



Modelling the effects of chorus species composition and caller density on acoustic masking interference in multispecies choruses of crickets and katydids



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ABSTRACT

Natural multispecies acoustic choruses such as the dusk chorus of a tropical rain forest consist of simultaneously signalling individuals of different species whose calls travel through a common shared medium before reaching their 'intended' receivers. This causes masking interference between signals and impedes signal detection, recognition and localization. The levels of acoustic overlap depend on a number of factors, including call structure, intensity, habitat-dependent signal attenuation and receiver tuning. In addition, acoustic overlaps should also depend on caller density and the species composition of choruses, including relative and absolute abundance of the different calling species. In this study, we used simulations to examine the effects of chorus species relative abundance and caller density on the levels of effective heterospecific acoustic overlap in multispecies choruses composed of the calls of five species of crickets and katydids that share the understorey of a rain forest in southern India. We found that on average species-even choruses resulted in higher levels of effective heterospecific acoustic overlap than choruses with strong dominance structures. This effect was found consistently across dominance levels ranging from 0.4 to 0.8 for larger choruses of forty individuals. For smaller choruses of twenty individuals, the effect was seen consistently for dominance levels of 0.6 and 0.8 but not 0.4. Effective acoustic overlap (EAO) increased with caller density but the manner and extent of increase depended both on the species' call structure and the acoustic context provided by the composition scenario. The *Phaloria* sp. experienced very low levels of EAO and was highly buffered to changes in acoustic context whereas other species experienced high EAO across contexts or were poorly buffered. These differences were not simply predictable from call structures. These simulation-based findings may have important implications for acoustic biodiversity monitoring and for the study of acoustic masking interference in natural environments.

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1. Introduction

Tropical forests are species-rich and known to harbour high levels of biodiversity (Rosenzweig, 1995). This diversity is also reflected in the diversity of signals used by acoustically communicating taxa such as cicadas, crickets, katydids, frogs and birds (Diwakar and Balakrishnan, 2007; Duellman and Pyles, 1983; Luther, 2009; Schmidt et al., 2013; Sueur, 2002). One of the most striking phenomena of the rain forest is the loud dusk chorus, which consists of individuals of different species, usually crickets, katydids, frogs and/or cicadas, all calling at the same time (Riede, 1996). Typically, the callers are males, who produce loud, often species-specific sound signals that serve to attract potential mates (females of the same species). Females recognise the presence of conspecific

males based on the acoustic signal patterns and also use these to locate them (Gerhardt and Huber, 2002). When a large number of species call together, the receivers are faced with the problem of detecting, discriminating and locating conspecific call patterns embedded in heterospecific 'noise' (Bee and Michéyl, 2008; Brumm and Slabbekoorn, 2005; Langemann and Klump, 2005). How this is achieved in the complex and noisy acoustic environment of the dusk chorus is little understood.

Acoustic niche partitioning has been proposed as a possible solution: signallers could in principle avoid overlap by partitioning calls in time and frequency (reviewed in Brumm and Slabbekoorn, 2005). The receivers could also restrict responses to specific, non-overlapping regions of acoustic signal space (Amézquita et al., 2011), thus occupying specific niches in multidimensional space. Previous studies on acoustic masking interference in forest environments have typically used such models based on the concept of ecological niche partitioning (Amézquita et al., 2011; Chek et al., 2003; Luther, 2009; Planqué and Slabbekoorn, 2008; Schmidt et al., 2013; Sueur, 2002). These studies have examined whether signal structures are spaced further apart in multidimensional space than predicted by chance alone or whether

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signallers show evidence of spatial, spectral or temporal partitioning of calls.

The levels and extent of acoustic masking interference experienced by individual receivers depend on a large number of factors. These include signal temporal and spectral structure, signal intensity at source, habitat effects on signal transmission, distance of each receiver from conspecific and heterospecific callers as well as hearing thresholds and frequency tuning of receivers (Jain et al., 2014; Schmidt and Römer, 2011; Schmidt et al., 2013). We recently developed a three-dimensional acoustic active space simulation model that allowed us to estimate effective acoustic overlap (EAO) in multispecies choruses, taking into account all of the above factors (Jain et al., 2014). EAO sets the upper limit to the levels of acoustic masking interference likely to be experienced by a receiver. The model was used to simulate the masking scenario in natural multispecies choruses of crickets and katydids in the understorey of a tropical rain forest. For the five species investigated, we found that median heterospecific EAO levels tended to be quite low and close to zero in most cases. The low levels of EAO estimated in these natural choruses could stem from two main factors: 1) temporal and spectral segregation of signals in combination with relative call intensities and receiver tuning (Jain et al., 2014) and 2) low total abundance of callers or low chorus density. In addition, chorus composition in terms of relative abundance of different calling species may affect the levels of acoustic interference experienced by receivers in these multispecies choruses.

In this study, we used our previously developed three-dimensional active space simulation model to explore the effects of chorus species composition (relative abundance), chorus size and density on effective acoustic overlap (EAO) in multispecies choruses of crickets and katydids. We examined the same five species used in our previous study but constructed artificial choruses. First, we examined whether choruses with higher species evenness resulted in lower acoustic overlaps for receivers than choruses with high levels of species dominance. Second, we examined the effects of chorus density on EAO by increasing the total number of callers of all five species in a fixed volume of space. Although EAO is expected to increase with caller density, the extent and manner of increase is likely to be different for different species. Our third objective was to examine whether some species were better buffered than others (in terms of levels of heterospecific acoustic overlap experienced) against changes in chorus density and composition (species relative abundance) in these multispecies choruses.

