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No phenotypic signature of acoustic competition in songs of a tropical cricket assemblage

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Efficient acoustic communication in multispecies assemblages is challenging due to the presence of heterospecific signals. Masking interference and signal confusion of similarly structured signals can impose fitness costs and, thus, drive evolutionary processes that shape acoustic signals to reduce their overlap in signal space. Although the partitioning of signal space has been frequently studied in frog and bird communities, this topic has received much less attention with reference to insects that communicate acoustically. In this study, we examined the role of acoustic competition in a tropical cricket community and tested the following hypotheses: 1) cosignaling species are expected to exhibit more dissimilar calling songs as compared with species that are spatially and/or temporally separated and 2) species signaling with similar song frequencies, who are thereby subject to energetic masking, are more likely to differ in the temporal domain of their calling songs. Using non-metric multidimensional scaling and pairwise comparison methods to measure acoustic dissimilarity, we found no evidence for either hypothesis: the acoustic signals of species pairs that cosignaled or used similar calling frequencies did not significantly differ from those of species that were spatially/temporally segregated or had large song frequency differences. In conclusion, for the acoustically communicating cricket community investigated, no supportive evidence for the partitioning hypothesis and the widespread belief that acoustic competition has led to divergent selection pressures on signal structure to avoid masking interference was found. Instead, we argue that selection pressures on sensory/neuronal mechanisms seem to more strongly drive reliable communication.

Key words: **acoustic assemblages, acoustic communication, acoustic masking interference, insects, signal divergence, signal space partitioning.**

INTRODUCTION

Acoustic signaling in animals plays a key role in mate attraction, mate choice decisions, and in the process of sexual selection and speciation (Gray and Cade 2000; Panhius et al. 2001; Mendelson and Shaw 2005; Boul et al. 2007; Hoskin and Higgie 2010; Wilkins et al. 2013). The messages encoded in acoustic signals, which usually include information about the sender's identity, condition, and location, must emerge from a background of concurrent signals from other individuals, both conspecifics and heterospecifics. Thus, it is not surprising that the acoustic environment is a major constraint factor that evidently affects acoustic signal evolution (Otte 1992; Gröning and Hochkirch 2008; Grant BR and Grant PR 2010; Brumm 2013; Wilkins et al. 2013). The influence of interfering signals in species-rich assemblages on acoustic communication

systems has frequently been studied, especially in birds (Luther 2009; Tobias et al. 2014), frogs (Chek et al. 2003; Amézquita et al. 2006, 2011), and insects (Sueur 2002; Schmidt et al. 2011, 2013; Balakrishnan et al. 2014; Jain et al. 2014).

Irrespective of the taxonomic group, acoustic signal interference in multispecies assemblages impairs the detection, recognition, and localization of relevant (mating) signals (Wiley 2006). Moreover, signals that are greatly similar might cause signal confusion and lead to mate choice errors (Blackwell and Jennions 1993; Gerhardt et al. 1994; Wiley 2013) that can result in high fitness costs for both the sender and receiver. Heterospecific mating can impose both direct and indirect fitness costs, but even without interbreeding, acoustic interference could lead to waste of time and energy due to the acoustic displays produced, or increases the risk of predation and parasitization while the insects call and search for mates. Selection should, therefore, act on signals and signaling behaviors that reduce their overlap in signal space (Otte 1992; Gröning and

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Hochkirch 2008; Mendelson and Shaw 2012). In fact, a typical result of competition for signal space consists of spatial and temporal partitioning; insects simply signal at different locations or at different times (Hödl 1977; Greenfield 1988; Römer et al. 1989; Sueur 2002; Brumm and Slabbekoorn 2005).

Signal space partitioning (usually with respect to song frequency) is another option for which mixed results have been reported (Sueur 2002; Chek et al. 2003; Planqué and Slabbekoorn 2008; Luther 2009; Amézquita et al. 2011; Schmidt et al. 2013; Tobias et al. 2014). In a comparative study in which 11 frog communities were investigated, Chek et al. (2003) found evidence for acoustic resource partitioning in only 3 communities. Additionally, in 2 studies with Amazonian birds, one found significant less spectral overlap between species, indicating spectral partitioning (Planqué and Slabbekoorn 2008), whereas another yielded opposite results (Tobias et al. 2014). Only a few studies have demonstrated acoustic interference to be a key factor for song divergence (Kirschel et al. 2009; Grant BR and Grant PR (2010). Grant BR and Grant PR (2010), for example, found that temporal features of finch songs (i.e., trill rate and song duration) diverged as a result of changes in a community, supporting the idea that acoustic interactions in species-rich environments can trigger species-specific song parameter shifts with important implications for song evolution and speciation.

