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THE ASSEMBLAGE OF ACOUSTICALLY COMMUNICATING CRICKETS OF A TROPICAL EVERGREEN FOREST IN SOUTHERN INDIA: CALL DIVERSITY AND DIEL CALLING PATTERNS

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ABSTRACT

This study provides the first description of the call structures of twenty ensiferan species constituting the nocturnal acoustic community of an evergreen forest in Southern India. Of the twenty species, ten belonged to the superfamily Grylloidea, nine to the superfamily Tettigonioidea and one to the superfamily Gryllacridoidea. The calls of the gryllid species were narrow-band with dominant frequencies ranging from 3 – 7 kiloHertz. The calls of the tettigoniids covered a wide spectral range, reaching far into the ultrasound in some species. Four of the nine tettigoniid species had narrow-band, relatively low frequency calls centred at 3, 9, 11 and 15 kiloHertz respectively. The temporal patterns of the species were diverse, with syllable durations ranging from eight to 63 milliseconds and syllable periods from 17 milliseconds to two seconds. The calls of the species showed considerable overlap in both spectral and temporal features. Calling activity peaked between six o'clock in the evening and midnight and died down subsequently. We found no diel partitioning of calling time between acoustically communicating ensiferan species. Species accumulation curves suggest that the acoustic community has been almost completely sampled.

Keywords**:** acoustic community, diel calling patterns, Ensifera, India, tropical forests

INTRODUCTION

Sound is used by animals such as birds, frogs, mammals and insects for long distance communication. In insects, mainly Orthoptera (crickets, katydids and grasshoppers) and Homoptera (cicadas) have developed the ability of sound production and reception in the context of long distance intra-specific communication. Adult male crickets produce acoustic signals or calling songs to attract potential mates (females of their species) from a distance (Bailey 1991). The call of each species is typically unique, with a specific, stereotyped combination of spectral and temporal features, which is used by females to recognise

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and approach conspecific males. In species-rich tropical forests, large numbers of insect species along with birds and frogs use acoustic signals for mate attraction and territory defence. The ensemble of acoustically communicating species may be considered as an acoustic community similar to other ecological guilds, competing for acoustic broadcast channels (Riede 1993).

The diversity of arthropod fauna in tropical forests has been studied in detail, though much of the focus has been on the abundant and speciose insect groups such as Coleoptera and Hymenoptera, particularly the ants (Formicidae) (Stork 1991; Basset *et al.* 1992). Studies from the Bornean lowland rainforest have shown that orthopteran insects account for between 1 to 3% of the species in the canopy (Stork 1991). The order Orthoptera is divided into two major groups: the Caelifera (grasshoppers) that are diurnal and the Ensifera (crickets and katydids) that are mainly nocturnal. Our knowledge of tropical forest orthopteran communities is scarce due to the limited number of studies. Most of the work on grasshopper community composition has been done in temperate grasslands (e.g. Kemp *et al.* 1990). Amédégnato (1997) studied grasshopper community structure and resource partitioning in the Amazonian forest canopies.

Preliminary studies at the community level in Ensifera have been carried out both in the Neotropics and Palaeotropics. Floren *et al.* (2001) have described the composition of an orthopteran community from Bornean lowland forests. They found adults belonging to 127 morphospecies representing both gryllid and tettigoniid superfamilies from the forest canopies. Desutter-Grandcolas (1997) studied a cricket community in the understorey of evergreen forests in New Caledonia. She found twenty-three species belonging to various gryllid subfamilies occupying four different habitat guilds. Riede (1993, 1997, 1998) characterised insect communities in tropical rainforests in Ecuador and Borneo using recordings from singing animals. His work provided a new method for monitoring rainforest biodiversity based on putative species clusters formed by plotting carrier frequency and repetition rate of calls, but there were no taxonomic descriptions of species. Nischk and Otte (2000) have described the species composition of cricket communities as well as the diversity of calling songs in two tropical forest ecosystems in Ecuador. Their work focussed mainly on the subfamily Phalangopsinae. Nischk and Riede (2001) described the call diversity of two Neotropical cloud forest ecosystems in Ecuador and compared it with a lowland rainforest. They found differences in species richness between the high and low altitude forests. Studies on the ensiferan fauna of the Indian subcontinent are limited only to systematics and no study has been carried out on the bioacoustics and community structure of Ensifera in evergreen forests.

Multi-species acoustic communities in tropical forests have been studied mainly in cicadas (Gogala & Riede 1995; Sueur 2002) and frogs (Hödl 1977; Drewry & Rand 1983; Duellman & Pyles 1983). Calls of syntopic species were more different from each other than allopatric species. Also, syntopic species with similar calls were found to have different calling sites or seasons. These studies suggested that temporal and spectral partitioning could be used by species calling in multi-species assemblages to combat interspecific acoustic interference.

Time has been viewed as a niche axis on which organisms can segregate to avoid competition for limited resources (Carothers & Jaksic 1984; Kronfeld-Schor & Dayan 2003). Time can be partitioned on both a diel and a seasonal scale (Case & Gilpin 1974). Among acoustically communicating animals, diel partitioning of calling time has been considered as a way to avoid interspecific acoustic interference among sympatric species (Reide 1997). Diel partitioning of calling time has been mainly studied in frogs (Drewry & Rand 1983; Gottsberger & Gruber 2004; Hsu *et al.* 2006), cicadas (Gogala & Reide 1995) and birds (Ficken & Ficken 1974). Studies on the calling activity of Ensifera are few and qualitative (Reide 1997). To our knowledge no study has quantitatively investigated the diel calling patterns in ensiferan communities of tropical forests.

The aim of this paper was 1) to examine the taxonomic and call structure diversity of the acoustically communicating ensiferan assemblage of a tropical evergreen forest in India and 2) to examine the diel calling patterns of species constituting the acoustic community. We were also interested in examining the assemblage for the presence of tettigoniid species with narrow-band, low frequency calls, which have been reported from tropical evergreen forests in other parts of the world (Heller 1995; Montealegre & Morris 1999, 2004).

MATERIALS AND METHODS

Study site and period

The study was carried out in the Kudremukh National Park (600.32 sq. km) located in the Western Ghats in Karnataka state in Southern India (13º 16'N, 75º 08'E). The forests consist of evergreen and semi evergreen vegetation. The region is characterised by tropical climate with an average annual rainfall of 4000 mm. All investigations were conducted in the dry season between October and March 2003–2006.

Song recording and analysis

Calls of individual males were recorded in the field between 1900 hrs and 2200 hrs. Individual calling insects were first tracked and located by ear. Recordings were made by holding a microphone at a distance of 0.5–2 m from the calling animal. Recordings were made in two ways, either using a Sony stereo microphone (ECM-MS957, frequency response: 50-18,000 Hz) and stereo cassette recorder (Sony WM-D6C Professional Walkman) or by using an ultra sound detector (D 980, Pettersson Elektronik AB, Sweden, frequency range 2–200 kHz) whose output was digitised on a laptop computer (IBM® ThinkPad® R32) using a data acquisition card (DAS 16/330 Measurement Computing) at a sampling rate of 200 kHz. The binary files were then converted to wave files using Matlab (1997, Version 5.1.0.421, The Mathworks Inc., Natick, MA) for spectral and temporal analysis. In the former case, sound recordings were sampled via an analogue-digital converter (Creative Sound Blaster A/D Card) at a sampling rate of 44 kHz. The tapes and compact discs of all the recordings are stored at the Centre for Ecological Sciences (CES), Indian Institute of Science (IISc), Bangalore, India for reference.

