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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chance simply because they have had more time to diverge, exaggerating the evidence for partitioning. Conversely, species co-occurring at local scales may be less divergent because they are segregated by habitat across a study site and therefore are unlikely to signal together. Although some studies (7, 11) partially overcome these issues by sampling assemblages from single points in space, none has considered the effects of habitat and the potential role of competitive interactions among related species (16). Moreover, previous studies have generally assessed partitioning in relatively small assemblages (<30 species), reducing both the likelihood of competition over transmission optima and the power of statistical tests.

Here, we sample >90 signaling assemblages (Fig. S1) containing a combined total of >300 species (Dataset S1) to assess the role of species interactions in structuring and organizing the dawn chorus of Amazonian rainforest birds. Each assemblage comprised species producing acoustic signals, identified from standardized 120-min sound recordings taken at points distributed across a single study locality. We also restricted analyses to 10-min time blocks and assumed that assemblages of species signaling in these blocks were forced to discriminate among each other (i.e., they were each other's background noise) and also that they had an increased likelihood of signaling simultaneously (i.e., directly masking each other's signals). We use the term cosignaling to describe pairs of species signaling during the same 10- or 120-min time block and thus not necessarily signaling simultaneously. We coded all assemblages for habitat and time of day, calculated the acoustic similarity of cosignaling species using spectrographic analyses of voice recordings, and estimated the evolutionary relatedness of cosignaling species using a hierarchical taxonomic framework.

Our null hypothesis states that species interactions have no effect on chorus structure and thus that species with similar signals are randomly distributed in space and time (Fig. 1*A*). The distance between signals in observed choruses should not differ significantly from that expected by chance, accounting for habitat and evolutionary relationships. We envisage two scenarios that may falsify the null. The partitioning hypothesis predicts that signal design is evenly spaced across communities, with a larger distance between co-occurring signals than predicted by chance (Fig. 1*B*). The network hypothesis predicts that competing species interact using phylogenetically conserved signals and thus that signals are clustered in distribution, with a smaller distance between co-occurring signals than predicted by chance (Fig. 1*C*). The partitioning and network hypotheses involve different forms of species interaction with opposing effects on chorus structure. Although we do not measure species interactions directly, we follow standard approaches in assuming that such interactions predict patterns in the trait structure of assemblages (25).

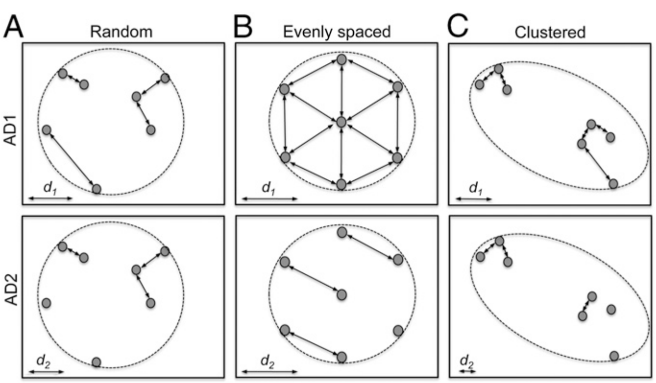

Fig. 1. Predictions of three hypotheses proposed to structure multispecies choruses, illustrated using hypothetical seven-species choruses with signal design plotted in multivariate signaling space. The null hypothesis that species interactions have no effect predicts that signal structure is random (*A*), generating an intermediate mean nearest-neighbor distance *d*. The partitioning hypothesis predicts an evenly spaced signal structure (*B*) reflected in larger values for *d*. The network hypothesis predicts that related species will signal together, causing signals to be clustered around optima (*C*), and generating small values for *d*. We test these predictions by assessing whether *d*, viewed across a sample of communities, is higher or lower than expected by chance. We calculated *d* in two ways: d_1 (*Upper*) is the mean nearest neighbor distance [nnd] across all community members; and d_2 (*Lower*) is the mean nnd across the three pairs of species with most similar signals.

