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## Co-occurrence of Australian land birds: Diamond's assembly rules revisited

Nicholas J. Gotelli, Neil J. Buckley and John A. Wiens

Gotelli, N. J., Buckley, N. J. and Wiens, J. A. 1997. Co-occurrence of Australian land birds: Diamond's assembly rule revisited. – *Oikos* 80: 311–324.

Using null model simulations, we tested for non-random patterns of local co-occurrence in 28 congeneric guilds of the Australian avifauna. At the scale of 1° latitude–longitude blocks, species in most guilds co-occurred more often than expected by chance. However, coexistence was significantly less than expected for six of the 28 guilds. In four of these guilds (*Climacteris*, *Cinclosoma*, *Manorina*, and *Psophodes*), the species were segregated by habitat use and/or geographic range. The remaining two cases were complicated by uncertainty in taxonomy (*Malurus*) and unreliable field records (*Corvus*). We also examined distribution patterns in five Australian guilds that are analogs of avian guilds designated by Diamond for the Bismarck Archipelago. For two of the five guilds (*Pachycephala* and *Zosterops*), co-occurrence in Australia was less than expected, mirroring an insular pattern of “checkerboard distributions” in the Bismarck Archipelago. For the remaining three guilds (*Ptilonopus*, *Myzomela*, and *Lonchura*), co-occurrence was significantly greater than expected. Overall, our results suggest that competitive-based assembly rules are not important in determining species coexistence within most congeneric guilds of the Australian avifauna, at least at the large spatial scale of our analysis.

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The idea that the species composition of a community is governed by deterministic “assembly rules” (Diamond 1975, Case and Diamond 1986) is a pervasive theme in community ecology. These rules emphasize the importance of interspecific interactions in determining which particular species are found in an assemblage (Drake 1990). The significance and even the reality of assembly rules have been widely debated. Proponents have argued for the importance of resource exploitation (Diamond 1975), competitive hierarchies (Gilpin et al. 1986), and priority effects (Drake 1991) in producing assembly rules. Critics have complained that many of the rules are trivial tautologies that lack predictive power (Connor and Simberloff 1979) and that the evidence for consistent patterns of community struc-

ture, much less for assembly rules, is hardly compelling (Wiens 1980, Wilson 1991).

The origin of this controversy was Diamond's (1975) treatise on the distribution of 141 land-bird species on New Guinea and its satellite islands in the Bismarck Archipelago. Diamond (1975) summarized many years of his own field studies and described species-area relationships, incidence functions, species combinations, and patterns of resource use in the archipelago. His analyses implied that interspecific competition within groups of related species (ecological guilds) was the most important determinant of observed species combinations. Diamond (1975) codified and generalized his findings in a list of seven “rules” of community assembly. Two of these rules discussed the occurrence of

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“checkerboard distributions” of species that never occupied the same island (or local habitat patch). Diamond (1975) presented seven examples of checkerboard distributions from the Bismarck Archipelago.

Connor and Simberloff (1979) argued that most of the rules were tautologies and that checkerboard patterns must be tested against an appropriate null model. For a number of island archipelagoes, they compared expected and observed numbers of species combinations with exclusive distributions and claimed that observed data fit the expected values closely. They concluded that Diamond’s (1975) evidence was insufficient to support the creation of general assembly rules.

Connor and Simberloff’s (1979) critique touched off an acrimonious debate, which has continued for nearly two decades (Wiens 1989, Gotelli and Graves 1996). Much of the controversy has surrounded the statistical details of Connor and Simberloff’s (1979) null model (Alatalo 1982, Diamond and Gilpin 1982, Gilpin and Diamond 1982, 1984, 1987, Wright and Biehl 1982, Connor and Simberloff 1983, 1984, Gilpin et al. 1984, Wilson 1987, Roberts and Stone 1990, Stone and Roberts 1990, 1992). Other issues, such as guild designation, source-pool construction, and habitat affinities are perhaps more important to the outcome of the analysis, but these factors have rarely been investigated systematically (Gotelli and Graves 1996).

Because Diamond (1975) never published the complete data set on which his analyses were based, it is probably impossible to resolve the controversy about assembly of avian communities of the Bismarck Archipelago. However, it is possible to test for assembly rules in the avifauna of the Australian mainland because detailed species-distribution maps have been published (Blakers et al. 1984). The Australian avifauna has been the subject of many ecological (e.g., Schall and Pianka 1978), evolutionary (e.g., Cracraft 1986), and biogeographic (e.g., Kikkawa and Pierce 1969) studies. In this paper, we test for the existence of assembly rules within congeneric guilds of the Australian avifauna.

Our analyses incorporated several key elements that have frequently been neglected in previous tests. First, we used a null model that reliably detects unusual aggregation or segregation of species at sites. Second, we used explicit, a priori guild designations of congeneric, ecologically similar species. These units are the most appropriate for detecting checkerboards (Graves and Gotelli 1993). Third, we incorporated information on habitat affinities of each species, which can refine null-model tests (Schoener and Adler 1991). Fourth, we examined the effect of differing definitions of residency status on the outcome of null-model tests. Finally, we were able to test for patterns in guilds that were analogous to those delineated in Diamond (1975). These analyses provide an independent test of co-occurrence patterns for certain sets of species common to the Bismarck Archipelago and the Australian mainland.

## Materials and methods

### Data sources

Between 1977 and 1981, the Royal Australian Ornithologists’ Union organized a distributional survey of the breeding birds of Australia, Tasmania, and the surrounding islands. The continent was divided into 812 1° × 1° longitude–latitude blocks (100 × 100 km), each of which was surveyed by teams of volunteer observers. Observers documented the presence or absence of species, and whenever possible, also collected breeding records.

Results of the survey were published as occurrence maps in *The Atlas of Australian Birds* (Blakers et al. 1984), which forms the basis for our analyses. The maps distinguish between breeding blocks and other blocks where the presence of species was recorded. Different sized circles indicate the “reporting rate” for a species in a particular block. The reporting rate for a species was the percentage of all record sheets for that block in which the species was recorded. The three reporting categories (≤10%, 11–40%, and >40%) indicate relative frequency of occurrence, which should correlate with relative abundance. The reporting rate is appropriate to compare relative abundance within a species across blocks, but it is not appropriate for comparing relative abundance among species (Schoener 1990), and we have not used it for that purpose.

### Habitat distributions

The *Atlas* volume also presents a simple map of habitat types. Each block of the Australian mainland was assigned by Blakers et al. (1984) to one of eight mutually exclusive habitat types: rainforest, forest, woodland, acacia scrub, mallee, spinifex, saltbush, and tussock grassland. Although this is a coarse level of habitat description, we used this information as a constraint in our null models and used it to test for simple patterns of habitat partitioning within guilds.

### Data reduction

We converted the *Atlas* maps to digitized computer maps. In the digitized maps, all breeding records were stored, and presence data were indicated as “common” (>40% recording rate) or “rare” (≤40% recording rate). Because the mechanisms controlling the composition of continental vs island avifaunas may be distinct (Lack 1976, Schluter 1988), we excluded offshore islands (including Tasmania) from our digitized maps. Data from 763 mainland 1° blocks were included in our maps and analyses. We also constructed a computerized map of the habitat types designated by Blakers et al. (1984) for each block of the mainland.

## Occupancy criteria

Although most null-model studies of birds define "occurrence" on the basis of breeding records, this definition may be problematic (Connor and Simberloff 1978). Important species interactions may occur away from breeding sites and these would be missed in such an analysis. In addition, breeding status may be difficult to determine, and the reliability of breeding records is likely to vary among species and among observers. This is particularly true in the current study, in which occurrence data were systematically collected but breeding records were not (Blakers et al. 1984).

For these reasons, we tested the effects of occupancy definition on null-model results. We used three definitions of site occupancy:

(1) "Breeding" included only those blocks in which there were breeding records for a species.

(2) "Common" included those blocks in which there were breeding records and/or the recording rate was >40%.

(3) "All" included those blocks in which there was any occurrence or breeding record.

## Guild designations

A major issue of contention in the assembly-rules debate has been the assignment of species to guilds. Ideally, such guilds would represent sets of species that use resources in a similar fashion (Root 1967). In practice, guilds are rarely designated solely by resource use, but are often based on taxonomic groupings (Jaksic and Medel 1990, Simberloff and Dayan 1991). The rationale is that closely related species are more similar in morphology and resource use, and hence are more likely to compete for limiting resources (Darwin 1859, Elton 1946).

