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A rain forest dusk chorus: cacophony or sounds of silence?

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Abstract A rain forest dusk chorus consists of a large number of individuals of acoustically communicating species signaling at the same time. How different species achieve effective intra-specific communication in this complex and noisy acoustic environment is not well understood. In this study we examined acoustic masking interference in an assemblage of rain forest crickets and katydids. We used signal structures and spacing of signalers to estimate temporal, spectral and active space overlap between species. We then examined these overlaps for evidence of strategies of masking avoidance in the assemblage: we asked whether species whose signals have high temporal or spectral overlap avoid calling together. Whereas we found evidence that species with high temporal overlap may avoid calling together, there was no relation between spectral overlap and calling activity. There was also no correlation between the spectral and temporal overlaps of the signals of different species. In addition, we found little evidence that species calling in the understorey actively use spacing to minimize acoustic overlap. Increasing call intensity and tuning receivers however emerged as powerful strategies to minimize acoustic overlap. Effective acoustic overlaps were on average close to zero for most individuals in natural, multispecies choruses, even in the absence of behavioral avoidance mechanisms such as inhibition of calling or active spacing. Thus, call temporal structure, intensity and frequency together provide sufficient parameter space for several species to call together yet

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communicate effectively with little interference in the apparent cacophony of a rain forest dusk chorus.

Keywords Katydids · Acoustic interference · Western Ghats · Acoustic communication network · Paleotropical cricket assemblage

Introduction

A rain forest dusk chorus consists of a large number of acoustically active individuals, usually male crickets, katydids, cicadas and frogs, calling to attract potential mates (Gerhardt and Huber 2002). Since females of these species typically locate conspecific males using temporal and spectral features of the signals, call structures are usually species-specific (Gerhardt and Huber 2002). These signals must however traverse a common medium, the habitat, where they suffer degradation and acoustic interference from other signals (Römer 1998). Detection, recognition and localization of acoustic signals are known to be impaired under such conditions of high background noise and masking interference (Römer 1998; Wollerman and Wiley 2002; Langemann and Klump 2005). Given the obviously large fitness consequences, one expects selection on both senders (males) and receivers (females) for adaptive features that reduce acoustic masking interference.

A number of strategies have been proposed, including partitioning of calling in time and place between species or partitioning frequency by evolving narrow bandwidth signals and tuned receivers (Römer 1998). Most previous studies have examined this using the concepts of ecological resource partitioning, examining multivariate acoustic distances or overlap between signals in relation to community-wide null models or acoustic co-occurrence (Chek et al. 2003; Planqué and Slabbekoorn 2008; Luther 2009; Amézquitas et al. 2011; Schmidt et al. 2013). Studies on frogs have provided mixed support for signal partitioning driven by acoustic competition or spatiotemporal segregation of species with similar calls (Chek et al. 2003; Amézquitas et al. 2011). Evidence for acoustic signal partitioning was found in only 3 out of 11 frog assemblages that were tested against null models (Chek et al. 2003). In a study on an assemblage of ten acoustically signaling species of dendrobatid frogs (Amézquitas et al. 2011), acoustic co-occurrence was not related to multivariate distances in signal structure, providing little support for spatiotemporal partitioning of calling activity as a mechanism to reduce inter-specific masking interference. Two studies on neo-tropical bird assemblages however provide some evidence for frequency partitioning and over-dispersion of signals in acoustic space at small spatiotemporal scales (Planqué and Slabbekoorn 2008; Luther 2009). A recent study examining acoustic partitioning in a neotropical cricket assemblage (Schmidt et al. 2013) found some evidence for spectral partitioning of calls (as compared with a null model) but not for partitioning in call timing on a diel scale.

Sender strategies to reduce acoustic masking include reduction of overlap in time, frequency and space (Brumm and Slabbekoorn 2005). Temporal overlap may be effectively reduced over four different temporal scales: different species may be (1) acoustically active at different seasons; (2) acoustically active in the same season but at different hours of the day or night (diel partitioning of calling time); (3) acoustically active during the same diel period but avoid calling together (over time scales of the order of minutes) by, for example, inhibition of calling of one species by another and/or (4) call temporal structures may result in low levels of overlap (on the scale of seconds or milliseconds) by chance alone even if different species call simultaneously without avoiding each other.

Over the past 10 years, we have been studying an assemblage of acoustically communicating crickets (Order Orthoptera: Family Gryllidae) and katydids (Order Orthoptera: Family Tettigoniidae) in a paleotropical rain forest in Southern India. The assemblage consists of twenty species of acoustically communicating crickets and katydids whose call structures have been characterised (Diwakar and Balakrishnan 2006; Nityananda and Balakrishnan 2006). Previous studies have shown that 14 of the 20 species have their peak breeding season at the same time of year (December to March) and there was no evidence for partitioning of calling time of these species on a diel scale (Diwakar and Balakrishnan 2006). In this study, we therefore investigated whether these species may avoid overlap of their calls on a finer temporal scale (scale 3 above). We hypothesized that species pairs with temporal or spectral structures that would result in high acoustic overlap (scale 4 above) will avoid calling together (temporal scale 3 above).

Considering receivers, in dendrobatid Amazonian frogs, there is a match between species call features and those that elicit responses, but the 'recognition spaces' were typically larger than the acoustic space of the corresponding signals (Amézquitas et al. 2011). In crickets, however, there is good evidence both for narrow bandwidth signals and matched frequency tuning (Kostarakos et al. 2008; Schmidt et al. 2011; Schmidt and Römer 2011). In a recent study on two neotropical rain forest cricket species, frequency tuning was found to be not only well matched to conspecific signals but was narrower than in temperate species (Schmidt et al. 2011). Neuronal representation of conspecific signals in the ambience of the nocturnal rain forest was also good, suggesting that masking levels may be overestimated from laboratory studies (Schmidt and Römer 2011). The reason is most likely because laboratory studies typically do not take into account a number of factors that influence masking levels in the field (Schmidt and Römer 2011). Most laboratory studies play back ambient noise from a single or two speakers, creating an acoustic situation that is quite different from the natural one, where there are multiple sound sources, each at a different location (Bee and Micheyl 2008).

The level of heterospecific acoustic masking interference experienced by a receiver in a natural environment depends on several factors. Firstly it depends on the effective temporal overlap (ETO), the overlap due to the probability of a heterospecific male calling simultaneously with the focal male times the probability that overlap will occur depending on their relative temporal structures. Secondly, it depends on the spectral overlap (SO). The relation between signal SO and the resultant masking is however, not straightforward. Whether a given level of SO between signals actually translates into masking for a receiver depends on a number of factors. These include (1) the positions of conspecific and masking heterospecific males in relation to the receiver, (2) the sound pressure levels (SPLs) at which they call, (3) the habitat and call structure-specific attenuation of the signals (Jain and Balakrishnan 2012) and (4) the hearing sensitivity and frequency response of the receiver. These together determine the overlap of active spaces, where active space is defined as the above-ground volume of space around a focal sender where it can be heard by a specific receiver. From previous work on the same assemblage, we have evidence for both vertical stratification and microhabitat selection by senders of different species (Diwakar and Balakrishnan 2007; Jain and Balakrishnan 2011) but how this translates into overlap of active spaces has not been investigated yet.