2. Material and methods

2.1. Study species and calls

We used the acoustic characteristics of three species of crickets (Order Orthoptera, Family Gryllidae) and two species of katydids (Order Orthoptera, Family Tettigoniidae), the males of which form a large part of the nocturnal multispecies choruses in the understorey of the tropical rain forests of Kudremukh National Park in Southern India (Diwakar and Balakrishnan, 2007). Their calls have been described previously (Diwakar and Balakrishnan, 2007; Nityananda and Balakrishnan, 2006) and are detailed in Fig. 1 and Table 1. The three cricket species include *Landreva* sp. (subfamily Gryllinae), *Phaloria* sp. (subfamily Itarinae) and 'Whiner' (subfamily Podoscirtinae). The two katydid species include *Mecopoda* 'Two-Part' (subfamily Mecopodinae) and *Pirmeda rosetta* (subfamily Pseudophyllinae). These five species overlap in call season and diel call timing and call together from the forest understorey (Diwakar and Balakrishnan, 2007). In addition, their calls cover a wide range of values of call intensity (Jain et al., 2014), temporal structure, dominant frequency and bandwidth (Diwakar and Balakrishnan, 2007; Nityananda and Balakrishnan, 2006). The calling activity patterns, habitat-dependent signal attenuation and spacing between individual callers have been previously measured for these

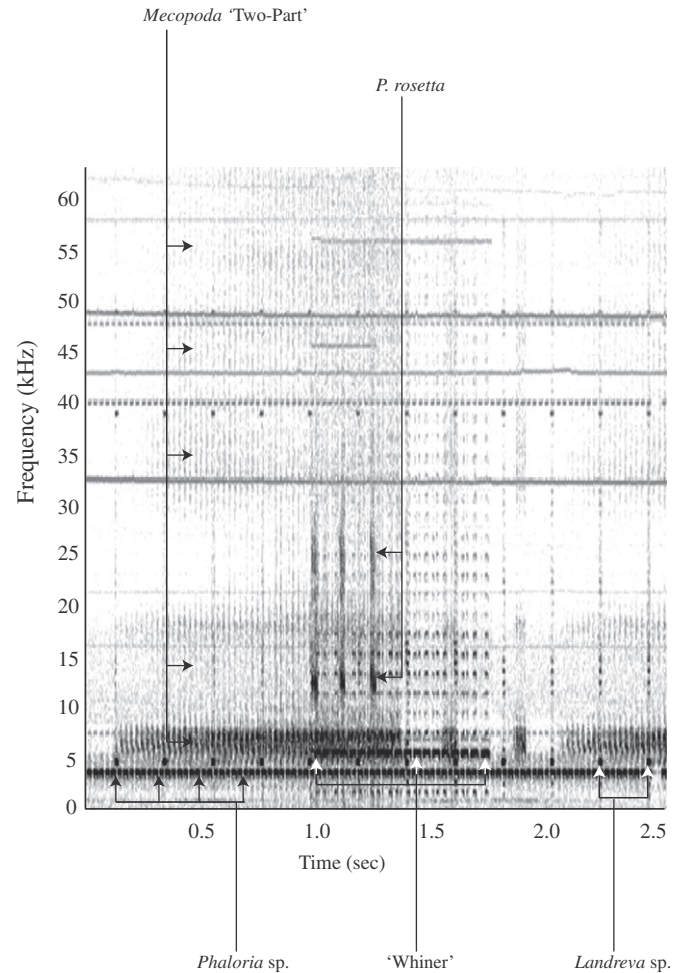


Fig. 1. Call structures. Spectrogram showing the spectral and temporal features of the calls of the five species of crickets and katydids and the overlaps between them.

species (Diwakar and Balakrishnan, 2007; Jain and Balakrishnan, 2012; Jain et al., 2014).

2.2. Study design

To examine how EAO changed as a function of chorus relative abundance, we generated six types of artificial multispecies choruses: the first was even, with callers of each of the five species being equally abundant (probability of occurrence of each species = 0.2). The other five choruses had a strong dominance structure (probability of occurrence of the dominant species = 0.8 and probability of occurrence of each of the other species was equal and set at 0.05). Each dominant

Table 1
Call features of the five species of crickets and katydids.

Species name	Dominant frequency (kHz) mean (SE)	Bandwidth ^a (kHz) mean (SE)	Duty cycle (%) mean	SPL ^b (dB) mean
<i>Mecopoda</i> 'Two-part'	N.A. ^c	78 (0.85)	94.7	80.4
<i>Pirmeda rosetta</i>	13.96 (0.60)	16.6 (0.82)	4.2	80.8
<i>Phaloria</i> sp.	4.57 (0.16)	0.39 (0.08)	77.8	80.1
<i>Landreva</i> sp.	4.86 (0.28)	0.43 (0.08)	8.4	66.7
'Whiner'	5.91 (0.10)	0.42 (0.13)	6.4	73.3

^a The bandwidth of the frequency spectrum was measured at 20 dB below the frequency of peak amplitude. Based on data from Diwakar and Balakrishnan, (2007); Nityananda and Balakrishnan (2006); Jain et al. (2014).

^b Sound pressure level.

^c N.A. = not applicable (due to multiple dominant frequency peaks in the spectrum).

chorus type had one of the five species as the dominant one. To examine the effect of chorus density on EAO, for each of the six chorus types, we varied the total number of calling individuals from 20 (which is close to the observed number) to 40, 60, 80, 100 and 120 individuals, keeping the physical space available constant at $30 \times 30 \times 12$ (height) m^3 (corresponding with the average volume occupied by the understorey in these forests: Jain and Balakrishnan, 2011). To examine the effect of different degrees of dominance, the average EAO values were estimated for each species for every iteration of the simulation across four different dominance levels (0.2, 0.4, 0.6 and 0.8) for chorus sizes of 20 and 40. Each chorus composition was spatially iterated 100 times, with caller position being randomly varied (within the spatial limits specified below) in every iteration.

2.3. Simulation and estimation of acoustic overlap

The model was built in three distinct steps: 1) Generating the choruses of given species composition and relative abundance, 2) Assigning random positions to the individuals of a given chorus in each iteration 3) Calculating EAO in multispecies choruses. The algorithmic details of the computations of each step are given below. Source codes are also available on request.

2.3.1. Generating the choruses

In order to generate choruses containing individuals (totalling N) from S species given the relative proportion of each species we use the following method.

Algorithm. Generate_Population (Species Count S, Individual Count N, Distribution D.)

Step a. Assign each species s to a region of the number line $[L, U]$ between 0..1 such that $U-L = \text{Distribution}[s]$.
 Step b. For each Individual i from 1...N.
 Step b.1 R Random Number between 0, 1.
 Step b.2 Find region where R falls and assign Individual i to Species s to which the region belongs.

