

# Species interactions and the structure of complex communication networks

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**A universal challenge faced by animal species is the need to communicate effectively against a backdrop of heterospecific signals. It is often assumed that this need results in signal divergence to minimize interference among community members, yet previous support for this idea is mixed, and few studies have tested the opposing hypothesis that interactions among competing species promote widespread convergence in signaling regimes. Using a null model approach to analyze acoustic signaling in 307 species of Amazonian birds, we show that closely related lineages signal together in time and space and that acoustic signals given in temporal or spatial proximity are more similar in design than expected by chance. These results challenge the view that multispecies choruses are structured by temporal, spatial, or acoustic partitioning and instead suggest that social communication between competing species can fundamentally organize signaling assemblages, leading to the opposite pattern of clustering in signals and signaling behavior.**

acoustic niche | Amazonia | dawn chorus | interspecific communication | signal partitioning

One of the core principles of animal communication is that signals should be detectable and convey an accurate message against a noisy background (1–3). This background can involve direct overlap of sounds, as in the case of masking by simultaneous signals (4, 5), or simply the co-occurrence of different species using confusingly similar signals at the same location (6–8). As most animals communicate within assemblages of related species, the problem of signal interference is widespread and may have far-reaching implications for the evolution of signals and signaling behavior. This concept—variously termed the “noisy neighbors” hypothesis (9) or “cocktail party problem” (10)—has attracted much attention over recent years. However, the extent to which it provides a general explanation for patterns of signaling in animal communities remains contentious (6, 8).

The traditional view is that the signaling strategies of animals are shaped by limiting similarity among competitors, much as competition for ecological resources is thought to promote partitioning of niche space (11–13). Partitioning of signal space may occur if species compete for position near overcrowded transmission optima, and, concurrently, if overlap in signal design impairs the detection or discrimination of signals mediating mate choice and resource competition (14). Under these conditions, mechanisms of selection against misdirected aggression (e.g., character displacement) or the production of unfit hybrids (e.g., reinforcement) are predicted to drive phenotypic divergence (9), whereas similar mechanisms may lead to related species signaling at different times or in different locations (13). These pathways theoretically lead to structural, temporal, and spatial partitioning of signals and signalers in animal assemblages, but tests of these patterns have produced mixed results (6, 11, 15).

A contrasting possibility is that selection for signal divergence is weak and that co-occurring species instead show the opposite

pattern of signal clustering (16). One potential driver of this pattern is that shared habitats can exert convergent selection on signals (17). Another is that signals often have dual function in mate attraction and resource defense (18), potentially mediating competition among closely related species for ecological resources (19). Thus, multispecies choruses may operate to some degree as extended communication networks, not only within species (20) but between species. The effect of such a network would be to increase the likelihood of interspecific communication involving closely related species with similar signals. A pattern of signal clustering caused by communication among similar congeners may be further exaggerated when competitive interactions among species promote signal similarity (16). This process may occur when individuals with convergent agonistic signals have higher fitness because they are better at defending resources against both conspecific and heterospecific competitors, driving convergent evolution (21, 22). Taken together, these alternative views suggest that the most pervasive effect of species interactions on animal communication systems may not be partitioning, as generally proposed, but synchrony and stereotypy among competing species.

Progress in resolving these opposing viewpoints has been limited because most studies of signaling assemblages have compiled lists of species co-occurring at particular localities and then compared multiple assemblages across regional scales (6, 15). This approach may be misleading because of spatial biases in phylogenetic relationships and habitat. On the one hand, sympatric species tend to be significantly older than allopatric species, at least within radiations (23, 24), and thus the signals of co-occurring lineages may be more divergent than expected by

## Significance

**Social signals used in multispecies choruses are generally assumed to be partitioned across temporal, spatial, or design axes to minimize the costs of misidentification. In contrast, we show that Amazonian bird species signaling in temporal and spatial proximity use acoustic signals that are more similar in design than expected by chance. We also show evidence that this pattern emerges because phylogenetically conserved (or potentially convergent) signals mediate interspecific competition among species with similar ecological niches. Together, these results suggest that acoustic choruses can be fundamentally organized by social communication extending beyond species boundaries and that such communication networks are inherently clustered by increased stereotypy and synchrony among species.**