In the second part of this study, we therefore developed a three-dimensional simulation model of acoustic active spaces for a set of five abundant, understorey species (two katydid and three cricket species) that are acoustically co-active (at temporal scales 1–3). These five species together span the extremes of call SPL, spectral and temporal structure (Appendix: Table S1). We used data on spacing of individuals measured in natural choruses, measurements of species-specific call SPLs and habitat-dependent signal transmission to probe how changes in call SPL and receiver tuning affect active space overlap (ASO) between pairs of species. Active space overlap (ASO) is the proportion of the active space of a calling male in which the calling male/s of another species is/are likely to be heard by a female receiver. It is therefore an estimate of the probability of being masked in space for that receiver.

We hypothesized that communication conditions for individuals of different species are likely to be optimized so that the effective acoustic overlap (EAO) is close to zero in natural choruses. The EAO is defined as the resultant acoustic overlap for a receiver in the active space of a specific caller, when temporal and active space overlaps (ASOs) are both taken into account. To test this in natural choruses, we extended the simulation model from pairwise comparisons between species to estimating EAOs based on the combined effects of all relevant heterospecific neighbours, for individuals of different species in natural choruses. Finally, we investigated whether the observed levels of EAO were an outcome of active spacing between individuals of the different species or could result from random spacing of individuals in these multispecies choruses.

To summarise, in this study, we have (1) investigated whether senders in multispecies choruses use relative call timing to decrease heterospecific acoustic overlap and thereby masking interference. (2) We have developed a three-dimensional simulation model of acoustic active spaces that allows exploration of acoustic overlap in a framework that integrates the relative temporal, spatial, spectral and amplitudinal characteristics of the calls of multiple senders in multispecies choruses. We have used this model (3) to probe the role and efficacy of call SPL and receiver tuning as strategies to minimize active space overlap (ASO), (4) to provide estimates of effective acoustic overlap (EAO) in natural choruses, which we hypothesised would be close to zero if communication conditions are optimal and (5) to investigate whether senders in natural choruses use active spacing as a mechanism to minimize EAO.

Materials and methods

Study site and animals

The fieldwork for the study was carried out in the tropical rain forests of Kudremukh National Park (13°01′–13°29′N, 75°01′–75°25′E), situated in the Western Ghats in southern India, during the post-monsoon dry season in 2004–2005 (December–March) and 2007–2009 (October to March). The forests have a stratified vegetation structure (Jain et al. 2010) consisting of a herb layer ($\leq$1 m), understorey (1–8 m) and canopy (12–30 m).

Fourteen species of crickets and katydids were studied, including seven species of katydids (Family Tettigoniidae), six species of crickets (Family Gryllidae) and one gryllacridoid (Family Anostostomatidae: Genus *Gryllacropsis*). Their calls have been described in detail previously (Diwakar and Balakrishnan 2006; Nityananda and Balakrishnan 2006): not all of them could be classified to the species level and some could represent new species. The seven katydid species (Family Tettigoniidae) were: *Onomarchus uninotatus* (subfamily Pseudophyllinae), *Elimaea* sp. (subfamily Phaneropterinae), ‘15 kHz’ (subfamily Phaneropterinae), *Phyllomimus* sp. (subfamily Pseudophyllinae), *Mecopoda* ‘Helicopter’ (subfamily Mecopodinae), *Mecopoda* ‘Two-Part’ (subfamily

Mecopodinae) and *Pirmeda rosetta* (subfamily Pseudophyllinae). The six cricket species (Family Gryllidae) studied included: *Landreva* sp. (subfamily Gryllinae), *Phaloria* sp. (subfamily Itarinae), "Whiner" (subfamily Podoscirtinae), *Xabea* sp. (subfamily Oecanthinae), *Ornebius* sp. (subfamily Mogoplistinae) and *Micrornebius* sp. (subfamily Mogoplistinae).

Temporal and spectral overlap (Objective 1)

To test the hypothesis that species pairs with high temporal or spectral overlap will avoid calling together, we first estimated, for each species, the probability that it would be overlapped in calling time (in 5-min time windows during peak calling time) by each of the other 13 species that call during the same diel period (Gross Temporal Overlap or GTO). This depends upon whether or not each of the other species calls in the same 5-min time window as the focal species (temporal scale 3 in the introduction). We then examined, for all pairs of species, the probability of call overlap by chance alone if species call continuously and simultaneously without avoiding each other (Fine Temporal Overlap or FTO): this overlap (temporal scale 4 in the introduction) is determined only by the temporal structures of the calls. We also computed, for all pairs of species, the spectral overlap (SO) between their calls. We then tested whether there was evidence for a negative correlation between GTO and FTO/SO.

Gross Temporal Overlap (GTO)

Data from acoustic spot sampling along transects (method validated in an earlier study: Diwakar et al. 2007) were analyzed for co-occurrences of calling of each species pair in 240 5-min time windows sampled during peak calling time (Diwakar and Balakrishnan 2006). Two transects 500 m in length that were similar in vegetation and elevation were chosen. In each transect, ten spots 50 m apart were marked. Acoustic spot sampling was carried out for 5 min in each spot. The number of calls heard of each of the14 species was recorded in every 5 min window. All sampling was carried out by one listener (SD) and the reliability of her acoustic identification has been established previously (Diwakar et al. 2007). Sampling was carried out in both transects between 1800 to 2100 and 2100 to 0000 hours following a randomized protocol. Six replicates of each sampling period were carried out in each transect. Occurrences in a total of 240 5-min windows were considered to estimate the GTO between species pairs.

A matrix with species identity in columns and 240 5-min sampling points in rows was generated based on the above data, wherein each cell depicted the presence or absence of a particular species in that particular sampling window. This matrix was imported into MATLAB (version 7, The Mathworks Inc, Natick MA) and a custom-written program (Vivek Nityananda, CES, IISc) was used to calculate the total number of incidences in which any given species pair called together across the 240 sampling points. Gross Temporal Overlap on species A by B was then calculated as the total number of incidences when both A and B called together divided by the total incidences of calling of species A. This was calculated for the 14 × 14 species-pairs, resulting in a matrix of 182 pairwise heterospecific GTO values (note that this is an asymmetric matrix since overlap of species A on B will be different from that of species B on A). For the five species that were examined in greater detail for ASO (see below), the total dataset (of 240 time windows) for the 20 combinations of species pairs was divided into ten subsets, each consisting of 24 time windows, such that there was equal representation of sampling from each transect and time period. GTO was then calculated for each of the 24 time windows and the median of these 24 values was determined.

Fine Temporal Overlap (FTO)

Fine Temporal Overlap (FTO) measures the actual temporal overlap between the calls of two species when two individuals, one of each species, are calling simultaneously, assuming no acoustic interaction between them. The proportion of sound on-time during a 60 s calling bout of an individual that was overlapped by sound from another simultaneously calling individual of a different species was calculated using a simulation. For each species, a 60 s recording of the call of an individual was selected that had call features (call period, duration and syllable period) similar to the mean call features for that species (Diwakar and Balakrishnan 2006; Nityananda and Balakrishnan 2006). This recording was then compared with a recording of the average call of each of the other species using custom-written programs (Vivek Nityananda, CES, IISc) in MATLAB (version 7, The Mathworks Inc, Natick MA). Since the calls are typically discontinuous, the total time out of 60 s during which sound was actually produced was calculated for the focal species' call. The proportion of this total time that was overlapped by the call of the other species was then calculated to obtain the FTO value which therefore ranged from 0 (no overlap) to 1 (100 % overlap).

