Report **Klaus Riede**

Monitoring Biodiversity: Analysis of Amazonian Rainforest Sounds

Recent estimates of the number of species inhabiting tropical forests, exceed those described scientifically by one order of magnitude. This diversity is threatened by the ongoing rapid destruction of tropical habitats and has led to the necessity for quick surveys to identify biodiversity rich areas. Sound recordings can represent a valuable tool for monitoring biodiversity of singing animals, especially in tropical areas under threat. Recordings from an Amazon lowland forest are analyzed and sound patterns, mainly generated by crickets (Gryllidae), are described. Plotting of song parameters such as carrier frequency and repetition rate, reveals clusters which can be attributed to putative cricket species. This allows diversity and abundance of the individuals composing a tropical cricket community to be assessed from the acoustic record only. Amplitude spectra of recordings from the canopy show a comb-like distribution of carrier frequencies which suggests optimal repartition of acoustic transmission channels, while those from secondary vegetation reveal reduced diversity by their "gappy" appearance.

INTRODUCTION

At present, the number of species inhabiting the earth can only be estimated and is a matter of vigorous debate mainly among zoologists (1, 2). However, there is general agreement that their number exceeds those described scientifically by one order of magnitude (3). Depending on who is presenting the figures, estimates vary between 5 and 80 millions and this is mainly due to the fact that an unknown number of insect species inhabit the tropical forests (4, 5). Because of ongoing rapid destruction of their tropical habitats, many of these species will have become extinct before they are even documented by science (6), thus, the mere inventorying of the planet's biodiversity is a race against time and has led to the necessity of making rapid surveys of the tropical forests in an attempt to identify areas rich in biodiversity (7). Inventory studies are especially difficult in rainforests, as the complexity of jungle architecture provides numerous niches and many species inhabit inaccessible regions of the canopy. Up to now, every new collection technique such as fogging with insecticide (8), tree-felling (9) or attraction by chemicals (10) has revealed a hitherto unknown community of invertebrates. In these samples, a great proportion of the species revealed is often represented by only one or a few individuals, and low population density is a characteristic feature of many rainforest species. This finding has puzzled many observers (11). Rarity, together with excellent camouflage, cryptic lifestyles and nocturnal habits of a great proportion of species, makes visual censuses extremely difficult. However, a considerable number of rainforest creatures indicate their presence acoustically, and the sensorial impression of a rainforest concerto rivals or even surpasses the visual one. Sound analysis could therefore provide a good means of relieving the problem of monitoring fauna in the rainforest. This report presents data on local diversity of the cricket community of a tropical lowland forest in Ecuador and is based on the analysis of sound recordings. These results can stimulate further bioacoustic assays which, if standardized and routinely applied, could act as a valuable complement for mapping endeavors in biosphere reserves under threat.

METHODS AND MATERIALS

Two transects of 200-m length and 10 recording points were marked along primary forest trails in the surroundings of the indigenous settlement San Pablo de Kantesiya, Rio Aguarico, latitude 0°15'S, longitude 76°27'W, Province of Sucumbias, Ecuador. At every point, tape recordings (minimum duration 5 minutes) were repeated for 2 weeks, twice per day at different hours. All hours of the day were covered. At each study point, individual songs were recorded by approaching the songster as close as possible. In a few cases, individuals were captured. Recordings were made with a condenser microphone (capsule CK8 with pre-amplifier C451, AKG) on a Sony TC-D5PRO cassette recorder (frequency response 40-16 000 Hz ± 3dB (NAB)) and analyzed with a spectrum analyzer (Spectro 2000, MEDAV) which produced an on-line fast Fourier Transform visible on a color monitor (Fig. 1). Segments of 2 sec. length were averaged and displayed as amplitude spectrum (Fig. 4).