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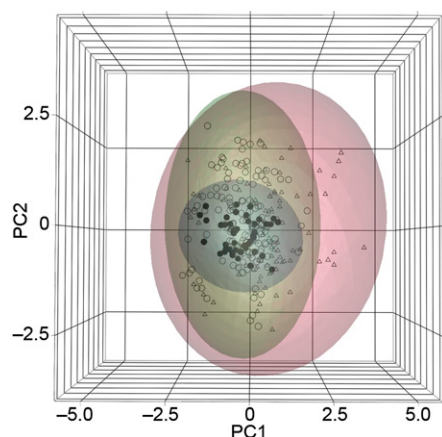
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**Fig. 2.** Acoustic structure of the Amazonian dawn chorus. Each signal (one per bird species,  $n = 283$ ) is plotted in multivariate trait space described by three principal components (PCs) derived from seven acoustic parameters; PC1 (x axis) correlates with pitch, PC2 (y axis) correlates with duration, and PC3 (not labeled but represented by depth) correlates with pace. High values for PC1 reflect high-pitched signals with broad bandwidths; for PC2 reflect long signals with high note number; and for PC3 reflect signals with high pace. Normal contour ellipsoids (coverage = 90%) show that signal variation is more extreme among nonpasserines (pink, triangles) than passerines (circles). Most families showed relatively high clustering in trait space; for example, antbirds (*Thamnophilidae*; blue, closed circles) are nested within the passerine radiation (green, open circles).

space, our models rejected the partitioning hypothesis. Instead, they provide clear evidence that species signaling together have more similar signals than expected by chance. In all models, habitat, time of day, and chorus diversity (species richness) had a significant effect on signal similarity (Tables S1 and S2), yet strong signal clustering was detected when taking these potentially confounding effects into account. Specifically, we found that the mean acoustic distance (AD) separating species cosignaling in 10-min choruses was significantly lower in observed choruses than in randomly generated (null) choruses for all acoustic traits (Fig. 3 and Figs. S2 and S3) and for both methods used to calculate AD (all  $P < 0.0001$ ; Tables S1 and S2). Evidence for clustering was strongest for the three most similar species pairs ( $AD_2$ ), suggesting that overall effects may be driven by cosignaling species with particularly similar songs, often congeners.

Analyses at the 10-min scale focus on groups of species likely to signal together, perhaps simultaneously and certainly within earshot, whereas analyses at the 120-min scale focus on groups of species occurring at the same site but not necessarily signaling together. One hundred twenty-minute choruses thus shed light on spatial vs. temporal partitioning, as well as removing the problem of temporal autocorrelation (SI Text). When we focused more broadly on 120-min choruses, we found no evidence of spatial partitioning among species with similar signals. Instead, AD of observed 120-min communities was either more similar or not significantly different from AD among species signaling within randomly generated communities, depending on the acoustic trait and method of calculating AD (Table S3). Specifically, we found that observed 120-min choruses comprised species with signals that were significantly more similar in terms of temporal structure (PC2 and PC3) but did not differ in terms of pitch (PC1). Again, habitat and species richness had an effect on signal similarity, but the pattern of clustering remained strongly significant when controlling for these effects (Table S3).

Tests of acoustic partitioning were conducted after removing nocturnal species and species identified by their distinctive flight calls, such as parrots. Nocturnal species mainly belong to a few families (owls, nightjars, and potoos) that signal together with

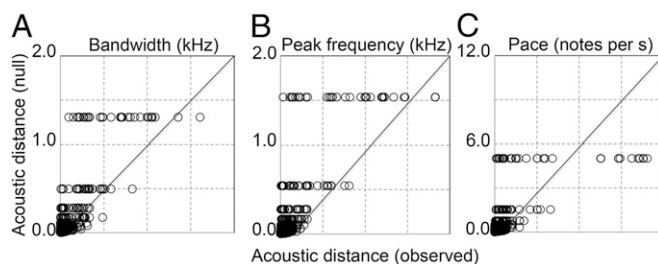
similar signals because of their predawn activity. Likewise, parrots tend to signal in mixed-species groups at similar times of day (mid to late morning) with acoustically similar signals. Thus, we note that including these nonpasserine groups in our analyses would very likely strengthen the main finding of clustered acoustic properties among cosignalers.