This FTO computation was carried out for 11 values of initial phase difference between the calls of the two species and the median FTO calculated. This procedure was carried out for each of the 182 species-pair combinations. The variance around the median was low in all cases (shown for 20 species pairs in the Appendix: Figure S2) and the central tendency was thus a good descriptor. Effective Temporal Overlap (ETO) for each of the 182 species pairs was then calculated by multiplying GTO and FTO values (Figure S2).

Spectral overlap (SO)

Spectral overlap between pairs of species was computed using a custom-written program (Natasha Mhatre, University of Bristol) in MATLAB (version 7, The Mathworks Inc, Natick MA). Representative calls with dominant frequency and bandwidth close to the mean values (see Diwakar and Balakrishnan 2006; Nityananda and Balakrishnan 2006) were chosen and subjected to a Fast Fourier Transform (FFT) using a Hamming window and a window length of 2,048 sampling points in MATLAB (version 7, The Mathworks Inc, Natick MA) and their power spectra plotted. To compute spectral overlap between a pair of species A and B, the two relevant power spectra were aligned and normalised to unit power (to equalise their sound intensities). The spectral overlap of species A by B was computed as the proportion of the total area under the curve of the spectrum of A that was overlapped by the spectrum of B. The overlap of species B by A was the converse i.e. the proportion of the total area under the curve of spectrum B that was overlapped by the spectrum of A. Values of spectral overlap can thus range from 0 (no overlap) to 1 (complete overlap). Spectral overlap was computed in this manner for the 182 species-pair combinations.

Active space overlap (ASO) (Objective 2)

We carried out this analysis on five acoustically co-active and co-occurring, abundant, frequently calling understorey species with high temporal and/or spectral overlap, (Appendix:

Figs. S1, S2; Table S1). These five species, including two katydids (*Mecopoda* 'Two-Part' and *Pirmeda rosetta*) and three crickets (*Landreva* sp., *Phaloria* sp. and an unidentified podoscirtine species 'Whiner') also span the extremes of call SPL, temporal structure, dominant frequency and bandwidth (Diwakar and Balakrishnan 2006; Nityananda and Balakrishnan 2006), (Appendix: Figure S1; Table S1), thus representing the subset of species likely to experience or cause the most difficult masking problems. Other taxa are unlikely to have major masking effects on the above five species: of the other nine species previously recorded during this season (Diwakar and Balakrishnan 2006), five were present at low densities, two were small mogoplistines (scaly crickets) with low intensity or very low duty-cycle calls and the other two were katydids with low duty-cycle, high-frequency calls (Diwakar and Balakrishnan 2006). Frogs and cicadas were not a source of interference since they are temporally partitioned from crickets and katydids in these forests on a seasonal and diel scale respectively (Diwakar and Balakrishnan 2006).

The objective was to calculate ASO based on the spatial position of other simultaneously calling individuals, the call SPLs of different species, the differences in the transmission profiles of their calls and the receiver's hearing sensitivity. Each step is described in detail below.

Spacing of calling individuals

The crickets and katydids in these forests typically call in distinct and discontinuous patches, thereby forming well-defined choruses. We located active natural choruses of individuals of the five selected species during peak calling time (Diwakar and Balakrishnan 2006). All calling individuals of these five species were acoustically located in these choruses and their position flagged without disturbing the animal. After flagging the spatial location of all participants of the chorus, we revisited the flags to locate the exact position of the individuals to record their height of calling. The location of the chorus in the forest was noted and the patch was never sampled again. The following morning the patch was re-visited and the distance of each flag to every other flag was measured using a meter tape. In some cases, spacing was measured using triangulation. On the next sampling night, a different patch of forest was sampled (that was at least 500 m away to avoid pseudo-replication) and the exercise repeated. Ten active choruses were mapped in this way.

Species-specific call SPLs

At least ten calling individuals of each of the five species were located to measure the sound pressure level (SPL) close to source. All SPL measurements were made using a sound level meter (Brüel and Kjær, type: Observer 2,260, Brüel and Kjær ½ inch microphone type 4,189; frequency response: 6 Hz to 20 kHz) using the fast root mean square (RMS) setting (re: 2×10^{-5} N/m^2) at a distance of 0.5 m from the calling individual. The mean SPL for each species was calculated and used for calculation of call broadcast radii (see below).

Active space overlap (ASO)

Active space was defined as the above-ground volume of a sphere whose centre was a calling male and radius was calculated based on mean species call SPL, attenuation profile and assumed receiver hearing threshold of 40 (or 35) dB SPL (Kostarakos et al. 2008;

Hummel et al. 2011; Schmidt et al. 2011; Schmidt and Römer 2011) (details in Appendix: Table S2). We considered a listener falling within any of the regions of the focal sphere intersected by other spheres to be affected by overlap in the spatial domain. Therefore, to calculate ASO, we determined the proportion of an animal's above-ground broadcast volume that was overlapped by the broadcast sphere of a neighbor (see Appendix for details).

Examining the role of call SPL and receiver tuning in ASO (Objective 3)

We examined ASO for each species-pair combination in four scenarios: all receivers untuned and individuals of all species assumed to (1) call at the same SPL (72 dB) or (2) at species-specific SPLs; all receivers tuned to the frequency spectrum of their conspecific calls as matched filters (Capranica and Moffat 1983; Wehner 1989) and all calls (3) produced at the same SPL (72 dB) or (4) species-specific SPLs. Untuned and tuned katydid and cricket receivers were approximated using appropriate filters (500 Hz high-pass and one-third octave band-pass with centre frequencies matched to call carrier frequency, respectively) during the attenuation measurements, which were carried out in the habitat using both a standard (72 dB) and the mean species-specific source SPLs (see Appendix). The ASO for each pair of individuals was estimated by simulating the acoustic fields using these measurements and then calculating the proportion of active space of each calling individual that was overlapped by a (for pairwise interactions) or all neighbouring (for multispecies choruses) heterospecific calling individual/s (see Appendix for details). We carried out ASO estimation in two scenarios, one with random positions of receivers within the active space and the other with stratified receivers and compared the results. We did this because real receiver positions are unknown, but we expect, based on sender vertical stratification (Diwakar and Balakrishnan 2007), that receivers may be confined to the same strata.

Effective acoustic overlap (EAO) (Objective 4)

While the active space of a focal animal may be spatially overlapped by neighbouring callers, a listener present at such a point suffers masking only if at least one of the neighboring calls intersects with the focal animal's calls in time. Thus, we needed to combine the ASO with the temporal overlap to get at Effective Acoustic Overlap (EAO) suffered by a caller. In the case of species pairs, this was calculated by multiplying the ASO and ETO values. However, in the case of multispecies choruses, GTO for a species pair in the chorus was assumed to be 1 (individuals were assumed to be calling uninterruptedly, a conservative assumption) therefore ETO was taken as equal to FTO. Thus, the probability that a focal receiver in a multispecies chorus suffers masking at any given point is described by P_{mask} as given below:

$$P_{mask} = (1 - P_{nomask})$$

where, P_{nomask} is the probability that none of the neighbors' calls intersect with the focal animal's call in time. It can be calculated as follows:

$$P_{nomask} = \prod_{s \in S} (1 - P_s)$$

Here P_s is the FTO probability from sphere (or neighboring animal) s and S is the set of all spheres (all heterospecific neighbours for a given focal animal) that contribute to intersection at that sampling point. In the case of multispecies overlap, we incorporated the calculation of EAO within the simulation by incrementing dV_{shared} for each sampling point by P_{mask} instead of 1.