RESULTS

Figure 1 shows the spectral analysis of a recording. Frequency bands below 3 kHz are mainly occupied by frogs, birds and mammals which were identified by the indigenous inhabitants in the area. Short broad-band signals are produced by katydids (Tettigoniidae). Probably as an anti-predator strategy, most of them produce faint songs with a low repetition rate (12). Conspicuous, repetitive signals with a narrow-band carrier frequency between 4 and 9 kHz, are principally generated by the rhythmic wing-strokes of male crickets (Gryllidae). During inward movement of the fore wings, a file-and-scraper mechanism excites specialized resonance areas which radiate sound in a narrow carrier frequency band, at a pulse rate determined by the wing strokes (Fig. 2a). Besides these basic features, pulses can be arranged to form complex secondary and tertiary structures called chirps (Fig. 2b). Carrier frequency, pulse rate and chirp structure are species specific and important cues for the innate releasing mechanism of searching conspecific females (13). To differentiate the recorded songs, the pulse rate and carrier frequency (CF) of individual songs were plotted against each other (Fig. 3). Such a CF/pulse rate diagram reveals clusters which can be attributed to putative species (Fig. 3). These were subsequently called ethospecies, as this classification is based on behavior. The CF/pulse rate space is densely packed between 5 and 8 kHz and 20 to 80 pulses per second. Relatively few ethospecies sing below 4 or above 8 kHz or produce more than 100 pulses per second. The

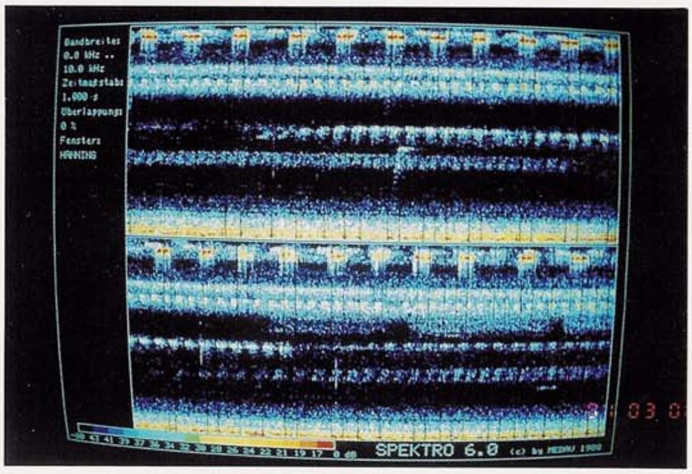


Figure 1. Color spectrogram of a sound track recorded in primary forest. The monitor is divided into two halves, each of which contains 10 sec. made up of segments of fast Fourier Transformation, showing the frequency composition between 0 and 10 kHz (y-axis). Intensity is color coded (highest intensities red). Frequency bands between 4 and 10 kHz are densely packed with cricket sounds; the chirp structure can be recognized for several species.

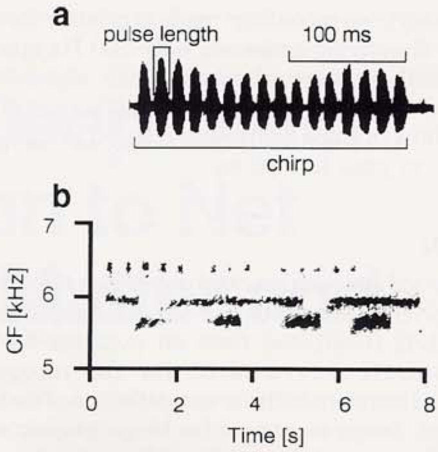


Figure 2. a. Oscillogram of a recording of a single cricket revealing the time structure of cricket song (individual 1; Fig. 3). Every pulse is produced by an inward wing stroke and is the envelope containing the carrier frequency of 5.9 kHz. Several pulses make up a chirp. b. Spectrogram of a simultaneous recording of different species singing at nearby frequencies. Every species is characterized by its carrier frequency and characteristic chirp structure, composed of a species-specific number of pulses. However, pulse rate can only be analyzed at a much higher temporal resolution, which reduces frequency resolution. Note that time resolution is not fine enough to recognize the pulse rate within a chirp.