Diamond (1975) designated a few guilds for the Bismarck avifauna, but did not state explicit rules or criteria for establishing guilds. Some of his guilds were strictly congeneric (e.g., *Pachycephala* flycatchers), but others included species from several genera (e.g., the cuckoo-dove guild, which included *Reinwardtoena* and *Macropygia*). Connor and Simberloff (1979) objected that these examples did not constitute a systematic evaluation of the entire avifauna, which would be necessary to establish the generality of assembly rules. However, their own analyses of complete avifaunas and of confamilial and congeneric groups have been criticized for including comparisons of species pairs that would never interact – the so-called "dilution effect" (Grant and Abbott 1980, Diamond and Gilpin 1982). For our analyses of the Australian avifauna, we established guilds as subsets of ecologically similar congeneric species. The rationale for this choice was a previous study by Graves and Gotelli (1993). In their

analyses of mixed-species flocks of Amazonian birds, significant checkerboard distributions could only be detected for congeneric species in the same feeding guild.

In spite of the importance of delineating guilds in assembly-rules studies, it is probably impossible to describe explicit "rules" for inclusion and exclusion of particular species. At the start of our study, one of us (JAW) divided the lists of congeners from Blakers et al. (1984) into guilds of ecologically similar species, based primarily on foraging ecology. These designations were made without reference to range maps in Blakers et al. (1984), but were influenced by previous field experience with the Australian avifauna (Wiens 1991a, b). We limited our analyses to guilds that contained four or more species, to ensure adequate statistical power for detecting unusual co-occurrence patterns. The final list contains 28 guilds of congeneric land-bird species with similar feeding ecology (Appendix 1). If competition is important in determining the distribution of species, its effects are most likely to be revealed within these groups. There is no overlap of species among guilds, which we treat as statistically and biologically independent of one another.

As part of our analysis, we also examined the distribution of species and genera indicated in Diamond's (1975) guilds. Appendix 2 lists Diamond's (1975) guilds for the Bismarck Archipelago and the closest set of species we could analyze for the Australian mainland. For this analysis, we relaxed our rule of a minimum of four species. In most cases, the species lists were not identical, although we were able to test the mainland distribution of *Pachycephala pectoralis* and *P. melanura*, two species that show a striking checkerboard distribution in the Bismarck Archipelago (Fig. 21 in Diamond 1975).

## Data limitations

Null-model analyses that rely on published range maps are limited by the quality of the data collected, and the current taxonomy of the group studied (Gotelli and Graves 1996). The state of taxonomy is especially important in the analysis of the Australian avifauna (Ford 1974, Keast 1981, Cracraft 1986). In particular, there is considerable disagreement over the status of species and subspecies with isolated, disjunct populations (Keast 1981). Blakers et al. (1984) did not recognize many disjunct populations as distinct species, even though they may exhibit morphological differentiation (Cracraft 1986). Moreover, the taxonomy in Blakers et al. (1984) was based largely on Schodde (1975). Many of these genera are now believed to be poly- or paraphyletic (Christidis and Boles 1994). Our initial list of guilds was kindly examined by Dr. Leslie Christidis, of the Museum of Victoria. He indicated changes in tax-

onomy and range status, which we have incorporated into Appendices 1 and 2. These lists now represent our best estimate of guilds of potentially competing species and reflect currently accepted taxonomy and systematics of the Australian avifauna.

### Quantifying co-occurrence patterns

How should unusual co-occurrence patterns be quantified? Diamond (1975) suggested that exclusive distributions of species (checkerboards) are indicative of assembly rules. Fox and Brown (1993) used the criterion of "favored" and "unfavored" states to identify particular combinations of functional groups in their analyses of coexisting rodent species. Whittam and Siegel-Causey (1981) examined the relative frequency of all possible combinations of species coexisting in Alaskan seabird colonies.

Although checkerboard distributions are the simplest and most clear-cut of the possible assembly rules (Graves and Gotelli 1993), the statistical requirement is very severe. If two species occurred together only in a single site, the pattern would not be scored as a checkerboard distribution. Checkerboards among three or more species of a guild would be even less likely to occur, even if competition were strong.

For these reasons, we favor a quantitative index of co-occurrence that reveals patterns of high and low overlap of species within a guild. That index is simply the total number of unique pairwise occurrences of species summed across all blocks. Suppose there is a set of  $k$  blocks, and  $n_x$  is the number of species within a guild coexisting in block  $x$ . We defined a simple index of co-occurrence,  $C$ :

$$C = \sum_{x=1}^k (n_x)(n_x - 1)/2 \quad (1)$$

This index is one of many possible measures of species co-occurrence (Gotelli and Graves 1996). The minimum value of the index is zero, when no species in the guild co-occur. The more blocks that contain two or more species, the larger the index. The maximum value of the index depends on the number of blocks, the number of species, and their degree of co-occurrence. For this reason, comparison of the observed  $C$  with an appropriate null model is essential.

### Null models for species co-occurrence

Our null models retained the observed number of occurrences for each species, but randomly placed these on the digitized map of Australia, subject to certain constraints. Because our analysis was not conducted at the level of the entire avifauna, we did not place restrictions or limitations on the total number of species

that could coexist in a single block. However, we recognize that habitat affinities are an important component of distribution that should be incorporated into null models of species co-occurrence. We used three versions of our null model that incorporated various degrees of habitat specificity:

(1) No restrictions. The block occurrences of each species were randomly redistributed among all continental blocks in Australia. In all simulations, a species could not be placed twice in the same block. For example, suppose a species was present in 6 blocks of rainforest, 3 blocks of woodland, and 1 block of acacia scrub. The simulation would place the species in 10 randomly chosen blocks of the Australian mainland, regardless of habitat type.

(2) Qualitative habitat restriction. Each species was randomly placed in blocks that contained habitat that it actually occurred in. For the hypothetical example, the simulation would place the species in 10 randomly chosen blocks that were designated as either rainforest, woodland, or acacia scrub.

(3) Quantitative habitat restriction. For each species, its occurrences in each habitat type were randomly redistributed to blocks with that habitat type. This simulation retains the observed habitat affinities for each species. For the hypothetical example, the simulation would place the species in 6 randomly chosen blocks of rainforest, 3 randomly chosen blocks of woodland, and 1 randomly chosen block of acacia scrub.

Note that in all three algorithms, species occurrences are assigned randomly to blocks, so that the structure of the geographic range is disrupted. A more realistic simulation procedure would choose randomly a starting block and then add site occurrences contiguously (e.g., Beven et al. 1984). However, this procedure would not be appropriate for many Australian bird species that have large geographic ranges with disjunct populations. In our discussion, we explicitly address the issue of geographic range and co-occurrence patterns.

Using one of the three algorithms and one of the three occupancy criteria, all species in a guild were placed randomly and independently of one another. Next, we calculated the co-occurrence index  $C$  for the simulated maps. We repeated the procedure 1000 times and compared the observed index  $C$  to the histogram of values from the 1000 simulated assemblages. The number of simulated distributions  $\leq$  or  $\geq$  the observed index is a measure of the tail probability that observed co-occurrences are unusually aggregated (large observed  $C$ ) or segregated (small observed  $C$ ).

Because there is no overlap in the species composition of different guilds, we treated them as statistically independent of one another in terms of their distributions. Therefore, tendencies towards unusual occurrence can be assessed for the entire avifauna by tabulating the frequencies of guilds with statistically

significant ( $p \leq 0.05$  or  $p \geq 0.95$ ) patterns. Digitized maps in ASCII files and the simulation program in a Pascal file are available from the senior author by request.

### Type I and Type II errors in the null model

In order to assess the power and reliability of our null model, we compared it to some idealized species distributions. First, we assembled a hypothetical guild of four species, each with an occurrence frequency of 180, 120, 60, or 30 blocks on the map of Australia. These occurrence frequencies represent typical range sizes for the Australian avifauna.

We began with two idealized distributions, one in which all four species were entirely allopatric ( $C = 0$ ), and one in which all four species were perfectly sympatric, with the smaller ranges progressively nested within the larger ones ( $C = 330$ ). Both distributions were highly non-random by the null model randomization ( $p < 0.001$ ), which generated an expected index of  $C = 66.5$ . Next, we randomly redistributed a certain fraction of the block occurrences of each species. These redistributions progressively degraded the pattern of perfect allopatry or perfect sympatry. The fraction of the range that was redistributed is a measure of the signal-to-noise ratio of the pattern. Thus, if 10% of the occurrences were redistributed, the signal-to-noise ratio was 9.0, whereas if 50% of the occurrences were redistributed, the signal-to-noise ratio was 1.0. When all of the occurrences were redistributed, the original pattern was completely degraded (signal-to-noise ratio = 0.0).

