

Assembly of avian mixed-species flocks in Amazonia

(assembly rules/interspecific competition/null models)

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ABSTRACT Diamond's "assembly rules" model posits that competitive interactions among species govern the composition of avifaunas. Although originally applied to islands in archipelagoes, this controversial set of hypotheses is difficult to test because islands differ in habitat and resource availability, colonization history, and stochastic effects. Permanent mixed-species flocks of Amazonian birds are a model system for testing the assembly rules hypothesis because flocks occur in relatively homogeneous tracts of rain forest and because resident species are potentially interactive from minute to minute. To analyze cooccurrence patterns of species in flocks, we used null models that incorporate realistic autecological colonization parameters. Potentially competing pairs of congeneric species with similar ecologies cooccur in flocks less often than expected by chance, resulting in perfect checkerboard distributions. Interactions among more distantly related species, however, appear to have little effect on the assembly of mixed-species flocks. Checkerboard distributions enhance local species diversity within habitats by generating different combinations of species in different flocks. This process may have contributed to the immense species richness of the Amazonian avifauna.

Diamond (1) suggested that the composition of avifaunas is governed by "assembly rules" mediated by interspecific competition, a concept that subsequently has been applied to many other taxa, including mammals (2, 3), lizards (4), fish (5–7), and ants (8, 9). The idea that local assemblages of species are determined more by the outcome of deterministic competitive processes than by autecological characteristics of species has generated considerable controversy (10–14). Much of the debate has centered around the choice of appropriate statistical tests, particularly the use of null models, and of biological realism in analyses (15–17). Among the many predictions of the assembly rules model (1, 13, 14), perhaps the simplest and most easily tested hypothesis is that competing pairs of species form "forbidden combinations" (1) that will be distributed in a mutually exclusive, checkerboard pattern. Within an island archipelago, a perfect checkerboard pattern for a pair of competitors results when each island is occupied by no more than one of the two species. However, analyses of checkerboard patterns on islands are complicated by interisland variation in habitats, resources, source pools, and colonization histories (18, 19). Because most archipelago-wide data represent at best a temporal snapshot of species distributions, investigators lack direct evidence that colonists of both species of a pair have ever reached an island currently inhabited by a single species. As a result, it has been difficult to detect the signature of interspecific competition in island communities.

Here we analyze cooccurrence patterns of species in permanent mixed-species flocks within a local Amazonian avifauna. In this system, the spatial scale is small enough that

any individual bird could potentially colonize any flock. Consequently, uncertainties about the interaction potential of competing species are absent. Flocks of Amazonian birds have figured prominently in natural history literature for over a century (20). Flocking may enhance foraging efficiency and reduce the risk of predation (21, 22). In eastern Peru, understory flocks are primarily insectivorous and have a permanent core of 4–10 species that participate year-round and form stable, life-long associations (23, 24). Each species is typically represented by a single individual, a mated pair, or a small family group. Core flocking species mutually defend territories, which define the home range of the flock. Approximately 60 additional resident species join understory flocks on a regular basis, although the total number of species in any single flock rarely exceeds 30. Thus, different combinations of species may occur in different flocks. Flock territories may therefore be considered analogs of islands that are colonized by different subsets of species from the local avifauna, with one important scalar difference—all competing species in an "archipelago" of mixed-species flocks are potentially interactive from minute to minute. Are mixed-species flocks governed by assembly rules? The purpose of this report is to determine if species cooccurrence patterns, as measured by the frequency of checkerboard distributions, are nonrandom among flocks.

METHODS

As a product of long-term studies, Munn (24, 25) and Terborgh *et al.* (26) documented the avifauna of an undisturbed, relatively homogeneous 97-ha (1 ha = 10,000 m²) study plot at Cocha Cashu (71°19'W, 11°51'S; elevation, *ca.* 400 m) in the drainage of the Río Manu, southeastern Peru. The predominant habitat on the study plot is tall (40 m) evergreen tropical forest with frequent emergent trees that exceed 50 m (see ref. 27 for additional descriptions of the Cocha Cashu forest). Ornithologically, the Cocha Cashu region is one of the richest sites in the world. More than 500 species have been recorded in the vicinity of the Cocha Cashu field station (28), and at least 245 species have home ranges on the 97-ha study plot. Seventy-one species regularly join understory mixed-species flocks.