The ambient temperature in the vicinity of the calling male was measured after each recording with a thermometer (Kestrel 3000 Pocket Weather Station). After obtaining the call recordings, the animals calling from the ground were captured by placing a plastic box over them and gently sliding the lid from underneath. The animals calling from herbs or the understorey were captured by trapping the leaf on which the animal was sitting between the plastic box and the lid. Animals calling from the canopy were also captured in the same manner after climbing the tree. The captured animals were preserved in 70% alcohol for taxonomic work. The collection is preserved at CES, IISc, Bangalore, India for reference. Information about the calling time, calling site and position, microhabitat, moon phase and the weather conditions at the time of recording were also noted for every individual recorded.

Spectral analysis was performed using the signal processing software Spectra Plus Professional (1994, Version 3.0, Pioneer Hill Software, Poulsbo, WA). The bandwidth of the frequency spectrum was measured at 20 dB below the frequency at peak amplitude. Temporal pattern analysis was performed using a custom-built program (Chandra Sekhar, ECE, IISc) in Matlab and the following call characters were measured: chirp duration, chirp period, syllable duration, syllable period and syllable repetition rate (SRR = 1/ syllable period). Means and standard errors were calculated for call features of each species. Each call feature was regressed against temperature to check for any significant effect of temperature. If a feature of a call showed a significant change with temperature, it was regressed to 24ºC (the temperature at which the calls of most other species were recorded) for comparisons between species.

Systematics

Collected specimens were identified using the taxonomic keys developed by Chopard (1969) for gryllids and Brunner von Wattenwyl (1888), Beier (1962) and Rentz (1996) for tettigoniids. The classification of Ensifera described in Orthoptera Species File 2 Online (Otte *et al.* 2006) was followed to assign specimens to families and subfamilies. Specimens were identified to the genus level in most cases. For two call types we were able to identify only up to the subfamily level and the temporary names 'Whiner' (Gryllidae: Podoscritinae) and '15 kHz' (Tettigoniidae: Phaneropterinae) have been used for now. We have refrained from a species level nomenclature since we have so far been unable to verify species identity due to problems of accessing type specimens. We have used the term 'species' as synonymous with 'call type' throughout the paper. We believe this to be a reasonable assumption since distinct calling songs are reliable indicators of reproductive isolation in crickets (Shaw 1999).

Diel Calling Patterns

The diel calling patterns of the species constituting the acoustic community of Kudremukh National Park were examined using acoustic spot sampling. The twenty-four hour sampling time was divided into eight sampling periods of three hours each. Sampling was carried out for two non-consecutive periods per day in a given transect. Acoustic spot sampling was carried out between December 2004 and March 2005 in two independent transects that were similar in vegetation and elevation. Six replicates of sampling time between 1500 h–0900 h and three replicates of sampling time between 0900 h–1500 h were conducted in each transect. Sampling was avoided during the period around full moon nights of the lunar cycle when calling activity is known to be low (Lang *et al.* 2006).

In each 500 m transect, ten spots were marked that were 50 m apart from each other. Acoustic spot sampling was carried out in each transect by standing on each of the ten spots for twelve minutes and listening to the calls. The number of different call types heard, number of individuals of each call type, direction of the call, approximate distance and height of the call were recorded. We preferred to use psychophysical acoustic sampling over recordings by instruments for two main reasons: 1) Some species such as *Gryllacropsis* sp. and *Mecopoda* sp. were not registered by the recorder even at high sensitivity settings and 2) most gryllid species in the community were calling at frequencies between 4–6 kHz. Species-specific temporal patterns in this frequency band were difficult to resolve in the spectrograms obtained using a recorder whereas they could be unambiguously identified by ear.

A three-way repeated measures ANOVA was carried out to analyse differences and interactions in diel patterning between transects, species and sampling periods. Differences in diel calling activity between species were investigated using *post hoc* pair wise Pearson correlations. Statistical analyses were carried out using Statistica (1999, Statsoft Inc., USA) software.

Community composition

Five transects of 500 m each in diverse evergreen, undisturbed forests (including dead and fallen logs) with vegetation stratified into herb, shrub and canopy layers, at more or less similar elevations (500–700 m above sea level), were selected in Kudremukh National Park. Sampling was carried out after sunset between 1900 h to 2100 h in the evening, which was found to be the peak calling activity of acoustically communicating Ensifera. Acoustic spot sampling as described above was carried out in five transects across Kudremukh National Park for 23 nights between December 2003 and March 2005.

The spot sampling data yielded counts of numbers of species and numbers of individuals of each species heard across transects on each sampling night. Two matrices of species by sampling nights were generated. The first matrix had the presence and absence of species and the second matrix had the number of individuals heard for each species in each transect. Presence or absence, frequency of occurrence and abundance of each species across sampling nights, number of species and individuals of each species in each sampling night were obtained from these matrices. The species by sampling night matrix was used to calculate species richness using the software EstimateS (Colwell 2005). Species richness was used to measure the diversity of the ensiferan assemblage. Species accumulation curves were plotted to assess the completeness of sampling (Colwell & Coddington 1994). A total of twenty-three sampling nights during which the acoustic spot sampling was done was used as the measure of sampling effort. Accumulation curves were constructed based on both the presence-absence and abundance of species. Curves were smoothed by 50 randomizations of the sample order using EstimateS.

RESULTS

The acoustic community

A total of 20 species of Ensifera constituting the nocturnal acoustic community of the evergreen forests of Kudremukh National Park was