**Taxonomic Relationships.** In all models, chorus diversity had a strong negative effect on taxonomic distance (TD): the greater the number of species recorded, the lower the TD of the community (Table S4 and Fig. S4). Habitat was also a significant predictor of TD in all models at the 10-min temporal scale and of TD<sub>1</sub> at the 120-min scale. When controlling for these effects by including chorus diversity and habitat in models, we detected no evidence of temporal or spatial partitioning of closer relatives within the dawn chorus. In contrast, we found that the TD between species in observed choruses was significantly lower than that in null choruses at both 10- and 120-min temporal scales, irrespective of the method used to calculate TD (Table S4). Thus, viewed across all species (i.e., including noncongeners), cosignalers were more closely related than expected by chance.

When we reassessed this pattern at a finer taxonomic scale, focusing on pairs of congeners, we again found that the observed frequency of cosignaling in 10-min choruses was significantly higher than null expectations ( $F_{1,300.6} = 11.84$ ,  $P < 0.0001$ ; Table S5 and Fig. 4A). However, congeners were significantly less likely to signal in the same 120-min chorus, as the observed frequency of cosignaling was significantly lower than null expectations ( $F_{1,271.6} = 24.35$ ,  $P < 0.0001$ ; Table S5 and Fig. 4B).

## Discussion

We conducted a detailed test of the processes structuring a megadiverse signaling assemblage, explicitly controlling for variation in evolutionary history, habitat, and species richness. Focusing on 120-min choruses, we found that congeneric rainforest birds occurred less frequently at the same recording sites than expected by chance, perhaps because the most similar lineages are spatially segregated by competitive exclusion (18, 29). However, the opposite pattern was detected in 10-min choruses as those congeneric lineages occurring in close conjunction signaled together more often than expected by chance. All other analyses were conducted across the entire community, revealing a similar lack of partitioning in both the design of signals and the timing of signal production, which instead were significantly clustered at both 10- and 120-min scales. These findings conflict with the classical view of acoustic (3) and temporal partitioning



**Fig. 3.** Tests of partitioning of acoustic signals produced during the dawn chorus by Amazonian birds ( $n = 283$  species). Shown are scatterplots of mean nearest-neighbor acoustic distance ( $AD_1$ ) in observed (x axis) 10-min choruses ( $n = 1,092$ ) vs. null (y axis), for three key acoustic traits: (A) bandwidth, (B) peak frequency, and (C) pace. For each trait, more points fall above the diagonal than below, indicating that species signaling together are more acoustically similar (i.e., smaller nearest-neighbor acoustic distance) than expected by chance for both spectral (A and B) and temporal (C) structure (GLM:  $P < 0.0001$ ).





and offers a new perspective on the architecture of social communication networks. Specifically, they indicate that the dominant mechanisms structuring such networks can lead to stereotypy and synchrony among species, generating a pattern of clustering in traits and behaviors, thereby helping to explain why so many studies of multispecies choruses have found the signature of partitioning to be weak (6, 7, 15, 30) or absent (8, 17).

## Materials and Methods

**Study System and Sampling.** We sampled the dawn chorus at Río Los Amigos (Centro de Investigación y Capacitación Río Los Amigos; 12°34'07"S, 70°05'57"W), southeast Peru, on 47 mornings in October–December 2007. Sound recordings were made with a digital (wav) recorder and an omnidirectional microphone at 91 sites spaced >100 m apart in three different habitat types (floodplain forest, terra firme forest, and bamboo; Fig. S1). All recordings started at nautical twilight (SI Text). Total recording time per sound file was 120 min (hereafter, 120-min choruses), and each file was automatically segmented into 12 × 10-min periods (hereafter, 10-min choruses;  $n = 1,092$ ) using Adobe Audition. We listed all species audible on these files, focusing exclusively on long-distance acoustic signals thought to play a role in mate attraction or territory defense. We included songs and other far-carrying mechanical sounds; we excluded short-range signals, such as alarm, begging, and foraging calls. Identifications were verified by inspecting sonograms, with reference to sound archives, online repositories, and commercially available collections. Ambiguous or uncertain identifications were excluded (<5% of detections).