We extracted raw data from these sources (24–26) to derive species richness, abundance, and guild membership of flocking species from 22 color-marked, mixed-species flocks with abutting territorial boundaries. Flocks contained from 4 to 32 species ($\bar{x} = 18.5 \pm 8.4$) and from 8 to 53 individuals ($\bar{x} = 30.3 \pm 12.6$), whereas the home range of flocks varied from 1.7 to 6.5 ha ($\bar{x} = 3.9 \pm 1.4$). The home range area of a flock was highly correlated with the number of individuals ($r^2 = 0.53$, $P < 0.0001$) and species ($r^2 = 0.46$, $P < 0.001$) participating in a flock. As expected, the number of species and individuals in a flock was also highly correlated ($r^2 = 0.89$, $P < 0.0001$).

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Abbreviations: SPEC model, species occurrence model; ABUN model, species abundance model; DEMO model, demographic model.

Each species was assigned to one of seven unique foraging guilds (Table 1). Guild designations of four species, *Veniliornis passerinus*, *Philydor rufus*, *Automolus rufipileatus*, and *Myrotherula ornata*, reported by Munn (25) but not included by Terborgh *et al.* (26) were provided by T. A. Parker, III.

Flock data were used to determine if species cooccurrence patterns were nonrandom. We conducted analyses at three nested organizational levels: (i) flocks, (ii) foraging guilds within flocks, and (iii) sets of congeneric species within guilds. This hierarchical classification groups species with increasing similarity in morphology and feeding ecology from flocks to guilds to congeners. If interspecific competition influences the composition of mixed-species flocks, then significantly more pairs of species should exhibit checkerboard distributions than expected by chance at each organizational level (flocks, guilds, congeners). Perfect checkerboards represent an extreme pattern of negative associations among species. Pairs of species that cooccur in one or more flocks may also exhibit significantly negative associations (29, 30), but we restricted our analyses to checkerboards for the sake of clarity.

The expected number of checkerboards at each organizational level was computed under three progressively more realistic simulation models (Table 1) based on (i) the frequency of occurrence of each species in flocks (SPEC), (ii) the abundance of each species in flocks (ABUN), and (iii) the demographic structure (paired adults, single adults, juveniles) of each species in flocks (DEMO).

Species occurrence model (SPEC). For each species the observed number of occurrences was randomized across 22 null flocks. The probability of a species being placed in a null flock was proportional to the total number of species in the corresponding real flock. This is a refinement over earlier null-model protocols, which randomized species occurrences equiprobably but constrained the total number of species that

could occur on an island (10, 11). In our simulations, each species can potentially be placed in any null flock. In this model, the expected total number of species in each null flock approximately equals the observed number in the corresponding real flock.

Species abundance model (ABUN). From the summed abundance of each species, individuals were distributed randomly among null flocks in proportion to the total number of individuals in real flocks. Because competitive exclusion ultimately occurs between individuals of interacting populations, abundance data should be used to construct null communities that are not influenced by competition (31). However, most null models have relied on presence-absence data (but see ref. 32), which may not be powerful enough to reveal competitive effects.