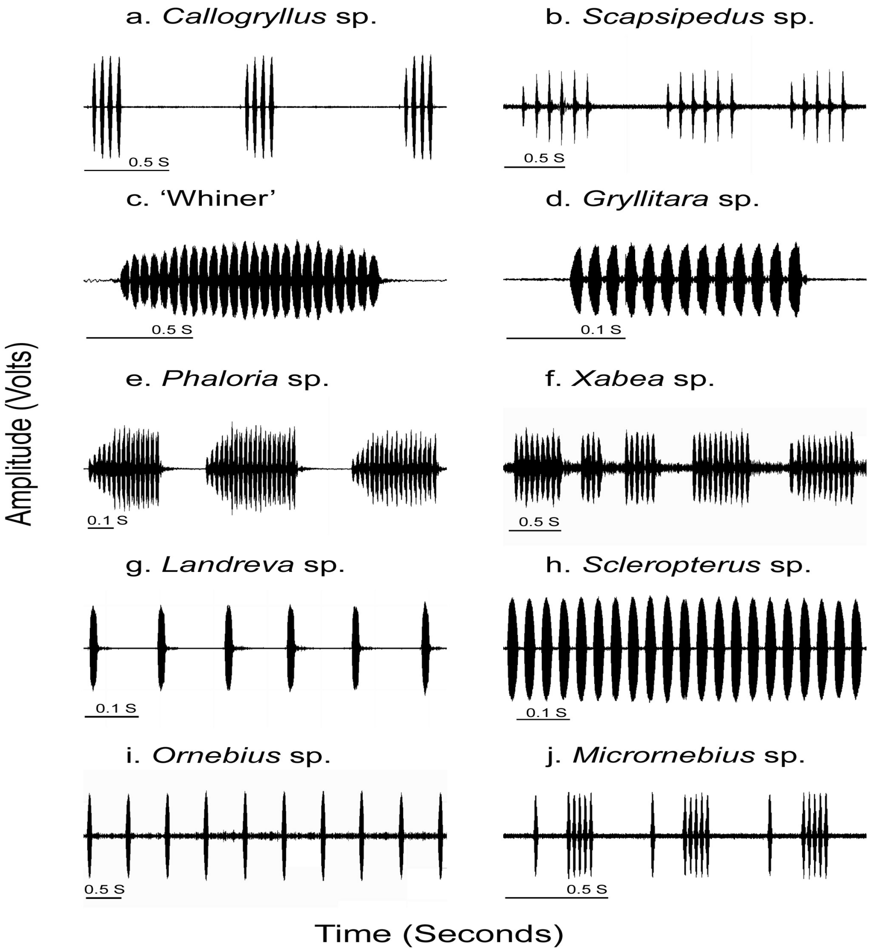

Figure 1. Oscillograms showing the temporal structure of the calls of gryllid species: a. *Callogryllus* sp., b. *Scapsipedus* sp., c. 'Whiner', d. *Gryllitara* sp., e. *Phaloria* sp., f. *Xabea* sp., g. *Landreva* sp., h. *Scleropterus* sp., i. *Ornebius* sp. and j. *Micrornebius* sp.

recorded. Of these, ten species belonged to the superfamily Grylloidea, nine to the superfamily Tettigonioidea and one to the superfamily Gryllacridoidea. Of the ten gryllids, eight species, namely, *Callogryllus* sp., *Scapsipedus* sp., *Landreva* sp., *Scleropterus* sp., *Phaloria* sp., *Xabea* sp., *Gryllitara* sp., 'Whiner' belonged to the family Gryllidae and two species, *Ornebius* sp. and *Micrornebius* sp. belonged to the family Mogoplistidae (scaly crickets).

The gryllid species exhibited a diversity of temporal patterns, ranging from short chirps to long uninterrupted trills (Figure 1). The calls of *Callogryllus* sp. and *Scapsipedus* sp. (Subfamily Gryllinae) consisted of short chirps of five-six syllables each (Figure 1 a, b).

TABLE 1

Temporal features of the calls of seventeen species of the ensiferan assemblage

Species	Call Duration (s) (s)	Call Period (s)	No. of Syllables/Call	Syllable Duration (s)	Syllable Period (s)
Callogryllus (N = 10)	0.21 (0.04)	0.91 (0.17)	4.56 (0.63)	0.024 (0.002)	0.051 (0.005)
Scapsipedus (N = 5)	0.49 (0.05)	1.48 (0.81)	5.88 (0.51)	0.021 (0.006)	0.069 (0.026)
Scleropterus (N = 6)	> 60	> 60	64.33 (1.86)*	0.017 (0.003)	0.030 (0.003)
Micrornebius (N = 2)	0.29 (0.01)	0.59 (0.00)	5.97 (0.04)	0.018 (0.001)	0.027 (0.001)
Gryllitara (N = 10)	0.19 (0.02)	4.14 (2.39)	11.45 (1.62)	0.010 (0.001)	0.017 (0.001)
Landreva (N = 10)	16.51 (12.9)	18.89 (15.25)	111.46 (38.67)*	0.018 (0.002)	0.214 (0.114)
Phaloria (N = 6)	0.2 (0.13)	0.58 (0.15)	31.59 (8.28)	0.014 (0.001)	0.018 (0.001)
Ornebius (N = 3)	8.83 (4.57)	12.44 (3.72)	19.67 (1.53)*	0.063 (0.002)	0.512 (0.048)
‘Whiner’ (N = 7)	0.94 (0.15)	14.68 (3.08)	20.5 (2.11)	0.037 (0.003)	0.045 (0.003)
Xabea (N = 3)	0.44 (0.23)	1.94 (1.89)	10.17 (5.93)	0.033 (0.002)	0.046 (0.004)
Onomarchus (N = 6)	0.15 (0.04)	1.17 (0.15)	2.32 (0.47)	0.044 (0.004)	0.084 (0.006)
Phyllomimus (N = 3)	0.46 (0.05)	1.52 (0.10)	2.80 (0.10)	0.056 (0.002)	0.222 (0.020)
Brochopeplus (N = 8)	1.96 (0.59)	13.82 (3.05)	23.68 (5.55)	0.033 (0.005)	0.086 (0.006)
‘15 kHz’ (N = 10)	n.a	n.a	n.a	0.008 (0.002)	2.379 (1.151)
Pirmeda (N = 9)	0.31(0.09)	7.44 (3.10)	2.99 (0.46)	0.036 (0.008)	0.128 (0.019)
Elimaea (N = 4)	0.43 (0.05)	11.39 (10.27)	7.1 (1.12)	0.038 (0.048)	0.04 (0.01)
Gryllacropsis (N = 6)	0.08 (0.00)	1.44 (0.15)	4 (0.0)	0.002 (0.000)	0.023 (0.002)

Values given are mean (S.E.) N = number of individuals analysed. *number of syllables in two seconds in *Scleropterus* and twenty seconds of call in *Landreva* and *Ornebius*. All values are for a temperature of 24°C.

'Whiner' (Subfamily Podoscirtinae) and *Gryllitara* sp. (Subfamily Itarinae) calls were composed of long chirps with 12–18 syllables per chirp (Figure 1 c, d). *Phaloria* sp. (Subfamily Phaloriinae) and *Xabea* sp. (Subfamily Oecanthinae) calls consisted of broken or continuous trills (Figure 1 e, f). *Landreva* sp. (Subfamily Landrevinae), *Scleropterus* sp. (Subfamily Sclerogryllinae) and *Ornebius* sp. (Subfamily Mogoplistinae) produced single syllables at different rates (Figure 1 g, h and i). The *Micrornebius* sp. call had an interesting structure (Figure 1 j) wherein each chirp consisted of a single syllable with a long inter syllable interval followed by five syllables. The values of call durations and periods for all the gryllid species are given in Table 1.

The ten gryllid species had calls that were narrow band with bandwidths ranging from 290 Hz in *Ornebius* sp. to about 1 kHz in *Scapsipedus* sp. (Table 2, Figure 2). The dominant frequencies of the ten gryllid species ranged from 3 kHz to 7 kHz (Table 2, Figure 2).

Of the nine tettigoniid species, four species *Onomarchus* sp., *Phyllomimus* sp., *Pirmeda* sp. and *Brochopeplus* sp. belonged to the subfamily Pseudophyllinae (false leaf katydids). Two species '15 kHz' and *Elimaea* sp. belonged to the subfamily Phaneropterinae. Three species belonged to the genus *Mecopoda* (Subfamily Mecopodinae). The power spectra and the temporal patterns of the tettigoniid species are shown in Figure 3. The calls of the tettigoniids were organized in short chirps of two or three syllables in *Onomarchus*, *Phyllomimus* and *Pirmeda* species (Figure 3 a, b and c). The *Brochopeplus* sp. call consisted of long chirps with a series of 16–32 syllables (Figure 3 d). The species '15 kHz' had a call consisting of single clicks (Figure 3 e). The calls of the *Elimaea* sp. consisted of chirps with an irregular syllable structure and varying rate (Figure 3 f). The call characteristics of the three species belonging to the genus *Mecopoda* have already been described (Nityananda & Balakrishnan 2006). The call of the 'Two part' call type of *Mecopoda* consisted of repeated verses with each verse consisting of a long trill followed by two or three short chirps. The calls of 'Helicopter' and 'Train' were complex with repeated trills having different start, middle and end segments (Nityananda & Balakrishnan 2006).