The effect of spacing (Objective 5)

To test whether the levels of EAO observed in multispecies choruses could occur by chance alone, we generated 100 spatially randomized versions of each natural chorus as follows. Given the number and species identity of each individual caller in the chorus, we assigned random positions to each individual such that the position fell within the volume and strata limits of that species. Random positions were assigned by dividing the total volume into pixels and picking a pixel using a random number generator; pixels once occupied could not be occupied by another individual. We then calculated EAO for each individual in the spatially randomized chorus using the algorithm described in (D) above. This procedure was repeated 100 times for each of nine observed choruses.

Statistical analyses

All statistical analyses were carried out in R (Version 2.14.0, The R Foundation for Statistical Computing). The overall comparisons of the distributions of GTO, FTO and ETO were made using the Wilcoxon matched-pairs sign rank test. To test for negative correlations between GTO, FTO and SO, we used Kendall-Tau correlations (since the distributions were not normal). Since each of these overlap matrices is asymmetric (the overlap proportion of species A on B is not equal to or predicted directly by the overlap proportion of species B on A) but the complementary pairs are not independent (the actual time or area overlapped by A on B will be the same as B on A), we did not compare all 182 species-pair values together. Instead, we re-sampled each matrix and picked half the number of values (e.g. either species A overlapped by B or B overlapped by A, but not both, in a random fashion). We generated 1,000 such matrices for each of GTO, FTO and SO, maintaining the pairing between the sampled cells in the three matrices for each randomization. We then compared GTO and FTO, GTO and SO, FTO and SO for each of the 1,000 randomly sub-sampled matrices to obtain a distribution of values of Kendall's Tau for each of the pairwise comparisons. The mean and confidence interval of each of these distributions of Tau values was calculated. The significance of the mean Tau value and those at the two ends of the confidence interval were examined and are reported.

To compare the effects on EAO of randomization of spatial positions of individuals in natural choruses, the distribution of observed EAO values for each species was compared with that of every spatially randomized chorus (100 randomized choruses in total). Comparisons between distributions were made in a pairwise fashion using a Wilcoxon matched-pairs sign rank test (since the distributions were not normal). For each species, we considered the observed distribution of EAO values to be significantly different from chance (at $\alpha = 0.05$) if more than 95 comparisons out of 100 had a P value of less than 0.05.

For pairwise ASO, the statistical models had one response variable, the proportion of active space overlapped, and three categorical explanatory variables: species-pair, call SPL and receiver tuning. As the response variable data were in the form of proportions, a generalized linear model (GLM) with binomial error was used for analysis (McCullagh and Nelder 1989; Crawley 2007). For multispecies choruses, the response variable was the proportion of the active space overlapped by multiple neighbouring heterospecific callers, and the explanatory variables were the species overlapped and the chorus (multispecies assemblage) it was in. The basic model had all the main effects and interaction terms. If there was over-dispersion in the model, the error structure was taken as quasi-binomial (McCullagh and Nelder 1989; Venables and Ripley 2002; Crawley 2007) to control for its effect. An analysis of deviance (McCullagh and Nelder 1989; Crawley 2007) was carried out for each model, where the significance of each explanatory term was checked. Each model was then simplified stepwise by removing the non-significant terms until a saturated model was obtained. The residuals from each saturated model were checked for normality and plotted against the fitted values (McCullagh and Nelder 1989; Venables and Ripley 2002; Crawley 2007). Models with acceptable fits were used for interpreting the results.

Results

Temporal and spectral overlap (Objective 1)

The distribution of Gross Temporal Overlap (GTO) values in the assemblage was broad (Fig. 1a, median = 0.31), with a number of species pairs calling together with high probability. We then examined the Fine Temporal Overlap (FTO), the overlap by chance alone between the calls of pairs of species if they were to call together without any acoustic interactions between them. The FTO values between pairs of species in the assemblage as a whole were dramatically lower (Fig. 1b, median = 0.09) than the GTO values (W = 22,143, $P < 0.001$), illustrating how differences in temporal structure between species result in low overlap levels between simultaneously calling heterospecific individuals. The ETO values for the assemblage were low (median = 0.04), being lower than 0.1 for 75 % of all species pairs (Fig. 1c). Spectral overlap (SO) between pairs of species was also low (Fig. 1d, median = 0.09), with a large number of species showing no overlap at all (mode = 0, first bar of histogram in Fig. 1d).

We then examined whether species pairs with structures resulting in high temporal overlap (FTO) avoid calling together by examining the correlation between GTO and FTO. We found a significant negative correlation between GTO and FTO for corresponding species pairs (mean Tau = −0.314, $P = 0.002$; Tau values at 95 % confidence intervals = −0.318 ($P = 0.002$) and −0.310 ($P = 0.003$)) indicating that species with high overlap due to their temporal structures have a significantly lower probability of calling together. There was however, no significant correlation between GTO and SO (mean Tau = 0.148 ($P = 0.16$); Tau values at 95 % confidence intervals = −0.143 ($P = 0.17$) and 0.153 ($P = 0.13$)) indicating that species with higher spectral overlap were not more likely to avoid calling together. We also examined the relation between FTO and SO and found no significant correlation (mean Tau = 0.172 ($P = 0.1$); Tau values at 95 % confidence intervals = 0.167 ($P = 0.11$) and 0.177 ($P = 0.091$). This indicates that call structures with high temporal overlap are not significantly more likely to have low spectral overlap and vice versa.

Active space overlap (ASO): the role of call SPL and tuning (Objectives 2 and 3)

The apparent lack of effect of spectral overlap on either temporal call properties or calling probability could be because the effects of spectral overlap as measured on signals are not manifested in real acoustic environments and a more realistic approach is to measure ASOs. We estimated ASOs assuming four different scenarios of call SPLs and receiver

