

Acoustic profiling of the landscape

by

Paul Brian Charles Grant

*Dissertation presented for the degree of Doctor of Philosophy
at the University of Stellenbosch*



Supervisor: Professor M.J. Samways

Faculty of AgriSciences

Department of Conservation Ecology and Entomology

Cr tki'4014

Declaration

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Paul B.C. Grant

Date: November 2013

Copyright © 2016 Stellenbosch University

All rights reserved

Abstract

Soft, serene insect songs add an intrinsic aesthetic value to the landscape. Yet these songs also have an important biological relevance. Acoustic signals across the landscape carry a multitude of localized information allowing organisms to communicate invisibly within their environment. Ensifera are cryptic participants of nocturnal soundscapes, contributing to ambient acoustics through their diverse range of proclamation songs. Although not without inherent risks and constraints, the single most important function of signalling is sexual advertising and pair formation. In order for acoustic communication to be effective, signals must maintain their encoded information so as to lead to positive phonotaxis in the receiver towards the emitter. In any given environment, communication is constrained by various local abiotic and biotic factors, resulting in Ensifera utilizing acoustic niches, shifting species songs spectrally, spatially and temporally for their optimal propagation in the environment.

Besides the importance of Ensifera songs from an ethological point of view, the multitude of species-specific signals provide an acoustic tapestry representing species diversity across ecological gradients and over time. Acoustic inventorying and monitoring of the landscape can reflect the environmental status of ecological systems, from natural to disturbed by human influence. In contrast to traditional survey techniques, sound recording and interpretation is a non-invasive method that allows for the detection and classification of highly cryptic, yet insightful indicators of ecosystem change. Here, acoustic monitoring was used across diverse ecological gradients to improve understanding of species diversity patterns, and how they change in response to both natural gradients and in response to the human dominated landscape mosaic.

This study was undertaken in three geographic locations from tropical rain forest of Brunei, Borneo, to the landscape mosaic of plantation forestry in KwaZulu-Natal, South Africa,

and to the botanically rich, mountain fynbos region of the Cape Floristic Region, also in South Africa. Each region provided a diverse and particular landscape to test the value of acoustic surveys for determining local diversity patterns across natural gradients and to assess the value of the technique for assessing the impact human influence across landscapes.

In tropical rainforests, an entire acoustic guild was investigated to determine how acoustic species partition their acoustic communication channels spectrally, temporally and spatially, to avoid acoustic interference. The overall assemblage showed considerable spectral partitioning. Diurnally active species showed low temporal niche overlap, whereas nocturnal species did not utilize temporal partitioning. Lack of nocturnal temporal partitioning suggests other mechanisms of acoustic avoidance are sufficient to avoid acoustic overlap, or that there are insufficient cues to partition nocturnal acoustic environments. Acoustic species also utilized spatial partitioning, with distinct acoustic assemblages at vertical heights and with elevation. Utilization of a range of different strategies allow many species to communicate with conspecifics with little or no interference from other species in a signal rich environment.

Acoustic profiling was also undertaken in KwaZulu-Natal, South Africa, across a plantation forestry landscape mosaic with diverse ecological gradients containing both alien and indigenous vegetation, as well as bordering large natural protected areas. Areas covered in alien timber or non-endemic grass were devoid of acoustic signals. Managed areas that were mowed and heavily grazed were not effective in maintaining the natural complement of nocturnal acoustic species. Within natural vegetation patches inside plantations, acoustic species richness increased with plant heterogeneity and patch size. Patches of indigenous vegetation within the plantation matrix effectively reduced the contrast of transformed landscapes with surrounding natural areas, with indigenous forest patches containing a highly characteristic acoustic species assemblage.

Within the botanically rich, mountain fynbos region of the Cape Floristic Region, acoustic profiling was conducted across gradients of elevation, season and vegetation. Across these gradients, katydid acoustic signals were identified and characterized for the first time. This resulted in the discovery of two new katydid species and a novel sound producing structure in a carabid beetle, a species previously unknown to produce sound. Acoustic diversity across seasonal and elevational gradients increased with increasing temperatures. Climatic variability along the elevational gradient produced variation in seasonal phenology. Katydids also utilized high frequency acoustic signals, which is probably an adaptation to overcome background noise from wind, so prevalent in this area. Furthermore, despite producing conspicuous signals for mate attraction and pair formation, katydids were found not to be part of bat-eared fox diet, an insectivorous, nocturnal predator that uses its characteristic large ears to detect sounds made by invertebrate prey.

This study shows the value of using acoustic emissions from katydids to identify acoustic diversity patterns across ecological gradients and in response to human impacts on the landscape.

Opsomming

Sagte, rustige insek liedjies voeg 'n intrinsieke estetiese waarde aan die landskap. Tog is hierdie liedjies ook van belangrike biologiese waarde. Akoestiese seine oor die landskap dra 'n magdom plaaslike inligting wat organismes in staat stel om onsigbaar te kommunikeer binne hul omgewing. Langhoringsprinkane is kriptiese deelnemers van die nagtelike klankomgewing en dra by tot die omringende akoestiek deur hul verskeidenheid van proklamasieliedjies. Alhoewel dit nie sonder inherente risiko's en beperkings is nie, is die belangrikste funksie van seine seksuele advertering en paarvorming. Vir akoestiese kommunikasie om effektief te wees, moet seine hul geënkodeerde inligting handhaaf, sodat dit sal lei tot positiewe fonotaksis in die ontvanger teenoor die emittor. In enige gegewe omgewing, word kommunikasie beperk deur verskeie plaaslike abiotiese en biotiese faktore. Dit lei tot die gebruik van akoestiese nisse deur langhoringsprinkane, wat hulle liedjies spektraal, ruimtelik en temporeel aanpas vir optimale verspreiding in die omgewing.

Benewens die belang van die langhoringsprinkaan liedjies uit 'n etologiese oogpunt, bied die menigte spesie-spesifieke seine 'n akoestiese tapisserie wat spesiesdiversiteit verteenwoordig oor ekologiese gradiënte en oor tyd. Akoestiese opname en monitering van die landskap kan die omgewingstoestand van ekologiese stelsels weerspieël, van natuurlike tot menslik versteurde stelsels. In teenstelling met tradisionele opnametegnieke, is klankopname en interpretasie 'n nie-indringende metode wat dit moontlik maak om hoogs kriptiese, nog insiggewende indikatore van ekosisteemverandering op te spoor en te klassifiseer. In hierdie studie is akoestiese monitering gebruik oor diverse ekologiese gradiënte om ons begrip te verbeter van spesies diversiteitspatrone, en hoe dit verander in reaksie op beide natuurlike gradiënte en in reaksie op die menslik gedomineerde landskapmosaïek.

Hierdie studie is onderneem in drie geografiese liggings: tropiese reënwood in Brunei, Borneo, die landskapmosaïek van plantasiebosbou in KwaZulu-Natal, Suid-Afrika, en die plantryke, bergfynbos-streek van die Kaap Floristiese Streek, ook in Suid-Afrika. Elke streek het 'n diverse en besondere landskap verskaf om die waarde van akoestiese opnames te toets vir die bepaling van plaaslike diversiteitspatrone in natuurlike gradiënte, asook om die waarde van die tegniek te bepaal vir die beoordeling van die impak van menslike invloed oor landskappe.

In tropiese reënwoorde, is 'n hele akoestiese gilde ondersoek om te bepaal hoe akoestiese spesies hul akoestiese kommunikasiekanale spektraal, ruimtelik en temporeel verdeel om akoestiese inmenging te vermy. Die algehele groep het aansienlike spektrale verdeling getoon. Dagaktiewe spesies het lae temporele nisoorvleueling getoon, terwyl nagtelike spesie nie temporele verdeling benut het nie. Gebrek aan nagtelike temporele verdeling dui daarop dat ander meganismes van akoestiese vermyding voldoende is om akoestiese oorvleueling te vermy, of dat daar onvoldoende seine is om nagtelike akoestiese omgewings te verdeel. Akoestiese spesies het ook ruimtelike verdeling benut, met verskillende akoestiese spesiesversamelings op vertikale hoogtes en met hoogte bo seevlak. Die gebruik van 'n verskeidenheid van strategieë maak dit moontlik vir spesies om te kommunikeer met min of geen inmenging van ander spesies in 'n seinryke omgewing.

Akoestiese profielsamestelling is ook onderneem in KwaZulu-Natal, Suid-Afrika, oor 'n plantasiebosbou landskapmosaïek met diverse ekologiese gradiënte wat beide uitheemse en inheemse plantegroei, sowel as groot, natuurlike, beskermde gebiede ingesluit het. Gebiede wat bestaan het uit uitheemse timmerhoutbome of nie-endemiese gras, was heeltemal sonder akoestiese seine. Bestuursgebiede wat gesny en swaar beweë was, het nie doeltreffend die natuurlike komplement van nagtelike akoestiese spesies gehandhaaf nie. In natuurlike

plantegroei fragmente binne plantasies, het akoestiese spesiesrykheid toegeneem met plantverskeidenheid en fragmentgrootte. Fragmente van inheemse plantegroei binne die plantasie-matriks het effektief die kontras van getransformeerde landskappe met omliggende natuurlike gebiede verminder, en inheemse woudefragmente het hoogs kenmerkende akoestiese spesiesversamelings gehad.

Binne die plantryke bergfynbosstreek van die Kaap Floristiese Streek, was akoestiese profielsamestelling gedoen oor gradiënte van hoogte bo seevlak, seisoen en plantegroei. Oor hierdie gradiënte, is langhoringsprinkaan akoestiese seine geïdentifiseer en gekenmerk vir die eerste keer. Dit het gelei tot die ontdekking van twee nuwe langhoringsprinkaan spesies en 'n nuwe klankvervaardiging struktuur in 'n Carabid kewer, 'n spesie wat nie voorheen bekend was om klank te produseer nie. Akoestiese diversiteit oor gradiënte van seisoen en hoogte bo seevlak het toegeneem met toenemende temperature. Variasie in klimaatstoestand oor die gradiënt van hoogte bo seevlak het variasie in seisoenale fenologie veroorsaak. Langhoringsprinkane het ook hoë frekwensie akoestiese seine benut, wat waarskynlik 'n aanpassing is om agtergrondgeraas van die wind, wat so algemeen is in hierdie gebied, te bowe te kom. Verder, ten spyte van die vervaardiging van opvallende seine vir maataantrekking en paarvorming, het langhoringsprinkane nie deel gevorm van die bakoerjakkals se dieet nie. Hierdie is 'n insekvetende, nagtelike roofdier wat gebruik maak van sy kenmerkende groot ore om klanke op te spoor wat gemaak word deur invertebraatprooi.

Hierdie studie toon die waarde van die gebruik van akoestiese seine van langhoringsprinkane om akoestiese diversiteitspatrone te identifiseer oor ekologiese gradiënte en in reaksie op menslike impakte op die landskap.

Acknowledgements

I would like to thank my supervisor Michael Samways for providing the opportunity to take on this stimulating project and for his constant source of enthusiasm for science, acoustics, katydids and life in general. His outlook and perspective have been a wonderful influence.

This project would not have been possible without the generous financial support of the Mauerberger Foundation and the National Research Foundation. I am also indebted to various people who provided assistance over the course of this project including Klaus Riede for sharing his knowledge on acoustics and providing incredibly enjoyable field excursions abroad. Piotr Naskrecki for sharing his extensive knowledge on katydids both in the lab and in the field. Anne Ropiquet for providing tremendous assistance with genetic analysis. Francois Roets for assistance in the field and with beetle identifications. Kenneth Oberlander for assistance with plant identifications. James Harvey for assistance identifying frog calls. Andrew Rodgers for assistance identifying bird calls. Johan Hoekstra for permission to use his artwork of the bat-eared fox. René Gaigher for the Afrikaans translation of the abstract. Colleen Louw, Adam Johnson and Marlene Isaacks who provided significant logistical and administrative support throughout the project. The Universiti Brunei Darussalam, including D.J. Marshall, A.S. Kamariah, H.M. Masnah, A.K. Rafhiah, B.A.W. Rodzay and M.A.B. Salleh for making the stay in Brunei possible. Mondi South Africa, including C. Burchmore, P. Gardiner, J. Pryke and L. Shaw for providing maps and accommodation at field sites. Ezemvelo KZN Wildlife; iSimangaliso Wetland Authority and Mondi-Shanduka and SiyaQhubeka Plantations for permitting solo nocturnal sampling on their holdings. SENTEC for providing access to the Jonaskop service road.

I would also like to thank all my friends and colleagues for making this such an amazing experience. It has been an incredible journey.

Finally, a very special thanks to my family for all their love and constant support.

Table of Contents

Declaration.....	1
Abstract.....	2
Opsomming.....	5
Acknowledgements.....	8
1. General introduction	19
References.....	43
2. Niche partitioning of acoustic communities in a Bornean rain forest	65
Abstract.....	65
Introduction.....	67
Methods.....	70
Results.....	76
Discussion.....	81
References.....	88
3. Elevational zonation of acoustic communities in Bornean rain forest	111
Abstract.....	111
Introduction.....	112
Methods.....	113
Results.....	119
Discussion.....	120
References.....	124
4. Implementing acoustic profiling of the landscape mosaic	136
Abstract.....	136
Introduction.....	138
Methods.....	141
Results.....	146
Discussion.....	149
References.....	158
5. Acoustic patterns of katydids (Orthoptera: Tettigoniidae) across ecological gradients on a significant mountain	179
Abstract.....	179

Introduction.....	181
Methods.....	184
Results.....	188
Discussion.....	191
References.....	199
6. Acoustic prey and a listening predator: interaction between calling katydids and the bat-eared fox	226
Abstract.....	226
Introduction.....	227
Methods.....	230
Results.....	232
Discussion.....	234
References.....	238
7. Sound characterization and structure of the stridulatory organ in <i>Gonogenia tabida</i> (Coleoptera: Carabidae)	248
Abstract.....	248
Introduction.....	249
Methods.....	252
Results.....	254
Discussion.....	256
References.....	260
8. General discussion	266
References.....	270

List of Figures

Figure 1.1. Viewing the landscape from an acoustic perspective provides insight into intricate interactions between abiotic and abiotic factors. Anthropogenic influences often mask or inhibit communication channels. Acoustic interference from abiotic or biotic sources can cause acoustic communicating taxa to shift signals spectrally, spatially or temporally to avoid acoustic interference 62

Figure 1.2. Bioacoustic monitoring provides rapid, non-invasive data to assess and monitor the recovery or degradation of biodiversity, providing critical feed back for conservation strategies 63

Figure 1.3. Within acoustic signals elements are defined as pulses (P), chirps (C), trills (T). Intervals between these elements are defined as pulse intervals (Pi), chirp intervals (Ci) and trill intervals (Ti). Pulses are the smallest discrete amplitude modulations within signals, grouped together as chirps or generated continuously as trills. Chirps, comprised of multiple pulses can occur singularly or within groups known as also known as trills. 64

Figure 2.1. Total acoustic species signaling across all vertical heights per hour for 24 hours. Acoustic species are partitioned into probable taxa. Distinct diurnal (06:00-18:00 hrs) and nocturnal (19:00-05:00) acoustic communities were present. Solid line indicates the number of new species which start to signal within each hour. Peaks of new species occur at dawn (06:00 hrs) and dusk (19:00 hrs). Diurnal species have relatively low total number of acoustic species signaling per hour, but a relatively high number of new species which start to signal each hour, indicating high species turn over and low temporal overlap. Nocturnal species had higher total number of species signaling per hour, with very low number of new species signaling each hour, indicating high temporal overlap of species 105

Figure 2.2. Spectral partitioning of center frequency (kHz) nocturnal (left) and diurnal (right) acoustic species utilize. Acoustic taxa are represented by the following symbols: katydids (o) had; cricket (■); cicada (*); frog (+); bird (Δ). Katydid signals were above 10 kHz; crickets 2.4-11.4 kHz; cicada 2.22-12.48 kHz; and frogs and birds below 4 kHz. Nocturnal species show usage of higher frequencies. Overall, acoustic species displayed low spectral niche overlap (0.157) (Table 2.3) 106

Figure 2.3. Spectrograms (A & C) display unfiltered, species-specific signals in frequency (kHz) versus time (s) with darker colours representing higher decibels (dB). Frequency spectrums (B & D) were produced using Hann windows with hop size of 1000. Spectrogram A and its associated frequency spectrum B, show a representative nocturnal soundscape, with a large number of acoustic species signaling across the frequency spectrum. The frequency spectrum shows greater utilization of upper frequency ranges. Spectrogram B and its associated

frequency spectrum display a representative diurnal soundscape, in this case with signal from cicada species #135. Diurnal soundscapes have less species calling per hour and utilize less upper frequency ranges than nocturnal soundscapes 107

Figure 2.4. Calling heights within the forest structure (ground 0 m; mid 30 m; top 50 m) were equally utilized by nocturnal and diurnal species. The mean number of nocturnal species signaling concurrently at each height was greater than the mean number of diurnal species ($w = 94.7, p = 0.00$)..... 108

Figure 2.5. Venn diagrams and Jaccard indices for A) total acoustic species composition B) katydid and C) cicada species composition across vertical calling heights at (ground 0 m; mid 30 m; top 50 m). While some acoustic species had overlapping calling height preference, distinct acoustic assemblages occurred at each height within the forest structure for all taxa with the exception of cicadas. Cicadas showed no vertical stratification of calling heights. 109

Figure 2.6. Diagram represents spatial and temporal niche partition in nocturnal katydid and diurnal cicada species. Both species utilize spectral partitioning (Table 2.3). For purposes of clarity, diagram only includes 12 selected species of each. The pattern that emerges clearly shows that katydids do not utilize temporal partitioning but rely on spatial and spectral acoustic niche partitioning, whereas cicadas rely on temporal and spectral but not spatial partitioning to communicate effectively 110

Figure 3.1. Location of Kuala Belalong Field Studies Centre (KBFSC), and Bukit Belalong (913 m asl), in the Temburong district of Brunei Darussalam in northern Borneo. Locations of acoustic sampling plots at 200, 500 and 850 m asl are shown, corresponding to prior research on elevational zonation of vegetation 132

Figure 3.2. Across all elevations, acoustic taxa displayed differences in center frequencies ($w = 100.22, p = 0.00$). Katydids generally had broad band signals covering a wide spectral range above 10 kHz; cricket signals were narrow band signals between 2.4-10.4 kHz; cicada signals ranged from 3.8-5.4 kHz, while frogs and birds were generally <4 kHz 133

Figure 3.3. Venn diagrams and Jaccard indices for acoustic species composition across elevations (200, 500 and 850 m asl). Distinct elevational zonation of unique species assemblages occurred with little species overlap..... 134

Figure 3.4. Spectrograms display unfiltered, species-specific signals in frequency (kHz) versus time (s) with darker colours representing higher decibels (dB). Spectrograms at 200, 500 and 850 m asl display representative nocturnal soundscapes at each elevation with a large number of unique acoustic species signaling across the frequency spectrum 135

Figure 4.1. Scale of heterogeneity was determined visually. Sites were ranked on a scale of 1-10. A site with a score of 1 was a uniform biotope of one structural vegetation type, a site with a score of 2 contained two structural vegetation types and so on until culminating in a score of 10, indicating a very diverse biotope 173

Figure 4.2. Spectrogram of a large natural protected grassland area displaying frequency (kHz) versus time (s) with darker colours representing higher decibels (dB). Various species signals have been selected within this spectrogram (boxes 1-7) showing the variation in frequency and pulse rates species utilize to avoid acoustic interference. Classification of these acoustic parameters allows for the identification of acoustic species (Table 4.1). Box 7 and 6 display high frequency, broadband, signals used by katydids (*Ruspolia* sp. 2; *Eurycorypha proserpinae*) compared to low frequency, narrow band signals used by crickets in boxes 2-5 (*Gryllidae* sp. 1; *Gryllidae* sp. 13; *Gryllidae* sp. 12; *Gryllidae* sp. 22). Box 1 displays a low frequency signal with complex amplitude modulations characteristic of the fiery-necked nightjar 174

Figure 4.3. Distribution of acoustic species based on pulse rate and center frequency (kHz). Katydid acoustic signals (♦) occupied highest frequency ranges, followed by crickets (○), with bird (■) frog (*) species occupying the lowest frequency ranges..... 175

Figure 4.4. Difference in mean species richness between site categories ($w = 179.50$, $p = 0.000$), with Shannon-Wiener Index (H') diversity scores above. Rs= Reserve sites; Wt= Wetland sites; Gr= Grassland sites; IF= Indigenous forest sites; Gz= Grazed sites; M= Managed sites; Euc= *Eucalyptus* stands 176

Figure 4.5. Difference in mean species richness between patch size categories ($w = 74.39$, $p = 0.00$), with Shannon-Wiener Index (H') diversity scores above. Size categories were 1= < 1 ha; 2= 1–3 ha; 3= 3–10 ha; 4= 10–150 ha; 5= > 150 ha..... 177

Figure 4.6. Relationship between maximum entropy (μ) and the number of acoustic species calling across sites ($w = 79.25$, $p = 0.00$) 178

Figure 5.1. Mean temperature and standard error (°C), humidity (%), and wind speed (m/s) across seasons are on the left and across elevations on the right for the study site 217

Figure 5.2. Acoustic signals of *Ceresia pulchripes*, *Ceresia rooi*, *Ceresia* sp., *Alfredectes semiaeneus*, *Aprosphyllus olszanowskii* and *Hetrodes pupus*. Spectrogram (above) displays frequency (kHz) versus time (s) with darker colours representing higher decibel levels (dB). Waveform associated with spectrogram (middle) displays signal structure of amplitude

modulations over time (8 seconds). Marked section in middle waveform is expanded in time (0.2 seconds) to display distinct pulses within each chirp..... 218

Figure 5.3. Acoustic signals of *Clonia melanoptera*, *C. minuta*, *C. vansoni*, *Conocephalus maculatus*, *C. peringueyi* and *Plangia compressa*. Spectrogram (above) displays frequency (kHz) versus time (s) with darker colours representing higher decibels (dB). Waveform associated with spectrogram (middle) displays signal structure of amplitude modulations over time (8 seconds). Marked section in middle waveform is expanded in time (0.2 seconds) to display distinct pulses within each chirp 220

Figure 5.4. Acoustic signal of *Tylopsis continua*. Spectrogram (above) displays frequency (kHz) versus time (s) with darker colours representing higher decibels (dB). Waveform associated with spectrogram (middle) displays signal structure of amplitude modulations over time (8 seconds). Marked section in middle waveform is expanded in time (0.2 seconds) to display distinct pulses within each chirp 222

Figure 5.5. Acoustic diversity patterns of katydids (mean and standard error) across elevations (above) and seasons (below). Peak acoustic activity along the elevational gradient occurred between 690-1044 m asl. Below 690 m asl, transition to Karoo vegetation occurred, resulting in the lowest acoustic activity across the botanical and elevational gradient. Peak seasonal acoustic activity occurred in January-February. Higher acoustic diversity patterns was positively correlated with increasing temperatures..... 223

Figure 5.6. Species ID are listed in Table 5.1. Zero = no species recorded signaling. *Hetrodes pupus* was acoustically active within a lower temperature range than all other katydid species ($w = 102.79$, $p = 0.00$). At low mean temperature thresholds (Zero) species generally ceased signalling completely (mean and standard error: 13.75 ± 0.74 °C)..... 224

Figure 5.7. Variation in pulse rates (number of pulses per second) with temperature for *Ceresia pulchripes* (●), *C. rooi* (*), *Ceresia* sp. (○), *Alfredectes semiaeneus* (+) and *Hetrodes pupus* (Δ) 225

Figure 6.1. The bat-eared fox by Johan Hoekstra, 1996..... 243

Figure 6.2. This spectrogram (above) displays frequency versus time with darker colour representing higher decibels (dB). It represents a typical nocturnal soundscape at the study site i.e. generally fairly quiet, punctuated with acoustic signals from katydids, in this case *Ceresia pulchripes*..... 244

Figure 6.3. Cumulative diversity of prey items against the number of scats 245

Figure 6.4. Diet of the bat-eared fox based on percentage of occurrence of food items. Total diet above. Breakdown of the 68% invertebrate diet below. ‘Other’ comprises Gryllacrididae, Termitidae, Chrysomelidae and Stenopelmatidae 246

Figure 6.5. Diet of the bat-eared fox based on mass of the food items. Total diet above. Breakdown of the 64% invertebrate diet below. ‘Other’ comprises Acrididae, Gryllacrididae, Termitidae, Formicidae, Stenopelmatidae, and Chrysomelidae 247

Figure 7.1. A) *Gonogenia tabida*; B) Cross section through abdomen and elytra of *G. tabida* showing the stridulatory structure and how the *pars stridens* and *plectrum* fit together; C, E) tooth like *pars stridens* on ventral side of elytra; D, F) ridge like *plectrum* on first abdominal sternite; G, I) fine stridulatory surface of the *pars stridens*; H, I) stridulatory surface of the *plectrum*. Scale bars: A, C, D = 5 mm; B, E, F = 100 µm; G, H = 10 µm; I, J = 2 µm..... 264

Figure 7.2. Acoustic signal of *Gonogenia tabida* at different temporal resolutions. Waveforms A, B and C display amplitude of signal over time. Spectrogram (below waveform B) displays frequency of signal over time, with darker colour representing higher decibels (dB). Waveform A) displays the temporal pattern of trills over a time period of approximately 40 seconds (s). Waveform B) displays the temporal expansion of a single trill and the discrete chirps that compose it. The associated spectrogram of waveform B displays the broad frequency range of *G. tabida* signals. Waveform C) displays the temporal expansion a single chirp and the discrete pulses which compose it 265

List of Tables

Table 2.1. Nocturnal acoustic species detected across all vertical heights (T= Top 50 m; M= Mid 30 m; G= Ground 0 m), with hours in which they were detected (time), signal parameters of pulse rate (pulse r.) and center frequency (kHz). All acoustic species were assigned a probable taxa category based on signal characteristics (k= katydid; cr= cricket; ci= cicada, f= frog; b= bird).....	102
Table 2.2. Diurnal acoustic species detected across all vertical heights (T= Top 50 m; M= Mid 30 m; G= Ground 0 m), with hours in which they were detected (time), signal parameters of pulse rate (pulse r.) and center frequency (kHz). All acoustic species were assigned a probable taxa category based on signal characteristics (k= katydid; cr= cricket; ci= cicada, f= frog; b= bird).....	103
Table 2.3. The amount of niche overlap (spectral; temporal; spatial) calculated between all species pairs, nocturnal species, diurnal species and probable taxa group (katydid, cricket, cicada, frog, bird). Observed and simulated indices of the model are indicated. The calculated indices range from 0 (species share no resource) and 1 (species have identical resource use)	104
Table 3.1. Acoustic species detected across all elevations (2= 200 m; 5= 500 m; 8= 850 m asl), with their signal parameters of pulse rate (pulse r.) and center frequency (kHz). All acoustic species were assigned a probable taxa category based on signal characteristics (k= katydid; cr= cricket; ci= cicada, f= frog; b= bird). ID= unique species identification number; #= position and number of species within the table.....	131
Table 4.1. Acoustic species detected across sites. PA= Protected area; Wt= Wetland sites; Gr= Grassland sites; IF= Indigenous forest sites; Gz= Grazed sites; Rd= Road sites; M= Managed sites; RA= % relative abundance across all 210 sites; PR= pulse rate; kHz= center frequency (kHz) of signals. Frequency species were detected (%) is listed under each site category (PA, Wt, Gr, IF, Gz, Rd, & M).....	170
Table 4.2. Structural vegetation cover (%) of sites. PA= Protected area; Wt= Wetland sites; Gr= Grassland sites; IF= Indigenous forest sites; Gz= Grazed sites; Rd= Road sites; M= Managed sites; Euc= <i>Eucalyptus</i> stands	172
Table 5.1. Katydid (Orthoptera: Ensifera: Tettigoniidae) species detected across elevational, seasonal and vegetation gradients at the study site	214

Table 5.2. Characterization of katydid acoustic signals. Acoustic parameters were taken from a minimum of 20 individuals per species between 17-19 C°. Species ID are listed in Table 5.1. T= trill duration (s), ti= trill interval (s), C= chirp duration (s), ci= chirp interval (s), P= pulse duration (s), pi= pulse interval (s), p/c= number of pulses per chirp, CR= chirp rate (number of chirps per second), PR= pulse rate (number of pulses per second), Min= minimum frequency range (kHz), Max= maximum frequency range (kHz), Center= center frequency (kHz).215

Table 5.3. Acoustic diversity patterns of katydid species across elevational, seasonal and botanical gradients. Species ID are listed in Table 5.1216

Table 6.1. Katydid (Orthoptera: Ensifera: Tettigoniidae) species recorded at the study site. Center frequency (kHz) is listed for all species242

1. General introduction

Acoustic communication in Ensifera: evolutionary opportunities and constraints

The evolution of Ensifera song

Long before mankind was around to notice, disturb or appreciate orthopteroid songs, katydids and crickets (Ensifera) were already cryptically singing within diverse environments across the world (Sharov 1968; Gwynne 2001). Yet this was not always the case, as ancestral Ensifera lacked tegminal stridulation and tibial ears (Gwynne 1995; Desutter-Grandcolas 2003) and therefore relied on non-acoustic sensory signals such as chemical attractants, visual cues or substrate vibrations for mate attraction (Gwynne 1995; Brown & Gwynne 1997). Visual displays for mate attraction involving wing movement are considered to be a possible origin of tegminal stridulation (Alexander 1962; Alexander & Brown 1963). Also, wing movement to disperse pheromones (Bailey & Rentz 1990), potentially in combination with visual displays, are another possible explanation of the origin of tegminal (wing) stridulation (Greenfield 1997). These displays likely developed into acoustic signals when the tegmina evolved rudimentary file and scraper mechanisms capable of producing sound (Brown & Gwynne 1997), thus augmenting other sensory signals. However, according to Desutter-Grandcolas (2003), evolution of sound producing structures in Ensifera developed in a strict communication context numerous times independently, possibly each time in different contexts. Specialized structures to produce, amplify, modify and receive sounds then evolved (Greenfield 1997). Current olfactory, vibratory, tactile, and visual cues used among various modern Ensifera species (Bailey & Rentz 1990; Greenfield 1997) are now only a supplement to highly developed acoustic communication (Greenfield 1997).

Whether sound production or the ability to detect sound developed first, has been debated. A number of drivers certainly exist for the development of both including predator

avoidance as a major driver for evolution of sound reception, as Riede (1987) suggested, and a pre-adaptation for sound production (Otte 1977; Riede *et al.* 1990; Greenfield 1997). The fossil record shows that sound production and reception organs likely developed concurrently ± 250 million years ago in the late Permian (Sharov 1968; Sharov 1971; Gwynne 2001). Therefore, hearing did not necessarily precede song production (Otte 1977; Riede *et al.* 1990; Greenfield 1997) nor did sound production, in the form of startle signals against predators, necessarily precede hearing (Field 1993). Processes and drivers involved in the propagation of acoustic signals likely coevolved with reception, with one system driving the other (Bailey & Rentz 1990).

The overlapping mechanisms driving song diversification remain somewhat variable and have been reviewed by Otte (1992) and Greenfield (1997). The impressive diversity of acoustic signals today ranges from intricate to minimalistic, resulting from a combination of abiotic and biotic influences acting synergistically or independently to varying degrees. While the primary function of acoustic communication is pair formation, and therefore shaped by sexual selection, other factors including genetic drift, and natural selection through male competition, predation and acoustic interference are also significant in constraining and shaping development of acoustic signals (Darwin 1871; Cade 1975; Bell 1979; Sakaluk & Belwood 1984; Searcy & Anderson 1986; Belwood & Morris 1987; Bailey & Rentz 1990; Belwood 1990; Otte 1992; Robert *et al.* 1992; Stumpner & von Helverson 1992; Morris *et al.* 1994; Greenfield 1997; Korsunovskaya 2008; Korsunovskaya 2009).

The role of sexual selection in the evolution of acoustic signals has been demonstrated by female preference for males with higher energy content (Gerhardt 1994; Greenfield 2002), through more complex calls (Stumpner & von Helverson 1992), longer and louder calls (Latimer & Sippel 1987; Galliard & Shaw 1991; Greenfield & Roizen 1993; Tuckerman *et al.*

1993; Greenfield 2002), calls repeated at a higher rate (Bailey & Rentz 1990), or higher frequency calls (Latimer & Sippel 1987; Bailey & Yeoh 1988; Bailey & Rentz 1990). At a proximal level, high energy signals may be more attractive to females as they impart greater stimulation to receptor organs and evoke a higher rate of action potentials (Greenfield 2002). At an ultimate level, louder calls have increased signal range and reach more females. However females may also select high-energy calling males as these characters are either attractive (Fisherian) and/or are indicators of higher viability (good-genes) (Greenfield 2002). Although female preference across species is not limited to high energy calls, it is safe to consider Fisherian or good-genes sexual selection as a realistic driver behind diverse and sometimes exaggerated signals (Jennions & Petrie 2000). Additionally, as certain call features can also predict size of calling males (Simmons & Zuk 1992; Tuckerman *et al.* 1993) female preference for these call features represent a direct benefit in terms of potentially receiving a larger nutritive spermatophylax, resulting in larger or more numerous egg production, maximizing parental investment (Greenfield 2002). Similarly, quality of song may indicate level of parasites (Simmons & Zuk 1992; Greenfield 2002) or fitness, and therefore female preference for high-quality songs is effectively a preference for high-quality males (Greenfield 2002). This is a genetic feedback cycle, where female mate attraction leads to longer and louder high energy calls.

Male competition has resulted in the development of aggression signals and alteration of acoustic signals, notably from continuous to discontinuous calls (Bailey 1976; Bailey & McCrae 1978). Irrespective of whether males are spaced regularly in preferred habitat or guarding a natural resource, they listen to and monitor acoustic signals from nearby conspecifics (Gerhardt & Huber 2002). As sensitive reception generally does not occur during sound production (Counter 1977; Brush *et al.* 1985; Bailey & Rentz 1990; Greenfield 1990; Greenfield 2002), continuous calls can shift to discontinuous calls, so as to provide acoustic

windows to detect proximity of conspecific males (Bailey 1976; Bailey & McCrae 1978; Greenfield 1990) without altering female preference (Walker 1957). In the case of satellite males, acoustic signals are infrequent or entirely suppressed when in relatively close proximity to high quality male signallers in order to intercept females without being detected (Greenfield 1997). Alteration of male acoustic signals can also occur through interspecific competition, by adjusting their calls spectrally, spatially, temporally or through call hybridization with closely related species as a result of landscape change (Samways 1977a; Samways 1977b; Samways 1977c; Riede 1993; Riede 1997; Diwakar & Balakrishnan 2007b; Schmidt *et al.* 2012; Jain *et al.* 2013).

Natural selection, particularly through being driven by predation, normally counters and constrains the influence of sexual selection for exaggerated, high energy, male acoustic signals, at a level below that which females would most prefer (Greenfield 2002). High energy signals can include greater risk of attracting unwanted predators (Burk 1982; Zuk & Kolluru 1998) ranging from predatory katydids, parasitoid sarcophagid and tachinid flies (Cade 1975; Burk 1982; Robert *et al.* 1992; Greenfield 2002), other predatory invertebrates to a host of vertebrate predators (Walker 1964a; Bell 1979; Sakaluk & Belwood 1984; Belwood & Morris 1987; Bailey & Rentz 1990; Morris *et al.* 1994). Interestingly, the appearance of bat predators 55 million years ago also coincides with the developed ability of katydids to detect ultrasound (Rust *et al.* 1999). Different bat predation pressure has also resulted in divergent acoustic signals, with neotropical katydids utilizing more ultrasonic signals, compared to narrow low-frequency signals of paleotropical katydids, due to greater risk of bat predation in the neotropics (Heller 1995). While modern cryptic defensive strategies aid avoidance of diurnal predators, acoustic signals that are short in duration and infrequent over time also reduce detection by nocturnal predators (Belwood & Morris 1987). Temporal patterns of Ensifera can also shift to avoid peak foraging times of predators (Belwood 1990) or alternatively result in higher

cautionary behaviour instead of reduced exaggerated signals (Greenfield 2002). Such cautionary behaviour can include exhibiting negative phonotaxis away from high frequency bat eco-locations (Libersat & Hoy 1991; Schulze & Schul 2001). Counter selection for call length also comes from trade-off between metabolic costs of sound production and mating effort, dependent of food availability and quality (Gwynne 1984; Thornhill & Gwynne 1986; Simmons & Gwynne 1991; Bailey 2006). Overall, acoustic signals shaped by various evolutionary drivers to different degrees, have resulted in remarkable diversity within modern Ensifera songs.

How do katydids and crickets sing? An overview of the mechanics of acoustic communication

In modern katydids, sound production by tegminal stridulation entails a file of minute teeth (pars stridens) along the underside of the left tegmen moving over a hardened scraper (plectrum) on the upper surface of the right tegmen during the closing stroke of the wings. Tooth strikes across the plectrum cause an associated membrane (mirror) surrounded by a sclerotized U-shape frame to resonate and amplify sound (Morris & Pipher 1967; Bailey 1970; Bailey & Broughton 1970; Ewing 1989; Bailey 1991; Morris & Mason 1995; Greenfield 1997; Desutter-Grandcolas 2003). Crickets also produce sound by tegminal stridulation using a similar mechanism. However unlike katydids, both tegmen are equipped files and scrapers, allowing species to switch forewing positions. Tooth strike across the plectrum cause a similar associated membrane (harp) surrounded by a sclerotized U-shape frame to resonate and amplify sound (Greenfield 2002). While crickets generally have conspicuous, simple repetitive signals within a narrow-band frequency range between 1 and 11 kHz (Riede 1998), katydids generally have broad frequency ranges between 6 and 130 kHz (Greenfield 2002; Montealegre-Z *et al.* 2006; Rössler *et al.* 2006). However, there are also numerous katydid species that produce

narrow-band frequency signals (Riede 1996; Riede 1998; Gerhardt & Huber 2002; Deily & Schul 2006). By definition, sound is the propagation of longitudinal waves in a compressible medium (Greenfield 1997), yet Ensifera breathe remarkable species-specific diversity into it. Diversity of signal characters such as intensity (dB), frequency (kHz), amplitude modulation (comprised of pulses grouped into chirps or generated continuously as trills), in addition to direction of source, provides critical information with regards to identity, location, and fitness (Greenfield 1997).

Signal reception, critical for detection of conspecifics, is also important for detection of predators (Rössler *et al.* 2006), and results in anti-predator behaviour. Reception is accomplished through tympanal organs, thin membranes located on the forelegs. This system is effectively driven by sound waves arriving at external membrane surfaces directly and inner surfaces indirectly by tracheal tubes, triggering specialized sensory neurons connected to the central nervous system. This is effectively a pressure-difference system in which binaural intensity and time cues correspond to internal and external differences between the two sides, providing directionality and allowing Ensifera to localize signal source (Gerhardt & Huber 2002). It is also possible that wide positioning the forelegs, and therefore the tympanal organs farther apart, could increase sensitivity of pressure-difference system and localization of signal source.

Why do Ensifera sing? Function of acoustic signals

These songs take on a major perspective: this is, one that risks everything in an overwhelming drive to pass on genes. Signalling may not only attract potential conspecific mates, but also undesired predators that may be listening in the darkness. Given the inherent risks, signalling is predominantly a male feature in the majority of Ensifera species (Bailey & Rentz 1990) with

the female being a silent receiver due to higher reproductive investment. Although examples of motile and stationary signaling or duetting females do occur, often in these cases, female signalling is generally a response to male signalling, similar in frequency but not homologous, consisting of short chirps (Heller & von Helverson 1986; Robinson 1990; Hartley 1993; Greenfield 1997). The single most important function of male signalling is sexual advertising and pair formation (Gerhardt & Huber 2002). While enabling the female to identify a potential conspecific mate, male signalling may also indicate access to an environmental resource such as high quality feeding or oviposition sites (Searcy & Anderson 1986; Brown & Gwynne 1997). Ensifera acoustic communication also plays an important role in agonistic interactions. Male signalling can also influence conspecific males to adjust their calls spatially (Thiele & Bailey 1980; Shaw *et al.* 1982) and temporally for synchrony or alteration of calls to avoid acoustic interference (Fulton 1934; Samways 1976; Sismondo 1990) and in some cases, to jam signals from other males (Greenfield & Roizen 1993; Greenfield 1997). Male signalling also functions in defence of resources (Greenfield 1997), warning rival males to withdraw or face imminent attack, therefore allowing conspecifics to assess fitness and potentially avoid direct physical contests (Gerhardt & Huber 2002). However, honesty of signals could be an issue in some cases and bluffing may occur where males lower the frequency of their calls indicating to rivals the signaler is larger than he actually is (Grafen 1990; Gerhardt & Huber 2002). Additionally, in some cases, Ensifera acoustic signals also act as a startle mechanism for predator deterrence (Greenfield 1997).

Acoustic limitations and solutions

Acoustic communication in Ensifera relies on transfer of detectable, clear signals that can be accurately interpreted and localized by conspecifics. Constraints to acoustic communication

include physical limitations based on body size, intra- and interspecific acoustic interference, in addition to various environmental factors such as habitat structure and climatic conditions (Greenfield 2002). To various degrees, these factors all impose restrictions on signal propagation and reception. In order for acoustic communication to be effective, the signal cannot be degraded to a degree where the receiver can no longer interpret encoded information. In response, Ensifera have developed some effective structural and behaviour mechanisms to adapt to acoustic constraints, and in some cases, to utilize them to their advantage (Greenfield 2002).

Within their given environment, Ensifera can distinguish fine differences in received sound, differentiating between calls that differ slightly in amplitude modulation (structure), in frequency or in intensity (1-2db) (Bailey *et al.* 1990; Greenfield 1997). Despite low signal to noise ratios in some environments, females in some species are still able to recognize and locate conspecific males (Römer 1993). The tympanum not only functions as a receptor, but to some degree, can also function as a filter, selectively admitting specific frequencies, and allowing species to focus on nearby conspecific males (Greenfield 2002; Schmidt *et al.* 2011). Frequency matching between dominant frequencies in sound production and optimal frequencies in sound reception has been demonstrated (Hill & Boyan 1977; Hill & Oldfield 1981; Lin *et al.* 1993; Dobler *et al.* 1994; Schmidt *et al.* 2011), and some species are even able to adjust optimal frequencies by opening their acoustic spiracles to become more sensitive to high frequencies, while then closing spiracles to become more sensitive to low frequencies (Greenfield 1997). This provides an ability to focus on high frequency conspecifics in addition to low frequency sounds produced by potential predators (Greenfield 1997).

Body size, influenced by various selection pressures, poses a physical problem for both propagating and receiving acoustic sensory information, limiting the nature of signals

transmitted, the sensitivity they can be detected, and the degree of accuracy in which they can be localized (Greenfield 2002; Cocroft & De Luca 2006). Based on size and stiffness, the mirror or harp vibrates at a natural frequency which increases proportionately with the inverse square root of its size, resulting in a negative relationship between body size and sound frequency (Ryan & Brenowitz 1985; Bennet-Clark 1998; Gerhardt & Huber 2002). There is also a physical relationship between body size, frequency and the efficiency at which sound is generated. For smaller species, higher frequencies are more efficient to produce than lower frequencies which require larger sound producing structures (Ryan 1988). Consequently, constraining small species to communicate within higher frequencies places a lower limit but not an upper limit on frequency of sounds used to communicate (Michelsen & Nocke 1974; Bennet-Clark 1998; Gerhardt & Huber 2002). While high frequency sounds are energetically efficient, they are also more subject to attenuation and signal degradation and therefore limit communication range (Wiley & Richards 1978; Gerhardt & Huber 2002). In order to adapt to these constraints, some species produce sounds whose frequency is near the lower limit of efficiency for their body size, favouring slightly lower frequency sounds for long distance transmission (Bennet-Clark 1998; Cocroft & De Luca 2006). Other species use body parts to amplify and even direct sound (Greenfield 2002). Enlarged pronotal shields in many katydid species, concealing modified wings, are elaborate structures designed to amplify sound and allow species to call cryptically with increased signal range (Morris & Mason 1995). Crickets also amplify sound through various means including the use of burrows, baffles or raising tegmen to amplify sound (Gerhardt & Huber 2002; Greenfield 2002).

Climatic conditions also influence Ensifera communication. Ensifera are subject to the direct effects of temperature through muscle contraction speed and ensuing sound production, as well as indirectly through temperature effects on the acoustic channel (Greenfield 2002). Fluctuating ambient temperatures effect the speed of Ensifera wing stroke muscle contraction

(Toms *et al.* 1993; Greenfield 1997) leading to a positive relationship between increased pulse rates with higher temperatures (Walker 1975; Greenfield 1997; Greenfield 2002; Gerhardt & Huber 2002; Sanborn 2006). This relationship first noted by Brooks (1882), and expounded by Bessey & Bessey (1898), who derived a formula to determine temperature based on pulse rates of tree crickets, has consequences for signal structure in regard to mate selection. In katydids and crickets, it likely results in shifting female preferences for specific pulse rates at given temperatures (Walker 1957; Doherty 1985; Pires & Hoy 1992; Greenfield 1997). Another option is that certain species may simply wait for environmental windows that are most suitable for producing pulse rates preferred by females. In this case, optimal temperature windows would have to occur fairly regularly within the given environment to allow for ample reproductive opportunities. Another strategy available to larger Ensifera to deal with temperature fluctuations, is to thermoregulate so as to maintain optimal pulse rates (Heath & Josephson 1970; Josephson & Halverson 1971; Josephson 1973; Sanborn 2006). Additionally, some species can alter the rate of their call to remain in synchrony at different temperatures (Samways 1976; Sanborn 2006). Indirect influences of temperature include thermal layers in the air, which can impede or enhance the propagation of acoustic signals (Van Staaden & Römer 1997; Gerhardt & Huber 2002). For example, colder temperatures near the ground with warmer air temperatures above, can result in an acoustic channel for ground-level signals which would experience much less attenuation and travel greater distances (Wiley & Richards 1978; Van Staaden & Römer 1997; Gerhardt & Huber 2002; Sanborn 2006).

Acoustic interference along acoustic channels through biotic and abiotic factors including vegetation, rocks, topography, wind, temperature gradients, humidity, and other sounds in the environment may attenuate, deflect, mask, absorb, refract, reverberate, scatter and alter the spectral composition of sound waves as sound radiates outward from a source (Richards & Wiley 1980; Römer & Lewald 1992; Römer 1993; Gerhardt & Huber 2002;

Greenfield 2002). High frequency sounds are disproportionately attenuated in the frequency spectrum, with broader, higher frequency ranges at the source and lower frequencies with distance (Griffin 1971; Lawrence & Simmons 1982). In response, Ensifera use various mechanisms to minimize localized interference across acoustic channels. Louder signals or signals transmitted in broadband frequencies help preserve call characteristics (Greenfield 2002). Attenuation is also unlikely to affect entire frequency range in katydid broadband signals (Römer & Lewald 1992). A great majority of Ensifera species call from elevated perches to reduce or avoid attenuating influences of vegetation and surface microtopography (Paul & Walker 1979; Arak & Eiríksson 1992; Römer & Lewald 1992; Greenfield 2002). Although high frequency signals are less susceptible to wind disruption, Ensifera possibly utilize windows of favourable environmental conditions to propagate signals (Richards & Wiley 1980; Greenfield 2002).

Acoustic communication channels are well defined resource for many species which results in strong intra- and interspecific competition and resource partitioning within an acoustic guild (Riede 1993). The use of different dominant frequencies and temporal patterns in addition to separation in horizontal or vertical space are therefore also mechanisms to reduce acoustic interference (Fulton 1934; Samways 1977b; Duellman & Pyles 1983; Latimer & Broughton 1984; Greenfield 1988; Römer *et al.* 1989; Schatral 1990; Schatral & Yeoh 1990; Riede 1993; Riede 1997; Riede 1998; Sueur 2002; Diwakar & Balakrishnan 2007b; Jain & Balakrishnan 2011; Schmidt *et al.* 2012; Jain *et al.* 2013). Riede (1997) demonstrated that crickets, katydids, frogs and cicadas combined as an acoustic guild, utilized temporal partitioning within tropical forests to minimize acoustic interference with each other. In turn, Diwakar & Balakrishnan (2007b) showed that Ensifera also utilize vertical stratification to reduce acoustic interference.

In any given habitat, communication is constrained by various local factors. As a result, *Ensifera* will utilize acoustic niches, signalling within specific frequency ranges, places or times to reduce attenuation, to increase communication ranges, or to reduce predation risk (Korsunovskaya 2009; Krause *et al.* 2011; Truax & Barrett 2011). The acoustic niche concept predicts that species communication has evolved to maximize optimal signal propagation and to minimize acoustic interference (Greenfield 1994; Korsunovskaya 2009). Within this physical acoustic space, each species in the acoustic guild occupies its own acoustic niche, utilizing communication channels in a specific manner (Korsunovskaya 2009).

The evolutionary drivers and constraints of acoustic communication have resulted in a remarkable diversity of songs, occurring across a range of environments. From an ensiferan perspective, songs are a critical communication channel necessary for mate attraction. From a human perspective, *Ensifera* songs not only create ambient acoustic orchestras that are aesthetically appealing, but the signals themselves provide an acoustic window to cryptic diversity patterns across ecological gradients and over time.

Listening to the diversity of landscapes

Sound and the ability to detect sound waves are evolutionary adaptations allowing organisms to propagate and receive acoustic sensory information invisibly within their environment. Although not without inherent risks and constraints, the advantages have driven development of acoustic communication in a spectacular diversity of forms in many aquatic and terrestrial organisms. Often these acoustic signals are as diverse and flamboyant as visual displays in regards to intensity, variation and complexity. Aside from the evolutionary value and function of acoustic signals, from a humanistic perspective, there is also an intrinsic aesthetic value to hearing the landscape. Often we associate serene, silent evenings with soft tranquil chirping of

orthopteran songs. Modern day orthopterans have been evolving and diversifying acoustically and in body form for millions of years (Sharov 1968; Sharov 1971). Among extant Orthoptera, katydids (Ensifera: Tettigoniidae) are the champions of this diversity, exhibiting rich and complex varieties of cryptic appearances and songs across 7061 known species in 1222 genera and 20 subfamilies (Eades *et al.* 2014), followed by crickets (Ensifera: Gryllidae) which contain 4829 species in 614 genera and 21 subfamilies (Eades *et al.* 2014). Estimates of both katydids and crickets are a great underestimate of their actual numbers given their cryptic lifestyles. This diversity has allowed Ensifera to flourish and occupy a broad range of niches in practically every habitat throughout the globe, as omnivorous generalists or specialists. Within these habitats, they are critical in food webs, consumed by an extensive range of invertebrate or vertebrate predators, making predation an influential driver of anti-predator behaviour and cryptic, camouflaged body designs. Yet despite being visually and behaviourally cryptic, so as to continue their evolutionary success, Ensifera announce themselves acoustically, producing, propagating, receiving and reacting to acoustic sensory information. Despite their broad acoustic abilities, the literature is sparse in terms of utilization of these sounds on a landscape scale to answer ecological questions. With current technology-infused advances in bioacoustic techniques, detecting, recording and analyzing Ensifera songs are developing into powerful tools for measuring and monitoring diversity within complex communities and habitats.

Resolution of soundscapes: a factor of scale

Sound drifting intermittently across landscapes in various forms, carries a multitude of localized information. Shifting focus from a visual to an acoustic spectrum provides a unique perspective of the landscape and the intricate interactions within (Fig. 1.1). These acoustic

landscapes, defined by distinctive abiotic and biotic acoustic factors that vary spectrally, spatially and temporally have been termed soundscapes (Southworth 1969; Farina *et al.* 2011; Pijanowski *et al.* 2011a; Pijanowski *et al.* 2011b; Truax & Barrett 2011; Villanueva-Rivera *et al.* 2011). Shifts in temporal patterns within soundscapes can occur across extremely rapid scales to exceptionally slow geologic time scales, where strong evolutionary undercurrents steadily alter signals and landscapes. Spatial shifts can occur in vertical or horizontal space as well as across various spatial scales.

Ensifera are key participants of nocturnal soundscapes, enhancing ambient acoustics through their diverse range of attracting songs. Significant insights have been positively correlated with technological advancements, appreciably amplifying our understanding of Ensifera communication dynamics at the species level. As a study taxon, Ensifera have been used to address behavioural, evolutionary and neurophysiological aspects of acoustic communication (Greenfield & Roizen 1993; Greenfield 1994; Schul & Sheridan 2006; Beckers & Schul 2008; Bush *et al.* 2009). Ensifera communication signals have a diverse range of functions, affected by a range of factors, shifting species songs spectrally, spatially and temporally for their optimal propagation in the environment (Samways 1977a; Samways 1977b; Samways 1977c; Arak & Eiríksson 1992; Riede 1993; Greenfield 1994; Riede 1997; Diwakar & Balakrishnan 2007a; Diwakar & Balakrishnan 2007b; Schmidt *et al.* 2012; Jain *et al.* 2013). Knowledge of these species level patterns can have important implications for acoustic sampling. While biodiversity estimates and classification of acoustic species have already become fairly standard for bats (MacSwiney *et al.* 2008), frogs (Malkmus & Riede 1996; Villanueva-Rivera 2007), birds (Goyette *et al.* 2011; Farina *et al.* 2011), and insects (Riede 1993; Riede 1998; Gogala & Riede 1995), including Ensifera (Morris & Beier 1982; Riede 1996; Riede 1998; Diwakar & Balakrishnan 2007b; Diwakar *et al.* 2007), on a landscape level, soundscapes incorporate not only focal taxa, but numerous other species which broadcast

signals in the same acoustic space and time (Römer *et al.* 1989; Römer 1993; Diwakar & Balakrishnan 2007b).