Interestingly, four of the nine tettigoniid species (*Onomarchus* sp., *Phyllomimus* sp., *Brochopeplus* sp. and '15 kHz') had narrow band calls similar to gryllids (Figure 3 g, h, j and k) with relatively low dominant frequencies of 3.2, 9, 11 and 15 kHz respectively. The other five species had broadband calls. In *Pirmeda* sp. and *Elimaea* sp., the bandwidths were 16 kHz and 17 kHz respectively (Figure 3 i and 1, Table 2). The three species of *Mecopoda* had similar spectra and a very high bandwidth of 68 kHz ranging from 2–70 kHz. Detailed call characteristics of the tettigoniid species are given in Tables 1 and 2. The single species belonging to the Gryllacridoidea (genus *Gryllacropsis*) has been described in detail elsewhere (Diwakar &

TABLE 2

Spectral features of the calls of seventeen species of the ensiferan assemblage.

Species	Dominant frequency (kHz)	Bandwidth (kHz)	Season	Microhabitat
Callogryllus (N = 10)	3.61 (0.15)	0.70 (0.16)	Oct-Nov	Ground
Scapsipedus (N = 5)	4.10 (0.21)	1.03 (0.13)	Nov-Dec	Ground
Scleropterus (N = 6)	6.73 (0.56)	0.67 (0.133)	Nov	Leaf litter
Micrornebius (N = 2)	6.95 (0.22)	0.99 (0.10)	Jan-Mar	Leaf litter
Gryllitara (N = 10)	4.89 (0.19)	0.99 (0.17)	Feb-Apr	Leaf litter, Herb
Landreva (N = 10)	4.86 (0.28)	0.43 (0.08)	Sep-Apr	Dead log
Phaloria (N = 6)	4.57 (0.16)	0.39 (0.08)	Sep-Apr	Stream side
Ornebius (N = 3)	5.8 (0.10)	0.29 (0.15)	Sep-Apr	Understorey
'Whiner' (N = 10)	5.91 (0.10)	0.42 (0.13)	Dec-Feb	Understorey
Xabea (N = 8)	3.28 (0.09)	0.39 (0.03)	Sep-Apr	Canopy
Onomarchus (N = 10)	3.23 (0.10)	0.4 (0.06)	Nov-Mar	Canopy
Phyllomimus (N = 3)	8.78 (0.16)	1.02 (0.05)	Nov-Mar	Canopy
Brochopeplus (N = 9)	11.61 (0.34)	1.42 (0.39)	Oct, Mar	Understorey
'15 kHz' (N = 10)	14.78 (0.34)	2.00 (0.55)	Nov-Mar	Understorey
Pirmeda (N = 9)	13.96 (0.60) (12–28)	16.6 (0.82)	Nov-Mar	Understorey
Elimaea (N = 4)	11.03 (0.61) (8–25)	16.78 (1.26)	Nov-Mar	Understorey
Gryllacropsis (N = 5)	1.71 (0.05) (1–3)	2.00 (0.56)	Sep, Mar	Tree trunks

Values given are mean (S.E.) N = number of individuals analysed. All values are for a temperature of 24°C.

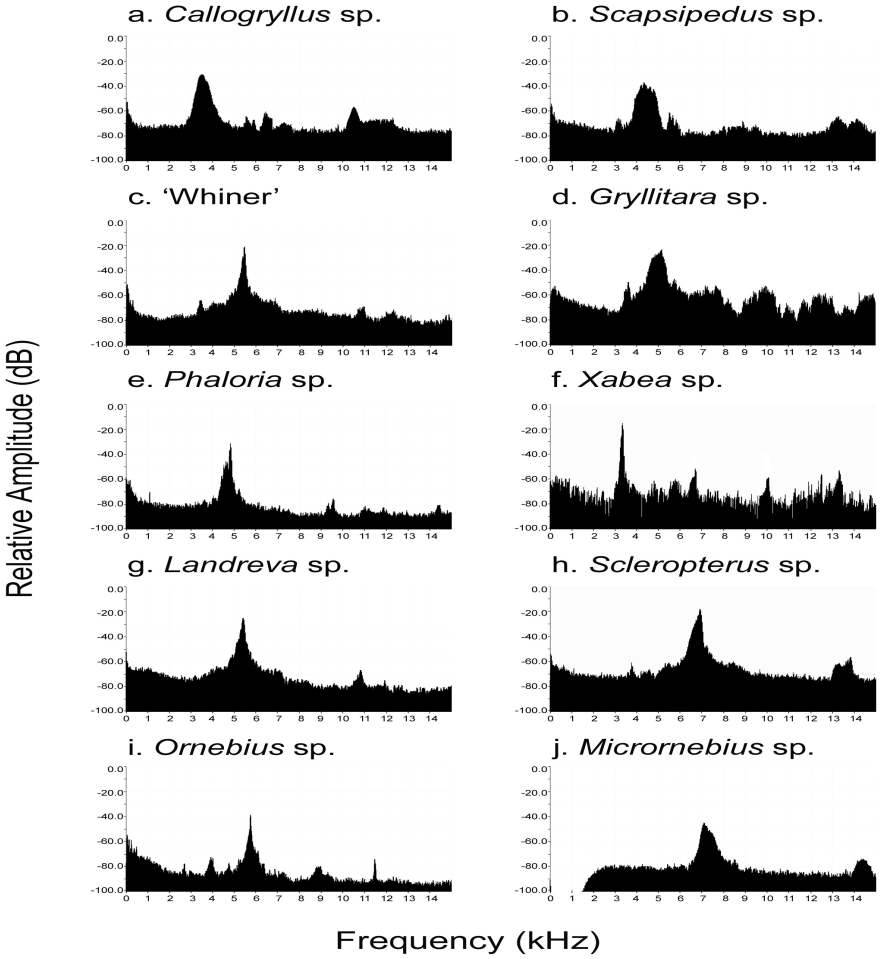

Figure 2. Amplitude spectra showing the narrow band call frequencies of ten gryllid species: a. *Callogryllus* sp., b. *Scapsipedus* sp., c. 'Whiner', d. *Gryllitara* sp., e. *Phaloria* sp., f. *Xabea* sp., g. *Landreva* sp., h. *Scleropterus* sp., i. *Ornebius* sp. and j. *Micrornebius* sp.

Balakrishnan 2006) but a brief summary of the call characteristics has been provided (Table 1, 2).

