Acoustic interference and recognition space within a complex assemblage of dendrobatid frogs

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In species-rich assemblages of acoustically communicating animals, heterospecific sounds may constrain not only the evolution of signal traits but also the much less-studied signal-processing mechanisms that define the recognition space of a signal. To test the hypothesis that the recognition space is optimally designed, i.e., that it is narrower toward the species that represent the higher potential for acoustic interference, we studied an acoustic assemblage of 10 diurnally active frog species. We characterized their calls, estimated pairwise correlations in calling activity, and, to model the recognition spaces of five species, conducted playback experiments with 577 synthetic signals on 531 males. Acoustic co-occurrence was not related to multivariate distance in call parameters, suggesting a minor role for spectral or temporal segregation among species uttering similar calls. In most cases, the recognition space overlapped but was greater than the signal space, indicating that signal-processing traits do not act as strictly matched filters against sounds other than homospecific calls. Indeed, the range of the recognition space was strongly predicted by the acoustic distance to neighboring species in the signal space. Thus, our data provide compelling evidence of a role of heterospecific calls in evolutionarily shaping the frogs' recognition space within a complex acoustic assemblage without obvious concomitant effects on the signal.

Amazonia | animal communication | bioacoustics | perception

Mate-recognition signals mediate successful breeding and, therefore, are often affected by strong selective forces that may lead to adaptation and reproductive isolation (1, 2). Although the causes (3, 4) and consequences (5, 6) of signal evolutionary divergence are relatively well studied, much less is known about the evolution of physiological mechanisms underlying the sensory processing of signals (7, 8). At the most basic level, signal detection and signal recognition are prerequisites for the appropriate re-action of receivers, rendering signal-processing traits at least as important as signal traits in potentially affecting the evolutionary fate of a lineage (9–11).

Signals must encode a minimum amount of information allowing for species recognition because of the high costs of reacting toward heterospecific signals as if they were homospecific ("false alarms") (12, 13). Signal recognition occurs when receivers compare detected signals to preexisting templates, often in the central nervous system. It is usually tested with playback experiments and is assumed when tested receivers exhibit overt behavioral responses (14, 15), i.e., when they "treat as valid" the stimulus signal (16). The recognition space of a given signal is thus estimated as the range of signal values that elicit effective (meeting some minimum criterion) behavioral responses in the receivers (13).

The recognition space may be larger than necessary for the recognition of conspecific signals (17, 18), presumably because sensory systems trade off their communicative function with other ecological functions such as predator or prey detection (19). The role of heterospecific signals in shaping the recognition space has received less attention (20). One example would be the effect of masking interference on acoustic communication in birds (21),

insects (22), and frogs (23, 24). Because heterospecific sounds may represent noise that interferes with signal detection (25, 26), the communication systems should reveal adaptations that reduce its effects. To date, most research to validate this idea has been conducted on the characteristics of the signals or on the pattern of signaling activity (27, 28), but compelling evidence suggests that recognition systems can evolve without concomitant variation in the signals (20, 29). We present here a manipulative study on a species-rich assemblage of diurnal frogs to test the general hypothesis that the recognition space is shaped in a way that minimizes the overlapping of signal space with those of co-occurring species.

The importance of acoustic communication for anuran reproduction is well established (30, 31). Typically, male breeding success depends on producing advertisement calls that attract females. In a fairly less-studied scenario, male breeding success depends on the successful and prolonged defense (against other males) of a territory containing resources essential for reproduction (32). Males of the latter species announce territory ownership by producing redundant series of advertisement calls throughout the breeding season; they also react toward conspecific calling intruders by increasing signaling rate or intensity and by attacking them (33). Because both levels of reaction increase energy expenditure and conspicuousness to potential predators, natural selection on signal-detection and signal-recognition mechanisms should be evident in the male–male communication systems of territorial species (20).