Landscape level patterns to a great degree are based on a species level understanding of acoustic species communication. Soundscapes, comprising of a range of natural sources (insects, birds, amphibians, mammals, waterfalls, rivers, wind) and anthropogenic sources (humans, vehicles, machinery, sirens), also vary spectrally, spatially and temporally. At a macro-scale, sound is not merely interactions between signallers and receivers but can reflect the environmental status of dynamic systems. Soundscapes, based on the principles of landscape ecology, can therefore determine the relationship between natural and anthropogenic, abiotic and biotic sounds with corresponding environmental processes, encompassing landscape and climatic induced changes (Pijanowski *et al.* 2011a).

Acoustic inventorying and monitoring provides necessary ecological data on community structure and diversity patterns along environmental gradients and over time (Riede 1998; Depaetere *et al.* 2011). This type of analysis allows for habitat assessment and monitoring to determine the level of restoration or deterioration from anthropogenic or environmental landscape change (Fischer *et al.* 1997) (Fig. 1.2). In contrast to many traditional survey techniques, sound recording is a non-invasive method that allows for the detection and classification of highly cryptic, yet insightful indicators of ecological gradients and change. Ensifera are among such cryptic animals, behaviourally and visually, and that without conspicuous calls, would otherwise be difficult to detect. Yet, acoustic signals of many Orthoptera are sensitive indicators of biodiversity and for habitat quality and deterioration (Samways 1977c; Peter *et al.* 1997; Fischer *et al.* 1997; Riede 1998; Brandes *et al.* 2006). Implementation of acoustic monitoring can be used for inventorying and monitoring individual species on a micro-scale and whole soundscapes on a macro-scale to improve understanding

of ecological integrity of the landscape (Riede 1998; Dumyahn & Pijanowski 2011; Pijanowski *et al.* 2011a). Long term monitoring of entire soundscapes also become a time stamped series of acoustic fossils enabling insight into long term changes in acoustic diversity through landscape alteration or climate change (Dumyahn & Pijanowski 2011; Pijanowski *et al.* 2011a). Evidence also demonstrates that bioacoustics can be used as an early warning system of perturbations, even when not directly affecting individual fitness (Lailo 2010). In spite of these advantages, the potential of acoustic surveys is still underexploited.

Anthropogenic impact on acoustic guilds

The study of landscape structure, function and underlying ecological processes have traditionally relied on visual aspects, ignoring auditory information. However, landscapes characterized by their soundscapes give a considerably different view on human and environmental changes. Current anthropogenic influences on the natural world are virtually ubiquitous, having profound effects on soundscapes and major shaping influences on acoustic communication (Laiolo 2010; Shieh *et al.* 2011). Development has resulted in habitat fragmentation (Saunders *et al.* 1991; Andr en 1994; Lane *et al.* 2011), and alteration, resulting in reduction of acoustic diversity within populations (Laiolo & Tella 2006). As gene flow is affected by connectivity between patches (Arnaud 2003; Laiolo & Tella 2006) so are acoustic signals. Edge effects also affect soundscapes, altering species composition and acoustic guilds (Ries *et al.* 2004; Pijanowski *et al.* 2011a). Climate change compounds these deleterious effects and further alters distributions of populations (Parmesan 2006; Lane *et al.* 2011).

Additionally, pollution in the form of chemical, light and sound stemming from anthropogenic influences have serious consequences to acoustic guilds. Various pollutants, transported atmospherically can resulting in negative effects on wildlife (Ross & Grant 2008),

including potential developmental abnormalities in Ensifera, resulting in signal alteration and failure to attract conspecific mates. Light pollution also has major implications for taxa that have evolved specific diel patterns within their acoustic guilds to propagate their signals. Darkness is an ecological resource for many species which has evolved with natural light and dark cycles (Gerrish *et al.* 2009). As nocturnal behaviour varies as a function of light intensity (Gerrish *et al.* 2009) and Ensifera activity is reduced during bright periods of full moon (Lang *et al.* 2006), it is likely that their behaviour is altered due to light pollution from urban contexts. Diurnal cicadas also call well into evening hours around light sources, potentially overlapping and masking local nocturnal Ensifera signals causing potential spatial shifts. Sound pollution has further direct consequences for Ensifera and acoustic guilds. Increasing anthropogenic noise in environments (Dumyahn & Pijanowski 2011; Pijanowski *et al.* 2011b; Truax & Barrett 2011) significantly alters species behaviour and distributions (Barber *et al.* 2011), resulting in reduced foraging efficiency (Siemers & Schaub 2010), disruption of mate attraction (Wollerman 1999; Barber *et al.* 2011), limiting signal reception and negatively impacting reproductive success in some species (Halfwerk *et al.* 2011), while increasing it in other species (Francis *et al.* 2009). Highlighting changes in acoustic guild structures are likely to adversely affect some species while others are able to exploit changes. Anthropogenic noise has resulted in species shifting acoustic communication channels spatially, temporally or spectrally to higher frequencies to avoid acoustic interference in proximity to roads and urban development (Slabbekoorn & Peet 2003; Patricelli & Blickley 2006; Barber *et al.* 2011; Dumyahn & Pijanowski 2011; Pijanowski *et al.* 2011a; Shieh *et al.* 2011).

Soundscape conservation

Natural soundscapes are becoming steadily eroded islands in a sea of encroaching anthropogenic change. Conserving soundscapes not only preserves biodiversity and function of ecological systems (Farina 2009; Dumyahn & Pijanowski 2011), but from a humanistic perspective, enables preservation of aesthetically pleasing acoustic environments, or the serenity of silence. Currently, the U.S. National Park Service identifies natural soundscapes as a critical resource to be monitored and protected (National Park Service 2006; Hults & Burson 2006; Miller 2008; Dumyahn & Pijanowski 2011). Management policies have been established to monitor soundscapes and take action to prevent or minimize all noise through frequency, magnitude or duration which adversely affects the natural soundscape. Katydid and their high frequency songs have been directly identified within this conservation strategy (National Park Service 2006). Keeping the acoustic perspective in mind when developing conservation or monitoring strategies is therefore an invaluable step forward towards protecting soundscapes and conserving biodiversity within.

Origins of bioacoustics

Soft serene insect songs have always surrounded human societies, subtly stimulating imagination and sparking enlightenment in our understanding of animal communication. Bioacoustics today has developed into a broad field studying all aspects sound production, propagation and reception in aquatic or terrestrial organisms, yet it began with a simple appreciation of listening to the landscape.

Recorded origins of the study of sound began with Pythagoras in the 6th century, followed by many others who initiated the science of sound waves. Parallel to the physical

aspects of sound, the recorded study of orthopteran songs arguably originated, somewhat appropriately, in music. Musical pieces which mimic cricket communication, such as *El Grillo* by Josquin des Prés in 1504, were a catalyst for using musical notation to record and describe species-specific songs within the literature, originating with Yersin (1854), followed soon after by Scudder (1868). Verbal descriptions to describe katydid and cricket songs using onomatopoeia, a method still used, broadened conceptualization and identification of species-specific calls (Scudder 1892; Walker 1905; Allard 1910; Fulton 1932; Morris & Walker 1976). Walker (1964b) emphasized the importance of species identification through sound, arguing there were a large number of cryptic species, difficult to differentiate through morphology but detectable through differences in song, establishing a strong link between Ensifera and their specific songs for mate attraction (Fulton 1932; Fulton 1934; Bailey & Robinson 1971; Morris & Walker 1976; Heller 2006; Diwakar *et al.* 2007).

Advancements in the field of bioacoustics are directly related to technological developments which provided insight into this invisible communication spectrum. This stepwise progression is illustrated by the introduction and adaptation of the telephone, resulting in the first unequivocal demonstration that female crickets orient and respond to male acoustic signals without additional sensory information (Regen 1913). Ultrasonic frequencies, were first detected and recorded for katydids by Pielemeier (1946) in his paper “Supersonic Insects”. The detection of ultrasonic frequencies ultimately unlocked a new realm in bioacoustics research, vastly improving our understanding of katydid communication (Pierce 1948). Adaptation of concurrent technological research and development led to further advances, most notably the quantification of Ensifera songs which had a major change on the field of bioacoustics.

This avalanche of advancement was the result of a butterfly effect of independent theories, triggering rapid flows of development through chemistry, physics and engineering

across the globe. Within this avalanche, there were some key elements which would have major impacts on the field of bioacoustics. One development that would continually gain momentum was the invention of Thomas Edison's phonograph in 1877, resulting in the first recording and reproduction of wildlife recordings. Technological development to record and reproduce sound waves radiated outward from this initial source, ultimately cumulating in the development of digital technology.

Concurrent to advancements in recording technology, was the development of signal analysis to graphically represent sound and measure structural details. Spectrum analysis usually consists of waveforms displaying signal structure over time (amplitude versus time), power spectra or bandwidth revealing major frequency bands (amplitude versus frequency) and spectrograms representing time on the horizontal axis, frequency on the vertical axis and relative intensity as colour scale value. Signals are then analyzed and described using an inventory of its physical properties. However, to date there has been no universal terminology for these acoustic elements in the literature. Terms such as pulse, impulse, syllable, note, echeme, chirp, element, and call have all been used to label the same acoustic unit (Pumphrey 1940; Thompson *et al.* 1994; Gerhardt & Huber 2002). Due to sheer diversity of structural signal units and terminology, explanation within the text or spectrograms labelled with the terms chosen should be considered to avoid confusion of differing terminology (Gerhardt & Huber 2002). Here, these elements are defined as pulses, chirps, trills and intervals. Pulses are the smallest discrete amplitude modulations within signals, grouped together as chirps or generated continuously as trills. Chirps, comprised of multiple pulses can occur singularly or within groups known as also known as trills. The gaps between pulses, chirps and trills are referred to as intervals (Fig 1.3).

Importantly, these species-specific acoustic parameters such frequency and amplitude modulation allow the definition of recognizable taxonomic units (Riede 1998). Classification of recognizable taxonomic units overcome taxonomic impediments due to declining expert knowledge and lack of adequate species descriptions. Consequently, songs are an excellent means for measuring Ensifera diversity (Riede 1993; Riede 1998; Nischk & Riede 2001; Diwakar *et al.* 2007). Bioacoustic signal recognition and identification range from trained human listeners, manual analysis of spectrograms to computer based recognition and classification software. Each of these methods has advantages and limitations, yet all provide accurate detection and identification of acoustic species (Riede 1998; Diwakar *et al.* 2007).

With the advancement of technology, so too has our understanding of Ensifera behaviour, biology, ecology, physiology, evolution, systematics and importantly, bioacoustics. Acoustic recordings of Ensifera songs, along with other members of acoustic guilds are a non-invasive tool to remotely assess and monitor species and landscapes. Digital sound archives, coupled with acoustic parameters and biological information, create a multimedia database that researchers can draw on to identify acoustic species, enhancing research into Ensifera communication at a species or landscape level (Eades *et al.* 2013; Riede *et al.* 2006; DORSA 2013).

Thesis objectives and outline

This research project was initiated to investigate acoustic diversity patterns of *Ensifera* and other acoustic species across diverse ecological gradients and the associated ecological influences which drive them. Gradients chosen ranged from tropical rain forests in Brunei, Borneo, to the landscape mosaic of plantation forestry in KwaZulu-Natal, South Africa and the botanically rich, mountain fynbos region of the Western Cape, South Africa. Each region provided a diverse and unique landscape to implement acoustic surveys to determine underlying diversity patterns and the different ecological processes that influence acoustic communication. The aim of utilizing the acoustic method was therefore to contribute to fundamental knowledge on the technique and to highlight its application in answering diverse ecological questions at both the species and landscape level. In the following section, I briefly describe the objectives of each chapter in context of the thesis theme.

Chapter 2: Niche partitioning of acoustic communities in a Bornean rain forest.

Tropical rain forests contain a rich ensemble of acoustically communicating species, creating complex acoustic environments. This research was therefore conducted within the Ulu Temburong National Park in Brunei, the most protected and pristine forest in Borneo. In this chapter, I investigate how an entire acoustic community of katydids, crickets, frogs, cicada and birds partition their acoustic communication channels spectrally, temporally, and spatially to maintain conspecific communication, yet reduce acoustic interference. How multiple acoustic taxa partition acoustic communication channels in signal rich environments has direct implications for monitoring acoustic species to ensure comparable coverage of focal taxa or entire acoustic guilds.

Chapter 3: Elevational zonation of acoustic communities in Bornean rain forest.

Using nocturnal bioacoustic signals, elevational zonation of acoustic species was assessed

within a pristine tropical rain forest in Brunei, Borneo. Here acoustic surveys provided a rapid method to detect otherwise cryptic creatures in an architecturally complex environment and determined their changing acoustic diversity patterns over an elevational gradient. This chapter highlights the value of the acoustic technique in determining cryptic species diversity patterns over ecological gradients and the potential ecological influences driving this change.

Chapter 4: Implementing acoustic profiling of the landscape mosaic. The research for this chapter was conducted in KwaZulu-Natal, South Africa. Acoustic profiling was implemented across a plantation forestry landscape mosaic with diverse ecological gradients, containing both alien and indigenous vegetation, as well as bordering large natural protected areas. Biodiversity assessment of this landscape therefore offered an opportunity to determine the ecological influences on acoustic diversity patterns across a landscape in need of identifying conservation priorities to ensure sustainable management. Utilizing acoustic signals across landscapes provided an extremely effective method to investigate diversity patterns across the landscape mosaic.

Chapter 5: Acoustic patterns of katydids (Orthoptera: Tettigoniidae) across ecological gradients on a significant mountain. Within the Cape Floristic Region, South Africa, how acoustic diversity patterns are influenced by gradients in elevation, season and vegetation types has direct implications for acoustic monitoring. Consequently, within this chapter, katydid acoustic signals were identified on a botanically rich mountain previously selected as an important gradient to monitor the effects of climate change. Detection of acoustic signals resulted in the discovery of two new katydid species, highlighting the effectiveness of the acoustic technique in detecting cryptic species.

Chapter 6: Acoustic prey and a listening predator: interaction between calling katydids and the bat-eared fox. While conducting acoustic research in the Cape Floristic

Region (Chapter 5), it became apparent there was an overlapping population of nocturnal, acoustically communicating katydids with an insectivorous, nocturnal predator that uses sound to detect invertebrate prey. Despite being visually and behaviourally cryptic, katydids rely on acoustic signals for mate attraction, producing, propagating, receiving and reacting to acoustic sensory information. Therefore within this chapter, I explore the interaction and potential level of predation between this listening, insectivorous predator with acoustically active katydids. This chapter highlights the effective strategies that katydids employ to avoid predators, emphasizing their detectability through acoustic surveys and the difficulties with traditional capture techniques to assess their diversity.

Chapter 7. Sound characterization and structure of the stridulatory organ in *Gonogenia tabida* (Coleoptera: Carabidae). Research for this chapter was conducted within the Cape Floristic Region, South Africa, and highlights the effectiveness of the acoustic technique in detecting novel acoustic signals. While identifying katydid acoustic signatures across ecological gradients, I encountered an acoustic signal emitted by a carabid beetle not known to produce sound. Within this chapter, this acoustic signal and the sound producing structure are characterized. Detection and characterization of novel acoustic signals across landscapes, enables their identification in future surveys, increasing the effectiveness of acoustic surveys.

In the final chapter (Chapter 8: General discussion), I discuss the most important overall findings in the context of the thesis themes.

References

- Alexander, R. D. 1962. Evolutionary change in cricket acoustical communication. *Evolution* 16:443–467.
- Alexander, R. D., Brown, W. D. 1963. Mating behavior and the origin of insect wings. *Occasional Papers of the Museum of Zoology, University of Michigan* 628:1–9.
- Allard, H. A. 1910. Musical crickets and locusts in north Georgia. *Proceedings of the Entomological Society of Washington* 12:32–43.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with suitable proportions of suitable habitat: A review. *Oikos* 71:355–366.
- Arak, A. & Eiríksson, T. 1992. Choice of singing sites by male bush crickets (*Tettigonia viridissima*) in relation to signal propagation. *Behavioural Ecology and Sociobiology* 30:365–372.
- Arnaud, G. W. 2003. Metapopulation genetic structure and migration pathways in the land snail *Helix aspersa*: influence of landscape heterogeneity. *Landscape Ecology* 18:333–346.
- Bailey, W. & Robinson, D. 1971. Song as a possible isolating mechanism in the genus *Homorocoryphus* (Tettigonioidea, Orthoptera). *Animal Behaviour* 19:390–397.
- Bailey, W. J. 1970. The mechanics of stridulation in bush crickets (Tettigonioidea, Orthoptera). I. The tegminal generator. *Journal of Experimental Biology* 52:495–505.
- Bailey, W. J. 1976. Species isolation and song types of the genus *Ruspolia schulthes* (Orthoptera: Tettigonioidea) in Uganda. *Journal of Natural History* 10:511–528.
- Bailey, W. J. 1991. *Acoustic behaviour of insects. An evolutionary perspective*. Chapman & Hall, London.
- Bailey, W. J. 2006. Insect Songs – The evolution of signal complexity. In: Drosopoulos, S. & Claridge, M. F (eds.). *Insect sounds and communication. Physiology, behaviour, ecology and evolution*. Taylor and Francis Group, Florida.

- Bailey, W. J. & Broughton, W. B. 1970. The mechanics of stridulation in bush crickets (Tettigonioidae, Orthoptera). II. Conditions for resonance in the tegminal generator. *Journal of Experimental Biology* 52:507–517.
- Bailey, W. J., Cunningham, R. J. & Lebel, L. 1990. Song power, spectral distribution, and phonotaxis in the bush cricket *Requena verticalis* (Orthoptera, Tettigoniidae) active choice or passive attraction. *Animal Behaviour* 40:33–42.
- Bailey, W. J. & McCrae, A. W. R. 1978. The general biology and phenology of swarming in the East African tettigoniid *Ruspolia differens* (Serville) (Orthoptera). *Journal of Natural History* 12:259–288.
- Bailey, W. J. & Rentz, D. C. F. 1990. The Tettigoniidae – their diversity and importance in biological research. In: Bailey, W. J. & Rentz, D. C. F. (eds.). *The Tettigoniidae: biology, systematics and evolution*. Crawford House Press, Australia.
- Bailey, W. J. & Yeoh, P. B. 1988. Female phonotaxis and frequency discrimination in the bush cricket *Requena verticalis* (Tettigoniidae: Litroscelidinae). *Physiological Entomology* 13:363–372.
- Barber, J. R., Burdett, C. L., Reed, S. E., Warner, K. A., Formichella, C., Crooks, K. R., Theobald, D. M. & Fristrup, K. M. 2011. Anthropogenic noise exposure in protected natural areas: estimating the scale of ecological consequences. *Landscape Ecology* 26:1281–1295.
- Beckers, O. M. & Schul, J. 2008. Developmental plasticity of mating calls enables acoustic communication in diverse environments. *Proceedings of the Royal Society B: Biological Sciences* 275:1243–1248.
- Bell, P. D. 1979. Acoustic attraction of herons by crickets. *Journal of New York Entomological Society* 87:126–127.

- Belwood, J. J. 1990. Anti-predator defences and ecology of neotropical forest katydids, especially the Pseudophyllinae. In: Bailey, W. J. & Rentz, D. C. F. (eds.). *The Tettigoniidae: biology, systematics and evolution*. Crawford House Press, Australia.
- Belwood, J. J. & Morris, G. K. 1987. Bat predation and its influence on calling behavior in neotropical katydids. *Science* 238:64–7.
- Bennet-Clark, H. C. 1998. Size and scale effects as constraints in insect sound communication. *Philosophical Transactions of the Royal Society B: Biological Sciences* 353:407–419.
- Bessey, C. A. & Bessey, E. A. 1898. Further notes on thermometer crickets. *The American Naturalist* 32:263–264.
- Brandes, T. S., Naskrecki, P. & Figueroa, H. K. 2006. Using image processing to detect and classify narrow-band cricket and frog calls. *Journal of the Acoustical Society of America* 120:2950–2957.
- Brooks, M. W. 1882. Influence of temperature on the chirp rate of the cricket. *Popular Science Monthly* 20:268.
- Brown, W. D., Gwynne, D. T. 1997. Evolution of mating in crickets, katydids, and wetas (Ensifera). In: Gangwere, S. K., Muralirangan, M. C. & Muralirangan, M. (eds.). *The bionomics of grasshoppers, katydids and their kin*. CAB International, Oxford.
- Brush, J. S., Gian, V. G. & Greenfield, M. D. 1985. Phonotaxis and aggression in the coneheaded katydid *Neoconocephalus affinis*. *Physiological Entomology* 10:23–32.
- Burk, T. E. 1982. Evolutionary significance of predation on sexually signalling males. *The Florida Entomologist* 65:90–104.
- Bush, S. L., Beckers, O. M. & Schul, J. 2009. A complex mechanism of call recognition in the katydid *Neoconocephalus affinis* (Orthoptera: Tettigoniidae). *The Journal of Experimental Biology* 212:648–55.

- Cade, W. H. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* 190:1312–1313.
- Cocroft, R. B. & De Luca, P. 2006. Size-frequency relationships in insect vibratory signals. In: Drosopoulos, S. & Claridge, M. F. (eds.). *Insect sounds and communication. Physiology, behaviour, ecology and evolution*. Taylor and Francis Group, Florida.
- Counter, S. A. 1977. Bioacoustics and neurobiology of communication in the tettigoniid *Neoconocephalus* (Orthoptera). *Journal of Insect Physiology* 23:817–824.
- Darwin, C. 1871. *The descent of man, and sexual selection in relation to sex*. Murray, London.
- Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S. & Sueur J. 2011. Monitoring animal diversity using acoustic indices: Implementation in a temperate woodland. *Ecological Indicators* 13:46–54.
- Desutter-Grandcolas, L. 2003. Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta* 32:525–561.
- Deily, J. A. & Schul, J. 2006. Spectral selectivity during phonotaxis: a comparative study in *Neoconocephalus* (Orthopter: Tettigoniidea). *The Journal of Experimental Biology* 209:1757–1764.
- Diwakar, S. & Balakrishnan, R. 2007a. The assemblage of acoustically communicating crickets of a tropical evergreen forest in southern India: call diversity and diel calling patterns. *Bioacoustics* 16:113–135.
- Diwakar, S. & Balakrishnan, R. 2007b. Vertical stratification in an acoustically communicating ensiferan assemblage of a tropical evergreen forest in southern India. *Journal of Tropical Ecology* 23:479–486.
- Diwakar, S., Jain, M. & Balakrishnan, R. 2007. Psychoacoustic sampling as a reliable, non-invasive method to monitor orthopteran species diversity in tropical forests. *Biodiversity and Conservation* 16:4081–4093.

- Dobler, S., Stumpner, A. & Heller, K. G. 1994. Sex-specific spectral tuning for the partner's song in the duetting bush cricket *Ancistrura nigrovittata* (Orthoptera: Phaneropteridae). *Journal of Comparative Physiology A* 175:303–310.
- Doherty, J. A. 1985. Temperature coupling and 'trade-off' phenomena in the acoustic communication system of the cricket, *Gryllus bimaculatus* (Orthoptera, Gryllidae). *Journal of Comparative Physiology A* 156:787–801.
- DORSA. 2013. *Digital Orthoptera Specimen Access*. Accessed November 2013. (Online: <http://www.dorsa.de>).
- Duellman, W. E., Pyles, R. E. 1983. Acoustic resource partitioning in anuran communities. *Copeia* 3:639–649.
- Dumyahn, S. L. & Pijanowski, B. C. 2011. Soundscape conservation. *Landscape Ecology* 26:1327–1344.
- Eades, D. C., Otte, D., Cigliano, M. M. & Braun, H. 2014. *Orthoptera species file online*. Version 5.0/5.0 Accessed January 2014. (<http://Orthoptera.SpeciesFile.org>).
- Ewing, A. W. 1989. *Arthropod bioacoustics*. Comstock, Ithaca and London.
- Farina, A. 2009. *Ecology, cognition and landscape: linking natural and social systems*. Springer, New York.
- Farina, A., Lattanzi, E., Malavasi, R., Pieretti, N. & Piccioli, L. 2011. Avian soundscapes and cognitive landscapes: theory, application and ecological perspectives. *Landscape Ecology* 26:1257–1267.
- Field, L. H. 1993. Structure and evolution of stridulatory mechanisms in New Zealand wetas (Orthoptera: Stenopelmatidae). *International Journal of Insect Morphology and Embryology* 22:163–183.

- Fischer, P. F., Schulz, U., Schubert, H., Knapp, P. & Schmöger, M. 1997. Quantitative assessment of grassland quality: acoustic determination of population sizes of orthopteran indicator species. *Ecological Applications* 7:909–920.
- Francis, C. D., Ortega, C. P. & Cruz, A. 2009. Noise pollution changes avian communities and species interactions. *Current Biology* 19:1415–1419.
- Fulton, B. B. 1932. North Carolina's singing Orthoptera. *Journal of the Mitchell Society* January:55–69.
- Fulton, B. B. 1934. Rhythm, synchronism, and alternation in the stridulation of Orthoptera. *Journal of the Mitchell Society* December:263–267.
- Galliard, P. I. & Shaw, K. C. 1991. Role of weight and acoustic parameters, including nature of chorusing, in the mating success of males of the katydid, *Amblycorypha parvipennis* (Orthoptera, Tettigoniidae). *The Florida Entomologist* 74:453–464.
- Gerhardt, C. H. & Huber, F. 2002. *Acoustic communication in insects and anurans: Common problems and diverse solutions*. The University of Chicago Press, Chicago.
- Gerhardt, H. C. 1994. Selective responses to long-range acoustic signals in insects and anurans. *American Zoologist* 34:706–714.
- Gerrish, G. A, Morin, J. G., Rivers, T. J. & Patrawala, Z. 2009. Darkness as an ecological resource: the role of light in partitioning the nocturnal niche. *Oecologia* 160:525–36.
- Gogala, M. & Riede, K. 1995. Time sharing of song activity by cicadas in Temengor Forest Reserve, Hulu Perak, and in Sabah, Malaysia. *Malayan Nature Journal* 48:297–305.
- Goyette, J. L., Howe, R. W., Wolf, A. T. & Robinson, W. D. 2011. Detecting tropical nocturnal birds using automated audio recordings. *Journal of Field Ornithology* 82:279–287.
- Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144:517–46.
- Greenfield, M. D. 1988. Interspecific acoustic interactions among katydids. *Neoconocephalus*: inhibition-induced shifts in diel activity. *Animal Behaviour* 36:684–695.

- Greenfield, M. D. 1990. Evolution of acoustic communication in the genus *Neoconocephalus*: discontinuous songs, synchrony, and interspecific interactions. In: Bailey, W. J. & Rentz, D. C. F. (eds.). *The Tettigoniidae: biology, systematics and evolution*. Crawford House Press, Australia.
- Greenfield, M. D. 1994. Cooperation and conflict in the evolution of signal interactions. *Annual Review of Ecology, Evolution, and Systematics* 25:97–126.
- Greenfield, M. D. 1997. Acoustic communication in Orthoptera. In: Gangwere, S. K., Muralirangan, M. C. & Muralirangan, M. (eds.). *The bionomics of grasshoppers, katydids and their kin*. CAB International, Oxford.
- Greenfield, M. D. 2002. *Signalers and receivers. Mechanisms and evolution of arthropod communication*. Oxford University Press, Oxford.
- Greenfield, M. D. & Roizen, I. 1993. Katydid synchronous chorusing is an evolutionary stable outcome of female choice. *Nature* 364:618–620.
- Griffin, D. R. 1971. Importance of atmospheric attenuation for echolocation of bats (Chiroptera). *Animal Behaviour* 19:55–61.
- Gwynne, D. T. 1984. Courtship feeding increases female reproductive success in bush crickets. *Nature* 307:361–363.
- Gwynne, D. T. 1995. Phylogeny of the Ensifera (Orthoptera): A hypothesis supporting multiple origins of acoustic signalling, complex spermatophores, and maternal care in crickets, katydids, and weta. *Journal of Orthoptera Research* 4:203–218.
- Gwynne, D. T. 2001. *Katydid and bush-crickets: reproductive behavior and evolution of the Tettigoniidae*. Cornell University Press, Ithaca.
- Halfwerk, W., Holleman, L. J. M., Lesselis, C. M. & Slabbekoorn, H. 2011. Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology* 48:210–219.

- Hartley, J. C. 1993. Acoustic behaviour and phonotaxis in the duetting ephippigerines, *Steropleurus nobrei* and *Steropleurus stali* (Tettigoniidae). *Zoological Journal of Linnean Society* 107:155–167.
- Health, J. E. & Josephson, R. K. 1970. Body temperature and singing in the katydid, *Neoconocephalus robustus* (Orthoptera, Tettigoniidae). *Biological Bulletin* 138:272–285.
- Heller, K. G. 1995. Acoustic signalling in palaeotropical bushcrickets (Orthoptera: Tettigoniodea: Pseudophyllidae): does predation pressure by eavesdropping enemies differ in the Palaeo- and Neotropics? *Journal of Zoology* 237:469–485.
- Heller, K. G. 2006. Song evolution and speciation in bush crickets. In: Drosopoulos, S. & Claridge M. F. (eds.) *Insect sounds and communication. Physiology, behaviour, ecology and evolution*. Taylor and Francis Group, Florida.
- Heller, K. G. & von Helverson, D. 1986. Acoustic communication in phaneropterid bushcrickets: species-specific delay of female stridulatory response and matching male sensory time window. *Behavioral Ecology and Sociobiology* 18:189–198.
- Hill, K. G. & Boyan, G. S. 1977. Sensitivity to frequency and direction of sound in the auditory system of crickets (Gryllidae). *Journal of Comparative Physiology A* 121:79–97.
- Hill, K. G. & Oldfield, B. P. 1981. Auditory function in Tettigoniidae (Orthoptera: Ensifera). *Journal of Comparative Physiology A* 142:169–180.
- Hults, C. & Burson, S. 2006. Soundscapes of Denali National Park and Preserve. *Alaska Park Science* 5:20–22.
- Jain, M., Diwakar, S., Bahuleyan, J., Deb, R. & Balakrishnan, R. 2013. A rain forest dusk chorus: cacophony or sounds of silence? *Evolutionary Ecology* doi:10.1007/s10682-013-9658-7.

- Jain, M. & Balakrishnan, R. 2011. Does acoustic adaptation drive vertical stratification? A test in a tropical cricket assemblage. *Behavioral Ecology* 23:343–354.
- Jennions, M. D. & Petrie, M. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews of the Cambridge Philosophical Society* 75:21–64.
- Josephson, R. K. 1973. Contraction kinetics of the fast muscles used in singing by a katydid. *Journal of Experimental Biology* 59:781–801.
- Josephson, R. K. & Halverson, R. C. 1971. High frequency muscles used in sound production by a katydid. I. Organization of the motor system. *Biological Bulletin* 141:411–433.
- Korsunovskaya, O. S. 2008. Acoustic signals in katydids (Orthoptera, Tettigonidae). Communication I. *Entomological Review* 88:1032–1050.
- Korsunovskaya, O. S. 2009. Acoustic signals in katydids (Orthoptera, Tettigonidae). Communication 2. *Entomological Review* 89:16–20.
- Krause, B., Gage, S. H. & Joo, W. 2011. Measuring and interpreting the temporal variability in the soundscape at four places in Sequoia National Park. *Landscape Ecology* 26:1247–1256.
- Laiolo, P. 2010. The emerging significance of bioacoustics in animal species conservation. *Biological Conservation* 143:1635–1645.
- Laiolo, P. & Tella, J. L. 2006. Landscape bioacoustics allow detection of the effects of habitat patchiness on population structure. *Ecology* 87:1203–1214.
- Lane, J. E., Forrest, M. N. K. & Willis, C. K. R. 2011. Anthropogenic influences on natural animal mating systems. *Animal Behaviour* 81:909–917.
- Lang, A. B., Kalko, E. K. V., Römer, H., Bockholdt, C. & Dechmann, D. K. N. 2006. Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia* 146:659–66.
- Latimer, W. & Broughton, W. B. 1984. Acoustic interference in bush crickets. *Journal of Natural History* 18:599–616.

- Latimer, W. & Sippel, M. 1987. Acoustic cues for female choice and male competition in *Tettigonia cantans*. *Animal Behaviour* 35:887–900.
- Laurence, B. D. & Simmons, J. A. 1982. Measurement of atmospheric attenuation of ultrasound frequencies and the significance for echolocation for bats. *Journal of the Acoustical Society of America* 71:585–590.
- Libersat, F. & Hoy, R. R. 1991. Ultrasonic startle behaviour in bush crickets (Orthoptera, Tettigoniidae). *Journal of Comparative Physiology A* 169:507–514.
- Lin, Y., Kalmring, K., Jatho, M., Sickman, T. & Rössler, W. 1993. Auditory receptor organs in the forelegs of *Gampsocleis gratiosa* (Tettigoniidae): morphology and function of the organs in comparison to the frequency parameters of the conspecific song. *Journal of Experimental Zoology* 267:377–388.
- MacSwiney, G., Cristina, M., Clarke, F. M. & Racey, P. A. 2008. What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. *Journal of Applied Ecology* 45:1364–1371.
- Malkmus, R. & Riede, K. 1996. Frogs from Kinabalu. Borneo. *Sauria* 18:37–37.
- Michelesen, A. & Noche, H. 1974. Biophysical aspects of sound communication in insects. *Advances in Insect Physiology* 10:247–296.
- Miller, N. P. 2008. US National Parks and management of park soundscapes: A review. *Applied Acoustics* 69:77–92.
- Montealegre-Z, F., Morris, G. K. & Mason, A. C. 2006. Generation of extreme ultrasonics in rainforest katydids. *Journal of Experimental Biology* 209:4923–4937.
- Morris, G. K. & Mason, A. C. 1995. Covert stridulation: novel sound generation by a South American katydid. *Naturwissenschaften* 82:96–98.

- Morris, G. K., Mason, A. C., Wall, P. & Belwood, J. J. 1994. High ultrasonic and tremulation signals in neotropical katydids (Orthoptera: Tettigoniidae). *Journal of Zoology* 233:129–163.
- Morris, G. K. & Pipher, R. E. 1967. Tegminal amplifiers and spectrum consistencies in *Conocephalus nigropleurum* (Bruner), Tettigoniidae. *Journal of Insect Physiology* 13:1075–1085.
- Morris, G. K. & Walker, T. J. 1976. Calling songs of *Orchelimum* meadow katydids (Tettigoniidae). *The Canadian Entomologist* 108:785–800.
- Morris, K. & Beier, M. 1982. Song structure and description of some Costa Rican katydids (Orthoptera: Tettigoniidae). *Transactions of the American Entomological Society* 108:287–314.
- National Park Service. 2006. *Management policies 2006*. U.S. Department of Interior, National Park Service, Washington, DC.
- Nischk, F. & Riede, K. 2001. Bioacoustics of two cloud forest ecosystems in Ecuador compared to lowland rainforest with special emphasis on singing cricket species. In: Nieder, J. & Barthlott, W. (eds.). *Epiphytes and canopy fauna of the Otongan rain forest (Ecuador). Results of the Bonn – Quito epiphyte project, funded by the Volkswagen Foundation (Vol. 2 of 2)*. Books on Demand GmbH, Bonn.
- Otte, D. 1977. Communication in Orthoptera. In: Sebeok, T. A. (ed.) *How Animals Communicate*. Indiana University Press, Bloomington, Indiana.
- Otte, D. 1992. Evolution of cricket songs. *Journal of Orthoptera Research* 1:25–49.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* 37:637–669.
- Patricelli, G. L. & Blickley, J. L. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. *Auk* 123:639–649.

- Paul, R. C. & Walker, T. J. 1979. Arboreal singing in a burrowing cricket, *Anurogryllua arboreus*. *Journal of Comparative Physiology A* 132:217–223.
- Peter, F., Schulz, U., Schubert, H., Knapp, P., Applications, S. E., Aug, N., Fischer, F. P. & Schmoeger, M. 1997. Quantitative assessment of grassland quality: Acoustic determination of population sizes of orthopteran indicator species. *Ecological Applications* 7:909–920.
- Pielemeier, W. H. 1946. Supersonic insects. *Journal of the Acoustical Society of America* 17:337–338.
- Pierce, G. W. 1948. *The songs of insects*. Harvard University Press, Cambridge, Massachusetts.
- Pijanowski, B. C., Farina, A., Gage, S. H., Dumyahn, S. L. & Krause, B. L. 2011a. What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology* 26:1213–1232.
- Pijanowski, B. C., Villanueva-Rivera, L. J., Dumyahn, S. L., Farina, A., Krause, B. L., Napoletano, B. M., Gage, S. H. & Pieretti, N. 2011b. Soundscape ecology: the science of sound in the landscape. *BioScience* 61:203–216.
- Pires, A. & Hoy, R. R. 1992. Temperature coupling in cricket acoustic communication, I. Field and laboratory studies of temperature effects on calling song production and recognition in *Gryllus firmus*. *Journal of Comparative Physiology A* 171:69–78.
- Pumphrey, R. J. 1940. Hearing in insects. *Biological Reviews* 15:107–132.
- Regen, J. 1913. Über die anlockung des weibchens von *Gryllus campestris* L. durch telephonisch übertragene der stridulationslaute des männchens. *Pflügers Archiv für die Gesamte Physiologie des Menschen und der Tiere* 155:193–200.
- Richards, D. G. & Willey, R. H. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: Implications for animal communication. *The American Naturalist* 115:381–399.

- Riede, K. 1987. A comparative study of mating behaviour in some neotropical grasshoppers (Acridoidea). *Ethology* 76:265–296.
- Riede, K. 1993. Monitoring biodiversity: analysis of Amazonian rainforest sounds. *Ambio* 22:546–548.
- Riede, K. 1997. Bioacoustic diversity and resource partitioning in tropical calling communities. In: Ulrich, H. (ed.). *Tropical biodiversity and systematics. Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems*, Bonn 1994. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.
- Riede, K. 1998. Acoustic monitoring of Orthoptera and its potential for conservation. *Journal of Insect Conservation* 2:217–223.
- Riede, K., Kämper, G. & Höffler, I. 1990. Tympana, auditory thresholds, and projection area of tympanal nerves in singing and silent grasshoppers (Insecta, Acridoidea). *Zoomorphology* 109:223–230.
- Riede, K., Nischk, F., Thiel, C. & Schwenker, F. 2006. Automated annotation of Orthoptera songs: first results from analysing the DORSA sound repository. *Journal of Orthoptera Research* 15:105–113.
- Ries, L., Fletcher, R. J., Battin, J., Sisk, T. D. 2004. Biological responses to habitat edges: mechanisms, models and variability explained. *Annual Review of Ecology, Evolution and Systematics* 35:491–522
- Robert, D., Amoroso, J., Hoy, R. R. 1992. The evolutionary convergence of hearing in a parasitoid fly and its cricket host. *Science* 258:1135–1137.
- Robinson, D. 1990. Acoustic communication between the sexes in bush crickets. In: Bailey, W. J. & Rentz, D. C. F. (eds.). *The Tettigoniidae: biology, systematics and evolution*. Crawford House Press, Australia.

- Römer, H. 1993. Environmental and biological constraints for the evolution of long-range signaling and hearing in acoustic insects. *Philosophical Transactions of the Royal Society B: Biological Sciences* 340:179–185.
- Römer, H., Bailey, W. & Dadour, I. 1989. Insect hearing in the field. III. Masking by noise. *Journal of Comparative Physiology A* 164:609–620.
- Römer, H. & Lewald, J. 1992. High-frequency sound transmission in natural habitats: implications for the evolution of insect acoustic communication. *Behavioral Ecology and Sociobiology* 29:437–444.
- Ross, P. S. & Grant, P. B. C. 2008. Persistent Organic Pollutants. In: Melnick, E. L. & Everitt, B. S. (eds.). *Encyclopedia of quantitative risk analysis and assessment*. Wiley, New York.
- Rössler, W., Jatho, M. & Kalmring, K. 2006. The auditory – vibratory sensory system in bushcrickets. In: Drosopoulos, S. & Claridge, M. F. (eds.). *Insect sounds and communication. Physiology, behaviour, ecology and evolution*. Taylor and Francis Group, Florida.
- Rust, J., Stumpner, A. & Gottwald, J. 1999. Singing and hearing in a Tertiary bush cricket. *Nature* 399:650.
- Ryan, M. J. 1988. Energy, calling and selection. *American Zoologist* 28:885–898.
- Ryan, M. J. & Brenowitz, E. A. 1985. The role of body size, phylogeny and ambient noise in the evolution of bird song. *The American Naturalist* 126:87–100.
- Sakaluk, S. K., Belwood, J. J. 1984. Gecko phonotaxis to cricket calling song: a case of satellite predation. *Animal Behaviour* 32:659–662.
- Samways, M. J. 1976. Song modification in the Orthoptera. I. Proclamation songs of *Platypleis* spp., (Tettigoniidae). *Physiological Entomology* 1:299–303.

- Samways, M. J. 1977a. Song modification in the Orthoptera. IV. The *Platycleis intermedia/P.affinis* interaction quantified. *Physiological Entomology* 2:301–315.
- Samways, M. J. 1977b. Bush cricket interspecific acoustic interactions in the field (Orthoptera, Tettigoniidae). *Journal of Natural History* 11:155–168.
- Samways, M. J. 1977c. Effect of farming on population movements and acoustic behaviour of two bush crickets (Orthoptera, Tettigoniidae). *Bulletin of Entomological Research* 67:471–481.
- Sanborn, A. F. 2006. Acoustic signals and temperature. In: Drosopoulos, S. & Claridge, M. F. (eds.). *Insect sounds and communication. Physiology, behaviour, ecology and evolution*. Taylor and Francis Group, Florida.
- Saunders, D. A., Hobbs, R. J. & Margules, C. R. 1991. Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* 5:18–32.
- Schatral, A. 1990. Interspecific acoustic behaviour among bush crickets. In: Bailey, W. J. & Rentz, D. C. F. (eds.). *The Tettigoniidae: biology, systematics and evolution*. Crawford House Press, Australia.
- Schatral, A. & Yeoh, P. 1990. Spatial distribution, calling and interspecific acoustic interactions in two species of Australian tettigoniid genus *Tympanophora* (Orthoptera, Tettigoniidae). *Journal of Zoology* 221:375–390.
- Schmidt, A. K. D., Riede, K. & Römer, H. 2011. High background noise shapes selective auditory filters in a tropical cricket. *Journal of Experimental Biology* 214:1754–1762.
- Schmidt, A. K. D., Römer, H. & Riede, K. 2012. Spectral niche segregation and community organization in a tropical cricket assemblage. *Behavioral Ecology* 24:470–480.
- Schul, J. & Sheridan, R. A. 2006. Auditory stream segregation in an insect. *Neuroscience* 138:1–4.

- Schulze, W. & Schul, J. 2001. Ultrasonic avoidance behaviour in the bush cricket *Tettigonia viridissima* (Orthoptera, Tettigoniidae). *Journal of Experimental Biology* 204:733–740.
- Scudder, S. H. 1886. Notes on stridulation of some New England Orthoptera. *Proceedings of the Boston Society of Natural History* 11:306–313.
- Scudder, S. H. 1892. The songs of our grasshoppers and crickets. *Entomological Society of Ontario* 1891:62–78.
- Searcy, W. A. & Anderson, M. 1986. Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics* 17:507–533.
- Sharov, A. G. 1968. Phylogeny of the Orthopteroidea. *Paleontological Institute, Russian Academy of Sciences*. 188:1–216.
- Sharov, A. G. 1971. *Phylogeny of the Orthopteroidea*. Israel Program for Scientific Translations, Jerusalem.
- Shaw, K. L., Bitzer, R. J. & North, R. C. 1982. Spacing and movement of *Neoconocephalus ensiger* males (Conocephalinae: Tettigoniidae). *Journal of Kansas Entomological Society* 55:581–592.
- Shieh, B. S., Liang, S. H., Chen, C. C., Loa, H. H. & Liao, C. Y. 2011. Acoustic adaptations to anthropogenic noise in the cicada *Cryptotympana takasagona* Kato (Hemiptera: Cicadidae). *Acta Ethologica* (On-line: DOI 10.1007/s10211-011-0105-x)
- Siemers, B. M. & Schaub, A. 2011. Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. *Proceedings of the Royal Society B: Biological Sciences* 278:1646–1652.
- Simmons, L. W. & Gwynne, D. T. 1991. The refractory period of female katydids (Orthoptera: Tettigoniidae): sexual conflict over the re-mating interval? *Behavioral Ecology and Sociobiology* 10:263–269.

- Simmons, L. W. & Zuk, M. 1992. Variability in call structure and pairing success of male field crickets, *Gryllus bimaculatus*: the effect of age, size and parasite load. *Animal Behaviour* 44:1145–1152.
- Sismondo, E. 1990. Synchronous, alternating, and phase-locked stridulation by a tropical katydid. *Science* 249:55–58.
- Slabbekoorn, H. & Peet, M. 2003. Birds sing at a higher pitch in urban noise. *Nature* 424:267.
- Southworth, M. 1969. The sonic environment of cities. *Environment and Behaviour* 1:49–70.
- Stumpner, A., von Helverson, D. 1992. Recognition of a two-element song in the grasshopper *Chorthippus dorsatus* (Orthoptera, Gomphocerinae). *Journal of Comparative Physiology A* 169:765–772.
- Sueur, J. 2002. Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico. *Biological Journal of the Linnean Society* 75:379–394.
- Thiele, D. & Bailey, W.J. 1980. The function of male spacing behaviour in bush-crickets (Tettigoniidae, Orthoptera). *Australian Journal of Ecology* 5:275–286.
- Thompson, N. S., Le Doux, K. & Moody, K. 1994. A system for describing bird song units. *Bioacoustics* 5:267–79.
- Thornhill, R. & Gwynne, D. T. 1986. The evolution of sexual differences in insects. *American Scientist* 74:382–389.
- Toms, R. B., Ferguson, J. W. H. & Becker, S. 1993. Relationship between body temperature and air temperature in stridulating male crickets, *Gryllus bimaculatus* (Orthoptera: Gryllidae). *South African Journal of Zoology* 28:71–73.
- Truax, B. & Barrett, G. W. 2011. Soundscape in a context of acoustic and landscape ecology. *Landscape Ecology* 26:1201–1207.

- Tuckerman, J. F., Gwynne, D. T. & Morris, G. K. 1993. Reliable acoustic cues for female mate preference in a katydid (*Scudderia curvivauda*). *Behavioral Ecology and Sociobiology* 4:106–113.
- Van Staaden, M. J. & Römer, H. 1997. Sexual signaling in bladder grasshoppers: Tactical design for maximizing call range. *Journal of Experimental Biology* 200:2597–2608.
- Villanueva-Rivera, L. J. 2007. Digital recorders increase detection of *Eleutherodactylus* frogs. *Herpetological Review* 38:59–63.
- Villanueva-Rivera, L. J., Pijanowski, B. C., Doucette, J. & Pekin, B. 2011. A primer of acoustic analysis for landscape ecologists. *Landscape Ecology* 26:1233–1246.
- Walker, E. M. 1905. Notes on the Locustidae of Ontario. *The Canadian Entomologist* 37:34–38.
- Walker, T. J. 1957. Specificity in the response of female tree crickets (Orthoptera, Gryllidae, *Oecanthinae*) to calling songs of the males. *Annals of the Entomological Society of America* 50:626–636.
- Walker, T. J. 1964a. Experimental demonstration of a cat locating orthopteran prey by the prey's calling song. *The Florida Entomologist* 47:163–165.
- Walker, T. J. 1964b. Cryptic species among sound producing Ensiferan Orthoptera (Gryllidae and Tettigoniidae). *Quarterly Review of Biology* 39:345–355.
- Walker, T. J. 1975. Effects of temperature on rates in poikilotherm nervous systems. Evidence from the calling songs of meadow katydids (Orthoptera, Tettigoniidae: *Orchelimum*) and reanalysis of published data. *Journal of Comparative Physiology A* 101:57–59.
- Wiley, R. H. & Richards, D. G. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* 3:69–94.

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

Yersin, A. 1854. Mémoire sur quelques faits relatifs à la stridulation des Orthoptères et à leur distribution géographique en Europe. *Bulletin Société Vaudoise des Sciences Naturelles* 4:108–128.

Zuk, M. & Kolluru, G. 1998. Exploitation of sexual signals by predators and parasitoids. *Quarterly Review of Biology* 73:415–438.

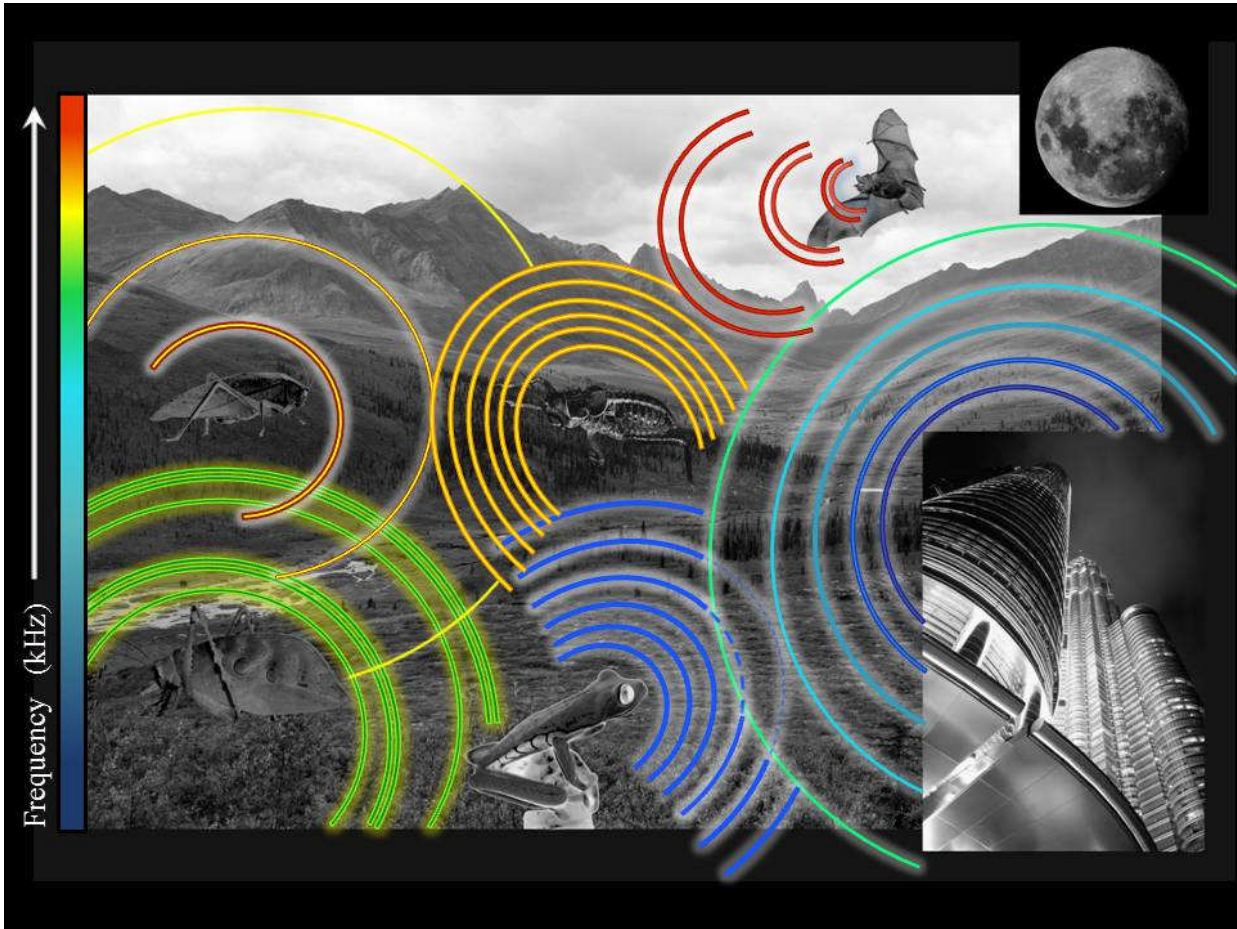


Figure 1.1. Viewing the landscape from an acoustic perspective provides insight into intricate interactions between abiotic and abiotic factors. Anthropogenic influences often mask or inhibit communication channels. Acoustic interference from abiotic or biotic sources can cause acoustic communicating taxa to shift signals spectrally, spatially or temporally to avoid acoustic interference.

