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Original Article

Spectral niche segregation and community organization in a tropical cricket assemblage

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In species-rich biomes such as tropical rainforests, the efficiency of intraspecific acoustic communication will strongly depend on the degree of signal overlap. Signal interference deteriorates detection, recognition, and localization of conspecific signals. Thus, the communication space should be partitioned sufficiently to reduce masking interference and to promote intraspecific communication. Here, we studied the community organization of a tropical cricket assemblage with respect to its multidimensional niche axes, such as song frequencies, space (horizontal and vertical), and time, affecting acoustic communication. We used the null model approach to test whether observed community patterns differed from those expected by chance. The assemblage clearly showed partitioning in the spectral domain of calling frequencies of their songs. Furthermore, the range of song frequencies occupied by species is positively correlated with the distance to the average calling frequency of its adjacent neighbors. Thus, species tended to use a greater range of frequency channels for intraspecific communication if the frequency space is available. Our results support the idea that competition for the acoustic communication channel may have resulted in niche segregation along the frequency axes. Concerning the spatiotemporal organization at the community level the spatial (horizontal) distribution appeared to be randomly structured, whereas we found a significant vertical stratification between species. At a temporal scale, the assemblage aggregated their calling activity with an observed niche overlap significantly greater than expected by chance. However, combining the spatial and temporal distribution resulted in low co-occurrence of pairwise species association, consequently reducing chances for masking events. *Key words:* acoustic communication, community pattern, competition, insects, niche segregation, null models. *[Behav Ecol]*

INTRODUCTION

Acoustic advertisement signals in animals are used to attract mates from a distance or in competitive interactions between males (Bradbury and Vehrencamp 2011). The communication channel used to convey the information can principally be regarded as an ecological resource, which—like other resources—may also be limited depending on the number of senders (competitors) and their overlap of channel (resource) exploitation. Thus, an increasing number of species and individuals using the same channel will inevitably decrease the chances of successful communication. In biological systems, competition for a communication channel has been investigated for the first time for chemical communication in moths (Greenfield and Karandinos 1979; Greenfield 1983; Löfstedt and Pers 1985; Löfstedt et al. 1991), and more recently for orchid bees (Zimmermann et al. 2009).

Most impressive examples from mixed-species choruses of birds (Klump 1996), anurans (Narins 1982; Gottsberger and Gruber 2004), and insects (Gogala and Riede 1995; Sueur 2002; Diwakar and Balakrishnan 2007a) demonstrate that acoustically communicating animals compete for communication channels as well. Signal interference due to heterospecific songs with overlapping frequencies hinders detection, recognition, and localization of conspecific signals (Wollerman 1999; Wollerman and Wiley 2002; Brumm and Slabbekoorn 2005; Bee 2008; Bee and Micheyl 2008; Schmidt and Römer 2011). Recent work has also revealed the negative impact of acoustic masking events with its consequences on reproductive success and foraging efficiency in birds (Halfwerk et al. 2011) and bats (Siemers and Schaub 2011), respectively. In technical systems, transmission of information through analog channels has been extensively investigated (since Shannon 1948), and the optimal distribution of neighboring radio frequencies seems to be analogous to the problems of interspecific acoustic competition in rainforests investigated here.

Thus, in order to avoid these negative effects of acoustic competition, communication space should be partitioned among species. Indeed, various strategies and mechanisms have been reported to reduce signal overlap. On the one hand, species are able to partition their calling activity in space and/or time as it has been shown for frogs (Hödl 1977; Duellman and Pyles 1983; Chek et al. 2003), birds (Ficken et al. 1974; Popp et al. 1985; Planqué and Slabbekoorn 2008; Luther 2009), and insects (Greenfield 1988; Römer et al. 1989; Sueur 2002; Diwakar and Balakrishnan 2007b). Masking interference can also be minimized by partitioning of the frequency domain (Drewry and Rand 1983; Heller and Helversen 1989; Kingston et al. 2000; Amézquita et al. 2005; Jones and Siemers 2010).

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In habitats with high species diversity such as tropical rainforests (Erwin 1982), the likelihood that species with similar traits co-occur is higher compared with temperate zones and thus one would expect increased acoustic competition. Indeed, especially the nighttime choruses in tropical forests result in elevated acoustic noise levels mainly due to signaling insects (Ellinger and Hödl 2003; Lang et al. 2005; Diwakar and Balakrishnan 2007a) with background noise levels reaching 70 dB SPL (sound pressure level) (Lang et al. 2005). A great proportion of the acoustic energy in the background is caused by crickets in a rather restricted audio frequency band from 3 and 9 kHz (Riede 1993; Nischk and Riede 2001; Diwakar and Balakrishnan 2007a; Schmidt et al. 2011). Male crickets emit calling songs by rubbing their wings, generating species-specific carrier frequencies (CFs) (i.e., the signal frequency with the greatest amount of acoustic energy, see Figure S1 in Supplementary Data). Calling songs ranging from 1.5 to 11 kHz (Bennet-Clark 1998) attract females from some distance as a first step in mate choice (Gerhardt and Huber 2002; for exceptions of cricket taxa also exploiting high sonic or ultrasonic frequencies, see Robillard 2009). Besides frequency calling songs exhibit well-defined, species-specific temporal patterns (Figure S2), thereby providing reliable features for classification of recognizable taxonomic units, equivalent to morphospecies (Riede 1993; Sueur et al. 2008) or even providing better taxonomic resolution (e.g., in the case of cryptic species; Walker 1964). Thus, species-specific songs are an ideal opportunity for rapid classification and mapping of a species-rich community (Riede 1993; Diwakar et al. 2007; Sueur et al. 2008; Depraetere et al. 2012).

The situation of high cricket diversity combined with the relatively narrow frequency range used for intraspecific communication in each species provides an ideal example of an assemblage prone to acoustic competition. Following Greenfield's suggestion to consider the communication channel as niche space (Greenfield 1983), one can distinguish 3 dimensions: frequency, space (both horizontal and vertical), and time. Although calling songs differ considerably in their temporal pattern (see Figure S2), this does not prevent acoustic masking if songs are broadcast with similar CFs (i.e., within the same frequency channel). In this study, we investigated acoustic resource partitioning in a species-rich tropical cricket community based on acoustic sampling of their species-specific songs. We analyzed the cricket assemblage with respect to its acoustic (spectral), spatial, and temporal composition and used null models to test if observed community patterns differed from those expected by chance. In null models, randomized data sets (null communities) are generated in the absence of any potential mechanisms (e.g., competition), thus providing a useful statistical tool in community ecology and biogeography (Gotelli and Graves 1996; Gotelli 2001).

We hypothesize that, at least partly, sufficient separation can be expected along the frequency axes between species of the assemblage. Support for this idea comes from previous results showing that frequency tuning in receivers is more selective for tropical rainforest species compared with their European counterparts with low interspecific acoustic competition, suggesting a possible adaptive role in frequency partitioning (Schmidt and Römer 2011; Schmidt et al. 2011).

As a consequence of narrowing frequency tuning, we also expect that interindividual variation of CFs in conspecific senders should be reduced (matched filter hypothesis; Capranica and Moffat 1983; Wehner 1987). This would allow the community to partition the frequency space efficiently, resulting in a more densely packed, species-rich assemblage. Moreover, spatial and/or temporal segregation might lead to further reduction of acoustic interference.

MATERIALS AND METHODS

Study site

The study site Barro Colorado Island (BCI; 9°9′N, 79°51′W, Republic of Panama) is a 1600 ha–sized island within Gatun Lake formed in the course of construction of the Panama Canal in the early 1900s. BCI holds diverse, moist lowland tropical forest protected from human disturbance, but highly accessible thanks to a well-documented net of trails. The reserve forms part of the Smithsonian Tropical Research Institute (STRI), which coordinated intensive research providing a wealth of long-term climatic, faunistic, and floristic data (Leigh et al. 1982) including a 50-ha plot (Harms et al. 2001). Rainfall is highly seasonal, with a mean dry season of 107 days from January to March (Condit 1998). The research was conducted during both the rainy seasons in September/October 2008, May to July 2010 and the dry season from January to April 2009.