Demographic model (DEMO). The most biologically realistic of the three, this model takes into account the prevalent pattern of intraspecific territoriality among understory species. For each species territorial pairs were first distributed randomly in null flocks subject to the constraint that pairs cannot coexist with one another. This constraint reflects intraspecific territoriality, which prevents more than a single adult pair of a species from occurring in a flock. Single birds were then distributed but were not allowed to coexist with pairs. Singles assigned to null flocks already containing a single were allowed to pair 50% of the time, assuming a 50:50 sex ratio within species. Lastly, individuals of a species in excess of a pair in any flock were defined as independent juveniles. These were distributed randomly with the restriction that no null flock could contain more than the maximum number of juveniles observed in real flocks for that species. For all null models, the number of checkerboards was calculated for each simulated assemblage of null flocks. The procedure was repeated 100 times at the flock level and 1000 times at the guild and generic levels. The probability of an

Table 1. Observed and expected numbers of perfect checkerboard distributions among pairs of bird species in mixed flocks under three null models: SPEC (species occurrence), ABUN (species abundance), DEMO (demographic)

| Level | Species, <i>n</i> | Obs. | Null model | | | | | |
|---|----------------------|------|-------------------------------------|------------|-------------------------------------|------------|-------------------------------------|------------|
| | | | SPEC | | ABUN | | DEMO | |
| | | | Exp. | <i>P</i> * | Exp | <i>P</i> * | Exp. | <i>P</i> * |
| Flock | 71 | 1012 | 1018.91 | 0.63 | 927.58 | <0.01 | 992.47 | 0.25 |
| Guild† | | | | | | | | |
| 1 | 27 | 111 | 122.11 | 0.912 | 94.04 | 0.027 | 114.73 | 0.706 |
| 2 | 14 | 36 | 38.12 | 0.758 | 40.47 | 0.876 | 38.34 | 0.783 |
| 3 | 8 | 10 | 7.29 | 0.137 | 6.37 | 0.046 | 7.28 | 0.123 |
| 4 | 3 | 3 | 2.63 | 0.667 | 2.46 | 0.526 | 2.65 | 0.687 |
| 5 | 10 | 14 | 11.04 | 0.142 | 10.14 | 0.095 | 9.84 | 0.046 |
| 6 | 7 | 15 | 14.70 | 0.576 | 14.81 | 0.602 | 14.62 | 0.556 |
| 7 | 2 | 1 | 0.89 | 0.887 | 0.88 | 0.879 | 0.89 | 0.893 |
| Fisher's combined probabilities test‡ (df = 14) | | | $\chi^2 = 10.77$ <i>P</i> > 0.50 | | $\chi^2 = 20.91$ <i>P</i> > 0.10 | | $\chi^2 = 13.68$ <i>P</i> > 0.50 | |
| Genera | | | | | | | | |
| <i>Monasa</i> | 2 | 0 | 0.03 | 1.000 | 0.13 | 1.000 | 0.09 | 1.000 |
| <i>Xiphorhynchus</i> | 4 | 2 | 0.35 | 0.041 | 0.24 | 0.024 | 0.32 | 0.036 |
| <i>Philydor</i> | 2 | 0 | 0.00 | 1.000 | 0.00 | 1.000 | 0.00 | 1.000 |
| <i>Automolus</i> | 3 | 3 | 1.28 | 0.045 | 0.09 | 0.014 | 1.30 | 0.052 |
| <i>Xenops</i> | 2 | 1 | 0.05 | 0.054 | 0.07 | 0.067 | 0.06 | 0.062 |
| <i>Thamnomanes</i> | 2 | 0 | 0.00 | 1.000 | 0.00 | 1.000 | 0.00 | 1.000 |
| <i>Myrotherula</i> | 7 | 3 | 1.30 | 0.119 | 0.89 | 0.048 | 0.95 | 0.051 |
| <i>Hylophilus</i> | 2 | 1 | 0.19 | 0.189 | 0.02 | 0.020 | 0.14 | 0.142 |
| Fisher's combined probabilities test‡ (df = 16) | | | $\chi^2 = 24.76$ <i>P</i> < 0.10 | | $\chi^2 = 33.43$ <i>P</i> < 0.01 | | $\chi^2 = 27.86$ <i>P</i> < 0.05 | |

*Probability that the observed number of checkerboards \geq simulated number of checkerboards under the null hypothesis of no species interactions.

†Guilds: 1, arboreal gleaning insectivores; 2, arboreal sallying insectivores; 3, arboreal dead-leaf searching insectivores; 4, bark interior insectivores; 5, superficial bark insectivores; 6, arboreal omnivores; 7, arboreal frugivores.