PRINCIPLE OF ACOUSTIC PROFILING

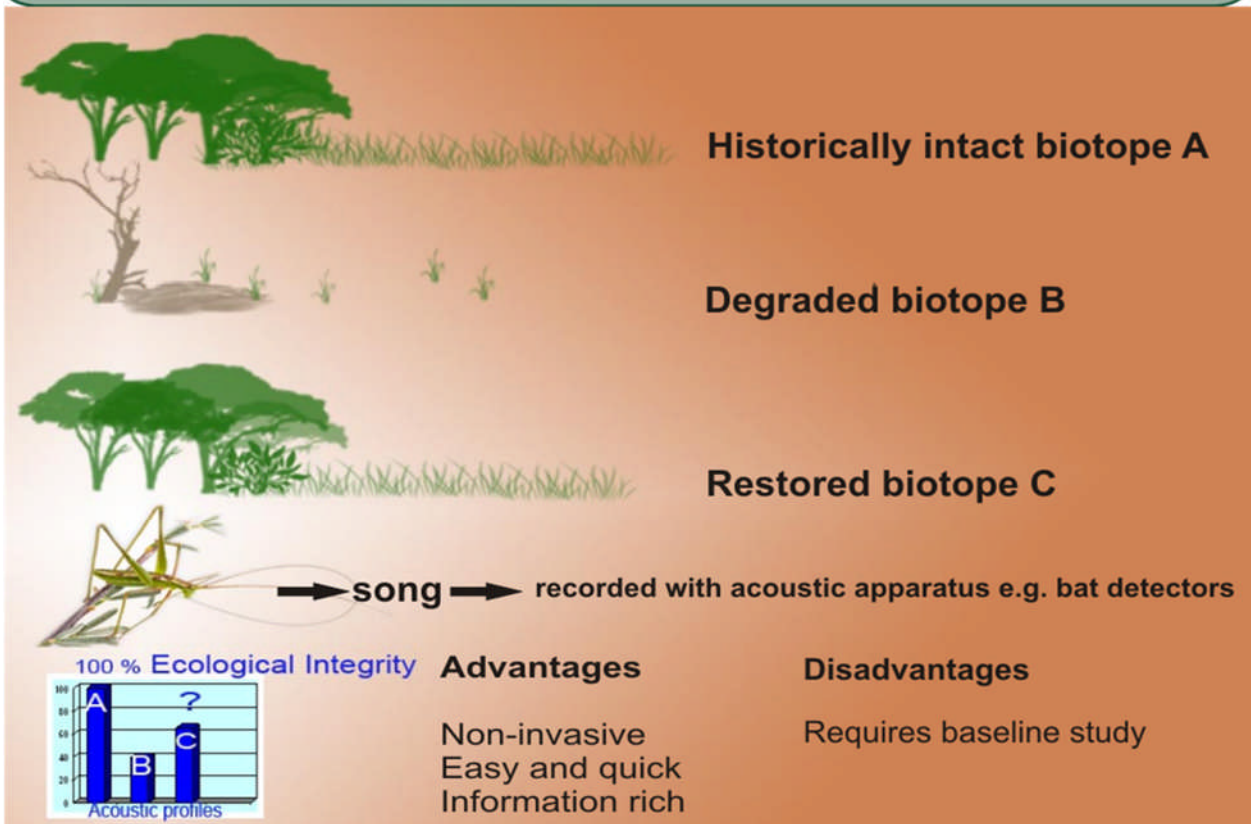


Figure 1.2. Bioacoustic monitoring provides rapid, non-invasive data to assess and monitor the recovery or degradation of biodiversity, providing critical feedback for conservation strategies.

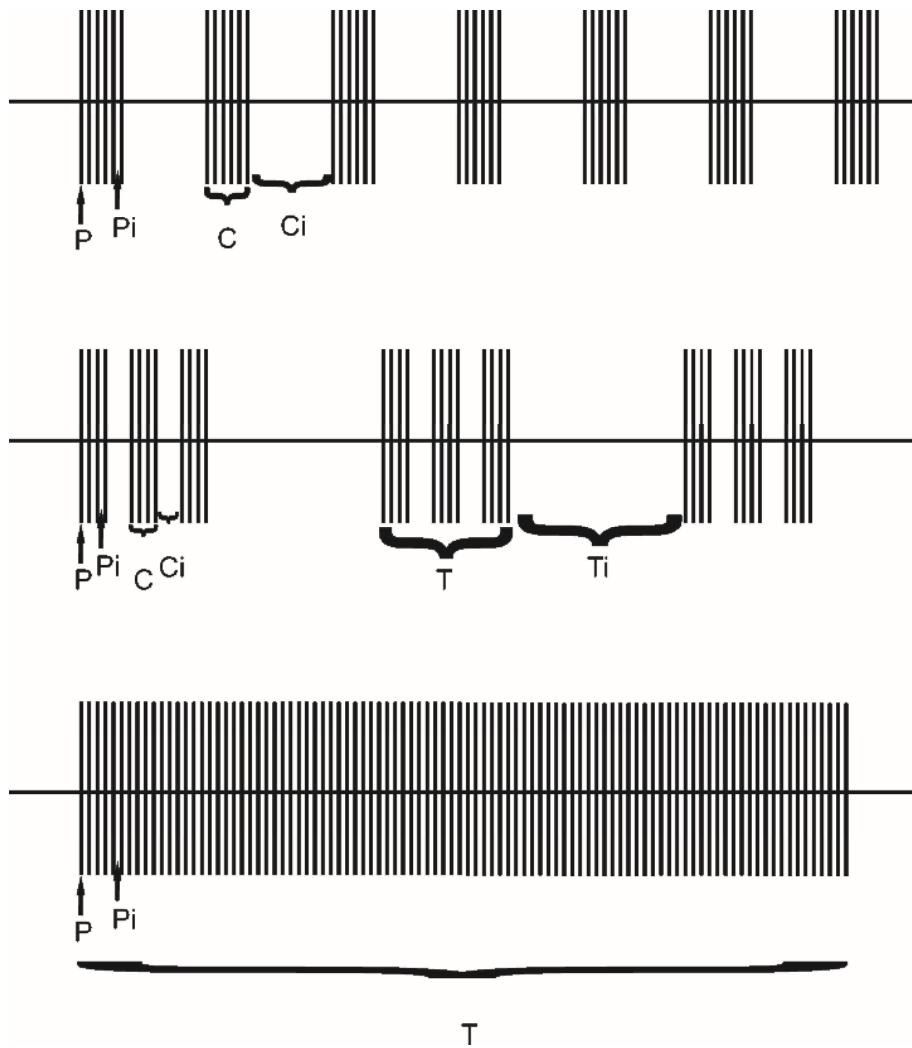


Figure 1.3. Within acoustic signals elements are defined as pulses (P), chirps (C), trills (T). Intervals between these elements are defined as pulse intervals (Pi), chirp intervals (Ci) and trill intervals (Ti). Pulses are the smallest discrete amplitude modulations within signals, grouped together as chirps or generated continuously as trills. Chirps, comprised of multiple pulses can occur singularly or within groups known as also known as trills.

2. Niche partitioning of acoustic communities in a Bornean rain forest

Abstract

Tropical rain forests contain a rich ensemble of acoustically communicating species, creating complex acoustic environments. To communicate effectively, acoustic species need to minimize signal interference to detect, recognize and localize conspecific signals. Here, I examine an entire acoustic community of 172 species of katydids, crickets, frogs, cicadas and birds. I then investigate their acoustic communication channels spectrally, temporally and spatially to determine how these species maintain conspecific communication yet reduce signal interference from other species. The overall assemblage showed considerable partitioning in the calling frequencies of their signals, displaying low spectral niche overlap. Diurnally active species, consisting mostly of cicadas and birds, showed low temporal niche overlap, with species signalling only within narrow time windows. Nocturnal species, which were mostly katydids, crickets and frogs, did not utilize temporal partitioning, displaying high temporal niche overlap. This overlap transcended the taxon level, as diurnally active katydids, crickets and frogs partitioned temporal acoustic space, whereas nocturnal cicadas and birds did not. Lack of nocturnal temporal partitioning suggests other mechanisms of acoustic avoidance are sufficient to avoid acoustic overlap, or that there are insufficient cues to partition nocturnal acoustic environments. In terms of vertical stratification of calling heights, corresponding to tree canopy crown, understory and ground levels, the three elevations were utilized equally by acoustic species. Nevertheless, there were unique acoustic assemblages at each calling height. This vertical stratification occurred across all taxa, with the exception of cicadas which displayed high spatial overlap across vertical heights. For cicadas, it is likely that spectral and temporal niche partitioning were sufficient to avoid acoustic interference. Furthermore, there

was no correlation between calling height of species and call features, including dominant frequency and pulse rate. Overall, the entire acoustic assemblage utilizes a range of different strategies so as to allow many species to communicate with conspecifics with little or no interference from other species in a signal rich environment.

Introduction

Tropical rain forests support exceptional fauna diversity within an architecturally complex and diverse flora matrix (Wallace 1869; Erwin 1982; Whitmore 1991; Stork 1991; Riede 1996; Floren *et al.* 2001; Sterck *et al.* 2001). Due to restricted visibility and nocturnal habits of many rainforest animals, species-specific acoustic signals are an important communication medium for mate recognition and orientation (Elton 1973; Riede 1996; Greenfield 2002).

For communication to be effective, propagated signals need to reach receivers with minimal loss of information. In tropical rain forests, the distant signals that are detected and recognized, are constrained by abiotic factors such as dense foliage, which reduces the total energy content of signals through attenuation (Jain & Balakrishnan 2011a). Propagation of signals through this medium also causes temporal and spectral distortion of signals, which render them unrecognizable to conspecifics (Wiley & Richards 1978; Wiley & Richards 1982; Römer *et al.* 1989; Greenfield 2002). In addition, these singing organisms are also often highly sought after prey, and they need to be alert to the approach of predators which disturb the vegetation (Samways 1976a). Furthermore, biotic constraints include signal interference from competing sound produced by other acoustically communicating animals, hindering detection, recognition and localization of conspecific signals (Römer *et al.* 1989, Riede 1996; Wollerman 1999; Wollerman & Wiley 2002; Brumm & Slabbekoorn 2005; Bee 2008; Bee & Micheyl 2008; Schmidt & Römer 2011; Jain & Balakrishnan 2011a; Jain *et al.* 2013). When there is interference, there can be distortion of the species-specific song (Samways & Broughton 1976).

The high diversity of acoustic signals in tropical rain forests creates a complex acoustic environment in which species need to compete for, and partition, acoustic transmission channels to minimize acoustic interference while maximizing broadcast range (Morton 1975; Römer *et al.* 1989; Römer 1993; Endler 1993; Riede 1993; Gogala & Riede 1995; Sueur 2002;

Diwakar & Balakrishnan 2007a; Diwakar & Balakrishnan 2007b; Jain & Balakrishnan 2011a; Schmidt *et al.* 2012.) Various strategies, including increasing call intensity (Jain *et al.* 2013) and partitioning frequency, temporal and spatial domains, are mechanisms which reduce signal interference in order to communicate effectively within signal rich environments (Hödl 1977; Henwood & Fabrick 1979; Duellman & Pyles 1983; Endler 1993; Riede 1996; Riede 1997; Nemeth *et al.* 2001; Sueur 2002; Diwakar & Balakrishnan 2007a; Diwakar & Balakrishnan 2007b; Diwakar & Balakrishnan 2011; Schmidt *et al.* 2012; Jain *et al.* 2013).

Use of different dominant frequencies allows both vertebrate and invertebrate species to call simultaneously with minimal signal interference within the same temporal and spatial domain (Drewry & Rand 1983; Heller & Helversen 1989; Riede 1998; Kingston *et al.* 2000; Sueur 2002; Gerhardt & Huber 2002; Amézquita *et al.* 2005; Brandes *et al.* 2006; du Preez & Carruthers 2009; Jones & Siemers 2010; Amézquita *et al.* 2011; Schmidt *et al.* 2012). Within tropical rain forests, increased competition for acoustic transmission channels has resulted in enhanced frequency tuning in species, allowing more species to communicate with overlapping temporal and spatial signals within the frequency spectrum (Schmidt *et al.* 2011; Schmidt *et al.* 2012). Preference for different temporal or spatial patterns also minimizes signal interference while optimizing signal transmission (Ficken *et al.* 1974; Samways 1976b; Hödl 1977; Henwood & Fabrick 1979; Drewry & Rand 1983; Duellman & Pyles 1983; Greenfield 1988; Römer *et al.* 1989; Endler 1993; Riede 1993; Gogala & Riede 1995; Riede 1996; Riede 1997; Sueur 2002; Gottsberger & Gruber 2004; Hsu *et al.* 2006; Diwakar & Balakrishnan 2007a; Diwakar & Balakrishnan 2007b; Planqué & Slabbekoorn 2008; Luther 2009; Krause *et al.* 2011; Goyette *et al.* 2011; Schmidt *et al.* 2012; Jain *et al.* 2013).

Temporal partitioning of species can occur over different time scales, ranging from different seasons of the year, different hours of the day (diel patterns), or within small calling

windows of minutes or seconds (Jain *et al.* 2013). Within diel patterns, dawn and dusk are often peaks of acoustic activity, with many individuals signaling at the same time (Gogala & Riede 1995; Riede 1996; Riede 1997; Sueur 2002; Gerhardt & Huber 2002; Diwakar & Balakrishnan 2007a; Goyette *et al.* 2011; Bormpoudakis *et al.* 2013; Jain *et al.* 2013). This is particularly important where both the spectral characteristics and temporal patterning of the song are similar, as among closely related congeners (Samways 1976b).

Vertical stratification of acoustic transmission channels are also an important resource partitioning strategy employed by many taxa, including birds (Marten & Marler 1977; Dabelsteen *et al.* 1993; Mathevon *et al.* 1996; Nemeth *et al.* 2001), frogs (Hödl 1977; Lamb 1987; Ptacek 1992; Kime *et al.* 2000; Mathevon *et al.* 2005), cicadas (Sueur 2002; Sueur & Aubin 2003), crickets and katydids (Samways 1976d; Arak & Eiriksson 1992; Nischk & Otte 2000; Diwakar & Balakrishnan 2007b; Jain & Balakrishnan 2011a; Schmidt *et al.* 2012).

Most songs in Bornean rain forests can be attributed to birds, frogs, cicadas, crickets and katydids, which produce species-specific signals with various spectral and temporal features for mate recognition (Otte 1992; Riede 1993; Riede 1998; Greenfield 2002; Diwakar & Balakrishnan 2007a). While these taxonomic groups have different general diel patterns, signal features such as carrier frequency and pulse rates provide reliable features for classification of recognizable taxonomic units which address the taxonomic challenge, particularly of tropical faunas (Riede 1998). Acoustic species, defined by their species-specific call features coincide with morphospecies and provide an ideal opportunity for rapid classification and mapping of species rich communities (Riede 1993; Riede 1998; Nischk & Riede 2001; Diwakar & Balakrishnan 2007a; Diwakar *et al.* 2007) Acoustic surveys therefore provide an extremely effective, reliable, non-invasive tool to assess and monitor biodiversity.

While many studies concentrate on specific taxonomic groups, within tropical rain forests, there are a diverse ensemble of acoustically communicating taxa all of which compete for optimal communication channels while minimizing acoustic interference through niche partitioning of frequency and temporal and spatial domains (Samways 1977a; Römer *et al.* 1989; Römer 1993; Riede 1993; Diwakar & Balakrishnan 2007a; Schmidt *et al.* 2012). The aim here is to investigate acoustic resource partitioning in a species rich Bornean tropical rain forest so as to determine which acoustic features enable them to co-exist. I analyze the entire acoustic assemblage with respect to its spectral, temporal and spatial composition. Additionally, I examine whether species-specific call features are related to calling height of species in the assemblage.

Methods

Study site and period

Investigations were conducted in August 2008 at the Kuala Belalong Field Study Centre (KBFSC), Universiti Brunei Darussalam in northern Borneo. The KBFSC (4°33'N, 115°09'E) is situated on the north-western boundary of the Ulu Temburong National Park, within the Batu Apoi Reserve in the Temburong district. The region is characterized by steep hills covered in virgin mixed dipterocarp tropical rain forest (Cranbrook 1993). Ulu Temburong National Park is the most protected and pristine forest in Borneo, actively protected from both legal and illegal logging (Bryan 2013). The climate is typically equatorial, with average daily relative humidity of 80% and maximum temperatures ranging between 30-35°C, with little variation between months (Dykes 2000). While there is no distinct dry season, precipitation peaks around April-May and November (Dykes 2000), with an annual precipitation of >4000 mm (Cranbrook 1993). As a highly protected tropical rain forest reserve, this region contains exceptionally high

biodiversity (Cranbrook 1993). While limited biodiversity surveys have been conducted within the Ulu Temburong National Park, one study recorded 324 butterfly species within a 1 km radius (Orr & Hauser 1996), and another recorded 278 tree species within a 1 ha plot (Small *et al.* 2004). On a broader geographic scale, the island of Borneo has ± 630 bird species (Myers 2009), >150 frog species (Inger & Stuebing 1997); 154 snake species (Inger & Stuebing 1999); 353 phasmid species (Bragg 2001); 300 dragonfly species (Orr 2003) and 330 Ensifera species which is comprised of 206 katydids (Tettigoniidae) (Eades *et al.* 2013) and 107 crickets (Gryllidae) (Eades *et al.* 2013). Another study conducted in a mixed dipterocarp lowland rain forest in Sabah, Borneo found 127 arboreal Ensifera species, 85 of which were new to science (Floren *et al.* 2001). These investigations emphasize the richness of Bornean biodiversity, and highlight the acoustic complexity of Bornean rain forests, rich in overlapping signals from acoustically active animals such as birds, frogs, cicadas, crickets and katydids.

Acoustic sampling

The KBFSC constructed a 50 m canopy research tower in Ulu Temburong National Park, nestled within the forest, containing platforms at 50 m and 30 m above ground. Canopy research towers eliminate the logistical difficulties in accessing various levels of the forest and allow ease of movement, without causing interference to taxa being studied (Baker & Pinard 2001). The KBFSC tower was divided into three sections, ground level (0 m), mid-level (30 m) and at the top of the emergent canopy (50 m). These heights corresponded to forest structure, characterized by tall emergent trees >50 m in height and 150 cm dbh, followed by canopy level trees up to 20-40 m in height with diameters less than 150 cm dbh (Small *et al.* 2004). Sub-canopy trees had diameters less than 50 cm dbh, and had considerable height variation, with mature individuals reaching the bottom of the canopy at 20 m (Small *et al.* 2004). Understorey trees were generally >10 m in height with diameters <10 cm dbh (Small *et al.* 2004). Of 278

tree species in the region, the most abundant families were *Euphorbiaceae*, *Lauraceae*, *Myristicaceae*, *Myrtaceae* and *Dipterocarpaceae* (Small *et al.* 2004).

At each height (0 m, 30 m and 50 m) ambient acoustic recordings of 1 minute in duration were made every hour, continuously for six 12 hour shifts. This included 3 nocturnal shifts from 21:00-09:00 hrs, and 3 diurnal shifts from 09:00-21:00 hrs for a total of 216 acoustic recordings. Recording schedule was organized to incorporate uninterrupted recording of dusk and dawn periods.

Recordings were made using a Sennheiser (Sennheiser, Germany) ME 67 long gun microphone in conjunction with a Marantz PD660 (Marantz, USA) solid state digital recorder. The Sennheiser microphone has a frequency range of <20 kHz and is highly directional, preventing sound colouration from off-axis sources, making it ideal for recording call structure with minimal background noise. The directional microphone was strictly aligned horizontally. The Marantz PD660 recording parameters were set to a sampling rate of 48 kHz with an uncompressed file format (.wav).

Signal characterization

Acoustic signals within ambient recordings were analyzed manually using Raven Pro (Cornel Laboratories, USA). Spectrograms were produced for each ambient recording in which each 1 kHz frequency band was isolated and examined in detail for species-specific signals. Signal structure measures and playback features within selected frequency bands provided a means to identify acoustic species. Highly stereotyped species-specific signals allow for trained listeners to distinguish between morphologically similar species with a high degree of accuracy (Riede 1996; Diwaker *et al.* 2007). Signals from acoustic species were also characterized according to their signal structure based on center frequency and pulse rate (number of pulses per second). Pulses are the smallest discrete amplitude modulations within signals, grouped together as

chirps or generated continuously as trills. Chirps, comprised of multiple pulses can occur singularly or within groups known as also known as trills. The gaps between pulses, chirps and trills are referred to as intervals. For each signal these elements were measured along with minimum, maximum and center frequency (the smallest discrete frequency which contains 50% of total energy). Collection of acoustic species was not possible, therefore each acoustic species was assigned a likely taxon (bird, frog, cicada, cricket, katydid) based on the psychoacoustic sound of signals in addition to the temporal and spectral features of the signal.

In Bornean forests, a large portion of acoustic space, both in number of species signaling and in the nocturnal acoustic energy, is generated by crickets (Orthoptera: Ensifera: Gryllidae). Crickets have conspicuous, simple repetitive signals within a narrow-band frequency range between 1 and 11 kHz (Riede 1998). Male crickets generate acoustic signals by tegminal stridulation, where a file and scrapper mechanism on the forewings cause the harp to resonate at narrow species-specific frequency ranges (Greenfield 2002). Pulse repetition rate and frequency range permit easy acoustic classification of cricket species (Riede 1998).

Katydids (Orthoptera: Ensifera: Tettigoniidae) are also nocturnal insects that produce species-specific signals by tegminal stridulation, where a functionally similar appendage to crickets called the mirror, resonates at generally high, broad frequency ranges between 6 and 130 kHz (Montealegre-Z *et al.* 2006; Greenfield 2002). However, some katydid species produce narrow frequency ranges (Riede 1996). Katydid signals have a diverse range of temporal amplitude modulations comprising pulses grouped into chirps or generated continuously as trills. (Greenfield 2002).

Cicadas (Cicadidae), generally active during the day generate high intensity signals using tymbals on both sides of the first abdominal segments. Their characteristic species-

specific songs incorporate a great deal of higher harmonics which can be readily classified and reliably identified by trained listeners (Riede 1996).

Birds are most acoustically active during dawn, but contain a rich variety of diurnal and some nocturnal species. Their acoustic signals are recognizable through complex fluctuating intensity across lower frequency ranges below 3 kHz (Riede 1993). Comparatively, frogs generally utilize frequency ranges below 3 kHz, although some species are known to utilize frequencies up to 8 kHz, are more nocturnally active and have relatively simple call structures easily classified by frequency range and pulse rates (Malkmus & Riede 1992; Riede 1993; Malkmus & Riede 1996; Gerhardt & Huber 2002; du Preez & Carruthers 2009).

While classification of bird and cicada calls is fairly reliable, some acoustic signals are difficult to differentiate between frog, cricket or katydid taxa. Therefore, assigned categories only represent the most probable taxonomic group.

Data analyses

Acoustic recordings were analyzed using Raven Pro 1.5 (Cornel Laboratories, USA). Spectrograms were produced without filtering. Frequency spectrums were produced using Hann windows with hop size of 1000.

Generalized Linear Models (GLMs) with Poisson distribution and log-link functions, were used to compare species richness and signal characters across vertical heights, and time (Dobson 1990; Bolker *et al.* 2009; O'Hara 2009; Zuur *et al.* 2010) in Statistica 8 (Statsoft 2012). GLMs provide a flexible, robust approach for analyzing categorical and continuous data that are non-normal by using Poisson distributions with log-link functions (Bolker *et al.* 2009). Tests for the significance of the effects in the model were performed via the Wald statistic (w) (Yi & Wang 2011). The Jaccard similarity coefficient was used to compare species

composition at vertical calling heights. Data from the 3 nocturnal shifts from 21:00-09:00 hrs, and 3 diurnal shifts from 09:00-21:00 hrs were pooled and analyzed together to investigate temporal, spectral and spatial segregation of acoustic species.

Niche overlap and null model analyses were used to analyze acoustic community structure in three niche axes: spectral, temporal and spatial. The degree of competition between species is reflected by the degree of overlap within these independent niche domains (Gotelli & Graves 1996). Overlap in resource use was calculated using the Czechanowski index (Feinsinger *et al.* 1981) of niche overlap between pairs of species:

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

In this formula, O_{12} is the overlap of species 1 with species 2 and p_{i1} , p_{i2} is the frequency of utilization of resource state i by species 1 and 2 respectively. The calculated indices range from 0 (species share no resource) and 1 (species have identical resource use). The null models tests variation among species niche utilization. In other words, they test whether or not species significantly differ in resource use as compared to a baseline level of overlap in resource use that would be found even in the absence of species mutualistic or competitive interactions (Entsminger 2012). Data for null models are organized as a matrix with rows for species and columns for categorical resource states. Bin widths were 1 kHz for spectral niche utilization, 1 hour for temporal niche utilization and the three vertical heights (top, middle, bottom) for were spatial niche utilization. Generation of the null community utilized the RA3 algorithm (Winemiller & Pianka 1990), where the observed niche breadths were retained by randomizing the utilization values within each row of the matrix and reshuffling zero states (Entsminger 2012). Thus, resource states are randomized, but the degree of specialization of each species is preserved (Entsminger 2012). The RA3 algorithm is recommended because of its robustness

for niche overlap studies (Gotelli and Graves 1996) and is an appropriate measure to detect any non-random patterns in community structure (Schmidt *et al.* 2012). All simulations were carried out with EcoSim Professional (Entsminger 2012). To compare observed and simulated indices 1000 null assemblages were created for each niche axes.

Results

The acoustic community

I found a highly diverse acoustic community, with 172 acoustic species distributed across the spectral, temporal and spatial domains (Tables 2.1 & 2.2). Classification of these signals based on their spectral, temporal and psychoacoustic features, resulted in bird (n = 47), frog (n = 20), cicada (n = 19), cricket (n = 57), and katydid (n = 29) acoustic species (Tables 2.1 & 2.2). These categories represent the most likely taxon in which acoustic signals belong, but were visually unconfirmed.

Temporal partitioning

Across all vertical calling heights, there were distinct nocturnal (19:00-05:00 hrs) (Table 2.1) and diurnal (06:00-18:00 hrs) (Table 2.2) acoustic communities which only overlapped during the dawn chorus (06:00 hrs) ($w = 957.38$, $p = 0.00$). Dawn and dusk choruses were transition periods between nocturnal and diurnal communities, with some species only signaling at dawn (06:00 hrs) (Table 2.2) or dusk (19:00 hrs) (Table 2.1; Fig. 2.1). The transition from diurnal to nocturnal acoustic communities was heralded by two intensely loud cicada species (acoustic species 125 & 135) at the onset of dusk, followed by only nocturnal acoustic species signaling at dusk (19:00 hrs). By the end of 19:00 hrs, a total of 51 nocturnal species across all vertical heights had started to signal, increasing to a peak of acoustic activity at 21:00 hrs, with 74

acoustic species signaling. Acoustic activity then slowly declined to 30 species signaling at 05:00 hrs. Dawn (06:00 hrs) was the peak of acoustic activity for diurnal hours with 31 species signaling.

While the number of diurnal species ($n = 75$) and nocturnal species ($n = 97$) was similar, there was higher species turnover during diurnal hours. Across all vertical heights combined, the number of diurnal species signaling per hour was 10 ± 2.19 (mean and standard error SE), compared to 57.72 ± 4.47 for nocturnal acoustic species ($w = 31.37$, $p = 0.00$). Duration diurnal species signaled was therefore less (1.76 ± 0.15 hrs) compared to nocturnal species (6.59 ± 0.37 hrs) ($w = 46.79$, $p = 0.00$).

In terms of the likely acoustic taxa, katydids, crickets and frogs were mainly nocturnal, while birds and cicadas were predominantly diurnal. However, each of these taxonomic groups had both diurnal and nocturnal species. Interestingly, nocturnal species of all taxa signalled for longer durations than diurnal species of the same taxa. Nocturnal katydids ($n = 25$) signaled for 7.9 ± 0.75 hr (mean \pm SE) compared to diurnal katydids ($n = 4$) which signaled for 1.5 ± 0.28 hr ($w = 11.65$, $p = 0.00$). Nocturnal crickets ($n = 49$) signaled for 6.38 ± 0.50 hr compared to diurnal species ($n = 8$) which signaled for 1.12 ± 0.12 hr ($w = 17.62$, $p = 0.00$). Nocturnal cicadas ($n = 3$) signaled for 7.0 ± 3.05 hr while diurnal species ($n = 16$) only signaled for 3.06 ± 0.51 hr ($w = 5.5$, $p = 0.03$). Nocturnal frogs ($n = 15$) signaled for 5.9 ± 0.87 hr compared to diurnal frogs ($n = 5$) which signaled for 2.0 ± 0.44 hr ($w = 6.3$, $p = 0.02$). Nocturnal birds ($n = 5$) signaled for 4.0 ± 1.76 hr while diurnal birds ($n = 42$) signaled within much smaller time windows of 1.3 ± 0.12 hr ($w = 15.6$, $p = 0.00$).

Niche overlap and null model analyses of acoustic community structure indicate that temporal niche overlap of the entire acoustic assemblage (using the Czenachowski index) resulted in a low observed mean for all acoustic species (0.218) (Table 2.3). This indicates that

at the community level, there is strong diel temporal partitioning among species. At a finer scale, the nocturnal acoustic assemblage did not utilize temporal patterns (0.658) and had greater overlap of temporal patterns than expected by chance. Comparatively, the diurnal acoustic assemblage relied heavily on partitioning of temporal patterns (0.155). On the taxon scale, this pattern was also seen within nocturnal and diurnal species. Nocturnal species such as katydids, crickets and frogs did not partition the temporal domain, having much greater overlap of temporal patterns than expected by chance. In contrast, cicadas and birds, which are predominantly acoustically active during the day, displayed strong partitioning of the temporal domain (Table 2.3).

Spectral partitioning

The call structure of the entire acoustic assemblage showed considerable spectral separation of signals, although some spectral overlap between species occurred (Fig. 2.2). Katydid generally had broad band signals covering a wide spectral range >10 kHz. Due to microphone frequency range (<20 kHz), detection of ultrasonic signals was limited, and high-frequency katydid species are likely under reported here. Other acoustic taxa with lower frequency signals were recorded and detected relatively easily. Cricket signals were narrow band signals between 2.4 and 11.4 kHz. Cicada signals ranged from 2.25 to 12.48 kHz, while frogs and birds were generally <4 kHz. Owing to the great number of high-frequency nocturnal katydid species, the nocturnal acoustic spectrum utilized a greater portion of higher frequency ranges, with mean and SE center frequencies of 12.6 ± 0.8 kHz, compared to the diurnal spectrum of 5.1 ± 0.5 ($w = 27.5$, $p = 0.00$). Representative nocturnal and diurnal spectrograms displayed higher frequency ranges, and a greater number of acoustic species signaling within the spectral domain (Fig. 2.3).

Niche overlap and null model analyses of acoustic community structure showed that spectral overlap of the entire acoustic assemblage (using the Czenachowski index) resulted in a very low observed mean (0.157) (Table 2.3), indicating that all acoustic species partition the spectral domain and rely on different dominant frequencies to communicate effectively. This pattern was similar across taxa and for nocturnal and diurnal species. However, nocturnal species had slightly greater partitioning of the spectral domain than diurnal species (Table 2.3). Despite overall low spectral overlap between all acoustic species, observed values of niche overlap were slightly higher than those expected by chance.

Spatial partitioning

The tower divided into three sections, ground (0 m), mid-level (30 m) and top of the canopy (50 m), had similar mean number of species signaling at each height ($w = 2.17, p = 0.33$) (Fig. 2.4). While the mean number of nocturnal species per height level was higher than diurnal species ($w = 94.7, p = 0.00$), number (mean \pm SE) of nocturnal species signaling at ground level 19.5 ± 2.25 , mid-level 23.5 ± 1.17 and at the top of the canopy 20.5 ± 1.09 did not vary significantly ($w = 4.17, p = 0.12$). Diurnal species also had similar numbers of species signaling at ground level 5.3 ± 0.99 , mid-level 5.04 ± 1.08 and at the top of the canopy 4.76 ± 1.17 ($w = 0.09, p = 0.95$).

Although number of species signaling was fairly constant at the various heights, species composition was very different (Fig. 2.5). While there were generalist species throughout the forest structure, distinct acoustic species were also found at the ground level, mid-level and at the top of the canopy (Fig. 2.5). Jaccard similarity coefficient indicated ground and mid-levels had the greatest degree of similarity (0.55) in terms of species composition, followed by mid and top canopy levels (0.52), with the top and ground levels being the most dissimilar (0.49). Similar Jaccard coefficients between vertical heights indicate fairly equal distribution of unique

and generalist species at each calling height. This vertical stratification, with distinct acoustic assemblages at the various canopy heights, was similar for both nocturnal and diurnal species, as well as for katydid, cricket, bird and frog taxa (Tables 2.1 & 2.2). For cicadas, a different pattern emerged. No vertical stratification of calling heights occurred in cicadas and almost 90% of cicada species signalled at all levels of the forest (Fig. 2.5). Jaccard similarity coefficients for cicadas between vertical heights were extremely high, with 0.89 for mid and top levels, 0.94 for mid and ground levels and 0.94 for top and ground levels. In contrast, katydids had distinct vertical stratification of calling heights, with low Jaccard similarity coefficients between heights of 0.35 for mid and top levels, 0.29 for mid and ground levels, and 0.21 for bottom and top levels (Fig. 2.5).

I found that while both cicadas and katydids use spectral stratification, cicadas relied more on temporal than spatial stratification to avoid acoustic interference, as opposed to katydids which used spatial rather than temporal stratification (Fig. 2.6).

Spatial niche overlap for the entire acoustic assemblage resulted in a fairly equal mix between resource partitioning and resource overlap (0.507). This highlights that while some species partitioned the vertical space in the forest structure, there were also species which were acoustically active at all heights. Nocturnal species partitioned this vertical space to a greater degree than diurnal species, which was highlighted by spatial resource partitioning in katydids (0.470), and a greater amount of resource overlap than expected by chance in cicadas (0.897) (Fig. 2.6).

Is calling height correlated with call features?

The acoustic assemblage did not show any correlation with height preference and call structure in terms of pulse rate ($w = 6.39$, $p = 0.269$) and center frequency ($w = 6.9$, $p = 0.226$). This pattern was the same for nocturnal and diurnal species, as well as individual acoustic taxa.

Discussion

Tropical rain forests, characterized by a rich diversity of acoustic species, create a complex acoustic environment (Wallace 1869; Ryan & Brenowitz 1985; Riede 1997; Diwakar & Balakrishnan 2007a). The high diversity of acoustic species and architectural complexity of tropical rain forests challenges the ability of receivers to detect conspecific signals and discriminate those signals from heterospecifics (Römer *et al.* 1989; Römer 1993; Greenfield 2002; Hartbauer 2012). To further distinguish among different variants of conspecific signals in the context of mate choice poses and even greater challenge for receivers (Andersson 1994; Gerhardt & Huber 2002; Greenfield 2002; Hartbauer 2012). Acoustic interference of intraspecific communication can therefore lead to call inhibition (Schatral 1990; Greenfield 2002) with quantifiable post-inhibitory rebound (Samways 1977a) and call distortion (Samways 1976c), or a decreased efficiency in the detection and discrimination of conspecific signals (Guilford & Dawkins 1991; Endler 1993; Sueur 2002). As signaling is energetically expensive (Taigen & Wells 1985; Bailey *et al.* 1993; Hoback & Wagner 1997; Wells 2001; Gerhardt & Huber 2002), signals and signaling behaviour evolves to minimize effects of interference from other species (Sueur 2002). Coexisting species of an acoustic community therefore compete for, and partition, acoustic transmission channels in terms of spectral, temporal and spatial domains decreasing the risk of signal interference and the destruction of information encoded within energetically costly acoustic signals (Morton 1975; Hödl 1977; Henwood & Fabrick 1979; Duellman & Pyles 1983; Römer *et al.* 1989; Samways 1989; Endler 1992; Endler 1993; Römer 1993; Gogala & Riede 1995; Riede 1996; Riede 1997; Sueur 2002; Morris 2003; Diwakar & Balakrishnan 2007a; Diwakar & Balakrishnan 2007b; Jain & Balakrishnan 2011a; Schmidt *et al.* 2012; Jain *et al.* 2013).

While a fundamental and long standing goal in ecology has been to determine how species partition environmental niches at the local community level in order to coexist (MacArthur 1958; Hutchinson 1959; Kunz 1973; Schoener 1974; Shigesada *et al.* 1979; Dueser & Shuggart 1979; Winemiller & Pianka 1990; Wright 2002; Levine & HilleRisLambers 2009; Corrêa *et al.* 2011; Schmidt *et al.* 2012; Stuble *et al.* 2013; Jain *et al.* 2013) few studies have investigated interspecies acoustic interactions of an entire acoustic community. In this study we show acoustic species employ different partitioning strategies to communicate effectively in signal rich environments.

Spectral partitioning

The acoustic community of this Bornean tropical rain forest consisted of 172 acoustic species all with a low degree of spectral overlap. This implies that some species groups rely strongly on spectral partitioning to communicate effectively with little interference (Jain *et al.* 2013). While overall low spectral overlap occurred between acoustic species, observed values of niche overlap were slightly higher than those expected by chance. This indicates that some resource sharing of dominant frequencies occurs, and spectral competition is not the only structuring force (Gotelli & Graves 1996). While null models can be used to establish whether observed niche overlap is more or less than expected by chance, it is still difficult to infer the mechanisms responsible for such patterns (Gotelli & Graves 1996). Competition in temporal or spatial domains, as well as correlated ecological or evolutionary factors, may all play various roles in division of spectral acoustic space (Samways 1976d; Jain & Balakrishnan 2011; Schmidt *et al.* 2012). There is also a physical relationship between body size, frequency and the efficiency at which sound is generated, placing a lower limit on signal range acoustic taxa can generate (Greenfield 2002; Gerhardt & Huber 2002).

Irrespective of the mechanisms involved, partitioning the frequency spectrum, reduces interference by heterospecific signals and allows for a more densely packed acoustic community (Riede 1997). According to the matched-filter hypothesis (Capranica & Moffat 1983; Gerhardt & Schwarz 2001) receivers gain an advantage from being tuned to the carrier frequency of conspecific signals, which is critical in signal rich environments with high ambient noise (Kostarakos *et al.* 2008; Sueur *et al.* 2010; Schmidt *et al.* 2011; Schmidt & Römer 2011; Hartbauer 2012; Jain *et al.* 2013).

Spectral partitioning is therefore an effective strategy to maximize probability of conspecific signal reception, utilized by katydids and crickets (Riede 1993; Riede 1996; Nityananda & Balakrishnan 2006; Diwakar & Balakrishnan 2007a; Schmidt *et al.* 2011; Jain *et al.* 2013), cicadas (Sueur 2002), birds (Planqué & Slabbekoorn 2008; Luther 2009) and frogs: (Hödl 1977; Duellman & Pyles 1983; Lüddecke *et al.* 2000; Chek *et al.* 2003; Amézquita *et al.* 2006; Amézquita 2011). However, among closely-related species which are constrained by their evolutionary past, spectral partitioning is not ways be possible, which places extreme selection pressure on species to adopt other strategies such as temporal or spatial partitioning (Samways 1976d).

Temporal partitioning

There was a notable change in the total number of acoustic species signaling over a 24-hour period. Diurnal calling activity peaked during the dawn chorus (06:00 hrs) and subsequently declined until the dusk chorus (19:00 hrs) when nocturnal acoustic species became active. Nocturnal signaling was fairly constant between 19:00-0:500 hrs, with a peak at 23:00 hrs, and no new species detected after 01:00 hrs. The nocturnal activity levels here are similar to those in nocturnal Ensifera species in Southern India (Diwakar & Balakrishnan 2007a).

On a diel scale, the entire acoustic assemblage displayed temporal partitioning, with distinct nocturnal and diurnal acoustic assemblages. Diurnal acoustic assemblages, signaled within narrow time windows with extremely low temporal overlap between species, resulted in fewer species signaling per hour but with higher turnover. In contrast, the nocturnal acoustic assemblage did not use temporal partitioning, but signaled for long durations with extremely high temporal overlap between species. Therefore, nocturnal acoustic species such as katydids, crickets, frogs did not utilize temporal partitioning, whereas diurnal cicadas and bird acoustic species displayed a high degree of temporal partitioning. Interestingly, diurnally active katydids, crickets and frogs signalled within narrower time windows, whereas nocturnally active cicadas and birds did not utilize temporal partitioning. Temporal partitioning therefore appears to transcend general temporal patterns of taxa, where diurnal species utilize temporal partitioning as a strategy to communicate effectively, and nocturnally active species do not, at least here in Borneo, partition the temporal niche.

Lack of nocturnal temporal partitioning suggests other mechanisms of acoustic avoidance are sufficient to avoid acoustic overlap (Jain *et al.* 2013), or that there are insufficient cues to partition nocturnal acoustic environments. As light levels are an important cue for many species, including cicadas which exhibit precise temporal windows (Morrison 1978; Crawford & Dadone 1979; Daly *et al.* 1992; Sueur 2002; Lang *et al.* 2006; Gerrish *et al.* 2009; Narendra *et al.* 2010; Amor *et al.* 2011), lack of sufficient light levels may alter how nocturnal acoustic species partition acoustic communication channels.

These findings correspond to previous research which has documented temporal partitioning in various diurnal taxa (Talbot 1946; Albrecht & Gotelli 2001; Stuble *et al.* 2013), including birds (Ficken *et al.* 1974; Popp *et al.* 1985; Brumm 2006; Luther 2009) and cicadas (Gogala & Riede 1995; Sueur 2002), along with diel partitioning between cicadas and katydids

(Gogala & Riede 1995). Previous research also failed to find any evidence of temporal partitioning within nocturnally active acoustic assemblages of crickets and katydids (Diwakar & Balakrishnan 2007a; Schmidt *et al.* 2012; Jain *et al.* 2013). However, while katydids and crickets do not utilize nocturnal temporal partitioning on the scale of hours, they may call within narrow time windows of minutes or seconds to avoid signal interference (Jain *et al.* 2013).

Spatial partitioning

Our study revealed that vertical heights of the forest (0 m, 30 m and 50 m) were equally utilized by acoustic species, yet unique species assemblages occurred at each of these heights. Spatial niche overlap for the entire acoustic assemblage reflects a roughly equal distribution between resource partitioning and resource overlap due to a mix of species with specific calling height preferences and those without. This tendency was similar across taxa, with the exception of cicadas. Cicadas displayed a high degree of spatial overlap, indicating that partitioning temporal and spectral domains, rather than spatial, may be sufficient mechanisms to avoid acoustic interference. With certain katydids, where this spatial partitioning is violated (as by landscape fragmentation), the result is acoustic interference and song modification (Samways 1977b; Samways 1977c).

Vertical stratification has been noted to occur in assemblages of crickets and katydids (Arak & Eiriksson 1992; Nischk & Otte 2000; Diwakar & Balakrishnan 2007b; Jain & Balakrishnan 2011a; Schmidt *et al.* 2012; Jain *et al.* 2013) frogs (Hödl 1977; Drewry & Rand 1983; Lamb 1987; Ptacek 1992; Lüddecke *et al.* 2000) and birds (Marten & Marler 1977; Mathevon *et al.* 2005). However, in contrast to our study, Sueur (2002) found that nine species of cicada in Mexico had calling height preferences related to microhabitat preferences.

Vertical stratification of calling sites could be driven by a number of mechanisms including predator avoidance, microhabitat preference, or selection of calling sites that optimize signal transmission (Arak & Eiriksson 1992; Diwakar & Balakrishnan 2007b; Jain & Balakrishnan 2011a; Jain & Balakrishnan 2011b). Optimization of signals could be related to avoidance of inter- and intraspecific interference or abiotic factors such as selecting microhabitat structure that minimizes attenuation and signal degradation (Gerhardt & Huber 2002; Greenfield 2002; Jain & Balakrishnan 2011b). As there was no correlation between call features and calling height in this study or others (Asquith *et al.* 1988; Höbel & Gerhardt 2003; Diwakar & Balakrishnan 2007b), it is unlikely that signal parameters drive vertical stratification of acoustic assemblages on larger scales than the microhabitat level.

Implications for acoustic interference

To reduce signal interference and communicate effectively within this signal rich Bornean tropical rain forest, the entire acoustic assemblage partitioned spectral, temporal and spatial domains. For diurnal species such as cicadas, partitioning spectral and temporal domains alone was sufficient to avoid acoustic interference. Comparatively, nocturnal species such as katydids and crickets partitioned spectral and spatial domains, but did not utilize temporal partitioning to avoid acoustic interference. For an entire acoustic assemblage, utilization of different strategies allows many species to communicate with little interference in acoustically complex tropical forests.

How species communicate has direct implications for acoustic monitoring of species and environments. Using bioacoustic signals is a rapid, non-invasive and reliable method to detect otherwise cryptic animals in architecturally complex environments (Riede 1998). Using acoustic parameters of species-specific signals also allows them to be defined as acoustic species, addressing the taxonomic challenge (Riede 1998). However, as species partition the

acoustic environment into spectral, temporal and spatial domains, acoustic surveys need to take into account inter- and intraspecific variability of signal patterns.

References

- Albrecht, M. & Gotelli, N. J. 2001. Spatial and temporal niche partitioning in grassland ants. *Oecologia* 126:134–141.
- Amézquita, A., Castellanos, L. & Hödl, W. 2005. Auditory matching of male *Epipedobates femoralis* (Anura: Dendrobatidae) under field conditions. *Animal Behaviour* 70:1377–1386.
- Amézquita, A., Flechas, S. V., Lima, A. P., Gasser, H. & Hödl, W. 2011. Acoustic interference and recognition space within a complex assemblage of dendrobatid frogs. *Proceedings of the National Academy of Sciences of the United States of America* 108:17058–17063.
- Amor, F., Ortega, P., Cerdá, X. & Boulay, R. R. 2011. Solar elevation triggers foraging activity in a thermophilic ant. *Ethology* 117:1031–1039.
- Andersson, M. 1994. *Sexual selection*. Princeton University Press, Princeton.
- Arak, A. & Eiriksson, T. 1992. Choice of singing sites by male bush crickets (*Tettigonia viridissima*) in relation to signal propagation. *Behavioral Ecology and Sociobiology* 30:365–372.
- Asquith, A., Altig, R. & Zimba, P. 1988. Geographic variation in the mating call of the green tree frog *Hyla cinerea*. *American Midland Naturalist* 119:101–110.
- Bailey, W. J., Withers, P. C., Endersby, M. & Gaull, K. 1993. The energetic cost of calling in the bush cricket *Requena verticalis* (Orthoptera: Tettigoniidae: Listroscelidinae). *Journal of Experimental Biology* 178:21–37.
- Barker, M. G. & Pinard, M. A. 2001. Forest canopy research: sampling problems, and some solutions. *Plant Ecology* 153:23–38.
- Bee, M. A. & Micheyl, C. 2008. The cocktail party problem: what is it? How can it be solved? And why should animal behaviorists study it? *Journal of Comparative Psychology* 122:235–251.

- Bee, M. A. 2008. Finding a mate at a cocktail party: spatial release from masking improves acoustic mate recognition in grey tree frogs. *Animal Behaviour* 75:1781–1791.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J. S. S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–35.
- Bormpoudakis, D., Sueur, J. & Pantis, J. D. 2013. Spatial heterogeneity of ambient sound at the habitat type level: ecological implications and applications. *Landscape Ecology* 28:495–506.
- Bragg, P. E. 2001. *Phasmids of Borneo*. Natural History Publications, Borneo.
- Brandes, T. S., Naskrecki, P. & Figueroa, H. K. 2006. Using image processing to detect and classify narrow-band cricket and frog calls. *The Journal of the Acoustical Society of America* 120:2950–2957.
- Brumm, H. 2006. Signalling through acoustic windows: nightingales avoid interspecific competition by short-term adjustment of song timing. *Journal of Comparative Physiology A* 192:1279–1285.
- Brumm, H. & Slabbekoorn, H. 2005. Acoustic communication in noise. *Advances in the Study of Behavior* 35:151–209.
- Bryan, J. E., Shearman, P. L., Asner, G. P., Knapp, D. E., Aoro, G. & Lokes, B. 2013. Extreme differences in forest degradation in Borneo: comparing practices in Sarawak, Sabah, and Brunei. *PLOS ONE* 8(7):e69679.
- Capranica, R. R. & Moffata, J. M. 1983. Neurobehavioral correlates of sound communication in anurans. In: Ewert, J. P., Capranica, R. R. & Ingle, D. (eds.). *Vertebrate Neuroethology*. Plenum Press, New York.
- Chek, A. A., Bogart, J. P. & Lougheed, S. C. 2003. Mating signal partitioning in multi-species assemblages: a null model test using frogs. *Ecology Letters* 6:235–247.

- Corrêa, C. E., Albrecht, M. P. & Hahn, N. S. 2011. Patterns of niche breadth and feeding overlap of the fish fauna in the seasonal Brazilian Pantanal, Cuiabá River basin. *Neotropical Ichthyology* 9:637–646.
- Cranbrook, E. 1993. Research and management of the Batu Apoi Forest Reserve, Temburong, Brunei: the Universiti Brunei Darussalam / Royal Geographical Society Rainforest. *Global Ecology and Biogeography Letters* 3:267–276.
- Crawford, C. S. & Dadone, M. M. 1979. Onset of evening chorus in *Tibicen marginalis* (Homoptera: Cicadidae). *Environmental Entomology* 8:1157–1160.
- Dabelsteen, T., Larsen, O. N. & Pedersen, S. B. 1993. Habitat-induced degradation of sound signals: quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-to-noise ratio in blackbird song. *Journal of the Acoustical Society of America* 93:2206–2220.
- Daly, M., Behrends, P. R., Wilson, M. I. & Jacobs, L. F. 1992. Behavioral modulation of predation risk – Moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Animal Behaviour* 44:1–9.
- Diwakar, S. & Balakrishnan, R. 2007a. The assemblage of acoustically communicating crickets of a tropical evergreen forest in southern India: call diversity and diel calling patterns. *Bioacoustics* 16:113–135.
- Diwakar, S. & Balakrishnan, R. 2007b. Vertical stratification in an acoustically communicating ensiferan assemblage of a tropical evergreen forest in southern India. *Journal of Tropical Ecology* 23:479–486.
- Diwakar, S., Jain, M. & Balakrishnan, R. 2007. Psychoacoustic sampling as a reliable, non-invasive method to monitor orthopteran species diversity in tropical forests. *Biodiversity and Conservation* 16:4081–4093.
- Dobson, A. J. 1990. *An introduction to generalized linear models*. Chapman & Hall, New York.

- Drewry, G. E., Rand, A. S. 1983. Characteristics of an acoustic community: Puerto Rican frogs of the genus *Eleutherodactylus*. *Copeia* 1983:941–953.
- Du Preez, L. & Carruthers, V. 2009. *A complete guide to the frogs of southern Africa*. Struik Nature, Cape Town.
- Duellman, W. E. & Pyles, R. E. 1983. Acoustic resource partitioning in anuran communities. *Copeia* 3:639–649.
- Dueser, R. D., Shuggart, H. H. 1979. Niche pattern in a forest-floor small mammal fauna. *Ecology* 60:108–118.
- Dykes, A. P. 2000. Climatic patterns in a tropical rainforest in Brunei. *The Geographical Journal* 166:63–80.
- Eades, D. C., Otte, D., Cigliano G. G. & Braun, H. *Orthoptera Species File*. Version 5.0/5.0. (Accessed September 2013). <<http://Orthoptera.SpeciesFile.org>>.
- Elton, C. S. 1973. The structure of invertebrate populations inside neotropical rain forest. *Journal of Animal Ecology* 42:55–104.
- Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. *The American Naturalist* 139:125–153.
- Endler, J. A. 1993. Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society of London, Series B* 340:215–225.
- Entsminger, G. L. 2012. *EcoSim Professional: Null modeling software for ecologists, Version 1*. Acquired Intelligence Inc., Kesey-Bear & Pinyon Publishing. Montrose.
- Erwin, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin* 36:74–75.
- Feinsinger, P., Spears, E. E. & Poole, R. W. 1981. A simple measure of niche breadth. *Ecology* 62:27–32.