Using a 10% increment of redistribution, we tested each co-occurrence pattern against the null model with no habitat restrictions (Fig. 1). For the allopatric distribution, the observed  $C$  increased as more occurrences were redistributed. The statistical significance of the pattern ( $p < 0.05$ ) disappeared when between 50 and 60% of the occurrences were redistributed. For the sympatric distribution,  $C$  decreased as more occurrences were redistributed. The statistical significance of the pattern disappeared when between 60 and 70% of the occurrences were redistributed.

These results show that our null model could detect aggregation and segregation even when there was a moderate amount of noise in the data. As long as the signal-to-noise ratio was greater than 1.0, the null model correctly revealed both positive and negative co-occurrence patterns. Moreover, the null hypothesis was not rejected for random or nearly random patterns, indicating that the model does not suffer from Type I errors.

### Null models for habitat associations

The habitat data were used as constraints in the null model for co-occurrence, but it is possible that habitat

affinities themselves reflect interspecific competition. If competition is an important force over evolutionary time, then current habitat affinities within a guild may exhibit unusually low overlap (the "ghost of competition past"; Connell 1980).

Habitat affinities can be tested most easily by using null models of niche overlap (Sale 1974, Inger and Colwell 1977, Lawlor 1980). Lawlor (1980) developed four randomization algorithms (RA) that could be used to study niche overlap. Winemiller and Pianka (1990) and Gotelli and Graves (1996) have compared the performance and power of these algorithms. For our purposes, the most useful are RA2 and RA3. In RA2, the observed frequencies of occurrence of each species in each habitat are replaced by a random uniform frequency. The only restriction is that habitats that were not used by a species in nature are also forbidden in the simulation. RA2 retains the observed habitat restrictions, but allows species to utilize habitats randomly within that restricted set. In RA3, observed frequencies of habitat use for each species are randomly re-assigned to different habitats. RA3 does not restrict species to particular habitats, but does retain the overall degree of habitat specialization (= niche breadth) for each species.

Next, the overlap in habitat use is calculated for all unique species pairs. We used Pianka's (1974) symmet-

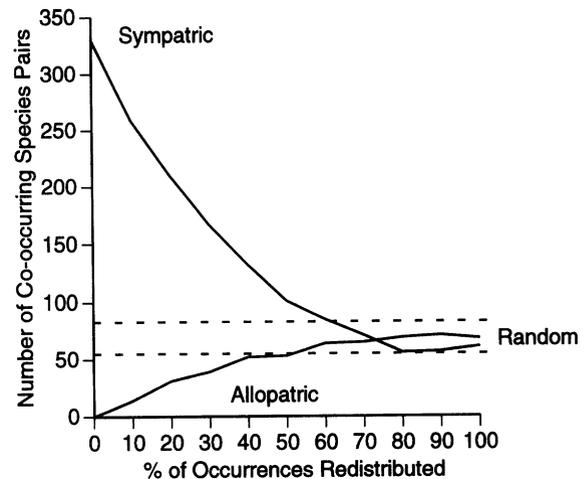


Fig. 1. Power test for null model of co-occurrence. The analysis begins with an idealized sympatric or allopatric distribution of four species ranges placed on the digitized map of Australia. For the allopatric distribution, the co-occurrence index is 0. For the sympatric distribution, the co-occurrence index is 330. At 10% intervals, a fraction of each species' occurrences is randomly redistributed across the map. The co-occurrence index is recalculated and compared to the null-model expectation. Distributions that could not be distinguished from the null model are bounded by the dashed lines, which indicate an approximate 95% confidence interval. The null model detected both aggregated and segregated distributions until approximately 50% of the block occurrences were randomized.

Table 1. Effects of residency criteria and habitat restrictions on null model results. Each entry is the number of guilds for which there were fewer co-occurring species than expected by chance ( $p < 0.05$ ; one-tailed test). The expected number of entries in each cell is approximately 1.4. By a binomial test, there were significantly more guilds than expected in the tail of the distribution (4 guilds,  $p = 0.01$ ; 5 guilds,  $p = 0.002$ ; 6 guilds,  $p = 0.0004$ ).

Null model	Residency		
	Breeding	Common	All sites
Unrestricted	0	0	6
Qualitative habitat restriction	0	0	5
Quantitative habitat restriction	1	1	4

ric overlap index  $O_{ij}$  to quantify the overlap in habitat utilization between species  $i$  and  $j$ :

$$O_{ij} = \frac{\sum_{x=1}^n P_{ix}P_{jx}}{\sqrt{\sum_{x=1}^n P_{ix}^2 \sum_{x=1}^n P_{jx}^2}} \quad (2)$$

For a set of  $n$  habitats,  $P_{ix}$  is the fraction of block occurrences of species  $i$  in habitat  $x$ . These pairwise values were averaged to give a single value that summarized niche overlap for the entire guild. Finally, the mean pairwise habitat overlap for the guild was compared to the histogram of means for 1000 randomizations. Randomizations followed one of the three occupancy criteria (breeding, common, or all) described earlier.

## Results

### Co-occurrence patterns

With three residency criteria and three co-occurrence null models, there were nine scenarios in which individual guilds were tested for negative and positive co-occurrence patterns. Residency criteria had a large effect on the number of guilds with negative co-occurrence patterns. Significant patterns were detected more often when all blocks were analyzed than when the analysis was restricted to “common” or “breeding” blocks. The type of null model used also affected the results. When all blocks were analyzed, significant deviations were more common for the unrestricted model. For breeding and common blocks, significant deviations were found only for the model with quantitative habitat restrictions (Table 1).

Regardless of the null model used, however, the frequency distribution of tail probabilities for different

guilds was bimodal and highly non-random (Fig. 2). Most guilds fell in the right-hand tail of the distribution, with a larger co-occurrence index than expected by chance. A small but substantial number of guilds also showed much less co-occurrence than expected. The co-occurrence index was random in very few guilds, although randomness was more common in the most restrictive null model (quantitative habitat restriction).

### Habitat overlap patterns

Few of the guilds were segregated in patterns of habitat use. Under RA2, only one or two guilds overlapped less

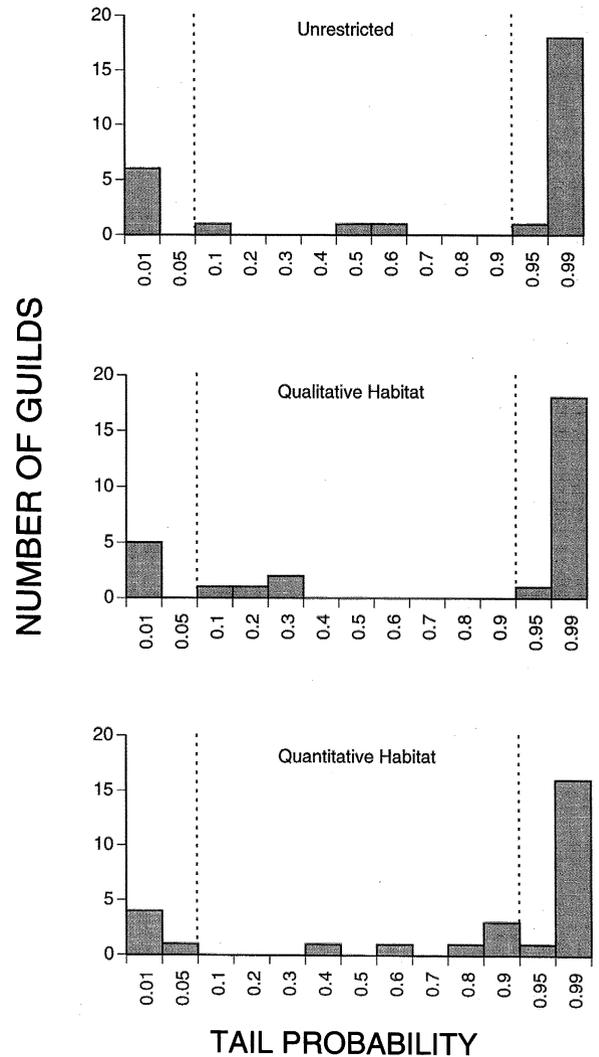


Fig. 2. Histogram of tail probabilities for co-occurrence patterns. Each element of the histogram is the probability that the observed co-occurrence index ( $C$ ) was less than or equal to the expected index for a particular guild ( $n = 28$ ). The dashed lines indicate the 95% boundaries. The three histograms represent three different null-model simulations (see text).