According to the sensory drive framework, signals are selected and optimized for the local environment in which they are used (Endler 1992, 1993; Boughman 2002). Therefore, in order to minimize the effects of attenuation and distortion, acoustic signals of different species may adaptively evolve to the habitat acoustics in which the species communicate (acoustic adaptation hypothesis; Morton 1975; Couldridge and van Staaden 2004).

Across species, adult male crickets (Orthoptera: Grylloidea) produce stereotypical, genetically fixed songs with their modified forewings (tegmina) to attract females from a distance. Most importantly, males produce calling songs that are almost pure in tone within a species-specific, relatively small frequency band that ranges between 2 and 10 kHz (Bennet-Clark 1998; Gerhardt and Huber 2002; for an exception, see Robillard et al. 2007). However, the temporal domain of songs is equally important for species recognition (Thorson et al. 1982; Stout and McGhee 1988). The difference in temporal patterns between species is striking (Otte 1992), suggesting that the temporal domain plays at least some role in the way acoustic communities are assembled to ensure efficient communication. This is particularly true for tropical cricket communities, which usually consist of a large number of species (Schmidt et al. 2013; Jain et al. 2014). Thus, crickets are ideally suited to test the hypothesis that signal structuring and adaptation occur as a result of acoustic competition.

In this study, we tested the following hypotheses about community composition in a tropical cricket assemblage: 1) cosignaling species are expected to exhibit more dissimilar calling songs as compared with species that are spatially and/or temporally separated and 2) species signaling with similar song frequencies and, thus, subject to energetic masking are more likely to differ in the temporal domain of their calling songs.

MATERIAL AND METHODS

Sound recordings

Field and laboratory recordings were conducted on Barro Colorado Island in Panama (9°9′N, 79°51′W) during September and October in 2008, from January to April in 2009 and from May to July in 2010. We used a Marantz PDM670 digital recorder (D&M Holdings Inc., Kanagawa, Japan; sampling rate 44.1 kHz) and a Telinga parabolic microphone (Pro7W, Tobo, Sweden) to record sounds in the field. The acoustic census consisted of 5-min recordings taken along marked trails, whereby each recording point was spaced at least 100 m apart. Due to the strong attenuation of cricket songs over a distance (about 30 dB over 16 m; Jain and Balakrishnan 2012 and our own unpublished data), we were confident that the song community recorded at one spot did not overlap with the one recorded 100 m away.

Site sampling was generally conducted in a time window between 6 and 11 PM, at a time of night when the highest level of call activity in the rainforest was expected (up to 70-dB sound pressure level, Lang et al. 2005). During 7 out of 43 nights, we extended the time window to 6 AM the following morning. Some sites were sampled more intensively than others or repeatedly during the same night at regular intervals of 1 h (Schmidt et al. 2013). In 2008, we sampled a total of 16 sites and collected 121 recordings (mean number of recordings per site: 8.64 ± 12.53), in 2009, 94 recordings were obtained at 37 sites (mean number of recordings per site: 2.47 ± 2.06), and in 2010, we obtained 23 recording at 22 different sites (mean number of recordings per site: 1 ± 0.22). In total, we obtained 237 recordings at 54 different sites to determine the rate of cosignaling. There was no significant difference in the rate of cosignaling between years (Kruskal–Wallis test, chi square = 2.671, $P = 0.263$).

To generate a reference sound library, individual male crickets were captured and recorded in the laboratory using an automated setup with electret microphones (frequency range: 50–16.000 Hz, LM-09, Hama, Monheim, Germany) and digitized at a sampling rate of 20 kHz (PowerLab 4/25, series 4/25, ADInstruments, Sydney, Australia). Analyses of song features (carrier frequency, pulse rate, pulse duration, pulse interval, pulses/chirp, chirp duration, and chirp interval; Figure 1) from field and reference recordings were performed using audio software CoolEdit Pro 2.0 (Syntrillium, Phoenix, now Adobe Audition). Temporal features were evaluated manually from oscillograms, and carrier frequencies were determined from power spectra at a frequency resolution of 86 Hz. Where necessary, field recordings were bandpass filtered at a cutoff frequency 150 Hz above and below the respective carrier frequency to extract clear temporal features of the song. Song features of a total of 18 species were analyzed (Table 1).