- Ficken, R. W., Ficken, M. S. & Hailman, J. P. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. *Science* 183:762–763.
- Floren, A., Riede, K. & Ingrisch, S. 2001. Diversity of Orthoptera from Bornean lowland rain forest trees. *Ecotropica* 7:33–42.
- Gerhardt, C. H. & Huber, F. 2002. *Acoustic communication in insects and anurans: Common problems and diverse solutions*. The University of Chicago Press, Chicago.
- Gerhardt, H. C. & Schwarz, J. J. 2001. Auditory tuning and frequency preferences in anurans. In: Ryan, M. J. (ed.). *Anuran communication*. Smithsonian Institution Press, Washington.
- Gerrish, G. A, Morin, J. G., Rivers, T. J. & Patrawala, Z. 2009. Darkness as an ecological resource: the role of light in partitioning the nocturnal niche. *Oecologia* 160:525–36.
- Gogala, M. & Riede, K. 1995. Time sharing of song activity by cicadas in Temengor Forest Reserve, Hulu Perak, and in Sabah, Malaysia. *Malayan Nature Journal* 48:297–305.
- Gotelli, N. J. & Graves, G. R. 1996. *Null models in ecology*. Smithsonian Institution Press. Washington.
- Gottsberger, B. & Gruber, E. 2004. Temporal partitioning of reproductive activity in a neotropical anuran community. *Journal of Tropical Ecology* 20:271–280.
- Goyette, J. L., Howe, R. W., Wolf, A. T. & Robinson, W. D. 2011. Detecting tropical nocturnal birds using automated audio recordings. *Journal of Field Ornithology* 82:279–287.
- Greenfield, M. D. 1988. Interspecific acoustic interactions among katydids *Neoconocephalus*: inhibition-induced shifts in diel periodicity. *Animal Behaviour* 36:684–695.
- Greenfield, M. D. 2002. *Signalers and receivers. Mechanisms and evolution of arthropod communication*. Oxford University Press, Oxford.
- Guilford, T. & Dawkins, M. S. 1991. Receiver psychology and the evolution of animals signals. *Animal Behaviour* 42:1–14.

- Hartbauer, M., Siegert, M. E., Fertschai, I. & Römer, H. 2012. Acoustic signal perception in a noisy habitat: lessons from synchronising insects. *Journal of Comparative Physiology. A* 198:397–409.
- Heller, K. G. & Helversen, O. 1989. Resource partitioning of sonar frequency bands in Rhinolophoid bats. *Oecologia* 80:178–186.
- Henwood, K. & Fabrick, A. 1979. A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. *The American Naturalist* 114:260–274.
- Hoback, W. W. & Wagner, E. W. 1997. The energetic costs of calling in the variable field cricket, *Gryllus lineaticeps*. *Physiological Entomology* 22:286–290.
- Höbel, G. & Gerhardt, H. C. 2003. Reproductive character displacement in the acoustic communication system of green tree frogs (*Hyla cinerea*). *Evolution* 57:894–904.
- Hödl, W. 1977. Call differences and calling site segregation in anuran species from Central Amazonian floating meadows. *Oecologia* 28:351–363.
- Hsu, M. Y., Kam, Y. C. & Fellers, G. M. 2006. Temporal organization of an anuran acoustic community in a Taiwanese subtropical forest. *Journal of Zoology (London)* 269:331–339.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* 93:145–159.
- Inger, R. E. & Stuebing, R. B. 1999. *A field guide to the snakes of Borneo*. Natural History Publications, Borneo.
- Inger, R. E. & Stuebing, R. B. 1997. *A field guide to the frogs of Borneo*. Natural History Publications, Borneo.
- Jain, M. & Balakrishnan, R. 2011a. Does acoustic adaptation drive vertical stratification? A test in a tropical cricket assemblage. *Behavioral Ecology* 23:343–354.

- Jain, M. & Balakrishnan, R. 2011b. Microhabitat selection in an assemblage of crickets (Orthoptera: Ensifera) of a tropical evergreen forest in Southern India. *Insect Conservation and Diversity* 4:152–158.
- Jain, M., Diwakar, S., Bahuleyan, J., Deb, R. & Balakrishnan, R. 2013. A rain forest dusk chorus: cacophony or sounds of silence? *Evolutionary Ecology* doi:10.1007/s10682-013-9658-7.
- Jones, G. & Siemers, B. M. 2010. The communicative potential of bat echolocation pulses. *Journal of Comparative Physiology A*. 197:447–457.
- Kime, N. M., Turner, W. R. & Ryan, M. J. 2000. The transmission of advertisement calls in Central American frogs. *Behavioural Ecology* 11:71–83.
- Kingston, T., Jones, G., Zubaid, A. & Kunz, T. H. 2000. Resource partitioning in Rhinolophoid bats revisited. *Oecologia* 124:332–342.
- Kostarakos, K., Hartbauer, M. & Römer, H. 2008. Matched filters, mate choice and the evolution of sexually selected traits. *PLOS ONE* 3:e3005.
- Krause, B., Gage, S. H. & Joo, W. 2011. Measuring and interpreting the temporal variability in the soundscape at four places in Sequoia National Park. *Landscape Ecology* 26:1247–1256.
- Kunz, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. *Journal of Mammalogy* 54:14–32.
- Lamb, T. 1987. Call site selection in a hybrid population of tree frogs. *Animal Behaviour* 35:1140–1144.
- Lang, A. B., Kalko, E. K. V, Römer, H., Bockholdt, C. & Dechmann, D. K. N. 2006. Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia* 146:659–66.
- Levine, J. M., Hillerislambers, J. 2009. The importance of niches for the maintenance of species diversity. *Nature* 461:254–257.

- Lüddecke, H., Amézquita, A., Bernal, X. & Guzmán, F. 2000. Partitioning of vocal activity in a neotropical highland-frog community. *Studies on Neotropical Fauna and Environment* 35:185–194.
- Luther, D. A. 2009. The influence of the acoustic community on songs of birds in a neotropical rain forest. *Behavioural Ecology* 20:864.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599–619.
- Malkmus, R. & Riede, K. 1993. Nachtrag zu *Leptolalax pictus* Malkmus, 1992 (Anura: Pelobatidae). *Sauria* 15:7–9.
- Malkmus, R. & Riede, K. 1996. Frogs from Kinabalu Borneo. *Sauria* 18:37–37.
- Marten, K. & Marler, P. 1977. Sound transmission and its significance for animal vocalization. *Behavioral Ecology and Sociobiology* 2:271–290.
- Mathevon, N., Aubin, T. & Dabelsteen, T. 1996. Song degradation during long-range propagation: importance of song post in the wren *Troglodytes troglodytes*. *Ethology* 102:397–412.
- Mathevon, N., Dabelsteen, T. & Blumenrath, S. H. 2005. Are high perches in the blackcap *Sylvia atricapilla* song or listening posts? A sound transmission study. *Journal of the Acoustical Society of America* 117:442–449.
- Montealegre-Z, F., Morris, G. K. & Mason, A. C. 2006. Generation of extreme ultrasonics in rainforest katydids. *Journal of Experimental Biology* 209:4923–4937.
- Morris, D.W. 2003. Toward an ecological synthesis: a case for habitat selection. *Oecologia* 136:1–13.
- Morrison, D. W. 1978. Lunar phobia in a Neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera Phyllostomidae). *Animal Behaviour* 26:852–855.

- Morton, E. S. 1975. Ecological sources of selection on avian sounds. *The American Naturalist* 109:17–34.
- Myers, S. 2009. *Birds of Borneo: Brunei, Sabah, Sarawak, and Kalimantan*. Princeton Field Guides, Princeton University Press. Princeton.
- Narendra, A., Reid, S. F. & Hemmi, J. M. 2010. The twilight zone: ambient light levels trigger activity in primitive ants. *Proceedings of the Royal Society of London B* 277:1531–1538.
- Nemeth, E., Winkler, H. & Dabelsteen, T. 2001. Differential degradation of antbird songs in a neotropical rainforest: adaptation to perch height? *Journal of the Acoustical Society of America* 110:3263–3274.
- Nischk, F. & Otte, D. 2000. Bioacoustics, ecology and systematics of Ecuadorian rainforest crickets (Orthoptera: Gryllidae: Phalangopsinae), with a description of four new genera and ten new species. *Journal of Orthoptera Research* 9:229–254.
- Nischk, F. & Riede, K. 2001. Bioacoustics of two cloud forest ecosystems in Ecuador compared to lowland rainforest with special emphasis on singing cricket species. In: Nieder, J. & Barthlott, W. (eds.). *Epiphytes and canopy fauna of the Otongan rain forest (Ecuador). Results of the Bonn – Quito epiphyte project, funded by the Volkswagen Foundation (Vol. 2 of 2)*. Books on Demand GmbH, Bonn.
- Nityananda, V. & Balakrishnan, R. 2006. A diversity of songs among morphologically indistinguishable katydids of the genus *Mecopoda* (Orthoptera: Tettigoniidae) from Southern India. *Bioacoustics* 15:223–250.
- O’Hara, R. B. 2009. How to make models add up – a primer on GLMMs. *Annales Zoologici Fennici* 46:124–37.
- Orr, A.G. 2003. *A guide to the dragonflies of Borneo: Their identification and biology*. Natural History publications, Borneo.

- Orr, A. G. & Hauser, C. L. 1996. Temporal and spatial patterns of butterfly diversity in a lowland tropical rainforest. In: Edwards, D. S., Booth, W. E. & Choy, S. C. (eds.). *Tropical rainforest research – current issues*. Kluwer, Dordrecht.
- Otte, D. 1992. Evolution of cricket songs. *Journal of Orthoptera Research* 1:25–49.
- Parker, G. G. 1995. Structure and microclimate of forest canopies. In: Lowman, M. D. & Nadkarni, N. M. (eds.). *Forest canopies*. Academic Press, San Diego.
- Planqué, R., Slabbekoorn, H. 2008. Spectral overlap in songs and temporal avoidance in a Peruvian bird assemblage. *Ethology* 114:262–271.
- Popp, J. W., Ficken, R. W. & Reinartz, J. A. 1985. Short-term temporal avoidance of interspecific acoustic interference among forest birds. *Auk* 102:744–748.
- Ptacek, M. B. 1992. Calling sites used by male gray tree frogs, *Hyla versicolor* and *Hyla chrysoscelis*, in sympatry and allopatry in Missouri. *Herpetologica* 48:373–382.
- Riede, K. 1993. Monitoring biodiversity: analysis of Amazonian rainforest sounds. *Ambio* 22:546–548.
- Riede, K. 1996. Diversity of sound-producing insects in a Bornean lowland rain forest. In: Edwards, D. S., Booth, W. E. & Choy, S. C. (eds.). *Tropical Rainforest Research – Current Issues*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Riede, K. 1997. Bioacoustic diversity and resource partitioning in tropical calling communities. In: Ulrich, H. (ed.). *Tropical biodiversity and systematics. Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems, Bonn 1994*. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.
- Riede, K. 1998. Acoustic monitoring of Orthoptera and its potential for conservation. *Journal of Insect Conservation* 2:217–223.

- Römer, H. 1993. Environmental and biological constraints for the evolution of long-range signaling and hearing in acoustic insects. *Philosophical Transactions of the Royal Society of London Series B* 340:179–185.
- Römer, H., Bailey, W. J. & Dadour, I. 1989. Insect hearing in the field. III. Masking by noise. *Journal of Comparative Physiology A* 164:609–620.
- Ryan, M. J. & Brenowitz, E. A. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *The American Naturalist* 126:87–100.
- Schatral, A. 1990. Interspecific acoustic interactions in bushcrickets. In: Bailey, W. J. & Rentz, D. C. F. (eds.). *The Tettigoniidae: biology, systematics and evolution*. Springer-Verlag, Berlin.
- Samways, M. J. 1976a. Effect of vegetation noise on the singing behaviour of *Platycleis intermedia* (Orthoptera, Tettigoniidae). *Biophon* 4:4–8.
- Samways, M. J. 1976b. Song modification in the Orthoptera. I. Proclamation songs of *Platycleis* spp. (Tettigoniidae). *Physiological Entomology* 1:131–149.
- Samways, M. J. 1976c. Song modification in the Orthoptera. II. Microsyllabic echemes in *Platycleis* spp. *Physiological Entomology* 1:299–303.
- Samways, M. J. 1976d. Habitats and habits of *Platycleis* spp. (Orthoptera, Tettigoniidae) in southern France. *Journal of Natural History* 10:643–667.
- Samways, M. J. 1977a. Song modification in the Orthoptera. IV. The *Platycleis intermedia/P. affinis* interaction quantified. *Physiological Entomology* 2:301–315.
- Samways, M. J. 1977b. Bush cricket interspecific acoustic interactions in the field (Orthoptera, Tettigoniidae). *Journal of Natural History* 11:155–168.
- Samways, M. J. 1977c. Effect of farming on population movements and acoustic behaviour of two bush crickets (Orthoptera, Tettigoniidae). *Bulletin of Entomological Research* 67:471–481.

- Samways, M. J. 1989. Insect conservation and landscape ecology: a case-history of bush crickets (Tettigoniidae) in southern France. *Environmental Conservation* 16:217–226.
- Samways, M. J. & Broughton, W. B. 1976. Song modification in the Orthoptera. III. Types of acoustic interaction between *Platycleis intermedia* and other species of the genus. *Physiological Entomology* 1:287–297.
- Schmidt, A. K. D. & Römer, H. 2011. Solutions to the cocktail party problem in insects: selective filters, spatial release from masking and gain control in tropical crickets. *PLOS ONE* 6:e28593.
- Schmidt, A. K. D., Riede, K. & Römer, H. 2011. High background noise shapes selective auditory filters in a tropical cricket. *Journal of Experimental Biology* 214:1754–1762.
- Schmidt, A. K. D., Römer, H. & Riede, K. 2012. Spectral niche segregation and community organization in a tropical cricket assemblage. *Behavioral Ecology* 24:470–480.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–30.
- Shigesada, N., Kawasaki, K. & Teramoto, E. 1979. Spatial segregation of interacting species. *Journal of Theoretical Biology* 79:83–99.
- Small, A., Martin, T. G., Kitching, R. L. & Wong, K. M. 2004. Contribution of tree species to the biodiversity of a 1ha Old World rainforest in Brunei, Borneo. *Biodiversity and Conservation* 13:2067–2088.
- Statsoft, Inc. 2012. Statistica (data analysis software system), version 11. www.statsoft.com.
- Sterck, F. J., Bongers, F. & Newbery, D. M. 2001. Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. *Plant Ecology* 153:279–292.
- Stork, N. E. 1991. The composition of the arthropod fauna of Bornean lowland rain forest trees. *Journal of Tropical Ecology* 7:161–180.

- Stuble, K. L., Rodriguez-Cabal, M. A., McCormick, G. L., Jurić, I., Dunn, R. R. & Sanders, N. J. 2013. Tradeoffs, competition, and coexistence in eastern deciduous forest ant communities. *Oecologia* 171:981–92.
- Sueur, J. & Aubin, T. 2003. Is microhabitat segregation between two cicada species (*Tibicina haematodes* and *Cicada orni*) due to calling song propagation constraints? *Naturwissenschaften* 90:322–326.
- Sueur, J. 2002. Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera: Cicadomorpha: Cicadidae). *Biological Journal of the Linnean Society* 75:379–394.
- Sueur, J. M., Windmill, J. F. C. & Robert, D. 2010. Sound emission and reception tuning in three cicada species sharing the same habitat. *The Journal of the Acoustical Society of America* 127:1681–1688.
- Taigen, T. L. & Wells, K. D. 1985. Energetics of vocalizations by an anuran amphibian. *Journal of Comparative Physiology* 155:163–170.
- Talbot, M. 1946. Daily fluctuations in aboveground activity of three species of ants. *Ecology* 27:65–70.
- Wallace, A. R. 1869. *The Malay archipelago*. Tynron Press, Scotland.
- Wells, K. D. 2001. The energetics of calling in frogs. In: RYAN, M. J. (ed.). *Anuran Communication*. Smithsonian Institution Press, Washington.
- Whitmore, T. C. 1991. *An introduction to tropical rain-forests*. Clarendon, Oxford.
- Wiley, R. H. & Richards, D. G. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: Kroodsma, D. E. & Miller, E. H. (eds.). *Acoustic communication in birds*. Academic Publishers, Ithaca, New York.

- Wiley, R. H. & Richards, D. G. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behavioural Ecology and Sociobiology* 3:69–94.
- Winemiller, K. O. & Pianka, E. R. 1990. Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60:27–55.
- Wollerman, L. 1999. Acoustic interference limits call detection in a Neotropical frog *Hyla ebraccata*. *Animal Behaviour* 57:529–536.
- Wollerman, L. & Wiley, R. H. 2002. Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. *Animal Behaviour* 63:15–22.
- Wright, S. J. 2002. Plant diversity in tropical forests: a review of the mechanisms of species coexistence. *Oecologia* 130:1–14.
- Yi, Y. & Wang, X. 2011. Comparison of Wald score and likelihood ratio tests for response adaptive designs. *Journal of Statistical Theory and Applications* 10:553–569.
- Zuur, A. F., Elena, N. I. & Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:1–14.

Table 2.1. Nocturnal acoustic species detected across all vertical heights (T= Top 50 m; M= Mid 30 m; G= Ground 0 m), with hours in which they were detected (time), signal parameters of mean pulse rate (pulse r.) (number of pulses per second) and mean center frequency (kHz). All acoustic species were assigned a probable taxa category based on signal characteristics (k= katydid; cr= cricket; ci= cicada, f= frog; b= bird).

ID	taxa	pulse r.	kHz	TMG	time	ID	taxa	pulse r.	kHz	TMG	time	ID	taxa	pulse r.	kHz	TMG	time
1	b	0.15	0.54	t mg	19–24	34	ci	27.03	4.04	t mg	21–5	66	cr	16.82	7.56	mg	20–5
2	b	0.09	0.93	t mg	5–7	35	cr	2.29	4.05	t mg	19–5	67	cr	24.39	7.71	m	19–22
3	f	3.33	0.96	t mg	19–3	36	cr	12.99	4.10	m	3	68	k	4.76	7.96	t mg	19–4
4	b	0.07	1.02	g	19	37	cr	6.41	4.34	mg	20–3	69	cr	43.48	8.17	mg	19–5
5	f	2.74	1.10	t mg	19–3	38	cr	5.05	4.36	t mg	20–1	70	k	13.75	8.25	t	20–4
6	f	0.05	1.13	t	22–24	39	ci	29.41	4.37	t mg	19–5	71	cr	2.40	8.75	g	20–3
7	f	0.29	1.27	mg	22–2	40	k	0.07	4.56	m	5	72	cr	27.78	8.87	t mg	19–1
8	f	0.25	1.31	t	24	41	cr	66.67	4.58	t mg	19–5	73	ci	100.00	8.88	m	19
9	f	9.01	1.49	t mg	19–24	42	cr	12.45	4.76	g	20–24	74	cr	18.96	9.49	t mg	20–24
10	b	0.12	1.54	mg	20–5	43	cr	31.33	4.82	t m	22–23	75	k	10.51	10.35	m	19–4
11	f	0.07	1.59	t mg	19–3	44	cr	9.21	4.84	g	22–4	76	cr	8.47	10.42	t mg	19–3
12	f	0.04	1.75	mg	20–23	45	k	9.90	4.97	m	19–4	77	k	11.33	10.58	m	5
13	f	1.54	1.99	t mg	19–5	46	cr	2.73	5.06	t m	19–2	78	k	94.38	10.75	mg	21–5
14	f	1.08	2.04	t mg	19–24	47	cr	9.18	5.11	m	4	79	k	2.19	11.27	mg	19–3
15	b	0.44	2.38	m	5	48	cr	23.49	5.18	t mg	5	80	k	0.35	11.38	mg	19–5
16	cr	32.26	2.41	mg	23–5	49	cr	25.74	5.25	g	20–1	81	cr	8.68	11.40	t m	19–3
17	f	4.53	2.60	t m	19–3	50	cr	2.80	5.26	g	1	82	k	2.08	12.70	t m	19–4
18	cr	1.57	2.72	t mg	19–5	51	cr	15.15	5.39	t m	19–3	83	k	0.58	12.86	t m	20–4
19	cr	18.52	2.91	t m	20–3	52	cr	14.72	5.54	mg	19–5	84	k	30.30	13.58	m	21
20	cr	1.46	2.96	t mg	19–4	53	cr	9.10	5.74	mg	5	85	k	0.51	13.63	t m	19–5
21	cr	35.71	3.07	mg	20–3	54	cr	14.99	5.94	t	19–2	86	k	5.69	14.44	t	20–4
22	cr	6.42	3.22	t mg	19–3	55	cr	15.20	6.12	t mg	20–3	87	k	5.85	14.48	t m	19–5
23	cr	13.54	3.41	t mg	19–1	56	cr	6.21	6.14	m	23	88	k	0.19	14.60	t m	19–4
24	cr	3.96	3.46	t mg	19–3	57	cr	25.00	6.54	t mg	19–5	89	k	9.98	14.73	t	19–4
25	cr	76.92	3.50	t mg	19–3	58	cr	45.45	6.61	mg	20–5	90	k	163.71	16.14	m	19–4
26	f	1.78	3.62	m	5	59	cr	1.70	6.66	m	23	91	k	250.00	18.79	t	19
27	cr	18.52	3.64	g	21	60	cr	3.70	6.90	m	22	92	k	0.32	18.94	t	21–4
28	cr	20.83	3.67	mg	20–1	61	cr	0.10	6.91	m	23	93	k	43.48	20.75	mg	19–4
29	f	1.51	3.71	t	19–24	62	f	0.07	6.96	m	21	94	k	226.56	21.00	g	19–5
30	f	83.33	3.76	g	20–5	63	cr	19.61	7.02	t m	19–23	95	k	2.92	21.33	t m	19–3
31	cr	10.63	3.84	t mg	19–1	64	cr	3.91	7.37	g	22–4	96	k	54.08	23.23	m	19
32	cr	2.38	3.94	t	24	64	cr	3.91	7.37	g	22–4	97	k	5.70	33.00	t	19–4
33	cr	2.00	3.98	m	19–21	65	cr	1.63	7.41	t mg	19–3						

Table 2.2. Diurnal acoustic species detected across all vertical heights (T= Top 50 m; M= Mid 30 m; G= Ground 0 m), with hours in which they were detected (time), signal parameters of mean pulse rate (pulse r.) (number of pulses per second) and mean center frequency (kHz). All acoustic species were assigned a probable taxa category based on signal characteristics (k= katydid; cr= cricket; ci= cicada, f= frog; b= bird).

ID	taxa	pulse r.	kHz	TMG	time	ID	taxa	pulse r.	kHz	TMG	time	ID	taxa	pulse r.	kHz	TMG	time
98	b	1.34	0.47	t m	6	130	b	0.50	3.00	mg	5	162	b	1.16	6.56	t m	6
99	f	1.04	0.63	m	16	131	b	0.80	3.00	mg	5	163	cr	2.07	6.80	t mg	7
100	b	5.78	0.74	t mg	9–10	132	b	0.27	3.00	t mg	9	164	cr	0.14	8.06	m	17
101	f	0.56	0.75	m	17	133	b	1.13	3.05	t mg	6	165	cr	4.59	8.18	t mg	6
102	b	1.00	0.81	t m	11	134	b	4.31	3.06	t	9	166	ci	500.00	8.23	t mg	6–11
103	b	0.09	0.93	t	10	135	ci	3.74	3.09	t mg	17–18	167	ci	110.41	9.00	t mg	16–17
104	b	3.02	0.94	t m	17	136	b	13.70	3.09	t mg	6	168	ci	35.77	12.38	mg	11–1
105	b	1.79	1.03	t	5	137	ci	166.67	3.15	t mg	6–11	169	ci	333.33	12.48	t mg	8–13
106	b	3.70	1.10	t	10	138	b	3.18	3.26	t mg	6	170	k	0.26	13.92	t mg	6
107	b	0.37	1.10	m	17	139	ci	135.66	3.38	t mg	9–11	171	k	340.35	16.83	t mg	6
108	b	1.09	1.13	m	15	140	ci	8.55	3.66	t mg	10–12	172	k	9.33	18.19	t m	11–12
109	b	0.87	1.13	m	16–17	141	b	0.16	3.66	t m	6						
110	b	0.21	1.20	t	6	142	ci	200.00	3.75	t mg	13–17						
111	f	1.06	1.23	t m	9–11	143	ci	492.68	3.75	t mg	16						
112	f	0.87	1.78	mg	6	144	b	0.51	3.80	t mg	6						
113	f	16.42	1.86	t mg	9–11	145	b	4.72	3.94	m	17						
114	b	6.06	1.86	t m	9–11	146	cr	4.96	4.41	t	10–11						
115	b	12.05	1.88	t	12	147	b	0.59	4.50	t mg	6						
116	b	2.80	1.88	t mg	6	148	b	0.40	4.66	t mg	6						
117	b	5.95	1.92	t mg	6	149	b	1.71	4.91	m	9						
118	b	0.65	1.99	t mg	7	150	ci	100.00	4.97	t mg	6						
119	b	7.75	2.02	t	10	151	b	0.67	5.06	t	12						
120	b	2.45	2.02	t mg	7	152	b	1.32	5.06	t	12						
121	b	0.81	2.05	t	10–12	153	cr	0.25	5.06	g	6						
122	b	7.35	2.06	mg	6	154	cr	9.43	5.12	g	10						
123	b	7.12	2.16	t	5	155	cr	0.18	5.25	g	6						
124	b	8.21	2.25	t	12	156	cr	0.85	5.91	t	9						
125	ci	0.62	2.25	t mg	18	157	ci	200.00	6.00	t mg	11–16						
126	b	3.69	2.34	g	6	158	b	1.93	6.19	t m	6						
127	b	2.08	2.77	m	9	159	b	0.36	6.45	t m	6						
128	ci	142.86	2.81	t mg	6	160	ci	44.60	6.56	t mg	15–16						
129	ci	43.70	3.00	t mg	12	161	k	20.83	6.56	m	16						

Table 2.3. The amount of niche overlap (spectral; temporal; spatial) calculated between all species pairs, nocturnal species, diurnal species and probable taxa group (katydid, cricket, cicada, frog, bird). Observed and simulated indices of the model are indicated. The calculated indices range from 0 (species share no resource) and 1 (species have identical resource use).

Niche Overlap	All sp.	Noc. sp.	Diur. sp.	katydid	cricket	cicada	frog	bird
Spectral								
Observed mean	0.157	0.075	0.120	0.044	0.136	0.128	0.284	0.200
mean of simulated indices	0.045	0.030	0.031	0.030	0.031	0.031	0.031	0.031
p - value	0.000	0.000	0.000	0.047	0.000	0.000	0.000	0.000
Temporal								
Observed mean	0.218	0.658	0.155	0.699	0.517	0.107	0.320	0.157
mean of simulated indices	0.153	0.273	0.049	0.303	0.035	0.015	0.032	0.045
p - value	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Spatial								
Observed mean	0.507	0.492	0.538	0.470	0.498	0.897	0.492	0.493
mean of simulated indices	0.494	0.474	0.523	0.410	0.486	0.896	0.485	0.462
p - value	0.000	0.002	0.010	0.005	0.043	0.000	0.027	0.002

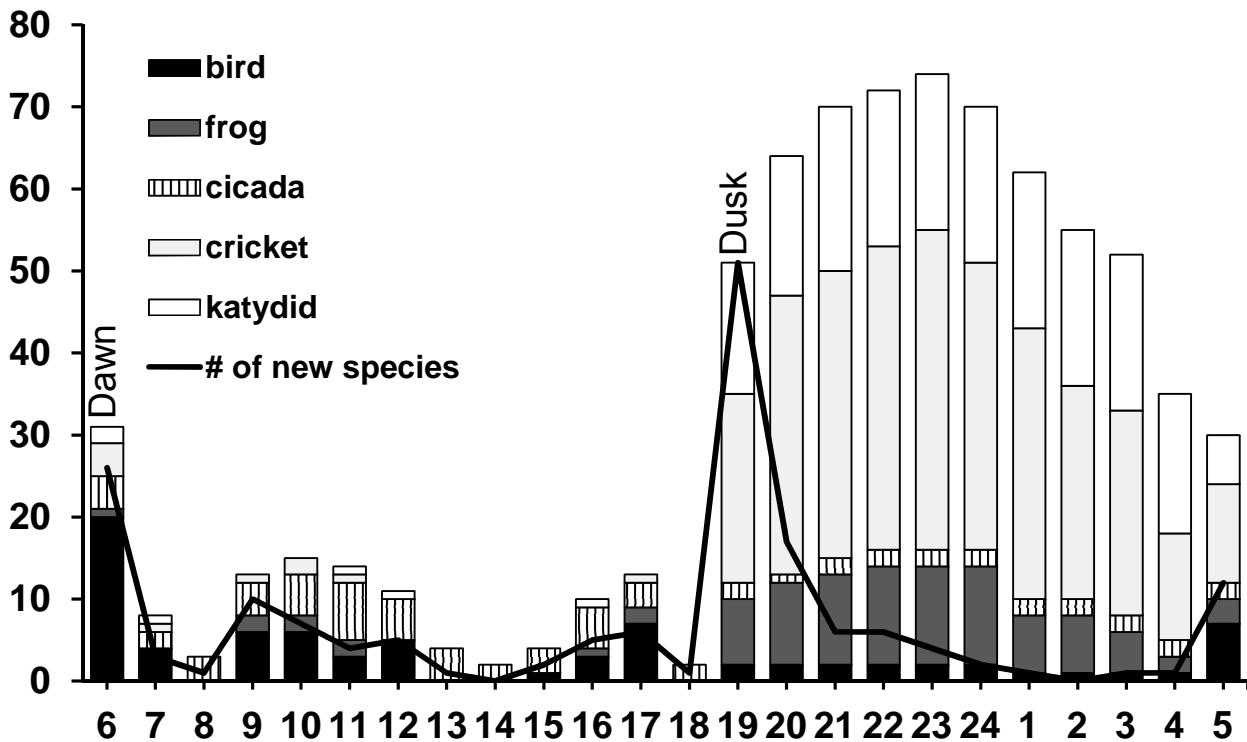


Figure 2.1. Total acoustic species signaling across all vertical heights per hour for 24 hours. Acoustic species are partitioned into probable taxa. Distinct diurnal (06:00-18:00 hrs) and nocturnal (19:00-05:00) acoustic communities were present. Solid line indicates the number of new species which start to signal within each hour. Peaks of new species occur at dawn (06:00 hrs) and dusk (19:00 hrs). Diurnal species have relatively low total number of acoustic species signaling per hour, but a relatively high number of new species which start to signal each hour, indicating high species turn over and low temporal overlap. Nocturnal species had higher total number of species signaling per hour, with very low number of new species signaling each hour, indicating high temporal overlap of species.

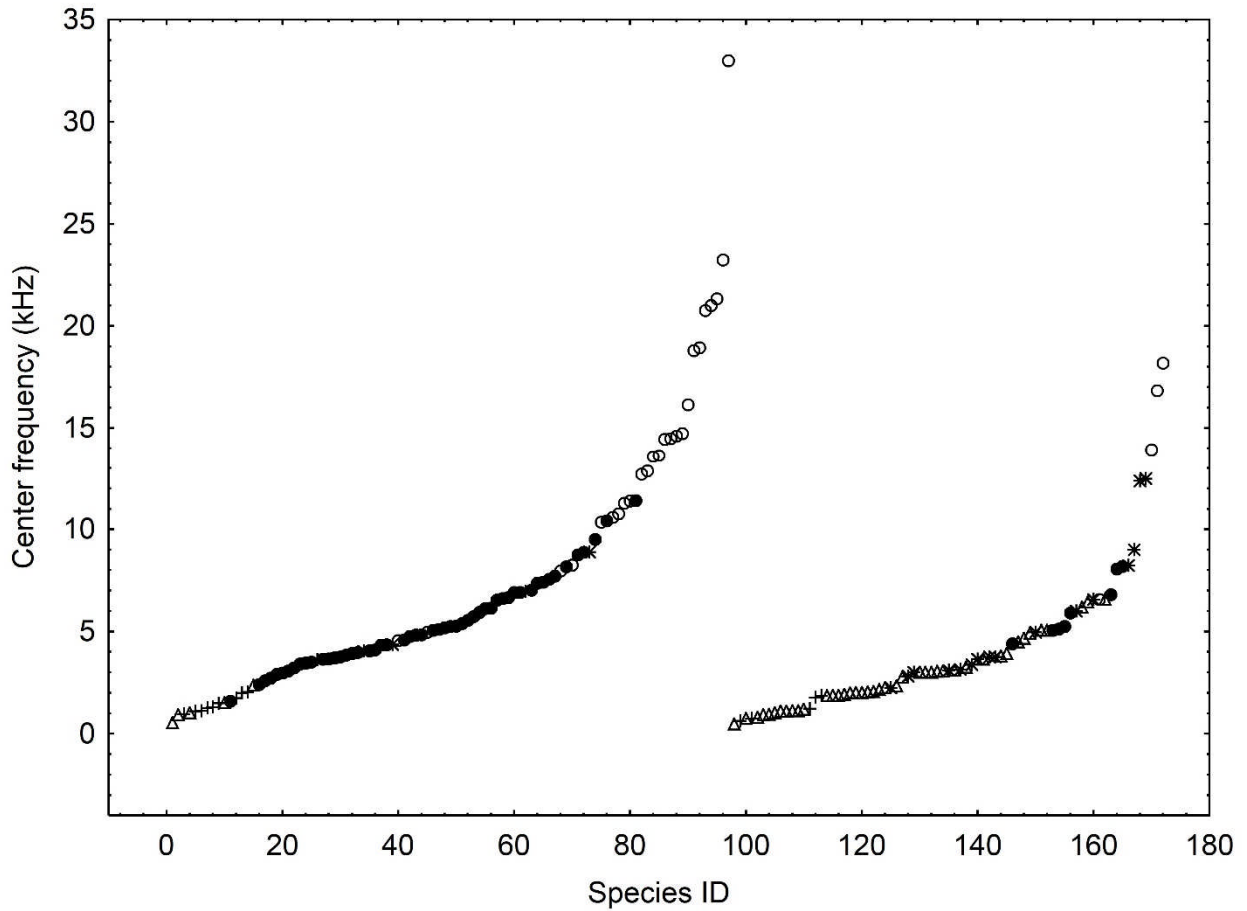


Figure 2.2. Spectral partitioning of center frequency (kHz) nocturnal (left) and diurnal (right) acoustic species utilize. Acoustic taxa are represented by the following symbols: katydids (o) had; cricket (\blacksquare); cicada (*); frog (+); bird (Δ). Katydid signals were above 10 kHz; crickets 2.4-11.4 kHz; cicada 2.22-12.48 kHz; and frogs and birds below 4 kHz. Nocturnal species show usage of higher frequencies. Overall, acoustic species displayed low spectral niche overlap (0.157) (Table 2.3).

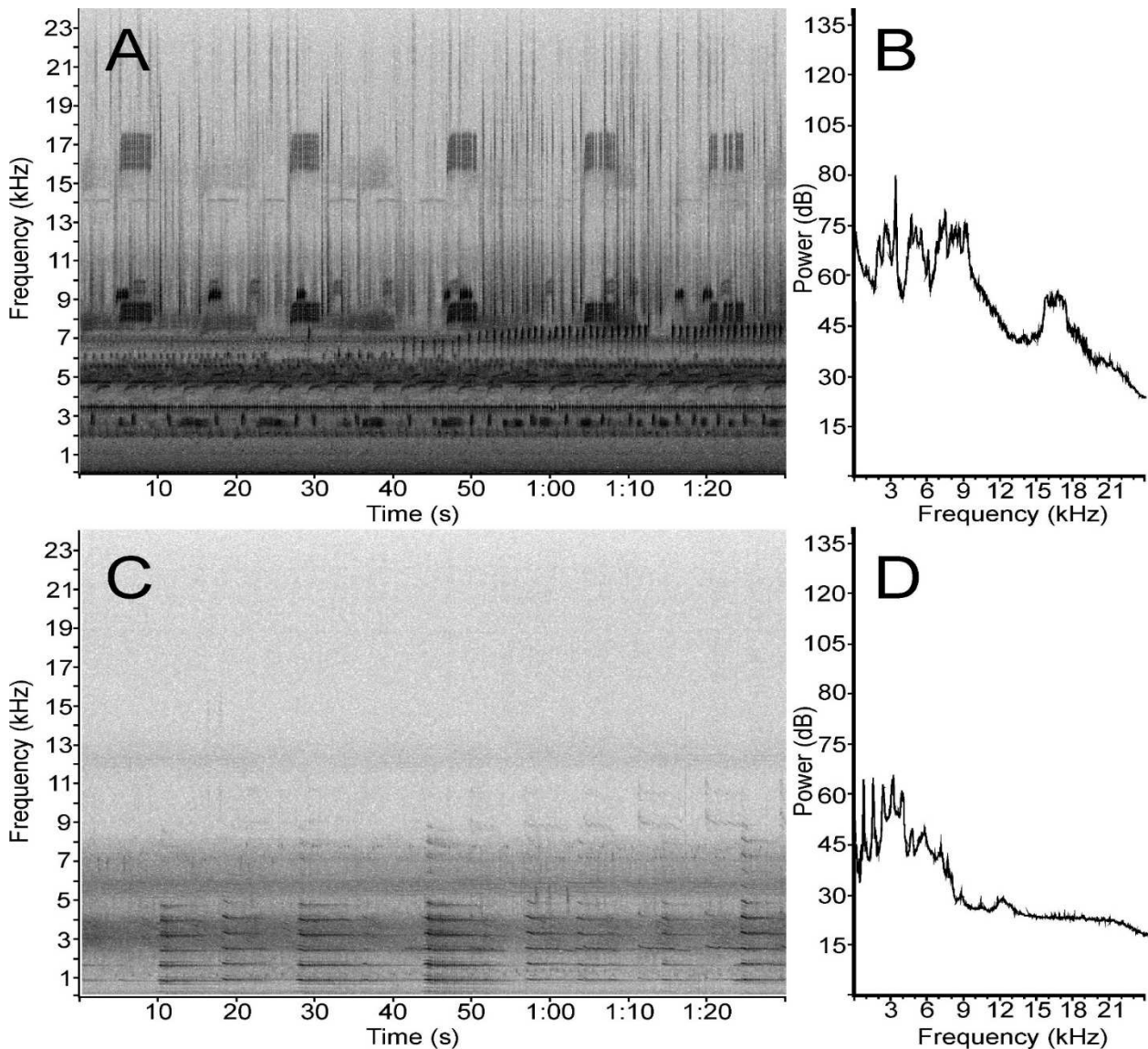


Figure 2.3. Spectrograms (A & C) display unfiltered, species-specific signals in frequency (kHz) versus time (s) with darker colours representing higher decibels (dB). Frequency spectrums (B & D) were produced using Hann windows with hop size of 1000. Spectrogram A and its associated frequency spectrum B, show a representative nocturnal soundscape, with a large number of acoustic species signaling across the frequency spectrum. The frequency spectrum shows greater utilization of upper frequency ranges. Spectrogram C and its associated frequency spectrum D display a representative diurnal soundscape, in this case with signal from cicada species #135. Diurnal soundscapes have less species calling per hour and utilize less upper frequency ranges than nocturnal soundscapes.

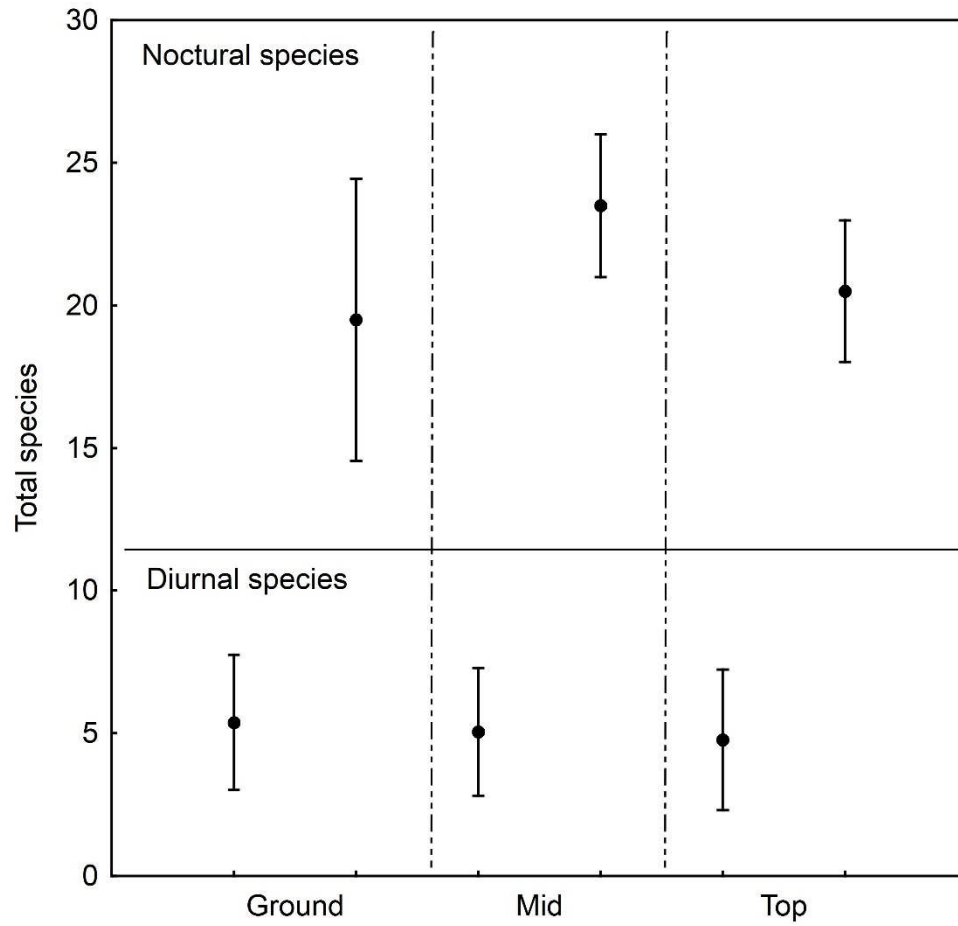


Figure 2.4. Calling heights within the forest structure (ground 0 m; mid 30 m; top 50 m) were equally utilized by nocturnal and diurnal species. The mean number of nocturnal species signalling concurrently at each height was greater than the mean number of diurnal species ($w = 94.7, p = 0.00$).

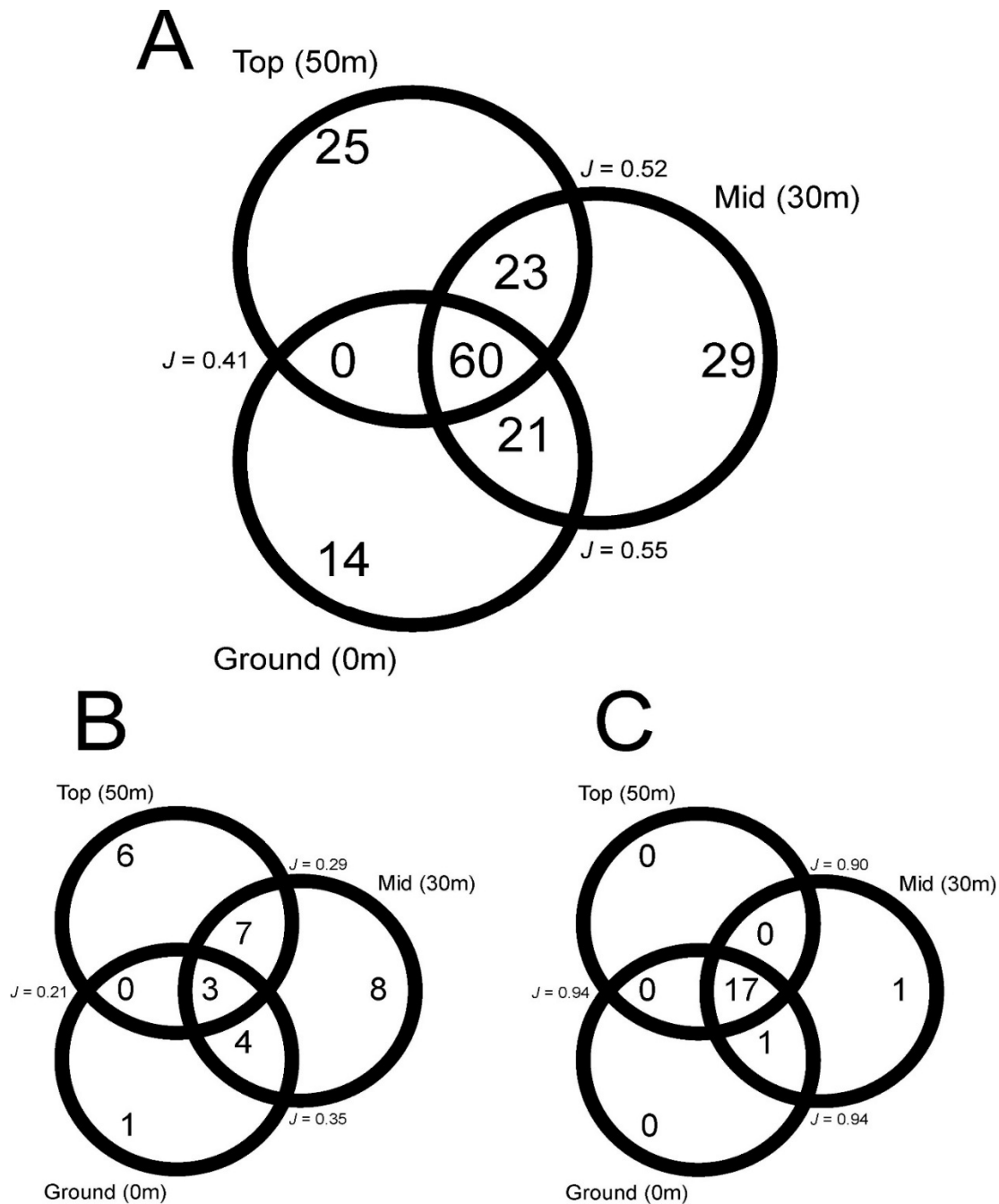


Figure 2.5. Venn diagrams and Jaccard indices for A) total acoustic species composition B) katydid and C) cicada species composition across vertical calling heights at (ground 0 m; mid 30 m; top 50 m). While some acoustic species had overlapping calling height preference, distinct acoustic assemblages occurred at each height within the forest structure for all taxa with the exception of cicadas. Cicadas showed no vertical stratification of calling heights.

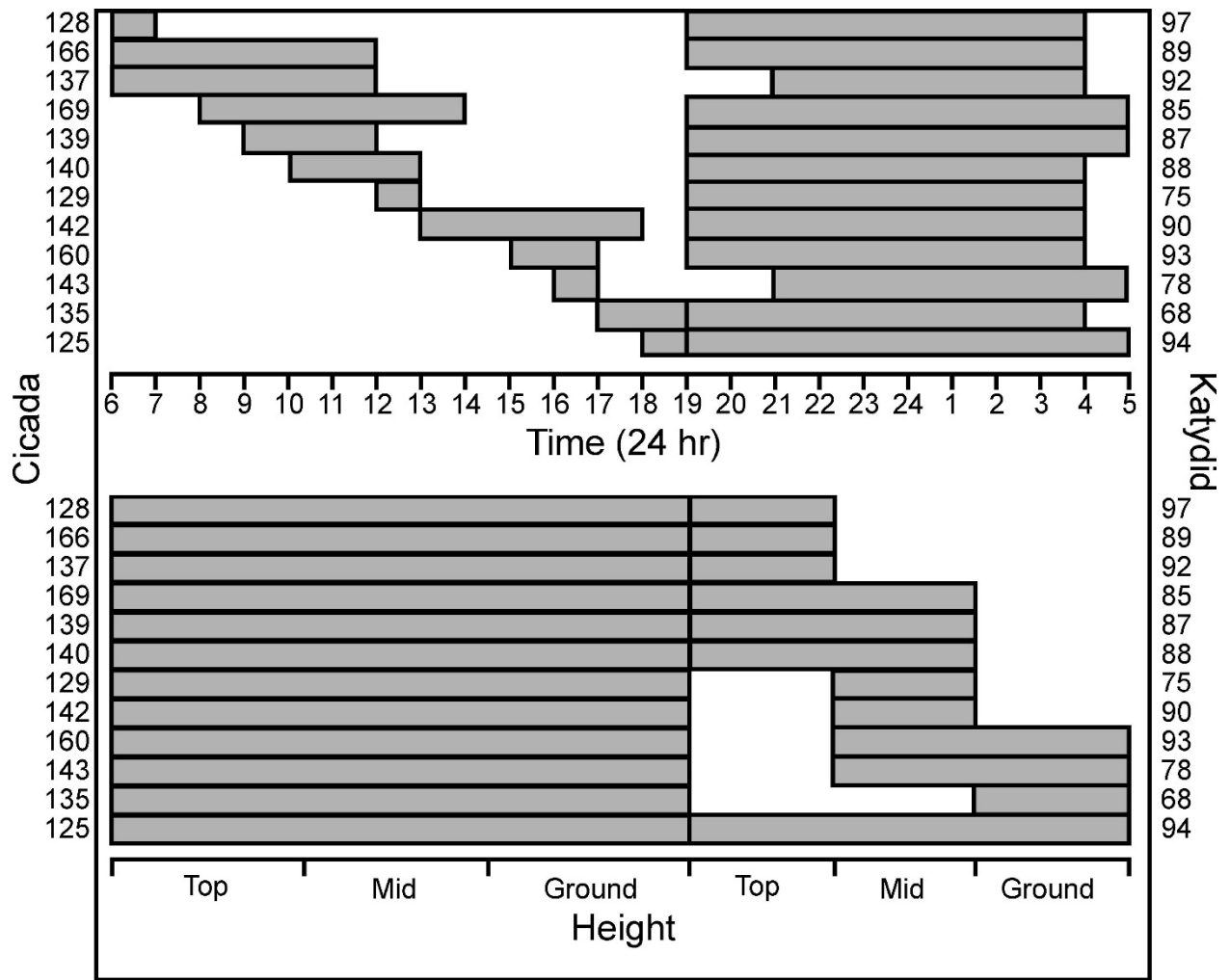


Figure 2.6. Diagram represents spatial and temporal niche partition in nocturnal katydid and diurnal cicada species. Both species utilize spectral partitioning (Table 2.3). For purposes of clarity, diagram only includes 12 selected species of each. The pattern that emerges clearly shows that katydids do not utilize temporal partitioning but rely on spatial and spectral acoustic niche partitioning, whereas cicadas rely on temporal and spectral but not spatial partitioning to communicate effectively.

3. Elevational zonation of acoustic communities in Bornean rain forest

Abstract

Tropical forests are acoustically rich environments with a diverse ensemble of songs mostly used in the context of mate attraction. Acoustic parameters of species-specific signals allows for the definition of acoustic species and provides a rapid, non-invasive method to detect otherwise cryptic animals. Using bioacoustics signals, elevational zonation of acoustic species was assessed on Bukit Belalong (913 m asl), Borneo and compared to known diversity patterns of vegetation. This small mountain lacks a permanent cloud cap, characteristic of higher elevation mountains, providing a unique opportunity to investigate elevational zonation across a relatively smooth gradient. In total, 105 acoustic species were detected consisting of nocturnal katydids, crickets, frogs, cicadas and birds, highlighting the rich acoustic diversity of tropical forests. Species richness of this acoustic assemblage decreased with increasing elevation. Distinct elevational zonation also occurred with unique acoustic assemblages at 200, 500 and 850 m asl with little overlap. Changes in acoustic species composition are matched by changes in vegetation along the same elevational gradient, likely corresponding either directly to environmental conditions or indirectly through other influences such as resource availability, predation or competition.

Introduction

Many species rely on acoustic communication to attract, detect, recognize and locate conspecifics for pair formation (Greenfield 2002). Nowhere is this more evident than within tropical rain forests, where an exceptionally diverse ensemble of acoustically communicating taxa create a rich and complex acoustic environment (Wallace 1869; Whitmore 1991; Riede 1997; Diwakar & Balakrishnan 2007). Within Bornean tropical rain forests, the intricate assemblage of songs can be attributed mainly to birds, frogs, cicadas, crickets and katydid, which produce species-specific signals with various spectral and temporal features (Otte 1992; Riede 1993; Riede 1998; Greenfield 2002; Diwakar & Balakrishnan 2007). These signal features, allow for the recognition and classification of acoustic species (Riede 1998), and as they coincide with morphospecies, they provide an effective, reliable, non-invasive tool to assess and monitor biodiversity across ecological gradients (Riede 1993; Riede 1998; Nischk & Riede 2001; Diwakar & Balakrishnan 2007; Diwakar *et al.* 2007).

Elevational zonation within South East Asian tropical rain forests has been the subject of numerous studies (Whitmore 1991; Hodkinson 2005). The most detailed occur on high elevation mountains where vegetation is heavily influenced by persistent cloud caps (Proctor *et al.* 1988; Kitayama 1992; Aiba & Kitayama 1999). Within these high elevation mountains, forest stature decreases and becomes stunted with increasing elevation, corresponding to lower temperatures (Kitayama 1992; Pendry & Proctor 1996), decreasing nutrient availability (Proctor & Woodell 1975; Grubb 1977; Bruijnzeel *et al.* 1993), and increasingly strong winds (Pendry & Proctor 1996). Species composition within tropical forests can also vary dramatically between different soils and substrates at similar elevations (Austin *et al.* 1972; Proctor *et al.* 1983).