observed pulse rates of 135 and 150 Hz lie among the highest known rates for crickets. In one ethospecies, pulse rate is variable and can be doubled in one chirp, which corroborates the observations of Otte (14) in Hawaiian crickets. Other ethospecies change their carrier frequency within one pulse, sweeping from the higher to the lower frequency. Their frequency range overlaps considerably with those singing at a constant carrier frequency. For several clusters in the CF/pulse-rate space, intraspecific variation is so small that classification is not difficult. In problematic cases, song features like frequency modulation, number of pulses per chirp and chirps per second provide additional criteria for classification. For example, in the recordings symbolized by D and T (Fig. 3), chirps are made up of double or triple pulses, respectively.

Such an "acoustical fingerprinting" of ethospecies allows noninvasive mapping and considerations about the structure of the "acoustic community". For a full description of a community consisting of N individuals it is necessary to know not only the number of species, but also their relative abundance defined as $p_i = N_i N^{-1}$ where N_i is the number of individuals of each species. Considering N_i as the number of recordings of the *i*th ethospecies and N as the total number of recordings, diversity indices as manifested in ecological theory can be calculated. They combine both species richness and relative abundance into a single statistic. The most commonly used is the Shannon-Wiener Index, which is derived from information theory and is calculated as $H = -\Sigma p_i \ln p_i$. For the acoustic community under consideration (Fig. 3), the Shannon-Wiener Index amounted to 2.789. This is rather low compared with diversities based on trapping tropical morphospecies, which can reach a value as high as H = 5.0 for moths attracted to light in Papua-New Guinea (15). Caswell (16) observed reduced diversity in communities with strong biotic interaction, which could be the explanation for the low diversity of the acoustic community under study. Biotic interaction could, in the present case, be interpreted as competition for acoustic transmission channels. This interpretation is corroborated by the rather regular spacing of different carrier frequencies (Fig. 4) which could be a consequence of male–male interactions like spatial rearrangement of songsters singing on nearby frequencies. Such interactions could explain the comblike appearance of

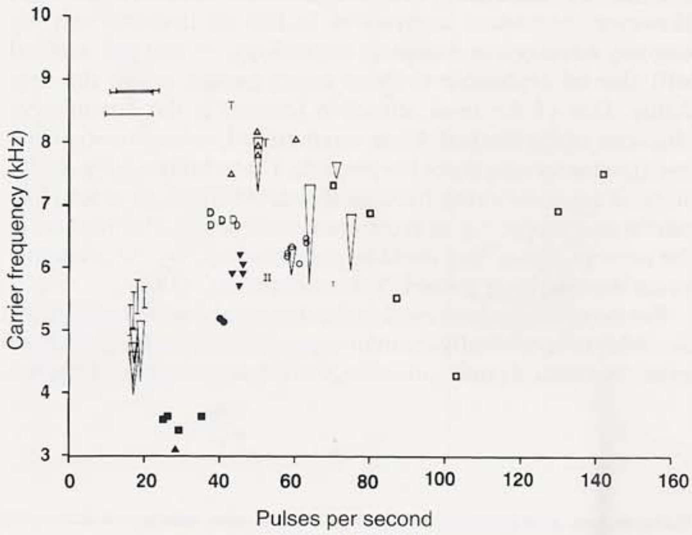
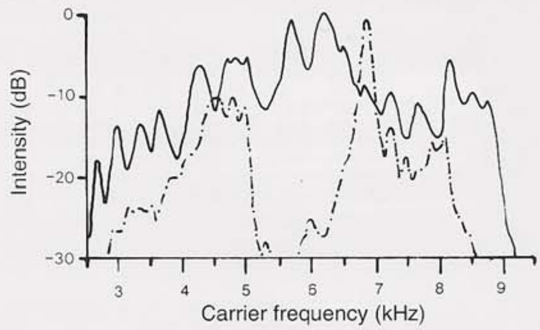