Forest habitats on BCI can be differentiated between 2 types of secondary forests (80–130 and 120–130 years old) and old-growth forests with and without palms, which are at least more than 400 years old (Leigh 1999; Mascaro et al. 2011). Our sample points included all types of forest, including the 50-ha plot and an observation tower within the Lutz catchment allowing canopy access, which reached 48 m at this locality. A detailed forest age map is available as GIS file at STRI's GIS data portal (http://mapserver.stri.si.edu/geonetwork/srv/en/main.home), together with trail markers, soil, and elevation information.

Acoustic census and sampling protocol

This study focused solely on crickets (Orthoptera: Grylloidea) because masking interference of acoustic signals with other taxonomic groups was negligible. Cicadas on BCI are not very prominent and only active during the day. Co-occurring katydids on the island are characterized with calling songs well above 10 kHz and do not overlap with crickets in this respect. The cricket and frog calling activity was fairly disjoined. Choruses of frogs mostly coincide with periods of precipitation, and this, in turn, suppressed cricket calling activity, which recovered soon after frogs stopped calling. Moreover, calling sites of frogs on BCI are usually restricted to small pools of standing water (Ryan 1983), thus indicating spatial separation as well.

The singing cricket community was assessed by regular recordings within the habitat and complemented by recordings of captured males in the laboratory. Habitat recordings were made using a Telinga parabolic microphone Pro7W (Telinga, Tobo, Sweden) and a Marantz PDM670 digital recorder (D&M Holdings Inc., Kanagawa, Japan) at a sampling rate of 44.1 kHz. The parabolic microphone was used to "pick out" calling songs of individuals to obtain unobstructed songs for identification. Acoustic census was carried out between 18 and 23 h, and it regularly extended throughout the night. Sampling of sites consisted of 5-min recordings obtained along marked trails, where every recording point was spaced at least 100 m apart. In total, we sampled 56 different sites and obtained 253 recordings. Some sites were sampled intensively, across different nights and also repeatedly at the same night in a regular interval of 1 h. Thus, sites were sampled ranging from 1 to 13 recordings per night and up to 4 different nights in a respective season (maximum number of recordings per site and season = 37). Additional 112 recordings were performed on a canopy tower to obtain information about the vertical stratification of calling heights.

The analysis of acoustic features was performed using audio software CoolEdit Pro 2.0 (Syntrillium, Phoenix, USA, now Adobe Audition). A spectral analysis of field recordings contained several simultaneously singing cricket species and individuals (Schmidt et al. 2011). Recordings were filtered by a bandpass with a cut-off frequency 150 Hz above and below the respective CF (see Figure S1 in Supplementary Data). This provided clear, identifiable oscillograms of calling songs from which additional cues like pulse rate and secondary/tertiary pulse structure (chirps) were derived to identify species-specific temporal features (see Figure S2). Individual CFs were determined with a frequency resolution of 86 Hz.

To assign classified songs recorded in the habitat to a respective morphospecies, we caught adult male crickets by sweep-netting and hand collection in the forest and at lights around the research station. All captured crickets were kept in plastic terrariums and fed ad libitum with fish flakes, oats, fruits, lettuce, and water. Calling songs of males were recorded in the laboratory at an ambient temperature of 24 °C. Songs were recorded from isolated males with an automated setup using electret microphones (frequency range: 50–16 000 Hz, LM-09, Hama, Monheim, Germany) placed near the animal and digitized with an analog to digital converter at a sampling rate of 20 kHz (PowerLab 4/25, series 4/25, ADInstruments, Sydney, Australia). In order to later correlate CF with body size, we determined pronotum width of the 15 most frequent species as mass-independent measure based on digital photo images using ImageJ 1.4 (Rasband 1997–2011).

Taxonomy

The highest concentrations of insect species in the world can be found in Mesoamerica and the Isthmus of Panama (Quintero and Aiello 1992). A first checklist of Panamanian Orthoptera was published by Nickle (1992), but a recent large-scale collecting effort covering all insects and arthropods from soil to canopy at 2 Panamanian sites (IBISCA, Pennisi 2005) yielded a considerable number of orthopterans whose identities have not yet been determined (Sperber G, personal communication). Like most other neotropical insects, the taxonomy of crickets is insufficiently known, but solid fundamental work has been done by Hebard and Rehn in the 1920s, based on material collected in the canal area (Hebard 1928). We continued with an inventory, trying to document a maximum of songs from identified voucher specimen recorded in captivity. Original descriptions such as those by Hebard (1928) are detailed, but lack information about genital morphology as being used in more recent taxonomy (cf. Otte 2006). His studies from Costa Rica (Otte 2006) and the Caribbean (Otte and Perez-Gelabert 2009) revealed a surprising number of species new to science. Their numerous descriptions of new species are often based on male genitalian anatomy, but lack data about songs. Ideally, a comprehensive description should contain morphology including male genitalia, bioacoustic analysis of songs, and molecular data ("integrative taxonomy": Dayrat 2005). For the time being, it is evident that the neotropical cricket fauna in general, and the Panamanian fauna in particular, is surprisingly rich and insufficiently known, with high regional but limited local diversity. In addition, delimitation of genera and higher taxonomy is heavily disputed and in flux. Therefore, we have deposited voucher specimens at the Zoological Research Museum Alexander Koenig for subsequent taxonomic determination or reexamination and subsequent genetic barcoding analysis (sensu Hebert et al. 2003). For references and higher taxonomy of crickets, we followed the Orthoptera Species File online (Eades et al. 2012).

Niche overlap and null model analyses

The community structure was analyzed with respect to its composition in 3 niche axes: frequency, space, and time. The degree of competition between the species is reflected by the amount of overlap in any of the 3 axes. To determine the overlap in resource use, we calculated the Czechanowski index (Feinsinger et al. 1981) of niche overlap between each pair of species:

$$O_{12} = O_{21} = 1 - 0.5\sum_{i=1}^{n} \left| p_{i1} - p_{i2} \right|$$

where O_{12} is the overlap of species 1 on species 2 and p_{i1}, p_{i2} is the frequency of utilization of resource state i by species 1 and 2, respectively. The calculated indices range from 0 (species share no resource at all) and 1 (species have identical resource utilization distribution).

Next, we used the null model approach to test whether the observed overlap of the assemblage differs from those by chance, that is, the expected overlap in the absence of mutualistic or competitive interactions. Data for each null model are organized as a matrix in which rows are species and columns are resource states (frequency channel occupied by each individual, locality in the habitat, and hours of the night). To generate the null community, a number of different randomization algorithms (RA1–RA4) have been proposed (Winemiller and Pianka 1990), which differ from each other in the dispersion of allowed states for each species and the nature of the distribution used for shuffling. To create randomized assemblages, we used RA3 to calculate frequency and temporal overlap and RA2 for spatial overlap. Both algorithms are the ones, which are usually recommended because of their robustness for niche overlap studies (Gotelli and Graves 1996).

Algorithm RA3: In this algorithm, the observed resource utilizations are randomly reassigned to different resource categories. The niche breadth (frequency and temporal distribution) of each species was not replaced but zero states in the matrix were reshuffled. If selection would have favored a community structure with decreased spectral overlap in order to reduce acoustic masking, the RA3 would be the appropriate measure to detect any nonrandom pattern in species composition by shuffling the 18 community species (out of potentially 52) used in the analysis freely in the frequency space.

In contrast to cicada with some very narrow temporal niche partitioning (Riede 1997; Sueur 2002) there is little evidence for such segregation in rainforest crickets and consequently times of a night should be accessible for all species. Thus, the use of the RA3 algorithm should also be appropriate to investigate the null-community hypothesis in the temporal domain.

Algorithm RA2: In this algorithm, the observed resource utilizations greater than zero are replaced by a random number and resource states, which were not occupied by a species in the observed community were left in the zero state. Species in the real community that never occupied a certain locality in the habitat were not allowed to occupy those in the null community. The rationale for the choice of this algorithm comes from the observation that apparently not all sites were equally accessible for every species (e.g., due to different demands with respect to microhabitats). Some species were categorically absent at certain sites, which were repeatedly and extensively measured over the course of a night, at different nights, and even across different seasons.