2.3.2. Assigning random positions to individuals of a chorus

Given a population, volume, strata information for each species we assign random positions to each individual in the population such that the position falls within the volume and strata of the species. The assigned locations are also such that no two individuals are within 1 unit of distance (m) of each other. In order to assign individuals to 3-D space we split the volume into cells of dimensions $1 \times 1 \times 1$. If the total volume is X, Y, Z there are $X \times Y \times Z$ cells in the volume. Given any cell at coordinate (i,j,k) where

$$0 \leq i \leq X, 0 \leq j \leq Y, 0 \leq k \leq Z,$$

we can transform the coordinate into an integer from $0 \dots X \times Y \times Z$

using the following formula

$$F(i, j, k) = (X \cdot Y \cdot k + (X \cdot j + i))$$

and an integer to a coordinate using

$$C(I) = I \% X, (I/X) \% Y, I/(X \cdot Y), \text{ where } \% \text{ is the modulus operation.}$$

A stratum is defined as comprising of the least co-ordinate of the lowest plane to the greatest co-ordinate of the highest plane. This means that it will be a continuous integer from $S_{lo} = F(x_{lo}, y_{lo}, z_{lo})$ to $S_{hi} = F(x_{hi}, y_{hi}, z_{hi})$ and the individual must be placed in this range. To assign random positions to individuals we generated random numbers in the range $[S_{lo}, S_{hi}]$ and assigned each to an individual of species S.

2.3.3. Calculating EAO for a focal animal in multispecies choruses

The algorithm for this is the same as described in Jain et al. (2014).

2.4. Statistical analyses

Statistical analyses were carried out in R (Version 2.14.0, The R Foundation for Statistical Computing). The statistical models had one response variable, the mean EAO, and three categorical explanatory variables: species (call structure, which included temporal and spectral features and call intensity), relative abundance (composition) and chorus size. We used a generalized linear model (GLM) to investigate the effect of the explanatory variables on the response variable (EAO) (Crawley, 2007; McCullagh and Nelder, 1989). A binomial error structure was used for the GLM as the data was in the form of proportions. However, due to over-dispersion in the models, we used a quasi-binomial error structure for all model constructions (Crawley, 2007; McCullagh and Nelder, 1989; Venables and Ripley, 2002). We carried out an analysis of deviance (Crawley, 2007; McCullagh and Nelder, 1989) to investigate the statistical significance of each of the explanatory variables and all the interaction terms (two-way and three-way interactions).

Post-hoc pairwise comparisons were carried out using the Mann-Whitney test. To investigate the effect of species composition, pairwise comparisons were carried out for chorus sizes of 20 and 40. For each species and chorus size, we carried out pairwise comparisons between EAO distributions of species-even versus worst-masker and species-even versus one randomly picked other dominance scenario (for a dominance level of 0.8). The worst-masker scenario was the species composition scenario that resulted in the highest median value of EAO for a given species and chorus size. This resulted in a total of 20 pairwise comparisons of EAO distributions (medians). To examine the effects of degrees of dominance, two pairwise comparisons were carried out for each of the three uneven dominance levels (0.4, 0.6 and 0.8). In pairwise comparisons, the even composition was compared with the chorus composition that had the highest and the third highest masking scenario.

3. Results

Chorus composition (relative abundance of species), size (and hence caller density) and the nature of the species' call structure all had significant main effects on the EAO (Table 2). In addition, all two-way interactions between chorus composition, size and species call structure were significant (Table 2).

3.1. The effect of chorus composition: species evenness versus dominance

3.1.1. Dominance level of 0.8

Mecopoda 'Two-Part' dominant choruses caused the highest levels of EAO for all the other species across chorus sizes (Figs. 2, 3: composition scenario 2 in each panel). *Mecopoda* 'Two-Part' itself experienced the highest levels of EAO in *P. rosetta*-dominant choruses (Figs. 2, 3: composition scenario 3). Interestingly, the choruses with high species evenness (composition scenario 1 in Figs. 2, 3) typically resulted in high levels of EAO (relative to four out of five other composition scenarios) for all five species. The median EAO levels of species-even choruses were the second highest of the six composition scenarios across chorus sizes (Figs. 2, 3); Mann-Whitney test statistic values ranged from 0 to 1489 for species-even versus worst-masker comparisons ($n = 10$) and from 5593 to 8878 for species-even versus other-dominant comparisons ($n = 10$) with $P < 0.0001$ in all cases). Thus, for all of the species, four out of five species dominance scenarios resulted in lower levels of median EAO than in species-even choruses (Figs. 2, 3).