Figure 3. Distribution of song parameters of 54 recordings in the frequency/pulse repetition rate space. Common symbols reflect tentative grouping of 20 species taking into account additional song parameters like chirp structure (Fig. 2) and frequency sweeps. Frequency sweeps within a pulse are symbolized by wedges and bars delimiting upper and lower frequencies; during the sweep the frequency is always reduced. "Sweeping" of pulse rate occurs in some species (horizontal bars), where pulse rate switches between 10 and 20 Hz, probably as a result of pulse drop-outs. Considerable overlap between different species can be observed in the middle frequency range between 5 and 8 kHz. 1 symbolizes the song parameters of a captured individual with a body length of only 5 mm. D = double pulses, T = triple pulses, squares = species documented by singular record.

amplitude spectra from recordings made in primary forest. Some of the clearly discernible peaks are only 200 Hz apart, which suggests optimal partition of transmission channels among songsters. In secondary growth, the amplitude spectrum shows gaps (Fig. 4, broken line), indicating reduced cricket diversity within successory plant formations.

Figure 4. Amplitude spectrum of overall recordings with microphone directed towards the canopy in primary forest (solid line) and from secondary old growth (stippled). Intensity scaled to loudest peak. Note dense packing in canopy record compared with "frequency holes" in secondary growth, reflecting different architectural complexity of the vegetation.



DISCUSSION

The data presented suggest that extrovert calling behavior can be exploited for diversity assays in rainforests. The species specific songs of crickets (Gryllidae) form an excellent tool for the taxonomist because they evolved for the recognition of conspecifics, and therefore fulfil the very definition of the biological species concept. Songs were used for biogeographic studies of speciation in Hawaiian crickets (14) and helped to detect several undescribed crickets in an Australian rainforest (17).

The observed assembly of ethospecies at one locality probably represents only a small fraction of the regional, Northwest Amazonian cricket fauna. A comparison of local with regional diversity will only be possible with a larger data base. This could be achieved by automatized evaluation employing sophisticated algorithms like feature-detecting "neural networks". The development of a "cricket detector" is under way which allows a preliminary analysis in the field by displaying relevant parameters like frequency and pulse rate. This allows mapping of ethospecies in the field. Songs of other insects like katydids (Tettigoniidae) and cicadas (Cicadidae) are more complex than cricket songs. However, acoustical analysis is facilitated tremendously by ongoing advances in computer technology, so that this method will also be applicable to these insect groups within the near future. One of the most attractive features is the noninvasive character of the method. Once standardized, automatization and even remote sensing should be possible. The technique is especially suitable for monitoring habitats that are difficult to reach, like rainforest canopy; e.g. microphones could be installed high up in the treetops. Recording could be done routinely by the personnel in national parks or trained "parataxonomists" (18).

For the ecologist interested in the structure of communities, the assembly of acoustically communicating species can be considered as the "acoustical guild", in analogy to other assemblies of species belonging to certain ecological categories such as feeding guilds. Members of the "acoustical guild" are interrelated by using the same modality for intra- and interspecific information transfer and they exhibit all kinds of biotic interaction like competition (for transmission channels), niche displacement, or even acoustic mimicry.

Tropical entomologists face a number of problems: Due to the extreme rarity of most species, species collection may interfere with the composition of small populations, but is necessary for a reliable classification of morphospecies. In many cases, such interference has to be avoided, so ecological and behavioral studies have often been limited to colorful, diurnal species like butterflies or grasshoppers (19, 20). In spite of its limitation to singing insects, the study of the acoustical guild could help to open an additional window to our understanding of tropical insect communities.

Insects are particularly subtle indicators of habitat quality and diversity (19); as cricket habitats are strongly determined by local microclimate, these data could serve as a subtle indicator of climatic change in the area. On the basis of these findings I suggest the incorporation of standardized sound recordings into current and future programs for measuring biodiversity.