Taxonomy

Taxonomic identification of cricket species was performed by following the original descriptions published by Hebard (1928) and Nickle (1992). However, a comprehensive state of the art description of
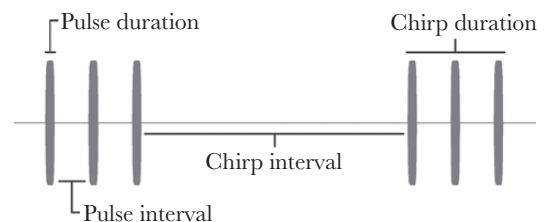

Figure 1
Terminology for temporal features of the cricket calling song. Pulse rates are calculated as pulses/second, based on the number of pulses/chirp, or, in case of trilling species (i.e., those that produce continuous pulse trains), the time of the trill with 10 pulses.

Table 1
Summary of species-specific acoustic parameters and calling height (mean ± standard deviation)

	N	Carrier frequency (kHz)	Pulse rate (Hz)	Pulse duration (ms)	Pulse interval (ms)	Pulses/chirp	Chirp duration (ms)	Chirp interval (ms)	Calling height (m)
Aclodes sp. 2	24	3.13±0.17	27.5±2.0	28.5±1.7	8.2±1.8	13±1	452±56	977±231	1.5±1.4
Aclodes sp. 1	19	3.16±0.12	69.8±3.0	9.8±0.5	4.3±0.5	38±5	550±82	14706±9511	6.3±5.6
Paroecanthus podagrosus	26	3.84±0.25	206.2±17.0	2.3±0.7	2.0±0.7	5±1	23.7±3.3	13.2±2.1	38.5±2.2
Orocharis sp. 2	19	4.07±0.38	270.8±30.2	2.2±0.4	1.1±0.4	58±22	209±62	887±742	28.7±8.0
Amblyrhethus sp.	20	4.41±0.20	16.7±1.5	30.0±2.6	33.0±6.3	—	—	—	33.5±5.0
Aclodes sp. 3	25	4.77±0.19	36.0±2.8	21.0±1.3	10.6±1.4	3±0	83.1±6.5	1226±356	1.6±2.0
Ethospecies 1	14	4.91±0.18	46.5±5.0	16.9±1.3	7.1±0.8	2±0	44.4±5.7	269±70	36.2±4.8
Diatrypa sp. 1	14	5.20±0.14	134.9±4.3	5.7±0.5	1.1±0.4	18±2	137±13	319±70	34.8±6.0
Orocharis sp. 1	18	5.34±0.15	90.6±3.4	6.9±0.7	3.3±0.8	95±12	1050±145	3197±367	9.6±7.4
Ethospecies 2	22	5.77±0.26	20.2±2.1	37.4±3.2	23.4±2.2	2±0	101±8	1345±288	28.9±8.7
Ethospecies 3	13	5.92±0.26	156.2±5.1	3.6±0.5	1.9±0.3	70±15	452±99	1165±453	—
Diatrypa sp. 2	22	6.38±0.20	15.2±0.8	24.3±2.3	45.4±4.3	—	—	—	10.6±5.6
Anaxipha sp. 1	32	7.43±0.35	54.9±9.8	13.7±3.0	4.9±1.5	8±1	137±20	1046±390	24.9±10.6
Anaxipha sp. 2	31	7.49±0.58	70.1±5.7	9.9±1.4	3.8±1.3	10±3	151±42	884±305	32.9±8.9
Anaxipha platyptera	19	7.61±0.30	45.4±3.0	14.4±1.5	7.5±1.4	—	—	—	—
Ornebius sp. 1	33	8.37±0.24	83.6±4.7	8.6±1.1	3.0±0.8	9±1	109±11	304±22	27.3±9.4
Ornebius sp. 2	31	8.50±0.29	76.9±5.1	9.3±0.9	3.9±0.7	4±0	52.1±3.7	164±14	18.1±9.7
Cycloptiloides sp.	22	9.39±0.32	3.8±0.5	13.9±1.9	323±28	—	—	—	4.5±1.7

Panamanian cricket species is still lacking, and their taxonomic determinations are still under discussion. While a consensus that the superfamily Grylloidea is monophyletic exists (Song et al. 2015), the hierarchical structure and relationships among the subfamilies, particularly within the Gryllidae, are controversial (see Jost and Shaw 2006, and most recent references in the Orthoptera Species File, Eades et al. 2015). Voucher specimens were deposited at the Zoological Research Museum Alexander Koenig in Bonn, Germany and the Muséum National d'Histoire Naturelle in Paris, France, for further examination, and if necessary, will be redescribed and phylogenetically analyzed.