Our aims were to (*i*) quantify acoustic properties of signals transmitted in the dawn chorus; (*ii*) estimate the degree of signal similarity among cosignaling species; and (*iii*) compare the observed distribution of signal properties with that expected by chance. We also consider spatial explanations for chorus structure, including the reduced cosignaling of species with similar signals through spatial partitioning. This form of segregation may occur because ecological competition is elevated in tropical bird communities (26), causing parapatric (27) or "checkerboard" distributions (28) among closely related species, thus potentially leading to apparent signal partitioning by competitive exclusion. The network hypothesis predicts the opposite pattern as closely related species should synchronize their signaling activity using shared territorial signals. We test these predictions by comparing 120-min (spatially segregated) and 10-min (nonsegregated) choruses and using taxonomic relatedness to estimate the degree of cosignaling between close relatives.

The Amazonian dawn chorus provides one of the world's most diverse multispecies signaling assemblages and an ideal system for exploring the effects of competition on signaling strategies for three reasons. First, visibility is hampered by dense vegetation, and thus long-distance signaling is forced into one modality (acoustic communication). Second, background noise levels are extremely high as a result of other organisms, including insects, amphibians, and primates, suggesting that selection for partitioning of acoustic signals should be maximized (12). Finally, many tropical species are permanently resident and apparently interspecifically territorial, using acoustic signals to mediate competitive interactions with heterospecifics (18, 26, 29). In combination, these factors imply that large numbers of species compete both for ecological resources and a narrow window of optimal signaling space (7, 30), providing a context in which to test the relative importance of acoustic partitioning and interspecific communication networks.

Results

Chorus Structure. Plotting the acoustic structure of signals according to principal component (PC)1 (correlated with pitch), PC2 (correlated with duration), and PC3 (correlated with pace) suggested a pattern of clustering, potentially around transmission optima (Fig. 2). Although all species have diagnostic signals (*SI Text*), we found that most are located toward the center of community signaling space in an area of low to intermediate pitch (25–75% quartile: 1.7–3.4 kHz) and slow pace (2.0–8.1 notes/s). The edge of trait space contains correspondingly few species. Nonpasserine bird species in our dataset are highly variable in body size, from white-chinned sapphire *Hylocharis cyanus* (8 cm) to razor-billed curassow *Mitu tuberosum* (90 cm), whereas size variation in passerines is less extreme (6.5–41 cm). Coupled with the covariance of many signal traits with body size (31), this may explain why passerines occupy a smaller area of signal space despite being more speciose. We also detected obvious clustering of families within broader acoustic space (Fig. 2), a pattern indicating that related species have similar songs.

Tests of Partitioning. Despite this restricted variation in signal properties, and thus potential competition for transmission

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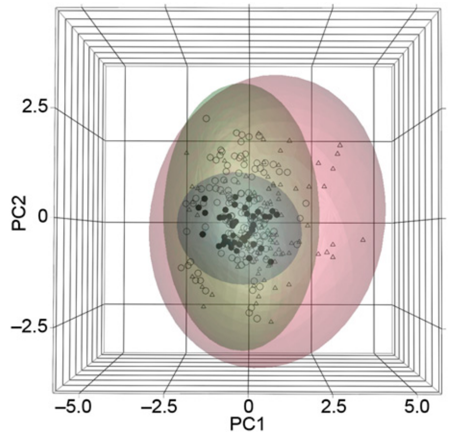

Fig. 2. Acoustic structure of the Amazonian dawn chorus. Each signal (one per bird species, $n = 283$) is plotted in multivariate trait space described by three principal components (PCs) derived from seven acoustic parameters; PC1 (x axis) correlates with pitch, PC2 (y axis) correlates with duration, 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 strcture (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_1 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. 4*A*). 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. 4*B*).

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

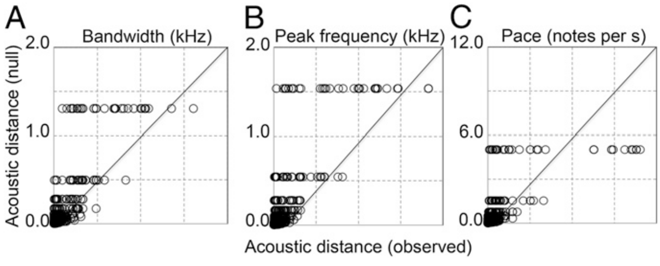

Fig. 3. Tests of partitioning of acoustic signals produced during the dawn chorus by Amazonian birds ($n = 283$ species). Shown are scatterplots of mean nearest-neighbor acoustic distance (AD_1) in observed (x axis) 10-min choruses ($n = 1,092$) vs. null (y axis), for three key acoustic traits: (*A*) 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: $P < 0.0001$).