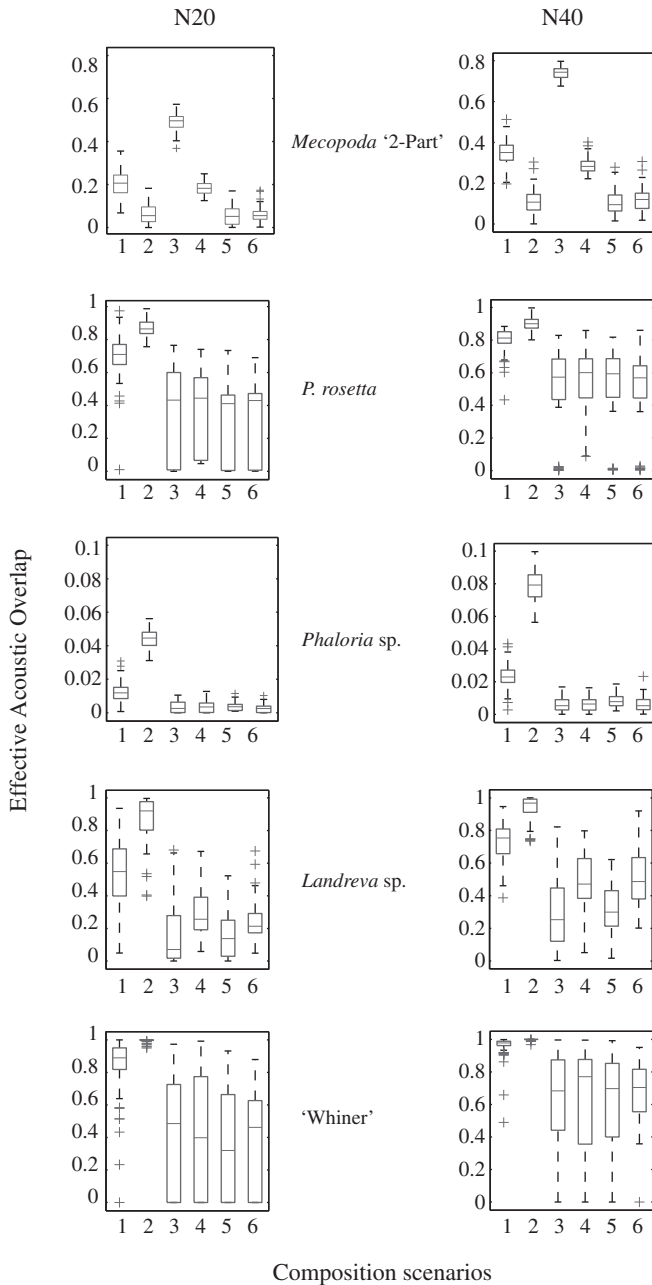
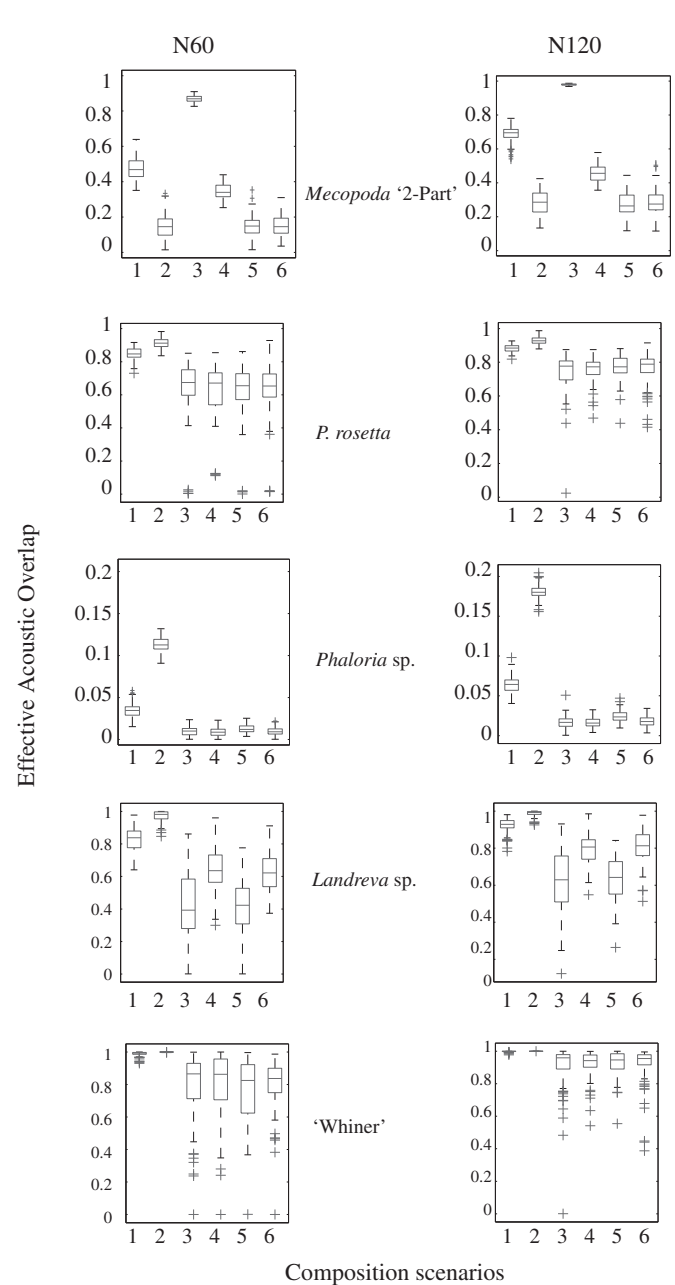
3.1.2. Dominance levels varying from 0.2 to 0.8

The median EAO values of all the species in the species-even composition scenario were significantly lower than in the worst-masker scenario (W ranging from 0 to 2564 and $P < 0.0001$) across different

Table 2

The effects of species call structure, chorus composition and caller density on effective acoustic overlap examined using an analysis of deviance.

Categories	Degrees of freedom	Deviance	Residual degrees of freedom	Residual deviance	F statistic	P value
Null			16955	1.36×10^{14}		
Species (Sp)	4	7.02×10^{13}	16951	6.66×10^{13}	13948.45	<0.0001
Composition (Comp)	5	1.40×10^{13}	16946	5.25×10^{13}	2233.30	<0.0001
Density (Dens)	5	1.50×10^{13}	16941	3.75×10^{13}	2388.32	<0.0001
Sp: Comp	20	1.26×10^{13}	16921	2.49×10^{13}	500.92	<0.0001
Sp: Dens	20	4.18×10^{11}	16901	2.45×10^{13}	16.63	<0.0001
Comp: Dens	25	6.71×10^{11}	16876	2.38×10^{13}	21.33	<0.0001
Sp: Comp: Dens	100	3.11×10^{11}	16776	2.35×10^{13}	2.47	<0.0001

**Fig. 2.** Effect of species composition on Effective Acoustic Overlap at lower chorus sizes. Box and whisker plots showing the distributions of EAO values for each of the five species in six different composition scenarios (X axes of each panel) and two chorus sizes (N = 20, left column; N = 40, right column) for dominance levels of 0.2 (even) and 0.8. Scenarios: 1 = even, 2 = *Mecopoda* 'Two-part' dominant; 3 = *P. rosetta* dominant; 4 = *Phaloria* sp. dominant; 5 = *Landreva* sp. dominant; 6 = 'Whiner' dominant. Note differences in Y axis scales between species. Dominance level = 0.8.**Fig. 3.** Effect of species composition on Effective Acoustic Overlap at higher chorus sizes. Box and whisker plots showing the distributions of EAO values for each of the five species in six different composition scenarios (X axes of each panel) and two chorus sizes (N = 60, left column; N = 120, right column) for dominance levels of 0.2 (even) and 0.8. Scenarios: 1 = even, 2 = *Mecopoda* 'Two-part' dominant; 3 = *P. rosetta* dominant; 4 = *Phaloria* sp. dominant; 5 = *Landreva* sp. dominant; 6 = 'Whiner' dominant. Note differences in Y axis scales between species.