Cosignaling

Based on the 237 outdoor sound recordings taken, species presence–absence data extracted from each of the single 5-min recordings were evaluated. To quantify the degree of cosignaling, a similarity index after Kulczynski (Krebs 1999) was measured between each species pair (15 species in total, 105 pairwise comparisons) using the software package PAST (Hammer et al. 2001). The Kulczynski index for binary data (presence–absence, encoded as 1 or 0) was calculated as: $d_{jk} = [M/(M + N_1) + M/(M + N_2)]/2$. When comparing 2 rows (i.e., species), a match M was counted for all columns (i.e., recordings) when a presence was observed in both rows. N is the total number of presence occurrences for either of the species (N_1 and N_2 refer to the 2 rows being compared). Values could range between 0 (species pairs never detected in the same recordings) and 1 (species co-occurring in all recordings). Not included in this data set were *Paroecanthus podagrosus*, *Anaxipha* sp. 2, and *Anaxipha platyptera*, which were not or were only rarely detected in sound recordings.

Tropical rainforests are characterized by their complex vertical structure (Leigh 1999). Thus, in order to identify species composition in this dimension more precisely, sound recordings were obtained at 5 m intervals from a canopy tower (height 40 m) in order to estimate the vertical stratification of signalers, incorporating a total of 16 species (not detected: ethospecies 3 and *A. platyptera*). Sampling was performed between 7 and 11 PM on 4 sampling nights in 2009 and 10 nights in 2010, resulting in a total of 112 recordings.

Acoustic dissimilarities, spatiotemporal, and signal space partitioning

To determine the differences in signal space among all 18 species, mean values for carrier frequency, pulse rate, pulse duration, and pulse interval (Table 1) were log transformed, and the Euclidean distances were calculated using PAST (Hammer et al. 2001). We used only these 4 acoustic parameters for 2 reasons: 1) because they are the most important ones for species recognition (Gerhardt and Huber 2002) and 2) to ensure that all species pair comparisons made among the 18 chirping and trilling species were based on the same acoustic parameters when calculating the similarity/dissimilarity matrix (i.e., the Euclidean distance).

In order to investigate partitioning between species within the community, the differences in cosignaling and acoustic dissimilarity were tested separately for randomness. During the first step, the presence–absence matrix of cosignaling and the mean acoustic values were subjected to a non-metric multidimensional scaling (NMDS) analysis. The NMDS analysis allowed us to project object similarities in a 2D scatterplot while preserving pairwise object distances (indicated by a stress factor for which a value <0.2

was considered acceptable; Clarke 1993). In our case, the selected similarity index of cosignaling was based on that of Kulczynski (Figure 2a) and for acoustic parameters, on Euclidean distance (Figure 3a); differences among all multidimensional acoustic features between any 2 species were considered. The resulting similarity/distance matrix was then projected into a 2D space based on ranked differences such that the relative distance between the species was retained. The point pattern distribution of NMDS was then statistically analyzed using Ripley's K method (PAST, Hammer et al. 2001). This method reveals patterns that deviate from random distribution effects (clustered or dispersed patterns) by incorporating distance effects such as regularity on a small scale or dispersion on a large scale (Dixon 2002; Wiegand and Moloney 2004). A 95% confidence interval for complete spatial randomness was estimated using 1000 Monte Carlo simulations (PAST, Hammer et al. 2001).

We also considered phylogenetic correlations with reference to acoustic distance and cosignaling. However, because of the current lack of clarity about phylogenetic relationships among Panamanian crickets, we followed the method applied by Tobias et al. (2014). We used standard taxonomic sources to generate pairwise taxonomic distances between all species and scored pairs of congeners as 1,
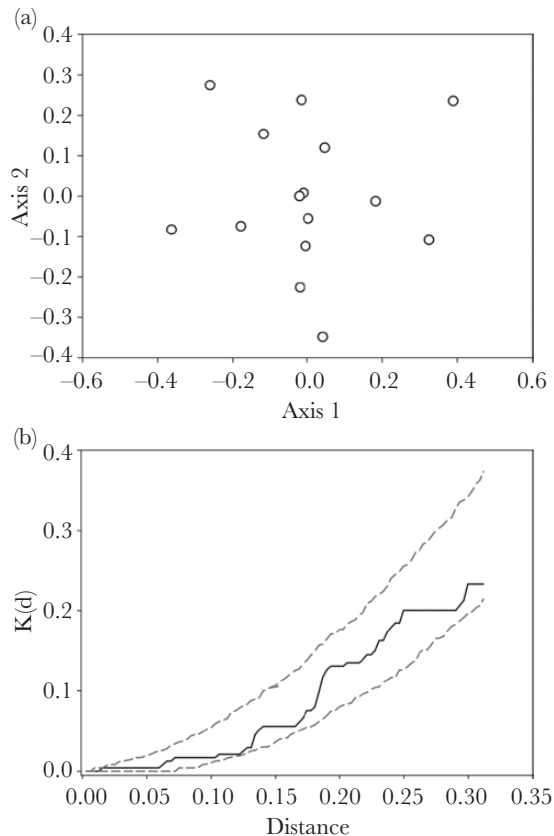
members of the same subfamily as 2, members of the same family as 3, and members of different families as 4. We then tested these taxonomic relationships for their effects on acoustic distance and cosignaling using general linear models. Acoustic distances were Box–Cox transformed to ensure normal distribution.