The call structures of the species in the ensiferan assemblage showed considerable overlap in both spectral and temporal features. Especially in the gryllids, there was a high overlap of dominant frequencies between 3 and 7 kHz (Figure 4 a). Calls of *Callogryllus* sp., *Scapsipedus* sp., *Landreva* sp., *Gryllitara* sp., *Phaloria* sp. and 'Whiner' overlapped extensively in the spectral domain. Calls of species such as *Callogryllus* and *Scapsipedus* (syllable repetition rate 20 and 17 syllables/second respectively), *Phaloria* and *Gryllitara*

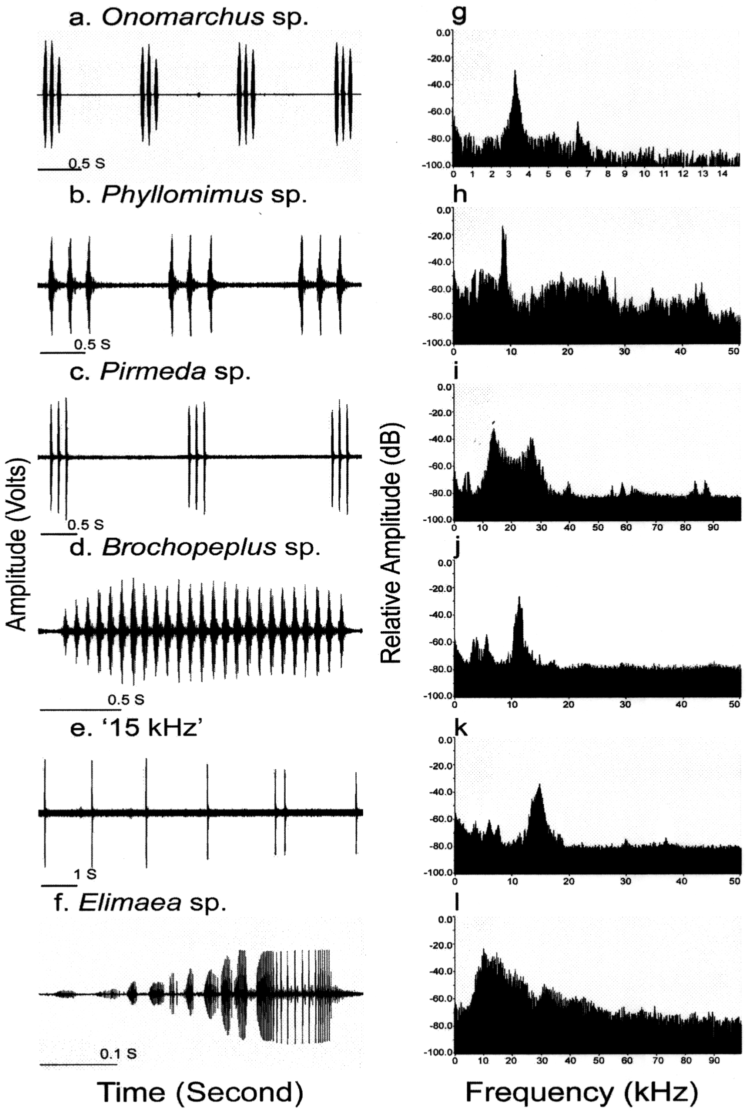

Figure 3. Oscillograms and power spectra of the calls of six tettigoniid species. *Onomarchus* sp. (a and g), *Phyllomimus* sp. (b and h), *Pirmeda* sp. (c and i), *Brochopeplus* sp. (d and j), '15 kHz' (e and k) and *Elimaea* sp. (f and l).

(syllable repetition rate 55 and 59 syllables/second respectively), *Scleropterus* and *Micrornebius* (syllable repetition rate 34 and 37 syllables/second respectively) overlapped both in dominant frequency and syllable repetition rates (Figure 4 a, Table 1 and 2). The calls

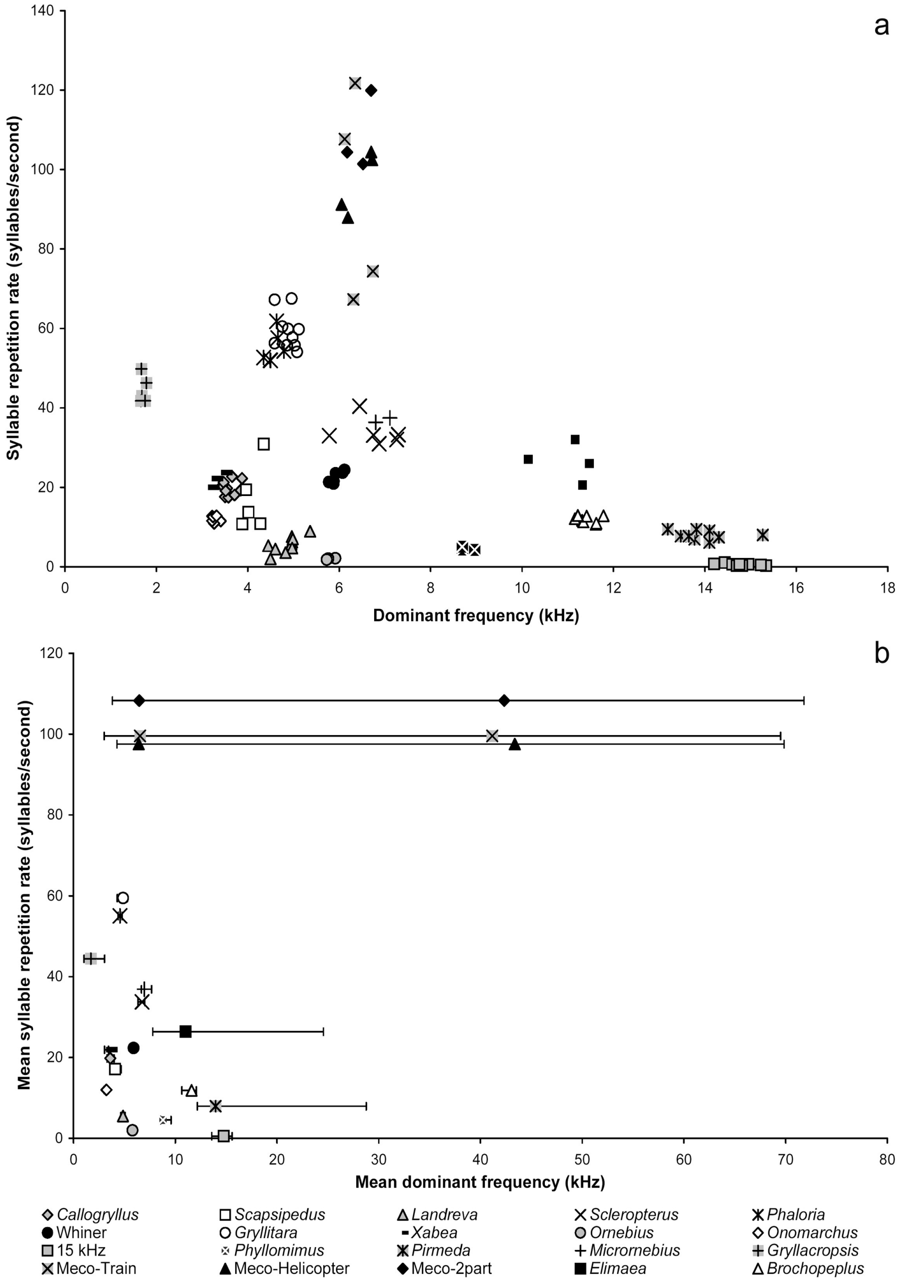

Figure 4. Spectral and temporal features of the calls of twenty ensiferan species constituting the acoustic community of Kudremukh National Park. (a) The distribution of dominant frequencies and syllable repetition rates. Each point represents one individual. (b) Mean frequency and syllable repetition rate for each species with the frequency bandwidth plotted as horizontal bars.