levels of dominance for both chorus sizes (40 and 20: Figs. S1, S2). For a chorus size of 40 (Fig. S1), EAO values of all the five species in the species-even composition scenario were significantly higher than in the next-worst composition scenario ($W = 6557\text{--}9107$, $P < 0.0001$ – < 0.01) across all the dominance levels (with only one exception, 'Mecopoda Two-part' for the dominance level of 0.4 ($W = 4934$, $P = 0.87$) out of 15 comparisons). Thus the species-even composition scenario was the second-worst masking condition for all five species across different dominance levels.

For a chorus size of 20 (Fig. S2), the EAO values of four out of five species were significantly higher than the next-worst composition scenario ($W = 5464\text{--}6458$, $P < 0.001$) for a dominance level of 0.6. The EAO values of 'Mecopoda Two-Part' were not significantly different from the next-worst composition scenario for a dominance level of 0.6 ($W = 5026$, $P = 0.07$). For a dominance level of 0.4, the EAO values of two out of five species were significantly higher than the next-worst composition scenario ($W = 6076$, $P < 0.01$ and $W = 5756.5$, $P < 0.01$). The EAO values of three out of five species ('Mecopoda Two-Part', *P. rosetta* and 'Whiner') in the even composition scenario were not significantly higher than the next-worst composition scenario for the dominance level of 0.4 with a chorus size of 20 ($W = 5331.5$, $P = 0.23$; $W = 5503$, $P = 0.0768$ and $W = 4698$, $P = 0.99$).

3.2. The effect of chorus size and caller density

The EAO increased significantly with chorus size and density as expected (Table 2) but the nature and extent of the increase was different for different species and composition scenarios (Fig. 4). For the two katydid species *Mecopoda* 'Two-Part' and *P. rosetta*, who were mutually the worst maskers for each other, the worst-masker-dominant choruses (*Mecopoda*-dominant for *P. rosetta* and *P. rosetta*-dominant for *Mecopoda*) resulted in high median EAO levels (above 0.8) even at intermediate chorus sizes (Fig. 4B,C). Species-even choruses were the second worst for the two katydid species, also resulting in high EAO levels at intermediate chorus sizes (Fig. 4A). The katydid species *Mecopoda* 'Two-Part' fared well in cricket dominant choruses, with median EAO levels between 0.25 and 0.6, even in the densest choruses (Fig. 4D, E, F, diamond symbols). In comparison, the other katydid species *P. rosetta* faced high EAO levels in cricket species dominant choruses, with median EAO rising to about 0.8 in the densest choruses (Fig. 4D, E, F, open circles).

The cricket species 'Whiner' and *Landreva* sp., both experienced high levels of EAO even at low chorus sizes (Fig. 4A, B, open triangles and crosses respectively) in species-even and *Mecopoda*-dominant choruses. In the other species dominance scenarios, they experienced moderate EAO levels at low chorus sizes, with median EAO rising with