Finally, to test the hypothesis that cosignaling species are expected to exhibit more dissimilar calls than those that do not signal together, we compared the acoustic dissimilarity of species pairs between 3 groups that had 1) low, intermediate, and high rate of cosignaling and 2) small, intermediate, and large calling height differences, respectively. To examine whether species that use spectrally similar calling songs differed in their temporal call structures, we compared the temporal acoustic dissimilarity of species pairs between 3 groups with small, intermediate, and large differences in song frequency. In order to create the 3 groups, the total number of species pairs obtained for the rate of cosignaling ($N = 105$), calling height differences ($N = 120$), and differences in song frequency ($N = 153$) were divided into thirds. Statistical comparisons between the 3 groups were based on repeated measurements with Anova. To ensure the normality of data, values were Box–Cox transformed. Mean values are presented ± standard deviation.

Figure 2
(a) Result of NMDS, illustrating the differences in cosignaling among 15 cricket species recorded in their natural habitat. The small and large distances between points (i.e., species) indicate the high and low degrees of cosignaling, respectively. (b) Statistical analysis of data points in (a) with $K(d)$ values for interspecific differences of cosignaling, conducted using Ripley's K-test to determine randomness. $K(d)$ values (solid line) show random distribution, suggesting that cosignaling between species in the community is randomly structured over distance (scale of analysis: relative difference of cosignaling). The 95% confidence interval (gray dashed lines) indicates the range of complete spatial randomness.
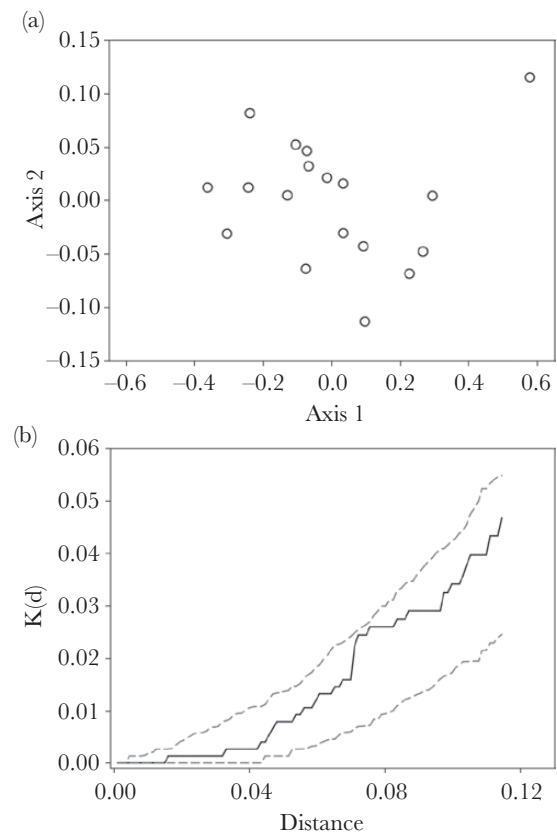

Figure 3
(a) NMDS scatter plot of the species' ($N = 18$) acoustic dissimilarities based on the Euclidean distance of 4 acoustic parameters (i.e., carrier frequency, pulse rate, pulse duration, and pulse interval). (b) Spatial analysis of data points in (a), with $K(d)$ values for interspecific acoustic dissimilarity, conducted using Ripley's K-test to determine randomness, suggesting that signal space is randomly structured. $K(d)$ values (solid line) within the 95% confidence interval (gray dashed lines) over distance (scale of analysis: relative difference of acoustic dissimilarity).