All simulations were carried out with EcoSim7 (Gotelli and Entsminger 2004). To compare observed and simulated indices of overlap pairs, 1000 and 5000 null assemblages were created for the temporal/spatial and spectral niche axes, respectively.

Spectral niche overlap

To calculate the spectral overlap of songs and to estimate the degree of frequency partitioning within the community, we determined for every species the number of individuals utilizing a certain frequency channel (i.e., the CF of the calling song used by an individual; e.g., see Supplementary Data, Figure S1). To draw a reliable frequency distribution, only species with a minimum number of 15 individuals or more were chosen for the analysis. In field recordings, individuals were attributed to distinct species when individual CFs differed by at least 100 Hz (Riede 1993). To avoid pseudoreplicas, recording points were spaced 100 m apart, and for those sites where multiple recordings at the same season were performed, a respective CF for a given species was evaluated only once. For the community analysis, we used the 18 most abundant species accounting for 84.3% (908 individuals) of all detected individuals on the island. The cricket community occupied a frequency range from 2.8 to 10 kHz, which we subdivided in 73 frequency channels of 100 Hz for further analysis.

Subsequent analyses of the spatial and temporal domains were carried out only for the 15 most abundant species that were detected in field recordings in the rainforest.

Temporal niche overlap

In order to determine the species' temporal activity pattern over the course of a night, we analyzed a total of 253 recordings in years 2008–2010 and evaluated the occurrence of singing individuals within every hour between 18:00 and 06:00 h. We assigned calling individuals to a certain time slot, for example, 18:00 or 19:00 h, when they were detected between 17:30 and 18:30 h or 18:31 and 19:30, respectively. Because the number of recordings differed between hours, the data set was normalized; that is, for each species and hour, the total number of calling individuals was divided by the number of recordings obtained for a respective hour (varying from 6 to 53) and multiplied by the average number of total recordings (across all hours).

Spatial niche overlap (horizontal distribution)

To determine the spatial organization of the community with regard to the species site preference, we analyzed 142 recordings containing a total of 1334 calling individuals at 10 different sites in 2008 and 2009. Some of the sites considered for this analysis have been evaluated more extensively than others and the total number of obtained recordings ranged from 6 to 37. Therefore, we normalized the data set by calculating an average number of individuals at a respective site (see "Temporal niche overlap").

Spatial niche overlap (vertical stratification)

In addition to the horizontal distribution pattern of the assemblage, information about the vertical stratification was obtained based on recordings made in different heights on a walk-up tower located in the small Lutz catchment on the island. The tower was climbed in 5-m intervals and at each height the calling individuals in the vicinity were recorded. Attention was paid that the highly directional parabolic microphone was strictly aligned horizontally with a constant input level of the Marantz recorder, which allowed us to assign the most intense calling individual to a respective height. However, in some cases when at consecutive intervals no difference in intensity of recorded individuals was detected, its position has been determined in between. A total of 14 sampling nights were performed in 2009/2010 between 19:00 and 23:00 h. Furthermore, calling males in the habitat that were identified and localized by sight were also added to the data set.

Co-occurrence and null model analysis

In order to calculate the seasonal co-occurrence pattern of the assemblage, we created presence–absence matrices of the spatiotemporal activity (i.e., the activity of a species at a certain site and time). Therefore, single 5-min sound recordings made in the habitat were scanned for the species presence or absence. We used the C-score index (Stone and Roberts 1990) as a quantitative measure of community organization, where the average number of "checkerboard units" (CU) (i.e., the submatrix of the form 01/10 or 10/01) between each species pairs is calculated as: CU = $(R_i - S)(R_j - S)$, where R_i and R_j are the numbers of occurrences for species i and j and S the number of recordings occupied by both species. To assess a randomized null distribution of C-scores, we used the simulation algorithm with fixed row totals (species) and fixed column totals (recordings), an algorithm least prone to type I and type II errors (Gotelli 2000). The difference in C-scores between the observed and simulated community was expressed in the standardized effect size (SES) and calculated as: $(I_{\mathrm{obs}} - I_{\mathrm{sim}})/S_{\mathrm{sim}}$, where I_{obs} and I_{sim} corresponds to the mean of the observed and simulated indices, respectively and S_{sim} is the standard deviation of the simulated assemblage. The SES states the number of standard deviations the observed index is above or below the mean of the simulated index. Assuming a normal distribution of deviations, approximately 95% of the SES values should fall between −1.96 and 1.96 (i.e., random distribution). Values above 1.96 and below −1.96 indicate species separation and aggregation, respectively.

Furthermore, the presence–absence data of 237 recordings were used to quantify the degree of coactivity between species pairs by measuring the similarity index after Jaccard (Krebs 1999). The Jaccard index for binary data is calculated as $d_{12} = M/(M + N)$, where M is the number of matches and N the total number of the presence of either one of both species. Values ranged from 0 (species pairs were never detected in the same recordings) to 1 (species pairs co-occurred in all recordings).

Song frequency variation (niche breadth)

We calculated the species niche breadth as a quantitative measure of intraspecific variation of calling song CFs using Levins' index (Levins 1968) given by: $B = 1/\sum p_j^2$, where p is the proportion of individuals using a specific CF channel j. We standardized the niche breadth to express it on a scale from 0 to 1 as follows: BA = $(B - 1)/(n - 1)$, where B is Levins' index and n the number of possible resource states (frequency channels) (Krebs 1999). Here n is 17 because calling song variation for *Anaxipha* sp. 1 was highest with values ranging from 6.3 to 7.9 kHz and thus utilizing a total of 17 frequency channels.

With respect to the separation in the frequency domain, one can expect that the closer 2 species are on the frequency axis, the lower the intraspecific variability in CF should be, in order to reduce any potential frequency overlap and masking interference. To determine the relationship between the species variation of song CF and its proximity to another neighboring species with similar CF, we calculated for each species the mean distance to the adjacent species above and below its average CF (values given in Figure S2).

RESULTS

We found a highly diverse cricket community with representatives from most cricket families occurring in the Neotropics

(Grylloidea: Gryllotalpidae; Mogoplistidae: Mogoplistinae; and Gryllidae: Gryllinae, Eneopterinae, Nemobiinae, Oecanthinae, Phalangopsinae, Luzarinae, Podoscirtinae, Trigonidiinae). As in other tropical cricket communities, a high number of "new" species remains to be described, particularly for the Trigonidiinae.

In the acoustic census of the cricket community, we registered 52 different cricket songs over the 3 years of field work. Of those, 75% could be assigned to distinct species, captured in the habitat. For the majority of species/ethospecies (species-specific calling songs) only a small number of individual songs were detected (on average 5 ± 3.39). Therefore, subsequent analysis was carried out only with the 18 most abundant species. Oscillograms of the calling songs of these species are shown in Figure S2 (Supplementary Data) with the average CF and its standard deviation denoted. In the figure, the 18 species are arranged according to their CF, and it is evident that independent of CF the calling songs differ strongly in their temporal pattern. Single syllables are either repeated at a high rate (trilling species Pp, Am, Di 3, and Anp) or arranged in chirps of varying duration (from a few milliseconds to more than a second) and repetition rate. Within chirps, the repetition rate of single syllables may also vary strongly.

Spectral niche overlap

The spectral overlap of calling songs of the 18 species in this community was calculated using the Czenachowski index, resulting in a rather low value with a mean of 0.069 ± 0.16. Out of 153 unique species combinations, only 9 pairs showed an overlap ≥50%, whereas the majority of species did not overlap with each other based on their individual CFs (Figure 1a). We used a simulated data set with 18 species randomly utilizing the frequency space occupied by the community in the original data set (2.8–10 kHz). The null model result suggests that the assemblage is structured by competition because the overlap index of the observed community was smaller than expected by chance (4989 of the 5000 simulated indices exceeded the observed mean, $P = 0.002$, mean simulated indices = 0.084).