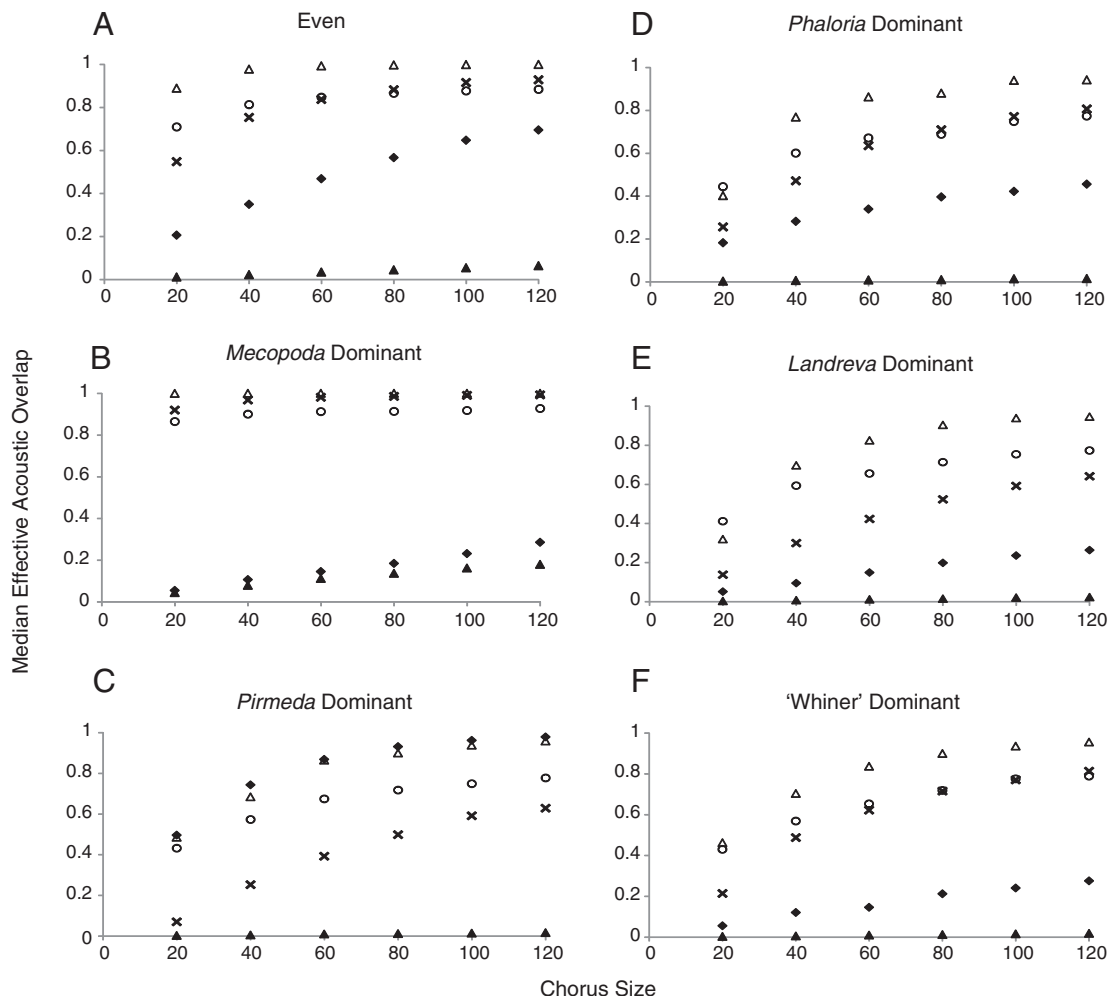


Fig. 4. Effect of chorus size on effective acoustic overlap. Each graph shows median EAO as a function of chorus size for the five species. Symbols: filled diamonds = *Mecopoda* 'Two-part'; open circles = *P. rosetta*; crosses = *Landreva* sp.; open triangles = 'Whiner'; closed triangles = *Phaloria* sp. Dominance level for 'Even' = 0.2, for all others = 0.8.

chorus size to a maximum of 0.8 in *Landreva* sp. and 0.95 in 'Whiner' (Fig. 4D, E, F, open triangles and crosses). *Phaloria* sp. was seen to experience very low EAO in all scenarios, ranging from 0.003 at low chorus densities to 0.18 in the densest, *Mecopoda* 'Two-Part' dominant choruses (Fig. 4A–F, filled triangles).

The chorus sizes at which median EAO levels reached saturation also varied depending on the species call structure and chorus composition. For species-even and *Mecopoda* dominant choruses (Fig. 4A, B), 'Whiner' (open triangles) experienced very high EAO levels (greater than 0.88) across all chorus sizes, followed by *P. rosetta* and *Landreva* sp. (open circles and crosses in Fig. 4A, B). In species-even choruses, *Landreva* sp. experienced EAO levels higher than 0.7 from chorus sizes of 40 onwards and saturated at a level of about 0.9 when chorus size reached 100 individuals (Fig. 4A, B, crosses). *Mecopoda* 'Two-Part' showed an increase of its median EAO from 0.2 to 0.7 and did not reach saturation even at a chorus size of 120 individuals in species-even choruses (Fig. 4A, diamonds).

3.3. Acoustic buffering: the effect of call structure

The species' call structure had significant effects on the EAO (Table 2) and resulted in differences in median levels of EAO and their distributions when pooled across chorus compositions and sizes (Fig. 5, Table 2). The *Phaloria* sp. was very well buffered against changes in its acoustic environment with extremely low levels of EAO across combinations of chorus species composition and size (Fig. 5). *Mecopoda* 'Two-part' emerged as the second best-buffered signal (Fig. 5; $P < 0.00001$ in pairwise comparisons with all four species), with about 75% of its EAO values being less than 0.5 across treatments. 'Whiner' suffered among the highest levels of EAO across chorus densities and compositions (Fig. 5; Mann–Whitney test: $P < 0.00001$ for 'Whiner' versus *P. rosetta* and 'Whiner' versus *Landreva* sp.), as did *P. rosetta*. The *Landreva* sp. was poorly buffered against changes in chorus composition and size (Fig. 5).

4. Discussion

4.1. Species evenness and dominance in choruses

The observation that species-even choruses resulted in high levels of acoustic overlap relative to species-dominant choruses across species and chorus densities for high dominance levels of 0.8 and 0.6 is intriguing and begs the question why. This observation can probably be explained in the context of the call structures and call intensities of the five species examined. *Mecopoda* 'Two-Part' has a loud, high-duty cycle, high-bandwidth call (Fig. 1, Table 1) which results in its being a major source of acoustic interference for all of the other calling species.

The calls of the other four species are relatively well separated from each other in spectral space (Fig. 1, Table 1) and, with tuned receivers, would result in relatively low levels of acoustic interference (Jain et al., 2014). The relative abundance of *Mecopoda* 'Two-Part' in choruses is therefore probably critical to the levels of acoustic masking experienced by the other species. In species-even choruses, the probability of occurrence of *Mecopoda* 'Two-Part' was much higher than in species-dominant choruses (except of course the *Mecopoda* 'Two-Part' dominant ones), resulting in the higher levels of EAO observed. For the masking experienced by *Mecopoda* 'Two-Part,' the main masker was *P. rosetta*, a species with which it shares extensive spectral overlap and which calls at the same intensity. Following the same logic, *Mecopoda* 'Two-Part' would, on average, experience higher levels of masking in species-even choruses than species-dominant choruses (other than *P. rosetta* dominant ones). We conclude that when there are some signals with extensive spectral overlap, species-even choruses will on average result in higher acoustic overlap than species-dominant ones in choruses with high levels of species dominance. This explanation is however speculative and needs to be further tested to examine whether the above observations represent a special case or are more generally true for different combinations of signal structures.

The above conclusions are based on comparisons between species-even choruses and those with extreme dominance structures. For intermediate dominance structures (0.4) in small choruses ($n = 20$), these conclusions held for only two out of five species (*Landreva* sp. and *Phaloria* sp.). Given that the natural choruses observed so far (Jain et al., 2014) have been of relatively small size (less than 20 individuals), the relevance of these results needs to be tested with more extensive empirical field studies to establish the range of variation in the size and species composition of natural choruses.