Within Borneo, Bukit Belalong (913 m asl) is a small mountain with no cloud cap and with no dramatically stunted forest (Pendry & Proctor 1997). It also has a uniform shale lithology, providing an ideal opportunity to study species zonation as a function of elevation alone (Pendry & Proctor 1997). Prior research on Bukit Belalong utilized the same plots at 200, 500 and 850 m, to investigate soils, forest structure, floristics (Pendry & Proctor 1997); herbaceous ground vegetation (Poulsen & Pendry 1995) and potential causes of elevational zonation (Pendry & Proctor 1996). These studies found that while tree structure (height and diameter), declined with elevation, species richness of both trees and ground vegetation increased, with distinct species communities at each elevation (Poulsen & Pendry 1995; Pendry & Proctor 1997). As no difference in soils, wind, or nutrient availability occur across elevations, it is believed forest structure and species composition are related to marginal changes in climatic conditions with slightly cooler temperatures, and precipitation at the summit (Pendry & Proctor 1997).

Given that elevational zonation of flora is fairly well described for Bukit Belalong, this study uses the same locations to explore patterns of elevational zonation in its faunal acoustic assemblage.

Methods

Study site and period

Investigations were conducted in August 2008 from the Kuala Belalong Field Study Centre (KBFSC), Universiti Brunei Darussalam in northern Borneo. The KBFSC (4°33'N, 115°09'E) is situated on the north-western boundary of the Ulu Temburong National Park, within the Batu Apoi Reserve in the Temburong district. Ulu Temburong National Park is the most protected

and pristine forest in Borneo, actively protected from both legal and illegal logging (Bryan 2013). Bukit Belalong rises to 913 m asl, 8 km to the south of KBFSC (Fig. 3.1).

The climate is typically equatorial with mean annual rainfall estimated to be 4 100 mm at the base of Bukit Belalong and 5 500 mm at the summit (Pendry & Proctor 1996). Mean temperatures of 25.7°C occur at the base, with a range of 20.9-35.0°C (Pendry & Proctor 1996). Temperatures at the summit are slightly cooler, with a mean of 21.8°C and a range of 17.7-31.0°C (Pendry & Proctor 1996).

The region is characterized by rugged topography with steep sloping hills and narrow ridges separating slender valleys. Bukit Belalong is composed almost entirely of strongly folded, dark grey shales with occasional thin beds of quartzitic sandstone from the Temburong Formation, dating from the Middle Oligocene to the Early Miocene (Brondijk 1963). Soils were identified as orthic Acrisols or Ultisols, containing shale fragments, indicative of landslides (Pendry & Proctor 1997).

Vegetation on Bukit Belalong is classified as tall evergreen lowland rain forest up to 750 m asl, above which it transitions to lower montane rain forest, distinctive both structurally and floristically (Pendry & Proctor 1997). Dipterocarpaceae was the most diverse tree family at 200 m asl and 500 m asl, but at 850 m asl its diversity was exceeded by Lauraceae, Myrtaceae, Euphorbiaceae and Clusiaceae (Pendry & Proctor 1997). Tree height and diameter decreased with increasing elevation with large trees 60 m tall and 161 cm in diameter at 200 m asl; 45 m tall and 115 cm in diameter at 500 m asl; and trees only 33 m tall and 76 cm in diameter at 850 m asl (Pendry & Proctor 1997). Elevations of 200 and 500 m asl were also characterized by flowering plants (Acanthaceae & Zingiberaceae), whereas 850 m asl was characterized by bryophytes and pteridophytes (Selaginellaceae & Thelypteridaceae). Species

richness of both tree and ground herb species increased with elevation and distinct flora communities were present at each elevation (Poulsen & Pendry 1996; Pendry & Proctor 1997).

Acoustic sampling

Flora plots used in prior studies (Poulsen & Pendry 1995; Pendry & Proctor 1996; Pendry & Proctor 1997) were re-visited at 200, 500 and 850 m asl (Fig. 3.1). Acoustic sampling was conducted over three consecutive evenings, with one evening spent at each elevation. Ambient acoustic recordings of 1 minute in duration were made every hour from 21:00-24:00 hrs, within three independent 0.25 ha plots. This resulted in a 12 acoustic recordings per elevation for a total of 36 acoustic recordings. Recording schedule was organized to avoid the influence of dusk choruses on site comparisons (Riede 1997).

Recordings were made using a Sennheiser (Sennheiser, Germany) ME 67 long gun microphone in conjunction with a Marantz PD660 (Marantz, USA) solid state digital recorder. The Sennheiser microphone has a frequency response sensitivity of <20 kHz and is highly directional, preventing sound colouration from off-axis sources, making it ideal for recording call structure with minimal background noise. However, the limited response frequency of the Sennheiser microphone, may have limited detection of ultrasonic signals >20 kHz. The Marantz PD660 recording parameters were set to a sampling rate of 48 kHz with an uncompressed file format (.wav).

Signal characterization

Acoustic signals within ambient recordings were analyzed manually using Raven Pro (Cornel Laboratories, USA). Spectrograms were produced for each ambient recording in which, each 1 kHz frequency band was isolated and examined in detail for species-specific signals. Signal

structure measures and playback features within selected frequency bands provided a means to identify acoustic species. Highly stereotyped species-specific signals allow for trained listeners to distinguish between morphologically similar species with a high degree of accuracy (Riede 1996; Diwaker *et al.* 2007). Signals from acoustic species were also characterized according to their signal structure based on center frequency and pulse rate (number of pulses per second). Pulses are the smallest discrete amplitude modulations within signals, grouped together as chirps or generated continuously as trills. Chirps, comprised of multiple pulses can occur singularly or within groups known as also known as trills. The gaps between pulses, chirps and trills are referred to as intervals. For each signal, these elements were measured along with minimum, maximum and center frequency (the smallest discrete frequency which contains 50% of total energy). Collection of specimens of the acoustic species was not possible (owing to their inaccessibility), therefore each acoustic species was assigned a likely taxon (bird, frog, cicada, cricket, katydid) based on the psychoacoustic sound of signals in addition to the temporal and spectral features of the signal.

In Bornean forests, a large portion of acoustic space, both in number of species signaling and in the nocturnal acoustic energy, is generated by crickets (Orthoptera: Ensifera: Gryllidae). Crickets have conspicuous, simple repetitive signals within a narrow-band frequency range between 1 and 11 kHz (Riede 1998). Male crickets generate acoustic signals by tegminal stridulation, where a file and scrapper mechanism on the forewings cause the harp to resonate at narrow species-specific frequency ranges (Greenfield 2002). Pulse repetition rate and frequency range permit easy acoustic classification of cricket species (Riede 1998).

Katydids (Orthoptera: Ensifera: Tettigoniidae) are also nocturnal insects that produce species-specific signals by tegminal stridulation, where a functionally similar appendage to crickets called the mirror, resonates at generally high, broad frequency ranges between 6 and

130 kHz (Greenfield 2002; Montealegre-Z *et al.* 2006). These signals have a diverse range of temporal amplitude modulations comprising pulses grouped into chirps or generated continuously as trills. (Greenfield 2002).

Cicadas (Cicadidae), which are generally active during the day, generate high intensity signals using tymbals on both sides of the first abdominal segments. Their characteristic species-specific songs incorporate intense higher harmonics, which can be readily classified and reliably identified by trained listeners (Riede 1996).

Birds are most acoustically active during dawn, but contain a rich variety of diurnal and some nocturnal species. Their acoustic signals are recognizable through complex fluctuating intensity across lower frequency ranges <3 kHz (Riede 1993). Comparatively, frogs, which also utilize frequency ranges <3 kHz, are more nocturnally active and have relatively simple call structures easily classified by frequency range and pulse rates (Riede 1993; Malkmus & Riede 1996; Gerhardt & Huber 2002; du Preez & Carruthers 2009).

Data analyses

Acoustic recordings were analyzed using Raven Pro 1.5 (Cornel Laboratories, USA). Spectrograms were produced without filtering. Generalized Linear Models (GLMs) with Poisson distribution and log-link functions, were used to compare species richness and signal characters across elevations (Dobson 1990; Bolker *et al.* 2009; O'Hara 2009; Zuur *et al.* 2010) in Statistica 8 (Statsoft 2012). GLMs provide a flexible, robust approach for analyzing categorical and continuous data that are non-normal by using Poisson distributions with log-link functions (Bolker *et al.* 2009). Tests for the significance of the effects in the model were performed via the Wald statistic (w) (Yi & Wang 2011). The Jaccard similarity coefficient was used to compare species composition at different elevations. Data from the three plots within each elevation zone were pooled and analyzed together.

Niche overlap and null model analyses were used to analyze elevational zonation of these acoustic assemblages. The degree of competition between species is reflected by the degree of overlap within these independent spatial niche domains (Gotelli & Graves 1996). Overlap in resource use was calculated using the Czechanowski index (Feinsinger *et al.* 1981) of niche overlap between pairs of species:

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

Where O_{12} is the overlap of species 1 with species 2 and p_{i1} , p_{i2} is the frequency of utilization of resource state i by species 1 and 2 respectively. The calculated indices range from 0 (species share no resource) and 1 (species have identical resource use). The null models tests variation among species niche utilization. In other words, they test whether or not species significantly differ in resource use as compared to a baseline level of overlap in resource use that would be found even in the absence of species mutualistic or complete interactions (Entsminger 2012). Data for null models are organized as a matrix with rows for species and columns for categorical resource states. Generation of the null community utilized the RA3 algorithm (Winemiller & Pianka 1990), where the observed niche breadths were relaxed, replaced by a uniform 0-1 value, thus all utilization levels are equiprobable for any resource (Entsminger 2012). The RA3 algorithm is recommended because of its robustness for niche overlap studies (Gotelli & Graves 1996) and is an appropriate measure to detect any non-random patterns in community structure (Schmidt *et al.* 2012). All simulations were carried out with EcoSim Professional (Entsminger 2012). To compare observed and simulated indices 1000 null assemblages were created for each niche axes.

Results

The acoustic community

We found a highly diverse acoustic community, with 105 acoustic species distributed across elevations at 200, 500 and 850 m asl (Table 3.1). Classification of these signals based on their spectral, temporal and psychoacoustic features, resulted in bird ($n = 5$), frog ($n = 21$), cicada ($n = 4$), cricket ($n = 49$), and katydid ($n = 26$) acoustic species (Table 3.1). Detection of cicada and bird acoustic species were comparatively low, as they are primarily diurnal taxa, with few nocturnal species.

Across all elevations, acoustic taxa displayed differences in center frequencies ($w = 100.22$, $p = 0.00$) (Fig. 3.2). Katydid generally had broad band signals covering a wide spectral range above 10 kHz. Due to microphone sensitivity (<20 kHz) and intense attenuation of high frequency signals, detection of ultrasonic signals was limited and high-frequency katydid species are likely under reported. Whereas other acoustic taxa with lower frequency signals were recorded and detected relatively easily. Cricket signals were narrow band signals between 2.4-10.4 kHz. Cicada signals ranged from 3.8-5.4 kHz, while frogs and birds were generally below 4 kHz.

Center frequency ($w = 11.21$, $p = 0.08$) and pulse rate ($w = 15.49$, $p = 0.16$) of acoustic species did not vary with elevation. This pattern was the same across taxa.

The number of acoustic species detected within each recording decreased with increasing elevation with 20.21 ± 0.79 (mean \pm standard error) at 200 m asl; 17.71 ± 1.01 at 500 m asl; 15.94 ± 0.37 at 850 m asl ($w = 14.03$, $p = 0.00$). Total number of species also declined with elevation with 51 at 200 m asl; 43 at 500 m asl and only 36 at 850 m asl (Fig. 3.3). While there were some species detected across multiple elevations there were far more

unique species at each elevation, indicating distinct acoustic assemblages (Fig. 3.3). Jaccard similarity coefficients were all fairly low, yet 200 and 500 m asl displayed the greatest degree of similarity (0.21), followed by 0.11 between 500 and 850 m, and the least similar were 200 and 850 m asl (0.03), indicating a high degree of elevational zonation.

Elevational niche overlap of the entire acoustic assemblage using the Czenachowski index resulted in a low observed mean (0.31), meaning little species overlap between elevations occur. The null model analyses resulted in high simulated mean of 0.69 with a variance of 0.00, indicating that acoustic species displayed much lower species overlap across elevations than those expected by chance ($p = 0.00$). Therefore, distinct species composition occurred across elevations. Representative spectrograms across elevations indicated unique acoustic assemblages (Fig. 3.4).

Discussion

Patterns of fauna diversity and distributions are often difficult to study within tropical forests where visibility is not only limited, but many species are highly cryptic with nocturnal habits. Poor taxonomic knowledge across many taxa amplifies the difficulties of accurately assessing tropical fauna (Novotny *et al.* 2005). However, many species rely on acoustic communication for attraction, detection, recognition and localization of conspecifics (Greenfield 2002). Therefore, utilization of these species-specific signals becomes a rapid, non-invasive and reliable method to detect otherwise cryptic creatures, in architecturally complex environments (Riede 1998).

Across the elevational gradient of Bukit Belalong 105 acoustic species were detected, consisting of nocturnal katydids, crickets, frogs, cicadas and birds, highlighting the rich acoustic diversity of tropical forests. The entire acoustic assemblage displayed decreasing

species richness with increasing elevation. There was also distinct elevational zonation with unique species assemblages at 200, 500 and 850 m asl, with little species overlap.

Changes in acoustic species assemblages are matched by changes in vegetation along the same elevational gradient on this mountain (Poulsen & Pendry 1995; Pendry & Proctor 1997). Forests showed gradual structural changes along the elevational gradient, with trees becoming shorter in stature and narrower in diameter with increasing elevation (Pendry & Proctor 1997). Forest species composition also shifts from a dominance of large emergent dipterocarps (Dipterocarpaceae) at low elevations, to increased species diversity within Lauraceae, Myrtaceae, Euphorbiaceae and Clusiaceae at higher elevations (Pendry & Proctor 1997). A study on herbaceous ground vegetation, including ferns and epiphytes, also showed increasing species diversity and abundance with increasing elevation (Poulsen & Pendry 1995). While flora diversity increased with elevation, opposite to acoustic species diversity, both contained unique species assemblages at 200, 500 and 850 m asl displaying distinct elevational zonation (Poulsen & Pendry 1995).

Although opposite diversity trends for the flora with acoustic species fauna seem counter intuitive, they can be explained by marginal changes in climatic conditions. While Bukit Belalong lacks a permanent cloud cap, the summit has cooler temperatures, increased precipitation and shorter forest stature which allows increased light to reach the forest floor (Poulsen & Pendry 1995). These conditions likely create more favorable conditions for herbaceous ground vegetation (Pendry & Proctor 1996; Poulsen and Pendry 1995). Smaller tree diameters at higher elevations also permit trees to grow closer together, increasing species richness within demarcated areas. These changes in forest structure and floristics along the elevational gradient of this mountain are also similar to other mountains in Borneo, including: Gunung Kinabalu, 4 101 m asl (Kitayama 1992; Aiba & Kitayama 1999); Gunung Mulu, 2 376

m asl (Proctor *et al.* 1983) and Gunung Silam, 884 m asl (Proctor *et al.* 1988). However, vegetation changes on these mountains are more abrupt, often coinciding with the occurrence of a cloud cap and colder temperatures (Stadtmuller 1987; Frahm & Gradstein 1991; Hamilton *et al.* 1993; Pendry & Proctor 1997).

The literature on fauna diversity patterns along elevational gradients is extensive and summarized by Hodkinson (2005). Increasing altitudinal gradients generally cause substantial species turnover and declines in species richness and abundance for a wide range of taxa (Alexander & Hilliard 1969; Holloway 1970; Kikkawa & Williams 1971; Janzen 1973; Hamilton 1975; Janzen *et al.* 1976; Hågvar 1976; Gagné 1979; Hebert 1980; Wolda 1987; McCoy 1990; Navarro 1992; Stevens 1992; Fernandes & Lara 1993; Olson 1994; Patterson *et al.* 1996; Vazquez & Givnish 1998; Givnish 1999; Brühl *et al.* 1999; Odland & Birks 1999; Grytnes & Vetaas 2002; Brehm *et al.* 2003; Novotny *et al.* 2005; Malsch *et al.* 2008). Although presence of invertebrate elevational specialists in tropical forest have been documented (De Vries 1987; Holloway 1987; Olson 1994) tropical species are generally more habitat specific and have narrower tolerance ranges to physical conditions than temperate species (Janzen 1967; Huey 1978; Pianka 1983; Stevens 1989). Consequently, species turnover across elevational gradients is fairly rapid with species exhibiting narrow elevational ranges (Olson 1994).

Declines in fauna species richness and abundance with increasing elevation have therefore been attributed to less than optimal environmental conditions at higher elevations, corresponding primarily to decreasing temperatures (Hodkinson 2005). However, while fauna diversity patterns across elevational gradients can be directly influenced by environmental parameters, they can also be indirectly influenced through shifts in resource availability, predation or competition (Hodkinson 2005). For herbivorous insects, vegetation along

elevational gradients may also vary in suitability as host plants influencing species distribution (Ayres 1993; Bowman & Conant 1994; Ayres *et al.* 1997; Erelli *et al.* 1998). Opposite diversity patterns along an elevational gradient therefore emphasize different optimal niche requirements across flora and fauna taxa.

Implications for biodiversity surveys

Using bioacoustic signals is a rapid, non-invasive and reliable method to detect otherwise cryptic creatures, in architecturally complex environments (Riede 1998). Using acoustic parameters of species-specific signals also allows them to be defined as acoustic species, overcoming the taxonomic impediment (Riede 1998). Although the acoustic species richness decreased with increasing elevations, there were nonetheless unique species assemblages at 200, 500 and 850 m asl, with little species overlap. Elevational zonation of species is therefore an important consideration when conducting biodiversity surveys to ensure accurate site comparisons, or complete species inventories when assessing conservation priorities in regions.

References

- Aiba, S. & Kitayama, K. 1999. Structure, composition and species diversity in an elevation-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecology* 140:139–157.
- Alexander, G. & Hilliard, J. R. 1969. Elevational and seasonal distribution of Orthoptera in the Rocky Mountains of northern Colorado. *Ecological Monographs* 39:385–431.
- Austin, M. P., Ashton, P. S. & Greig-Smith, P. 1972. The application of quantitative methods to vegetation survey. III. A re-examination of rain forest data from Brunei. *Journal of Ecology* 60:308–324.
- Ayres, M. P., Clausen, T. P., Maclean, S. F., Redman, A. M. & Reichart, P. B. 1997. Diversity of structure and anti-herbivore activity in condensed tannin. *Ecology* 78:1696–1711.
- Ayres, M. P. 1993. Global change, plant defense, and herbivory. In: Kareiva, P. M., Kingsolver, J. G. & Huey, R. B. (eds.). *Biotic interactions and global change*. Sinauer, Sunderland.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J. S. S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–35.
- Bowman, W. D. & Conant, R. T. 1994. Shoot growth dynamics and photosynthetic response to increased nitrogen availability in the alpine willow *Salix glauca*. *Oecologia* 97:93–99.
- Brehm, G., Homeier, J. & Fiedler, K. 2003. Beta diversity of geometrid moths (Lepidoptera: Geometridae) in an Andean montane rainforest. *Diversity and Distributions* 9:351–366.
- Brondijk, J. F. 1963. Reclassification of part of the Setap Shale Formation as the Temburong Formation. *British Borneo Geological Survey Annual Report* pp. 56–60.

- Brühl, C., Mohamed, M. & Linsenmair, K. E. 1999. Elevational distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology* 15:265–277.
- Bruijnzeel, L. A., Waterloo, M. J., Proctor, J., Kuiters, A. T. & Kotterink, B. 1993. Hydrological observations in montane rain forests on Gunung Silam, Sabah, Malaysia, with special reference to the ‘Massenerhebung’ effect. *Journal of Ecology* 81:145–167.
- Bryan, J. E., Shearman, P. L., Asner, G. P., Knapp, D. E., Aoro, G. & Lokes, B. 2013. Extreme differences in forest degradation in Borneo: comparing practices in Sarawak, Sabah, and Brunei. *PLOS ONE* 8(7):e69679.
- De Vries, P. J. 1987. *The butterflies of Costa Rica and their natural history. Papilionidae, Pieridae, Nymphalidae*. Princeton University Press, Princeton, USA.
- Diwakar, S. & Balakrishnan, R. 2007. The assemblage of acoustically communicating crickets of a tropical evergreen forest in southern India: call diversity and diel calling patterns. *Bioacoustics* 16:113–135.
- Diwakar, S., Jain, M. & Balakrishnan, R. 2007. Psychoacoustic sampling as a reliable, non-invasive method to monitor orthopteran species diversity in tropical forests. *Biodiversity and Conservation* 16:4081–4093.
- Dobson, A. J. 1990. *An introduction to generalized linear models*. Chapman & Hall, New York.
- Du Preez, L. & Carruthers, V. 2009. *A complete guide to the frogs of southern Africa*. Struik Nature, Cape Town.
- Entsminger, G. L. 2012. *EcoSim Professional: Null modeling software for ecologists, Version 1*. Acquired Intelligence Inc., Kesey-Bear & Pinyon Publishing. Montrose.
- Erelli, M. C., Ayres, M. P. & Eaton, G. K. 1998. Elevational patterns in host suitability for forest insects. *Oecologia* 117:133–142.

- Feinsinger, P., Spears, E. E. & Poole, R. W. 1981. A simple measure of niche breadth. *Ecology* 62:27–32.
- Fernandes, G.W. & Lara, A.C.F. 1993. Diversity of Indonesian gall-forming herbivores along elevational gradients. *Biodiversity Letters* 1:186–192.
- Frahm, J. P., & Gradstein, R. S. 1991. An elevational zonation of tropical rain forests using byrophytes. *Journal of Biogeography* 18:669–678.
- Gagné, W. C. 1979. Canopy-associated arthropods in *Acacia koa* and *Metrosideros* tree communities along an elevational transect on Hawaii Island. *Pacific Insects* 21:56–82.
- Gerhardt, C. H. & Huber, F. 2002. *Acoustic communication in insects and anurans: Common problems and diverse solutions*. The University of Chicago Press, Chicago.
- Givnish, T.J. 1999. On the causes of gradients in tropical tree diversity. *Journal of Ecology* 87:193–210.
- Gotelli, N. J. & Graves, G. R. 1996. *Null models in ecology*. Smithsonian Institution Press. Washington.
- Greenfield, M. D. 2002. *Signalers and receivers. Mechanisms and evolution of arthropod communication*. Oxford University Press, Oxford.
- Grubb, P. J. 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annual Review of Ecology and Systematics* 8:83–107.
- Grytnes, J. A. & Vetaas, O. R. 2002. Species richness and elevation: a comparison between null models and interpolated plant species richness along the Himalayan elevational gradient, Nepal. *The American Naturalist* 159:294–304.
- Hågvar, S. 1976. Elevational zonation of the invertebrate fauna on branches of birch (*Betula pubescens* Erh.). *Norwegian Journal of Entomology* 23:61–74.

- Hamilton, A. C. 1975. A quantitative analysis of elevational zonation in Uganda forests. *Vegetatio* 30:99–106.
- Hamilton, L. S., Juvik, J. O. & Scatena, F. N. 1993. *Tropical montane cloud forests*. United States Department of Agriculture Forest Service, Puerto Rico.
- Hebert, P. D. N. 1980. Moth communities in montane Papua New Guinea. *Journal of Animal Ecology* 49:593–602.
- Hodkinson, I. D. 2005. Terrestrial insects along elevation gradients: species and community responses to elevation. *Biological Reviews* 80:489–513.
- Holloway, J. D. 1970. The biogeographical analysis of a transect sample of the moth fauna of Mt Kinabalu, Sabah, using numerical methods. *Biological Journal of the Linnean Society* 2:259–286.
- Holloway, J. D. 1987. Macrolepidoptera diversity in the Indo-Australian tropics: geographic, biotopic and taxonomic variations. *Biological Journal of the Linnean Society* 30:325–341.
- Huey, R. B. 1978. Latitudinal patterns of between-elevation faunal similarity: mountains might be 'higher' in the tropics. *The American Naturalist* 112:225–229.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *The American Naturalist* 101:233–249.
- Janzen, D. H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54:687–708.
- Janzen, D. H., Ataroff, M., Farinas, M., Reyes, S., Rincon, A., Soler, A., Soriano, P. & Vera, M. 1976. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. *Biotropica* 8:193–203.
- Kikkawa, J., & Williams, E. E. 1971. Elevation distribution of land birds in New Guinea. *Search* 2:64–65.

- Kitayama, K. 1992. An elevational transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* 102:149–171.
- Malkmus, R. & Riede, K. 1996. Frogs from Kinabalu Borneo. *Sauria* 18:37–37.
- Malsch, A. K. F., Fiala, B., Maschwitz, U., Mohamed, M., Nais, J. & Linsenmair, K. E. 2008. An analysis of declining ant species richness with increasing elevation at Mount Kinabalu, Sabah, Borneo. *Asian Myrmecology* 2:33–49.
- McCoy, E. D. 1990. The distribution of insects along elevational gradients. *Oikos* 58:313–322.
- Montealegre-Z, F., Morris, G. K. & Mason, A. C. 2006. Generation of extreme ultrasonics in rainforest katydids. *Journal of Experimental Biology* 209:4923–4937.
- Navarro, A. G. S. 1992. Elevational distribution of birds in the Sierra Madre del Sur, Guerrero, Mexico. *Condor* 94:29–39.
- Nischk, F. & Riede, K. 2001. Bioacoustics of two cloud forest ecosystems in Ecuador compared to lowland rainforest with special emphasis on singing cricket species. In: Nieder, J. & Barthlott, W. (eds.). *Epiphytes and canopy fauna of the Otongan rain forest (Ecuador). Results of the Bonn – Quito epiphyte project, funded by the Volkswagen Foundation (Vol. 2 of 2)*. Books on Demand GmbH, Bonn.
- Novotny, V., Miller, S. E., Basset, Y., Cizek, L., Kaupa, B., Kua, J. & Weiblen, G. D. 2005. An elevational comparison of caterpillar (Lepidoptera) assemblages on *Ficus* trees in Papua New Guinea. *Journal of Biogeography* 32:1303–1314.
- O'Hara, R. B. 2009. How to make models add up – a primer on GLMMs. *Annales Zoologici Fennici* 46:124–37.
- Odland, A. & Birks, H. J. B. 1999. The elevational gradient of vascular plant species richness in Aurland, western Norway. *Ecography* 22:548–566.
- Olson, D. M. 1994. The distribution of leaf litter invertebrates along a Neotropical elevational gradient. *Journal of Tropical Ecology* 10:129–150.

- Otte, D. 1992. Evolution of cricket songs. *Journal of Orthoptera Research* 1:25–49.
- Patterson, B. D., Pacheco, V. & Solari, S. 1996. Distributions of bats along an elevational gradient in the Andes of southeastern Peru. *Journal of Zoology (London)* 240:637–658.
- Pendry, C. A. & Proctor, J. 1996. The causes of elevational zonation of rain forests on Bukit Belalong, Brunei. *Journal of Ecology* 84:407–418.
- Pendry, C. A. & Proctor, J. 1997. Elevational zonation of rain forest on Bukit Belalong, Brunei: soils, forest structure and floristics. *Journal of Tropical Ecology* 13:221–241.
- Pianka, E. R. 1983. *Evolutionary ecology*. Harper & Row, Publishers, New York, USA.
- Poulsen, A. D. & Pendry, C. A. 1995. Inventories of ground herbs at three elevations on Bukit Belalong, Brunei, Borneo. *Biodiversity and Conservation* 4:745–757.
- Proctor, J. & Woodell, S. R. J. 1975. The ecology of serpentine soils. *Advances in Ecological Research* 9:255–366.
- Proctor, J., Anderson, J. M., Chai, P. & Vallack, H. W. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. *Journal of Ecology* 71:237–260.
- Proctor, J., Lee, Y. F., Langley, A. M., Munro, C. M. & Nelson, T. 1988. Ecological studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia. I. Environment, forest structure and floristics. *Journal of Ecology* 76:320–340.
- Riede, K. 1993. Monitoring biodiversity: analysis of Amazonian rainforest sounds. *Ambio* 22:546–548.
- Riede, K. 1996. Diversity of sound-producing insects in a Bornean lowland rain forest. In: Edwards, D. S., Booth, W. E. & Choy, S. C. (eds.). *Tropical Rainforest Research – Current Issues*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Riede, K. 1997. Bioacoustic diversity and resource partitioning in tropical calling communities. In: Ulrich, H. (ed.). *Tropical biodiversity and systematics. Proceedings of the*

- International Symposium on Biodiversity and Systematics in Tropical Ecosystems, Bonn 1994*. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.
- Riede, K. 1998. Acoustic monitoring of Orthoptera and its potential for conservation. *Journal of Insect Conservation* 2:217–223.
- Schmidt, A. K. D., Römer, H. & Riede, K. 2012. Spectral niche segregation and community organization in a tropical cricket assemblage. *Behavioral Ecology* 24:470–480.
- Stadtmüller, T. 1987. *Cloud forests in the humid tropics: a bibliographic review*. United Nations University Press, Costa Rica.
- Statsoft, Inc. 2012. Statistica (data analysis software system), version 11. www.statsoft.com.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist* 133:240–256.
- Stevens, G. C. 1992. The elevational gradient in elevational range: an extension of Rapoport's latitudinal rule to elevation. *The American Naturalist* 140:893–911.
- Vazquez, J. A. & Givnish, T. J. 1998. Elevational gradients in the tropical forest composition, structure, and diversity in the Sierra de Manantlan. *Journal of Ecology* 86:999–1020.
- Wallace, A. R. 1869. *The Malay archipelago*. Tynron Press, Scotland.
- Whitmore, T. C. 1991. *An introduction to tropical rain-forests*. Clarendon, Oxford.
- Winemiller, K. O. & Pianka, E. R. 1990. Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60:27–55.
- Wolda, H. 1987. Elevation, habitat and tropical insect diversity. *Biological Journal of the Linnean Society* 30:313–323.
- Yi, Y. & Wang, X. 2011. Comparison of Wald score and likelihood ratio tests for response adaptive designs. *Journal of Statistical Theory and Applications* 10:553–569.
- Zuur, A. F., Elena, N. I. & Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:1–14.

Table 3.1. Acoustic species detected across all elevations (2= 200 m asl; 5= 500 m asl; 8= 850 m asl), with their signal parameters of pulse rate (pulse r.) and center frequency (kHz). All acoustic species were assigned a taxa category based on signal characteristics (k= katydid; cr= cricket; ci= cicada, f= frog; b= bird). ID= unique species identification number; #= position and number of species within the table.

#	ID	taxa	2	5	8	pulse r.	kHz	#	ID	taxa	2	5	8	pulse r.	kHz	#	ID	taxa	2	5	8	pulse r.	kHz
1	18	cr	X	X	X	1.57	2.72	36	37	cr	X			6.41	4.34	71	181	cr	X			2.11	5.63
2	57	cr	X	X	X	25.00	6.54	37	38	cr	X			5.05	4.36	72	182	k	X			19.23	5.63
3	5	f	X	X		2.74	1.10	38	39	ci	X			29.41	4.37	73	183	cr	X			0.92	6.38
4	11	f	X	X		0.07	1.59	39	41	cr	X			66.67	4.58	74	184	cr	X			5.38	5.44
5	13	f	X	X		1.54	1.99	40	50	cr	X			2.80	5.26	75	187	cr	X			0.37	2.72
6	19	cr	X	X		18.52	2.91	41	53	cr	X			9.10	5.74	76	189	cr	X			33.33	4.50
7	20	cr	X	X		1.46	2.96	42	55	cr	X			15.20	6.12	77	190	cr	X			7.17	4.78
8	42	cr	X	X		12.45	4.76	43	58	cr	X			45.45	6.61	78	191	f	X			0.24	1.13
9	44	cr	X	X		9.21	4.84	44	66	cr	X			16.82	7.56	79	45	k		X		9.90	4.97
10	48	cr	X	X		23.49	5.18	45	69	cr	X			43.48	8.17	80	192	f		X		0.21	0.81
11	49	cr	X	X		25.74	5.25	46	71	cr	X			2.40	8.75	81	193	ci		X		240.76	3.86
12	52	cr	X	X		14.72	5.54	47	74	cr	X			18.96	9.49	82	194	f		X		6.71	3.10
13	64	cr	X	X		3.91	7.37	48	76	cr	X			8.47	10.42	83	195	f		X		0.82	1.60
14	65	cr	X	X		1.63	7.41	49	78	k	X			94.38	10.75	84	196	f		X		3.40	1.97
15	68	k	X	X		4.76	7.96	50	80	k	X			0.35	11.38	85	197	f		X		1.24	2.77
16	72	cr	X	X		27.78	8.87	51	93	k	X			43.48	20.75	86	198	cr		X		17.53	4.29
17	79	k	X	X		2.19	11.27	52	94	k	X			226.56	21.00	87	199	cr		X		1.58	4.76
18	16	cr	X		X	32.26	2.41	53	77	k		X	X	11.33	10.58	88	200	cr		X		23.31	5.24
19	1	b	X			0.15	0.54	54	83	k		X	X	0.58	12.86	89	201	k		X		0.09	9.94
20	3	f	X			3.33	0.96	55	85	k		X	X	0.51	8.63	90	202	k		X		1.01	13.52
21	4	b	X			0.07	1.02	56	185	k		X	X	500.00	9.32	91	203	k		X		4.40	10.11
22	7	f	X			0.29	1.27	57	186	k		X	X	1.38	8.81	92	204	cr		X		4.52	6.05
23	9	f	X			9.01	1.49	58	188	b		X	X	47.62	6.84	93	205	cr		X		0.35	2.94
24	10	b	X			0.12	1.54	59	26	f		X		1.78	3.62	94	206	f		X		1.00	1.09
25	12	f	X			0.04	1.75	60	46	cr		X		2.73	5.06	95	207	ci		X		29.41	5.48
26	14	f	X			1.08	2.04	61	70	k		X		13.75	8.25	96	208	k		X		16.13	16.78
27	21	cr	X			35.71	3.07	62	87	k		X		5.85	9.48	97	209	f		X		10.20	1.57
28	22	cr	X			6.42	3.22	63	173	cr		X		1.98	3.40	98	210	k		X		0.95	6.27
29	23	cr	X			13.54	3.41	64	174	cr		X		6.58	5.82	99	211	k		X		0.07	15.07
30	24	cr	X			3.96	3.46	65	175	k		X		11.02	7.29	100	212	cr		X		1.51	2.46
31	25	cr	X			76.92	3.50	66	176	f		X		0.50	0.84	101	213	cr		X		1.86	4.27
32	30	f	X			83.33	3.76	67	177	f		X		0.36	0.61	102	214	cr		X		4.70	4.31
33	31	cr	X			10.63	3.84	68	178	B		X		6.45	1.73	103	215	k		X		1.85	7.13
34	34	ci	X			27.03	4.04	69	179	f		X		0.18	1.41	104	216	k		X		0.21	11.25
35	35	cr	X			2.29	4.05	70	180	k		X		32.26	8.20	105	217	k		X		15.13	2.63

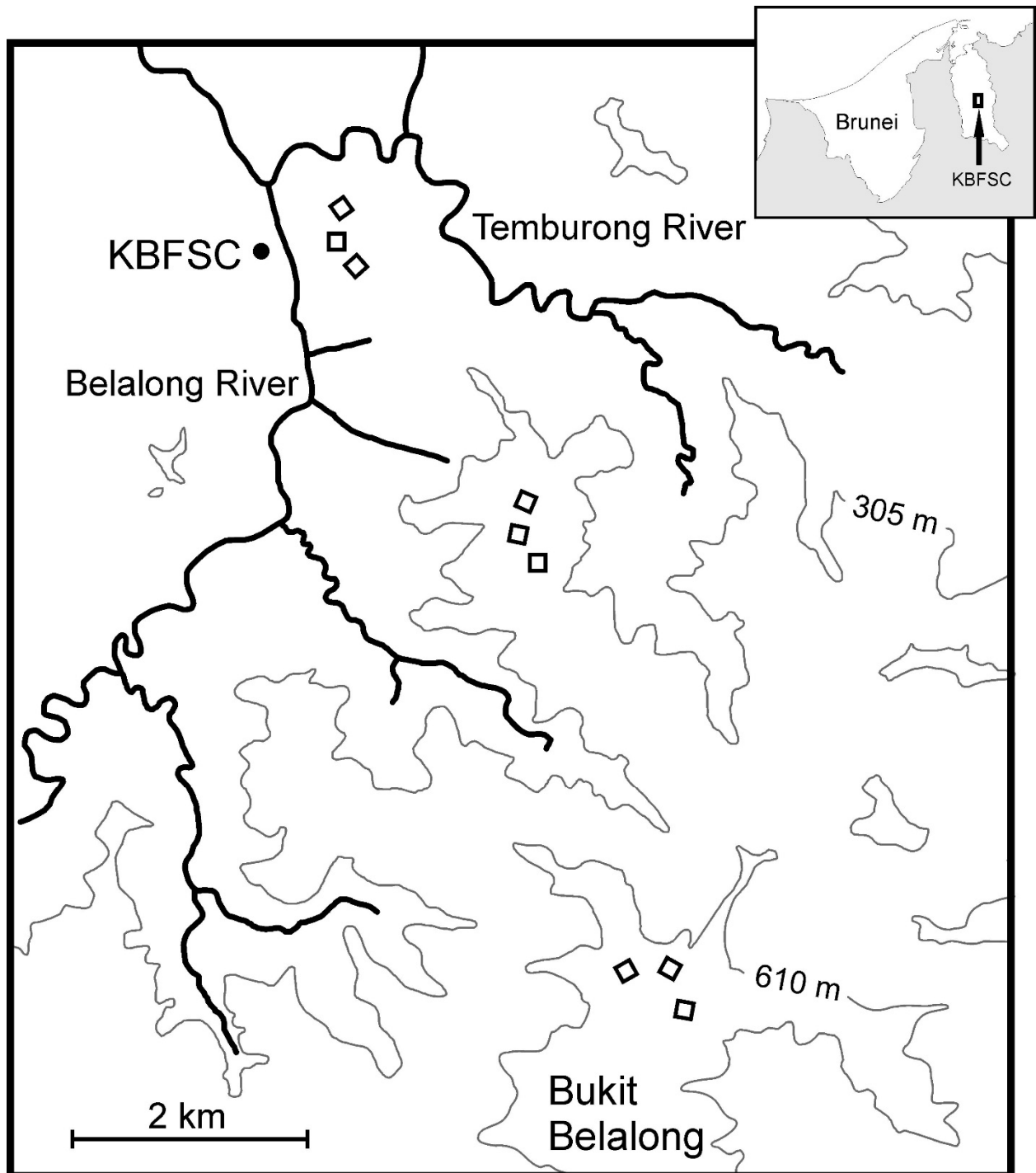


Figure 3.1. Location of Kuala Belalong Field Studies Centre (KBFSC), and Bukit Belalong (913 m asl), in the Temburong district of Brunei Darussalam in northern Borneo. Locations of acoustic sampling plots at 200, 500 and 850 m asl are shown, corresponding to prior research on elevational zonation of vegetation.

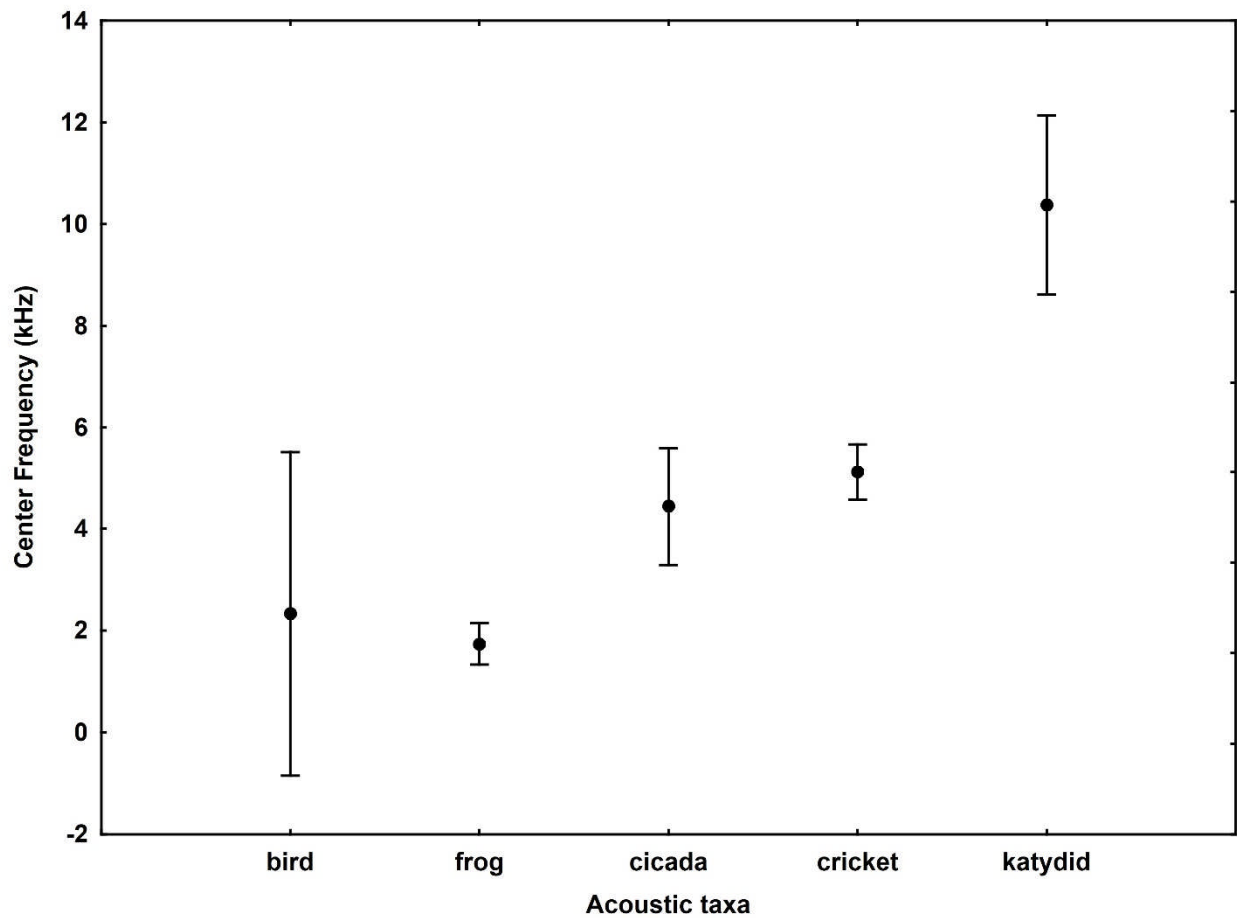


Figure 3.2. Across all elevations, acoustic taxa displayed differences in center frequencies ($w = 100.22$, $p = 0.00$). Katydids generally had broad band signals covering a wide spectral range above 10 kHz; cricket signals were narrow band signals between 2.4-10.4 kHz; cicada signals ranged from 3.8-5.4 kHz, while frogs and birds were generally <4 kHz.

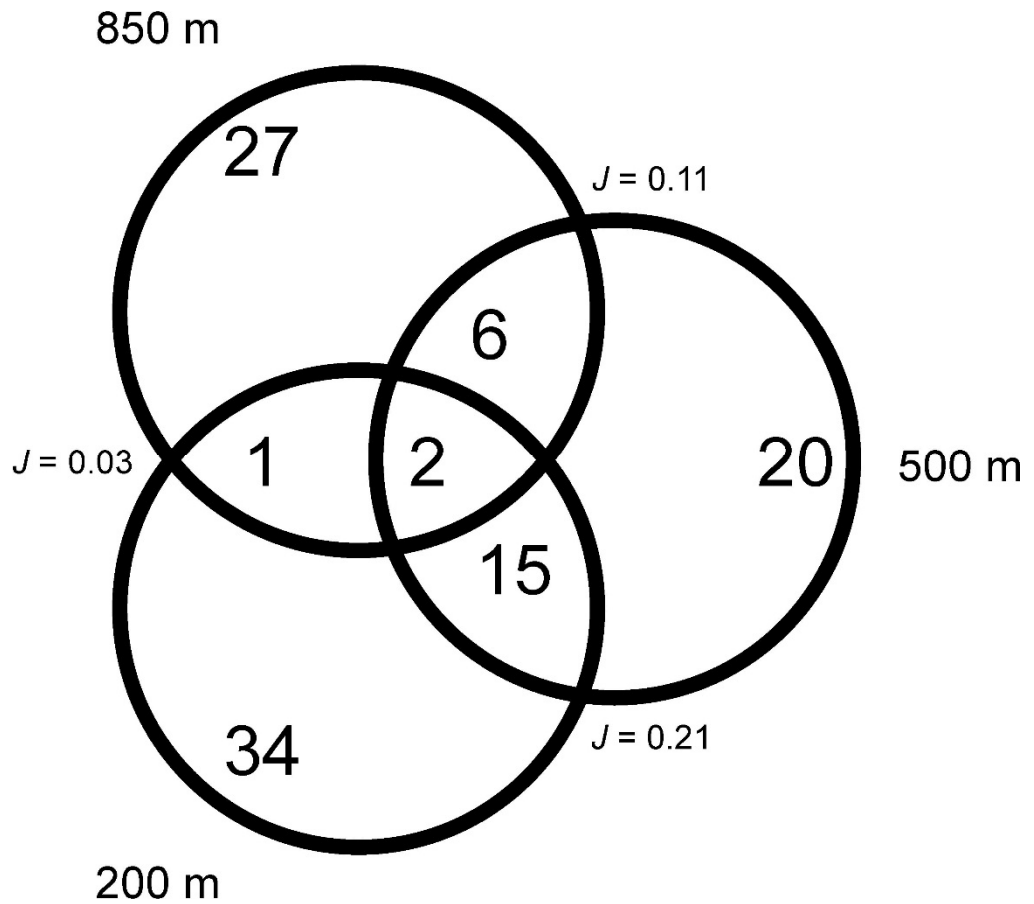


Figure 3.3. Venn diagrams and Jaccard indices for acoustic species composition across elevations (200, 500 and 850 m asl). Distinct elevational zonation of unique species assemblages occurred with little species overlap.

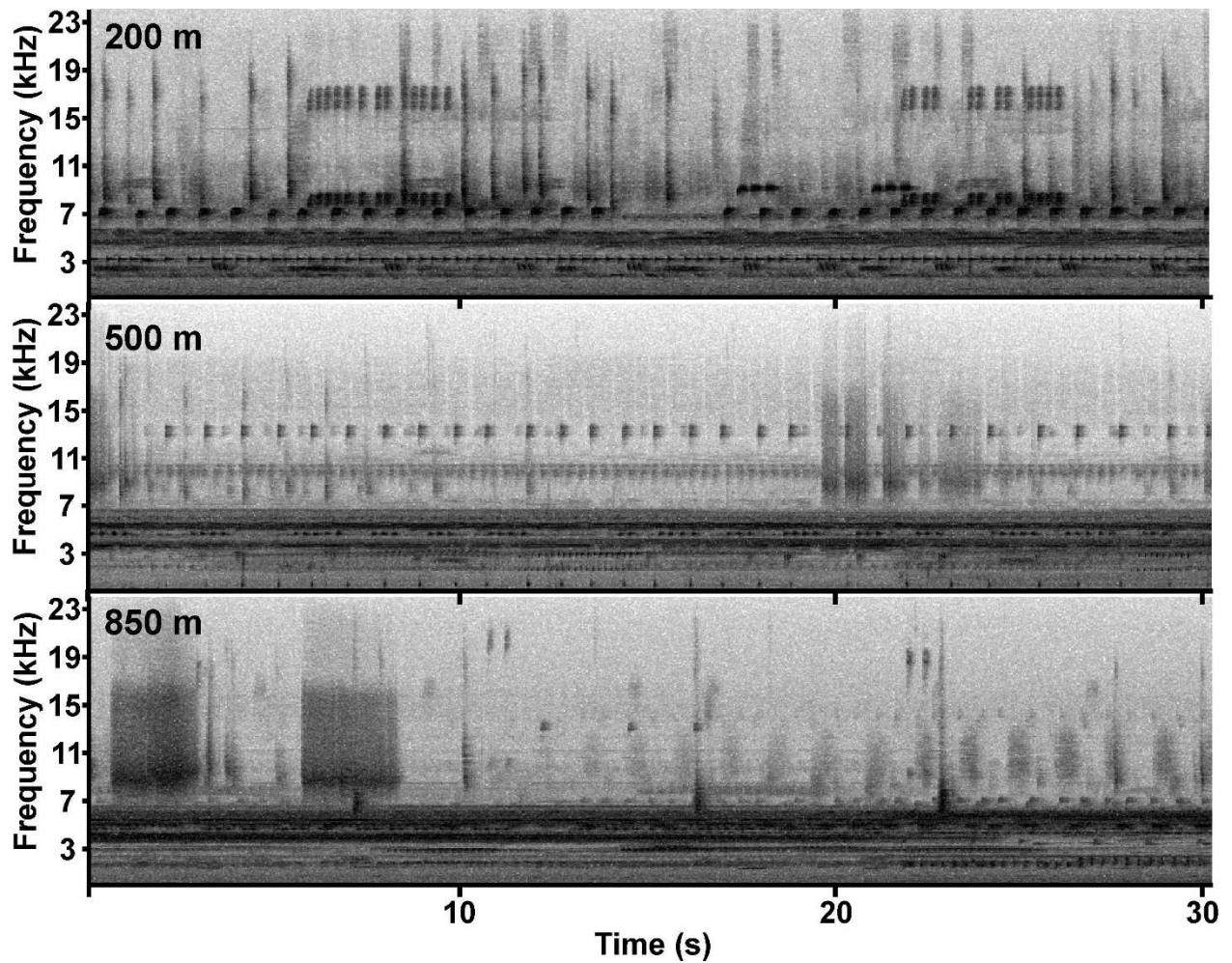


Figure 3.4. Spectrograms display unfiltered, species-specific signals in frequency (kHz) versus time (s) with darker colours representing higher decibels (dB). Spectrograms at 200, 500 and 850 m asl display representative nocturnal soundscapes at each elevation with a large number of unique acoustic species signaling across the frequency spectrum.

4. Implementing acoustic profiling of the landscape mosaic

Abstract

Sound carries a multitude of localized information providing a unique perspective of the landscape and the intricate interactions within. Acoustic profiling of the landscape mosaic is a non-invasive, effective method to investigate diversity patterns of acoustic taxa across ecological gradients. This method was implemented across a unique plantation forestry landscape mosaic with diverse ecological gradients, containing both alien and indigenous vegetation as well as bordering large natural protected areas. Biodiversity assessment of this landscape therefore offered an opportunity to determine the ecological influences on acoustic diversity patterns across a landscape in need of identifying conservation priorities to ensure sustainable management. Nocturnal acoustic profiling identified 65 acoustic species, including bird, frog, cricket and katydid species across the landscape. Areas covered in alien timber or non-endemic grass were devoid of acoustic signals and supported no acoustic species, emphasizing their negative impact on indigenous acoustic species. Managed areas that were mowed and heavily grazed were not effective in conserving late successional stage insects or other nocturnal acoustic species, highlighting the influence of plantation management actions on acoustic biodiversity. Within natural vegetation patches inside plantations, acoustic species richness increased with plant heterogeneity and patch size. Patches <1 ha, were heavily influenced by edge effects, and did not maintain the full complement of acoustic biodiversity. Large, natural, protected grassland sites outside plantations contained the highest acoustic diversity. Isolated grassland patches within plantations supported lower acoustic diversity, yet overall supported similar species composition, effectively reducing the contrast of transformed landscapes with surrounding natural areas. Indigenous forest patches within plantations contained a highly characteristic acoustic species assemblage, highlighting the significant

contribution of indigenous forests to biodiversity across the landscape. Measurement of the degree of entropy within sound signals also provided an estimate of biodiversity, yet lacked the high resolution required to determine differences in species composition between sites and which were of important conservation significance. Utilizing acoustic signals across landscapes therefore provided an extremely effective method to investigate diversity patterns across the landscape mosaic.

Introduction

Acoustic communication in the context of sexual advertisement and pair formation allows a wide range of cryptic taxa to propagate and receive acoustic sensory information invisibly within their environment (Greenfield 2002). Species-specific signals allow conspecifics to identify, locate and assess the fitness of potential mates (Simmons & Zuk 1992; Tuckerman *et al.* 1993; Greenfield 2002). In the absence of accurate species identification through poor taxonomic knowledge, classification of signal parameters allows for the definition of recognizable taxonomic units (Riede 1993; Riede 1998). Detection of these acoustic signals therefore provides a non-invasive, rapid, effective method for investigating diversity patterns of acoustic taxa across ecological gradients. Acoustic profiling of the landscape over time consequently provides a means of developing conservation strategies and for monitoring the result of their implementation by determining levels of restoration or deterioration of ecological integrity, based on acoustic diversity patterns (Riede 1993; Fischer *et al.* 1997; Riede 1998; Brandes *et al.* 2006; Sueur *et al.* 2008; Pijanowski *et al.* 2011; Dumyahn & Pijanowski 2011).