Song frequency constrained by body size and phylogeny

In the community investigated here, the body size of the crickets was negatively correlated with calling song CF (Figure 2, $R^2 = 0.70$, F-test: $F = 29.64$, $P < 0.001$). Dividing the data set into 2 naturally occurring subsets around species pronotum width of 2.4 mm, this correlation disappears (subset 1 [gray circles]: $R^2 = 0.37$, F-test: $F = 2.94$, $P = 0.15$; subset 2 [black circles]: $R^2 = 0.02$, F-test: $F = 0.12$, $P = 0.74$). Subset 1 consists predominantly of smaller species of the subfamilies Trigonidiinae and Mogoplistinae with relatively high CFs, whereas subset 2 comprises species of the 2 subfamilies Eneopterinae and Phalangopsinae with relatively low CFs. We reperformed the null model analysis for both subsets separately. The observed spectral overlap for species of the subset 1 appeared to be randomly structured compared with the null model (occupied frequency range: 5.6–10 kHz; observed mean = 0.20, simulated mean = 0.19; $P < 0.05$). On the other hand, the overlap index for the subset 2 was significantly smaller than expected by chance (occupied frequency range: 2.8–5.7 kHz; observed mean = 0.12, simulated mean = 0.16; $P = 0.011$).

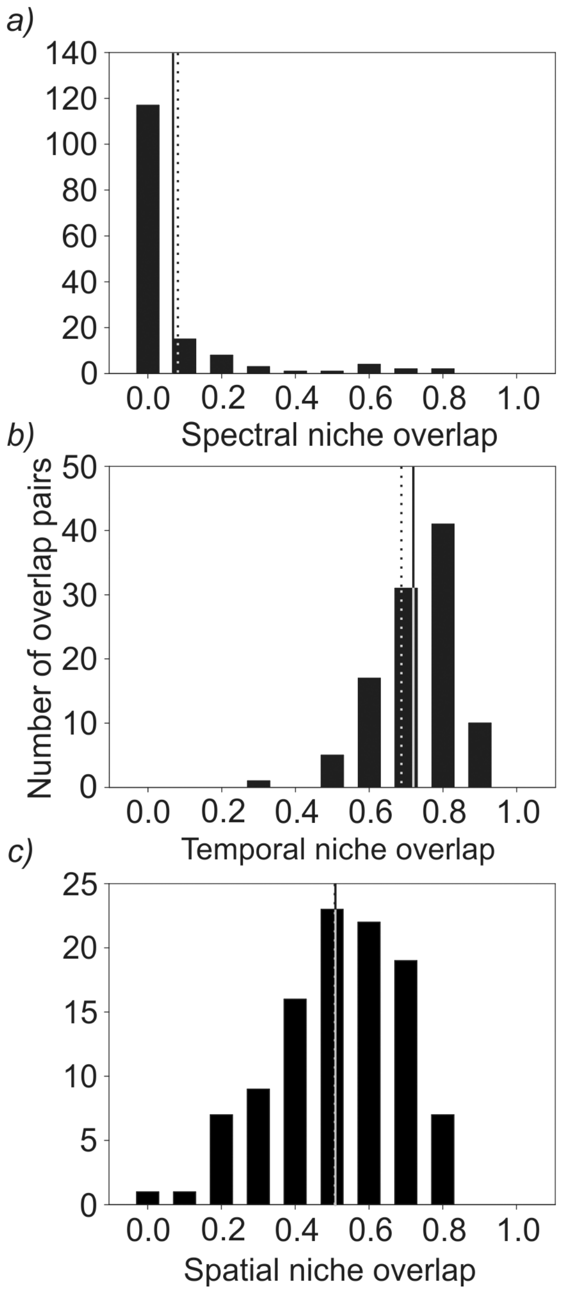

Figure 1
The amount of niche overlap (a: spectral; b: temporal; c: spatial) calculated between all species pair combinations, with the average overlap for the observed (solid vertical lines) and simulated random community (dotted vertical lines) of the null model indicated. Note the low spectral, high temporal, and intermediate spatial overlap of frequently sampled sites.

The frequency analysis in Figure 1 was based on a total of 18 species, 3 of which are ethospecies for which we do not have measures of pronotum size. Therefore, calculating pronotum sizes for the 3 ethospecies (Et 1–3, see Figure S2) based on the regression line shown in Figure 2 ($-1.412x + 9.859$) for the species-specific average CF one will obtain values of 3.5, 2.9, and 2.8 mm, respectively. Complementing the subset 2 by these 3 ethospecies (linear correlation: $R^2 = 0.09$, F-test: $F = 0.85$, $P = 0.38$), however, significant results became even stronger for the spectral domain ($P = 0.0016$).

Song frequency variation (niche breadth)

The calculated standardized niche breadths as a measure of intraspecific variation of CFs ranged from 0.17 to 0.6 with an

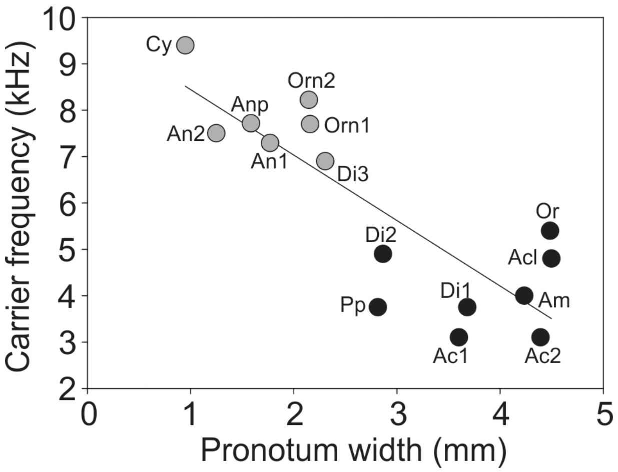

Figure 2
Relationship between a species' body size (pronotum width) and the average CF of calling songs. Number of measured individuals per species ranged from 1 to 39. For abbreviation of species names, see Figure S2 and Table S1 in Supplementary Data. Data points in this plot appearing in 2 clusters consisting of a small species using relatively high CFs (subset 1, gray circles) and large species with low CFs (subset 2, black circles).

average value of 0.38 ± 0.13. This is less compared with the European field cricket *Gryllus campestris*, a species suffering from low acoustic competition, exhibiting a niche breadth of 0.51. We also found a significant correlation ($R^2 = 0.4$, F-test: $F = 10.77$, $P = 0.005$) between the average neighbor distance of the mean calling frequency and the amount of sender variation (standardized niche breadth values; Figure 3). Therefore, species using more similar call frequencies also tend to occupy less frequency channels (i.e., smaller niche breadth).

Temporal niche overlap

The temporal activity pattern of the community included a total of 1907 calling individuals recorded between 18:00 and 06:00 h. The mean overlap was 0.72 ± 0.1, and 94% of all species pairs showed a temporal overlap ranging between 0.6 and 0.9 (Figure 1b). Moreover, the observed temporal niche overlap index was significantly greater than expected by chance; all 1000 randomized assemblages resulted in smaller value compared with the observed mean of 0.72 (mean of simulated indices = 0.69; $P < 0.001$). This suggests that the assemblage aggregated their calling activity.

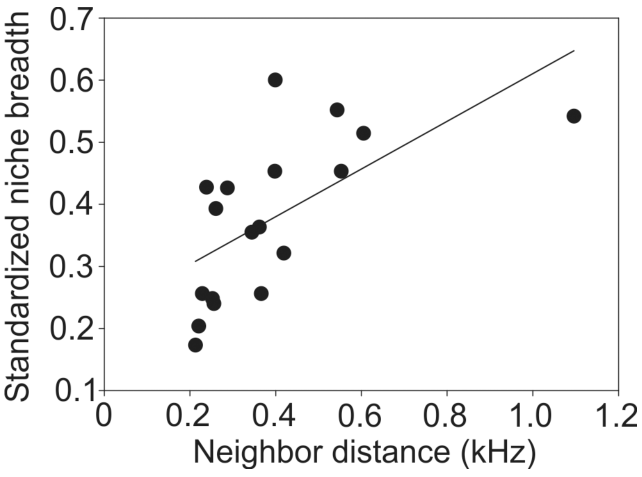

Figure 3
Relationship between the proximity of species' average CF and the occupied niche space. Species using similar average CFs (lower neighbor distance) tend to utilize fewer frequency channels (lower standardized niche breadth).