The simulated choruses however serve to illustrate the effects of chorus size and species dominance level on levels of acoustic masking and raise interesting questions regarding the structure and formation of natural acoustic choruses. Whether species-dominant choruses are indeed more frequently observed in the field than species-even ones and whether these depend on chorus size needs to be examined in future studies. Behavioural experiments also need to be conducted to verify whether callers of some species tend to move away from others that are simultaneously calling and whether these are as predicted by our active space models. These results are also important to verify empirically in the context of their implications for biodiversity monitoring by acoustic sampling. If the predictions we make regarding chorus structures are true, then the relative abundance of callers in large multispecies choruses is unlikely to be a good indicator of the relative abundance of species. This in turn would have implications for the spatial scales at which acoustic sampling for biodiversity monitoring (Aide et al., 2013 and references therein) needs to be carried out to obtain reliable

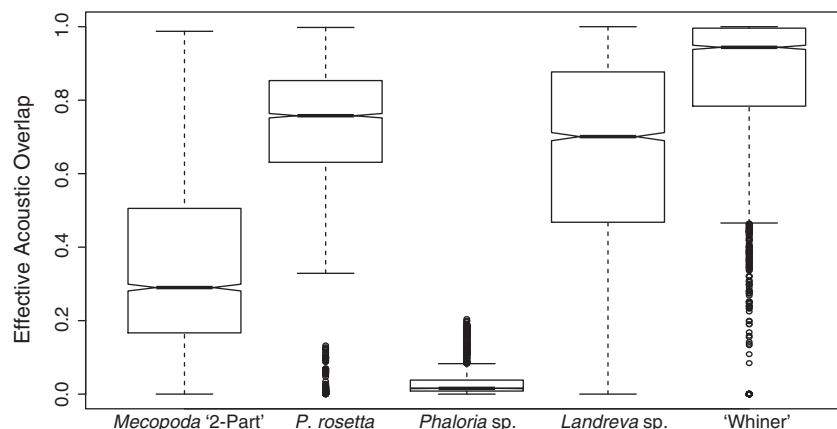


Fig. 5. Acoustic buffering. Box and whisker plots showing distributions of EAO values across treatments (species-even and five dominance scenarios with a dominance level of 0.8) for the five species.

estimates of species relative abundance. This is an important issue that merits further study, both theoretical and empirical.

4.2. Chorus size and density

The effects of increasing chorus size (and therefore the density in this study) were different across species. As a result, there is no general rule about how large or dense a given multispecies chorus might be. For example, *Phaloria* sp., with a maximum EAO of 0.18, could in principle co-exist with very high densities of heterospecific callers. On the other hand, 'Whiner', *P. rosetta* and *Landreva* sp. showed high levels of EAO even at low chorus sizes and one may predict that these species may be found in smaller, sparser multispecies choruses. Preliminary observations indicate that males of 'Whiner', the species that we expect to

experience the highest levels of EAO, in fact typically occur in smaller, 'Whiner' dominant choruses and only rarely in large, multispecies choruses. Based on this study, we predict low caller densities for species-even choruses and higher densities for species-dominant choruses except in cases of high spectral overlap between species. The generality of these predictions will however need to be verified both theoretically and empirically with multispecies choruses containing different combinations of signal structures.

4.3. Acoustic buffering

The five species examined provide interesting contrasts in the level of acoustic buffering: the *Phaloria* sp. not only experienced extremely low levels of acoustic overlap but was also remarkably well buffered

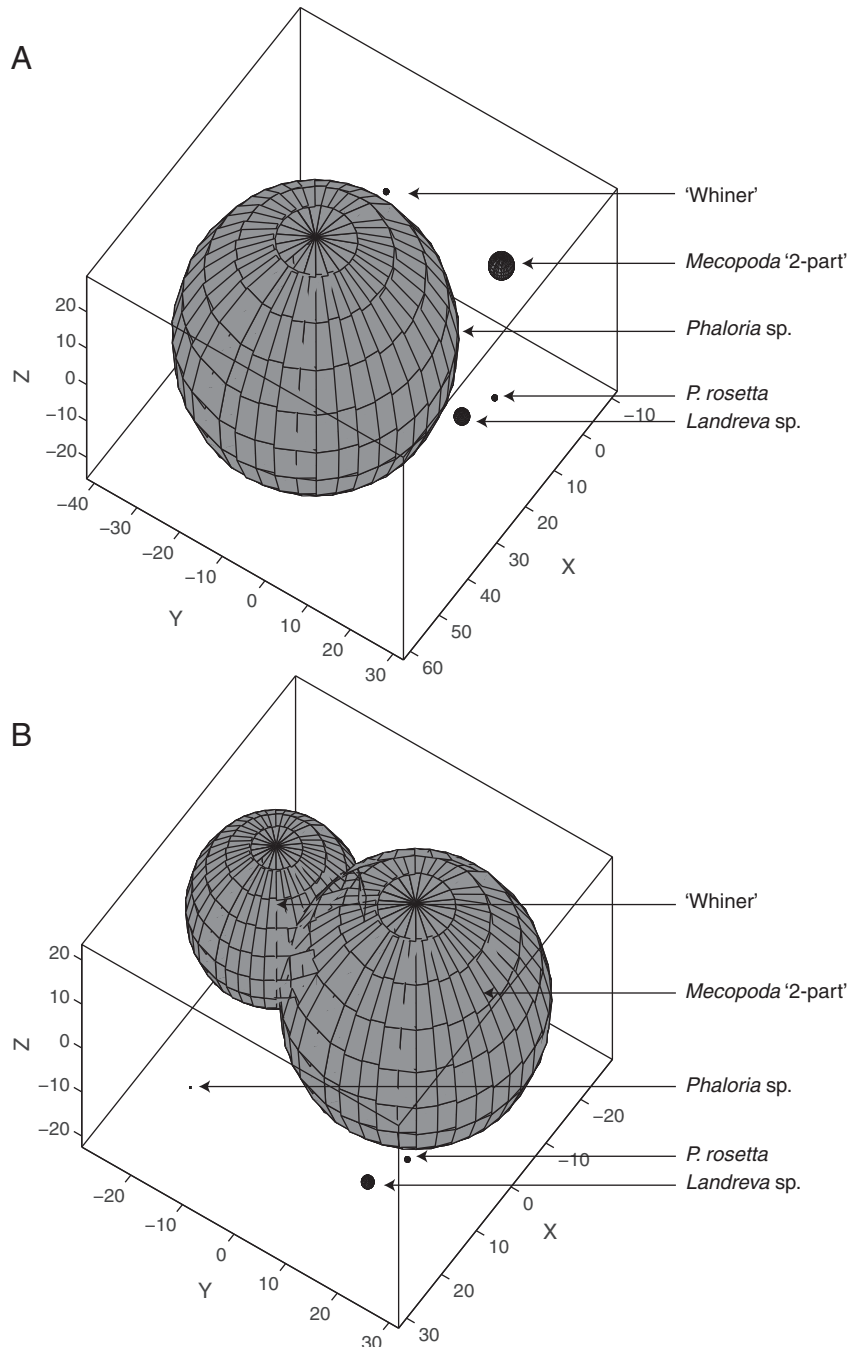


Fig. 6. Acoustic overlap depends on call intensity and receiver tuning. The 3-D active spaces of calling males of the five species are illustrated assuming that the receiver is a female of (A) *Phaloria* sp. and (B) 'Whiner' sp.