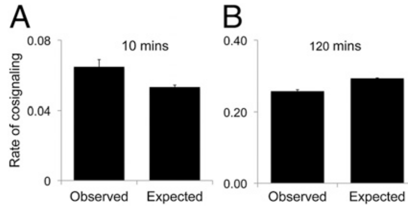

Fig. 4. Taxonomic structure of the Amazonian dawn chorus at two different temporal scales. Bars show the mean observed and expected rate (±SE) of cosignaling for 212 pairs of congeneric species in (*A*) 10-min choruses (n = 1,092) and (*B*) 120-min choruses (n = 91). The difference between observed and expected rate is significant at both scales (LMM: $P < 0.001$), although the effect is opposite in sign (Table S5).

(32) and instead suggest that related lineages with similar signals synchronize their signaling activity in both time and space, in line with the predictions of the network hypothesis.

One possible explanation for this finding is that our indices of clustering are somehow exaggerated because nearest-neighbor distances are reduced among species that tend to co-occur in highly diverse assemblages, as signals are then more crowded in trait space. Another possibility is that the similarity of signals among co-occurring species is not driven by species interactions but by consistent acoustic adaptation to shared signaling environments (17). We addressed these issues first by sampling across habitats known to drive acoustic adaptation at the same study locality (31) and then resampling solely within habitat types and constraining species richness and time of day. The results show that cosignalers have unexpectedly similar signals even when controlling for these effects. We conclude that signals are clustered in the Amazonian dawn chorus irrespective of community size and acoustic adaptation and thus that the pattern of clustering most likely arises through species interactions.

The absence of significant partitioning is striking given that we found an extremely high diversity of related species communicating with similar signals during the Amazonian dawn chorus (Fig. 2). Previous sound transmission experiments predict that slow-paced and low-pitched bird songs travel more effectively through rainforests if transmitted at ~2–4 kHz (31, 33). Faster-paced and higher-frequency signals suffer greater attenuation and reverberation (34), as well as masking by high-pitched choruses of amphibians and insects (35). Our findings confirm that most acoustic signals fall within this relatively narrow window of optimal transmission, a pattern usually interpreted as intense competition among rainforest bird species for signaling space (12, 30, 36).

The apparent lack of acoustic and temporal partitioning in this crowded transmission space suggests that rainforest birds may simply avoid interference by partitioning at finer temporal scales (37). Previous studies have shown that Amazonian birds use minor adjustments in the timing or acoustic structure of songs to reduce direct overlap of signals both within (38) and among species (30). This subtle form of partitioning is restricted to the scale of individual songs (mainly 1–2 s) and thus cannot be detected using 10-min choruses. Although we cannot rule out fine-scale avoidance of direct masking, this is simply a form of behavioral plasticity, whereas our sampling is designed to test for the signature of ecological and evolutionary mechanisms fundamentally shaping signals and signaling behavior across populations. At this broader scale, we find no evidence that the costs of signal similarity drive the evolution of structurally dissimilar signals or divergent signal schedules, so that optimal signal space is subdivided among species (3). These results conflict with the core predictions of the partitioning hypothesis (6, 15), suggesting that competition for signal space is weaker than generally assumed.

One likely reason is that receivers, whether mates or competitors, are capable of accurate signal detection and discrimination (39), even when extremely similar signals are perceived against high levels of background noise (1, 40, 41). Indeed, experimental studies reveal that receivers can even discriminate individuals on the basis of signals that have been digitally mixed with those of other species or individuals (42, 43). Moreover, a growing body of evidence suggests that selection for accurate discrimination of similar signals can lead to fine-tuning of recognition mechanisms (e.g., a narrowing of recognition space) without driving divergence of the signals themselves (8, 39, 44). These lines of evidence suggest that acoustic perception may be effective in complex choruses and that the costs of sharing similar signals and signaling schedules is lower than expected.

Reduced costs, and thus weaker selection for divergence, may explain the absence of partitioning. However, it cannot explain why we detect the opposite pattern of clustering in signals and signaling schedules. Rather, this result suggests that signals mediate communication among related species that share similar signals, signaling schedules, and perceptual biases as a result of their close evolutionary relationship. It is possible that congeners stimulate nonadaptive responses from each other, including misdirected aggression. However, this implies a cost to cosignaling that seems unlikely to result in acoustic and temporal clustering, as selection should then favor divergence in signals and signaling schedules over time. Alternatively, communication among congeners may be adaptive, leading to coordinated signaling among heterospecifics.