However, one species pair with a rather low temporal calling overlap of 0.3 seems to segregate their activity pattern in time. Individuals of Et1 were predominantly observed calling between 19 and 01 h, whereas calling songs of *Aclodes* sp. are predominately shifted toward the late night and early morning. Notably, these 2 species call at average CFs of about 4.8 and 4.9 kHz and are among those species pairs with the strongest frequency overlap.

Spatial niche overlap (horizontal distribution)

The acoustic survey at the 10 sites revealed a mean spatial overlap of 0.51 ± 0.17 with values ranging from 0 to 0.8, indicating that species pairs partitioned the space (sites) to a different degree (Figure 1c). Indeed, we found species that were missing at single sites, whereas other tended to be equally distributed throughout the habitat. However, compared with the randomized community (mean of 0.51), the observed assemblage overlap was not significantly different than expected by chance ($P < 0.05$), meaning that the community is randomly distributed. We found no significant difference in the magnitude of spatial overlap between 2008 (rainy season) and 2009 (dry season) (Mann–Whitney U-test, $U = 4378$, $z = -1.008$, $P = 0.314$, $N = 105/91$).

We observed no principal difference in the temporal and spatial (horizontal) domain when performing the null model analysis for the 2 subsets of species occurring in Figure 2 separately (see above). The temporal overlap was higher than expected by chance (subset 1: $P = 0.001$; subset 2: $P = 0.025$), whereas the spatial overlap was not significantly different than expected by chance (subset 1: $P = 0.07$; subset 2: $P = 0.86$).

Spatial niche overlap (vertical stratification)

The analysis of the vertical stratification is based on a total of 15 species and 304 calling individuals. The distribution pattern of calling height ranged from the ground region to the canopy (Figure S3, Supplementary Data), with significant differences between species (Kruskal–Wallis test, $H = 241.2$, $P < 0.001$). Species also differed with respect to the degree of variation in calling height. Some showed a very restricted range of calling height (e.g., *Aclodes* sp. and *Acla* sp. 2 near the forest floor), whereas the majority of species occupied a relatively wide range of forest strata.

The results of the null model analysis in the spectral, temporal, and spatial domain are independent from the selected algorithm and did not change the significance level if we apply RA2 instead of RA3 and vice versa (spectral, RA2: mean simulated indices = 0.08, $P < 0.001$; temporal, RA2: mean simulated indices = 0.61, $P < 0.001$; spatial, RA3: mean simulated indices = 0.52, $P < 0.05$).

Co-occurrence

Single 5-min recordings revealed 1–12 species simultaneously calling at the same time and the same place (average number of species 5.8 ± 2.5). Analyzing the assemblage's co-occurrence pattern, that is, the concurrent calling activity of species in single field recordings, we observed different results between years (Figure 4a). There was significant segregation among species in 2008 (SES = 13.1; number of recordings analyzed = 124), but a random pattern in 2009 (SES = −0.42;

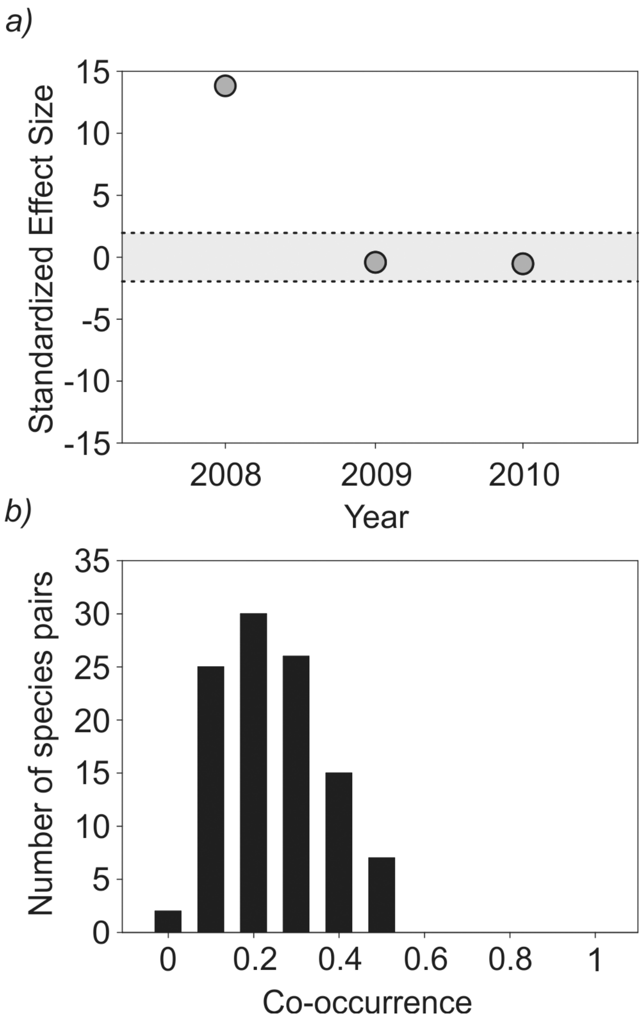

Figure 4

(a) Between year comparison of community organization. The gray area within dotted lines (1.96 standard deviations) depicts the range of random co-occurrence, whereas values above and below indicate segregation and aggregation, respectively. (b) The amount of co-occurrence/coactivity every species spend calling with every other species calculated across all habitat recordings.

number of recordings analyzed = 91) and 2010 (SES=−0.54; number of recordings analyzed = 22). We created subassemblages of the 2008 data set to test whether the strong segregation pattern is caused by the high sampling effort obtained for 4 sites (total number of recordings 11–37) in this year. The null model returned mixed results because 2 of 4 frequently sampled sites showed a nonrandom pattern (i.e., segregation, SES values of 4.85 and 3.98, respectively), whereas the other 2 sites were randomly structured (i.e., SES values of 1.12 and −0.31, respectively).

Additionally, we were interested in the total amount of coactivity that species pairs spend calling together at the same time and the same place. Between all 105 unique species pair combinations of the community, the average probability for a species pair to be detected in the same recording was merely 0.25 ± 0.12 with individual values ≤0.5 (Figure 4b).

In Figure S4, we summarized the results for the spatiotemporal domain for individual species pairs with an observed frequency overlap ≥0.2. A multivariate regression (MANOVA, $R^2 = 0.02$, $F = 0.21$, $P = 0.93$) revealed no significant relationship between CF overlap and any other spatiotemporal dimension (spatial overlap, temporal overlap, co-occurrence, or difference in calling height).

DISCUSSION

Natural auditory scenes like the nocturnal tropical rainforest are characterized by a rich diversity of vocalizing species and individuals, producing high levels of biotic noise (Ryan and Brenowitz 1985; Riede 1997; Diwakar and Balakrishnan 2007a). Auditory masking as a result of this situation will decrease the discrimination and/or detection of behaviorally relevant signals, depending on the degree of signal (spectral) overlap (Riede 1997; Wollerman and Wiley 2002; Brumm and Slabbekoorn 2005; Bee 2007; Bee and Micheyl 2008; Schmidt and Römer 2011). This is particularly true for the cricket community on BCI with 52 species/ethospecies identified so far and their almost pure-tone calling songs with CFs being concentrated within a relatively narrow frequency range between about 2.8 and 10 kHz. In the present paper, we hypothesized that the amount of overlap of song frequencies between species as direct source of masking should be reduced. Moreover, species using similar frequency channels of acoustic communication should furthermore reduce masking interference by having developed an alternative suite of behavioral adaptations over evolutionary time. These include, for example, exploiting the call activity at different times at night and/or at different places (both in the horizontal and vertical plane) in the habitat. We investigated the community organization of the singing cricket assemblage with respect to its multidimensional niche axes of acoustic communication, consisting of song CF, time, and space.