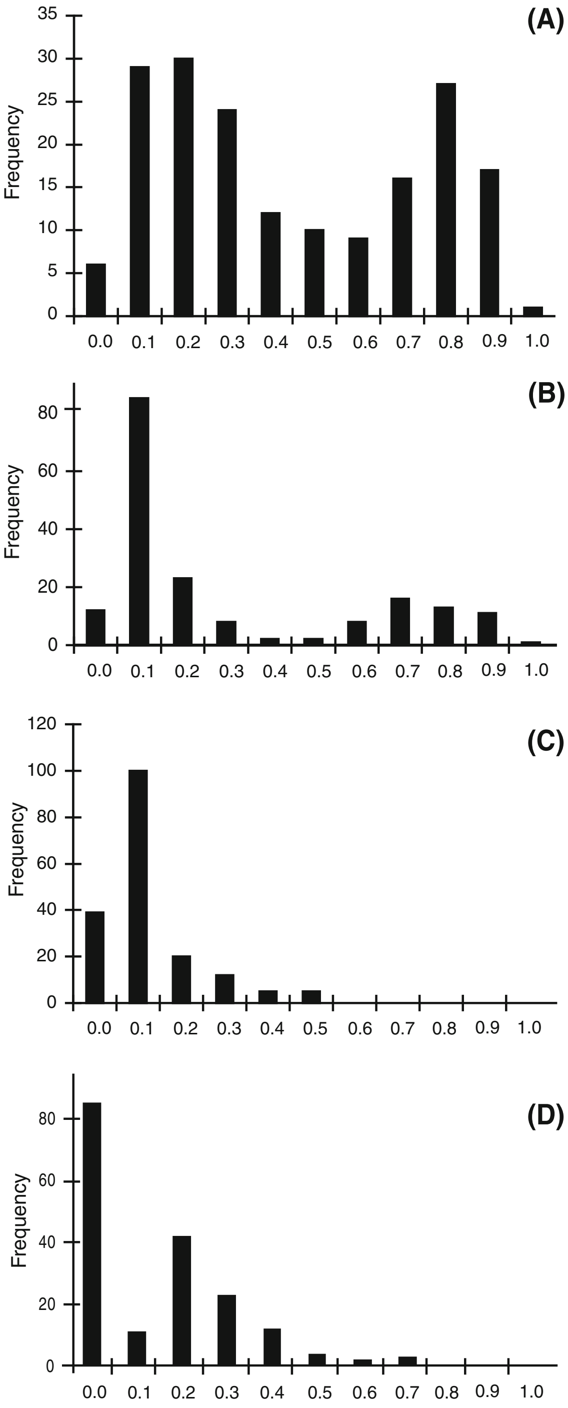


Fig. 1 Temporal and spectral overlap in the assemblage. Frequency distributions of pairwise temporal and spectral overlap probabilities for 14 species of crickets and katydids ($N = 182$ species-pair combinations). **a** Gross Temporal Overlap (GTO), **b** Fine Temporal Overlap (FTO), **c** Effective Temporal Overlap (ETO), **d** Spectral Overlap (SO). First bar indicates values <0.01, second bar 0.01–0.1, bin width from the third bar onwards is 0.1

tuning (Fig. 2). In the first case (Fig. 2a), an artificial baseline (with all calls produced at equal SPLs and all receivers untuned), there was large variance in ASO depending upon spacing and species pairs. When all species call at their natural SPLs and if all receivers are untuned, then the louder species of each pair maximizes its non-overlapped active space at the expense of the softer one, irrespective of call structure (Fig. 2b). Tuning receivers as matched filters had the effect of lowering ASO dramatically, including for species that called at much lower SPLs than their potential maskers (Fig. 2c, d). In fact, in the most realistic scenario of natural call SPLs and tuned receivers, 16 out of 20 species-pair combinations had median ASO levels close to zero (Fig. 2d), with little variance in spite of the range of pairwise distances considered (Figure S3 in Appendix).

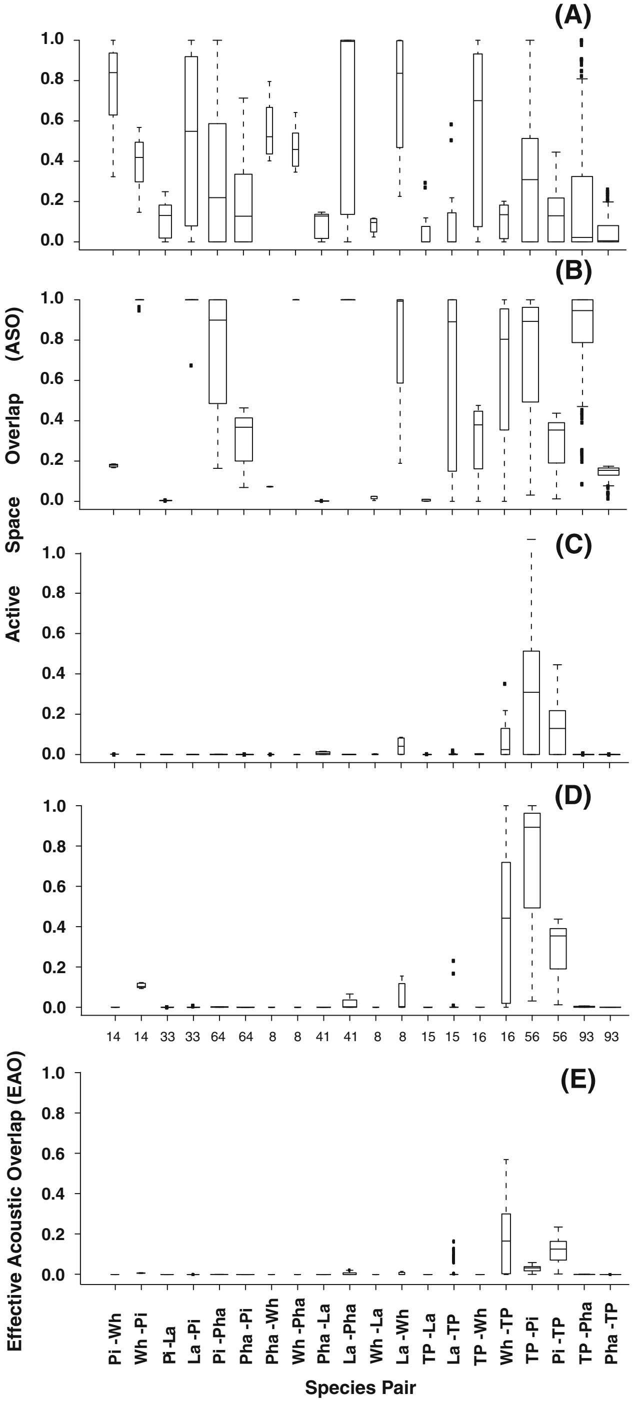
Call SPL and tuning had significant main effects on ASO (Table 1, $P < 0.001$ for both) but no significant interactions ($P = 0.92$), revealing them to be independent strategies that can effectively counter spatial masking. For tuned receivers and species-specific call SPLs, the median value of EAO was close to zero for 17 out of 20 species pairs (Fig. 2e). To test the robustness of these values, however, we needed to examine the assumptions. These included random receiver positions within the active space and receiver hearing thresholds of 40 dB SPL. Assuming a lower receiver hearing threshold of 35 dB SPL yielded similar results (Figure S4). Although stratification had a significant effect on the ASO, and its effects were independent of SPL and tuning (Appendix: Table S3), there were no dramatic differences in ASO for most species pairs between the case of unstratified and stratified receivers (compare Figs. 2, 3). For tuned receivers, stratification resulted in an increase in ASO for four species pairs, but median EAO still remained less than 0.05 for 17 out of 20 species pairs (Fig. 3).

Effective acoustic overlap (EAO) in natural multispecies choruses (Objective 4)

We have so far examined overlap between pairs of individuals, whereas in natural environments, an individual is surrounded by multiple calling individuals of other species. To examine this scenario, we reconstructed ten natural choruses (details of composition in Appendix: Table S4) and computed EAO for the active space of each individual. The median EAO for the five species ranged from 0 to 0.09 (Fig. 4) and the active spaces of 81 out of 110 individuals (74 %) had EAO lower than 0.05.There was, however, a significant interaction between species identity and chorus (Table 2, $P = 0.003$) and EAO for a species depended on which chorus it was in. For *P. rosetta* and 'Whiner', that have spectral overlap with *Mecopoda* 'Two-Part', EAO was clearly bimodal, being almost zero in choruses where *Mecopoda* was absent and high (>0.6) in choruses with large numbers of *Mecopoda* (Fig. 4a, c; Table S4: Appendix). For *Mecopoda* 'Two-Part', EAO was close to zero in all choruses except where it co-occurred with *P. rosetta*, and maximum EAO was 0.21 (Fig. 4d; Table S4). For *Landreva* sp., the softest caller, 9 out of 15 individuals had EAO less than 0.1 (Fig. 4b). *Phaloria* sp. suffered little EAO in any chorus (Fig. 4e). Thus, even when multiple calling neighbours were considered, overall EAO was low except when species pairs that had high spectral overlap occurred together in the same chorus.