Table 2. Effects of residency criteria and null model (RA2, RA3) on patterns of habitat overlap. Each entry is the number of guilds for which observed habitat overlaps were less than expected by chance ( $p < 0.05$ ; one-tailed test). The expected number of entries in each cell is approximately 1.4. See text for descriptions of residency criteria and null models.

Null model	Residency		
	Breeding	Common	All sites
RA2	1	2	2
RA3	0	0	0

in habitat use than expected by chance. Under RA3, none of the guilds had significantly low overlaps (Table 2). As in the co-occurrence analysis, many guilds showed significantly more overlap in habitat use than expected by chance (Fig. 3).

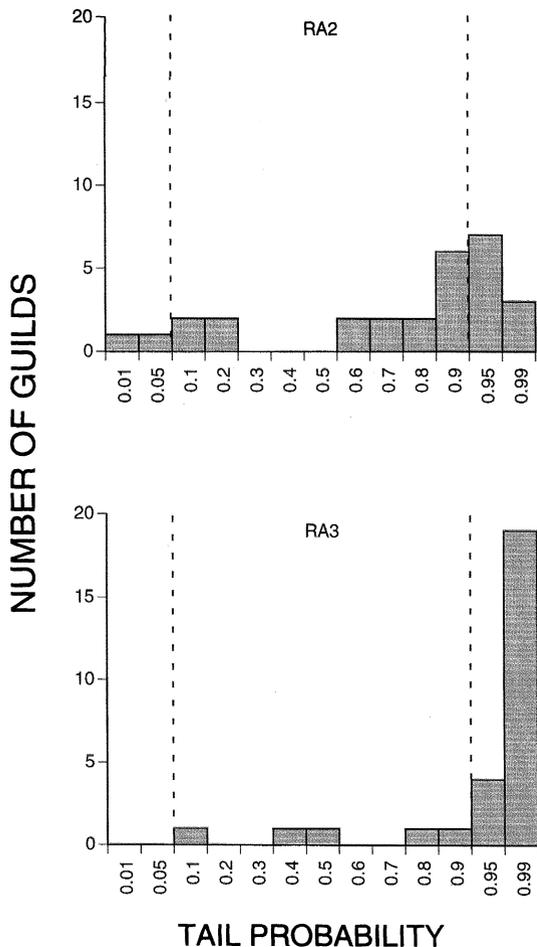


Fig. 3. Histogram of tail probabilities for habitat overlap patterns. Each element of the histogram is the probability that the observed habitat overlap was less than or equal to the expected overlap for a particular guild ( $n = 28$ ). The dashed lines indicate the 95% boundaries. The two histograms represent different randomization algorithms (RA) described in the text.

## Co-occurrence in Diamond's guilds

Table 3 depicts co-occurrence patterns in five guilds of Australian birds that are analogous to guilds with checkerboard distributions in the Bismarck Archipelago (Diamond 1975). None of these guilds displayed perfect checkerboards ( $C = 0$ ) on the Australian mainland. However, in two of the guilds (*Pachycephala* and *Zosterops*) the co-occurrence index was significantly less than expected by chance. In the remaining three guilds (*Ptilonopus*, *Myzomela*, and *Lonchura*), species co-occurrence was significantly greater than expected. Results were similar for all three null models of co-occurrence.

## Discussion

### Mechanisms producing checkerboard distributions

Much of the controversy surrounding assembly rules has been directed toward the statistical analysis of checkerboard distributions and the detection of non-random community patterns. Less attention has been devoted to interpreting checkerboards or other non-random patterns, once they have been revealed with an appropriate null model.

What accounts for assemblages of species that co-occur less often than expected by chance? The answer depends critically on the extent to which species overlap in habitat use and the extent to which their geographic ranges overlap. We suggest that patterns of low co-occurrence fall into one of three categories:

(1) Ecological segregation. Species have similar habitat requirements and overlap substantially in their geographic ranges, but co-occur less often than expected by chance, because exploitation or interference competition limits local coexistence. Examples include aggressive ant species that never co-occur on small mangrove islands (Cole 1983) and stem-boring insects that co-occur less often than expected because of interspecific aggression and murder (Stiling and Strong 1983).

(2) Habitat segregation. Species overlap substantially in geographic ranges but show unusually low overlap in habitat use. Consequently, local coexistence is less than predicted by null models. Habitat segregation may be the result of current or past competitive interactions, or may reflect the independent evolution of habitat affinities that is not driven by resource exploitation. Examples include desert rodent species that shift their habitat affinities in the presence of competitors (Rosenzweig 1973). Diamond (1975) also offers two examples of within-island checkerboards of Bismarck birds (*Lonchura*, *Melidectes*) that represent habitat shifts, possibly due to competition.

(3) Geographic segregation. Species show little or no overlap in their geographic ranges. They may or may

Table 3. Co-occurrence patterns for Diamond's (1975) guilds. For each Australian guild, the observed number of species and the co-occurrence index  $C$  is given. The expected value of  $C$  is the average of 1000 randomizations for each of three null models. A "+" indicates significantly more coexistence than expected by chance. A "-" indicates significantly less coexistence. One symbol  $p < 0.05$ ; two symbols  $p < 0.01$ ; three symbols  $p < 0.001$ . Guild members are listed in Appendix 2.

Guild	Number of species	Observed co-occurrence ( $C$ )	Expected co-occurrence ( $C$ )		
			Unrestricted	Qualitative habitat restriction	Quantitative habitat restriction
<i>Pachycephala</i>	2	2	8.2 <sup>-</sup>	9.3 <sup>--</sup>	10.5 <sup>---</sup>
<i>Ptilonopus</i>	4	66	5.5 <sup>+++</sup>	13.0 <sup>+++</sup>	35.5 <sup>+++</sup>
<i>Myzomela</i>	3	44	11.6 <sup>+++</sup>	19.7 <sup>+++</sup>	38.8 <sup>+++</sup>
<i>Zosterops</i>	2	3	15.5 <sup>---</sup>	14.9 <sup>---</sup>	14.7 <sup>---</sup>
<i>Lonchura</i>	2	12	1.6 <sup>+++</sup>	2.2 <sup>+++</sup>	3.5 <sup>+++</sup>

not overlap in habitat affinity. Geographic segregation may reflect the history of speciation and vicariance events or the evolution of distinct habitat preferences on a geographic scale. Alternatively, it may reflect short-term ecological interactions that ultimately set geographic range limits (Brown 1995). Examples include sister taxa that speciated because of geographical isolation and now exhibit allopatric or parapatric geographic ranges (Lynch 1989).

### Patterns of segregation in Australian guilds

At the scale of 1° blocks, our analyses revealed six guilds in which there was an unusually small number of species co-occurrences ( $p < 0.05$ ) in at least two of the three null models tested. For each of these guilds, we have plotted the geographic ranges of the species by drawing polygons around the recorded occurrences from the range maps in Blakers et al (1984; Figs 4 and 5). These maps, combined with the null-model analyses of habitat affinities, allow us to distinguish among the three types of low-overlap distributions.

Guilds in the genera *Cinclosoma* (Fig. 4a), *Psophodes* (Fig. 4b), and *Climacteris* (Fig. 4c) fit the pattern of geographic segregation. Most species in these guilds have allopatric or parapatric distributions, which accounts for the low overlap revealed by the null models. Species in these guilds exhibit random (RA2; *Climacteris*  $p = 0.241$ ) or low overlap in habitat use at this scale (RA2; *Cinclosoma*  $p = 0.054$ ; *Psophodes*  $p = 0.007$ ). In contrast, the *Manorina* (Fig. 4d) guild fits the pattern of habitat segregation. The geographic ranges of the four species are broadly overlapping, but there was significant segregation on the basis of habitats used within the ranges ( $p = 0.033$ ). This habitat segregation seems to be responsible for the low overlap revealed by the co-occurrence null models.

Guilds in the genera *Corvus* (Fig. 5a) and *Malurus* (Fig. 5b) conform to the pattern of ecological segregation: species in these guilds have broadly overlapping geographic ranges and overlap randomly in habitat use (*Corvus*  $p = 0.887$ ; *Malurus*  $p = 0.114$ ), but never-

theless co-occur in fewer blocks than expected. Superficially, these patterns are the best examples of competitively based assembly rules on a geographic scale.