References and Notes

1. Gaston, K. J. 1991. The magnitude of global insect species richness. *Conserv. Biol. 5*, 283–296.
2. Erwin, T. 1991. How many species are there?: Revisited. *Conserv. Biol. 5*, 330–333.
3. May, R.M. 1986. How many species are there? *Nature 324*, 514–515.
4. Erwin, T. L. 1982. Tropical forests: Their richness in Coleoptera and other Arthropod species. *Coleopterist's Bull. 36*, 74–75.
5. Stork, N.E. 1988. Insect diversity: facts, fiction and speculation. *Biol. J. Linn. Soc. 35*, 321–337.
6. Wilson, E.O. 1989. Threats to biodiversity. *Sci. Am. 60*, 60–66.
7. Roberts, L. 1988. *Science 241*, 1759–1761.
8. Erwin, T.L. 1983. Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. In: *Tropical Rain Forest Ecology and Management*. Sutton, S. L., Whitmore, T. C. and Chadwick, A. C. (eds). Blackwell, Oxford, p. 59–75.
9. Descamps, M. 1976. La faune dendrophile neotropicale. I. Revue des Proctolabinae (Orth. Acrdididae). *Acrida 5*, 63–167.
10. Dressler, R. L. 1982. Biology of the orchid bees (Euglossini). *Ann. Rev. Ecol. Syst. 13*, 373–380.
11. Elton, C. S. 1973. The structure of invertebrate populations inside neotropical rain forest. *J. Anim. Ecol. 42*, 55–104.
12. Belwood, J.J. and Morris, G. K. 1987. Bat predation and its influence on calling behaviour in neotropical katydids. *Science 238*, 64–67.
13. Schildberger K., Huber, F. and Wohlers, D. 1989. Central auditory pathway: neuronal correlates of phonotactic behavior. In: *Cricket Behavior and Neurobiology*. Huber, F., Moore, T.E. and W. Loher (eds). Cornell University Press, Ithaca, p. 423–458.
14. Otte, D. 1989. Speciation in Hawaiian crickets. In: *Speciation and its Consequences*. Otte, D. and Endler, J.A. (eds). Sinauer Associates, Sunderland, Massachusetts, p. 482–526.
15. Hebert, P.D. 1980. Moth communities in montane Papua New Guinea. *J. Anim. Ecol. 49*, 593–602.
16. Caswell, H. 1976. Community structure: a neutral model analysis. *Ecol. Monogr. 46*, 327–354.
17. Otte, D. and Alexander, R.D. 1983. *The Australian Crickets (Orthoptera: Gryllidae)*. Academy of Natural Sciences in Philadelphia, Philadelphia.
18. Coddington, J., Hammond, P., Olivieri, S., Robertson, J., Sokolov, V., Stork, N. and Taylor, E. 1991. Monitoring and inventorying biodiversity from genes to ecosystems. In: *From Genes to Ecosystems: A Research Agenda for Biodiversity*. Solbrig, O. T. (ed.). International Union of Biological Sciences, Cambridge Mass., p. 83–109.
19. Brown Jr, K.S. 1989. Conservation of neotropical environments: insects as indicators. In: *The Conservation of Insects and Their Habitats*. Collins, N. M. and Thomas, J. A. (eds). Academic Press, London, p. 349–404.
20. Riede, K. 1987. A comparative study of mating behaviour in some neotropical grasshoppers (Acridoidea). *Ethology 76*, 265–296.

21. I wish to thank the Secoya Indians from San Pablo for their hospitality, and especially Belisario Payaguaje for his enthusiastic company during cricket hunts and for the identification of vertebrate sounds. I also thank Professor Dr. H.-U. Schnitzler, Tübingen, for providing the MEDAV machine for sound analysis.
22. First submitted 9 July 1992, accepted for publication 27 January 1993.

Dr Klaus Riede is a zoologist at the University of Freiburg, Department of Animal Physiology and Behavior. He is participating in a German research project on tropical diversity funded by the German Research Council. He carried out a comparative study on the behavioral ecology of South American grasshoppers and became interested in issues of biodiversity during his research in tropical lowland forests of Ecuador. His address: Institut für Biologie I (Zoologie), Albertstr. 21 a, D-79104 Freiburg, Germany.