Our *null hypothesis* states that the recognition space of each species occupies the available signal space of the whole frog assemblage; males of each species should then indiscriminately react to every species' signal. We anticipated at least three scenarios that falsify the null hypothesis (Fig. 1). In our *matched-spaces hypothesis*, the recognition space is perfectly matched to the signal space, indicating pleiotropic relationships between signal-producing and signal-recognition traits or strong natural selection against detecting sounds other than the signals. Our matched-spaces hypothesis differs from the original matched-filter hypothesis (34) in including the whole signal space rather than only the spectral parameters and in emphasizing the signal parameters' range instead of the average values. In the *spectral-partitioning hypothesis*, the recognition space is partitioned in the spectral but not in the temporal domain of call parameters, suggesting an effect of masking interference in shaping the recognition space. The *filled-gaps hypothesis* adds to the spectral-partitioning hypothesis by including the temporal domain of the
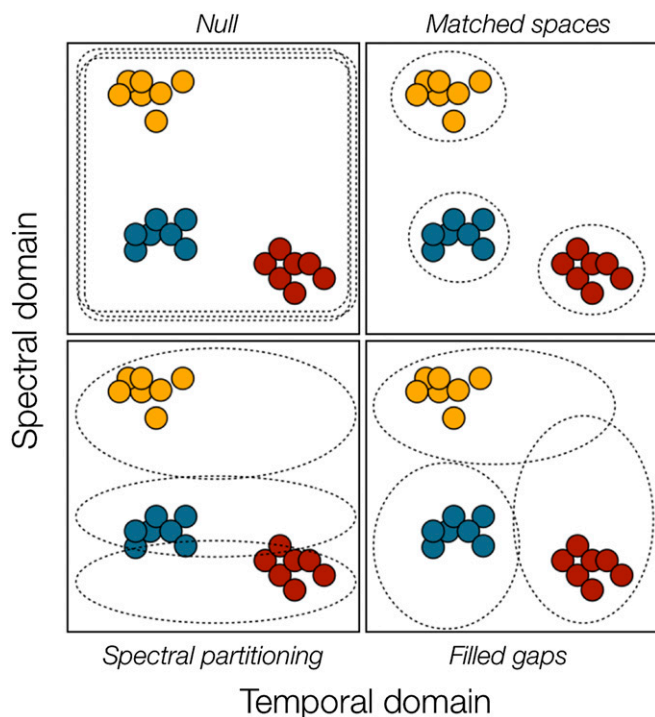

Fig. 1. Four hypotheses on the shape of the recognition space (dotted lines) and its relationship with the signal space defined by individual signals (filled circles) of three hypothetically co-occurring species (colored circles).

signal. The recognition space should then extend beyond the limits of the species-specific signals, depending on the multi-variate distance to the neighboring species in the signal space; this result would indicate that recognition spaces are constrained by the probability of heterospecific interference. Because the last two hypotheses imply a role for heterospecific signals, we quantified the actual magnitude of this influence by estimating species acoustic co-occurrence from recordings of the acoustic environment.

Our aims were thus (*i*) to estimate the degree of signaling co-occurrence between every pair of species in an assemblage of diurnal frogs, (*ii*) to characterize the parameters of their advertisement calls, (*iii*) to estimate the potential of call parameters to allow discrimination between homospecific and heterospecific signals, (*iv*) to estimate the recognition space of five species by conducting playback experiments, and, finally, (*vi*) to test the four hypotheses (Fig. 1) by mapping the recognition spaces onto the signal spaces estimated from the call traits.

Results

We registered 10 acoustically active frog species at the study site, nine of them calling during daytime hours (all belonging to the family Dendrobatidae) and one during the late afternoon (*Leptodactylus andreae*, Leptodactylidae). Regarding spatiotemporal segregation, only the calling activity of *Allobates femoralis* was inversely related to the calling activity of *Ameerega petersi* ($r = -0.62$, $P < 0.0001$, $n = 53$ acoustic environments). The whole pattern of species co-occurrence was successfully represented in two dimensions by multidimensional scaling (MDS; stress = 0.02). The transformed proximities between species pairs, our estimate of species co-occurrence, were not related to the multivariate difference in advertisement calls (Mantel $r = 0.17$, $P = 0.8011$, $n = 45$ species pairs, 9,999 permutations).