of *Xabea* sp. overlapped in frequency with *Onomarchus* sp. at 3 kHz but differed from it in syllable repetition rate (22 and 12 syllables per second respectively). The broadband calls of *Pirmeda* sp. and *Elimaea* sp. (frequency range: 12–28 and 8–25 kHz respectively) overlapped in frequency with *Brochopeplus* sp. and '15 kHz'. However, the calls of these species differed in their syllable repetition rates (Figure 4 b, Table 1). The broadband calls of *Mecopoda* species 'Helicopter', 'Two part' and 'Train' with frequency ranging from 2–70 kHz overlapped with narrow band calls in the frequency spectrum. Interestingly, *Mecopoda* species had high syllable repetition rates of 98, 100 and 108 syllables per second respectively and separated from the other gryllid and tettigoniid species along this axis.

Diel calling patterns

There was a significant change in the total calling activity of crickets over the 24-hour period (F = 86.92, *P* < 0.001, Table 3). Calling activity was largely restricted between 1800 h in the evening and 0600 h in the morning (Figure 5 a). There was a peak in calling activity from 1800 h in the evening till midnight. No calling activity peak was observed in the morning. Species accumulation curves over the 24-h cycle reached an asymptote by 2100–2200 hours and no new species were heard in subsequent sampling periods (Figure 5 b). The mean number of calling individuals was similar between the two transects (F = 0.41, *P* = 0.52) and the ambient calling profiles of the two transects were similar (F = 0.91, *P* = 0.5). There was a significant species x time interaction (F = 10.02, *P* < 0.001) indicating differences between the calling profiles of species over the 24-h period.

TABLE 3

Results of a three-way repeated measures ANOVA of diel calling patterns of the ensiferan acoustic community

	df Effect	MS Effect	df Error	MS Error	F	*P*-level
1	1	5.50	64	13.35	0.41	0.52
2	15	526.49	64	13.35	39.44	0.00*
3	7	742.74	448	8.55	86.92	0.00*
12	15	17.50	64	13.35	1.31	0.22
13	7	7.81	448	8.55	0.91	0.50
23	105	85.59	448	8.55	10.02	0.00*
123	105	7.34	448	8.55	0.86	0.83
1-TRANSECT, 2-SPECIES, 3-TIME						

* Differences significant at $\alpha = 0.01$.

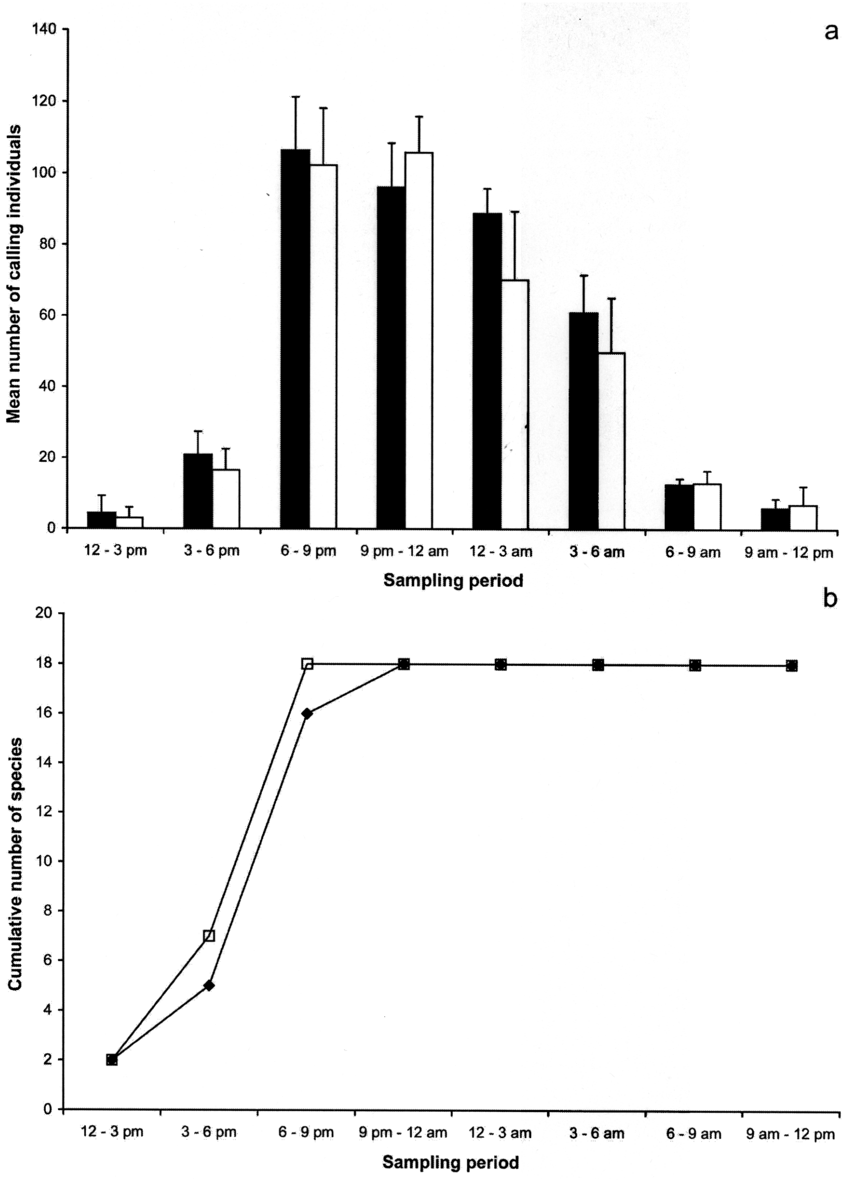

Figure 5. Diel calling profiles of the ensiferan acoustic community. a) The total number of calling individuals of all species heard over 24-hours. Black bar indicates transect 1 and white bar indicates transect 2. b) Species accumulation curve over 24 hours in two transects based on presence-absence data on 18 species. Filled diamonds represent transect 1 and empty squares represent transect 2. *Callogryllus* sp. and *Scleropterus* sp. were not observed in the data set as the diel pattern sampling was carried out between December and March.