Frequency partitioning

One way to improve the efficiency of intraspecific communication is to partition the acoustic space similarly to other ecological resources (Schoener 1974). Separating frequency channels among signals of cricket species would undoubtedly be advantageous to reduce the potential risk of masking interference by heterospecific callers (Riede 1997), thus allowing a more densely packed community. The tropical cricket community consisting of the most abundant 18 species on BCI revealed a surprisingly low degree of spectral overlap; with the majority of species pairs not overlapping at all (Figure 1a). When testing for nonrandomness of the observed community pattern, the null model analyses revealed a significant lower niche overlap than expected by chance (RA3; $P = 0.002$), indicating that some sort of mechanism eventually affected the composition of the community in this respect. We have some support to assume that the observed pattern of spectral niche segregation is the evolutionary result of acoustic competition. Not only is the overlap between species pairs strongly reduced but the intraspecific variation of song frequencies correlates positively with the distance of its closest neighbors on the frequency axis (Figure 3). In other words, species tend to use a greater range of frequency channels (i.e., a greater niche breadth) for intraspecific communication if the frequency space is available and not constrained by an overlapping frequency range of another species. These results suggest that a number of different frequency channels might exclusively be used by different species for intraspecific communication, thus providing a "private communication channel" (but see below).

A decrease in signal overlap due to frequency partitioning has also been reported for other taxa at the community level (cicadas: Sueur 2002; birds: Planqué and Slabbekoorn 2008; frogs: Hödl 1977; Duellman and Pyles 1983; Chek et al.

2003). However, even when only 2 species utilize spectrally similar signals, this can result in complete suppression of calling activity of one species by the other, or a shift in the diurnal calling activity of one species (Schwartz and Wells 1983; Greenfield 1988; Römer et al. 1989). Similarly, the potential role of frequency partitioning as an important factor for reproductive isolation and speciation has been suggested for bats, based on the observed separation of species-specific CF bands of echolocation calls in bat communities (Heller and Helversen 1989; Kingston et al. 2000; Jones and Siemers 2010; Schuchmann and Siemers 2010). However, in contrast to insects species, discrimination in vertebrates probably involves some form of cognitive processes, for example, learning and memory (Bee and Micheyl 2008; Schuchmann and Siemers 2010). This might explain why complete spectral separation of signals seems not to be necessary for efficient species recognition at least in bat (Jones and Siemers 2010; Schuchmann and Siemers 2010) and frog communities (Amézquita et al. 2011).

In addition to selection acting on the sender side a reduction of signal interference could also be achieved by modification of the receiver's sensory system. Similarly, we have evidence that the strong acoustic interference in the tropical cricket community also acted on the receiver side and resulted in a more selective frequency tuning in the afferent auditory pathway compared with the European counterparts *G. campestris* and *Gryllus bimaculatus*, species for which almost no acoustic competition exists (Schmidt et al. 2011). As a result of such changes, masking interference by frequencies around the receivers' best frequency was significantly reduced. This, in turn, provided a strongly improved neuronal representation of species-specific calling songs in receivers under natural outdoor conditions (Schmidt and Römer 2011). Evidence for a similar scenario comes from a recent analysis of the male–male communication system of territorial tropical frogs (Amézquita et al. 2011). In the dendrobatid frog *Allobates femoralis*, the occurrence of only 1 additional frog species, calling in an overlapping frequency range, significantly predicted narrower and asymmetric frequency response curves (Amézquita et al. 2006). As a consequence of such a change in receivers, strong selection would act on senders to call exactly at those CFs to which receivers are tuned, and this view is indeed supported by the cricket data. The calculated standardized niche breadth in CF for the rainforest cricket assembly is lower compared with the European field cricket *G. campestris* (see results for song frequency variation/niche breadth).

Frequency partitioning constrained by body size and phylogeny

In crickets, body size is negatively correlated with calling song frequency, both in a comparison between species and at the interindividual level within a species (Figure 2; Bennet-Clark 1998; Gerhardt and Huber 2002). Thus, the observed spectral separation of the cricket community might have emerged from correlated ecological and/or evolutionary factors rather than selection to avoid acoustic masking. In the analysis of the correlation between body size and calling song CF (Figure 2), 2 clusters of species can be separated. The 2 size subgroups also delimit phylogenetic groups, with Mogoplistinae and Trigonidiinae belonging to the small, high frequency moiety (subset 1), Phalangopsinae and Eneopterinae with the exception of 1 species (Di 3, Figure 2) to the large low frequency group (subset 2). Consequently, our size subdivision provides us also with a meaningful phylogenetic subdivision, thereby taking into account potential phylogenetic biases. When examining the 2 clusters separately, one could obtain a measure of frequency overlap not confounded by body size. This separate analysis revealed that the observed spectral overlap in subset 1 appeared to be randomly structured when compared with the null community, whereas the index of the observed community was significantly smaller than expected by chance in subset 2. We argue that species in subset 2 will be more subject to acoustic competition than smaller species due to a larger active space of their signals. The active space describes the range over which a receiver can detect a signal. The size of the active space depends on (1) signal intensity, (2) sound attenuation properties of the transmission channel, and (3) receiver sensitivity (Bradbury and Vehrencamp 2011). Species with larger body size produce more intense signals and thus will have a larger active space (Bennet-Clark 1998). Our own preliminary measurements of signal intensity indicate that species of the subset 1 produce indeed fainter songs (e.g., *Ornebius* sp. 1 and 2 about 54 dB SPL/m, *Anaxipha* sp. 1 60 dB SPL/m) compared with larger species of subset 2 (e.g., *Diatrypa* sp., *Orocharis* sp. about 75–80 dB SPL/m).

With respect to the sensitivity of receivers, we have further evidence that smaller species of subset 1 (e.g. *Anaxipha* sp. 1) are less sensitive: neurophysiological thresholds at the best frequency are on average at 46.2 ± 2.9 dB SPL ($N = 15$, unpublished data). This was approximately 13 dB SPL higher compared with the 2 larger sympatric species *Paroecanthus podagrosus* and *Diatrypa* sp. 1 (Schmidt and Römer 2011; Schmidt et al. 2011). A reduced sensitivity might be a potential proximate mechanism to overcome masking interference at high ambient noise levels (Narins 1987; Witte et al. 2005), even though it reduces the active space of a signal.

In cluttered environments like the dense rainforest, sound propagation for larger species and their relatively lower frequencies might be also less affected in terms of signal attenuation when compared with species using higher frequencies (Marten and Marler 1977; Bradbury and Vehrencamp 2011). This effect probably amounts to only a few decibels but eventually will further limit the active space.

Temporal organization

Temporal adjustment and partitioning of calling behavior is a well-known strategy to reduce acoustic interference in birds (Brumm 2006; Luther and Wiley 2009), frogs (Schwartz and Wells 1983), and insects (Greenfield 1988; Römer et al. 1989). Among insects, cicadas are known for their impressively precise timing of call on and offset with species-specific short calling periods during dusk and dawn choruses, resulting in temporal segregation between species (Gogala and Riede 1995; Riede 1997; Sueur 2002). By contrast, the temporal organization of the cricket community investigated here revealed that the assemblage aggregated their calling activity with an observed niche overlap significantly greater than expected by chance.

Spatial organization

Release of acoustic competition can also be realized by the spatial organization of signalers (Brumm and Slabbekoorn 2005). Indeed, when comparing the community composition at frequently sampled sites, we found that some species were never detected at some locations. This difference appeared to be due to hitherto unknown factors (most probably microhabitat or temporal food resources) and was clearly not driven by the amount of spectral overlap of their signals (Figure S4). However, at the community level, we found no support for partitioning of horizontal space.

Sound recordings covered a relatively large radius when scanning for calling individuals. This could principally lead to an overestimation of the amount of overlap. Site segregation between species of a community has been reported at much finer scales (Joern 1982; Jain and Balakrishnan 2011a). The vertical stratification of calling heights identified in our study (Supplementary Data, Figure S3; see also Sueur 2002; Diwakar and Balakrishnan 2007b; Jain and Balakrishnan 2011b) further contributes to the spatial segregation. However, microhabitat segregation can be of limited value because separation by only a few meters in distinct forest strata or broadcast positions in the vegetation would still allow considerable acoustic crosstalk (Riede 1993). Again, the active, 3D space is essential in determining the amount of segregation in this respect (see above). For example, in the case of the 2 *Ornebius* species with their high spectral, and large spatial and temporal overlap the average calling height difference of 9.2 m (Figures S3 and S4) might already be sufficient to reduce signal interference because signal intensities for these species are rather low with about 54 dB/m. It is likely that with such a vertical separation distance the heterospecific signal will not interfere with the detection of the conspecific signal at all after transmission through the habitat (Römer and Lewald 1992).