Each species' call (Fig. 2) consisted basically of frequency-modulated notes uttered in seven species as long series of uninote
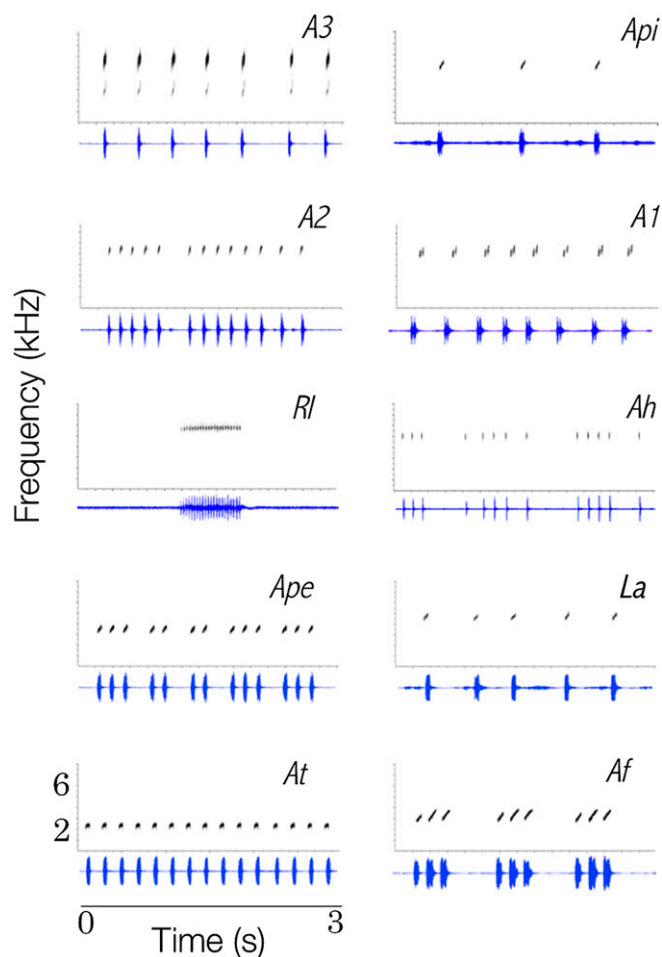

Fig. 2. Oscillogram (lower, blue) and sonogram (upper, gray) of the advertisement calls of 10 acoustically co-occurring frog species at Panguana, Peru. A1, *Allobates* sp. 1; A2, *Allobates* sp. 2; A3, *Allobates* sp. 3; Af, *Allobates femoralis*; Ah, *Ameerega hahneli*; Ape, *Ameerega petersi*; Api, *Ameerega picta*; At, *Ameerega trivittata*; La, *Leptodactylus andreae*; Rl, *Ranitomeya lamasi*.

calls and arranged in three species as multinote calls. Call parameters were successfully combined in two discriminant axes that explained 92.0% of variance and classified very well (98.7% of correct classifications) each species' call (Fig. 3). The variables that most contributed to discriminate calls were low frequency (discrimination coefficient = 0.63) in the first discriminant function (explaining 66.2% of variance) and note duration (discrimination coefficient = 0.62) on the second discriminant function (25.8%). Therefore, we estimated a 2D recognition space by manipulating note frequency and note duration.

The effect of manipulating call parameters on the probability of male reaction differed among species (Table 1 and Fig. 4). Whereas *A. femoralis* males reacted to synthetic stimuli with deviations up to 10–15 SD, *Ameerega picta*, males restricted their reactions to stimuli within 2 SD of the average values. In addition, three of four species tolerated lower deviations in peak frequency than in note duration (Fig. 4).