However, it is risky to infer competition from the distribution of these particular guilds because of limitations in the data. In the genus *Malurus*, there is still considerable controversy over species limits and the status of disjunct populations (Serventy 1951, Ford 1974, Cracraft 1986). In particular, *M. lamberti* may include several closely related forms (Schodde 1982). Based on biochemical studies, L. Christidis (pers. comm.) suggests that the nine species of *Malurus* can be partitioned into three distinct lineages: (1) *M. lamberti*, *M. amabilis*, *M. pulcherrimus*, and *M. elegans*; (2) *M. splendens*, *M. cyaneus*, and *M. coronatus*; and (3) *M. leucopterus* and *M. melanocephalus*. We plotted range maps of these three lineages and discovered that ranges were largely allopatric and parapatric. In other words, most of the co-occurrence depicted in Fig. 4b is between species that belong to different putative lineages. These results underscore the importance of systematic and taxonomic boundaries to the results of null-model analyses (Gotelli and Graves 1996).

Ecological segregation in the *Corvus* guild is complicated by the fact that Australian crows and ravens are difficult to identify in the field, and the published maps may not be accurate. Blakers et al. (1984: 644) established the distribution of the corvids by "querying all records outside the range previously accepted by three people experienced with corvids. Only extralimital records accepted by all three are shown on the map". More precise records of corvid distributions might increase or decrease the pattern of local coexistence.

Thus, of the six Australian guilds with unusually low overlap, four cases (*Climacteris*, *Cinclosoma*, *Manorina*, and *Psophodes*) involve species that separate on the basis of geographic range and/or habitat use. The two remaining cases may represent true ecological segregation, but the patterns may also reflect taxonomic and systematic uncertainty (*Malurus*) or unreliable occurrence records (*Corvus*).

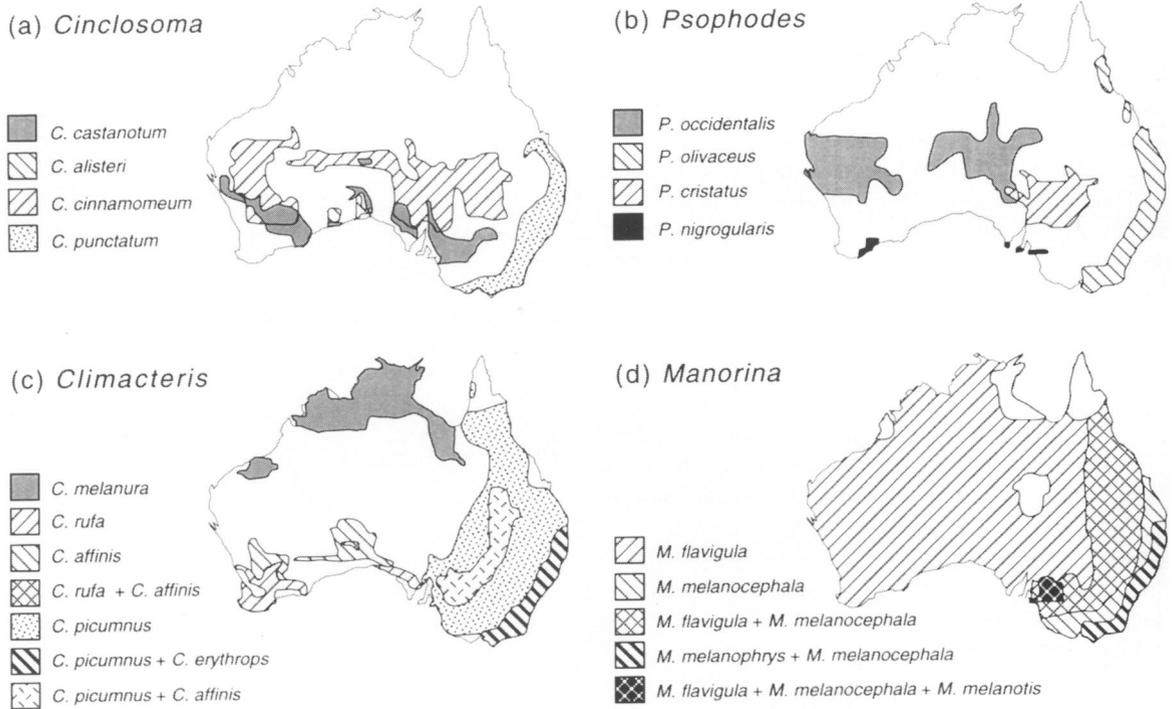


Fig. 4. Geographic ranges for guilds in which the co-occurrence index was significantly less than expected. These species segregate on the basis of geographic range and/or habitat use. (a) *Cinclosoma*; (b) *Psophodes*; (c) *Climacteris*; (d) *Manorina*.

### Patterns of segregation in Diamond's guilds

We were unable to confirm a pattern of low co-occurrence for three of Diamond's (1975) five guilds. In *Ptilonopus*, *Myzomela*, and *Lonchura*, the co-occurrence index was significantly greater than expected (Table 3). However, two of the five analogs of Diamond's (1975) guilds, *Zosterops* and *Pachycephala*, co-occurred less often than expected on the Australian mainland. Diamond (1975) has argued that these island checkerboard distributions reflect interspecific competition and "forbidden species combinations" that cannot coexist. Connor and Simberloff (1979) argued for the *Zosterops* example that five of the species in the Bismarck Archipelago represented a superspecies complex that was by definition allopatric or parapatric and should not be interpreted as an ecological checkerboard. For *Pachycephala*, Connor and Simberloff (1979) conceded that the pattern was statistically improbable, but they argued that checkerboards might still arise by chance because there were so many species combinations in the Bismarck Archipelago. In other words, because Diamond (1975) did not present guild designations for the entire avifauna, it is impossible to assess the significance of a handful of examples of checkerboard distributions.

Fig. 6 depicts the distribution of the two-species guilds with negative co-occurrence patterns on the Australian mainland. In both guilds, the two species have nearly exclusive coastal distributions, with only a few

blocks of co-occurrence. Although it is difficult to infer process from non-random patterns of geographic ranges, we believe these distributions reinforce Diamond's (1975) arguments about competition in these specific guilds.

For *Pachycephala* in particular (Fig. 6a), the two species exhibit a perfect checkerboard island distribution in the Bismarck Archipelago and co-occur less than expected by chance on the Australian mainland. Low co-occurrence cannot be explained on the basis of coarse habitat affinities, because all three of the co-occurrence null models were rejected, and because this species pair shows a high degree of habitat overlap (RA2;  $p = 0.912$ ). For this particular example, Connor and Simberloff's (1979) argument of chance factors can probably be rejected. If the *Pachycephala* island checkerboard in the Bismarcks were not due to competition, it seems unlikely that the same species pair would have a low-overlap mainland distribution in Australia. The *Zosterops* example is more difficult to interpret because the species pair that occurs in Australia does not occur in the Bismarcks, and because of the uncertain taxonomic status of some of the Bismarck species.

### Dilution effects

An important criticism of many null-model analyses is that negative co-occurrence patterns, such as checker-

board distributions, have been obscured by analyses of whole-island faunas or large taxonomic groups, such as avian families or genera (Grant and Abbott 1980, Diamond and Gilpin 1982). Empirical support for the dilution effect comes from an analysis of avian co-occurrence in mixed-species flocks of Amazonia (Graves and Gotelli 1993). In that study, co-occurrence patterns at the level of the entire avifauna or of exclusive ecological guilds were random or inconsistent. Only at the level of congeners within guilds was there evidence of significant ecological checkerboards.