Co-occurrence

The pattern of species co-occurrence at the community level revealed a random community structure for 2009 and 2010, whereas for 2008, species tended to be significantly segregated (SES = 13.1). Interestingly, a detailed view of the subassemblages of the data in 2008 showed that this pattern strongly depended on the recording site. The 2 significant results (i.e., segregation) were obtained in an area of secondary forest and a light gap, whereas the randomly structured subassemblages were located in parts of the island covered by old-growth forest. Clearly, it will be necessary to gather more data of species composition and assemblage stability over longer periods of time and at various sites in order to account for the observed differences of the co-occurrence pattern, which we currently pursue with automated acoustic monitoring on BCI.

In addition to the findings at the community level we also calculated the respective magnitude of coactivity for each species pair. We found rather low values of co-occurrence between species pairs with an average level of 0.25, which means that the chance of an actual masking event is less likely when spatial and temporal distribution is combined. In addition, the sampling protocol of 5-min recordings provides a relative crude temporal measurement, in which we did not consider temporal overlap at a microscale level. Because masking only occurs when 2 or more species exhibit an overlapping time window of their calls, we would expect even lower values than the one given in Figure 4b, at least for a number of chirping species that do not call continuously (Figure S2). Indeed, comparing, for example, the *Acla* species 1 and 2, we rarely found incidences of such direct signal overlap. This is due to the low duty cycles of about 3% (i.e., the duration of song in relation to song period) they produce, thus providing sufficient probabilistic events of nonoverlap calling and further reducing incidences of masking interference.

For the spatial–temporal dimension, segregation over evolutionary time might not (e.g., spatial [horizontal] and temporal distribution) or only partly (vertical distribution, co-occurrence) be accomplished at the community level; however, at a pairwise species association, the results showed that successful intraspecific communication especially for those pairs sharing identical frequency channels is likely (summarized in Figure S4).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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REFERENCES

Amézquita A, Castellanos L, Hödl W. 2005. Auditory matching of male *Epipedobates femoralis* (Anura: Dendrobatidae) under field conditions. Anim Behav. 70:1377–1386.

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. 108:17058–17063.

Amézquita A, Hödl W, Lima AP, Castellanos L, Erdtmann L, de Araulo MC. 2006. Masking interference and the evolution of the acoustic communication system in the Amazonian dendrobatid frog *Allobates femoralis*. Evolution. 60(9):1874–1887.

Bee MA. 2007. Sound source segregation in grey treefrogs: spatial release from masking by the sound of a chorus. Anim Behav. 74:549–558.

Bee MA. 2008. Finding a mate at a cocktail party: spatial release from masking improves acoustic mate recognition in grey treefrogs. Anim Behav. 75:1781–1791.

Bee MA, Micheyl C. 2008. The cocktail party problem: what is it? How can it be solved? And why should animal behaviorists study it? J Comp Psychol. 122:235–251.

Bennet-Clark HC. 1998. Size and scale effects as constraints in insect sound communication. Philos Trans R Soc B. 353:407–419.

Bradbury JW, Vehrencamp SL. 2011. Principles of animal communication. Sunderland (MA): Sinauer Associates, Inc., Publishers.

Brumm H. 2006. Signalling through acoustic windows: nightingales avoid interspecific competition by short-term adjustment of song timing. J Comp Physiol A. 192:1279–1285.

Brumm H, Slabbekoorn H. 2005. Acoustic communication in noise. Adv Stud Behav. 35:151–209.

Capranica RR, Moffat AJM. 1983. Neurobehavioral correlates of sound communication in anurans. In: Ewert JP, Capranica RR, Ingle D, editors. Advances in vertebrate neuroethology. New York: Plenum. p. 701–730.

Chek AA, Bogart JP, Lougheed SC. 2003. Mating signal partitioning in multi-species assemblages: a null model test using frogs. Ecol Lett. 6:235–247.

Condit R. 1998. Ecological implications of changes in drought patterns: shifts in forest composition in Panama. Climatic Change. 39:413–427.

Dayrat B. 2005. Towards integrative taxonomy. Biol J Linn Soc. 85:407–415.

Depraetere M, Pavoine S, Jiguet F, Gasc A, Duvail S, Sueur J. 2012. Monitoring animal diversity using acoustic indices: implementation in a temperate woodland. Ecol Indic. 13:46–54.

Diwakar S, Balakrishnan R. 2007a. The assemblage of acoustically communicating crickets of a tropical evergreen forest in southern India: call diversity and diel calling patterns. Bioacoustics. 16:113–135.

Diwakar S, Balakrishnan R. 2007b. Vertical stratification in an acoustically communicating ensiferan assemblage of a tropical evergreen forest in southern India. J Trop Ecol. 23:479–486.

Diwakar S, Jain M, Balakrishnan R. 2007. Psychoacoustic sampling as a reliable, noninvasive method to monitor orthopteran species diversity in tropical forests. Biodivers Conserv. 16:4081–4093.

Drewry GE, Rand AS. 1983. Characteristics of an acoustic community: Puerto Rican frogs of the genus *Eleutherodactylus*. Copeia. 4:941–953.

Duellman WE, Pyles RA. 1983. Acoustic resource partitioning in anuran communities. Copeia. 3:639–649.

Eades DC, Otte D, Cigliano MM, Braun H. 2012. Orthoptera species file online. Version 2.0/4.0. [6/3/2012].

Ellinger N, Hödl W. 2003. Habitat acoustics of a neotropical lowland forest. Bioacoustics. 13:297–321.

Erwin TL. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. Coleopts Bull. 36:74–75.

Feinsinger P, Spears EE, Poole RW. 1981. A simple measure of niche breadth. Ecology. 62:27–32.

Ficken RW, Ficken MS, Hailman JP. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. Science. 183:762–763.

Gerhardt HC, Huber F. 2002. Acoustic communication in insects and anurans: common problems and diverse solutions. Chicago: University of Chicago Press.

Gogala M, Riede K. 1995. Time sharing of song activity by cicadas in Temengor Forest Reserve, Hulu Perak, and in Sabah, Malaysia. Malay Nat J. 48:297–305.

Gotelli NJ. 2000. Null model analysis of species co-occurrence patterns. Ecology. 81:2606–2621.

Gotelli NJ. 2001. Research frontiers in null model analysis. Global Ecol Biogeogr. 10:337–343.

Gotelli NJ, Entsminger GL. 2004. EcoSim: null models software for ecology. Jericho (VT): Acquired Intelligence Inc. & Kesey-Bear. Available from http://garyentsminger.com/ecosim/index.htm [accessed 2012 October 24].

Gotelli NJ, Graves GR. 1996. Null models in ecology. Washington: Smithsonian Institution Press.

Gottsberger B, Gruber E. 2004. Temporal partitioning of reproductive activity in a neotropical anuran community. J Trop Ecol. 20:271–280.

Greenfield MD. 1983. Reproductive isolation in clearwing moths (Lepidoptera: Sesiidae): a tropical-temperate comparison. Ecology. 64:362–375.

Greenfield MD. 1988. Interspecific acoustic interactions among katydids Neoconocephalus: inhibition-induced shifts in diel periodicity. Anim Behav. 36:684–695.

Greenfield MD, Karandinos MG. 1979. Resource partitioning of the sex communication channel in clearwing moths (Lepidoptera: Sesiidae) of Wisconsin. Ecol Monogr. 49:403–426.

Halfwerk W, Holleman LJM, Lessells CM, Slabbekoorn H. 2011. Negative impact of traffic noise on avian reproductive success. J Appl Ecol. 48:210–219.

Harms KE, Condit R, Hubbell SP, Foster RB. 2001. Habitat associations of trees and shrubs in a 50-Ha neotropical forest plot. J Ecol. 89:947–959.

Hebard M. 1928. Studies in the Gryllidae of Panama (Orthoptera). Trans Am Entomol Soc. 54:233–294.

Hebert PDN, Cywinska A, Ball SL, deWaard JR. 2003. Biological identifications through DNA barcodes. Proc R Soc B. 270:313–321.

Heller KG, Helversen O. 1989. Resource partitioning of sonar frequency bands in rhinolophoid bats. Oecologia. 80:178–186.