Do senders use active spacing to minimize EAO? (Objective 5)

To test whether the observed levels of EAO were a result of active spacing between individuals, we then compared the observed distribution of EAO values for each of the five species with each of 100 artificial choruses in which the spatial positions of all individuals in the choruses was randomised. For 'Whiner', *P. rosetta* and *Landreva* sp., the observed


(A)
(B)
(C)
(D)
(E)
1.0
0.8
0.6
0.4
0.2
0.0
Space Overlap (ASO)
Active
Effective Acoustic Overlap (EAO)
14 14 33 33 64 64 8 8 41 41 8 8 15 15 16 16 56 56 93 93
Pi -Wh
Wh -Pi
Pi -La
La -Pi
Pi -Pha
Pha -Pi
Pha -Wh
Wh -Pha
Pha -La
La -Pha
Wh -La
La -Wh
TP -La
La -TP
TP -Wh
Wh -TP
TP -Pi
Pi -TP
TP -Pha
Pha -TP
Species Pair

◀**Fig. 2** Active space overlap in the assemblage. Box-and-whisker plots of the distributions of Active Space Overlap (ASO) values for five species of crickets and katydids (N = 20 species-pair combinations) in four scenarios: Individuals of all species calling at equal SPLs (72 dB) with **a** untuned or **c** tuned receivers; individuals calling at mean species-specific SPLs with **b** untuned or **d** tuned receivers. **e** Distributions of Effective Acoustic Overlap (EAO) values generated by multiplying all combinations of ETO and ASO values for species-specific call SPLs and tuned receivers. Numbers below X axis (**d**) and width of boxes indicate sample sizes. *La Landreva* sp. (66.7), *Pi Pirmeda rosetta* (80.8), *Ph Phaloria* sp. (80.1), *TP Mecopoda* 'Two-Part' (80.4), *Wh* 'Whiner' (73.3). Numbers in brackets above indicate mean species call SPL in dB. Convention: *Pi-Wh Pirmeda* overlapped by 'Whiner'

values of EAO were not significantly different from chance: the number of *P* values greater than 0.05 on comparison with the EAO values from 100 randomized choruses was 100 for 'Whiner' (median *P* value = 0.371), 95 for *P. rosetta* (median *P* value = 0.534) and 92 for *Landreva* sp. (median *P* value = 0.233). For *Phaloria* sp. and *Mecopoda* 'Two-Part,' however, the observed distribution of EAO values was significantly lower than those from the randomized choruses: the number of *P* values greater than 0.05 on comparison with the EAO values from 100 randomized choruses was zero for both *Phaloria* sp. (median *P* value = 0.002) and *Mecopoda* 'Two-Part' (median *P* value = 0.004). When the distributions of EAO values were examined, however, the difference between observed and randomized choruses (Fig. S5: Appendix) was negligible for *Phaloria* (median = 0 for both distributions, maximum EAO value = 0.003 for observed and 0.005 for randomized choruses). For *Mecopoda* 'Two-Part,' the observed choruses had a median EAO value of 0.09 as compared with a median value of 0.14 in randomized choruses (Fig. S5), indicating some decrease in heterospecific acoustic overlap by active spacing.

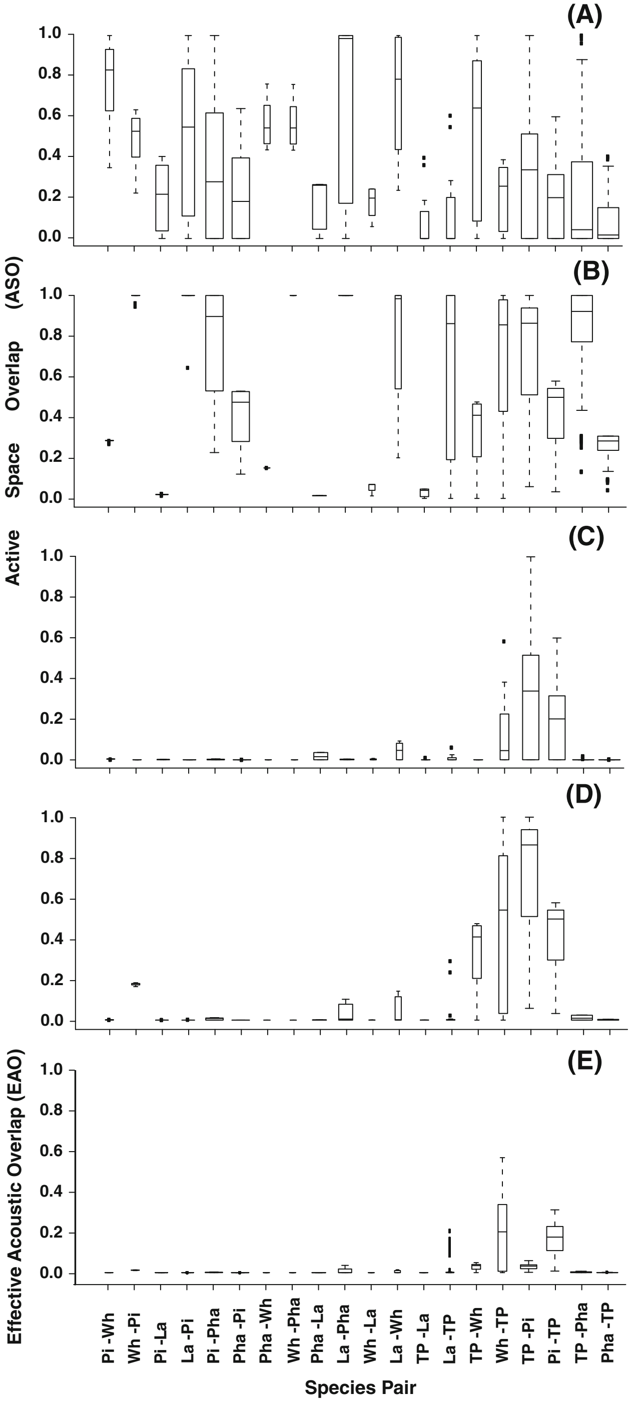
Discussion

In this study we have examined masking interference in an acoustically signaling assemblage of rain forest crickets and katydids using different approaches. We have used signal structures and spacing of signalers to estimate temporal, spectral and active space overlap between species. We then examined these overlaps for evidence of strategies of masking avoidance in the assemblage. Whereas we found evidence that species with signal temporal structures that result in high temporal overlap (temporal scale 4) may avoid calling together (temporal scale 3), there was no relation between spectral overlap and calling activity. There was also no correlation between the spectral and temporal overlaps (scale 4) of the signals of different species. In addition, we found little evidence that species calling in the understorey actively use spacing to minimise acoustic overlap.

We have, for the first time, developed a three-dimensional simulation model of acoustic active spaces that integrates temporal, spectral and amplitudinal characteristics of multiple signals to allow estimation of effective acoustic overlap (EAO). Using this, we show that EAOs are on average close to zero for most individuals in natural, multispecies choruses, even in the absence of behavioral avoidance mechanisms such as heterospecific inhibition of calling or active spacing. We also show that increasing call SPL and tuning receivers are powerful strategies to minimise acoustic overlap and thereby masking interference.