RESULTS

Spatiotemporal partitioning

Cosignaling species were sufficiently well represented in a 2D scatterplot, based on species presence–absence data in the habitat (NMDS analysis: stress factor = 0.18; Figure 2a). Small differences between the points indicated a high degree of cosignaling, whereas large differences illustrated small degree of cosignaling. In order to test for community-wide partitioning of cosignaling, the spatial distribution of data points in Figure 2a was analyzed. No segregation between species was revealed ($P > 0.05$, random distribution; Figure 2b).

Acoustic dissimilarity and signal space partitioning

The Euclidean distances, measures of acoustic dissimilarity between the species, ranged from 0.07 to 3.21 with a mean of 1.02 ± 0.67 ($N = 153$ species pairs, 18 species). Acoustic parameters were subjected to an NMDS analysis (stress factor = 0.02; Figure 3a), and the subsequent spatial analysis of data points (i.e., differences among acoustic signals between species) revealed a random distribution ($P > 0.05$; Figure 3b).

Effect of cosignaling on signal structure

We found no correlation between species cosignaling and the dissimilarity of their acoustic signals. Thus, the 3 groups with low (0.06–0.36), intermediate (0.36–0.49), and high (0.50–0.68) rates of cosignaling were not statistically different (Anova repeated measurements: $F_{0.165} = 0.350$, $P = 0.706$; N/group = 35; Figure 4a).

Likewise, the analysis of vertical stratification showed that signals communicated between species pairs that were signaling at similar heights (i.e., calling height differences of 0.1–8 m) were not significantly dissimilar as compared with those signaling with intermediate (8–23 m) and large (>23 m) differences in calling height (Anova repeated measurements: $F_{1.158} = 2.262$, $P = 0.111$, N/group = 40; Figure 4b).

Song frequency and temporal acoustic dissimilarity

We found no significant difference between temporal acoustic dissimilarity and the degree of song frequency difference (small = 0.03–1.23 kHz; intermediate = 1.24–2.73 kHz; large = 2.74–6.26 kHz; Anova repeated measurements: $F_{0.363} = 0.707$, $P = 0.496$; N/group = 51; 18 species; Figure 5a). Incorporating 3 additional temporal parameters such as pulses per chirp, chirp duration, and chirp interval in the analysis led to an overall increase in the temporal dissimilarity (Figure 5b), but again, no significant difference between the 3 groups could be measured (Anova repeated measurements: $F_{0.150} = 0.460$, $P = 0.634$; N/group = 30; 14 species). Taken together, none of the variables (i.e., song frequency difference, rate of cosignaling, and calling height difference) were predictors for the temporal acoustic dissimilarity of the species pairs (multiple regression analysis, Anova: $R^2 = 0.01$, $F_{0.129} = 0.245$, $P = 0.865$, $N = 91$).

Phylogenetic patterns of acoustic distance and cosignaling

When considering phylogenetic relationships, we found only a weak and inconsistent correlation between these and acoustic distance and cosignaling. Although the significance test for an overall effect of taxonomic distance on acoustic signals was positive
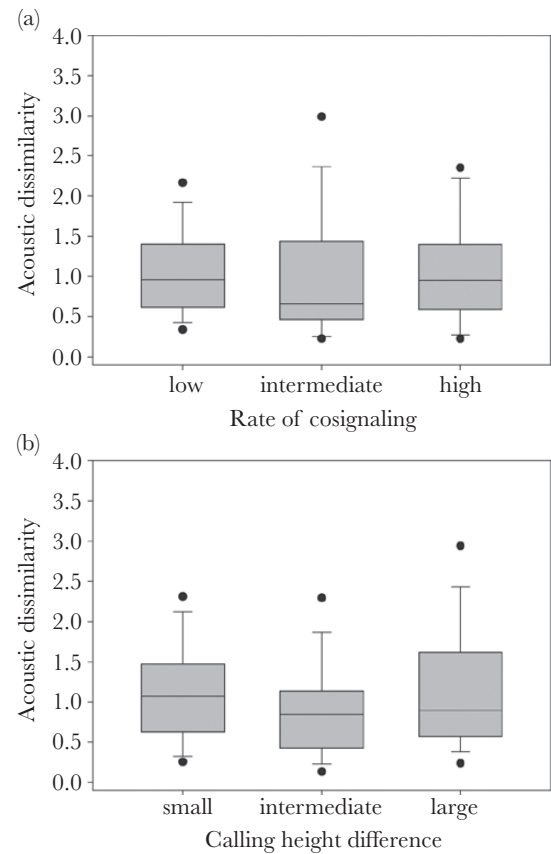

Figure 4

Comparison of acoustic dissimilarity of calling songs between species pairs depending (a) on the rate of cosignaling and (b) calling height difference. Boxes show the range from the 25th to 75th percentiles, the solid horizontal line depicts the median value, and circles represent the 5th and 95th percentile outliers.