Hödl W. 1977. Call differences and calling site segregation in anuran species from Central Amazonian Floating Meadows. Oecologia. 28:351–363.

Jain M, Balakrishnan R. 2011a. Microhabitat selection in an assemblage of crickets (Orthoptera: Ensifera) of a tropical evergreen forest in Southern India. Insect Conserv Diver. 4:152–158.

Jain M, Balakrishnan R. 2011b. Does acoustic adaptation drive vertical stratification? A test in a tropical cricket assemblage. Behav Ecol. 23:343–354.

Joern A. 1982. Vegetation structure and microhabitat selection in grasshoppers (Orthoptera: Acrididae). SW Nat. 27:197–209.

Jones G, Siemers BM. 2010. The communicative potential of bat echolocation pulses. J Comp Physiol A. 197:447–457.

Kingston T, Jones G, Zubaid A, Kunz TH. 2000. Resource partitioning in Rhinolophoid bats revisited. Oecologia. 124:332–342.

Klump GM. 1996. Bird communication in a noisy world. In: Kroodsma DE, Miller EH, editors. Ecology and evolution of acoustic communication in birds. Ithaca (NY): Cornell University Press. p. 321–338.

Krebs CJ. 1999. Ecological methodology. 2nd ed. Menlo Park (CA): Benjamin/Cummings.

Lang A, Teppner I, Hartbauer M, Römer H. 2005. Predation and noise in communication networks of neotropical katydids. In: McGregor P, editor. Animal communication networks. Cambridge: Cambridge University Press. p. 152–169.

Leigh EG. 1999. Tropical forest ecology: a view from Barro Colorado Island. Oxford: Oxford University Press.

Leigh EG Jr, Rand AS, Windsor DM. 1982. The ecology of a tropical forest: seasonal rhythms and long-term changes. Washington: Smithsonian Institution Press.

Levins R. 1968. Evolution in changing environments: some theoretical explorations. New Jersey: Princeton University Press.

Löfstedt C, Herrebout WM, Menken SBJ. 1991. Sex pheromones and their potential role in the evolution of reproductive isolation in small ermine moths (Yponomeutidae). Chemoecology. 2:20–28.

Löfstedt C, Pers JNC. 1985. Sex pheromones and reproductive isolation in 4 European small ermine moths. J Chem Ecol. 11:649–666.

Luther DA. 2009. The influence of the acoustic community on songs of birds in a neotropical rain forest. Behav Ecol. 20:864.

Luther DA, Wiley RH. 2009. Production and perception of communicatory signals in a noisy environment. Biol Lett. 5:183–187.

Marten K, Marler P. 1977. Sound transmission and its significance for animal vocalizations. I. Temperate habitats. Behav Ecol Sociobiol. 2:271–290.

Mascaro J, Asner GP, Muller-Landau HC, van Breugel M, Hall J, Dahlin K. 2011. Control over aboveground forest carbon density on Barro Colorado Island, Panama. Biogeosciences. 8:1615–1629.

Narins PM. 1982. Effects of masking noise on evoked calling in the Puerto Rican coqui (Anura: Leptodactylidae). J Comp Physiol A. 147:439–446.

Narins PN. 1987. Coding of signals in noise by amphibian auditory nerve fibers. Hearing Res. 26:145–154.

Nickle DA. 1992. The crickets and mole crickets of Panama (Orthoptera: Gryllidae and Gryllotalpidae). In: Quintero DA, Aiello A, editors. Insects of Panama and Mesoamerica: Selected Studies. Oxford: Oxford University Press. p. 185–197.

Nischk F, Riede K. 2001. Bioacoustics of two cloud forest ecosystems in Ecuador compared to lowland rainforest with special emphasis on singing cricket species. In: Nieder J, Barthlott W, editors. Epiphytes and canopy fauna of the Otongan rain forest (Ecuador). Results of the Bonn – Quito epiphyte project, funded by the Volkswagen Foundation (Vol. 2 of 2). Bonn: Books on Demand GmbH. p. 217–242.

Otte D. 2006. Eighty-four new cricket species (Orthoptera: Grylloidea) from La Selva, Costa Rica. Trans Am Entomol Soc. 132(3–4):299–418.

Otte D, Perez-Gelabert DE. 2009. Caribbean crickets. Philadelphia: The Orthopterists' Society.

Pennisi E. 2005. Sky-high experiments. Science. 309:1314–1315.

Planqué R, Slabbekoorn H. 2008. Spectral overlap in songs and temporal avoidance in a Peruvian bird assemblage. Ethology. 114:262–271.

Popp JW, Ficken RW, Reinartz JA. 1985. Short-term temporal avoidance of interspecific acoustic interference among forest birds. Auk. 102:744–748.

Quintero DA, Aiello A. 1992. Insects of Panama and Mesoamerica: selected studies. New York: Oxford University Press.

Rasband, WS. 1997–2011. ImageJ. Bethesda (MD): U.S. National Institutes of Health [cited 2012 October 30]. http://imagej.nih.gov/ij/.

Riede K. 1993. Monitoring biodiversity: analysis of Amazonian rainforest sounds. AMBIO. 22:546–548.

Riede K. 1997. Bioacoustic diversity and resource partitioning in tropical calling communities. In: Ulrich H, editor. Tropical biodiversity and systematics. Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems, Bonn 1994. Bonn: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn. p. 275–280.

Robillard T. 2009. Eneopterinae crickets (Insecta, Orthoptera, Grylloidea) from Vanuatu. Zoosystema. 31:577–618

Römer H, Bailey W, Dadour I. 1989. Insect hearing in the field III. Masking by noise. J Comp Physiol A. 164:609–620.

Römer H, Lewald J. 1992. High-frequency sound transmission in natural habitats: implications for the evolution of insect acoustic communication. Behav Ecol Sociobiol. 29:437–444.

Ryan MJ. 1983. Sexual selection and communication in a neotropical frog, *Physalaemus pustulosus*. Evolution. 37:261–272.

Ryan MJ, Brenowitz EA. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. Am Nat. 126:87–100.

Schmidt AKD, Riede K, Römer H. 2011. High background noise shapes selective auditory filters in a tropical cricket. J Exp Biol. 214:1754–1762.

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:e28593.

Schoener TW. 1974. Resource partitioning in ecological communities. Science. 185:27–39.

Schuchmann M, Siemers BM. 2010. Behavioral evidence for community-wide species discrimination from echolocation calls in bats. Am Nat. 176:72–82.

Schwartz JJ, Wells KD. 1983. The influence of background noise on the behavior of a neotropical treefrog, *Hyla ebraccata*. Herpetologica. 39:121–129.

Shannon CE. 1948. A mathematical theory of communication. Bell System Tech J. 27:379–423; 623–656.

Siemers BM, Schaub A. 2011. Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. Proc R Soc B. 278:1646–1652.

Stone L, Roberts A. 1990. The checkerboard score and species distributions. Oecologia. 85:74–79.

Sueur J. 2002. Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera: Cicadomorpha: Cicadidae). Biol J Linn Soc. 75:379–394.

Sueur J, Pavoine S, Hamerlynck O, Duvail S. 2008. Rapid acoustic survey for biodiversity appraisal. PLoS ONE. 3:e4065.

Walker TJ. 1964. Cryptic species among sound-producing ensiferan orthoptera (Gryllidae and Tettigoniidae). Q Rev Biol. 39:345–355.

Wehner R. 1987. “Matched filters”—neural models of the external world. J Comp Physiol A. 161:511–531.

Winemiller KO, Pianka ER. 1990. Organization in natural assemblages of desert lizards and tropical fishes. Ecol Monogr. 60:27–55.

Witte K, Farris HE, Ryan MJ, Wilczynski W. 2005. How cricket frog females deal with a noisy world: habitat-related differences in auditory tuning. Behav Ecol. 16:571–579.

Wollerman L. 1999. Acoustic interference limits call detection in a Neotropical frog *Hyla ebraccata*. Anim Behav. 57:529–536.

Wollerman L, Wiley RH. 2002. Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. Anim Behav. 63:15–22.

Zimmermann Y, Ramírez SR, Eltz T. 2009. Chemical niche differentiation among sympatric species of orchid bees. Ecology. 90:2994–3008.