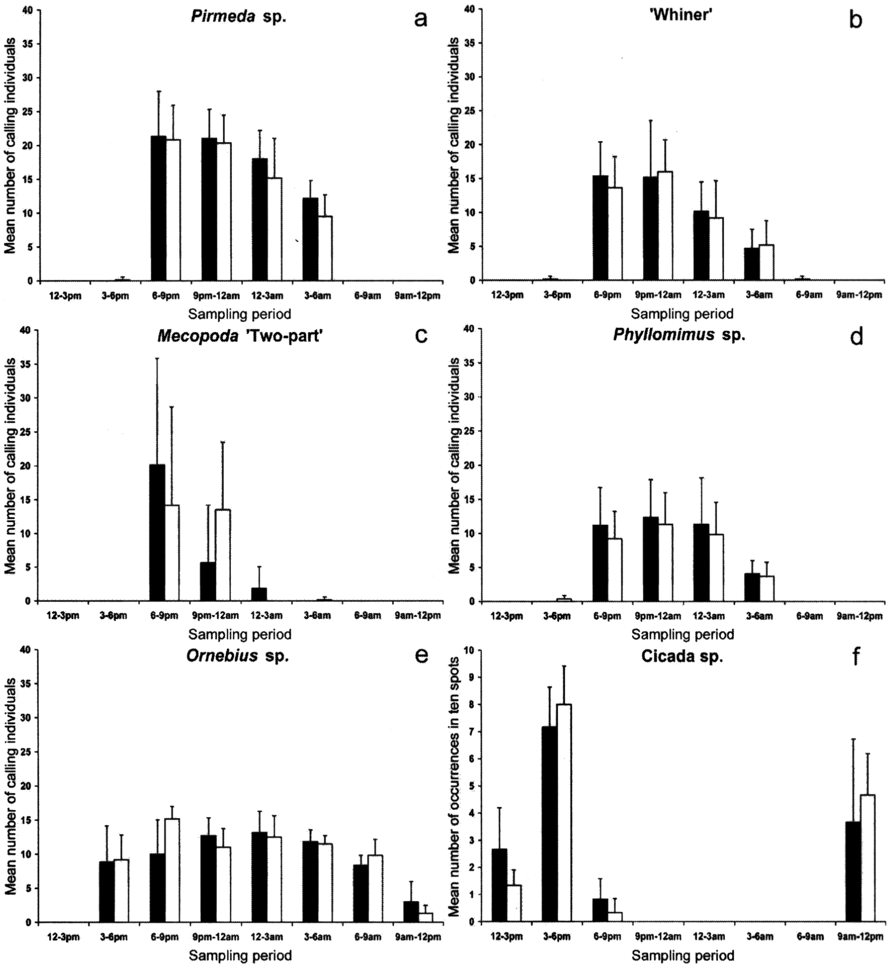

Figure 6. Calling patterns of (a) *Pirmeda* sp. (b) 'Whiner' (c) *Mecopoda* 'Two part' (d) *Phyllomimus* sp. (e) *Ornebius* sp. and (f) Cicada species over twenty-four hours. Black bar indicates transect 1 and white bar indicates transect 2.

The calling activity profiles of selected species occurring at relatively high density are shown in Figure 6 a–f. Calling activity of *Pirmeda* sp., 'Whiner', *Mecopoda* 'Two part' and *Phyllomimus* sp. increased during the 1800–2100 h sampling period and died down by 0300 h in the morning. Whereas the calling activity of these species was restricted from dusk till midnight, *Ornebius* sp. and *Micrornebius* sp., called during the daytime as well (Figure 6 e). Pair wise comparisons between species showed that there were many significant positive correlations in calling profiles but there were no significant negative correlations suggesting that the acoustically communicating ensiferan species were not partitioning their calling time over the diel cycle. We also recorded two species of cicada from the evergreen forests that had the peak calling activity during the day and stopped calling by dusk. The calling activity profile of one of the species of cicada is shown in Figure 6 f.

Completeness of the acoustic community

The average number of species heard on a sampling night by acoustic sampling along a 500 m transect was 14 ± 2. *Callogryllus* sp., *Gryllitara* sp., *Scapsipedus* sp. and *Brochopeplus* sp. had the least occurrences of 1, 2, 5 and 6 respectively across twenty-three sampling nights and accordingly lesser number of individuals. Individuals of *Pirmeda* sp., *Micrornebius* sp., 'Whiner', *Mecopoda* 'Two part', *Ornebius* sp. and *Phyllomimus* sp. were most commonly heard. Species accumulation curves based both on abundance (Figure 7 a) as well as presence-abundance (Figure 7 b) were close to asymptotic. The slope at the asymptote of the randomized curve based on the abundance data was 0.00044 (Figure 7 a) and that of the curve based on the incidence data was 0.036 (Figure 7 b) suggesting that the acoustic cricket community has been almost completely sampled.

DISCUSSION

Taxonomic diversity and species richness

The present study provides the first description of the calls of a multi-species ensiferan assemblage in a tropical evergreen forest of the Indian subcontinent. We have identified and described the calls of twenty ensiferan species constituting the nocturnal acoustic community of a tropical forest. Most previous studies on ensiferan assemblages have concentrated on specific taxonomic groups. Otte (1994) described the Hawaiian gryllid fauna and found that most species in the tropical montane forests belonged to the subfamilies

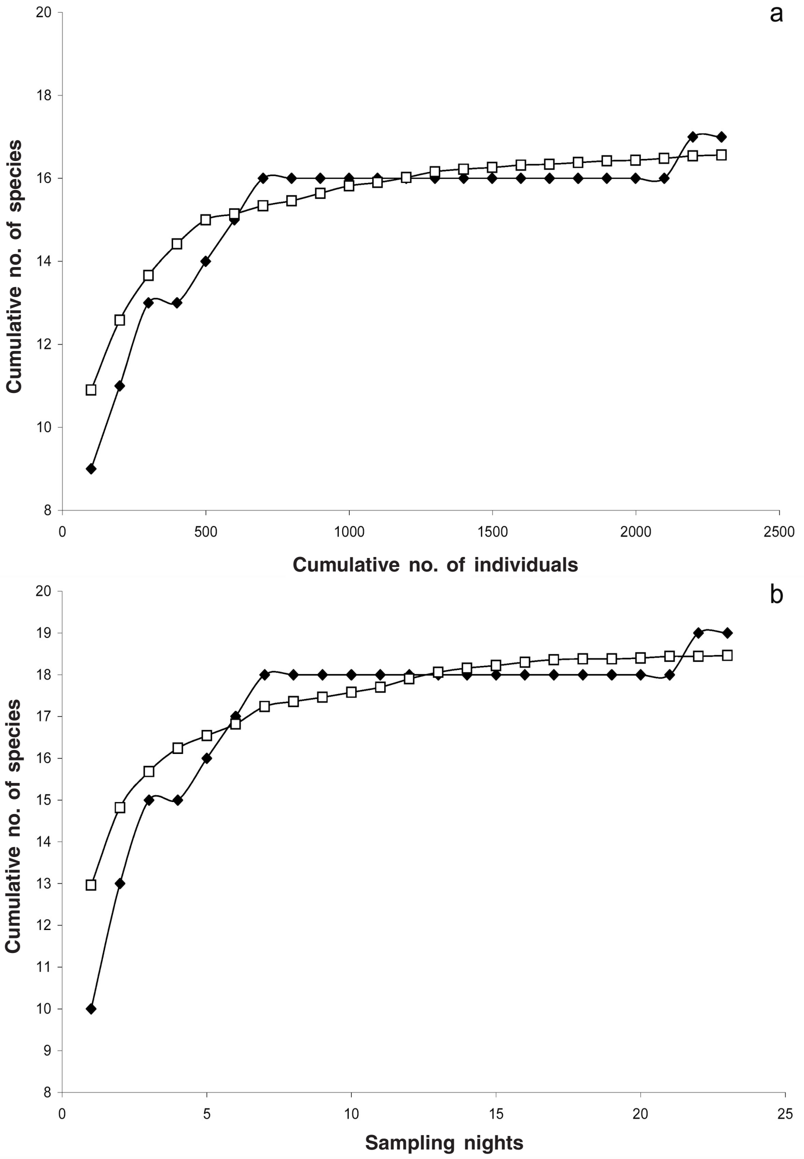

Figure 7. Species accumulation curves of the acoustically communicating ensiferan assemblage based on (a) the number of individuals and (b) the number of sampling nights. There were only 17 species in the observed data set in (a) due to the difficulty in correctly estimating the number of calling individuals of *Phaloria* sp. and *Xabea* sp., which call in chorus. There were 19 species in the observed data set in (b) as one species (*Scleropterus* sp.) was not recorded as the acoustic samplings were concentrated mainly between December to March whereas this species has a short calling season in November. Filled diamonds represent the observed data and the empty squares represent the smoothed curve produced by 50 randomisations.