Biodiversity estimates and classification of acoustic species have already become fairly standard for bats (MacSwiney *et al.* 2008), frogs (Malkamus & Riede 1996; Villanueva-Rivera 2007), birds (Goyette *et al.* 2011; Farina *et al.* 2011), and insects (Riede 1993; Riede 1998; Gogala & Riede 1995), including katydids (Orthoptera: Ensifera: Tettigoniidae) (Morris & Beier 1982; Riede 1998; Diwakar *et al.* 2007; Diwakar & Balakrishnan 2007a). On a landscape level, acoustic surveys are similar to a multi-taxon approach, as they incorporate not only focal taxa, but numerous other species which broadcast signals in the same acoustic space and time but within different dominant frequencies, (Römer 1993; Römer *et al.* 1989; Diwakar & Balakrishnan 2007a).

Forgoing identification of acoustic species within communities, biodiversity can also be estimated by measuring the degree of entropy within sound (Sueur *et al.* 2008). As more acoustic species occupy the same habitat, the more heterogeneous the soundscape becomes, providing a means to quickly estimate rough biodiversity levels through simple signal analysis (Sueur *et al.* 2008).

Acoustic profiling of the landscape is a powerful, yet underutilized tool to assess the landscape mosaic. Plantation forestry containing diverse environmental gradients, provides a unique landscape mosaic to implement acoustic profiling and rapidly assess biodiversity to develop conservation initiatives.

Large scale landscape transformation and associated habitat loss cause major disruptions to biodiversity and functional ecosystem integrity. Within South Africa, managed landscapes such as plantation forestry occur primarily within severely threatened grassland, wetland and indigenous forest biomes (Neke & du Plessis 2004; DWAF 2006; Samways *et al.* 2009). Blocks of alien trees stand in extreme contrast to these indigenous biomes and support little indigenous biodiversity at the patch scale (Samways & Moore 1991; Armstrong & van Hensbergen 1994; Pryke & Samways 2009; Bremer & Farley 2010; Pryke & Samways 2011; Pryke & Samways 2012). Timber plantations also act as barriers or filters to movement between grassland remnants (Samways & Moore 1991; Bieringer & Zulka 2003; Bazelet & Samways 2010), cause landscape fragmentation (Lindenmayer & Fischer 2006), have severe adverse effects on hydrology (Le Maitre *et al.* 1996; Samways *et al.* 2009) and have hard edges which negatively impact taxa on biodiversity in adjacent grassland biomes (Pryke & Samways 2001; Pryke & Samways 2011).

Currently, the timber industry in South Africa occupies 1.8 million ha, with 1.3 million ha planted mainly with alien *Eucalyptus* and *Pinus* species (DWAF 2006; Samways *et al.*

2009). The remaining 500 000 ha are left unplanted and are maintained within overall plantation landscapes as areas of protected grassland, wetland and indigenous forest, as well as firebreaks, power line servitudes and roads. This plantation matrix is overseen by national environmental regulations (DWAF 2005). However, in order to export timber products to Europe, large-scale forestry operations require Forest Stewardship Council (FSC) certification, which necessitates adherence to international standards for sustainable forestry (FSC 1996). Designing ecological networks within plantations effectively reduces the contrast of transformed landscapes with surrounding natural areas, resulting in plantation landscapes which are sustainably managed, and is economically beneficial as it opens critical European markets through FSC certification.

Ecological networks consist of interconnected corridors and nodes which improve connectivity between remnant patches and extensive natural areas to maintain structural, compositional and functional biodiversity (Jongman 1995; Samways *et al.* 2009). Connectivity of remnant habitat patches reduces the effect of isolation and improves dispersal ability of organisms (Fahrig 2003), which in turn, increases genetic variability and long-term survival of populations (Hilty *et al.* 2006; Wells *et al.* 2009). The aim of ecological networks is therefore to function equivalently to adjacent protected areas within transformed landscapes.

In addition to existing ecological networks, plantations contain numerous isolated patches of protected grassland, wetland and indigenous forest within a timber matrix. Biodiversity levels within these remnant patches are influenced by size, shape, heterogeneity and habitat quality (Saunders *et al.* 1991; Laurance *et al.* 2002; Kruess & Tschardtke 2002; Samways 2007; Costanza *et al.* 2011; Cabrera-Guzmán & Reynoso 2012). Irregularly shaped and small fragments also have a higher proportion of edge habitat, often reducing their value for biodiversity conservation (Didham *et al.* 1996; Yamaura *et al.* 2008). Optimization of

existing ecological network design includes selectively planting or removing timber stands in strategic areas to alter their size or shape to include areas with special landscape features or to enlarge corridors in key locations. In order to make informed design and management decisions, assessment of remnant patches is critical to prioritize areas with high conservation value and conversely, to identify areas that are relatively ineffective in conserving biodiversity. Consequently, there is a need to conduct reliable, rapid assessment surveys of remnant patches within plantations. And so, the aim here is to test the concept of acoustic profiling for landscape assessment and conservation planning in a diverse landscape mosaic.

Methods

Study area and design

I studied three jointly owned and managed commercial plantations within the Zululand region of the KwaZulu-Natal Province, South Africa. Nyalazi (28°12'S; 32°22'E), was northerly adjacent to DukuDuku (28°19'S; 32°22'E) and Kwambonambi (28°39'S; 32°10'E) was 20 km to the south of DukuDuku. Plantations were situated within threatened Maputaland Wooded Grassland or Maputaland Coastal Belt biomes (Mucina & Rutherford 2006) and consisted mainly of alien *Eucalyptus* and *Pinus* species (Kirkman & Pott 2002). The plantations all had similar elevations of 20-90 m asl and bordered the iSimangaliso Wetland Park (a World Heritage Site) to the east. As there is no fence between the plantations and iSimangaliso Wetland Park, many large animals including the African elephant (*Loxodonta africana*), white rhino (*Ceratotherium simum*), African buffalo (*Syncerus caffer*) and leopard (*Panthera pardus pardus*) occur in the ecological networks and protected nodes of the plantations.

A total of 210 sites of seven types were selected within plantations: indigenous forest patches (n = 34), wetland patches (n = 48), grassland patches (n = 43), *Eucalyptus* timber stands with no understory vegetation (n = 15), managed sites (areas under power line servitudes and firebreaks that were mowed biweekly) (n = 21), grazed patches (grassland and wetland areas grazed by wild game and domestic cattle) (n = 11) and road margins (narrow margin of tall grass (>30 cm) between *Eucalyptus* stands and road) (n = 21). Outside of plantations, protected area (PA) sites (large natural grassland areas over 150 ha) (n = 17) were also selected. PA sites were placed >1 km apart and located over 32 m away from plantation timber stands to avoid edge effects (Pryke & Samways 2011).

Variables, including site category, such as wetland or grassland patch and size (perimeter and area) were determined by GIS using Manifold System 8.0. Shape of sites was measured by the Shape Index, an area-independent measure in which a perfectly circular site receives a value of 1, with greater divergence from this shape proportionately increasing this value (Laurance & Yensen 1991). As size of PA sites were only categorical (>150 ha), other site sizes were made categorical for statistical analysis. Size classes were exponentially chosen to determine effects of small patches on biodiversity: 1 = <1 ha (n = 24); 2 = 1 – 3 ha (n = 29); 3 = 3 – 10 ha (n = 59); 4 = 10 – 150 ha (n = 71); 5 = >150 ha (n = 27).

As orthopteran species composition responds more strongly to native vegetation structure than to grass species composition (Gandar 1982; Chambers & Samways 1998; Hochkirch & Adorf 2007; Bazelet & Samways 2010), structural diversity of vegetation was surveyed. Within sites the percent cover of tall grass (>30 cm), short grass (<30 cm), bare ground, shrubs, small non-commercial trees (<2 m), and tall non-commercial trees (>2 m) were recorded visually. Additionally, percentage cover of non-native, invasive crow's foot grass (*Dactyloctenium australe*) was recorded.

The degree of variation within vegetation structure and cover was measured within each site, as this can have an influence on species diversity (Palmer 1990; Costanza *et al.* 2011). Local heterogeneity is frequently measured in terms of vegetation structure (Costanza *et al.* 2011), yet there is little consensus concerning its metrics (Costanza *et al.* 2011). Here, the level of heterogeneity was measured visually by a single observer, ranking each site on a scale of 1-10. A site with a score of 1 was a uniform biotope of one structural vegetation type, a site with a score of 2 contained two structural vegetation types and so on until culminating in a score of 10 containing ten or more structural vegetation types, indicating a highly diverse biotope (Fig. 4.1).

Acoustic sampling

Nocturnal acoustic surveys were carried out in the late summer (February 2010) corresponding with peak acoustic activity of katydids (Tettigoniidae), crickets (Gryllidae) and frogs. Many acoustic species sing more intently during dawn and dusk (Riede 1997; Sueur *et al.* 2008; Diwakar & Balakrishnan 2007b; Franklin *et al.* 2009; Pijanowski *et al.* 2011). Therefore, to avoid the influence of dawn and dusk choruses on site comparisons, all acoustic recordings were made an hour after sunset and ended an hour before dawn between 21h00 and 05h00 hrs. During acoustic sampling, the time, temperature, wind speed and humidity were recorded within each site. Within each site, three ambient acoustic recordings, each of a minute in duration, were made using a Sennheiser (Sennheiser, Germany) long barrel microphone in conjunction with a Marantz PD660 (Marantz, USA) solid state digital recorder. The Sennheiser microphone has a frequency response up to 20 kHz, ideal for recording call structure of various acoustic species with minimal background noise and without being concerned for severe attenuation of the very high frequencies. The Marantz PD660 recording parameters were the same for all sites and set to sampling rate of 48 kHz with an uncompressed file format (.wav).

Ambient recordings within sites were separated by 100 m to increase signal coverage, but sites small in size occasionally limited this distance to 50-100 m.

Signal analysis

Acoustic recordings were analyzed using Raven Pro 1.5 (Cornel Laboratories, USA). Spectrograms were produced for each recording to graphically display and analyze the energy within the temporal and frequency spectra. For each site, these spectrograms were used to calculate maximum energy (dB), center frequency (kHz), the smallest discrete frequency which contains 50% of total energy, and maximum entropy (μ), which measures the amount of disorder in sound by analyzing the energy distribution within a spectrogram. High entropy values correspond to greater disorder, whereas a single pure tone with energy in a narrow frequency band would have zero entropy.

Each 1 kHz frequency band within spectrograms were also isolated and examined in detail for species-specific signals (Fig. 4.2). Using signal structure measures, and playback features within selected frequency bands, provided a means to identify acoustic species. Highly stereotyped species-specific signals allow for trained listeners to distinguish between morphologically similar species with a high degree of accuracy (Riede 1996; Diwaker *et al.* 2007). Signals from acoustic species were also characterized according to their signal structure based on center frequency and pulse rate (number of pulses per second). Pulses are the smallest discrete amplitude modulations within signals, grouped together as chirps or generated continuously as trills. Chirps, comprised of multiple pulses can occur singularly or within groups known as also known as trills. The gaps between pulses, chirps and trills are referred to as intervals. For each species-specific signal these elements were measured along with center frequency (the smallest discrete frequency which contains 50% of total energy).

Classification of species based on pulse rate and center frequency allows for the definition of recognizable taxonomic units (Riede 1998). Once acoustic species are defined, signals can be used as sensitive indicators of biodiversity and habitat quality and deterioration (Riede 1998; Fischer *et al.* 1997; Brandes *et al.* 2006). Frog calls of southern Africa (du Preez 2009), along with bird calls (Xeno-canto 2012) are known, permitting the identification of these species within recordings.

Birds are most acoustically active during dawn, but contain a rich variety of diurnal and some nocturnal species. Their acoustic signals are recognizable through complex fluctuating intensity across lower frequency ranges <3 kHz (Riede 1993). Comparatively, frogs which also utilize frequency ranges <3 kHz, are more nocturnally active and have relatively simple call structures easily classified by frequency range and pulse rates (Riede 1993; Malkmus & Riede 1996; Gerhardt & Huber 2002; du Preez & Carruthers 2009).

Katydid (Orthoptera: Ensifera: Tettigoniidae) acoustic signals were identified in ambient recordings through recording, collecting and identifying the species of the signaler within sites. Katydid are nocturnal insects that produce species-specific signals by tegminal stridulation, where a file and scrapper mechanism on the forewings cause the mirror to resonate at generally high, broadband frequency ranges between 6 and 130 kHz (Montealegre-Z *et al.* 2006; Greenfield 2002). These signals have a diverse range of temporal amplitude modulations comprising of pulses grouped into chirps or generated continuously as trills. (Greenfield 2002).

A large portion of acoustic space both in terms of number of species signaling and the nocturnal acoustic energy is generated by crickets (Orthoptera: Ensifera: Gryllidae). Crickets have conspicuous, simple repetitive signals within a very narrowband frequency range between 1 and 11 kHz (Riede 1998). Male crickets also generate acoustic signals by tegminal stridulation, where a file and scrapper mechanism on the forewings cause the harp to resonate

at narrow species-specific frequency ranges (Greenfield 2002). Within sites, acoustic signals were located to identify the taxon of the signaler. Pulse repetition rate and frequency range permitted easy acoustic classification of cricket species (Riede 1998).

Data analysis

Generalized Linear Models (GLMs) with Poisson distribution and log-link functions, were used to compare species richness across environmental and acoustic variables (Dobson 1990; Bolker *et al.* 2009; O'Hara 2009; Zuur *et al.* 2010) in Statistica 8 (Statsoft 2012). GLMs provide a flexible, robust approach for analyzing categorical and continuous data that is non-normal by using Poisson distributions with log-link functions (Bolker *et al.* 2009). Tests for the significance of the effects in the model were performed via the Wald statistic (w) (Yi & Wang 2011). Data on time acoustic surveys were analyzed categorically, with all sampling events within each hour assigned to a unique category (i.e. 21h00 = 1, 05h00 = 9). The Shannon-Wiener Index (H') was used to calculate species diversity across site categories and size categories. This diversity index is analogous to entropy of species within a community, with values approaching zero equating to lower diversity. As the H' index is sensitive to rare species, it is recommended for landscape diversity assessments (Nagendra 2002).

Results

Between the three plantation landscapes, there were no differences in species composition, species richness ($w = 1.46$, $p = 0.48$) or their Shannon-Weiner biodiversity index ($w = 5.95$, $p = 0.51$), allowing sites across all plantations to be pooled for analyses.

All species were detected continually from 21h00-05h00 hrs. Time of sampling therefore did not have an effect on total species richness across sites ($w = 6.31$, $p = 0.38$). Meteorological

variables did not vary significantly across sites, with temperature ranges (mean and standard deviation) of ($25.6 \pm 1.3^{\circ}\text{C}$) ($w = 2.11, p = 0.14$), wind speed (0.26 ± 0.34 m/s) ($w = 2.19, p = 0.13$) and relative humidity ($74.9 \pm 4.7\%$) ($w = 0.04, p = 0.83$). Species richness across sites consequently did not vary with temperature ($w = 2.35, p = 0.12$), wind speed ($w = 6.19, p = 0.12$) or relative humidity ($w = 2.22, p = 0.13$).

In total, 65 acoustic species were identified across all sites (Table 4.1), including bird ($n = 1$), frog ($n = 11$), katydid ($n = 21$) and cricket ($n = 32$) species. There were no nocturnal anthropogenic noises detected at any site. Acoustic taxa separated out based on pulse rate and center frequency (Fig. 4.3). Katydid acoustic signals occupied highest frequency ranges, followed by crickets, with birds and frogs occupying the lowest frequency ranges.

The various site categories (*Eucalyptus* timber stands, managed areas, grazed areas, road margins, indigenous forest, grassland, wetland and protected areas) showed differences in vegetation structure (Table 4.2). Between these site types, there were significant differences in mean species richness ($w = 179.50, p = 0.00$) (Fig. 4.4; Table 4.1). Shannon-Wiener Index scores, showed a corresponding increase with mean species diversity. *Eucalyptus* stands contained no acoustic species. Managed sites, with the exception a single cricket species (*Gryllidae* sp. 13), contained no acoustic species. The grassy margin along roads had low mean species richness (13 species in total). Yet, *Ruspolia* sp. 5 was only detected within this site category and *Ruspolia* sp. 4 was detected predominantly within this site category. Grazed sites had higher mean species richness (19 species in total) than road sites, but contained no unique species, and significantly less mean species richness than indigenous forest, wetland, grassland and PA sites. There was no difference in mean species richness between indigenous forest (33 species), grassland (45 species) and wetland patches (50 species) ($w = 5.57, p = 0.06$), yet there were differences in species composition (Table 4.1). Indigenous forests had nine unique

species. Wetland patches had four unique species. While grassland patches had comparable mean species richness to wetland and indigenous forest, it contained no unique species and generally species within this habitat type were detected more frequently within other habitat types. PA sites had the highest mean species richness (49 species) and contained three unique species.

Site size had a significant effect on species richness ($w = 74.39, p = 0.00$) (Fig. 4.5). Sites <1 ha showed a large drop in mean species richness and Shannon-Wiener Index scores. Sites >1 ha and <150 ha supported similar mean species richness ($w = 2.14, p = 0.34$). Sites >150 ha supported the greatest mean number of species and had the highest Shannon-Wiener Index scores. Shape of sites also influenced total species richness, with increasing shape index resulting in decreased species richness ($w = 10.74, p = 0.00$). However, when managed areas, which contained relatively no species and had high SI index scores (being long and narrow), were removed from the analysis, SI did not have an effect on species richness ($w = 0.68, p = 0.41$). Higher heterogeneity within sites also increased species richness ($w = 140.81, p = 0.00$). Species richness also decreased significantly with increasing cover of invasive crow's foot grass ($w = 21.46, p = 0.00$). Sites with $>70\%$ cover of this invasive grass contained no acoustic species.

Analysis of maximum entropy (μ) across sites also revealed a positive correlation between entropy levels and species richness ($w = 79.25, p = 0.00$) (Fig. 4.6). However, this correlation was unable to discriminate between species richness of 6 and 16 ($w = 0.46, p = 0.91$). A positive correlation was also present between species richness and maximum energy (dB) ($w = 93.28, p = 0.00$).

Discussion

Excellent camouflage, cryptic lifestyles and nocturnal habits of many species make visual surveys difficult. However, a considerable number of species indicate their presence acoustically, providing a non-invasive, rapid, reliable method for their detection. Center frequency, pulse rate and chirp structure are species-specific cues that evolved for the recognition of conspecifics and therefore fulfil the definition of the biological species concept (Riede 1993). Intraspecific variation within these acoustic parameters is so small that classification and identification of acoustic species is relatively easy (Riede 1993). Katydid generally utilize high frequency, broadband signals compared to crickets which use low frequency narrowband signals, allowing the signaler to be identified. Identification of acoustic species through acoustic surveys therefore effectively bridges the taxonomic gap that currently exists in South Africa and elsewhere for many Orthoptera species that are taxonomically unknown.

Acoustic transmission channels are a critical resource for many species, resulting in competition and resource partitioning of different dominant frequencies and temporal patterns (Duellman & Pyles 1983; Riede 1993; Riede 1997; Diwakar & Balakrishnan 2007a; Diwakar & Balakrishnan 2007b; Schmidt *et al.* 2012; Jain *et al.* 2013). Therefore, strategies that acoustic species employ to avoid acoustic interference and maximize their signal propagation may have implications for acoustic surveys. Within the present study, only nocturnal species between dawn and dusk choruses were surveyed, as these species mostly utilize different dominant frequencies, rather than nocturnal temporal partitioning patterns to communicate (Diwakar & Balakrishnan 2007b; Schmidt *et al.* 2012). This allowed for comparisons between sites without time of sampling being factor. It is commonly accepted that weather conditions also affect calling rates in Orthoptera (Edes 1899; Franklin *et al.* 2009). Often, katydids call continually

through the night unless interrupted by cold temperatures or rain, which result in the cessation of calls (Franklin *et al.* 2009). Here, weather conditions were fairly consistent across sites allowing unbiased assessment of acoustic species richness. As temporal and meteorological factors influence how taxa communicate, acoustic sampling methods should occur only within uniform conditions to allow for unbiased biodiversity comparisons between sites.

Forestry plantations comprising of individual patches of indigenous vegetation and other features embedded within a timber matrix contained a diverse range of acoustic signatures. Alien vegetation had a distinct, detrimental impact on acoustic signals and species richness. *Eucalyptus* stands contained no acoustics species and sites with increasing cover of crow's foot grass experienced decreasing species richness resulting in no acoustic species occurring in sites with >70% cover. Alien vegetation is well known to negatively impact species diversity (Slobodchikoff & Doyen 1977; Olckers & Hulley 1991; Armstrong & van Hensbergen 1996; Samways *et al.* 1996; Gerber *et al.* 2008; Wu *et al.* 2009; Litt & Steidl 2010; Simao *et al.* 2010). Alien vegetation can often outcompete native vegetation, altering plant communities and affecting dynamics of resource and reproduction sites for insects (Pimentel *et al.* 1999; Bakker & Wilson 2001). Altering these dynamics causes noticeable deleterious changes within acoustic signals. While species are not utilizing either *Eucalyptus* stands or sites with >70% cover of crow's foot grass, they may still disperse silently through them to reach other suitable habitat patches (Pryke & Samways 2001). Unlike timber stands which have a direct economic benefit, non-endemic invasive grasses significantly reduce biodiversity, and management actions should incorporate their removal or control.

Managed sites that were mowed biweekly were acoustically similar to sites with alien vegetation and contained relatively no acoustic species diversity. The high disturbance and short grass within these sites did not provide suitable habitat for nocturnal acoustic species such

as katydids, crickets, frogs or birds. Katydid in particular, are generally highly cryptic, less mobile insects, which require vegetation for camouflage, traits characteristic of late successional species (Greenfield 2002). Within the same plantations, these managed areas had a high abundance and diversity of grasshoppers (Orthoptera: Caelifera) (Bazelet & Samways 2010). Managed areas simulate early successional stages after fire or heavy grazing, which benefits early successional stage insects like grasshoppers that are highly mobile, have fast generation times and have wide niche breadths (Brown 1985; Siemann *et al.* 1999; Picaud & Petit 2007; Bazelet & Samways 2010). While managed areas support early successional stage insects, they are not beneficial for late successional stage insects or other nocturnal acoustic species, highlighting that management actions in these areas benefits some taxa to the detriment of others. Incorporating diurnal acoustic surveys into the present study would have captured diurnal acoustically communicating taxa such as grasshoppers, cicada and birds, providing an additional assessment window. However, diurnal or nocturnal acoustic species would likely reflect similar overall distributions in biodiversity across large-scale environmental gradients (Howard *et al.* 1998; Eeley *et al.* 2001).

Grassland areas within plantations are often grazed by wild game and domestic cattle both of which play a significant role in shaping vegetation characteristics through succession (Mucina & Rutherford 2006; Lindenmayer & Fischer 2006). Disturbance through heavy grazing, particularly from domestic cattle have a highly impoverishing effect on invertebrate species (Bullock & Samways 2005; Samways *et al.* 2009). Grazed sites had a high proportion of short grass and bare ground, similar to managed areas, which again provides habitat for early successional species, but severely degrades habitat for late successional species resulting in an overall decline in diversity of nocturnal acoustic species.

Grassy margins between roads and forest edge can be considered extreme edge habitat. While these areas did not support high species diversity, the tall grass within these sites was a unique biotope for certain katydid species, therefore contributing marginally to overall biodiversity of the plantation matrix. On a landscape scale, this emphasizes the importance of special natural landscape features containing unique niches to maximize overall biodiversity.

While grassland, wetland and indigenous forest patches did not vary in terms of mean species diversity, there were notable differences in species composition between these categories. Most notable were indigenous forest patches within the plantation matrix, which contained a large number of unique acoustic species. Within the same region, they also contain other unique non-acoustic taxa (Pryke & Samways 2011), and have been identified as priority areas for conservation containing overlapping hotspots of species richness and rarity (Eeley *et al.* 2001), emphasizing their importance in conserving biodiversity (MacDevette *et al.* 1989; Lawes *et al.* 2000; Eeley *et al.* 2001). An estimated 42.5% of this indigenous forest biome has been transformed, mainly through plantation forestry (Eeley *et al.* 2001). While about 18% (128 500 ha) currently falls within PAs, it remains the smallest biome represented in the country (Low & Rebelo 1996). Currently, it is highly fragmented, with most individual patches being <100 ha (Low & Rebelo 1996). Given their overall small total area, it has been recommended that all indigenous forest in South Africa should be protected (Scheepers 1983; Eeley *et al.* 2001). Maintaining indigenous forest within ecological networks of plantations would likely help conserve biodiversity across the timber production landscape.

Wetland patches contained the highest total number of species, unique acoustic species and species that were predominantly detected within this biome, underscoring their contribution to overall biodiversity within plantations. PA sites with large grassland areas contained the greatest mean species richness in addition supporting unique species. However,

isolated grassland patches, had lower mean species richness, yet contained similar species composition to PA sites. This emphasizes that isolated grassland patches surrounded by a timber matrix function similarly to PA sites and contribute to reducing contrast between transformed landscapes and natural biomes. In order to maximize species richness however, there may be value in using the combined area of isolated grassland patches towards increasing connectivity and size of current grassland ecological networks.

How size of patches effects biodiversity has been studied extensively (Hokit & Branch 2003; Fahrig 2003; Horn *et al.* 2005; Lindenmayer & Fischer 2006; Fischer & Lindenmayer 2007; Laurance 2008; Cabrera-Guzmán & Reynoso 2012). Generally there is a positive association between patch size and either reproductive success or survival (Hokit & Branch 2003; Horn *et al.* 2005). Organisms in smaller patches are also more susceptible to edge effects (Horn *et al.* 2005). While some species respond positively to edge habitat (van Halder *et al.* 2011; Pryke & Samways 2012), from a biodiversity perspective, it is the interior zone which is important to conserve, yet also more difficult to do so, as it requires enough space for edge zone to surround it (Pryke & Samways 2012). Previous research within these plantations demonstrated species richness and assemblage composition is negatively impacted within 32 m of plantation edge (Pryke & Samways 2011). Theoretically this implies that remnant patches within a timber matrix that are circular in shape and contain a radius of <32 m (0.32 ha) could be considered entirely edge zone. Small patches of <1 ha are therefore likely highly impacted by edge effects. Within this study, patches sizes of <1 ha contained significantly lower species diversity. Yet sites between 1 and 150 ha did not significantly vary in species richness, while and sites >150 ha contained the highest species diversity. This means that within a plantation context, patches must be >1 ha in order to effectively avoid extreme edge effects and conserve biodiversity within plantations. Using the combined area of small remnant patches to contribute

towards ecological networks may contribute towards biodiversity conservation while enabling more effective management of timber stands in which they are currently located.

Another factor which influenced the degree of biodiversity within patches was heterogeneity. Habitats with greater heterogeneity host greater biodiversity due to the larger amount of available niches within them, regardless of the taxonomic group under consideration (Gaston 2000; Palmer *et al.* 2002; Hortal & Lobo 2005; Rocchini *et al.* 2010). While habitat heterogeneity does not necessarily ensure conservation of rare or endemic species, it does contribute to overall biodiversity across the landscape (Grant & Samways 2011). On a landscape scale, this has important implications for the design of ecological networks. Selecting habitats with special landscape features, and containing unique niches, maximizes the level of biodiversity conserved within plantation matrices (Samways *et al.* 2009). Conserving the natural structural aspects of a landscape therefore contributes towards conserving compositional, structural and functional biodiversity, improving the persistence of populations within transformed landscapes (Samways *et al.* 2009).

Biodiversity assessment at landscape scales requires rapid and reliable methods to accurately assess and compare species richness across environmental gradients and over time. Importantly, species-specific acoustic parameters such frequency and amplitude modulation provide an excellent means to measure acoustic species diversity and allow for the definition of recognizable taxonomic units where taxonomic challenges exist (Riede 1993; Riede 1998; Nischk & Riede 2001). Bioacoustic signal recognition and identification range from trained human listeners, manual analysis of spectrograms to computer based recognition and classification software (Riede 1998; Diwakar *et al.* 2007). Each of these methods has advantages and limitations, but both provide a powerful high resolution tool for monitoring species diversity.

Biodiversity can also be roughly estimated by measuring the degree of entropy within sound, forgoing identification of acoustic species within communities (Sueur *et al.* 2008). The ability to estimate species diversity using easily measured variables with limited resources is becoming increasingly important (Rocchini *et al.* 2010). Using entropy within the present study provided a quick, reliable estimate of biodiversity levels through simple signal analysis (Sueur *et al.* 2008). While proving to be an extremely effective tool, it lacked high resolution detail required to assess biodiversity at a species level. This is important from a conservation perspective, as species composition is often as important as species richness. Acoustic analysis at a species level also detects the disappearance of endemic species or appearance of invasive species, which can potentially prevent optimal signal propagation of endemic species (Pijanowski *et al.* 2011) or generate acoustic signals where previously there were none (Dumyahn & Pijanowski 2011). Furthermore, it does not distinguish between natural bioacoustics signals and anthropogenic noise pollution, limiting its application in certain contexts and potentially providing false high biodiversity estimates in areas with noise pollution. Sound pollution within landscapes can also result in species shifting spatially or altering acoustic communication channels to avoid acoustic interference (Slabbekoorn & Peet 2003; Patricelli & Blickley 2006; Barber *et al.* 2011; Dumyahn & Pijanowski 2011; Pijanowski *et al.* 2011; Shieh *et al.* 2011). Therefore, it is often necessary to have high resolution signal analysis to not only identify acoustic species but to distinguish between natural bioacoustics signals and anthropogenic noise.

Conclusions

To mitigate effect of landscape transformation, ecological networks and isolated patches of indigenous forest, wetland and grassland have been incorporated into the design of timber plantations. The landscape mosaic design within plantations effectively reduces the contrast of

transformed landscapes with surrounding natural areas, resulting in plantation landscapes which are sustainably managed, opening critical European markets through FSC certification. Optimization of ecological network design includes protecting strategic areas while afforesting less critical patches of natural vegetation. To make informed decisions to sustainably manage plantations and maximize conservation of biodiversity necessitates identification of biodiversity patterns across patches of indigenous vegetation. Acoustic profiling of the landscape provides an effective, rapid tool to investigate diversity patterns across these ecological gradients.

Results of acoustic profiling indicate that future optimization of ecological networks within forestry plantations should make indigenous forest patches and their connectivity a conservation priority, as this highly threatened biome supports a high diversity of unique acoustic species not detected in other wetland or grassland patches.

Grassland patches were acoustically similar to large protected grassland areas, highlighting that isolated grassland patches surrounded by a timber matrix were effective in reducing the contrast of transformed landscapes with surrounding natural areas. As larger areas support greater mean species richness, using the combined area of grassland patches within plantations to enlarge strategic areas and connectivity of current ecological networks would likely help increase biodiversity conservation across the plantation landscape.

Within natural vegetation patches, species richness increased with heterogeneity and patch size. Patches <1 ha, are heavily influenced by edge effects and were not suitable for conserving biodiversity. Increasing the size of small patches of natural vegetation within plantations would contribute to optimizing ecological networks while enabling more effective management of timber stands in which small patches are located.

Alien vegetation such as *Eucalyptus* stands, and sites containing >70% cover of invasive crow's foot grass did not support acoustic species, highlighting the negative impact alien vegetation can have on species diversity. While acoustic species are not utilizing these areas as resource, they may still disperse through them to reach other patches or large natural areas. Unlike timber stands which have an economic benefit, management actions should incorporate the removal or control of non-endemic, invasive grasses to maximize biodiversity within the plantation matrix.

Other features within plantations such as powerline servitudes and firebreaks are an integral part of the production landscape and require regular management. While these areas contribute over overall biodiversity of grasshoppers, their management was not beneficial to late successional stage insects or other nocturnal acoustic species, highlighting the influence of plantation management actions on biodiversity. Overall, acoustic profiling provided an effective tool to investigate acoustic diversity patterns across this landscape mosaic.

References

- Armstrong, A. J. & van Hensbergen, H. J. 1994. Comparison of avifaunas in *Pinus radiata* habitats and indigenous riparian habitat at Jonkershoek, Stellenbosch. *South African Journal of Wildlife Research* 24:48–55.
- Armstrong, A. J. & van Hensbergen, H. J. 1996. Impacts of afforestation with pines on assemblages of native biota in South Africa. *South African Forestry Journal* 175:35–42.
- Bakker, J. & Wilson, S. 2001. Competitive abilities of introduced and native grasses. *Plant Ecology* 157:117–125.
- Barber, J. R., Burdett, C. L., Reed, S. E., Warner, K. A., Formichella, C., Crooks, K. R., Theobald, D. M. & Fristrup, K. M. 2011. Anthropogenic noise exposure in protected natural areas: estimating the scale of ecological consequences. *Landscape Ecology* 26:1281–1295.
- Bazelet, C. S. & Samways, M.J. 2010. Relative importance of management vs. design for implementation of large-scale ecological networks. *Landscape Ecology* 26:341–353.
- Bieringer, G. & Zulka, K. P. 2003. Shading out species richness: edge effect of a pine plantation on the Orthoptera (Tettigoniidae and Acrididae) assemblage of an adjacent dry grassland. *Biodiversity and Conservation* 12:1481–1495.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J. S. S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–35.
- Brandes, T. S., Naskrecki, P. & Figueroa, H. K. 2006. Using image processing to detect and classify narrow-band cricket and frog calls. *Journal of the Acoustical Society of America* 120:2950–2957.

- Bremer, L.L. & Farley, K. A. 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land use transitions on plant species richness. *Biodiversity and Conservation* 19:3893–3915.
- Brown, V. K. 1985. Insect herbivores and plant succession. *Oikos* 44:17–22.
- Bullock, W. L & Samways, M. J. 2005. Conservation of flower–arthropod interactions in remnant grassland linkages among pine afforestation. *Biodiversity and Conservation* 14:3093–3103.
- Cabrera-Guzmán, E. & Reynoso, V. H. 2012. Amphibian and reptile communities of rainforest fragments: minimum patch size to support high richness and abundance. *Biodiversity and Conservation* 21:3243–3265.
- Chambers, B. Q. & Samways, M. J. 1998. Grasshopper response to a 40-year experimental burning and mowing regime, with recommendations for invertebrate conservation management. *Biodiversity and Conservation* 7:985–1012.
- Costanza, J. K., Moody, A. & Peet, R. K. 2011. Multi-scale environmental heterogeneity as a predictor of plant species richness. *Landscape Ecology* 26:851–864.
- Didham, R. K., Ghazoul, J., Stork, N. E. & Davis, A. J. 1996. Insects in fragmented forests: a functional approach. *Trends in Ecology & Evolution* 11:255–260.
- Diwakar, S. & Balakrishnan, R. 2007a. Vertical stratification in an acoustically communicating ensiferan assemblage of a tropical evergreen forest in southern India. *Journal of Tropical Ecology* 23:479–486.
- Diwakar, S. & Balakrishnan, R. 2007b. The assemblage of acoustically communicating crickets of a tropical evergreen forest in southern India: call diversity and diel calling patterns. *Bioacoustics* 16:113–135.

- Diwakar, S., Jain, M. & Balakrishnan, R. 2007. Psychoacoustic sampling as a reliable, non-invasive method to monitor orthopteran species diversity in tropical forests. *Biodiversity and Conservation* 16:4081–4093.
- Dobson, A. J. 1990. *An introduction to generalized linear models*. Chapman & Hall, New York.
- du Preez, L. & Carruthers, V. 2009. *A complete guide to the frogs of southern Africa*. Struik Nature, Cape Town.
- Duellman, W. E. & Pyles, R. E. 1983. Acoustic resource partitioning in anuran communities. *Copeia* 3:639–649.
- Dumyahn, S. L. & Pijanowski, B. C. 2011. Soundscape conservation. *Landscape Ecology* 26:1327–1344.
- DWAF (Department of Water Affairs and Forestry). 2005. *PCI&S final version 2005*. Department of Water Affairs and Forestry, Pretoria, South Africa. Available via <http://www.dwaf.gov.za>.
- DWAF (Department of Water Affairs and Forestry). 2006. *Abstract of South African forestry facts for the year 2004/2005*. Department of Water Affairs and Forestry, Pretoria, South Africa. Available via <http://www.dwaf.gov.za>.
- Edes, R. 1899. Relation of the chirping of the tree cricket (*Oecanthus niveus*) to temperature. *The American Naturalist* 33:935–938.
- Eeley, H. A. C., Lawes, M. J. & Reyers, B. 2001. Priority areas for the conservation of subtropical indigenous forest in southern Africa: a case study from KwaZulu-Natal. *Biodiversity and Conservation* 10:1221–1246.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487–515.

- Farina, A., Lattanzi, E., Malavasi, R., Pieretti, N. & Piccioli, L. 2011. Avian soundscapes and cognitive landscapes: theory, application and ecological perspectives. *Landscape Ecology* 26:1257–1267.
- Fischer, J. & Lindenmayer, D. B. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16:265–280.
- Fischer, P. F., Schulz, U., Schubert, H., Knapp, P. & Schmöger, M. 1997. Quantitative assessment of grassland quality: acoustic determination of population sizes of orthopteran indicator species. *Ecological Applications* 7:909–920.
- Franklin, M., Droege, S., Dawson, D., Royle, J. 2009. Nightly and seasonal patterns of calling in common true katydids (Orthoptera: Tettigoniidae: *Pterophylla camellifolia*). *Journal of Orthoptera Research* 18:15–18.
- FSC (Forest Stewardship Council). 1996. *FSC international standard: FSC principles and criteria for forest stewardship*. FSC-STD-01-001 (version 4-0). Available via <http://www.fsc.org>.
- Gandar, M. V. 1982. The dynamics and trophic ecology of grasshoppers (Acridoidea) in a South African savanna. *Oecologia* 54:370–378.
- Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* 405:220–227.
- Gerber, E., Krebs, C., Murrell, C. & Moretti, M. 2008. Exotic invasive knotweeds (*Fallopia* sp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. *Biological Conservation* 141:646–654.
- Gogala, M. & Riede, K. 1995. Time sharing of song activity by cicadas in Temengor Forest Reserve, Hulu Perak, and in Sabah, Malaysia. *Malayan Nature Journal* 48:297–305.
- Goyette, J. L., Howe, R. W., Wolf, A. T. & Robinson, W. D. 2011. Detecting tropical nocturnal birds using automated audio recordings. *Journal of Field Ornithology* 82:279–287.

- Grant, P. B. C. & Samways, M. J. 2011. Micro-hotspot determination and buffer zone value for Odonata in a globally significant biosphere reserve. *Biological Conservation* 144:772–781.
- Greenfield, M. D. 2002. *Signalers and receivers. Mechanisms and evolution of arthropod communication*. Oxford University Press, Oxford.
- Hilty, J. A., Lidicker, W. Z. & Merenlender, A. M. 2006. *Corridor ecology: the science and practice of linking landscapes for biodiversity conservation*. Island Press, Washington, DC.
- Hochkirch, A. & Adorf, F. 2007. Effects of prescribed burning and wildfires on Orthoptera in Central European peat bogs. *Environmental Conservation* 34:225–235.
- Hokit, D. G & Branch, L. C. 2003. Associations between patch area and vital rates: consequences for local and regional populations. *Ecological Applications* 13:1060–1068.
- Horn, D. J., Phillips, M. L., Koford, R. R., Clark, W. R., Sovada, M. & Greenwood, R. J. 2005. Landscape composition, patch size, and distance to edges: interactions affecting duck reproductive success. *Ecological Applications* 15:1367–1376.
- Hortal, J. & Lobo, J. M. 2005. An ED-based protocol for the optimal sampling of biodiversity. *Biodiversity and Conservation* 14:2913–2947.
- Howard, P. C., Viskanic, P., Davenport, T. R. B., Kigenyi, F. W., Baltzer, M., Dickinson, C. J., Lwanga, J. S., Matthews, R. A. & Balmford, A. 1998. Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature* 394:472–475.
- Jain, M., Diwakar, S., Bahuleyan, J., Deb, R. & Balakrishnan, R. 2013. A rain forest dusk chorus: cacophony or sounds of silence? *Evolutionary Ecology* doi:10.1007/s10682-013-9658-7.

- Jongman, R. H. G. 1995. Nature conservation planning in Europe: developing ecological networks. *Landscape and Urban Planning* 32:169–183.
- Kirkman, K. E. & Pott, R. M. 2002. Biodiversity conservation in plantation forestry. In: Pierce, S. M., Cowling, R. M., Sandwith, T. & MacKinnon, K. (eds.). *Mainstreaming biodiversity in development—case studies from South Africa*. The World Bank Environmental Department, Washington DC.
- Kruess, A. & Tschardt, T. 2002. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology* 16:1570–1580.
- Laurance, W. F. 2008. Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation* 141:1731–1744.
- Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., Gascon, C., Bierregaard, R. O., Laurance, S. G. & Sampaio, E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16:605–618.
- Laurance, W. F. & Yensen, E. 1991. Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* 55:77–92.
- Lawes, M. J., Eeley, H. A. C. & Piper, S. E. 2000. The relationship between local and regional diversity of indigenous forest fauna in KwaZulu-Natal Province, South Africa. *Biodiversity and Conservation* 9:683–705.
- Le Maitre, D. C., van Wilgen, B. W., Chapman, R. A. & McKelly, D. H. 1996. Invasive plants and water resources in the Western Cape Province, South Africa: modelling the consequences of lack of management. *Journal of Applied Ecology* 33:161–172.
- Lindenmayer, D. B. & Fischer, J. 2006. *Habitat fragmentation and landscape change: an ecological and conservation synthesis*. Island Press, Washington DC.

- Litt, A. R. & Steidl, R. J. 2010. Insect assemblages change along a gradient of invasion by a nonnative grass. *Biological Invasions* 12:3449–3463.
- Low, A. B. & Rebelo, A. G. 1996. *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria.
- MacDevette, D. R., MacDevette, D. K., Gordon, I. G. & Bartholomew, R. L. C. 1989. Floristics of the Natal indigenous forests. In: Geldenhuys, C. J. (ed.) *Biogeography of the mixed evergreen forests of Southern Africa*. Foundation for Research Development, Pretoria.
- MacSwiney, G., Cristina, M., Clarke, F. M. & Racey, P. A. 2008. What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. *Journal of Applied Ecology* 45:1364–1371.
- Malkmus, R. & Riede, K. 1996. Frogs from Kinabalu. Borneo. *Sauria* 18:37–37.
- Montealegre-Z, F., Morris, G. K. & Mason, A. C. 2006. Generation of extreme ultrasonics in rainforest katydids. *Journal of Experimental Biology* 209:4923–4937.
- Morris, K. & Beier, M. 1982. Song structure and description of some Costa Rican katydids (Orthoptera: Tettigoniidae). *Transactions of the American Entomological Society* 108:287–314.
- Mucina, L. & Rutherford, M. C. 2006. *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria.
- Nagendra, H. 2002. Opposite trends in response for the Shannon and Simpson indices of landscape diversity. *Applied Geography* 22:175–186.
- Neke, K. S., du Plessis, M. A. 2004. The threat of transformation: quantifying the vulnerability of grasslands in South Africa. *Conservation Biology* 18:466–477.

- Nischk, F. & Riede, K. 2001. Bioacoustics of two cloud forest ecosystems in Ecuador compared to lowland rainforest with special emphasis on singing cricket species. In: Nieder, J. & Barthlott, W. (eds.). *Epiphytes and canopy fauna of the Otongán rain forest (Ecuador). Results of the Bonn – Quito epiphyte project, funded by the Volkswagen Foundation (Vol. 2 of 2)*. Books on Demand GmbH, Bonn.
- O'Hara, R. B. 2009. How to make models add up – a primer on GLMMs. *Annales Zoologici Fennici* 46:124–37.
- Olckers, T. & Hulley, P. E. 1991. Impoverished insect herbivore faunas on the exotic bugweed *Solanum mauritianum* Scop. relative to indigenous *Solanum* species in Natal/KwaZulu and the Transkei. *Journal of the Entomological Society of Southern Africa* 54:39–50.
- Palmer, M. W. & Dixon, P. M. 1990. Small-scale environmental heterogeneity and the analysis of species distributions along gradients. *Journal of Vegetation Science* 1:57–65.
- Palmer, M. W., Earls, P., Hoagland, B. W., White, P. S. & Wohlgemuth, T. 2002. Quantitative tools for perfecting species lists. *Environmetrics* 13:121–137.
- Patricelli, G. L. & Blickley, J. L. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. *Auk* 123:639–649.
- Picaud, F. & Petit, D. P. 2007. Primary succession of Acrididae (Orthoptera): differences in displacement capacity in early and late colonizers of new habitats. *Acta Oecologica* 32:59–66.
- Pijanowski, B. C., Farina, A., Gage, S. H., Dumyahn, S. L. & Krause, B. L. 2011. What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology* 26:1213–1232.
- Pimental, D., Lach, L., Zuniga, R. & Morrison, D. 1999. Environmental and economic costs of nonindigenous species in the United States. *BioScience* 53:53–65.

- Pryke, J. S. & Samways, M. J. 2009. Recovery of invertebrate diversity in a rehabilitated city landscape mosaic in the heart of a biodiversity hotspot. *Landscape and Urban Planning* 93:54–62.
- Pryke, J. S. & Samways, M. J. 2011. Conservation management of complex natural forest and plantation edge effects. *Landscape Ecology* 27:73–85.
- Pryke, J. S. & Samways, M. J. 2012. Ecological networks act as extensions of protected areas for arthropod biodiversity conservation. *Journal of Applied Ecology* 49:591–600.
- Pryke, S. R. & Samways, M. J. 2001. Width of grassland linkages for the conservation of butterflies in South African afforested areas. *Biological Conservation* 101:85–96.
- Riede, K. 1993. Monitoring biodiversity: analysis of Amazonian rainforest sounds. *Ambio* 22:546–548.
- Riede, K. 1996. Diversity of sound-producing insects in a Bornean lowland rain forest. In: Edwards, D. S., Booth, W. E. & Choy, S. C. (eds.). *Tropical Rainforest Research – Current Issues*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Riede, K. 1997. Bioacoustic diversity and resource partitioning in tropical calling communities. In: Ulrich, H. (ed.). *Tropical biodiversity and systematics. Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems, Bonn 1994*. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.
- Riede, K. 1998. Acoustic monitoring of Orthoptera and its potential for conservation. *Journal of Insect Conservation* 2:217–223.
- Rocchini, D., Balkenhol, N., Carter, G., Foody, G. M., Gillespie, T. W., He, K. S. & Neteler, M. 2010. Remotely sensed spectral heterogeneity as a proxy of species diversity: Recent advances and open challenges. *Ecological Informatics* 5:318–329.

- Römer, H. 1993. Environmental and biological constraints for the evolution of long-range signaling and hearing in acoustic insects. *Philosophical Transactions of the Royal Society B* 340:179–185.
- Römer, H., Bailey, W. & Dadour, I. 1989. Insect hearing in the field. III. Masking by noise. *Journal of Comparative Physiology A* 164:609–620.
- Samways, M. J. 2007. Insect conservation: a synthetic management approach. *Annual Review of Entomology* 52:465–487.
- Samways, M. J., Bazelet, C. S. & Pryke, J. S. 2009. Provision of ecosystem services by large scale corridors and ecological networks. *Biodiversity and Conservation* 19:2949–2962.
- Samways, M. J., Caldwell, P. M. & Osborn, R. 1996. Ground-living invertebrate assemblages in native, planted, and invasive vegetation in South Africa. *Agriculture, Ecosystems & Environment* 59:19–32.
- Samways, M. J. & Moore, S. D. 1991. Influence of exotic conifer patches on grasshopper (Orthoptera) assemblages in a grassland matrix at a recreational resort, Natal, South-Africa. *Biological Conservation* 57:117–137.
- Saunders, D. A., Hobbs, R. J. & Margules, C. R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18–32.
- Scheepers, J. C. 1983. The present status of vegetation conservation in South Africa. *Bothalia* 14:991–995.
- Shieh, B. S., Liang, S. H., Chen, C. C., Loa, H. H. & Liao, C. Y. 2011. Acoustic adaptations to anthropogenic noise in the cicada *Cryptotympana takasagona* Kato (Hemiptera: Cicadidae). *Acta Ethologica* (On-line: DOI 10.1007/s10211-011-0105-x).
- Schmidt, A. K. D., Römer, H. & Riede, K. 2012. Spectral niche segregation and community organization in a tropical cricket assemblage. *Behavioral Ecology* 24:470–480.

- Siemann, E., Haarstad, J. & Tilman, D. 1999. Dynamics of plant and arthropod diversity during old field succession. *Ecography* 22:406–414.
- Simao, M. C., Flory, S. L. & Rudgers, J. A. 2010. Experimental plant invasion reduces arthropod abundance and richness across multiple trophic levels. *Oikos* 119:1553–1562.
- Simmons, L. W. & Zuk, M. 1992. Variability in call structure and pairing success of male field crickets, *Gryllus bimaculatus*: the effect of age, size and parasite load. *Animal Behaviour* 44:1145–1152.
- Slabbekoorn, H. & Peet, M. 2003. Birds sing at a higher pitch in urban noise. *Nature* 424:267.
- Slobodchikoff, C. N. & Doyen, J. T. 1977. Effects of *Ammophila arenaria* on sand dune arthropod communities. *Ecology* 58:1171–1175.
- StatSoft Inc. 2012. Statistica (data analysis software system), version 11. www.statsoft.com.
- Sueur, J., Pavoine, S., Hamerlynck, O. & Duvail, S. 2008. Rapid acoustic survey for biodiversity appraisal. *PLOS ONE* 3:e4065 (doi:10.1371/journal.pone.0004065).
- Tuckerman, J. F., Gwynne, D. T. & Morris, G. K. 1993. Reliable acoustic cues for female mate preference in a katydid (*Scudderia curvivauda*). *Behavioral Ecology and Sociobiology* 4:106–113.
- van Halder, I., Barbaro, L. & Jactel, H. 2011. Conserving butterflies in fragmented plantation forests: Are edge and interior habitats equally important? *Journal of Insect Conservation* 15:591–601.
- Villanueva-Rivera, L. J. 2007. Digital recorders increase detection of *eleutherodactylus* frogs. *Herpetological Review* 38:59–63.
- Wells, C. N., Williams, R. S., Walker, G. L. & Haddad, N. M. 2009. Effects of corridors on genetics of a butterfly in a landscape experiment. *Southeastern Naturalist* 8:709–722.

- Wu, Y., Wang, C., Zhang, X., Zhao, B., Jiang, L., Chen, J. & Li, B. 2009. Effects of saltmarsh invasion by *Spartina alterniflora* on arthropod community structure and diets. *Biological Invasions* 11:635–649.
- Xeno-canto. 2012. Sharing bird sounds from around the world. <http://www.xeno-canto.org/>.
- Yamaura, Y., Kawahara, T., Iida, S. & Ozaki, K. 2008. Relative importance of the area and shape of patches to the diversity of multiple taxa. *Conservation Biology* 22:1513–1522.
- Yi, Y. & Wang, X. 2011. Comparison of Wald score and likelihood ratio tests for response adaptive designs. *Journal of Statistical Theory and Applications* 10:553–569.
- Zuur, A. F., Elena, N. I. & Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:1–14.

Table 4.1. Acoustic species detected across sites. PA= Protected area; Wt= Wetland sites; Gr= Grassland sites; IF= Indigenous forest sites; Gz= Grazed sites; Rd= Road sites; M= Managed sites; RA= % relative abundance across all 210 sites; PR= pulse rate; kHz= center frequency (kHz) of signals. Frequency species were detected (%) is listed under each site category (PA, Wt, Gr, IF, Gz, Rd, & M).