‡Fisher's test gives an overall probability value for excess checkerboards among guilds and congeners.

excess of checkerboards was defined as the fraction of null communities for which the simulated number of checkerboards \geq observed number. The analysis provides a one-tailed test, which is appropriate because the assembly-rules model predicts only an excess, not a deficit, of checkerboards. Simulations were written in Turbo Pascal 6.0; a different random number seed was used for each simulation.

RESULTS

Simulation outcomes at the flock and guild organizational level were sensitive to model structure. Of the 2485 pairs of species in the Cocha Cashu assemblage of understory flocking birds, 1012 (41%) pairs never cooccur in flocks and form perfect distributional checkerboards. The ABUN model indicated that this fraction was significantly larger than expected by chance. In contrast, the observed number of distributional checkerboards did not differ significantly from the predictions of the SPEC and DEMO null models. These results may be sensitive to the inclusion of many noninteracting species pairs (e.g., woodpeckers and antwrens) in the analysis. To control for this dilution effect (12, 13), we repeated analyses for foraging guilds, groups of species that exploit the same spectrum of resources with similar foraging behaviors. The SPEC model, based solely on the presence or absence of species in flocks, revealed no significant patterns among guilds. However, the other models indicated excessive numbers of checkerboards in three guilds, arboreal gleaning insectivores (ABUN), arboreal dead-leaf searching insectivores (ABUN), and superficial bark insectivores (DEMO). These guilds are dominated by species of antbirds (Formicariidae), ovenbirds (Furnariidae), and woodcreepers (Dendrocolaptidae) (see refs. 33 and 34). However, four of seven guilds exhibited random distributional patterns with all simulation models. Overall probabilities across guilds were nonsignificant for all models.

Interspecific competition is expected to be the most intense between morphologically similar species in the same genus (35). Omitting rare species that occurred only in a single flock, Cocha Cashu understory flocks contained eight genera represented by two or more species that belong to the same guild. Five of the eight genera exhibited checkerboard distributions, all of which were significantly (or marginally) nonrandom by one or more simulation models. The most noteworthy example occurred among the *Xiphorhynchus* woodcreepers [*Xiphorhynchus guttatus*, body mass = 65 g (body masses from ref. 26), occurred in 13 flocks; *Xiphorhynchus obsoletus*, body mass = 39 g, 2 flocks; *Xiphorhynchus ocellatus*, body mass = 32 g, 9 flocks; *Xiphorhynchus spixii*, body mass = 40 g, 9 flocks; three flocks were unoccupied by any species in this genus]. The largest species, *Xiphorhynchus guttatus*, cooccurs with each of the smaller ones. Among the smaller-bodied species, two pairs, *Xiphorhynchus spixii/Xiphorhynchus ocellatus* and *Xiphorhynchus spixii/Xiphorhynchus obsoletus*, exhibited marked interspecific territoriality (36), resulting in checkerboard distributions among understory flocks. All three species had similar habitat preferences and foraging behaviors on the study site. Moreover, reciprocal turnover between *Xiphorhynchus spixii* and *Xiphorhynchus ocellatus* occurred following the death or disappearance of an original territory holder (36).

Other significant checkerboards may be due to competition, undetected patchiness in habitat, or a combination of both. For example, the three species of *Automolus* foliage-gleaners are distributed in a checkerboard pattern (*Automolus infuscatus*, occurred in 6 flocks; *Automolus ochrolaemus*, 4 flocks; *Automolus rufipileatus*, 2 flocks). Although 10 of the 22 understory flocks were unoccupied by any *Automolus* species, the observed pattern was unlikely to occur by chance under all three null models. Two other checkerboards

involved pairs of species that usually segregate vertically in tropical forests. *Xenops rutilans* (2 flocks), which normally forages with canopy flocks, occupied 2 of 8 understory flocks where *Xenops minutus* (14 flocks) did not occur. *Hylophilus hypoxanthus* (2 flocks), also of canopy flocks, was found with 2 of 11 understory flocks not occupied by *Hylophilus ochraceiceps* (11 flocks).