We restricted our analysis of the Australian avifauna to this same level, and found a small but significant number of guilds with negative co-occurrence patterns. Perhaps these analyses also suffer from a dilution effect, and more negative interactions would have been revealed if we had examined all possible species pairs. Pairwise analyses are problematic, because the individ-

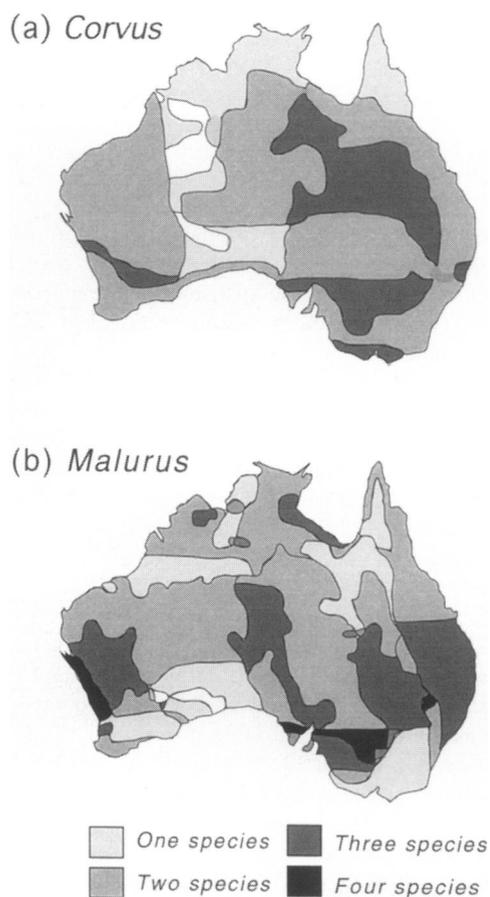


Fig. 5. Species densities for guilds in which the co-occurrence index was significantly less than expected. In these guilds, species overlapped substantially in geographic range and habitat use, but local co-occurrence was significantly less than expected by chance. See Appendix 1 for species names. (a) *Corvus*; (b) *Malurus*.

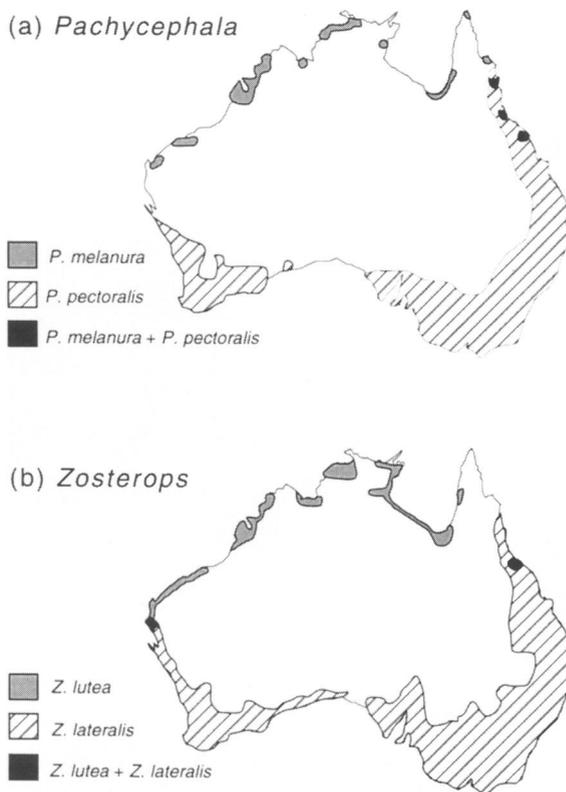


Fig. 6. Geographic ranges for analogs of Diamond's (1975) guilds in which the co-occurrence index was significantly less than expected. (a) *Pachycephala*; (b) *Zosterops*.

ual pairs are not statistically independent of one another and cannot be easily compared to null model randomizations (Gotelli and Graves 1996). Nevertheless, a pairwise analysis can at least suggest whether significant negative interactions are hidden within guilds that show an aggregate distribution that is overlapping or random.

To examine this possibility, we chose three guilds for more detailed analysis of pairwise co-occurrence patterns. Overall, these guilds showed strong patterns of aggregation (*Pachycephala*), randomness (*Amytornis*), or segregation (*Corvus*) in co-occurrence (the ground-foraging *Pachycephala* guild does not include the two species in Diamond's (1975) analysis). In general, pairwise analyses within guilds supported these patterns. There were five *Pachycephala* species in the low-foraging guild, which showed an aggregated pattern of co-occurrence. Of the 10 unique species pairs, 3 co-occurred in more blocks than expected by chance, 1 was significantly negative, and 6 were random (Table 4a). The *Amytornis* guild of eight species had a pattern of random co-occurrence, and this was reflected in all 28 pairwise interactions, which were non-significant (Table 4b). Finally, the *Corvus* guild of five species

Table 4. Tests for dilution effect. Three guilds are analyzed in detail which showed consistent patterns of (a) aggregation (*Pachycephala*), (b) randomness (*Amytornis*), and (c) segregation (*Corvus*) for all three null models. For each guild, co-occurrence patterns for all possible species pairs are summarized. + = co-occurrence significantly greater than expected by chance. - = co-occurrence significantly less than expected by chance. NS = co-occurrence random. One symbol =  $p < 0.05$ ; two symbols =  $p < 0.01$ ; three symbols =  $p < 0.001$ .

(a) *Pachycephala*. This guild exhibited positive co-occurrence patterns for all three null models. Note that this guild does not include the two species in Diamond's (1975) *Pachycephala* guild (Fig. 6a).

	<i>P. olivacea</i>	<i>P. lanioides</i>	<i>P. rufogularis</i>	<i>P. inornata</i>	<i>P. rufiventris</i>
<i>P. olivacea</i>		NS	NS	NS	++
<i>P. lanioides</i>			NS	NS	-
<i>P. rufogularis</i>				NS	+++
<i>P. inornata</i>					+++
<i>P. rufiventris</i>					

(b) *Amytornis*. This guild exhibited random co-occurrence patterns for all three null models.

	<i>A. housei</i>	<i>A. woodwardi</i>	<i>A. dorotheacea</i>	<i>A. striatus</i>	<i>A. goyderi</i>	<i>A. barbatus</i>	<i>A. textilis</i>	<i>A. purnelli</i>
<i>A. housei</i>		NS	NS	NS	NS	NS	NS	NS
<i>A. woodwardi</i>			NS	NS	NS	NS	NS	NS
<i>A. dorotheacea</i>				NS	NS	NS	NS	NS
<i>A. striatus</i>					NS	NS	NS	NS
<i>A. goyderi</i>						NS	NS	NS
<i>A. barbatus</i>							NS	NS
<i>A. textilis</i>								NS
<i>A. purnelli</i>								

(c) *Corvus*. This guild exhibited negative co-occurrence patterns for all three null models.

	<i>C. coronoides</i>	<i>C. tasmanicus</i>	<i>C. mellori</i>	<i>C. bennetti</i>	<i>C. orru</i>
<i>C. coronoides</i>		+++	+++	NS	---
<i>C. tasmanicus</i>			+++	---	NS
<i>C. mellori</i>				---	---
<i>C. bennetti</i>					--
<i>C. orru</i>					

showed a strong pattern of negative co-occurrence. Within the guild, 5 of the 10 possible pairwise patterns were negative, 3 were positive, and 2 were random (Table 4c).

These analyses indicate that patterns at the guild level generally reflect the pairwise interactions that occur among most species. In particular, there is no evidence that guilds with random (*Amytornis*) or positive (*Pachycephala*) co-occurrence patterns are obscuring large numbers of species pairs with low co-occurrence. On the other hand, guilds that show low-overlap patterns (*Corvus*) may nevertheless contain spe-

cies pairs that co-occur more often than expected. Overall, the results suggest that patterns in our guild analyses were not distorted by a dilution effect.

### Competition and community assembly

Much of the controversy over competition and community assembly has centered around the statistical properties of null models. In our analysis of the Australian avifauna, the null model we used had sufficient power to detect non-random distributions (Fig. 1), and our

classification of species into congeneric guilds was unlikely to have generated a dilution effect (Table 4). Thus, our results are unlikely to reflect simple statistical artifacts.

Very few guilds showed random co-occurrence patterns. The most typical result was that species in a guild co-occurred substantially more often than expected by chance (Fig. 2). Some of this co-occurrence undoubtedly reflected shared habitat preferences (Fig. 3) and the broad spatial scale of our analysis, although substantial co-occurrence was detected even in null models that controlled for observed habitat affinities.

A second group of guilds contained species that overlapped less often than expected by chance. These patterns are consistent with the hypothesis that competition within a guild limits local coexistence. However, most of these cases involved distributions that were segregated on the basis of available habitat or geographic range (Fig. 4). Habitat affinities and geographic ranges may also reflect the role of competition, but it is equally likely that they reflect phylogenetic and historical processes. Our results suggest that competition within guilds is not a strong organizing force, at least at the large spatial scale of this analysis.