The recognition and signal spaces overlapped but did not have the same boundaries or shape (Fig. 5). Four species reacted to supernormal stimuli, but the limits of their recognition spaces did not overlap. Only in *Allobates* sp. 1 did the recognition space include most calls of an acoustically neighboring species, *Allobates* sp. 2. We did not consider *Am. petersi* to be a neighboring species of *A. femoralis* in the communication space because both
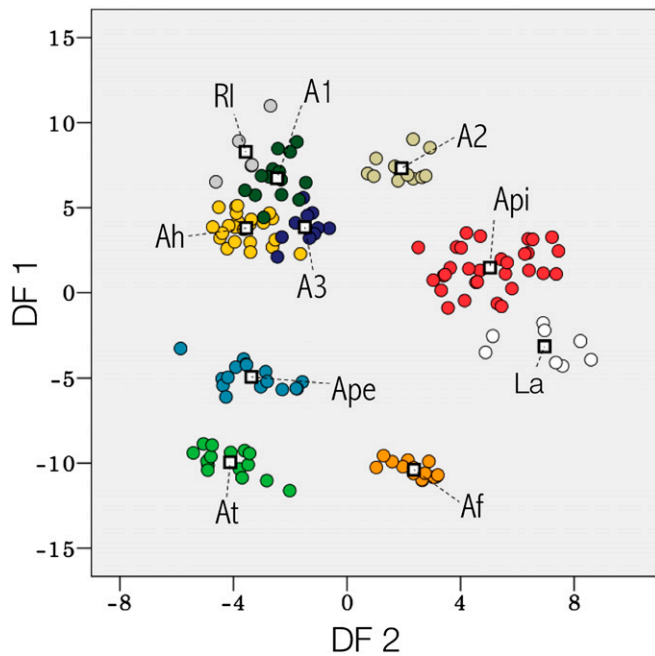
Fig. 3. Discriminant plot summarizing between individuals' (dots) and species' (colors) differences in five parameters of the advertisement calls. The first discriminant function (DF1; 66.2%) is correlated with high values of low ($r = 0.86$), peak ($r = 0.76$), and high ($r = 0.73$) frequency, whereas the second (DF2; 25.8%) is mainly correlated with note duration ($r = 0.69$). The discriminant axes were switched to improve data visualization and comparison with Figs. 1 and 5. Species abbreviations are as described in Fig. 2.

whole signal space of the frog assemblage (null hypothesis) nor did they match in range the signal space of the same species' call (matched-spaces hypothesis). Statistically, the matched-spaces hypothesis predicts that the recognition space should reach up to 3 SD from the bivariate centroid defined by peak frequency and note duration. Instead, the models (Fig. 5 and Table 1) show that they reached between 4 and 15 SD away from the centroid, often in an asymmetrical fashion. In one species (*Am. picta*), the model was not statistically significant as to reject or accept any hypothesis about the recognition space.

The lack of sender–receiver match apparently conflicts with the matched-filter hypothesis (34). The latter predicts an association between the peak frequency of an auditory signal and the peak spectral sensitivity of the peripheral auditory system (13), which would improve the signal-to-noise ratio and thereby reduce masking by heterospecific or abiotic noise. A direct comparison between the matched-filter hypothesis as it was applied to the tuning of auditory neurons and our matched-spaces hypothesis is misleading, however, because (*i*) we have emphasized the range and not the center of the recognition space, (*ii*) we have included temporal and not merely spectral parameters of the signal, and (*iii*) we have studied behavioral rather than physiological reactions to auditory stimuli.

Acoustically communicating species may not interfere with each other if their signaling activity is segregated in space and time (24, 35, 36). Our data do not support this explanation. Should species tend to segregate, then their calling activities would be negatively correlated across our recordings of acoustic environment; this happened for just 1 (*A. femoralis* and *Am. petersi*) of 18 species pairs. In addition, the MDS proximity, our estimate of pairwise species co-occurrence, was unrelated to concomitant differences in advertisement calls. Thus, contrary to another work (21), we found no general evidence that frogs uttering more similar calls are also better segregated in space and time.

Species' communication spaces might instead be partitioned along the spectral axis (spectral-partitioning hypothesis) because spectral overlapping could cause masking interference. The spectral-partitioning hypothesis received mixed support from our data. On the positive side, spectral traits performed much better than temporal traits did in discriminating species' calls (see Fig. 3 and corresponding discriminant coefficients). Regarding the recognition space, four of the five species tolerated lower deviations in note frequency than in note duration. On the negative side, we found substantial overlap between species in the call spectral axis (Figs. 3 and 5). Also, the recognition space of *Allobates* sp. 1 encompassed a significant fraction of the signal space of *Allobates* sp. 2 and spectrally overlapped with at least two other species (Fig. 5). One explanation for the latter case would be that

species appear segregated in the analysis of co-occurrence (see above). Finally, acoustic distance was a strong predictor of recognition distance [permutational regression, likelihood ratio test (LRT) = 8.5, $P = 0.0090$, $n = 18$ species pairs, 10,000 permutations] after controlling for concomitant variation in co-occurrence (LRT = 0.2, $P = 0.7012$). Because *Am. picta* males exhibited a conspicuously atypical and statistically nonsignificant recognition space (Figs. 4 and 5), we repeated the regression analysis, excluding the species pairs involving it; the pattern became even stronger (Fig. 6; acoustic distance: LRT = 21.2, $P = 0.0007$; co-occurrence: LRT = 3.1, $P = 0.1065$; $n = 14$ species pairs, 10,000 permutations).