Although we cannot directly test these hypotheses, there are two reasons why adaptive interspecific communication may be widespread among co-occurring congeners and other closely related lineages. First, congeners are often similar in ecology because of phylogenetic niche conservatism: the retention of niche-related traits over evolutionary time (45). Hence, individuals of congeneric species are more likely to compete over ecological resources, potentially incurring costs when their territories coincide. Second, if selection for partitioning is weak, then shared signals and signaling behavior may confer an advantage because individuals of both species are more successful in defending resources and deterring territorial intrusions against heterospecifics and conspecifics (16, 21).

The idea of interactive communication networks among heterospecifics is a simple extension of patterns demonstrated within species. Previous studies of birds reveal that territorial individuals often respond to the songs of neighboring conspecifics (46) and that the dawn chorus network connects many members of a single species (20, 47, 48). In addition, conspecific individuals often interact using song matching—i.e., responding with a similar song—as an honest signal of aggression (49). Importantly, both territorial song (50) and song matching (51) function as deterrent signals and therefore increase the fitness of signalers and receivers by limiting the costs of escalated contests. Although these factors are thought to promote signal stereotypy and synchrony within species, it seems plausible that similar adaptive communication networks extend beyond the species boundary, particularly as interactive singing (21) and song matching (19) are known to mediate competition between species. In support of this idea, we found that closely related Amazonian species known to be interspecifically territorial use highly similar signals within congruent signaling schedules (Fig. S5).

The concept of communication networks has previously been applied to alarm calls used in multispecies foraging flocks (52), leading to the proposal that these flocks are structured by interspecific communication (53). In contrast, our results provide evidence that communication networks may apply more generally to the primary long-distance signals of entire communities (54). We propose that these cascading networks of communication across species boundaries are widespread, in which case the signaling traits of heterospecific organisms often qualify as signal rather than noise. This viewpoint challenges conventional views about the processes shaping signals and signaling behavior 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 ± SD number of choruses per species = 15.3 ± 0.2 per species; range = 1–85). Mean ± SD diversity was 47.7 ± 9.2 species (range = 28–67) for 120-min choruses and 11.9 ± 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 ± SD number of 10-min choruses contributed to per species was only 2.8 ± 0.3, with 70.6 ± 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 ± SE = 5.4 ± 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

$$AD_1 = \mathrm{mean}\{\mathrm{nnd}(S_i), \quad i = 1, \ldots, n\}$$
$$AD_2 = \mathrm{mean}\{\mathrm{nnd}(S_i), \quad i = 1,2,3\},$$

where a chorus is represented by species $S_1,\ldots,S_n$, 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 $\mathrm{nnd}(S_i) = \min[d(S_i, S_j), j = 1,\ldots,n, j \neq i]$. Without loss of generality, we assume that $\mathrm{nnd}(S_1) \leq \mathrm{nnd}(S_2) \leq \ldots \leq \mathrm{nnd}(S_n)$, 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 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. 1*A*), evenly spaced (Fig. 1*B*), or clustered (Fig. 1*C*) distribution in space and time. The same approach was used to assess taxonomic relatedness among cosignalers (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 cosignaling by congeners; in contrast, signaling networks are expected to yield higher observed than expected rates of cosignaling.