Our analyses of Diamond's (1975) guilds showed that guilds exhibiting island checkerboards in the Bismarck Archipelago do not necessarily segregate on the Australian mainland, although we were able to confirm the low overlap pattern for *Pachycephala* and *Zosterops* (Fig. 6). Perhaps if the entire avifauna of the Bismarck Archipelago were classified according to guilds and subjected to a null-model analysis, it would reveal the same patterns that we have found for the Australian avifauna. Alternatively, island assemblages may be more structured by competition than mainland assemblages, as many authors have argued (Elton 1946, MacArthur 1972, Lack 1976). To assess the impact of competition on community structure, we need other studies of island assemblages that use a priori guild designations and appropriate null models.

### Large-scale geographic analyses

It is difficult to make inferences about local community structure from large-scale analyses. Each "site" in our analysis is very large and may encompass many different habitats and resources that can be partitioned by species. Thus, local segregation is almost certainly occurring in some of the guilds that show significantly aggregated overlap at the biogeographic scale. A definitive test of Diamond's (1975) assembly rules model would be to experimentally manipulate putative competitors, such as species in the genus *Pachycephala*. However, such field experiments are rarely possible for avian community studies. As Brown (1995) has argued, we must rely on large-scale "macroecology" studies to

address many ecological questions. In this case, we have independently confirmed some, but not all, of the checkerboard distributions first described by Diamond (1975). Our results are consistent with Diamond's (1975) explanation of competitive exclusion in these guilds, although they suggest that competitive structuring is not a general mechanism for all guilds in an assemblage.

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### References

- Alatalo, R. V. 1982. Bird species distributions in the Galapagos and other archipelagoes: competition or chance? – *Ecology* 63: 881–887.
- Beven, S., Connor, E. F. and Beven, K. 1984. Avian biogeography in the Amazon basin and the biological model of diversification. – *J. Biogeogr.* 11: 383–399.
- Blakers, M., Davies, S. and Reilly, P. 1984. The atlas of Australian birds. – Royal Australasian Ornithologists' Union, Melbourne.
- Brown, J. H. 1995. *Macroecology*. – Univ. of Chicago Press, Chicago.
- Case, T. J. and Diamond, J. M. 1986. *Community ecology*. – Harper & Row, New York.
- Christidis, L. and Boles, W. E. 1994. The taxonomy and species of birds of Australia and its territories. – Royal Australasian Ornithologists' Union monograph no. 2. Royal Australasian Ornithologists' Union, Melbourne.
- Cole, B. J. 1983. Assembly of mangrove ant communities: patterns of geographical distribution. – *J. Anim. Ecol.* 52: 339–347.
- Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. – *Oikos* 35: 131–138.
- Connor, E. F. and Simberloff, D. 1978. Species number and compositional similarity of the Galapagos flora and avifauna. – *Ecol. Monogr.* 48: 219–248.
- and Simberloff, D. 1979. The assembly of species communities: chance or competition? – *Ecology* 60: 1132–1140.
- and Simberloff, D. 1983. Interspecific competition and species co-occurrence patterns on islands: null models and the evaluation of evidence. – *Oikos* 41: 455–465.
- and Simberloff, D. 1984. Neutral models of species' co-occurrence patterns. – In: Strong, D. R., Jr., Simberloff, D., Abele, L. G. and Thistle, A. B. (eds), *Ecological communities: conceptual issues and the evidence*. Princeton Univ. Press, Princeton, NJ, pp. 316–331.
- Cracraft, J. 1986. Origin and evolution of continental biotas: speciation and historical congruence within the Australian avifauna. – *Evolution* 40: 977–996.
- Darwin, C. 1859. The origin of species by means of natural selection. – Murray, London.
- Diamond, J. M. 1975. Assembly of species communities. – In: Cody, M. L. and Diamond, J. M. (eds), *Ecology and evolution of communities*. Harvard Univ. Press, Cambridge, MA, pp. 342–444.
- and Gilpin, M. E. 1982. Examination of the "null" model of Connor and Simberloff for species co-occurrences on islands. – *Oecologia* 52: 64–74.
- Drake, J. A. 1990. Communities as assembled structures: do rules govern pattern? – *Trends Ecol. Evol.* 5: 159–164.
- 1991. Community-assembly mechanics and the structure of an experimental species ensemble. – *Am. Nat.* 137: 1–26.

- Elton, C. 1946. Competition and the structure of ecological communities. – *J. Anim. Ecol.* 15: 54–68.
- Ford, J. 1974. Concepts of subspecies and hybrid zones, and their application in Australian ornithology. – *Emu* 74: 113–123.
- Fox, B. J. and Brown, J. H. 1993. Assembly rules for functional groups in North American desert rodent communities. – *Oikos* 67: 358–370.
- Gilpin, M. E. and Diamond, J. M. 1982. Factors contributing to non-randomness in species co-occurrences on islands. – *Oecologia* 52: 75–84.
- and Diamond, J. M. 1984. Are species co-occurrences on islands non-random, and are null hypotheses useful in community ecology? – In: Strong, D. R., Jr., Simberloff, D., Abele, L. G. and Thistle, A. B. (eds), *Ecological communities: conceptual issues and the evidence*. Princeton Univ. Press, Princeton, NJ, pp. 297–315.
- and Diamond, J. M. 1987. Comment on Wilson's null model. – *Oecologia* 74: 159–160.
- , Diamond, J. M., Connor, E. F. and Simberloff, D. 1984. Rejoinders. – In: Strong, D. R., Jr., Simberloff, D., Abele, L. G. and Thistle, A. B. (eds), *Ecological communities: conceptual issues and the evidence*. Princeton Univ. Press, Princeton, NJ, pp. 332–343.
- , Carpenter, M. P. and Pomerantz, M. J. 1986. The assembly of a laboratory community: multi-species competition in *Drosophila*. – In: Diamond, J. and Case, T. J. (eds), *Community ecology*. Harper and Row, New York, pp. 33–40.
- Gotelli, N. J. and Graves, G. R. 1996. *Null models in ecology*. – Smithsonian Inst. Press, Washington.
- Grant, P. R. and Abbott, I. 1980. Interspecific competition, island biogeography and null hypotheses. – *Evolution* 34: 332–341.
- Graves, G. R. and Gotelli, N. J. 1993. Assembly of avian mixed-species flocks in Amazonia. – *Proc. Natl. Acad. Sci. USA* 90: 1388–1391.
- Inger, R. F. and Colwell, R. K. 1977. Organization of contiguous communities of amphibians and reptiles in Thailand. – *Ecol. Monogr.* 47: 229–253.
- Jaksic, F. M. and Medel, R. G. 1990. Objective recognition of guilds: testing for statistically significant species clusters. – *Oecologia* 82: 87–92.
- Keast, A. 1981. The evolutionary biogeography of Australian birds. – In: Keast, A. (ed.), *Ecological biogeography of Australia*. Junk, The Hague, pp. 1587–1635.
- Kikkawa, J. and Pearse, K. 1969. Geographical distribution of land birds in Australia – a numerical analysis. – *Austr. J. Zool.* 17: 821–840.
- Lack, D. L. 1976. *Island biology, illustrated by the land birds of Jamaica*. – Univ. of California Press, Berkeley, CA.
- Lawlor, L. R. 1980. Structure and stability in natural and randomly constructed competitive communities. – *Am. Nat.* 116: 394–408.
- Lynch, J. D. 1989. The gauge of speciation: on the frequencies of modes of speciation. – In: Otte, D. and Endler, J. A. (eds), *Speciation and its consequences*. Sinauer, Sunderland, MA, pp. 527–553.
- MacArthur, R. H. 1972. *Geographical ecology*. – Harper & Row, New York.
- Pianka, E. R. 1974. Niche overlap and diffuse competition. – *Proc. Natl. Acad. Sci. USA* 71: 2141–2145.
- Roberts, A. and Stone, L. 1990. Island-sharing by archipelago species. – *Oecologia* 83: 560–567.
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. – *Ecol. Monogr.* 37: 95–124.
- Rosenzweig, M. L. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. – *Ecology* 54: 111–117.
- Sale, P. F. 1974. Overlap in resource use, and interspecific competition. – *Oecologia* 17: 245–256.
- Schall, J. J. and Pianka, E. R. 1978. Geographical trends in numbers of species. – *Science* 201: 679–686.
- Schluter, D. 1988. The evolution of finch communities on islands and continents: Kenya vs. Galápagos. – *Ecol. Monogr.* 58: 229–249.
- Schodde, R. 1975. Interim list of Australian songbirds: passerines. – Royal Australasian Ornithologists' Union, Melbourne.
- 1982. *The Fairy-Wrens*. – Lansdowne, Melbourne.
- Schoener, T. W. 1990. The geographical distribution of rarity: misinterpretation of atlas methods affects some empirical conclusions. – *Oecologia* 82: 567–568.
- and Adler, G. H. 1991. Greater resolution of distributional complementarities by controlling for habitat affinities: a study with Bahamian lizards and birds. – *Am. Nat.* 137: 669–692.
- Serventy, D. L. 1951. The evolution of the chestnut-shouldered wrens (*Malurus*). – *Emu* 51: 113–120.
- Simberloff, D. and Dayan, T. 1991. The guild concept and the structure of ecological communities. – *Annu. Rev. Ecol. Syst.* 22: 115–143.
- Stiling, P. D. and Strong, D. R. 1983. Weak competition among *Spartina* stem borers, by means of murder. – *Ecology* 64: 770–778.
- Stone, L. and Roberts, A. 1990. The checkerboard score and species distributions. – *Oecologia* 85: 74–79.
- and Roberts, A. 1992. Competitive exclusion, or species aggregation? An aid in deciding. – *Oecologia* 91: 419–424.
- Whittam, T. S. and Siegel-Causey, D. 1981. Species interactions and community structure in Alaskan seabird colonies. – *Ecology* 62: 1515–1524.
- Wiens, J. A. 1980. Concluding comments: are bird communities real? – *Acta XVII Congr. Int. Ornithol.* 1088–1089.
- 1989. *The ecology of bird communities. Vol. 1. Foundations and patterns*. – Cambridge Univ. Press, Cambridge.
- 1991a. Ecological similarity of shrub-desert avifaunas of Australia and North America. – *Ecology* 72: 479–495.
- 1991b. Ecomorphological comparisons of the shrub-desert avifaunas of Australia and North America. – *Oikos* 60: 55–63.
- Wilson, J. B. 1987. Methods for detecting non-randomness in species co-occurrences: a contribution. – *Oecologia* 73: 579–582.
- 1991. Does vegetation science exist? – *J. Veg. Sci.* 2: 289–290.
- Winemiller, K. O. and Pianka, E. R. 1990. Organization in natural assemblages of desert lizards and tropical fishes. – *Ecol. Monogr.* 60: 27–55.
- Wright, S. J. and Biehl, C. C. 1982. Island biogeographic distributions: testing for random, regular, and aggregated patterns of species occurrence. – *Am. Nat.* 119: 345–357.