($F_{1.482} = 3.32$, $P = 0.023$), the post hoc pairwise comparisons of the 4 taxonomic rankings revealed no significant group differences (Tamhane T2 test for unequal group variances, $P > 0.05$). Testing the rate of cosignaling (i.e., species calling at the same time and place) for phylogenetic correlations yielded in a significant result ($F_{0.015} = 3.304$, $P = 0.026$). However, this effect was only detectable between taxonomic groups 3 (members of the same family) and 4 (members of different families) (post hoc analyses: Tukey test, $P = 0.017$).

DISCUSSION

In this study, we examined the role of acoustic competition on calling song structure in a species-rich, tropical cricket community. We hypothesized that species exhibiting 1) a high rate of cosignaling or 2) calling with similar song frequencies are expected to have songs that are acoustically dissimilar or differ in their temporal domains, respectively. However, based on the present results, we found no support for the hypothesis that signal structure in the observed acoustic community was shaped by acoustic competition. One explanation for this negative result may be the overall low degree of call overlap between species. Some conclusive evidence suggesting that acoustic overlap is weaker than is usually assumed has been presented for a paleotropic cricket and katydid acoustic assemblage in India, where the amount of masking interference was rigorously
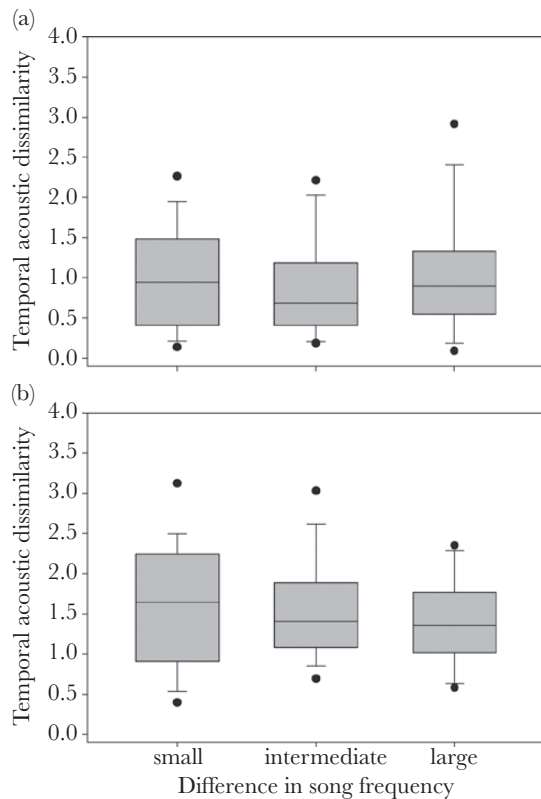
Figure 5
Analysis of temporal signal structure for 18 species based on pulse rate, pulse duration, and pulse interval (a) and for 14 chirping species based on pulse rate, pulse duration, pulse interval, pulses/chirp, chirp duration, and chirp interval (b) depending on differences in calling song frequencies. Species pairs using similar calling song frequencies were expected to show a higher degree of temporal acoustic dissimilarity. Boxes show the range from the 25th to 75th percentiles, the solid horizontal line depicts the median value, and circles represent the 5th and 95th percentile outliers.

tested (Balakrishnan et al. 2014; Jain et al. 2014). In these studies, in addition to temporal and spectral overlaps, as well as the relative positions of individuals in the habitat, the authors considered the hearing sensitivity and tuning properties of the receivers. Together with the call intensities and attenuation profiles of calls in the habitat, they integrated these data in 3D acoustic space simulation models and noted that the effective acoustic overlap (EAO) was close to 0 (Jain et al. 2014). Thus, where sufficiently large signal space is available, such a low level of acoustic overlap may be present in contemporary communities, suggesting that masking interference does not constitute a major problem. The observed contemporary community and its low associated EAO may be the result of a species sorting process, in which acoustic competition between any newcomer and the pre-existing species inevitably results in local extinction for one of them.

