third, supertramps occur on large central islands with a wide range of habitats but still lacking the usual slowly dispersing bird species of large islands because of defaunation by volcanic activity or tsunamis in recent centuries. Fourth, species with supertramp distributions on species-rich archipelagoes near New Guinea often prove not to have supertramp distributions but to occupy the largest central islands as well as small or remote islands on species-poorer archipelagoes further from New Guinea – for example, five species that behave as supertramps in the Bismarcks but occupy the largest islands of the Solomons, and two species that behave as supertramps in the Solomons but occupy the largest islands of the Vanuatu and Fijian archipelagoes. Fifth, on islands that supertramps do occupy, they are catholic rather than narrow in their habitat preference, occurring in a wide range of habitats from beach forests and gardens at sea level to lowland rainforests, montane forests, and sub-alpine shrubbery at high elevations. Finally, the presence or absence of a supertramp can usually be correlated with the absence or presence of one or more specific competitors or congeners – for example, *Macropygia mackinlayi* with *Macropygia nigrirostris*, *Myzomela pammelaena* with other *Myzomela* species or *Nectarinia sericea*, *Ptilinopus solomonenis* with *Ptilinopus rivoli*, and *Ducula pacifica* with several other *Ducula* species.

The explanation for why only certain genera tend to develop significantly non-overlapping island distributions (negative associations) of congeners follows straightforwardly from ecological differences within and between genera. Congeneric bird species may co-exist on the same island or in the same archipelago through either of two broad types of niche differences: spatial differences, such that the two species occupy different altitudes, habitats or island types and thereby live in mutually exclusive territories; or non-spatial differences, such that the two species have different body sizes or diets, or obtain food at different heights above the ground or by different foraging techniques, and are thereby able to co-occur in the same territory. In some Northern Melanesian genera (such as *Pachycephala* and *Zosterops*), ecological segregation must be predominantly spatial, because all Northern Melanesian species in the genus are of similar body sizes, diets, and foraging techniques. In other genera (such as *Accipiter*, *Falco*, *Aerodramus*, and *Coracina*), congeners commonly overlap spatially through differences in body size, diet or foraging technique. From this perspective, our two groups of 7 and 13 genera separate almost completely: the 7 genera tending to develop negative associations are ones in which ecological segregation is strictly spatial (2 genera) or either spatial or non-spatial (5 genera), but not predominantly non-spatial; while the 13 genera tending not to develop negative associations are ones in which ecological segregation is predominantly non-spatial (9 genera) or either spatial or non-spatial (3 genera), and in only one genus strictly spatial. The tendency of congeners in the former 7 genera, but not in the latter 13 genera, to segregate on different islands, as analysed in this paper, is thus part of a broader pattern of spatial segregation in the former 7 genera.

Extensions

Finally, our results exemplify a broader issue of strategy in community ecology studies, which we term the 'duck/flycatcher effect' (and also known as the 'dilution effect'). In many and perhaps most species communities, a given species has direct ecological interactions with some but not with most other species of the community. Such interactions include predator–prey relationships, mutualism, competition, infection, parasitism, co-evolution, and mimicry. Each such type of interaction can be documented in detail by study of the species pairs or groups involved, and many or most species of the community may be involved in that particular type of interaction with one or more other species. Nevertheless, it may still be difficult to demonstrate the importance of the interaction by a community-wide analysis of all species pairs or links, because most pairs or links (e.g. ducks and flycatchers) are not involved in that interaction. Hence a community-wide analysis may yield the appearance that the community is randomly organized and approximates predictions of a neutral model.

Three examples to date are: our present study of first-order pairwise associations, which we have documented with effort for congeners but not at the level of the whole community; co-evolution, abundantly documented in individual cases but lacking a signal at the level of whole food webs (Montoya *et al.*, 2006); and species–abundance relationships (Hubbell, 2001). Hence our practical conclusion for research strategies is that, realistically, community-wide searches for a role of species interactions are likely to require 'sieving' methods, such as those used in our Fig. 2, to extract the signal of the smaller number of meaningful interactions from the noise of the huge number of non-interacting pairs or links such as ducks and flycatchers.

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