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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1. Brumm H, Slabbekoorn H (2005) Acoustic communication in noise. *Adv Stud Behav* 35: 151–209.
2. Bradbury JW, Vehrencamp SL (2011) *Principles of Animal Communication* (Sinauer Associates, Sunderland, MA), 2nd Ed.
3. Wiley RH (2006) Signal detection and animal communication. *Adv Stud Behav* 36: 217–247.
4. Ficken RW, Ficken MS, Hailman JP (1974) Temporal pattern shifts to avoid acoustic interference in singing birds. *Science* 183(4126):762–763.
5. Hartbauer M, Siegert ME, Fertschai I, Römer H (2012) Acoustic signal perception in a noisy habitat: Lessons from synchronising insects. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 198(6):397–409.
6. Chek AA, Bogart JP, Lougheed SC (2003) Mating signal partitioning in multi-species assemblages: A null model test using frogs. *Ecol Lett* 6(3):235–247.
7. Luther D (2009) The influence of the acoustic community on songs of birds in a neotropical rain forest. *Behav Ecol* 20(4):864–871.
8. Amézquita A, Flechas SV, Lima AP, Gasser H, Hödl W (2011) Acoustic interference and recognition space within a complex assemblage of dendrobatid frogs. *Proc Natl Acad Sci USA* 108(41):17058–17063.
9. Noor MAF (1999) Reinforcement and other consequences of sympatry. *Heredity (Edinb)* 83(Pt 5):503–508.
10. Schmidt AKD, Römer H (2011) Solutions to the cocktail party problem in insects: Selective filters, spatial release from masking and gain control in tropical crickets. *PLoS ONE* 6(12):e28593.
11. Schmidt AKD, Römer H, Riede K (2013) Spectral niche segregation and community organization in a tropical cricket assemblage. *Behav Ecol* 24(2):470–480.
12. Luther DA, Wiley RH (2009) Production and perception of communicatory signals in a noisy environment. *Biol Lett* 5(2):183–187.
13. Nelson DA, Marler P (1990) The perception of birdsong and an ecological concept of signal space. *Comparative Perception Vol. II: Complex Signals*, eds Berkley MA, Stebbins WC (Wiley, New York), Vol 2, pp 443–478.
14. Endler JA (1992) Signals, signal conditions and the direction of evolution. *Am Nat* 139(Supplement):S125–S153.
15. Sueur J (2002) Cicada acoustic communication: Potential sound partitioning in a multispecies community from Mexico (Hemiptera: Cicadomorpha: Cicadidae). *Biol J Linn Soc Lond* 75(3):379–394.
16. Grether GF, Losin N, Anderson CN, Okamoto K (2009) The role of interspecific interference competition in character displacement and the evolution of competitor recognition. *Biol Rev Camb Philos Soc* 84(4):617–635.
17. Cardoso GC, Price TD (2010) Community convergence in birdsong. *Evol Ecol* 24(2): 447–461.
18. Tobias JA, Gamarra-Toledo V, García-Olaechea D, Pulgarín PC, Seddon N (2011) Year-round resource defence and the evolution of male and female song in suboscine birds: Social armaments are mutual ornaments. *J Evol Biol* 24(10):2118–2138.
19. Gorissen L, Gorissen M, Eens M (2006) Heterospecific song matching in two closely related songbirds (*Parus major and P. caeruleus*): Great tits match blue tits but not vice versa. *Behav Ecol Sociobiol* 60(2):260–269.
20. Burt JM, Vehrencamp SL (2005) Dawn chorus as an interactive communication network. *Animal Communication Networks*, ed McGregor PK (Cambridge Univ Press, Cambridge, UK), pp 320–343.
21. Tobias JA, Seddon N (2009) Signal design and perception in *Hypocnemis* antbirds: Evidence for convergent evolution via social selection. *Evolution* 63(12):3168–3189.
22. Laiolo P (2012) Interspecific interactions drive cultural co-evolution and acoustic convergence in syntopic species. *J Anim Ecol* 81(3):594–604.
23. Weir JT, Price TD (2011) Limits to speciation inferred from times to secondary sympatry and ages of hybridizing species along a latitudinal gradient. *Am Nat* 177(4):462–469.
24. Tobias JA, et al. Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature*, 10.1038/nature12874.
25. Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of community ecology and phylogenetic biology. *Ecol Lett* 12(7):693–715.
26. Jankowski JE, et al. (2012) The role of competition in structuring tropical bird communities. *Ornitol Neotrop* 23(Supplement):115–124.
27. Pigot AL, Tobias JA (2013) Species interactions constrain geographic range expansion over evolutionary time. *Ecol Lett* 16(3):330–338.
28. Graves GR, Gotelli NJ (1993) Assembly of avian mixed-species flocks in Amazonia. *Proc Natl Acad Sci USA* 90(4):1388–1391.