Oecanthinae and Trigonidiinae. Nischk and Riede (2001) found representative species mainly from the subfamilies Trigonidiinae, Phalangopsinae and Eneopterinae from the rainforest ecosystem in Ecuador. However, subfamily Trigonidiinae was absent from cloud forest ecosystems in the same region. The gryllid community in the understorey of New Caledonian forests studied by Desutter Grandcolas (1997) had representative species from six subfamilies namely, Nemobiinae, Brachytrupinae, Eneopterinae, Itarinae, Phalangopsinae and Podoscirtinae.

In our study, we found that the multi-species ensiferan assemblage consisted of diverse taxa representing subfamilies from the families Gryllidae, Tettigoniidae and Anostostomatidae. We found eight acoustically communicating species of the family Gryllidae belonging to subfamilies Gryllinae, Landrevinae, Sclerogryllinae, Oecanthinae, Phaloriinae, Itarinae and Podoscirtinae. Two species belonged to the subfamily Mogoplistinae in the family Mogoplistidae. Interestingly, each subfamily was mostly represented by only one genus. In the tettigoniids, we found representative species only from subfamilies Pseudophyllinae, Phaneropterinae and Mecopodinae. Also, phaneropterines were under-represented in the assemblage with only two genera as compared to four from the family Pseudophyllinae. Since the song recordings and collection were based on hearing the call and locating the animal, we are likely to have missed species with call frequencies in the ultrasonic range, especially the high frequency callers from the canopy due to both inaccessibility and the greater attenuation of high frequencies (Wiley & Richards 1978).

The species richness of the acoustically communicating cricket assemblage in the tropical evergreen forest of Kudremukh was low compared to the lowland rainforest in Ecuador (Nischk & Riede 2001). The number of singing cricket species in the low elevation forest in Ecuador was reported to be thirty-five. However, no species accumulation curves were shown so the number of species could be much larger. Twenty-three gryllid species were identified in the understorey of New Caledonian evergreen forests (Desutter Grandcolas 1997). This study also included the non-calling gryllid species. None of the above studies included tettigoniid species. Twenty putative species clusters were revealed from the song parameters based on the song recordings from Amazonian lowland forest (Riede 1993). Our study did not include non-calling species and is therefore an underestimate of the total ensiferan species richness.

Narrow versus broadband calls in gryllids and tettigoniids

The gryllid and tettigoniid species analyzed exhibited different frequency (both narrow and broadband) and temporal patterns.

Species belonging to the family Gryllidae had narrow band calls (with bandwidths not greater than 1 kHz) and had dominant frequencies mainly between 3 and 7 kHz that are typical dominant frequencies generated by gryllids (Riede 1993).

The calls of tettigoniids covered a wide spectral range reaching far into the ultrasound in species of the genus *Mecopoda*. Interestingly, of nine tettigoniid species, the calls of four (*Onomarchus* sp., *Phyllomimus* sp., *Brochopeplus* sp. and '15 kHz') were narrow band and in the audible range similar to those of gryllids. Of the calls of 15 species of pseudophyllines described by Montealegre and Morris (1999) in the Neotropical rainforests of Ecuador and Colombia, five had broadband calls and the other ten were narrow band. Narrow-band calls were produced at high carrier frequencies ranging from 13 kHz to as high as 29.3 kHz in *Tricentrus atrosignatus*. Studies on acoustic signals of Costa Rican (Morris & Beier 1982) and Ecuadorian katydids (Morris *et al.* 1989) showed that species utilized narrow band carrier frequencies predominantly in the ultrasonic range for mating calls. Calls were also produced at a very low duty cycle. The ultrasonic narrow-band calls produced infrequently have been suggested as an adaptation for avoidance of predation by bats (Belwood & Morris 1987).

Studies on the acoustic behaviour of nine species of the subfamily Pseudophyllinae from Malaysia (Heller 1995) showed that their carrier frequencies were in the audible range and a high proportion (six out of nine species) had narrow band calls with carrier frequencies ranging from as low as 600 Hz in *Tympanophyllum* to 11.6 kHz. In the Paleotropics, call frequencies were found to be lower than those in the Neotropics and this was suggested to be due to differences in predation pressure by bats between the two regions.

The occurrence of narrow band calls cannot be considered as typical only of pseudophyllines as Colombian species of *Panacanthus* belonging to the subfamily Conocephalinae were also found to have narrow band calls (Montealegre & Morris 2004). In our study also, we found the '15 kHz' species belonging to the subfamily Phaneropterinae calling at an audible narrow band frequency of 15 kHz. This suggests that the evolution of narrow-band calls in tettigoniids is more likely to be driven by ecological factors, perhaps peculiar to tropical evergreen forests. These factors may include habitat structure, predation pressure and high levels of acoustic interference.

Implications for acoustic interference

Differences in carrier frequencies and temporal patterns of calls within assemblages in frogs (Hödl 1977; Duellman & Pyles 1983;

Rutledge and Narins 2001) and cicadas (Riede & Kroker 1995; Sueur 2002) have been suggested as mechanisms to reduce acoustic interference. In our study, although there was a high overlap of call frequencies between 3 to 7 kHz, gryllid species separated in their syllable repetition rate, which varied from six syllables per second in *Landreva* to 60 syllables/second in *Gryllitara*. Species with overlapping syllable repetition rates of 10–20 syllables per second separated along the frequency axis (Figure 4 a, b). There were species such as those of *Phaloria* and *Gryllitara, Scapsipedus, Xabea* and *Callogryllus* that overlapped both in spectral features and syllable repetition rates. These species however, differed in other temporal features such as call duration, call period and number of syllables per call.

Separation in spectral and/or temporal patterns among calls in an assemblage is of prime importance in species recognition and to reduce acoustic interference (Drewry & Rand 1983). In our study, the spectral and temporal features of the calls of the ensiferan assemblage appear to separate many of the species acoustically, suggesting possible partitioning to avoid acoustic interference. This is important considering that all ensiferan species constituting the nocturnal acoustic community had their peak calling time between dusk and midnight and there was no diel partitioning of calling. Since the study was mainly concentrated in the post-monsoon dry season from December to March, the acoustic community did not have frog species. Frogs typically call during the monsoon season from June to October. Cicada calling was restricted to the daytime. Thus, frogs and cicadas that can be considered as acoustic competitors of the ensiferan assemblage appear to separate from crickets on a seasonal and diel scale respectively. Future studies will aim at investigating whether the ensiferan species try to avoid acoustic interference by spatial dispersion of calling sites both in the vertical and the horizontal dimension.

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