against changes in chorus species' relative abundance and caller density, with very low variance in EAO values. At the other extreme, the cricket species 'Whiner' experienced high levels of EAO and was poorly buffered against changes in its acoustic environment. We believe that the explanation for this difference in level and variance of EAO values may lie in the differences in call structure and intensity between these species. In general, species with low bandwidth signals and tuned receivers should experience lower levels of acoustic interference than species with high bandwidth signals since the receivers of the latter will have higher sensitivity to a wider range of frequencies (Jain et al., 2014). Both *Phaloria* sp. and 'Whiner' however have signals of comparably low bandwidth (0.39 and 0.42 kHz respectively: Diwakar and Balakrishnan, 2007) and are not very different in their carrier frequencies (4.6 and 5.9 kHz respectively: Diwakar and Balakrishnan, 2007). Yet one of them suffers very little acoustic interference and is well-buffered while the other is not. We believe there are two major reasons for this: the *Phaloria* sp. produces calls that are more than twice the amplitude (80 dB SPL versus 73 dB SPL on average) of 'Whiner,' which would contribute to reducing its EAO. This is because of the difference in their active space volumes: we have shown previously (Jain et al., 2014) that, independent of call structure and receiver tuning, louder callers tend to suffer less EAO simply because their active spaces are so large that the proportion of active space overlapped is relatively small. Further, the mean carrier frequency of 'Whiner' (5.9 kHz) is much closer to one of the dominant frequency bands at the lower end of the *Mecopoda* 'Two Part' call spectrum (6–7 kHz: Fig. 1, Nityananda and Balakrishnan, 2006). In fact the broadcast radius of a *Mecopoda* call is 22 m when the receiver is modelled as a tuned 'Whiner' female but only 2.5 m when the receiver is a tuned *Phaloria* sp. (illustrated in Fig. 6). A *Phaloria* sp. female would need to be within 2.5 m of a calling *Mecopoda* 'Two Part' male to suffer any masking whereas a 'Whiner' female would suffer masking if she were within 22 m of a calling *Mecopoda* 'Two Part' male. Thus, 'Whiner' is more likely to experience masking from *Mecopoda* 'Two Part' than *Phaloria* sp., which more effectively tunes out the *Mecopoda* call. 'Whiner' also experiences a higher variance in EAO than *Phaloria* sp. for the same reason: in choruses that contain few or no *Mecopoda* 'Two-Part', 'Whiner' suffers virtually no masking because it can effectively tune out all the other species whereas in *Mecopoda*-dominant choruses, it would experience high masking levels. On the other hand, the *Phaloria* sp., with its high-intensity call, narrow frequency tuning and lower spectral overlap with *Mecopoda* 'Two Part' and the other species, does not experience similar variance in EAO.

The *Landreva* sp. has a similar carrier frequency to *Phaloria* sp. and yet experiences much higher levels of masking when *Mecopoda* 'Two-Part' is the dominant species. The reason for this again lies in the difference in call intensities at source between the two species. Although the *Landreva* sp. is (in our model) as narrowly tuned as *Phaloria* sp., its call intensity (66.7 dB SPL) is much lower than *Mecopoda* 'Two Part' (80 dB SPL). For a *Landreva* receiver, the broadcast radii for both conspecific calls and *Mecopoda* 'Two Part' calls are thus almost equal (10 m) and this increases the probability of acoustic overlap in space.

A difference in acoustic buffering is also seen between the two katydid species, even though both of them have high bandwidth calls (Fig. 1, Table 1; Diwakar and Balakrishnan, 2007; Nityananda and Balakrishnan, 2006). Based on the bandwidth and the frequency span of the calls of the two species (Table 1), one may expect *Mecopoda* 'Two Part' to experience more acoustic masking than *P. rosetta*. Yet the results are exactly the opposite: *Mecopoda* 'Two Part' is surprisingly well buffered against changes in species composition and chorus density. The difference cannot be explained by call intensity, since both species call at similar high levels (80 dB SPL on average). The difference in duty cycle between the two calls probably explains the difference: *Mecopoda* 'Two Part' has a very high duty cycle call whereas *P. rosetta* produces brief, low duty cycle calls (Table 1). The proportion of a *Mecopoda* call that will be subject to overlap from another

simultaneously calling species is therefore much lower than that of a *P. rosetta* call, so that it experiences lower levels of acoustic overlap (see Jain et al., 2014, for temporal overlap estimates).

Both of the above examples serve to illustrate that effective acoustic overlap cannot be simply predicted by examining single call features in isolation: it can only be meaningfully estimated when a combination of call features is used in the appropriate spatial and acoustic context. The knowledge of signal structure alone is not sufficient to predict either the amount of acoustic overlap experienced or how well-buffered a particular species might be to changes in its acoustic environment due to changes in chorus composition and density.

5. Conclusions

In this study, we have examined the effects of caller species' relative abundance and density on heterospecific acoustic overlap in simulated multispecies choruses consisting of five species of crickets and katydids. We found that larger choruses with high species evenness had on average higher levels of acoustic overlap than choruses with strong species dominance. We also found that the effects of caller density on acoustic overlap depended both on chorus composition and on signal structure. Some species experienced low EAO levels and were strongly buffered against changes in the acoustic context, whereas others were not. These differences could not be simply predicted from an examination of call features alone.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.ecoinf.2013.11.006>.

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