Acoustic overlap avoidance using time and frequency

Previous studies on masking interference in acoustically signaling insect assemblages (reviewed in Brumm and Slabbekoorn 2005) have revealed diel partitioning of calling


(A)
(B)
(C)
(D)
(E)
1.0
0.8
0.6
0.4
0.2
0.0
Active Space Overlap (ASO)
Effective Acoustic Overlap (EAO)
Pi -Wh
Wh -Pi
Pi -La
La -Pi
Pi -Pha
Pha -Pi
Pha -Wh
Wh -Pha
Pha -La
La -Pha
Wh -La
La -Wh
TP -La
La -TP
TP -Wh
Wh -TP
TP -Pi
Pi -TP
TP -Pha
Pha -TP
Species Pair

◀**Fig. 3** Pairwise active space overlap for stratified receivers. Box-and-whisker plots of the distributions of ASO values for five species of crickets and katydids (N = 20 species-pair combinations) in four scenarios: Individuals of all species calling at equal SPLs (72 dB) with **a** untuned or **c** tuned receivers; individuals calling at mean species-specific SPLs with **b** untuned or **d** tuned receivers. **e** Distributions of Effective Acoustic Overlap (EAO) values generated by multiplying all combinations of ETO and ASO values for species-specific call SPLs and tuned receivers. Receivers were confined to the same strata as conspecific senders in all cases

between katydid species and potential partitioning of calling time and call frequencies in cicada species (Gogala and Riede 1995; Sueur 2002). Diel shifts in calling activity in the katydid species *Neoconocephalus spiza* and *Mygalopsis marki* have been shown to be due to masking interference from other syntopic calling species (Greenfield 1988; Römer et al. 1989). In a recent study on a neotropical cricket assemblage, however, Schmidt et al. (2013) failed to find evidence for diel partitioning of calling time between cricket species. Our previously published study (Diwakar and Balakrishnan 2006) also failed to find evidence for diel partitioning between different cricket and katydid species in the paleotropical assemblage examined in this study. In tropical forests, at least, there does not seem to be strong selection for partitioning on a diel scale in cricket and katydid assemblages, suggesting that other mechanisms of acoustic avoidance are probably sufficient to prevent acoustic overlap. Alternatively, lack of call partitioning on a diel scale may be because of benefits to calling between dusk and midnight, such as optimal atmospheric conditions for sound transmission or lowered risk of predation, both of which may exert a stronger selection pressure than masking interference.

Short-term adjustments of call timing to avoid interspecific interference have been shown in birds and frogs (Ficken et al. 1974; Popp et al. 1985; Brumm 2006; Wong et al. 2009). Although acoustically signaling insects are well-known to be capable of adjustments on a fine temporal scale, much of the work has focused on acoustic interactions between conspecific signalers in the context of call synchrony or alternation in choruses (Gerhardt and Huber 2002). Our results suggest that cricket and katydid species with call structures that result in greater levels of temporal overlap may avoid calling together, thus reducing acoustic overlap.

We found no evidence that species pairs with higher spectral overlap avoid calling together or have temporal structures that result in less overlap. There could be two reasons for this: firstly, the overall levels of spectral overlap for the assemblage as a whole were low (Fig. 1d, with a mode of zero and a median <0.1). A similar result was obtained for the neotropical cricket assemblage investigated by Schmidt et al. (2013). In both cases, the vast majority of species pairs showed little or no spectral overlap. It is possible that these low levels of spectral overlap do not provide a sufficiently large selection pressure to drive signals or signaling behaviour towards temporal avoidance simply because the spectral separation is great enough to avoid overlap. The second reason could be that spectral overlap measurements do not necessarily reflect the effective acoustic overlap. Our results, using an active space simulation model for five species do indicate, however, that even when spacing, SPL and receiver characteristics are taken into account, the only species that do suffer significant levels of ASO are those with extensive spectral overlap (Fig. 2: *Mecopoda* 'Two-Part'—*Pirmeda rosetta* and 'Whiner'—*Mecopoda* 'Two-Part'). In the two specific cases referred to above, however, one can clearly see how the low ETO effectively nullifies the large ASO to result in dramatically lower levels of EAO (compare the ASO levels with the EAO levels for these two pairs in Fig. 2d, e). Thus, specific cases of a negative relation between temporal and active space overlap do exist. Therefore the

Table 1 Analysis of deviance results for pairwise active space overlap in three scenarios

	Null	Species pair	Tuning	SPL	Species pair × tuning	Species pair × SPL	SPL × tuning	Species pair × SPL × tuning
40 dB threshold								
df		19	1	1	19	19	1	19
Deviance		5.30×10^{10}	2.86×10^{10}	2.28×10^{9}	2.31×10^{10}	4.55×10^{9}	1.12×10^{5}	3.44×10^{6}
Residual df	2,783	2,764	2,763	2,762	2,743	2,724	2,723	2,704
Residual deviance	1.42×10^{11}	8.90×10^{10}	6.01×10^{10}	5.78×10^{10}	3.46×10^{10}	3.01×10^{10}	3.01×10^{10}	3.01×10^{10}
P values		**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.91	1
40 dB threshold, stratified receivers								
df		19	1	1	19	19	1	19
Deviance		6.22×10^{8}	5.30×10^{9}	7.22×10^{8}	4.64×10^{9}	1.28×10^{9}	3.28×10^{5}	2.27×10^{7}
Residual df	2,783	2,764	2,763	2,762	2,743	2,724	2,723	2,704
Residual deviance	2.36×10^{10}	$1.73 \times \times 10^{10}$	1.20×10^{10}	1.12×10^{10}	6.60×10^{9}	5.32×10^{9}	5.32×10^{9}	5.30×10^{9}
P values		**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.66	0.83
35 dB threshold								
df		19	1	1	19	19	1	19
Deviance		4.04×10^{11}	2.02×10^{11}	2.58×10^{9}	1.66×10^{11}	3.69×10^{10}	2.49×10^{5}	5.31×10^{7}
Residual df	2,783	2,764	2,763	2,762	2,743	2,724	2,723	2,704
Residual deviance	8.59×10^{11}	4.55×10^{11}	2.53×10^{11}	2.55×10^{11}	8.46×10^{10}	4.77×10^{10}	4.77×10^{10}	4.77×10^{10}
P values		**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.9	1

Table 2 Analysis of deviance results for active space overlap in multispecies natural choruses

	Null	Species	Chorus	Species × Chorus
Multisphere masking				
df		4	9	18
Deviance		1.87×10^8	8.52×10^9	2.31×10^8
Residual df	109	105	96	78
Residual deviance	9.47×10^9	9.29×10^9	7.67×10^8	5.36×10^8
P value		**<0.001**	**<0.001**	**0.003989**

Analysis of deviance table of the primary model with quasi-binomial error structure is shown here. Significant *P* values are written in bold font

third reason for the lack of negative correlation may be because we are investigating assemblage-wide trends. If some pairs do actually diverge in call timing due to spectral overlap, this will be obscured in such assemblage-wide analyses, as also pointed out by Planqué and Slabbekoorn (2008).