## Appendix 1

Congeneric guilds of Australian birds. The number of species in the guild and the common name are given in parentheses. Guilds were designated a priori by JAW as species within a genus with similar feeding ecologies.

*Pachycephala* (5; flycatchers): *P. olivacea*, *P. lanioides*, *P. rufogularis*, *P. inornata*, *P. rufiventris*  
*Philemon* (4; friarbirds): *P. buceroides*, *P. corniculatus*, *P. argenticeps*, *P. citreogularis*  
*Meliphaga* (4; honeyeaters): *M. lewinii*, *M. notata*, *M. gracilis*, *M. albilineata*  
*Colluricincla* (4; shrike-thrushes): *C. megarhyncha*, *C. boweri*, *C. woodwardi*, *C. harmonica*  
*Cinclosoma* (4; quail-thrush): *C. cinnamomeum*, *C. alisteri*, *C. punctatum*, *C. castanotum*

Tyto (5; barn/grass owls): *T. alba*, *T. novaehollandiae*, *T. longimembris*, *T. tenebricosa*, *T. multipunctata*  
Ninox (4; owls): *N. rufa*, *N. strenua*, *N. novaeseelandiae*, *N. connivens*  
Ephthianura (4; chats): *E. tricolor*, *E. crocea*, *E. aurifrons*, *E. albifrons*  
Rhipidura (5; fantails): *R. rufifrons*, *R. fuliginosa*, *R. rufiventris*, *R. leucophrys*, *R. phasiana*  
Halcyon (4; kingfishers): *H. macleayii*, *H. pyrrhopygia*, *H. sancta*, *H. chloris*  
Corvus (5; crows): *C. coronoides*, *C. tasmanicus*, *C. mellori*, *C. bennetti*, *C. orru*  
Artamus (6; woodswallows): *A. leucorhynchus*, *A. personatus*, *A. superciliosus*, *A. cinereus*, *A. cyanopterus*, *A. minor*  
Cracticus (4; butcherbirds): *C. quoyi*, *C. torquatus*, *C. mentalis*, *C. nigrogularis*  
Manorina (4; miners): *M. melanophrys*, *M. melanocephala*, *M. flavigula*, *M. melanotis*  
Climacteris (5; treecreepers): *C. erythroptus*, *C. affinis*, *C. picumnus*, *C. rufa*, *C. melanura*  
Eopsaltria (4; robins): *E. pulverulenta*, *E. georgiana*, *E. australis*, *E. griseogularis*  
Coracina (4; cuckoo-shrikes): *C. novaehollandiae*, *C. papuensis*, *C. lineata*, *C. tenuirostris*  
Amytornis (8; grasswrens): *A. housei*, *A. woodwardi*, *A. dorotheae*, *A. striatus*, *A. goyderi*, *A. barbatus*, *A. textilis*, *A. purnelli*  
Neophema (4; parrots): *N. chrysostoma*, *N. elegans*, *N. chrysogaster*, *N. splendida*  
Cacatua (5; corellas): *C. roseicapilla*, *C. tenuirostris*, *C. sanguinea*, *C. leadbeateri*, *C. galerita*  
Malurus (9; fairy-wrens): *M. coronatus*, *M. cyaneus*, *M. splendens*, *M. lamberti*, *M. pulcherrimus*, *M. elegans*, *M. leucopterus*, *M. melanocephalus*, *M. amabilis*  
Acanthiza (11; thornbills): *A. katherina*, *A. pusilla*, *A. apicalis*, *A. uropygialis*, *A. robustirostris*, *A. inornata*, *A. reguloides*, *A. iredalei*, *A. chrysorrhoea*, *A. nana*, *A. lineata*  
Gerygone (8; gerygones): *G. mouki*, *G. magnirostris*, *G. tenebrosa*, *G. laevigaster*, *G. fusca*, *G. chloronota*, *G. palpebrosa*, *G. olivacea*  
Sericornis (5; scrubwrens): *S. keri*, *S. magnirostris*, *S. citreogularis*, *S. beccarii*, *S. frontalis*  
Pomatostomus (4; babblers): *P. temporalis*, *P. superciliosus*, *P. halli*, *P. ruficeps*  
Psephotus (4; rosellas): *P. haematonotus*, *P. varius*, *P. chrysopterygius*, *P. dissimilis*  
Psophodes (4; wedgebills/whipbirds): *P. olivaceus*, *P. nigrogularis*, *P. cristatus*, *P. occidentalis*

Ptilinopus (4; fruit-doves): *P. cinctus*, *P. superbus*, *P. regina*, *P. magnificus*

## Appendix 2

Australian analogs to avian guilds in the Bismarck Archipelago. The left-hand column gives the genus and species in the Bismarck guilds and the figure reference from Diamond (1975). The right-hand column gives the analogous guild on the Australian mainland for which there are two or more species.

Bismarck island guilds      Australian equivalents

### Pachycephala (Fig. 21)

*P. pectoralis*      *P. pectoralis*  
*P. melanura dahl*      *P. melanura*

### Ptilinopus (Fig. 22)

*P. rivoli*      *P. cinctus*  
*P. solomonensis*      *P. superbus*  
                                  *P. regina*  
                                  *P. magnificus*

### Myzomela (Fig. 23)

*M. sclateri*      *M. obscura*  
*M. erythromelas*      *M. erythrocephala*  
*M. pulchela*      *M. sanguinolenta*  
*M. cruentrata*  
*M. pammelaena*

### Zosterops (Fig. 24)

*Z. atriceps*      *Z. lutea*  
*Z. buruensis*      *Z. lateralis*  
*Z. chloris*  
*Z. griseotincta*  
*Z. hypoxantha*  
*Z. kuehni*  
*Z. mysorensis*  
*Z. novaeguineae*  
*Z. uropygialis*  
*Z. atrifrons*  
*Z. grayi*  
*Z. meeki*

### Lonchura (Fig. 33)

*L. castaneothorax*      *L. castaneothorax*  
*L. grandis*      *L. flaviprymna*  
*L. montana*  
*L. spectabilis*  
*L. tristissima*  
*L. vana*  
*L. teerinki*  
*L. caniceps*