Family	Acoustic Species	PA	Wt	Gr	IF	Gz	Rd	M	RA	PR	kHz
1 Caprimulgidae	<i>Fiery-necked Nightjar</i>	41	15	2	9				8.6	0.2	1.7
2 Arthroleptidae	<i>Leptopelis mossambicus</i>	35	20	35	12	36			18.6	16.8	1.4
3 Bufonidae	<i>Amietophrynus gutturalis</i>	6	2	5					1.9	6.6	1.3
4 Hemisotidae	<i>Hemisus guttatus</i>		1						1.0	15.9	2.1
5 Hyperoliidae	<i>Afrixalus aureus</i>		4	2					1.4	6.2	4.3
6 Hyperoliidae	<i>Hyperolius marmoratus</i>		4						1.0	0.9	3.1
7 Hyperoliidae	<i>Hyperolius pusillius</i>	6	4	2					1.9	2.7	4.9
8 Hyperoliidae	<i>Hyperolius semidiscus</i>	18	10	2		9			4.8	3.0	2.7
9 Hyperoliidae	<i>Kassina maculata</i>			2		9			1.0	1.3	1.7
10 Hyperoliidae	<i>Kassina senegalensis</i>	12	6			9			2.9	0.9	1.0
11 Ptychadenidae	<i>Ptychadena mossambica</i>		4						1.0	29.0	1.9
12 Ptychadenidae	<i>Ptychadena oxyrhynchus</i>	18	6	2	6				4.3	10.7	2.4
13 Gryllidae	Oecanthinae sp. 1	18	25	37	29	9	29		22.9	41.1	2.5
14 Gryllidae	Oecanthinae sp. 2	35	29	16		27	14		15.7	44.8	3.4
15 Gryllidae	Oecanthinae sp. 3	24	40	37		45	5		21.4	51.1	6.6
16 Gryllidae	Gryllidae sp. 1	76	42	47	85		14		40.5	1.0	3.6
17 Gryllidae	Gryllidae sp. 2	35	23	19		18	5		13.3	14.0	5.7
18 Gryllidae	Gryllidae sp. 3	6	19						4.8	25.2	6.5
19 Gryllidae	Gryllidae sp. 4	35	17	28	71				23.8	38.9	5.8
20 Gryllidae	Gryllidae sp. 5	59	54	49	21	27	5		32.4	34.9	4.9
21 Gryllidae	Gryllidae sp. 6	18	6	2	6				4.3	7.6	4.6
22 Gryllidae	Gryllidae sp. 7	12	21	23					1.9	29.7	10.7
23 Gryllidae	Gryllidae sp. 8	29	38	47	50	45	24		33.3	8.9	3.4
24 Gryllidae	Gryllidae sp. 9	29	27	23	50	18	14		23.8	13.6	3.1
25 Gryllidae	Gryllidae sp. 10	29	2	12					5.2	64.5	6.0
26 Gryllidae	Gryllidae sp. 11	29	4	21					7.6	32.4	6.4
27 Gryllidae	Gryllidae sp. 12	24	10	5	6				6.2	7.8	5.8
28 Gryllidae	Gryllidae sp. 13	59	38	33	29			5	25.2	12.9	4.2
29 Gryllidae	Gryllidae sp. 14	6	6	2					2.4	30.1	4.2
30 Gryllidae	Gryllidae sp. 15	24	8	9	44				12.9	20.4	4.8

Table 4.1. *Continued*

Family	Acoustic Species	PA	Wt	Gr	IF	Gz	Rd	M	RA	PR	kHz
31	Gryllidae	Gryllidae sp. 16	41	13	2	6	9		8.1	1.9	6.9
32	Gryllidae	Gryllidae sp. 17	12	2					1.4	22.4	6.0
33	Gryllidae	Gryllidae sp. 18	12						1.0	7.1	4.6
34	Gryllidae	Gryllidae sp. 19	53	17	19	6	46		15.2	3.1	3.9
35	Gryllidae	Gryllidae sp. 20	18						1.4	18.7	6.6
36	Gryllidae	Gryllidae sp. 21	12	2	9				3.3	76.1	7.5
37	Gryllidae	Gryllidae sp. 22	6		2				1.0	81.6	7.1
38	Gryllidae	Gryllidae sp. 23	24	27	2				8.6	2.9	6.2
39	Gryllidae	Gryllidae sp. 24	12	4	2	3			2.9	0.9	5.5
40	Gryllidae	Gryllidae sp. 25		6					1.4	19.9	7.1
41	Gryllidae	Gryllidae sp. 26	12	27	5				8.1	8.7	3.2
42	Gryllidae	Gryllidae sp. 27	47	8	26	6			11.9	1.0	6.0
43	Gryllidae	Gryllidae sp. 28							5.2	0.8	3.7
44	Gryllidae	Gryllidae sp. 29							9.0	26.3	5.8
45	Tettigoniidae	Tettigoniidae sp. 1							9.0	0.9	8.7
46	Tettigoniidae	Tettigoniidae sp. 2							5.7	1.8	14.0
47	Tettigoniidae	Tettigoniidae sp. 3							2.9	2.9	11.1
48	Tettigoniidae	Tettigoniidae sp. 4							2.9	23.5	10.1
49	Tettigoniidae	Tettigoniidae sp. 5							1.9	94.7	7.6
50	Tettigoniidae	Tettigoniidae sp. 6							1.9	15.8	13.7
51	Tettigoniidae	<i>Conchotopoda belcki</i>							5.7	46.7	7.3
52	Tettigoniidae	<i>Conocephalus caudalis</i>	12						1.0	198	4.2
53	Tettigoniidae	<i>Conocephalus iris</i>	24	17	5				6.7	27.5	14.2
54	Tettigoniidae	<i>Conocephalus maculatus</i>	65	21	26	3			15.7	48.2	20.0
55	Tettigoniidae	<i>Eulioptera atkinsonae</i>	24	8	9				5.7	1.0	9.8
56	Tettigoniidae	<i>Eurycorypha proserpinae</i>	12	6	9	3			4.8	0.9	12.1
57	Tettigoniidae	<i>Plangia graminea</i>	52	40	30	6	27		21.9	1.1	9.6
58	Tettigoniidae	<i>Ruspolia</i> sp. 1	82	44	53		73	14	32.9	38.1	14.3
59	Tettigoniidae	<i>Ruspolia</i> sp. 2	88	67	77	18	45	38	47.1	39.2	12.0
60	Tettigoniidae	<i>Ruspolia</i> sp. 3	18	23	12	3		19	11.4	196	12.9
61	Tettigoniidae	<i>Ruspolia</i> sp. 4	6	2	9	9		33	7.6	18.8	12.3
62	Tettigoniidae	<i>Ruspolia</i> sp. 5						48	4.8	8.6	8.6
63	Tettigoniidae	<i>Thoracistus viridifer</i>	12	44	5		27		13.3	380	14.3
64	Tettigoniidae	<i>Tylopsis continua</i>	41	29	26	15	9		18.1	2.2	15.4
65	Tettigoniidae	<i>Zuludectes modestus</i>	53	35	30		18		19.5	209	19.9

Table 4.2. Structural vegetation cover (%) of sites. PA= Protected area; Wt= Wetland sites; Gr= Grassland sites; IF= Indigenous forest sites; Gz= Grazed sites; Rd= Road sites; M= Managed sites; Euc= *Eucalyptus* stands.

Variable	PA	Wt	Gr	IF	Gz	Rd	M	Euc
Tall Grass > 30 cm	68	68	64	5	15	100	0	0
Short grass < 30 cm	3	5	9	2	62	0	90	0
Bareground	0	0	2	0	6	0	10	0
Shrubs < 1 m	5	6	7	5	6	0	0	0
Trees < 2 m	4	3	3	9	2	0	0	0
Trees > 2 m	2	2	3	80	3	0	0	100
Tree stumps	2	1	2	0	1	0	0	0
Crow's foot grass	15	13	10	0	5	0	0	0
Ferns	0	2	0	0	0	0	0	0

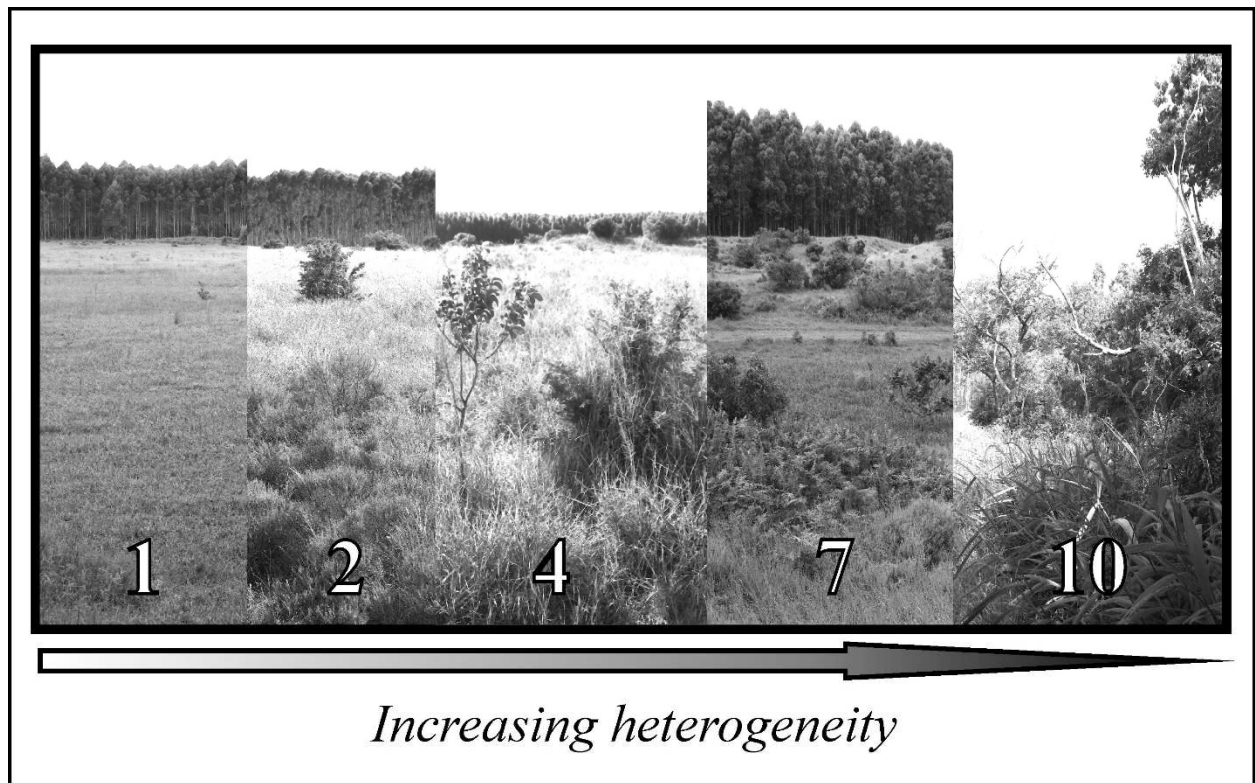


Figure 4.1. Scale of heterogeneity was determined visually. Sites were ranked on a scale of 1-10. A site with a score of 1 was a uniform biotope of one structural vegetation type, a site with a score of 2 contained two structural vegetation types and so on until culminating in a score of 10, indicating a very diverse biotope.

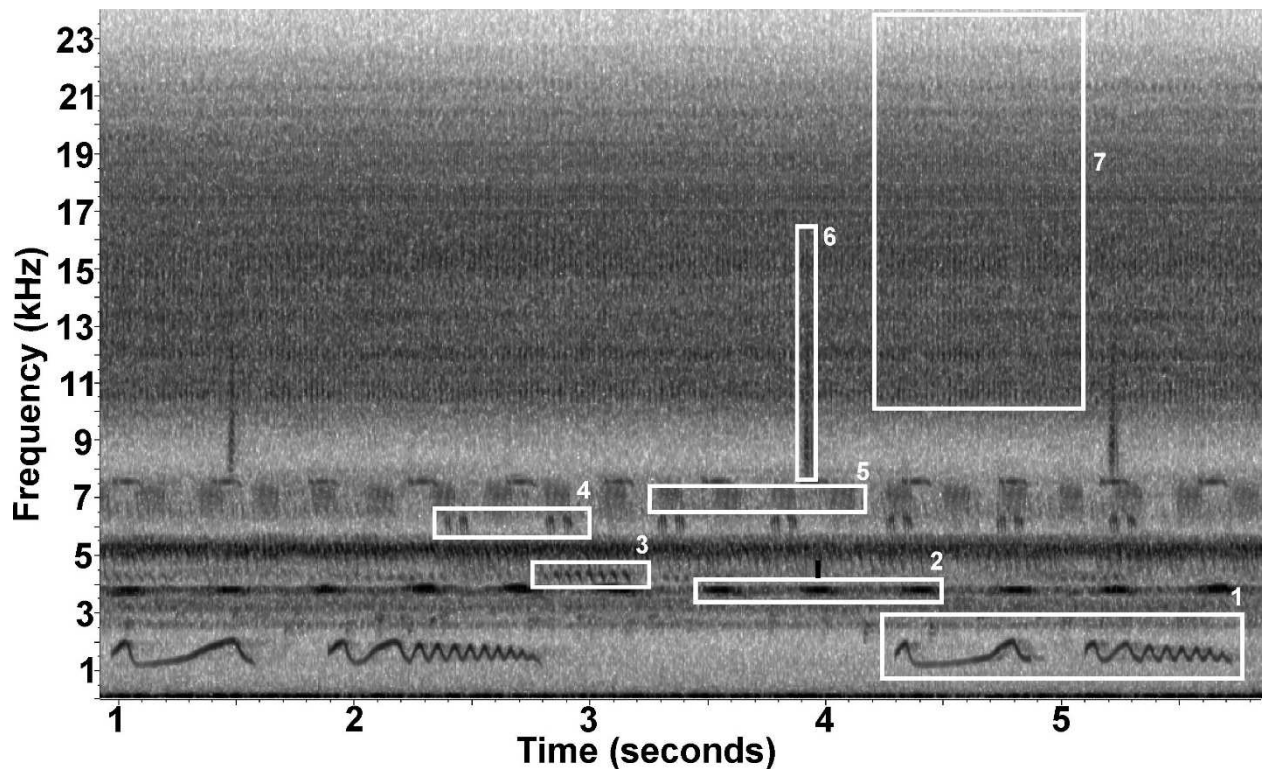


Figure 4.2. Spectrogram of a large natural protected grassland area displaying frequency (kHz) versus time (s) with darker colours representing higher decibels (dB). Various species signals have been selected within this spectrogram (boxes 1-7) showing the variation in frequency and pulse rates species utilize to avoid acoustic interference. Classification of these acoustic parameters allows for the identification of acoustic species (Table 4.1). Box 7 and 6 display high frequency, broadband, signals used by katydids (*Ruspolia* sp. 2; *Eurycorypha proserpinae*) compared to low frequency, narrow band signals used by crickets in boxes 2-5 (*Gryllidae* sp. 1; *Gryllidae* sp. 13; *Gryllidae* sp. 12; *Gryllidae* sp. 22). Box 1 displays a low frequency signal with complex amplitude modulations characteristic of the fiery-necked nightjar.

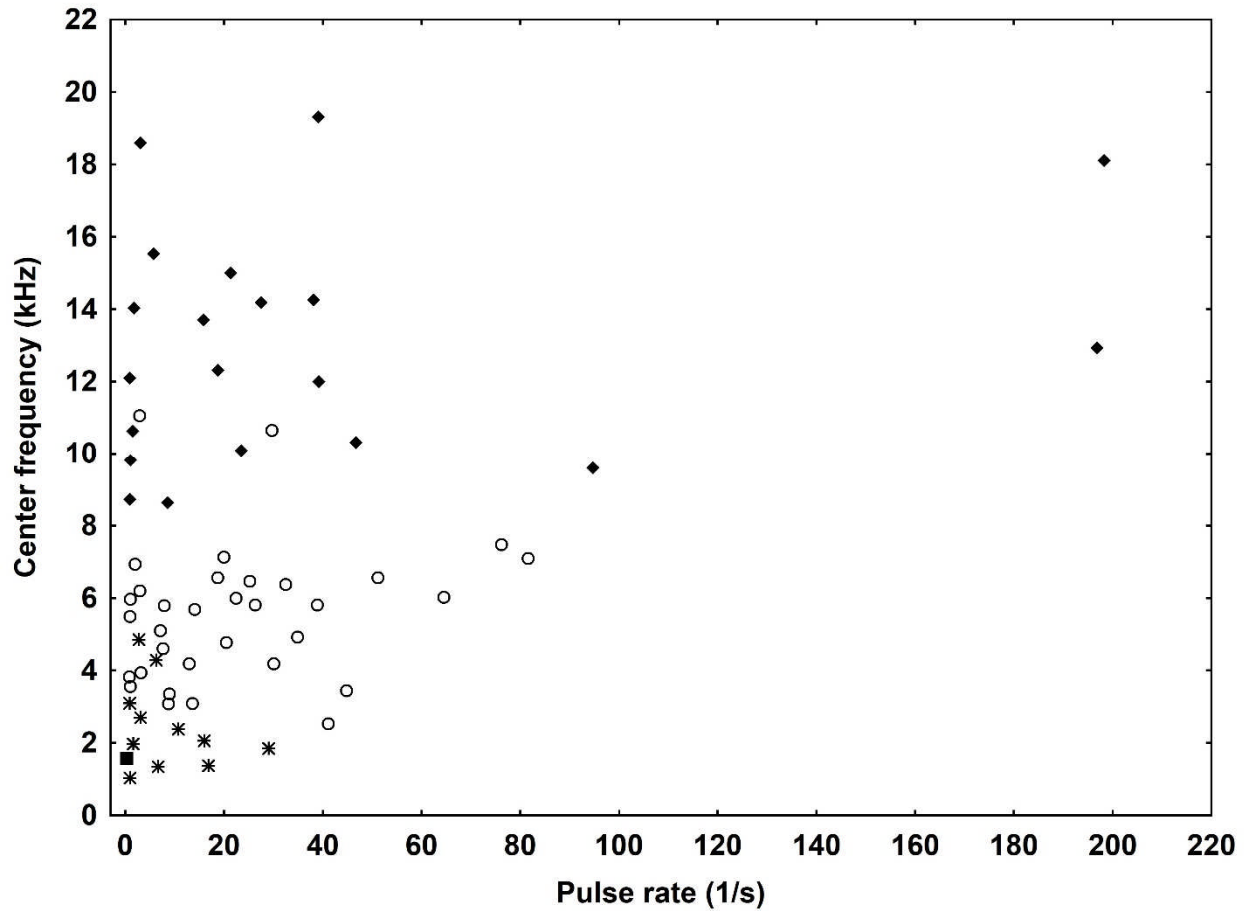


Figure 4.3. Distribution of acoustic species based on pulse rate and center frequency (kHz). Katydid acoustic signals (◆) occupied highest frequency ranges, followed by crickets (○), with bird (■) frog (*) species occupying the lowest frequency ranges.

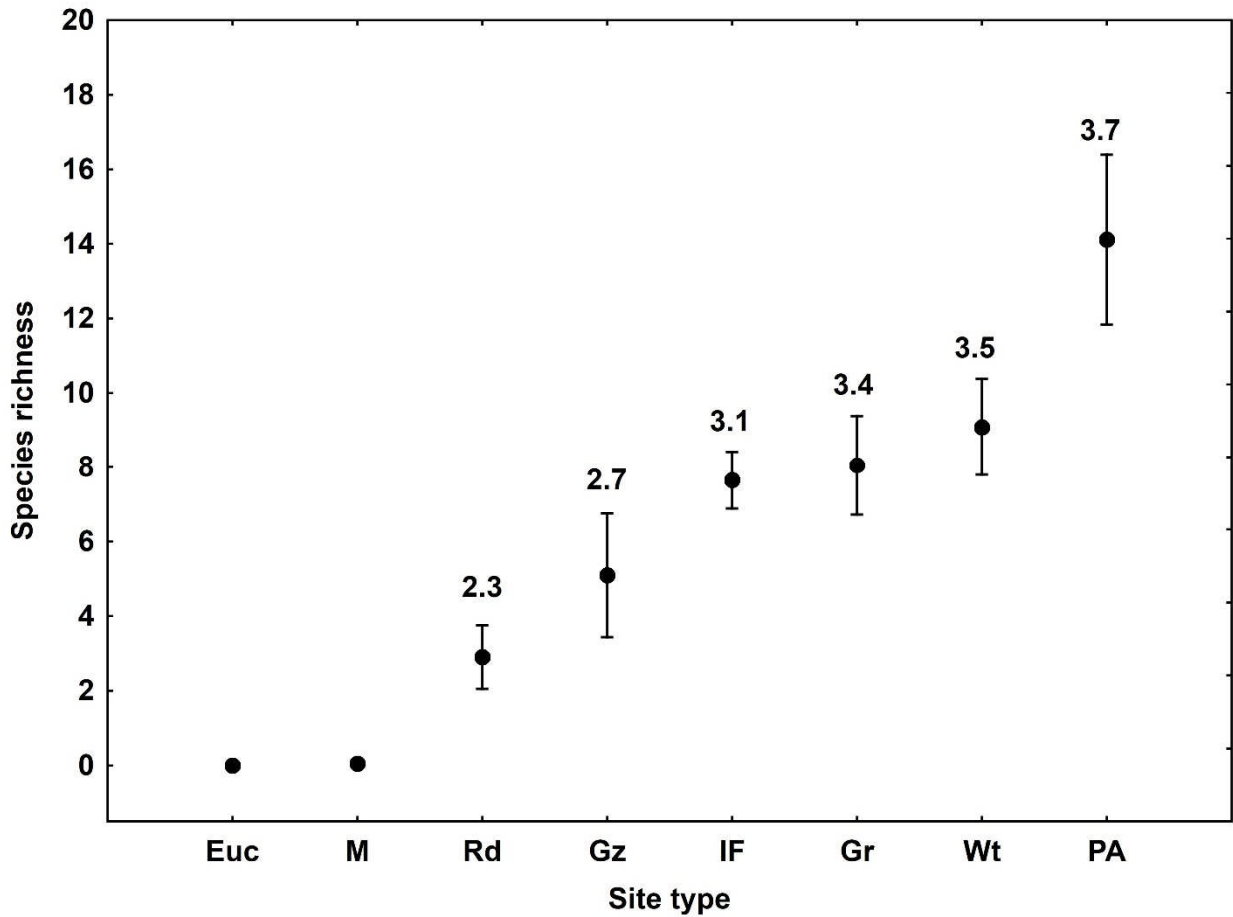


Figure 4.4. Difference in mean species richness between site categories ($w = 179.5$, $p = 0.00$), with Shannon-Wiener Index (H') diversity scores above. PA= Protected area; Wt= Wetland sites; Gr= Grassland sites; IF= Indigenous forest sites; Gz= Grazed sites; M= Managed sites; Euc= *Eucalyptus* stands.

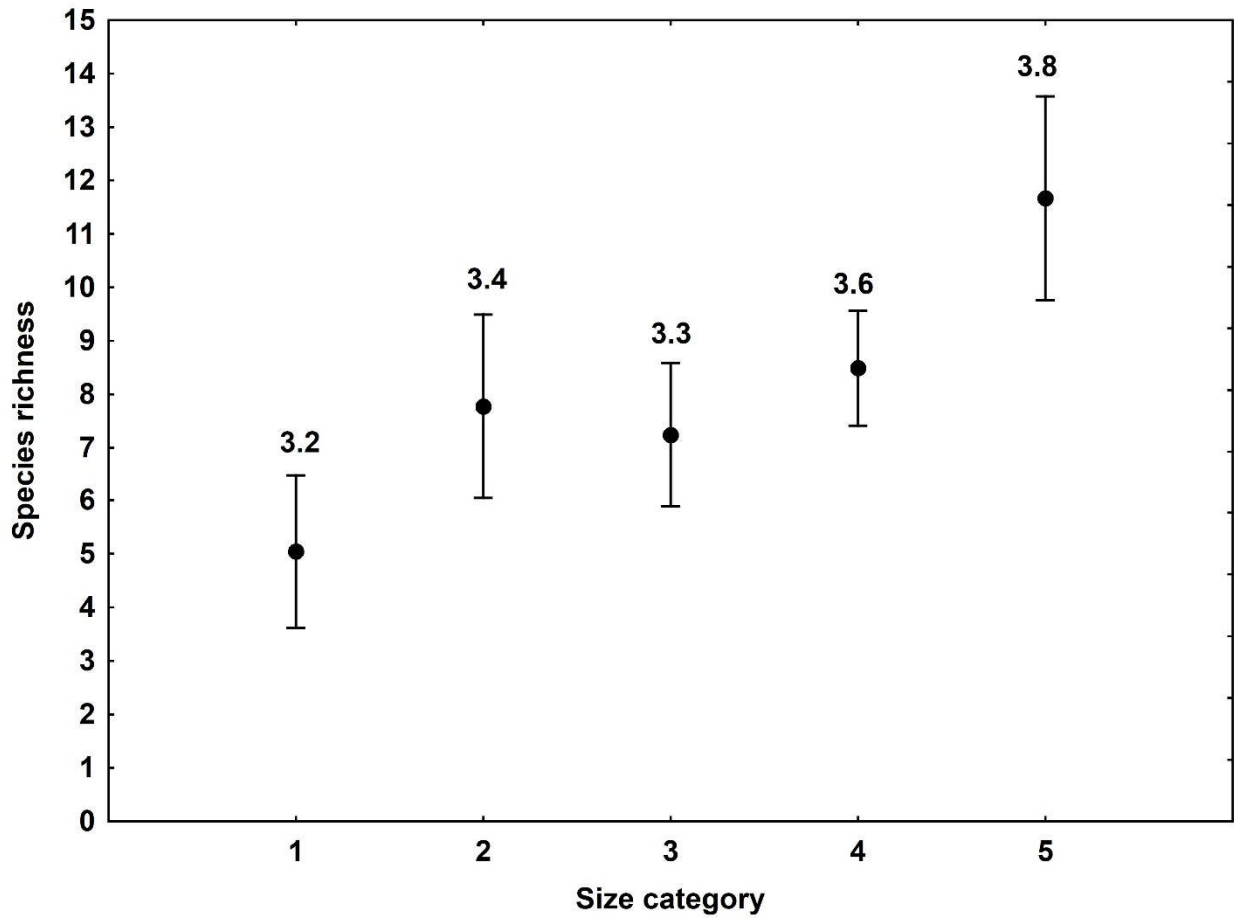


Figure 4.5. Difference in mean species richness between patch size categories ($w = 74.39$, $p = 0.00$), with Shannon-Wiener Index (H') diversity scores above. Size categories were 1= <1 ha; 2= 1–3 ha; 3= 3–10 ha; 4= 10–150 ha; 5= >150 ha.

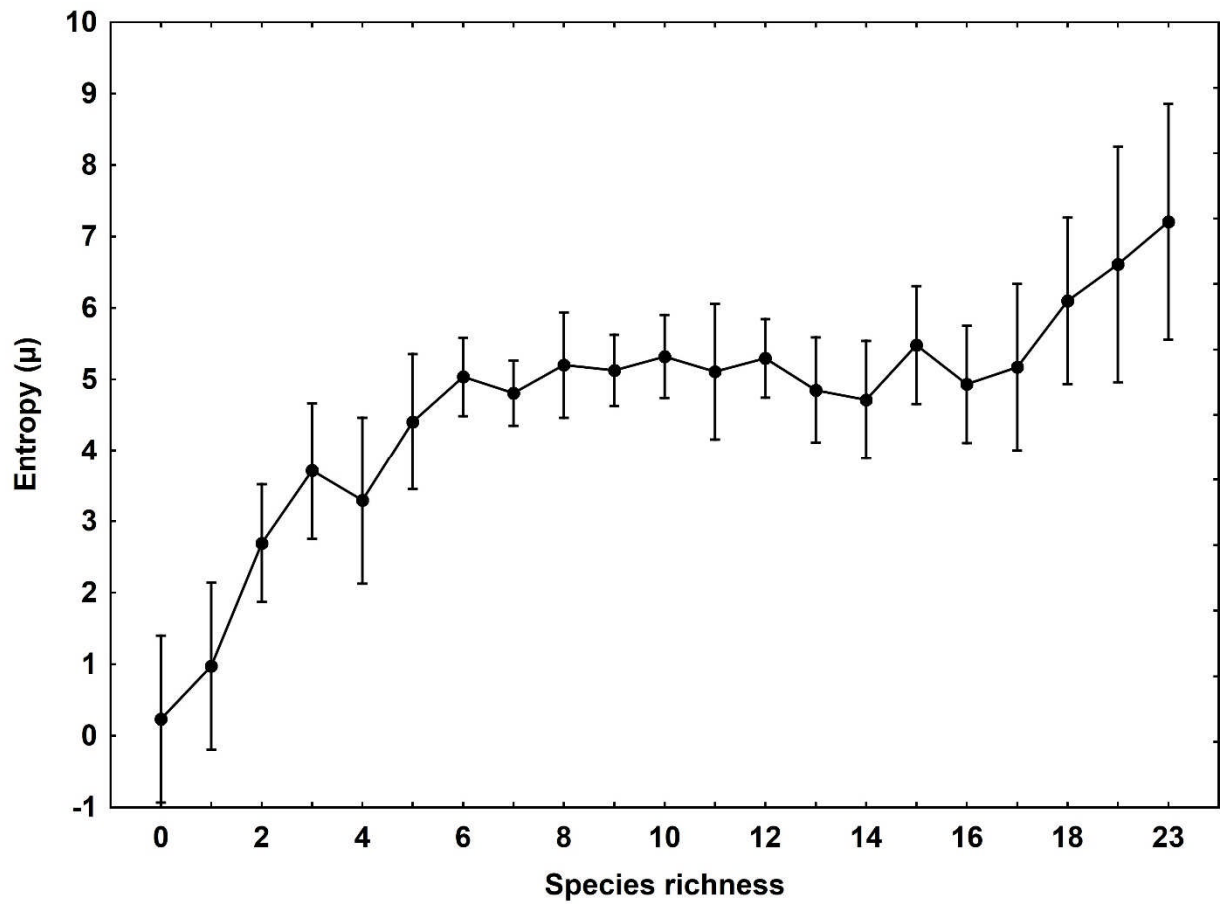


Figure 4.6. Relationship between maximum entropy (μ) and the number of acoustic species calling across sites ($w = 79.25$, $p = 0.00$).

5. Acoustic patterns of katydids (Orthoptera: Tettigoniidae) across ecological gradients on a significant mountain

Abstract

Katydid acoustic communication provides a non-invasive, effective method to investigate diversity patterns across ecological gradients. Long term monitoring of signals can detect declines in ecological integrity through absence of signals, or changing environmental conditions through spatial or temporal shifts in acoustic diversity. How acoustic diversity patterns are influenced by gradients in elevation, season and vegetation types therefore has direct implications for acoustic monitoring. Consequently, katydid acoustic signals were identified and characterized on a botanically rich mountain (1646 m asl), previously selected as an important gradient for monitoring the effects of climate change. Detection of novel acoustic signals resulted in the discovery of two new katydid species, highlighting the effectiveness of the acoustic technique in detecting cryptic species. Acoustic diversity patterns of katydids were influenced and constrained by various environmental factors such as habitat and climatic conditions. The botanical transition between dissimilar Karoo (545 m asl) and Ecotone (690 m asl) vegetation types created a hard barrier which restricted 92% of katydids above and 8% below. Acoustic diversity across seasonal and elevational gradients increased with increasing temperatures. Temperature lapse rate or decrease with respect to increasing elevation was 5.7 °C for each 1000 m of ascent, leading to a decrease in acoustic diversity with increasing elevation. However, acoustic patterns indicated species had wide elevational ranges, likely providing a limited buffer in a climatic warming scenario. Climatic variability along the elevational gradient also produced variation in seasonal phenology, resulting in delayed onset of acoustic activity by a month for each 300 m rise in elevation. Fluctuating ambient

temperatures effected the speed of katydid muscle contraction, leading to a positive linear relationship between increased pulse rate with higher temperatures. Katydids also utilized high frequency acoustic signals, likely as an adaptation to overcome background noise of wind, which is a common regional feature.

Introduction

Changes in the songs of katydids across the nocturnal landscape reflect cryptic species diversity across the various ecological gradients. Acoustic communication within this taxonomic group functions primarily in sexual advertisement and pair formation (Gwynne 2001). Although evolutionarily advantageous for mate attraction, production of acoustic signals also increases the risk of predation and parasitism (Cade 1975; Burk 1982; Zuk & Kolluru 1998; Gerhardt & Huber 2002). As a result, signalling is predominantly a male feature in the majority of katydid species, with females being silent receivers due to higher reproductive investment (Bailey & Rentz 1990; Gwynne 2001). Acoustic signals therefore provide receivers with information on the identity, location and fitness of the caller, to assess potential conspecific mates (Simmons & Zuk 1992; Tuckerman *et al.* 1993; Gwynne 2001; Greenfield 2002). High quality mates are also often associated with access to an environmental resource such as high quality feeding or oviposition sites (Searcy & Anderson 1986; Brown & Gwynne 1997). Accurate assessment of caller fitness is therefore crucial for enhanced reproductive success (Greenfield 2002).

For effective acoustic communication, propagated signals need to reach receivers with minimal loss of information. Signal information such as structure, intensity and frequency degrade over distance (Greenfield 2002). Furthermore, interference along acoustic channels through biotic and abiotic factors including vegetation, rocks, topography, wind, temperature gradients, humidity, and intra- and interspecific acoustic signals may attenuate, deflect, mask, absorb, refract, reverberate, scatter and alter the spectral composition of sound waves, rendering signals unrecognizable to a receiver (Richards & Wiley 1980; Römer & Lewald 1992; Römer 1993; Gerhardt & Huber 2002; Greenfield 2002; Jain & Balakrishnan 2011).

In any given habitat, communication is constrained by various local environmental factors. As a result, katydids have developed effective structural and behavioural mechanisms

to adapt to acoustic constraints (Greenfield 2002). Some of these mechanisms include transmitting signals in broadband frequencies to preserve call characteristics, as attenuation is unlikely to affect the entire frequency range (Römer & Lewald 1992). A great number of species also call from elevated perches to reduce or avoid attenuating influences of vegetation and surface microtopography (Paul & Walker 1979; Arak & Eiríksson 1992; Römer & Lewald 1992; Greenfield 2002). Although high frequency signals are less susceptible to wind disruption, katydids possibly utilize windows of favourable environmental conditions to propagate signals (Richards & Wiley 1980; Greenfield 2002). Intra- and interspecific acoustic interference can also be minimized through partitioning the frequency and spatial domains of acoustic transmission channels (Morton 1975; Römer *et al.* 1989; Riede 1993; Riede 1998; Sueur 2002; Diwakar & Balakrishnan 2007a; Diwakar & Balakrishnan 2007b; Schmidt *et al.* 2012; Jain *et al.* 2013). Temporal partitioning of katydid species occurs over large seasonal time scales, or within small calling windows of minutes or seconds (Jain *et al.* 2013). Generally however, no diel partitioning of calling time occurs within nocturnal species, and they tend to signal continuously during evening hours (Schmidt *et al.* 2012; Diwakar & Balakrishnan 2007a).

A significant communication constraint for these insects is temperature. Katydidids are subject to the direct effects of temperature through muscle contraction speed and ensuing sound production, as well as indirectly through temperature effects on the acoustic channel. Fluctuating ambient temperatures effect the speed of katydid muscle contraction (Toms *et al.* 1993; Greenfield 1997) leading to a positive relationship between pulse rate and temperature (Walker 1975; Greenfield 1997; Greenfield 2002; Gerhardt & Huber 2002; Sanborn 2006). Once specific lower temperature thresholds are reached, all species of katydid will cease calling (Franklin *et al.* 2009).

Temperature gradients often correspond with elevational and seasonal gradients (Hodkinson 2005). Declines in fauna species richness with increasing elevation has been attributed to less than optimal environmental conditions at higher elevations, corresponding primarily to decreasing temperatures (Grytnes & Vetaas 2002; Hodkinson 2005). However, while faunal diversity patterns across elevational gradients can be directly influenced by environmental parameters, they can also be indirectly influenced through shifts in predation, competition, resource availability and plant diversity (Siemann *et al.* 1998; Hodkinson 2005; Pijanowski *et al.* 2011).

The elevational gradient on Jonaskop Mountain in the Western Cape of South Africa is characterized by high plant species richness, with high species turnover with elevation (Agenbag *et al.* 2008). Yet, despite extensive botanical knowledge of its rich diversity of endemic species, nothing is known of its invertebrate taxa, especially katydids. How diversity patterns of katydid species are influenced by these various gradients can be characterized by their acoustic signals.

The aim of this study is therefore to identify the acoustic signals of katydids across vegetation, elevational and seasonal gradients on a significant mountain in the Cape Floristic Region biodiversity hotspot, South Africa, and to investigate how these gradients influence acoustic diversity patterns.

Methods

Study site

Jonaskop Mountain (33°58'00 S 19°30'00 E, elevation 1646 m asl) is one of the highest peaks of the east-west trending Riviersonderend Mountain Belt, within the Cape Floristic Region (CFR) of the Western Cape, South Africa. The CFR, with an area of ±90 000 km², is a global biodiversity hotspot (Myers *et al.* 2000) containing such exceptional high diversity and endemism that it forms one of the six flora kingdoms of the world (Goldblatt 1997; Goldblatt and Manning 1999). The botanical diversity of the CFR is largely a result of the Fynbos Biome, which contains 7000 of the 8700 vascular plants in the CFR, 80% of which are endemic to the region (Rebello 1998).

Jonaskop is a protected area managed by CapeNature as an important water source to the Riviersonderend River and contains a private service road leading to the mountain summit. Jonaskop has therefore been previously selected as an important gradient for monitoring the effects of climate change on vegetation (Agenbag *et al.* 2008). As a result, detailed botanical studies have been conducted across its elevation gradient on the equator-facing slope at 545, 690, 744, 953, 1044, 1196, 1303 and 1576 m asl (Agenbag *et al.* 2008).

The Jonaskop gradient spans a change of 1200 m in elevation between the foothills and the summit, across a distance of 6.3 km. Soils on the mountain are shallow and rocky, derived from quartzitic sandstone of the Table Mountain Group (Agenbag *et al.* 2008). Below 600 m asl, soils derived from arenaceous shale and argillaceous sandstone of the Bokkeveld Group, become finer grained and less rocky (Agenbag *et al.* 2008) resulting in agriculture (wheat, cattle) activities dominating lower elevations.

Distinct vegetation types occur across the elevation gradient. At 545 m asl vegetation is classified as Karoo, containing 56 plant species of which 45 (80%) are unique to this site (Agenbag *et al.* 2008). Dominant plant species here are unable to cross the soil barrier between this site and higher elevations (Agenbag *et al.* 2008). Vegetation from 690-744 m asl is classified as Ecotone, containing 73 and 59 species at the two respective sites. From 953-1303 m asl vegetation is classified as Mid-altitude Sandstone Fynbos, containing 85 species at 953 m asl, 56 at 1044 m asl, 62 at 1196 m asl, and 53 at 1303 m asl. Vegetation then shifts to High-altitude Sandstone Dwarf Fynbos containing 26 species at 1576 m asl. While 690-1576 m asl is characterized by high species turnover, common plant families also occur across these elevations (Agenbag *et al.* 2008), providing a softer transition than the Karoo-Fynbos boundary. The intersection of low elevation succulent karoo with fynbos at higher elevations therefore provides an interesting opportunity to investigate katydid acoustic signatures across this hard vegetation gradient.

Acoustic sampling

Botanical survey sites used in earlier studies (Agenbag *et al.* 2008) were re-visited at 545, 690, 744, 953, 1044, 1196, 1303 and 1576 m asl, as well as an additional site added at 1435 m asl. Nocturnal acoustic sampling was undertaken from early spring in September 2009 to early winter in April 2011, corresponding to start and end of katydid acoustic activity. Acoustic sampling took place within three permanent 100 m² plots 500 m apart at each elevation. Acoustic data for each three permanent plots were pool for each elevation. All elevation zones were acoustically sampled once a week for the duration of the study. Acoustic sampling occurred after dusk and before dawn between 20:00-05:00 hrs. Within half an hour after sunset, all katydid species present signalled continuously for the duration of evening hours. Acoustic sampling was restricted to evenings without rain and high winds (>13.9 m/s), which would

have influenced the detection of katydid signals. Within each site at each elevation, temperature (°C), wind speed (m/s) and humidity (%) were recorded using a Testo 410-2 (Testo, Germany).

Recordings were made of all species using a Sennheiser ME 67 long gun microphone (Sennheiser, Germany) in conjunction with a Marantz PD660 solid state digital recorder (Marantz, USA). Voucher specimens were collected to confirm species identity of the signaler. The Sennheiser microphone has a frequency response sensitivity of <20 kHz and is highly directional, preventing sound colouration from off-axis sources, making it ideal for recording call structure with minimal background noise. The Marantz PD660 recording parameters were set to a sampling rate of 48 kHz with an uncompressed file format (.wav). A Pettersson D230 Ultrasound Detector (Pettersson, Sweden) was also used to detect and locate katydids with ultrasonic signals. Additionally, a Pettersson D500X Ultrasound recorder (Pettersson Elektronik, Sweden) was used for a short duration towards the end of this study to detect high range ultrasonic song components. The D500X microphone sensitivity has a frequency range of <5-190 kHz, with a 500 kHz sampling rate and was used to record full spectrum calls of select katydid signals.

Data analyses

Acoustic recordings were analyzed using Raven Pro 1.5 (Cornel Laboratories, USA). Spectrograms were produced without filtering. Pulses are the smallest discrete structure or amplitude modulations within signals, grouped together as chirps or generated continuously as trills. Chirps, comprised of multiple pulses can occur singularly or within groups also known as trills. The gaps between pulses, chirps and trills are referred to as intervals. For each signal, these elements were measured along with minimum, maximum and center frequency (the smallest discrete frequency which contains 50% of total energy). The number of pulses within each chirp, chirp rate (number of chirps per second) and pulse rate (number of pulses per

second) were then calculated. In the absence of voucher specimens to confirm identification of signals, classification of species based these acoustic parameters allows for the definition of recognizable taxonomic units (Riede 1998).

Generalized Linear Models (GLMs) with Poisson distribution and log-link functions, were used to compare meteorological conditions (temperature, humidity, wind speed), species richness and signal characteristics across elevational, seasonal and vegetation gradients (Dobson 1990; Bolker *et al.* 2009; O'Hara 2009; Zuur *et al.* 2010) in Statistica 8 (Statsoft 2012). GLMs provide a flexible, robust approach for analyzing categorical and continuous data that are non-normal by using Poisson distributions with log-link functions (Bolker *et al.* 2009). Tests for the significance of the effects in the model were performed via the Wald statistic (w) (Yi & Wang 2011).

Niche overlap and null model analyses were used to analyze elevational zonation of katydid acoustic assemblages. The degree of competition between species is reflected by the degree of overlap within these independent spatial niche domains (Gotelli & Graves 1996). Overlap in resource use was calculated using the Czechanowski index of niche overlap between pairs of species, where calculated indices range from 0 (species share no resource) and 1 (species have identical resource use) (Feinsinger *et al.* 1981). The null models tests whether or not species differ significantly in resource use, as compared to a baseline level of overlap in resource use that would be found even in the absence of species mutualistic or competitive interactions (Entsminger 2012). Generation of the null community employed the RA3 algorithm, which is recommended because of its robustness for niche overlap studies (Gotelli & Graves 1996; Winemiller & Pianka 1990). All simulations were carried out with EcoSim Professional (Entsminger 2012). To compare observed and simulated indices 1000 null assemblages were created for each niche axes.

Results

Mean monthly temperatures were lowest in September and increased to peak temperatures in January-March, thereafter dropping significantly in April ($w = 105.77$, $p = 0.00$) (Fig. 5.1). Mean monthly humidity also varied across the season, generally decreasing with increasing mean monthly temperatures ($w = 196.61$, $p = 0.00$). Mean monthly wind speeds (below 13.9 m/s) varied over the season, displaying two peaks in November and February ($w = 83.02$, $p = 0.00$).

Along the elevation gradient, mean temperature decreased with increasing elevation ($w = 53.36$, $p = 0.00$). Temperature lapse rate was 5.7 °C for each 1000 m of ascent. Humidity also decreased with increasing elevation ($w = 20.57$, $p = 0.00$). Wind speed (below 13.9 m/s) did not significantly increase with increasing elevation, yet the summit had the highest mean wind speed ($w = 14.03$, $p = 0.08$). Fluctuating wind speeds occurred at all sites across elevational and seasonal gradients (Fig. 5.1).

Across elevational and seasonal gradients, we found a unique acoustic assemblage of katydids, consisting of 13 species from five subfamilies (Table 5.1). Of these species, *Ceresia rooi* and *Ceresia* sp. are new species to science, currently being described. With the exception of *Conocephalus maculatus*, *Plangia compressa*, *Tylopsis continua* and *Aprosphyllus olszanowskii*, the majority of katydids were brachypterous. The acoustic signals of all the katydids are described for the first time (Fig. 5.2-5.4). Signal characteristics for each species are listed in Table 5.2. Of the 13 species, *Alfredectes semiaeneus*, was the only katydid to have variable pulse rates within signals, consisting of a brief, slower pulse rate at the onset of the signal followed by a longer more rapid pulse rate. Pulse rate calculations for this species were therefore based on the faster pulse rate characteristic of the majority of the signal, ignoring the brief initial slower pulse rate. Measurements of acoustic parameters within Table 5.2 were

taken from a minimum of 20 individuals per species within a narrow temperature window between 17 and 19 °C. These katydids tended to use broadband, high frequency acoustic signals extending into ultrasound ranges for acoustic communication, with high center frequencies (mean and standard error) (17.4 ± 1.4 kHz). Comparatively, 14 katydids from the same subfamilies which have, to date, only been found in the KwaZulu-Natal (KZN) Province, of South Africa (*Alfredectes browni*, *Conocephalus iris*, *Conchotopoda belcki*, *Eulioptera atkinsonae*, *Eurycorypha proserpinae*, *Ruspolia* sp. 1-5, *Thoracistus semeniphagus*, *Thoracistus thyraeus*, *Thoracistus viridifer* and *Zuludectes modestus*) had significantly lower center frequencies (11.4 ± 0.6 kHz) ($w = 17.58, p = 0.00$) (Grant unpublished data). Mean wind speed across seasons and elevations at the site (2.75 ± 0.15 m/s) was also significantly higher than mean wind speeds in KZN during similar peaks in katydid acoustic activity (0.23 ± 0.03 m/s) ($w = 38.28, p = 0.00$) (Grant unpublished data).

Seasonal acoustic diversity started in September and increased to a peak in January-February before declining March-April, ceasing completely at the end of April ($w = 72.13, p = 0.00$) (Fig. 5.5). Increasing diversity across seasons corresponded to increasing mean monthly temperatures ($w = 72.47, p = 0.00$), decreasing humidity ($w = 6.21, p = 0.01$) and decreasing mean monthly wind speeds ($w = 6.75, p = 0.00$).

Across the elevation gradient, acoustic diversity was lowest at 545 m asl, highest at 744 m asl, and then declined with increasing elevation ($w = 69.70, p = 0.00$). Decreasing acoustic diversity with increasing elevation corresponded to decreasing temperatures ($w = 11.66, p = 0.00$); and humidity ($w = 34.65, p = 0.00$), but was not related to wind speed ($w = 2.50, p = 0.11$).

Acoustic diversity across the vegetation gradient was similar to that across the elevational gradient, decreasing in vegetation types at higher elevations ($w = 53.67, p = 0.00$).

However, Karoo vegetation (545 m asl), which was the lowest in elevation and highest in mean temperatures, had the lowest acoustic diversity (mean and standard error) (0.25 ± 0.16), falling outside of the expected diversity pattern explained by temperature alone. Ecotone vegetation (690-744 m asl) had the highest acoustic diversity (4.8 ± 0.91), followed by Mid-altitude Sandstone Fynbos (953-1303 m asl) (2.93 ± 0.48) and High-altitude Sandstone Dwarf Fynbos (1435-1576 m asl) (0.56 ± 0.27).

Acoustic diversity patterns of katydid species across elevational, seasonal and vegetation gradients are given in Table 5.3. Climatic variability along the elevation gradient produced variation in seasonal phenology, with delayed acoustic activity of roughly one month for each 300 m rise in elevation. Delayed phenology resulted in narrower acoustic activity windows with increasing elevation, corresponding to temperature. Acoustic activity for all species at 744 m asl was 8 months including onset, peaks and declines. At 300 m increases, acoustic activity was reduced to 7 months at 1044 m asl, 5 months at 1303 m asl and 2 months at 1576 m asl. While these results (Table 5.3) highlight diversity patterns of all species across these gradients, they also show species specific trends. Some species had different calling seasons, such as *Hetrodes pupus*, which was only acoustically active from late September-February, whereas *Alfredectes semiaeneus* was acoustically active from December-April. Above 1196 m asl, only six species (*Conocephalus maculatus*, *C. peringueyi*, *Hetrodes pupus*, *Alfredectes semiaeneus*, *Ceresia pulchripes*, *C. rooi* and *C. sp.*) could be detected acoustically. In turn, *Clonia vansoni* was the only katydid found below 690 m asl within Karoo vegetation. Elevational niche overlap of this katydid acoustic assemblage using the Czenachowski index resulted in an observed mean of 0.43. The null model analyses resulted in lower simulated mean of 0.31, indicating that acoustic species displayed a greater degree of niche overlap across elevations than expected by chance ($p = 0.00$).

Species were also acoustically active within different temperature ranges ($w = 102.79$, $p = 0.00$), and species were rarely recorded signaling during low temperatures (mean and standard error) (13.75 ± 0.74 °C) (Fig. 5.6). *H. pupus* displayed the lowest mean temperature calling ranges (14.97 ± 0.30 °C), while *C. vansoni* displayed the highest mean temperature range (21.53 ± 1.13 °C). However, when *H. pupus* was removed from the data set, katydids did not significantly differ in calling temperature range ($w = 15.89$, $p = 0.14$).

Acoustic signal parameters of all species were influenced by temperature. Trill durations ($w = 15.58$, $p = 0.00$), trill intervals ($w = 6.72$, $p = 0.00$), chirp durations ($w = 25.77$, $p = 0.00$), chirp intervals ($w = 101.84$, $p = 0.00$), pulse intervals ($w = 141.11$, $p = 0.00$), chirp rate ($w = 35.72$, $p = 0.00$) and pulse rate ($w = 183.96$, $p = 0.00$) all became longer in duration with decreasing temperatures. Pulse duration ($w = 0.04$, $p = 0.82$) and the number of pulses per chirp ($w = 0.95$, $p = 0.75$) did not vary with temperature. Variation in pulse rates with temperature for selected species is given in Fig. 5.7.

Discussion

Acoustic diversity patterns of katydids are influenced and constrained by various environmental factors such as habitat structure and climatic conditions. In response, katydids have developed effective structural and behaviour mechanisms to adapt to these acoustic constraints. Utilization of acoustic niches, by signalling from specific places or times during optimal environmental conditions reduces attenuation and increases the ability to communicate effectively.

Seasonal shifts in insect diversity typically correspond directly to environmental indicators such as photoperiod and temperature (Greenfield 2002; Gerhardt & Huber 2002;

Gullan & Cranston 2010). Temperature has a significant influence on the timing and synchronicity of montane insects, ensuring they only become active during favourable conditions for growth, development and reproduction (Butterfield 1976; Butterfield & Coulson 1988; Fielding *et al.* 1999; Butterfield *et al.* 1999; Butterfield *et al.* 2001; Hodkinson 2005). Here, along the seasonal gradient, acoustic activity of katydids was positively related to increasing temperatures, with peak acoustic activity during the hottest months of January and February. However, species displayed variation in the onset their seasonal acoustic activity, indicating potential differences in optimal thermal preferences (Greenfield 2002). Male katydids which begin signaling earlier in the season, prior to female activity, are often able to select, defend and signal from higher quality vegetation, providing an increased probability of encountering more females (Wang *et al.* 1990; Greenfield 2002). Therefore, onset of seasonal male signaling may not necessarily correspond to female mating activity.

Climatic variability along the elevation gradient produced variation in seasonal phenology, resulting in katydids at higher elevations experiencing delayed onset of acoustic activity by a month for each 300 m rise in elevation. Delayed onset of acoustic activity corresponded directly to temperature, yet could also be influenced indirectly through plant phenological events (Watt & McFarlane 1991; Hunter 1992; Hill & Hodkinson 1995; Hodkinson 1997; Hill *et al.* 1998; Virtanen & Neuvonen 1999; Hodkinson *et al.* 2001). Delayed phenology resulted in reduced acoustic activity windows at higher elevations, related to narrower optimal temperature windows. Narrow acoustic windows likely result in reduced mating opportunities.

Temperature here decreased with increasing elevation. Temperature lapse rate or decrease with respect to increasing elevation is generally between 5.5 and 6.5 °C for each 1000 m of ascent (Hodkinson 2005), which is consistent with the 5.7 °C change at the study site here

between 545 and 1576 m asl. However, temperature rate decrease on mountains can vary significantly with respect to both local topography, season and meteorological circumstances (Dodson & Marks 1997; Lookingbill & Urban 2003; Rolland 2003; Hodkinson 2005). Generally, temperature lapse rates and exposure to lower temperature extremes with increasing elevation causes a decreased annual thermal budget for insects, resulting in energy trade-offs between associated metabolic costs and sound production (Simmons & Gwynne 1991; Bailey *et al.* 1993; Ritchie *et al.* 1998). As acoustic signals are extremely metabolically costly to produce, energy limitations may restrict energy budget for acoustic activity at higher elevations (Cade 1975; Stevens & Josephson 1977; MacNally & Young 1981; Prestwich & Walker 1981; Bucher *et al.* 1982; Taigen & Wells 1985; Taigen *et al.* 1985; Ryan 1988; Prestwich *et al.* 1989; Simmons & Gwynne 1991; Bailey *et al.* 1993).

Additionally, lower temperatures may not provide optimal acoustic windows for acoustic communication. Fluctuating ambient temperatures affect the speed of katydid muscle contraction (Toms *et al.* 1993; Greenfield 1997) leading to a positive linear relationship between increased pulse rates with higher temperatures (Zweifel 1968; Walker 1975; Gerhardt 1978; Bauer & von Helverson 1987; Ewing 1989; Wagner 1989; Bennet-Clark 1989; Greenfield 1997; Greenfield 2002; Gerhardt & Huber 2002; Sanborn 2006). This relationship occurred across all katydid species at the study site here, and calling ceased altogether at low temperature thresholds. Alteration of pulse rate with temperature, first noted by Brooks (1882) and expounded by Bessey & Bessey (1898), who derived a formula to determine temperature based on pulse rates of tree crickets, has consequences for signal structure with regard to mate selection. In katydids, it usually results in shifting female preferences for specific pulse rates at given temperatures, as is the case in other Ensifera (Walker 1957; Doherty 1985; Pires & Hoy 1992; Greenfield 1997). Another response is that certain species may simply wait for environmental windows that are most suitable for producing a range of pulse rates preferred by

females. In this case, optimal temperature windows would have to occur fairly regularly within the given environment to allow for ample reproductive opportunities. Another strategy available to larger katydids to deal with temperature fluctuations, is to thermoregulate so as to maintain optimal pulse rates (Health & Josephson 1970; Josephson & Halverson 1971; Josephson 1973; Samways 1976; Sanborn 2006).