29. Robinson SK, Terborgh J (1995) Interspecific aggression and habitat selection by Amazonian birds. *J Anim Ecol* 64(1):1–11.
30. Planqué R, Slabbekoorn H (2008) Spectral overlap in songs and temporal avoidance in a Peruvian bird assemblage. *Ethology* 114(3):262–271.
31. Tobias JA, et al. (2010) Song divergence by sensory drive in Amazonian birds. *Evolution* 64(10):2820–2839.
32. Cody ML, Brown JH (1969) Song asynchrony in neighboring bird species. *Nature* 222(5195):778–780.
33. Marten K, Quine D, Marler P (1977) Sound transmission and its significance for animal vocalisation II. Tropical forest habitats. *Behav Ecol Sociobiol* 2(3):291–302.
34. Wiley RH (1991) Associations of song properties with habitats for territorial oscine birds of Eastern North America. *Am Nat* 138(4):973–993.
35. Ryan MJ, Brenowitz EA (1985) The role of body size, phylogeny and ambient noise in the evolution of bird song. *Am Nat* 126(1):87–100.
36. Slabbekoorn H (2004) Singing in the wild: The ecology of birdsong. *Nature's Music: The Science of Birdsong*, eds Marler P, Slabbekoorn H (Elsevier, San Diego), pp 178–205.
37. Brumm H (2006) Signalling through acoustic windows: Nightingales avoid interspecific competition by short-term adjustment of song timing. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 192(12):1279–1285.
38. Tobias JA, Seddon N (2009) Signal jamming mediates sexual conflict in a duetting bird. *Curr Biol* 19(7):577–582.
39. Seddon N, Tobias JA (2010) Character displacement from the receiver's perspective: Species and mate recognition despite convergent signals in suboscine birds. *Proc Biol Sci* 277(1693):2475–2483.
40. Aubin T, Jouventin P (1998) Cocktail party effect in king penguin colonies. *Proc Biol Sci* 265(1406):1665–1673.
41. Narins PM, Feng AS, Fay RR, Popper AN (2007) *Hearing and Sound Communication in Amphibians* (Springer, New York).
42. Benney KS, Braaten RF (2000) Auditory scene analysis in estrildid finches (*Taenopygia guttata* and *Lonchura striata domestica*): A species advantage for detection of conspecific song. *J Comp Psychol* 114(2):174–182.
43. Hulse SH, MacDougall-Shackleton SA, Wisniewski AB (1997) Auditory scene analysis by songbirds: Stream segregation of birdsong by European starlings (*Sturnus vulgaris*). *J Comp Psychol* 111(1):3–13.
44. Gerhardt HC, Huber F (2002) *Acoustic Communication in Insects and Anurans: Common Problems and Diverse Solutions* (Univ of Chicago Press, Chicago).
45. Wiens JJ, et al. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol Lett* 13(10):1310–1324.
46. Seddon N (2002) The structure, context and possible function of solos, duets and choruses in the subdesert mesite (*Monias benschi*). *Behaviour* 139(5):645–676.
47. Liu W-C, Kroodsma DE (2007) Dawn and daytime singing behavior of chipping sparrows (*Spizella passerina*). *Auk* 124(1):44–52.
48. Foote JR, Fitzsimmons LP, Mennill DJ, Ratcliffe LM (2008) Male chickadees match neighbors interactively at dawn: Support for the social dynamics hypothesis. *Behav Ecol* 19(6):1192–1199.
49. Vehrencamp SL (2001) Is song-type matching a conventional signal of aggressive intentions? *Proc Biol Sci* 268(1476):1637–1642.
50. de Kort SR, Eldermire ERB, Cramer ERA, Vehrencamp SL (2009) The deterrent effect of bird song in territory defense. *Behav Ecol* 20(1):200–206.
51. Akçay C, Tom ME, Campbell SE, Beecher MD (2013) Song type matching is an honest early threat signal in a hierarchical animal communication system. *Proc Biol Sci* 280(1756):20122517.
52. Magrath RD, Pitcher BJ, Gardner JL (2009) An avian eavesdropping network: Alarm signal reliability and heterospecific response. *Behav Ecol* 20(4):745–752.
53. Goodale E, Beauchamp G, Magrath RD, Nieh JC, Ruxton GD (2010) Interspecific information transfer influences animal community structure. *Trends Ecol Evol* 25(6): 354–361.
54. Krams I (2010) Interspecific communication. *Encyclopedia of Animal Behavior*, eds Breed MD, Moore J (Academic, Oxford), Vol 2, pp 196–202.
55. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO (2012) The global diversity of birds in space and time. *Nature* 491(7424):444–448.
56. Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. *Ecology* 81(9): 2606–2621.
57. Seddon N, et al. (2013) Sexual selection accelerates signal evolution during speciation. *Proc Biol Sci* 280(1766):20131065.
58. Pinheiro JC, Bates DM (2000) *Statistics and Computing: Mixed-Effects Models in S and S-Plus* (Springer, New York).