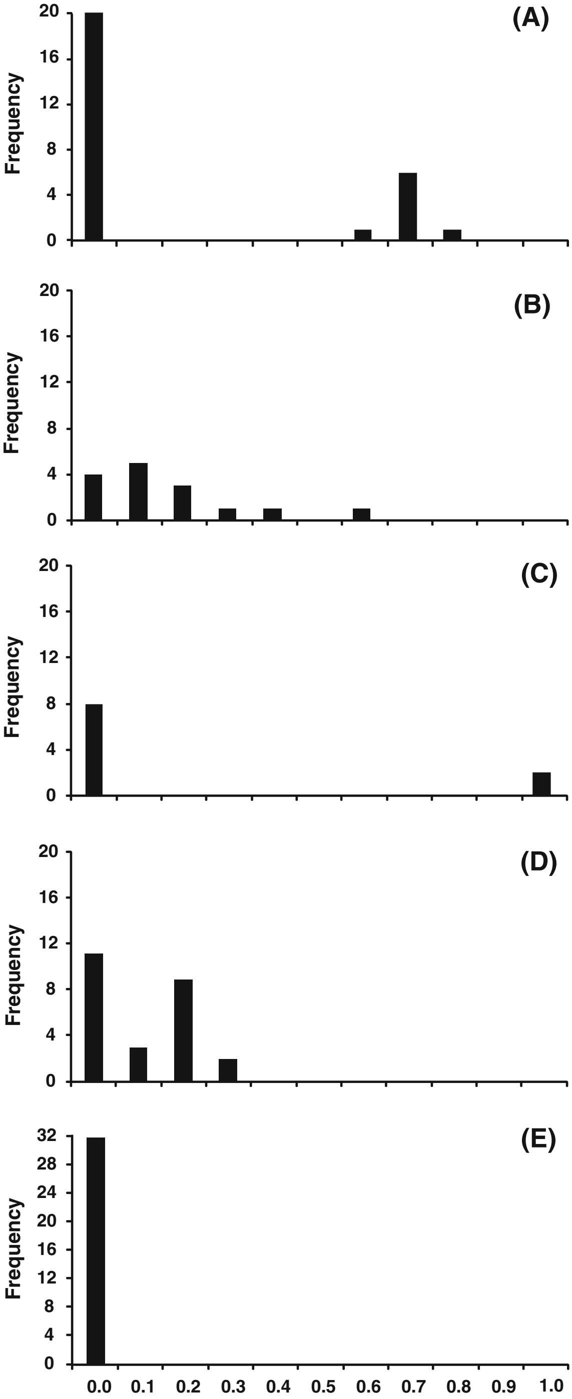
Active space models and effective acoustic overlap

We have developed simulation models that allow estimation of three-dimensional active space overlap either in pairwise interactions or taking into account multiple calling neighbours. We have also developed an integrated model that combines the effects of call temporal structures, spacing, relative intensity, propagation and tuning to estimate EAO in natural choruses. To the best of our knowledge, this is the first time that such an integrated model has been developed and used to study acoustic overlap. We believe that such quantitative models are an important tool to study acoustic masking interference and understand its role as a selective force driving the evolution of signal structures and signaling behaviour.

In this study, we have shown that the levels of EAO that occur in natural multispecies choruses are remarkably low, even for species with high temporal and spectral overlap, when call structure, timing, SPL, spacing, habitat effects and receiver tuning are all taken into account. The five understorey species that we examined represent worst-case masking scenarios and we expect even lower EAO for most other species in the assemblage, given their narrow bandwidth calls (Diwakar and Balakrishnan 2006) and low ETO (Fig. 1c). Although we did not directly measure masking using receivers, spatial masking probabilities are likely to be lower than implied by the ASO since ASO was calculated based on just the detection of a potentially masking heterospecific signal, whereas crickets and katydids are known to possess mechanisms of selective attention and neuronal gain control that should result in lower masking probabilities (Gerhardt and Huber 2002; Brumm and Slabbekoorn 2005; Schmidt and Römer 2011).

We also examined the robustness of our results by changing the assumptions of hearing sensitivity and taking into account the realistic possibility of receiver stratification. Our simulations show that the results are robust to changes in these assumptions. One of the key assumptions, receiver tuning, was not empirically tested, but is highly reasonable given the compelling evidence for matched frequency filtering in the tropical cricket and katydid species where this has been examined (Kostarakos et al. 2008; Schmidt et al. 2011; Schmidt and Römer 2011; Hummel et al. 2011).

Fig. 4 Effective acoustic overlap in natural multispecies choruses. Frequency histogram showing the distribution of Effective Acoustic Overlap (EAO) values for the five species (N = 10 choruses). **a** *P. rosetta* (0.004), **b** *Landreva* sp. (0.024), **c** 'Whiner' (0), **d** *Mecopoda* 'Two-Part' (0.09), **e** *Phaloria* sp. (0). Numbers in brackets indicate median values. Note the bimodality in EAO for *P. rosetta* and 'Whiner:' High and low values corresponded to presence or absence of *Mecopoda* 'Two-Part' in the chorus. Bin widths as in Fig. 1



Acoustic overlap avoidance by active spacing

Few previous studies on acoustic interference have considered the effects of spatial distribution. In a recent paper, Schmidt et al. (2013) examined the distribution of acoustically signaling males of different species in a neotropical cricket assemblage in both horizontal and vertical dimensions. Using a null model approach, they found that the horizontal spatial distribution was randomly structured. Their study however is not comparable to ours for several reasons. Most importantly, it was on a much larger spatial scale and examined occurrence probabilities across different sites rather than actual spacing between individuals of a multispecies chorus. Further, they did not use active space models to estimate acoustic overlaps. In the vertical dimension, Schmidt et al. (2013) did find evidence, as we had previously (Diwakar and Balakrishnan 2007), for vertical stratification of different calling cricket species. The relation between vertical stratification of the calling assemblage and EAO, however, remains to be explored in more detail.

We found evidence for active spacing in two out of five species tested but the actual overlap reduction gained was either negligible (<1 % in *Phaloria* sp.) or modest (3–5 % in *Mecopoda* 'Two-Part'). This is in sharp contrast to the large reductions in ASO gained by increasing call SPL or tuning receivers (Fig. 2). The role of acoustic interference as a driver of active spacing is therefore unclear. This will need to be clarified in the future using acoustic playback and behavioural experiments.

Acoustic overlap avoidance using receiver tuning and call SPL

Receiver tuning emerged as a powerful strategy to minimise acoustic overlap. Our results show that tuning allows narrow bandwidth callers to minimize acoustic overlap, yet call at lower SPLs (exemplified by *Landreva* sp.), facilitating safe and effective communication in the presence of potentially eavesdropping predators. Interestingly, calling loud was a highly effective strategy to minimize ASO, independent of spectral and temporal differences in call structure between species. Increasing call SPL has usually been evoked as a successful strategy in the context of sexual selection, with louder males of a species attracting more females (Forrest and Green 1991; Ryan and Keddy-Hector 1992; Farris et al. 1997). Our results suggest that minimizing acoustic spatial overlap with other species may represent another important selective pressure leading to high call SPLs. Calling louder is a well-known short-term behavioural strategy to increase signal-to-noise ratio in noisy environments (the Lombard Effect: Brumm and Slabbekoorn 2005) and our results suggest an analogous phenomenon in acoustically signaling insects on an evolutionary time scale. Species with high bandwidth calls in acoustically dense assemblages are thus predicted to call louder than those with narrow bandwidth calls to minimize acoustic masking, since they are less able to utilize frequency tuning.

Conclusion

The cricket and katydid species of this assemblage do not partition calling on a seasonal or diel time scale (Diwakar and Balakrishnan 2006) and in this study we have shown that a number of species pairs call together within time windows of a few minutes. The effective temporal overlap was, however, remarkably low for most species pairs due to a combination of behavioral avoidance of temporal overlap and the low levels of overlap by chance alone resulting from the different call temporal structures. Effective acoustic overlaps were also low, even in the absence of active spacing by senders. Increasing call SPL and tuning receivers minimizes active space overlap whereas the diverse temporal structures of the calls and active avoidance of calling together result in low temporal overlap. Taken together, these different strategies allow many species to call together yet communicate with little interference in the cacophony of a tropical rain forest, so evocatively described by Darwin (1988) as ‘A most paradoxical mixture of sound and silence…’

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