The total list of identified signals were produced by 320 bird species (Dataset S1), representing 67% of the local avifauna. Our sample included 13 species from nocturnal families, with signals largely restricted to the first 40 min after nautical twilight, when it remains dark beneath the forest canopy. These species were removed from analyses to avoid biasing tests of partitioning. The final dataset contained 307 diurnal species, of which 205 contributed to at least six 120-min choruses (mean  $\pm$  SD number of choruses per species =  $15.3 \pm 0.2$  per species; range = 1–85). Mean  $\pm$  SD diversity was  $47.7 \pm 9.2$  species (range = 28–67) for 120-min choruses and  $11.9 \pm 6.3$  species (0–28) for 10-min choruses. All choruses containing fewer than two species were excluded from analyses. We found that the mean  $\pm$  SD number of 10-min choruses contributed to per species was only  $2.8 \pm 0.3$ , with  $70.6 \pm 0.06\%$  of species contributing to fewer than three choruses.

**Signal Properties.** To examine the acoustic structure of signals identified in choruses, we collated high-quality recordings of single species made in the study area or surrounding region (southeast Peru). Our final dataset (Dataset S2) contained 1,518 signals for 283 diurnal species (92%; mean  $\pm$  SE =  $5.4 \pm 1.2$  signals per species, taken from up to six adults per species). We used Raven Pro v1.4 to digitize sound files and then quantify temporal and spectral traits from broadband spectrograms. We generated mean values per individual and per species and conducted a rotated principal components analysis (PCA) on the correlation matrix of species means (log-transformed) to quantify overall signal structure. We extracted three components: PC1 (correlating with signal pitch), PC2 (correlating with signal duration and note number), and PC3 (correlating with signal pace). Together, these axes accounted for 92% of the variance in the original acoustic dataset.

To visualize the acoustic space represented by the Amazonian dawn chorus, we plotted the signals of species according to these axes of variation (Fig. 2). AD. For each of the three PCs extracted from our signal measures, we first calculated mean nearest-neighbor distance to produce an estimate of overall AD ( $AD_1$ ). However, because in a typical chorus there are numerous species with highly divergent signals, this measure of AD might swamp the effect of interactions between species with less divergent signals. Therefore, for each PC we also calculated the mean nearest-neighbor distance between the three species with the most similar signals ( $AD_2$ ). Specifically, we defined AD as

$$AD_1 = \text{mean}\{\text{nnd}(S_i), \quad i = 1, \dots, n\}$$

$$AD_2 = \text{mean}\{\text{nnd}(S_i), \quad i = 1, 2, 3\},$$

where a chorus is represented by species  $S_1, \dots, S_n$ , the acoustic distance between species  $S_i$  and  $S_j$  is represented by  $d(S_i, S_j)$ ,  $i \neq j$ , and nearest neighbor distance for each species  $S_i$  is defined by  $\text{nnd}(S_i) = \min\{d(S_i, S_j), j = 1, \dots, n, j \neq i\}$ . Without loss of generality, we assume that  $\text{nnd}(S_1) \leq \text{nnd}(S_2) \leq \dots \leq \text{nnd}(S_n)$ , by renumbering the species numbers if necessary.

**TD.** Analyses of phylogenetic relationships among Amazonian birds are not possible because genetic sampling of lineages remains patchy in this region (55). Instead, we used standard taxonomic sources to generate a matrix of

pairwise TD between all species in each chorus, scoring pairs of congeners as 1, members of the same family as 2, members of the same order as 3, and members of different orders as 4. Low scores reflected lower TD and hence close taxonomic relationships. Using this matrix, we calculated overall TD of each chorus in two different ways, mirroring those used to calculate AD: mean nearest-neighbor distance to produce an estimate of overall TD ( $TD_1$ ) and mean nearest-neighbor distance between the three most closely related pairs of species ( $TD_2$ ).