Discussion

Our study provides sufficient evidence to reject two of the four initial hypotheses: the recognition spaces did not occupy the

Table 1. Summary of the GAM analyses on binary data to test the effect of note duration and note frequency on male reaction to the playback of synthetic calls in five frog species

Species	n	DE, %	Predictor	df	Deviance	P
Am. hahneli	57	16.2	Peak frequency	−2.9	−6.23	0.0925
			Note duration	−3.0	−10.9	0.0118
Am. picta	31	20.9	Peak frequency	−3.1	−6.40	0.0974
			Note duration	−2.8	−5.45	0.1243
Am. trivittata	51	33.2	Peak frequency	−0.6	−4.6	0.0148
			Note duration	−4.3	−19.0	0.0011
Allobates sp. 1	51	36.8	Peak frequency	−3.5	−17.4	0.0010
			Note duration	−3.0	−11.9	0.0075
A. femoralis	63	43.8	Peak frequency	−3.0	−18.6	0.0003
			Note duration	−3.5	−19.1	0.0004

The ability of the model to predict the outcome of the playback experiments is expressed as the percentage of deviation explained (DE).
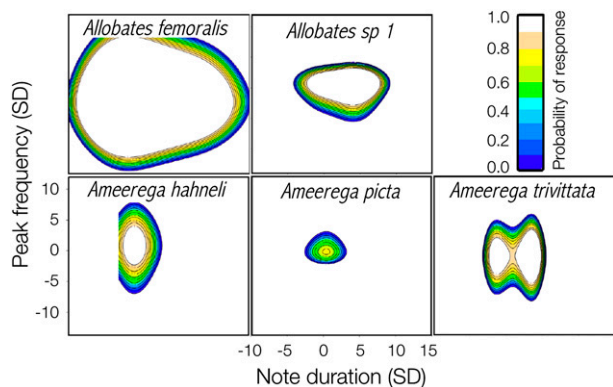
Fig. 4. Recognition space of five co-occurring frog species as estimated by a GAM on the phonotactic reaction of males to the playback of synthetic advertisement calls. The variables were manipulated beyond the natural range of variation (expressed as SD) until most individuals failed to react to the corresponding stimulus call.
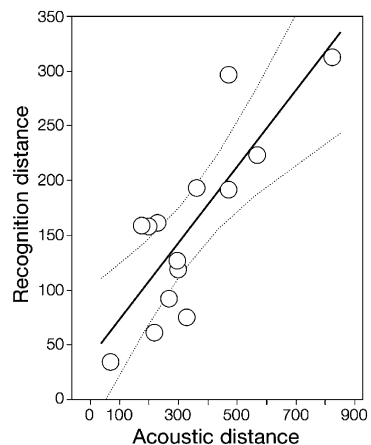

Fig. 6. Relationship between the projection of the recognition space (recognition distance) and pairwise differences in call traits (acoustic distance) while controlling for the degree of species co-occurrence in an acoustic community of diurnal frogs.

Allobates sp. 1 is the only species with microtemporal structuring of the call (Fig. 2), which we did not consider in our estimates of the signal space: Males utter series of calls, each consisting of two notes separated by a very short time interval.