Tobias et al. (2014) addressed the issue of signal space segregation in birds and argued that acoustic competition is too weak to exert significant costs that might drive the evolution of structurally dissimilar signals and signal partitioning. On the contrary, considering only the spectral axis of the signal as a direct source of masking interference for the cricket community investigated here, we found some support for the spectral niche hypothesis (Schmidt et al. 2013; see also acoustic niche hypothesis: Krause 1987; Farina 2014). The results of our study demonstrated that call frequency overlap

between most species pairs in the cricket assemblage was extremely low and significantly smaller than what was expected to occur by chance (Schmidt et al. 2013; Schmidt and Balakrishnan 2015). Nonetheless, even species that show no frequency overlap are not acoustically separated, but in one another's detection ranges when they use similar calling frequencies. This is especially true when species tend to call together, as demonstrated by Jain et al. (2014). The authors found low spectral overlap between the majority of species pairs in the assemblage, but a relatively high temporal overlap (i.e., species calling together) for a considerable number of pairs. However, when considering the differences in song frequencies, we found no partitioning in the temporal domain of signals (Figure 5).

Grasshopper communities should be more strongly affected by the problem of masking interference because of the broadband frequency spectra of their signals; only the temporal domain of their songs remains for species recognition. Moreover, because grasshoppers usually inhabit simply structured grassland areas, they have fewer possibilities for spatial segregation as compared with species distributed in communities in tropical rainforests. Therefore, one could expect a higher selection pressure on signal structure in a densely packed communication channel. Indeed, a few studies have provided evidence that songs in syntopic, species-rich Eurasian grasshopper communities exhibit pronounced differences in temporal fine structure, leading to partitioning of the acoustic signal space (Bukhvalova 2006; Tishechkin and Bukhvalova 2009).

Reasonable explanations for the absence of signal partitioning can be found when we look at the problem of signal interference from a receiver's perspective (the receiver psychology; Guilford and Dawkins 1991). For example, it has already been shown that some of the species in the cricket community investigated here possess a more sharply tuned song carrier frequency than field crickets, which communicate without the competitive signals of heterospecific signalers (Schmidt et al. 2011; Schmidt and Römer 2011). Such frequency selectivity enables receivers to effectively suppress the noise (i.e., adjacent neighboring frequencies) from heterospecific signalers and reliably extract the species-specific song pattern. Simulation models have indeed confirmed that frequency tuning is the most powerful mechanism used to reduce masking interference (Jain et al. 2014). With respect to the temporal song pattern, crickets possess very effective filters for species-specific song characteristics, and the respective filters in the brain do respond selectively to a given pulse pattern, even when only 2–3 pulse intervals have been perceived (Kostarakos and Hedwig 2012; see also Hennig et al. 2014). Thus, species-specific differences in song structure alone might be sufficient, allowing receivers to avoid confusing signals from conspecifics with those from other calling species in the community (Seddon and Tobias 2010; Amézquita et al. 2011; Tobias et al. 2014).

Apart from acoustic competition, other factors have been discussed that potentially influence signal diversity (Wilkins et al. 2013), one of which is related to physical features of the habitat and their sound transmission properties (Morton 1975; Hunter and Krebs 1979; Endler 1992; Couldridge and van Staaden 2004; Ey and Fischer 2009; Tobias et al. 2010). Although the role of transmission properties for the cricket songs was not explicitly addressed for the community examined in this study, no compelling evidence that sound signals of crickets and katydids are shaped for optimal transmission thus far exists (Diwakar and Balakrishana 2007; Jain and Balakrishnan 2012; Montealegre et al. 2014). A reason for this is that the transmission distance might be constrained by predation and and/or parasitization risks, which exert selective pressure

against conspicuous calling songs (Cade 1975; Zuk and Kolluru 1998; Gerhardt and Huber 2002; Zuk et al. 2006; Römer et al. 2010). In addition, no support has been presented for indirect selection in crickets due to pleiotropic effects that link song differentiation as a by-product to ecological or morphological adaptions to the environment (Otte 1992; Jones 1997; Podos 2001).

Acoustic competition has been hypothesized to lead to divergent selection pressures on signal structure in order to avoid masking interference (Wilkins et al. 2013). However, in this study, we found no support for the hypothesis that acoustic signal partitioning occurs. Instead, we argue that selection on sensory mechanisms seems to play a more important role for reliable communication. The community described here, however, is not complete and is possibly derived from a larger species pool. Specifically, not all existing species were considered in the analysis; some were left out because they were too rare, whereas others might not have been detected at all. Cricket populations can fluctuate considerably from season to season, thereby creating a strong stochastic element that would argue against stable evolutionary outcomes. For this reason, the current ecological factors (e.g., the presence of new species that compete for acoustic space with the existing, local pool of species) play important roles in determining the acoustic signature of the assemblage and reduce the importance of the fine-tuned evolutionary response of a single species.

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