### Tests of Partitioning. Analysis 1: Comparison of observed and null communities.

We used a standard independent swap algorithm (56) to generate null choruses by randomization and then ran general linear models (GLMs) to compare AD and TD of observed and null choruses. Given that species signaling together within a particular habitat may be significantly more similar than predicted by a null model drawn from across all habitats because of acoustic adaptation (31), we restricted randomizations to habitats, i.e., bamboo communities were only resampled from species recorded at bamboo sites. Given that signals may also be under selection for use during a particular time of day, we restricted randomizations to the same 10-min time period. We used the following randomization procedure. For a given habitat, we ran 10,000 swaps of the entire dataset. Each swap involved randomly selecting one 10-min chorus from within one 120-min chorus and then selecting the same 10-min time slot (i.e., same time of day) from a different randomly selected 120-min chorus in the same habitat. We then randomly selected one species from each of these two 10-min choruses and swapped them. Our method automatically conserves species occurrence among choruses and species richness within choruses during swapping, both for 10- and 120-min communities.

We repeated this process by reshuffling the original dataset 100 times and then computing distance measures (e.g.,  $AD_1$ ) for all shuffled datasets, thus yielding 100 different estimates of the distance measures for each original chorus. Further analyses were conducted on the means of these 100 values. The same procedure was applied to all combinations of chorus scale, habitat, and distance measure. We then used GLMs to compare the AD and TD of observed choruses with the same metrics extracted from null choruses of equivalent species richness. AD and TD were Box-Cox transformed to ensure normal distribution of model residuals. The main advantage of using GLMs as an analytical framework is that they enable us to include covariates relevant to each chorus, including habitat, time of recording, and species richness. Thus, we were able to explicitly control for the influence of acoustic adaptation driven by habitat variation, as well as the effect of varying species richness, on AD and TD. **Analysis 2: Species-pairs analysis.** To focus on pairs of taxa most likely to compete for ecological resources and signal space and to control for potential biases resulting from the inclusion of highly unrelated taxa, we compared the observed and expected rates at which pairs of congeners sang together in our sample. From species contributing to at least one dawn chorus, we generated a list of all unique pairs of congeneric species ( $n = 212$  pairs). Pairs containing duplicate species (i.e., a species occurring in another pair) were removed at random until all remaining pairs contained two unique species. For each of these pairs,  $P$ , we counted the 10-min choruses in which at least one of the two species signaled ( $m_P$ , ranging from 1 to 12). The total number of relevant 10-min blocks for each species pair is thus  $91m_P$ , i.e., the total number of dawn recordings (91) multiplied by  $m_P$ . Finally, we calculated the proportion of these blocks containing species 1 and species 2, denoted as  $p_{P1}$  and  $p_{P2}$ , respectively. The expected co-occurrence of these species was defined as  $p_{P1}p_{P2}$ . The observed co-occurrence is given by the fraction of the  $91m_P$  time blocks in which both species signaled together.

To compare the observed and expected rate at which pairs of congeneric species signaled together (i.e., the rate of cosignaling) we used a mixed effect model with restricted maximum likelihood estimation (REML) for normally distributed response variables [linear mixed-effect model (LMM)]. In these models, rate of cosignaling was the continuous dependent variable, and type of data (observed or expected) was the categorical fixed effect. To control for pseudoreplication introduced by repeated measures, we fitted both pair members as random effects (labeled species 1 and species 2 in Table S5). Lack of robust phylogenies for Amazonian birds precluded us from incorporating tree topologies and branch lengths into our models. Thus, to control for phylogenetic nonindependence, we included taxonomy (genus nested within family) as a random effect, following numerous studies (57, 58). In all cases, the mixed-effects model including taxonomy [family (genus)] had a significantly lower log-likelihood score than the model excluding taxonomy (Table S5). Before analysis, AD and TD were Box-Cox transformed, and frequency of cosignaling was cube-root-transformed, so that residuals were normally distributed.

We used the results of analysis 1 to test whether AD and TD showed a random (Fig. 1A), evenly spaced (Fig. 1B), or clustered (Fig. 1C) distribution in space and time. The same approach was used to assess taxonomic relatedness among consignalers (analysis 2). In analysis 1, signal partitioning is expected to yield significantly greater AD and TD in observed compared with null choruses; in contrast, signaling networks are expected to yield significantly smaller AD and TD. In analysis 2, signal partitioning is expected to yield lower observed than expected rates of consignaling by congeners; in contrast, signaling networks are expected to yield higher observed than expected rates of consignaling.

Full details of study site, sampling protocols, acoustic analyses, analytical approach, and statistical methods are given in [SI Text](#). Complete datasets and information on data sources are provided in [Datasets S1](#) and [S2](#).

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