We found unequivocal evidence favoring our filled-gaps hypothesis as the dominant pattern regarding the shape of the recognition space. The extent by which the recognition space exceeded the homospecific signal space was strongly related to the multivariate distance to other species' signals (Fig. 6). Thus, our results support the idea that recognition spaces subserve detection of sounds other than conspecific signals and that their shape is constrained by the probability of heterospecific interference. Moreover, because the filled-gaps hypothesis implies some degree of segregation along the spectral domain of the recognition space, we could also explain the evidence partly
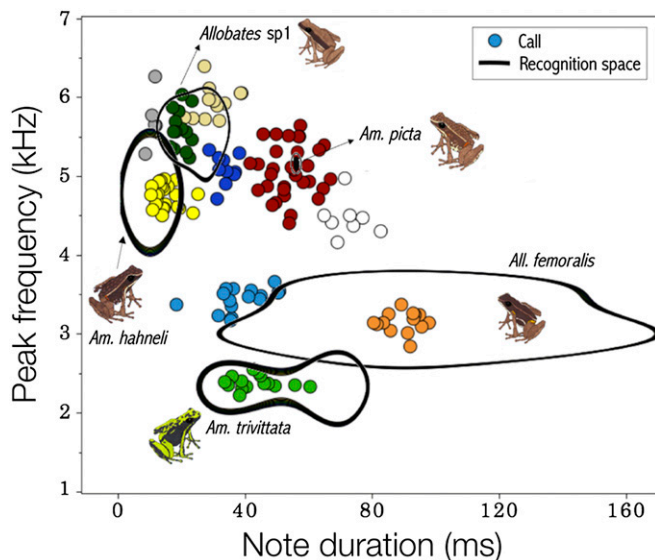

Fig. 5. Communication space depicting the relationships between the recognition space (5 species shown) and the signal space (10 species shown) as defined by two call parameters in an assemblage of diurnal frogs. Each dot represent average values of call parameters for a single frog. The line delimitates the call parameter values at which the probability of male reaction was estimated as 0.99 by a GAM.

supporting the spectral-partitioning hypothesis by accepting the filled-gaps hypothesis as valid.

The strong pattern we detected may have arisen from the negative consequences of heterospecific signals on communication, territory defense, and successful breeding. In agreement with an adaptive scenario, related species within our study system (e.g., within the genus *Ameerega* or *Allobates*) do not share similarly shaped recognition spaces, and previous studies have strongly suggested adaptive divergence in the signal spectral processing in *A. femoralis* without concomitant variation in the signal (29). Also, the physiological basis of intraspecific variation in spectral tuning has been previously tracked for other frog species (37). Alternatively, learning has been invoked to explain sensory biases (38) and thereby could explain the patterns we observed; the adaptive adjustment would then occur within a single generation of individuals. Although some signal characteristics are thought to be relatively conservative in frogs (39, 40) and pleiotropically linked to body size and perhaps sensory systems (13), the possibilities that signal-processing mechanisms are adjusted via learning or phenotypic plasticity deserve deeper exploration.

The recognition spaces may still depend on at least two factors that we did not manipulate here. Repeating the whole experiment at different sound-pressure levels might reveal interesting changes in recognition spaces perhaps associated to among-species differences in territory size. We chose, however, a sound-pressure level range that mimics a natural sound produced by an eventual intruder approaching within 1–2 m of the focal male. In our positive controls (synthetic sounds with the call average parameters), playbacks were recognized as "valid" intruders in every case. On the other hand, the whole experiment could also be done testing females, rather than males, in playback experiments. Females, in general, have shown to be more selective than males in the calls to which they respond (41, 42). However, territory ownership and successful defense against other males appears to be the most important factor determining reproductive success in basal dendrobatids such as the ones we studied here (32). In turn, dendrobatid females might use much more multimodal information than males do to recognize conspecific males. Courtship in dendrobatid frogs involves a complex exchange of auditory, visual, and tactile signals, often lasting several days (40). In any case, the conclusions we draw here apply to an ecologically relevant (male–male) communication system studied under realistic conditions of signal amplitude.

In sum, the co-occurrence of acoustically communicating species has been traditionally explained by invoking spatial and

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temporal segregation of signaling activity as well as spectral segregation of the signals. We found almost no evidence of spatiotemporal segregation and some evidence of signal spectral stratification in the male–male communication system of territorial frogs. Instead, our data support an additional explanation about how species overcome heterospecific noise while concurring for breeding purposes. They might develop a suite of sensory and perhaps cognitive processes that selectively deal with heterospecific signals according to the probability of interference: a context-dependent recognition space.

Methods

We conducted our field recordings and experiments at the Panguana Biological Field Station ($-9.614°$ N, $-74.936°$ W), in the Peruvian Amazon, during November 2005, November 2006, and November 2007–January 2008. Nine species of dendrobatid and one species of leptodactylid frogs were calling during daytime hours within an area of ~2.37 km^2 of old-growth forest. All dendrobatid species at Panguana appear to breed synchronously in advance of and throughout the rainy season (43). Males of these species utter relatively simple (easy to measure and synthesize) advertisement calls based on frequency-modulated tones (notes).