The list of genera in Table 1 includes all six species designated as "Type 1 core species" by Munn and Terborgh (23) [*Thamnomanes ardesiacus* (18 flocks), *Thamnomanes schistogynus* (18 flocks), *Myrmotherula axillaris* (22 flocks), *Myrmotherula longipennis* (13 flocks), *Myrmotherula menetriesii* (22 flocks), *Philydor ruficaudatus* (10 flocks)]. These species occurred in many or all understory flocks at Cocha Cashu and equally shared the jointly held flock territory (23). By virtue of their wide distribution among flocks, these species are not likely to form checkerboard patterns with congeners, even uncommon ones. Overall, at the generic level checkerboard patterns were significant under the constraints of the two more biologically realistic models, ABUN and DEMO.

DISCUSSION

Many congeneric species in Amazonia segregate ecologically by occupying different habitats (37), and species-specific habitat selection may be a consequence of past or present interspecific competition. However, because the habitat at Cocha Cashu was relatively uniform (26, 27), many potentially interacting species pairs present in the mosaic of regional habitats were absent from the study plot. Thus, the flock data provide a conservative test of competitive effects.

Our results cast doubt on the usual method of relying on a single simulation model or analytical technique to test a null hypothesis (1, 10–14). The least sophisticated of the three Monte Carlo models (SPEC) presented here is based on presence/absence data used in most previous null model tests. The other two models incorporate not only the abundance of individual species (ABUN) but also the demographic constraints evidenced in the age and sex structure of species in flocks (DEMO). All three models objectively address flock composition, yet variation in model structure and assumptions result in markedly different interpretations of the patterns observed in nature. For example, the SPEC model indicates that species cooccurrence is not significantly different from that expected by chance at the flock and guild level and only marginally different at the generic level. On the other hand, the ABUN model indicates more checkerboards than expected at the flock and generic levels. In this case, we believe that the ABUN model more accurately addresses the biology of mixed-species flocks than SPEC. However, a further refinement of the simulation model (DEMO) confirms significant deviations from the expected pattern only at the generic level. We interpret the inconsistent results at the flock level (ABUN vs. SPEC and DEMO) and especially the uniformly nonsignificant results at the guild level to indicate that competition between distantly related species has little effect on species cooccurrence and flock membership. On the other hand, at least some of the checkerboards at the generic level are probably due to interspecific territoriality caused by competitive processes rather than autecological segregation caused by microhabitat selection. The latter hypothesis might be addressed by examining the correlation between distributional patchiness of species and microhabitats. A second stronger test would be to experimentally alter habitat (17) or remove individuals of potentially competing species. However, manipulative field experiments in the protected Cocha Cashu reserve are neither practical nor ethical.

In sum, only at the generic level are cooccurrence patterns consistent with the least complex of Diamond's (1) assembly

rules, the checkerboard distribution of competing pairs of species. Our results suggest that interspecific territoriality may prevent ecologically similar congeners from joining the same flock. However, local competitive exclusion may enhance diversity at the regional scale by generating different species combinations in different flocks (38, 39). This process, in addition to the spatial segregation of congeners among habitats within regions (37) and geographic replacement of allospecies between regions (40, 41), may contribute to the remarkable richness of the Amazonian avifauna.

Finally, we point out that the prevalence of perfect checkerboards in this system is dependent on the spatial distribution of flocks and on sample size. Increased spatial sampling may incorporate flock territories that contain a different spectrum of microhabitats, permitting otherwise segregated species to coexist. If the number of monitored flocks was increased, some or perhaps all of the checkerboards would eventually disappear to be replaced by overlapping, yet significantly negative, associations. Thus, perfect checkerboards may have a limited utility in tests of the importance of interspecific competition in the assembly of ecological communities. Instead, emphasis should be shifted toward tests of all pairwise associations, employing a range of biologically realistic null models.

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