Acoustic Co-Occurrence. Throughout November 2006 and November 2007–January 2008, we recorded 53 samples of the acoustic environment to estimate the extent of overlap in calling activity between each species pair, following protocols published elsewhere (44) (*SI Methods*). To estimate the degree of acoustic co-occurrence, we ran an MDS analysis from the rectangular (acoustic environment sample × species) matrix of calling activity. MDS reproduces the pattern of similarity/distance among several objects (species) in two (or any number of user-defined) dimensions. We used the matrix of pairwise-transformed proximities between species as the covariate co-occurrence in further analyses.

Signal Space. To describe each species' advertisement call, we recorded between five and 29 spontaneously calling males by using standard methods published elsewhere (44, 45, 46) (*SI Methods*). To estimate the potential of measured call parameters for species recognition (25), we ran a canonical discriminant function analysis. The magnitude of between-species divergence in each call parameter was directly estimated from the standardized coefficients in the first two discriminant functions. We also used the result of discriminant function analysis to select the two call parameters that best discriminated between species and, therefore, were used as the main experimental treatments in our estimation of the recognition space.

Recognition Space. We conducted 577 valid playback experiments with 577 synthetic signals on 531 males of five frog species to estimate their recognition spaces. In brief, we (*i*) used the measured properties of each species' advertisement call to synthesize normal and supernormal (i.e., beyond the natural range of variation) stimulus calls, (*ii*) conducted playback experiments on territorial males, (*iii*) used male binary responses (to approach or not the loudspeaker) to build a statistical model of the recognition space,

and, finally, (*iv*) mapped each species' recognition space onto the 2D signal space created by the manipulated call features.

Call synthesis and playback experiments were conducted according to the protocols published elsewhere (29, 33, 47) (*SI Methods*). To estimate each species' recognition space, we built a generalized additive model (GAM) of male binary reactions with one spectral and one temporal call parameter (see *Signal Space* above) as predictor variables. In contrast to general linear models, GAMs fit isotropic nonlinear smooths of a number of predictors, and the response variable can be explicitly nonnormal (48), e.g., binomial in our study. To assess the significance of each predictor, we deleted it from the model and compared the incomplete and the complete models with ANOVA (49). To avoid overparameterization in the models, we ran separate GAMs for the subset of data corresponding to each species. Graphically, each species-specific recognition space was represented as a line encompassing the range of signal variation that would elicit positive phonotactic reactions with a probability of at least 0.99.

We further created a communication space by mapping the recognition spaces onto the 2D signal space. The resulting picture was visually contrasted against our four a priori hypotheses (Fig. 1). If our matched-spaces hypothesis holds, then the recognition space should extend up to about 3 SD of each relevant call parameter, no matter the multivariate distance to the signal of other co-occurring species. If the spectral-partitioning hypothesis holds, then recognition space should be much wider in the temporal than in the spectral domain, allowing it to overlap with the other species' signal space in the former but not in the latter case. Finally, if the filled-gaps hypothesis holds, then the projections of the recognition space should be longer toward the species that appear farther in the signal space.

To explicitly test the latter hypothesis, we tested whether the projection of the recognition space (recognition distance) could be predicted from the pairwise differences in call traits (acoustic distance) while controlling for the degree of species co-occurrence. The three variables were estimated for species pairs that were neighbors in the communication space (i.e., no other species' signal was between them) and that included at least one species used to estimate recognition spaces. Acoustic distance was interpolated from the communication space as the straight-line unitless distance between the centroids of signal parameters of each species pair. The recognition distance was concomitantly estimated from the intersection between the line used to estimate call distance and the line used to delimit a species recognition space. Co-occurrence was estimated from the MDS analysis on the acoustic environments (see *Acoustic Co-Occurrence* above). Because the statistical unit of analysis is a species pair, we ran the corresponding regression model (recognition distance = A*acoustic distance + B*co-occurrence + C + ε) by using permutation techniques on the R package "glmperm" (50) after the modification by W. Werft and A. Benner (51). Briefly, the significance of the regression coefficient (e.g., acoustic distance) was tested by permuting the regression residuals of a second predictor (e.g., co-occurrence).

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