Temperature can also indirectly influence katydid communication, as thermal layers in the air can impede or enhance propagation of katydid acoustic signals (Wiley & Richards 1978; Van Staaden & Römer 1997; Gerhardt & Huber 2002; Greenfield 2002; Sanborn 2006). Higher air temperatures adjacent to the ground with cooler temperatures above will limit ground level acoustic signals through refraction and attenuation. Conversely, colder temperatures near the ground can result in an acoustic channel for ground level signals which would experience much less attenuation and travel greater distances (Sanborn 2006). It is possible that ground dwelling *H. pupus*, which has a lower optimal temperature calling range than other sympatric katydids, are able to take advantage of this acoustic channel to enhance signal propagation.

Across the elevation gradient, katydid acoustic activity decreased with increasing elevation. Declines in fauna species richness with increasing elevation has been attributed to less than optimal environmental conditions at higher elevations, corresponding primarily to decreasing temperatures (Grytnes & Vetaas 2002; Hodkinson 2005). This trend has been well documented in other studies on a wide range of taxa (Alexander & Hilliard 1969; Holloway 1970; Kikkawa & Williams 1971; Janzen 1973; Hamilton 1975; Janzen *et al.* 1976; Hågvar 1976; Gagné 1979; Hebert 1980; Wolda 1987; McCoy 1990; Navarro 1992; Stevens 1992; Fernandes & Lara 1993; Olson 1994; Patterson *et al.* 1996; Vazquez & Givnish 1998; Givnish 1999; Brühl *et al.* 1999; Odland & Birks 1999; Grytnes & Vetaas 2002; Brehm *et al.* 2003; Novotny *et al.* 2005; Hodkinson 2005; Malsch *et al.* 2008). Here, species showed greater

overlap of elevational niche breadth than expected by chance, and also had wide elevational ranges. Species above 690 m asl therefore did not display distinct acoustic assemblages across elevations. This corresponds with elevational ranges of African dung beetles, which became wider with increasing elevation (Gaston & Chown 1999). Within these species, the critical thermal minima changed more rapidly than the critical thermal maxima, producing a wide tolerance band, allowing species to withstand wider variations in the climate that they experience (Gaston & Chown 1999; Hodkinson 2005). Conversely, tropical species are generally more habitat specific and have narrower tolerance ranges to physical conditions than temperate species (Janzen 1967; Huey 1978; Pianka 1983; Stevens 1989). Consequently, species turnover across tropical elevational gradients is fairly rapid with species exhibiting narrow elevation ranges (Olson 1994).

Set against the consequences of possible global warming, this trend has implications for katydid conservation. Species have individualistic responses to climate change (Graham & Grimm 1990; Warren *et al.* 2001), shifting their ranges to match optimal environmental conditions (Huntley & Birks 1983; Parmesan 1996; Parmesan *et al.* 1999; Hewitt 2000). Species ranges along an elevational gradient are geometrically constrained by hard boundaries (Colwell & Lees 2000; Grytnes & Vetaas 2002), yet are predicted to shift upwards as temperature rises (Woodward 1993). The broad elevational ranges of the katydid species here therefore provide a limited buffer allowing them to withstand greater climate variations in a global warming scenario. The high degree of brachypterous katydids at the study area may also reflect past habitat stability (Roff 1990; Wagner & Liebherr, 1992; Denno *et al.* 1996). Nevertheless, their potential elevational range shifts along known environmental gradients can consequently serve as a sensitive indicator of climate change (Hodkinson & Bird 1998).

While faunal diversity patterns across elevational gradients are directly influenced by environmental parameters such as temperature, they can also be indirectly influenced through shifts in predation, competition, resource availability and plant diversity (Siemann *et al.* 1998; Hodkinson 2005; Pijanowski *et al.* 2011). While plant diversity occurred within distinct zones along the elevational gradient here (Agenbag *et al.* 2008), above 690 m asl, katydids tended to have broad elevational distributions across vegetation gradients. The occurrence of common plant families, such as Restionaceae, which also occur across the elevation gradient (Agenbag *et al.* 2008), makes it difficult to determine the degree of influence plant composition had on katydid acoustic diversity. This is highlighted by two katydid species (*C. pulchripes* and *Ceresia* sp.), which were strongly affiliated with Restionaceae plant species. Whether they utilize these plants as a resource for a combination of ovipositioning, feeding, or concealment is unknown. However, they do use this plant structure as an elevated acoustic niche that rises above dominant vegetation to increase signal range. Given the high plant species diversity of the mountain here, and the high plant species turnover across the elevation gradient, it is likely that katydid species are more generalist in plant preferences, and possibly select structural aspects of vegetation families, rather than species themselves. However, more detailed knowledge on the acoustic niches, host plants, and ovipositioning of the katydids here is needed to shed greater light on the influence of plant species composition on acoustic diversity.

Nevertheless, below 690 m asl, the effect of plant composition on acoustic diversity was more pronounced. Acoustic diversity across the elevational gradient increased with increasing temperatures, corresponding to lower elevations, until the soil barrier between the Ecotone and Karoo site. The resulting vegetation gradient of Karoo vegetation was a hard edge, and a barrier to 12 of the 13 katydids here, restricting them to elevations above this vegetation type. The remaining species (*C. vansoni*), was restricted solely to this vegetation type. Karoo vegetation was almost entirely restricted to this elevation, unable to cross the soil barrier, and

also contained many unpalatable asteraceous shrubs, indicating vegetation had been degraded by overgrazing in the recent past (Agenbag *et al.* 2008). Vegetation along elevational gradients frequently varies in suitability as host plants and can influence species distribution (Ayres 1993; Bowman & Conant 1994; Ayres *et al.* 1997; Erelli *et al.* 1998; Kronfuss & Havranek 1999). Absence of katydid acoustic signatures within this Karoo vegetation reflects the unsuitability of these host plants, and or an effect of some unknown disturbance on katydid diversity.

The focal mountain was continually exposed to varying wind speeds which occurred across all elevational and seasonal gradients, a finding that corresponds with prior research (Agenbag *et al.* 2008), creating fairly constant levels of background noise. What is interesting, is that katydids here utilized significantly higher frequency acoustic signals for communication, compared to katydids from the same subfamilies, in a relatively wind free area of KwaZulu-Natal (see this thesis, Chapter 4). Acoustic communication is constrained by various abiotic and biotic factors affecting signal propagation and reception (Römer *et al.* 1989). Abiotic background noise from sources like wind, rain and waterfalls impairs effective communication (Riede 1996). As a result, signals evolve to minimize the effect acoustic interference from background noise (Brumm & Slabbekoorn 2005; Endler, 1992). Various taxa including katydids therefore tend to utilize signals of short duration, high intensity and high in frequency to overcome abiotic background noise (Dubois & Martens 1984; Ryan & Brenowitz 1985; Greenfield 1994; Riede 1996; Pijanowski *et al.* 2011). It seems likely that the high frequency signals of the katydids here are an adaptation to overcome constant background noise of wind. Using high frequency, broadband acoustic signals and acoustic niches above dominant vegetation also reduces attenuation of high frequency signals with surrounding vegetation and improves directionality and localization of signals (Paul & Walker 1979; Doolan & MacNally 1981; Dadour & Bailey 1985; Montealegre-Z *et al.* 2006; Greenfield 2002).

Conclusion

Katydid acoustic communication provides a non-invasive, effective method of investigating diversity patterns of these visually and behaviourally cryptic insects, across ecological gradients. Once species-specific signals are identified they enable long term monitoring of species across habitats and over time. This not only provides a means of detecting the absence of previously existing signals (indicating a decline in ecological integrity or changing environmental conditions) but also the presence of new signals which indicate range shifts, invasive species or new species discovery (Riede 1993; Sueur *et al.* 2008a; Sueur *et al.* 2008b; Pijanowski *et al.* 2011). The value of this is highlighted within this study by the discovery of two new species to science, based on the detection of novel acoustic signatures across the landscape. Acoustic diversity patterns are therefore an important consideration when assessing conservation priorities in regions, conducting biodiversity surveys, or monitoring impacts of climate change.

References

- Agenbag, L., Esler, K. J., Midgley, G. F. & Boucher, C. 2008. Diversity and species turnover on an altitudinal gradient in Western Cape, South Africa: baseline data for monitoring range shifts in response to climate change. *Bothalia* 191:161–191.
- Alexander, G. & Hilliard, J. R. 1969. Altitudinal and seasonal distribution of Orthoptera in the Rocky Mountains of northern Colorado. *Ecological Monographs* 39:385–431.
- Arak, A. & Eiríksson, T. 1992. Choice of singing sites by male bush crickets (*Tettigonia viridissima*) in relation to signal propagation. *Behavioural Ecology and Sociobiology* 30:365–372.
- Ayres, M. P. 1993. Global change, plant defense, and herbivory. In: Kareiva, P. M., Kingsolver, J. G. & Huey, R. B. (eds.). *Biotic interactions and global change*. Sinauer, Sunderland.
- Ayres, M. P., Clausen, T. P., Maclean, S. F., Redman, A. M. & Reichart, P. B. 1997. Diversity of structure and anti-herbivore activity in condensed tannins. *Ecology* 78:1696–1711.
- Bailey, W. J. & Rentz, D. C. F. 1990. The Tettigoniidae – their diversity and importance in biological research. In: Bailey, W. J. & Rentz, D. C. F. (eds.). *The Tettigoniidae: biology, systematics and evolution*. Crawford House Press, Australia.
- Bailey, W. J., Withers, P. C., Endersby, M. & Gaull, K. 1993. The energetic cost of calling in the bush cricket *Requena verticalis* (Orthoptera: Tettigoniidae: Listroscelidinae). *Journal of Experimental Biology* 178:21–37.
- Bauer, M. & von Helverson, O. 1987. Separate localization of sound recognizing and sound producing neural mechanisms in a grasshopper. *Journal of Comparative Physiology* 161:95–101.
- Bennet-Clark, H. C. 1989. Songs and the physics of sound production. In: Hubner, F., Moore, T. E. & Loher, W. (eds.). *Cricket behavior and neurobiology*. Cornell University Press, Ithaca, New York.

- Bessey, C. A. & Bessey, E. A. 1898. Further notes on thermometer crickets. *The American Naturalist* 32:263–264.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J. S. S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–35.
- Bowman, W. D. & Conant, R. T. 1994. Shoot growth dynamics and photosynthetic response to increased nitrogen availability in the alpine willow *Salix glauca*. *Oecologia* 97:93–99.
- Brehm, G., Homeier, J. & Fiedler, K. 2003. Beta diversity of geometrid moths (Lepidoptera: Geometridae) in an Andean montane rainforest. *Diversity and Distributions* 9:351–366.
- Brooks, M. W. 1882. Influence of temperature on the chirp rate of the cricket. *Popular Science Monthly* 20:268.
- Brown, W. D. & Gwynne, D. T. 1997. Evolution of mating in crickets, katydids, and wetas (Ensifera). In: Gangwere, S. K., Muralirangan, M. C. & Muralirangan, M. (eds.). *The bionomics of grasshoppers, katydids and their kin*. CAB International, Oxford.
- Brühl, C. A., Mohamed, M. & Linsenmair, K. E. 1999. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology* 15:265–2.
- Brumm, H. & Slabbekoorn, H. 2005. Acoustic communication in noise. *Advances in the Study of Behavior* 35:151–209.
- Bucher, T. L., Ryan, M. J., Bartholomew, G. 1982. Oxygen consumption during resting, calling, and nest building in the frog *Physalaemus pustulosus*. *Physiological Zoology* 55:10–22.
- Burk, T. E. 1982. Evolutionary significance of predation on sexually signalling males. *The Florida Entomologist* 65:90–104.

- Butterfield, J. 1976. Effect of photoperiod on a winter and on a summer diapause in two species of crane fly (Tipulidae). *Journal of Insect Physiology* 22:1443–1446.
- Butterfield, J., Telfer, G., Fielding, C. & Coulson, J. C. 1999. The diapause syndrome in the seed-eating caterpillar of *Coleophora alticolella*. *Entomologia Experimentalis et Applicata* 92:321–330.
- Butterfield, J., Whittaker, J. B. & Fielding, C. A. 2001. Control of the flexible annual/biennial life cycle of the heather psyllid *Strophingia ericae*. *Physiological Entomology* 26:266–274.
- Butterfield, J. & Coulson, J. C. 1988. The rate of development in the overwintering eggs of *Tipula pagana* Meigen. *Journal of Insect Physiology* 34:53–57.
- Cade, W. H. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* 190:1312–1313.
- Colwell, R. K. & Lees, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* 15:70–76.
- Dadour, I. & Bailey, W. J. 1985. Male agonistic behaviour of the bush cricket *Mygalopsis marki* Bailey in response to conspecific song (Orthoptera, Tettigoniidae). *Zeitschrift für Tierpsychologie* 70:320–330.
- Denno, R. E., Roderick, G. K., Peterson, M. A., Huberty, A. F., Dobel, H. G., Eubanks, M. D., Losey, J. E. & Langellotto, G. A. 1996. Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. *Ecological Monographs* 66:389–408.
- Diwakar, S. & Balakrishnan, R. 2007a. The assemblage of acoustically communicating crickets of a tropical evergreen forest in southern India: call diversity and diel calling patterns. *Bioacoustics* 16:113–135.

- Diwakar, S. & Balakrishnan, R. 2007b. Vertical stratification in an acoustically communicating ensiferan assemblage of a tropical evergreen forest in southern India. *Journal of Tropical Ecology* 23:479–486.
- Dobson, A. J. 1990. *An introduction to generalized linear models*. Chapman & Hall, New York
- Dodson, R. & Marks, D. 1997. Daily air temperature interpolated at high spatial resolution over a large mountainous region. *Climate Research* 8:1–20.
- Doherty, J. A. 1985. Temperature coupling and ‘trade-off’ phenomena in the acoustic communication system of the cricket, *Gryllus bimaculatus* (Orthoptera, Gryllidae). *Journal of Comparative Physiology A* 156:787–801.
- Doolan, J. M. & MacNally, R. C. 1981. Spatial dynamics and breeding ecology in the cicada *Cystosoma saundersii*: the interaction between distributions of resources and intraspecific behaviour. *Journal of Animal Ecology* 50:925–940.
- Dubois, A. & Martens, J. 1984. A case of possible vocal convergence between frogs and a bird in Himalayan torrents. *Journal of Ornithology* 125:455–463.
- Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. *The American Naturalist* 139:125–153.
- Entsminger, G. L. 2012. *EcoSim professional: null modeling software for ecologists, Version 1*. Acquired Intelligence Inc., Kesey-Bear & Pinyon Publishing. Montrose.
- Erelli, M. C., Ayres, M. P. & Eaton, G. K. 1998. Altitudinal patterns in host suitability for forest insects. *Oecologia* 117:133–142.
- Ewing, A. M. 1989. *Arthropod bioacoustics, neurobiology and behavior*. Cornell University Press, Ithaca, New York.
- Feinsinger, P., Spears, E. E. & Poole, R. W. 1981. A simple measure of niche breadth. *Ecology* 62:27–32.

- Fernandes, G. W. & Lara, A. C. F. 1993. Diversity of Indonesian gall-forming herbivores along altitudinal gradients. *Biodiversity Letters* 1:186–192.
- Fielding, C. A, Whittaker, J. B., Butterfield, J. E. L. & Coulson, J. C. 1999. Predicting response to climate warming? In: Harrington, R. & Stork, N. E. (eds.). *Insects in a changing environment* Academic press, London.
- Franklin, M., Droege, S., Dawson, D., Royle, J. A. 2009. Nightly and seasonal patterns of calling in common true katydids (Orthoptera: Tettigoniidae: *Pterophylla camellifolia*). *Journal of Orthoptera Research* 18:15–18.
- Gagné, W. C. 1979. Canopy-associated arthropods in *Acacia koa* and *Metrosideros* tree communities along an altitudinal transect on Hawaii Island. *Pacific Insects* 21:56–82.
- Gaston, K. J. & Chown, S. L. 1999. Elevation and climatic tolerance: a test using dung beetles. *Oikos* 86:584–590.
- Gerhardt, H. C. & Huber, F. 2002. *Acoustic communication in insects and anurans: Common problems and diverse solutions*. The University of Chicago Press, Chicago.
- Gerhardt, H. C. 1978. Temperature coupling in the vocal communication system of the gray tree frog, *Hyla versicolor*. *Science* 199:992–994.
- Givnish, T. J. 1999. On the causes of gradients in tropical tree diversity. *Journal of Ecology* 87:193–210.
- Goldblatt, P. & Manning J. C. 1999. *Cape flora – a conspectus of the cape flora of South Africa*. National Botanical Institute, Pretoria.
- Goldblatt, P. 1997. Floristic diversity in the cape flora of South Africa. *Biodiversity and Conservation* 6:359–377.
- Gotelli, N. J. & Graves, G. R. 1996. *Null models in ecology*. Smithsonian Institution Press. Washington.

- Graham, R. W. & Grimm, E. C. 1990. Effects of global climate change on the patterns of terrestrial biological communities. *Trends in Ecology and Evolution* 5:289–292.
- Greenfield, M. D. 1994. Cooperation and conflict in the evolution of signal interactions. *Annual Review of Ecology, Evolution, and Systematics* 25:97–126.
- Greenfield, M. D. 1997. Acoustic communication in Orthoptera. In: Gangwere, S. K., Muralirangan, M. C. & Muralirangan, M. (eds.). *The bionomics of grasshoppers, katydids and their kin*. CAB International, Oxford.
- Greenfield, M. D. 2002. *Signalers and receivers. Mechanisms and evolution of arthropod communication*. Oxford University Press, Oxford.
- Grytnes, J. A. & Vetaas, O. R. 2002. Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *The American Naturalist* 159:294–304.
- Gullan, P. J. & Cranston, P. S. 2010. *The insects: an outline of entomology 4th edition*. Wiley-Blackwell, Oxford.
- Gwynne, D. T. 2001. *Katydid and bush-crickets: reproductive behavior and evolution of the Tettigoniidae*. Cornell University Press, Ithaca.
- Hågvar, S. 1976. Altitudinal zonation of the invertebrate fauna on branches of birch (*Betula pubescens* Erh.). *Norwegian Journal of Entomology* 23:61–74.
- Hamilton, A. C. 1975. A quantitative analysis of altitudinal zonation in Uganda forests. *Vegetatio* 30:99–106.
- Health, J. E., Josephson, R. K. 1970. Body temperature and singing in the katydid, *Neoconocephalus robustus* (Orthoptera, Tettigoniidae). *Biological Bulletin* 138:272–285.
- Hebert, P. D. N. 1980. Moth communities in montane Papua New Guinea. *Journal of Animal Ecology* 49:593–602.

- Hewitt, G. M. 2000. The genetic legacy of the Quaternary ice ages. *Nature* 405:907–913.
- Hill, J. K., Hamer, K. C. & Hodkinson, I. D. 1998. Variation in resource exploitation along an altitudinal gradient: the willow psyllids (*Cacopsylla spp.*) on *Salix lapponum*. *Ecography* 21:289–296.
- Hill, J. K. & Hodkinson, I. D. 1995. Effects of temperature on phenological synchrony and altitudinal distribution of jumping plant lice (Hemiptera, Psylloidea) on dwarf willow (*Salix lapponum*) in Norway. *Ecological Entomology* 20:237–244.
- Hodkinson, I. D. 1997. Progressive restriction of host plant exploitation along a climatic gradient: The willow psyllid *Cacopsylla groenlandica* in Greenland. *Ecological Entomology* 22:47–54.
- Hodkinson, I. D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* 80:489–513.
- Hodkinson, I. D., Bird, J. M., Hill, J. K. & Baxter, R. 2001. Host plant growth characteristics as determinants of abundance and phenology in jumping plant-lice on downy willow. *Ecological Entomology* 26:376–387.
- Hodkinson, I. D. & Bird, J. 1998. Host-specific insect herbivores as sensors of climate change in arctic and alpine environments. *Arctic and Alpine Research* 30:78–83.
- Holloway, J. D. 1970. The biogeographical analysis of a transect sample of the moth fauna of Mt Kinabalu, Sabah, using numerical methods. *Biological Journal of the Linnean Society* 2:259–286.
- Huey, R. B. 1978. Latitudinal patterns of between-altitude faunal similarity: mountains might be 'higher' in the tropics. *The American Naturalist* 112:225–229.
- Hunter, M. D. 1992. A variable insect-plant interaction: the relationship between budburst phenology and population levels of insect herbivores among trees. *Ecological Entomology* 17:91–95.

- Huntley, B., Birks, H. J. B., 1983. *An atlas of past and present pollen maps for Europe, 0–13000 B.P.* Cambridge University Press, Cambridge.
- Jain, M. & Balakrishnan, R. 2011. Does acoustic adaptation drive vertical stratification? A test in a tropical cricket assemblage. *Behavioral Ecology* 23:343–354.
- Jain, M., Diwakar, S., Bahuleyan, J., Deb, R. & Balakrishnan, R. 2013. A rain forest dusk chorus: cacophony or sounds of silence? *Evolutionary Ecology* doi:10.1007/s10682–013–9658–7.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *The American Naturalist* 101:233–249.
- Janzen, D. H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54:687–708.
- Janzen, D. H., Ataroff, M., Farinas, M., Reyes, S., Rincon, A., Soler, A., Soriano, P. & Vera, M. 1976. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. *Biotropica* 8:193–203.
- Josephson, R. K. 1973. Contraction kinetics of the fast muscles used in singing by a katydid. *Journal of Experimental Biology* 59:781–801.
- Josephson, R. K. & Halverson, R. C. 1971. High frequency muscles used in sound production by a katydid. I. Organization of the motor system. *Biological Bulletin* 141:411–433.
- Kikkawa, J., & Williams, E. E. 1971. Altitude distribution of land birds in New Guinea. *Search* 2:64–65.
- Kronfuss, H. & Havranek, W. M. 1999. Effects of elevation and wind on the growth of *Pinus cembra* L. in a subalpine afforestation. *Phyton-Annales Rei Botanicae* 39:99–106.
- Lookingbill, T. R. & Urban, D. L. 2003. Spatial estimation of air temperature differences for landscape-scale studies in montane environments. *Agricultural and Forest Meteorology* 114:141–151.

- MacNally, R. C. & Young, D. 1981. Song energetics of the bladder cicada. *Journal of Experimental Biology* 90:185–196.
- Malsch, A. K. F., Fiala, B., Maschwitz, U., Mohamed, M., Nais, J. & Linsenmair, K. E. 2008. An analysis of declining ant species richness with increasing elevation at Mount Kinabalu, Sabah, Borneo. *Asian Myrmecology* 2:33–49.
- McCoy, E. D. 1990. The distribution of insects along elevational gradients. *Oikos* 58:313–322.
- Montealegre-Z, F., Morris, G. K. & Mason, A. C. 2006. Generation of extreme ultrasonics in rainforest katydids. *Journal of Experimental Biology* 209:4923–4937.
- Morton, E. S. 1975. Ecological sources of selection on avian sounds. *The American Naturalist* 109:17–34.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- Navarro, A. G. S. 1992. Altitudinal distribution of birds in the Sierra Madre del Sur, Guerrero, Mexico. *Condor* 94:29–39.
- Novotny, V., Miller, S. E., Basset, Y., Cizek, L., Kaupa, B., Kua, J. & Weiblen, G. D. 2005. An altitudinal comparison of caterpillar (Lepidoptera) assemblages on *Ficus* trees in Papua New Guinea. *Journal of Biogeography* 32:1303–1314.
- O’Hara, R. B. 2009. How to make models add up – a primer on GLMMs. *Annales Zoologici Fennici* 46:124–37.
- Odland, A. & Birks, H. J. B. 1999. The altitudinal gradient of vascular plant species richness in Aurland, western Norway. *Ecography* 22:548–566.
- Olson, D. M. 1994. The distribution of leaf litter invertebrates along a Neotropical altitudinal gradient. *Journal of Tropical Ecology* 10:129–150.
- Parmesan, C. 1996. Climate effects on species range. *Nature* 382:765–766.

- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kulberg, J., Tammaru, T., Tennett, W. J., Thomas, J. A. & Warren, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–583.
- Patterson, B. D., Pacheco, V. & Solari, S. 1996. Distributions of bats along an elevational gradient in the Andes of southeastern Peru. *Journal of Zoology (London)* 240:637–658.
- Paul, R. C., Walker, T. J. 1979. Arboreal singing in a burrowing cricket, *Anurogryllua arboreus*. *Journal of Comparative Physiology A* 132:217–223.
- Pianka, E. R. 1983. *Evolutionary ecology*. Harper & Row, Publishers, New York.
- Pijanowski, B. C., Farina, A., Gage, S. H., Dumyahn, S. L. & Krause, B. L. 2011. What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology* 26:1213–1232.
- Pires, A., Hoy, R. R. 1992. Temperature coupling in cricket acoustic communication, I. Field and laboratory studies of temperature effects on calling song production and recognition in *Gryllus firmus*. *Journal of Comparative Physiology A* 171:69–78.
- Prestwich, K. N. & Walker, T. J. 1981. Energetics of singing in crickets: effect of temperature in three trilling species (Orthoptera: Gryllidae). *Journal of Comparative Physiology B* 143:199–212.
- Prestwich, K., Brugger, K. E. & Topping, M. 1989. Energy and communication in three species of hylid frogs: power input, power output and efficiency. *Journal of Experimental Biology* 144:53–80.
- Rebelo, A. G. 1998. Fynbos Biome. In: Low, A. B. & Rebelo, A. G. (eds.). *Vegetation of South Africa, Lesotho and Swaziland: a companion to the vegetation map of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria.

- Richards, D. G. & Willey, R. H. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: Implications for animal communication. *The American Naturalist* 115:381–399.
- Riede, K. 1993. Monitoring biodiversity: analysis of Amazonian rainforest sounds. *Ambio* 22:546–548.
- Riede, K. 1996. Diversity of sound-producing insects in a Bornean lowland rain forest. In: Edwards, D. S., Booth, W. E. & Choy, S. C. (eds.). *Tropical Rainforest Research – Current Issues*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Riede, K. 1998. Acoustic monitoring of Orthoptera and its potential for conservation. *Journal of Insect Conservation* 2:217–223.
- Ritchie, M. G., Townhill, R. M. & Hoikkala, A. 1998. Female preference for fly song: playback experiments confirm the targets of sexual selection. *Animal Behaviour* 56:713–717.
- Roff, D. A. 1990. The evolution of flightlessness in insects. *Ecological Monographs* 60:389–422.
- Rolland, C. 2003. Spatial and seasonal variations of air temperature lapse rates in Alpine regions. *Journal of Climate* 16:1032–1046.
- Römer, H. 1993. Environmental and biological constraints for the evolution of long-range signaling and hearing in acoustic insects. *Philosophical Transactions of the Royal Society B: Biological Sciences* 340:179–185.
- Römer, H. & Lewald, J. 1992. High-frequency sound transmission in natural habitats: implications for the evolution of insect acoustic communication. *Behavioral Ecology and Sociobiology* 29:437–444.
- Römer, H., Bailey, W. J. & Dadour, I. 1989. Insect hearing in the field. III. Masking by noise. *Journal of Comparative Physiology A* 164:609–620.
- Ryan, M. J. 1988. Energy, calling and selection. *The American Zoologist* 28:885–898.

- Ryan, M. J. & Brenowitz, E. A. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *The American Naturalist* 126:87–100.
- Samways, M. J. 1976. Song modification in the Orthoptera. I. Proclamation songs of *Platycleis* spp., (Tettigoniidae). *Physiological Entomology* 1:299–303.
- Sanborn, A. F. 2006. Acoustic signals and temperature. In: Drosopoulos, S. & Claridge, M. F. (eds.). *Insect sounds and communication: physiology, behaviour, ecology and evolution*. Taylor and Francis Group, Florida.
- Schmidt, A. K. D., Römer, H. & Riede, K. 2012. Spectral niche segregation and community organization in a tropical cricket assemblage. *Behavioral Ecology* 24:470–480.
- Searcy, W. A., Anderson, M. 1986. Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics* 17:507–533.
- Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *The American Naturalist* 152:738–750.
- Simmons, L. W. & Gwynne, D.T. 1991. The refractory period of female katydids (Orthoptera: Tettigoniidae): sexual conflict over the re-mating interval? *Behavioral Ecology and Sociobiology* 10:263–269.
- Simmons, L. W. & Zuk, M. 1992. Variability in call structure and pairing success of male field crickets, *Gryllus bimaculatus*: the effect of age, size and parasite load. *Animal Behaviour* 44:1145–1152.
- Statsoft, INC. 2012. Statistica (data analysis software system), version 11. www.statsoft.com.
- Stevens, D. E. & Josephson, R. K. 1977. Metabolic rate and body temperature in singing katydids. *Physiological Zoology* 50:31–42.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist* 133:240–256.

- Stevens, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *The American Naturalist* 140:893–911.
- Sueur, J., Pavoine, S., Hamerlynck, O. & Duvail, S. 2008b. Rapid acoustic survey for biodiversity appraisal. *PLOS ONE* 3:e4065
- Sueur, J., Aubin, T. & Simonis, C. 2008a Seewave: a freemodular tool for sound analysis and synthesis. *Bioacoustics* 18:213–226.
- Sueur, J. 2002. Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera: Cicadomorpha: Cicadidae). *Biological Journal of the Linnean Society* 75:379–394.
- Taigen, T. L. & Wells, K. D. 1985. Energetics of vocalizations by an anuran amphibian. *Journal of Comparative Physiology* 155:163–170.
- Taigen, T. L., Wells, K. D. & Marsh, R. L. 1985. The enzymatic basis of high metabolic rates in calling frogs. *Physiological Zoology* 58:719–26.
- Toms, R. B., Ferguson, J. W. H. & Becker, S. 1993. Relationship between body temperature and air temperature in stridulating male crickets, *Gryllus bimaculatus* (Orthoptera: Gryllidae). *South African Journal of Zoology* 28:71–73.
- Tuckerman, J. F., Gwynne, D. T. & Morris, G. K. 1993. Reliable acoustic cues for female mate preference in a katydid (*Scudderia curvivauda*). *Behavioral Ecology and Sociobiology* 4:106–113.
- Van Staaden, M. J. & Römer, H. 1997. Sexual signaling in bladder grasshoppers: Tactical design for maximizing call range. *Journal of Experimental Biology* 200:2597–2608.
- Vazquez, J. A. & Givnish, T. J. 1998. Altitudinal gradients in the tropical forest composition, structure, and diversity in the Sierra de Manantlan. *Journal of Ecology* 86:999–1020.
- Virtanen, T. & Neuvonen, S. 1999. Performance of moth larvae on birch in relation to altitude, climate, host quality and parasitoids. *Oecologia* 120:92–101.

- Wagner, W. E. 1989. Social correlates of variation in male calling behavior in Blanchard's cricket frog, *Acris crepitans blanchardi*. *Ethology* 82:27–45.
- Wagner, D. L. & Liebherr, J. K. 1992. Flightlessness in insects. *Trends in Ecology & Evolution* 7:216–220.
- Walker, T. J. 1957. Specificity in the response of female tree crickets (Orthoptera, Gryllidae, *Oecanthinae*) to calling songs of the males. *Annals of the Entomological Society of America* 50:626–636.
- Walker, T. J. 1975. Effects of temperature on rates in poikilotherm nervous systems. Evidence from the calling songs of meadow katydids (Orthoptera, Tettigoniidae: *Orchelimum*) and reanalysis of published data. *Journal of Comparative Physiology A* 101:57–59.
- Wang, G. Y., Greenfield, M. D. & Shelly, T.E. 1990. Intermale competition for high- quality host-plants: the evolution of protandry in a territorial grasshopper. *Behavioral Ecology and Sociobiology* 27:191–198.
- Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M. G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S. G., Greatorex-Davies, J. N., Moss, D. & Thomas, C.D. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414:65–69.
- Watt, E. D. & McFarlane, A. M. 1991. Winter moth on sitka spruce: synchrony of egg hatch and budburst, and its effect on larval survival. *Ecological Entomology* 16:387–390.
- Wiley, R. H. & Richards, D. G. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* 3:69–94.
- Winemiller, K. O. & Pianka, E. R. 1990. Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60:27–55.

- Wolda, H. 1987. Altitude, habitat and tropical insect diversity. *Biological Journal of the Linnean Society* 30:313–323.
- Woodward, F. I. 1993. The lowland-to-upland transition modeling plant-responses to environmental-change. *Ecological Applications* 3:404–408.
- Yi, Y. & Wang, X. 2011. Comparison of Wald score and likelihood ratio tests for response adaptive designs. *Journal of Statistical Theory and Applications* 10:553–569.
- Zuk, M. & Kolluru, G. 1998. Exploitation of sexual signals by predators and parasitoids. *Quarterly Review of Biology* 73:415–438.
- Zuur, A. F., Elena, N. I. & Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:1–14.
- Zweifel, R. G. 1968. Effects of temperature, body size, and hybridization of mating calls of toads, *Bufo americanus* and *Bufo woodhousi fowleri*. *Copeia* 1968:269–285.

Table 5.1. Katydid (Orthoptera: Ensifera: Tettigoniidae) species detected across elevational, seasonal and vegetation gradients at the study site.

	Species ID	Subfamily	Species	Authority
1	Com	Conocephalinae	<i>Conocephalus maculatus</i>	Le Guillou, 1841
2	Cop	Conocephalinae	<i>Conocephalus peringueyi</i>	Uvarov, 1928
3	Hp	Hetrodinae	<i>Hetrodes pupus</i>	(Linné, 1758)
4	Pc	Phaneropterinae	<i>Plangia compressa</i>	(Walker, 1869)
5	Tc	Phaneropterinae	<i>Tylopsis continua</i>	(Walker, 1869)
6	Clme	Saginae	<i>Clonia melanoptora</i>	(Linné, 1758)
7	Clmi	Saginae	<i>Clonia minuta</i>	(Haan, 1842)
8	Clv	Saginae	<i>Clonia vansoni</i>	Kaltenbach, 1971
9	Ao	Tettigoniinae	<i>Aprosphylus olszanowskii</i>	Naskrecki, 1994
10	As	Tettigoniinae	<i>Alfredectes semiaeneus</i>	(Serville, 1838)
11	Cp	Tettigoniinae	<i>Ceresia pulchripes</i>	(Péringuey, 1916)
12	Cr	Tettigoniinae	<i>Ceresia rooi</i>	Grant, 2013
13	Csp	Tettigoniinae	<i>Ceresia</i> sp.	Grant, 2013

Table 5.2. Characterization of katydid acoustic signals. Acoustic parameters were taken from a minimum of 20 individuals per species between 17-19 C°. Species ID are listed in Table 5.1. T= trill duration (s), ti= trill interval (s), C= chirp duration (s), ci= chirp interval (s), P= pulse duration (s), pi= pulse interval (s), p/c= number of pulses per chirp, CR= chirp rate (number of chirps per second), PR= pulse rate (number of pulses per second), Min= minimum frequency range (kHz), Max= maximum frequency range (kHz), Center= center frequency (kHz).

Species ID	T	ti	C	ci	P	pi	p/c	CR	PR	Min	Max	Center
1 Com	0.8	1.5	0.016	0.005	0.001	0.000	11.1	48.2	535.6	9.4	23.4	20.0
2 Cop	5.3	0.9	0.068	0.039	0.001	0.003	16.1	17.5	211.0	8.7	23.4	20.0
3 Hp	15.1	339.0	0.049	0.024	0.001	0.003	11.3	14.7	164.3	5.8	19.4	10.9
4 Pc	0.2	2.1	0.019	0.032	0.001	0.003	4.7	19.9	93.0	6.9	14.6	10.5
5 Tc	–	–	1.878	4.396	0.001	0.133	14.0	0.2	2.2	9.0	23.5	15.4
6 Clme	> 60	–	0.036	0.021	0.001	0.010	3.5	17.7	63.1	7.5	22.3	12.0
7 Clmi	> 60	–	0.008	0.035	0.001	0.006	1.5	18.7	27.3	1.2	23.1	21.0
8 Clv	> 60	–	0.025	0.027	0.001	0.001	11.1	19.4	215.1	3.5	23.6	20.3
9 Ao	0.7	2.8	0.089	0.032	0.001	0.009	9.5	8.6	82.3	8.0	23.8	18.1
10 As	8.6	1.7	0.043	0.089	0.001	0.003	5.3	42.4	205.7	8.0	24.3	13.0
11 Cp	9.6	2.1	0.078	0.020	0.001	0.003	19.2	11.0	207.5	9.6	40.3	17.2
12 Cr	13.4	10.0	0.032	0.023	0.001	0.006	4.4	20.3	91.6	7.9	40.9	31.1
13 Csp	1.6	1.1	0.053	0.014	0.001	0.003	13.2	18.1	220.2	21.1	53.6	14.7

Table 5.3. Acoustic diversity patterns of katydid species across elevational, seasonal and botanical gradients. Species ID are listed in Table 5.1.

High-altitude Sandstone Dwarf Fynbos	1576					As	Csp As Com Cop		
	1435					As	As	Csp As	
Mid-altitude Sandstone Fynbos	1303			Hp	Hp As	Hp Cp Csp As	Cp Csp As	Cp Csp As	
	1196			Hp	Hp As	Hp Cp Csp As	Cp Csp As	Cp Csp As	As
	1044		Hp	Hp	Hp Cp Csp As Clme Pc	Hp Cp Csp Cr As Clme Clmi Pc	Hp Cp Csp Cr As Clme Clmi Pc	Cp Csp As Pc Tc	Cp Csp As
	953		Hp	Hp Ao	Hp Ao Cp Csp As Clme Pc	Hp Ao Cp Csp Cr As Clme Clmi Pc	Ao Cp Csp Cr As Clme Clmi Pc	Ao Cp Csp As Tc	Cp Csp As
Ecotone	744	Hp	Hp Ao Cp	Hp Ao Cp Csp Clme	Hp Ao Cp Csp As Clme Pc	Hp Ao Cp Csp Cr As Clme Clmi Pc Tc	Ao Cp Csp Cr As Clme Clmi Pc Tc Cop	Ao Cp Csp As Tc	Ao Cp
	690		Ao Cp	Ao Cp	Ao Cp Csp Clme Pc	Hp Ao Cp Csp Cr As Clme Clmi Pc Tc	Ao Cp Csp Cr As Clme Clmi Pc Tc Cop	Ao Cp Csp As Tc	
Karoo	545					Clv	Clv		
Veg.	Elev.	September	October	November	December	January	February	March	April

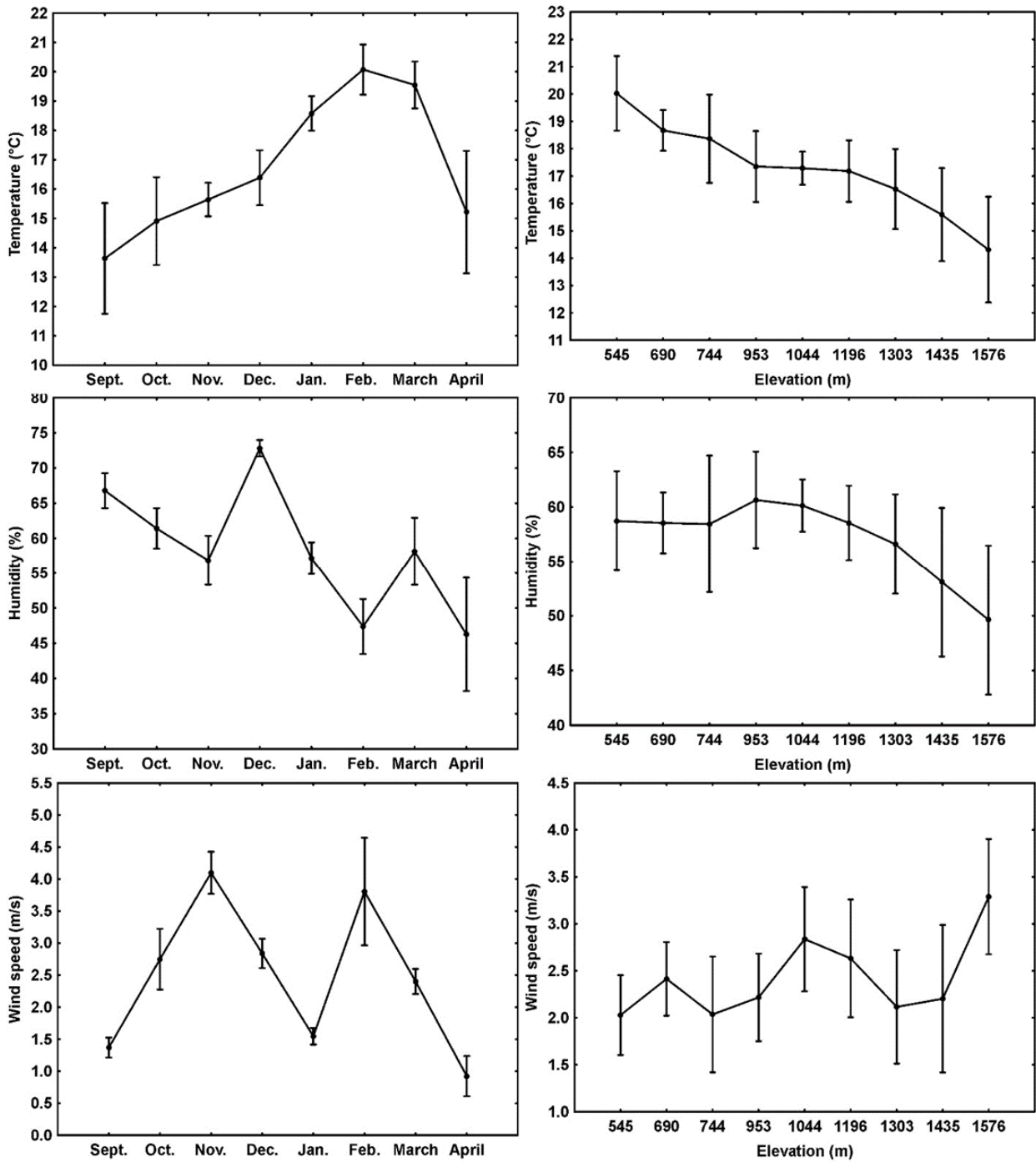


Figure 5.1. Mean temperature and standard error (°C), humidity (%), and wind speed (m/s) across seasons are on the left and across elevations on the right for the study site.

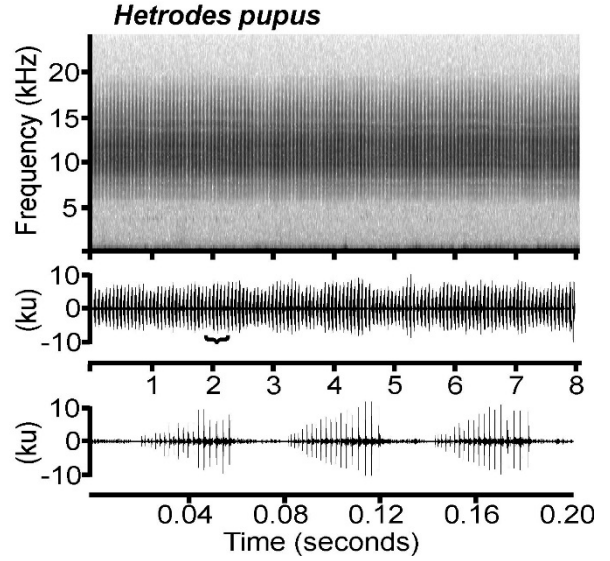
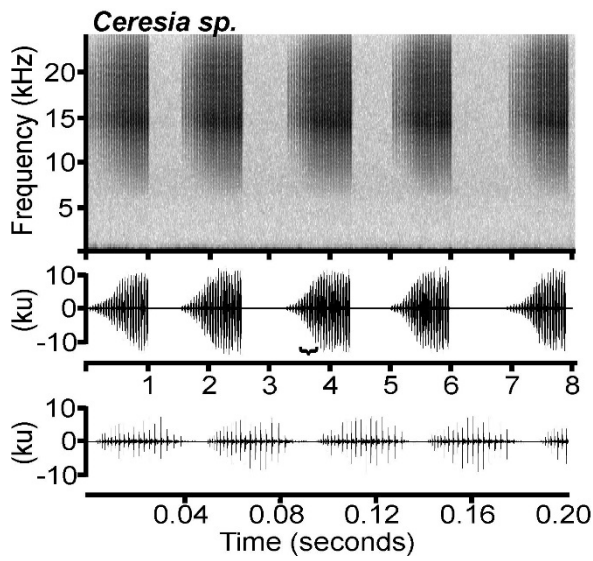
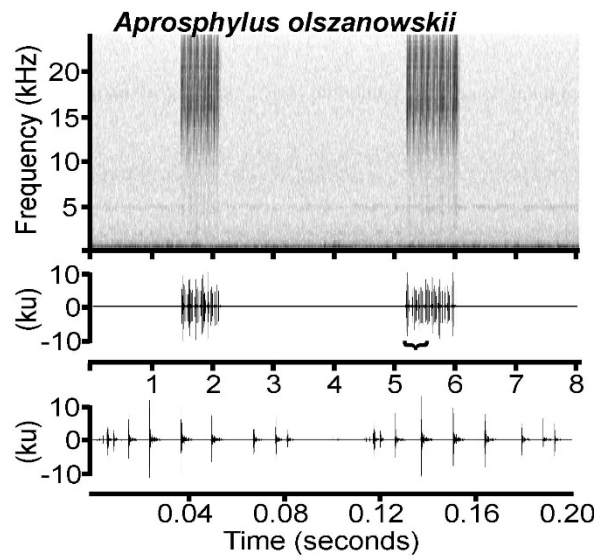
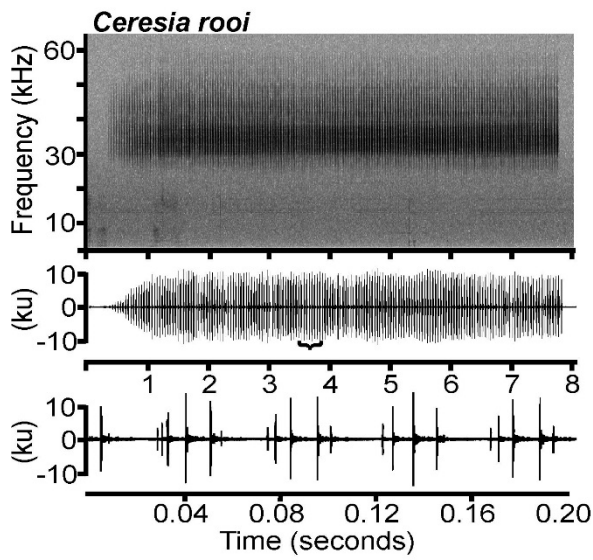
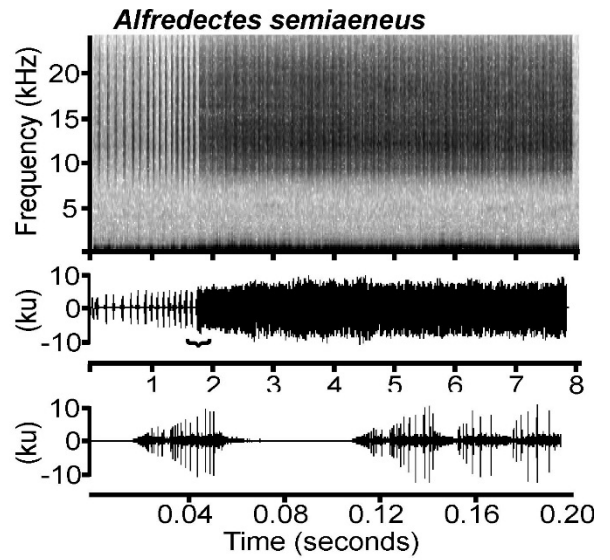
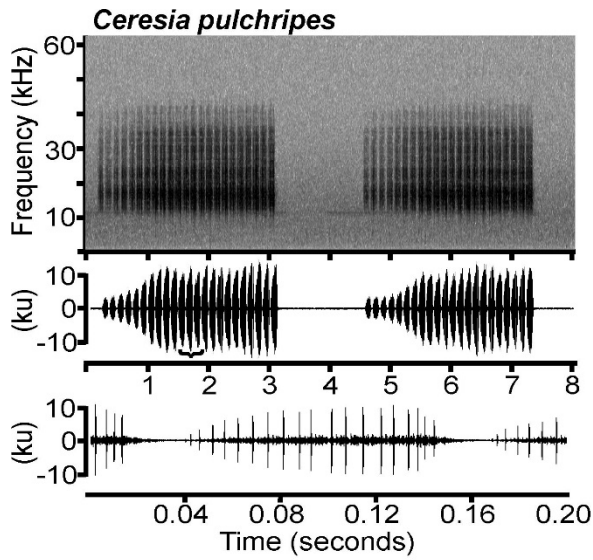


Figure 5.2. Acoustic signals of *Ceresia pulchripes*, *Ceresia rooi*, *Ceresia* sp., *Alfredectes semiaeneus*, *Aprosphylus olszanowskii* and *Hetrodes pupus*. Spectrogram (above) displays frequency (kHz) versus time (s) with darker colours representing higher decibel levels (dB). Waveform associated with spectrogram (middle) displays signal structure of amplitude modulations over time (8 seconds). Marked section in middle waveform is expanded in time (0.2 seconds) to display distinct pulses within each chirp.

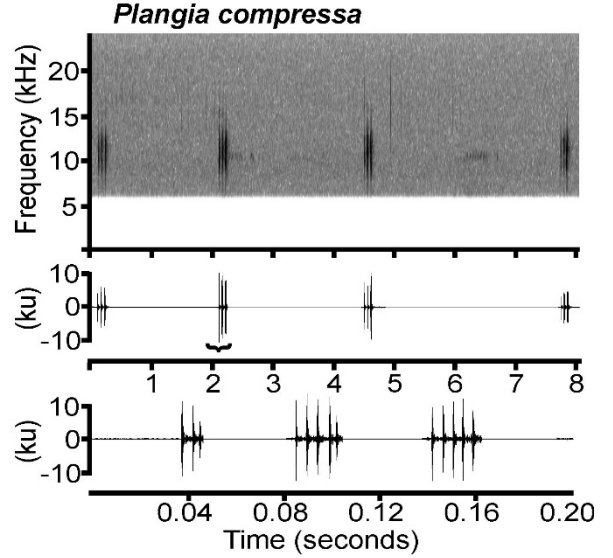
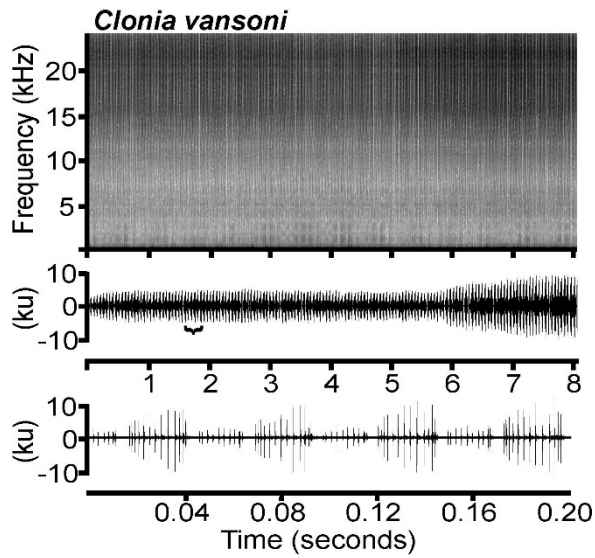
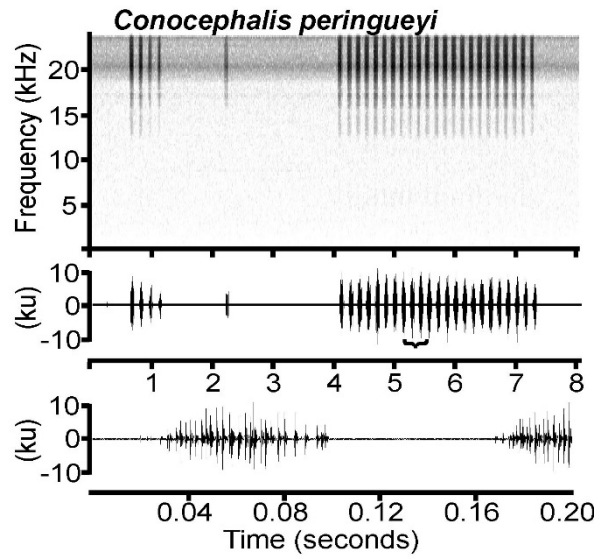
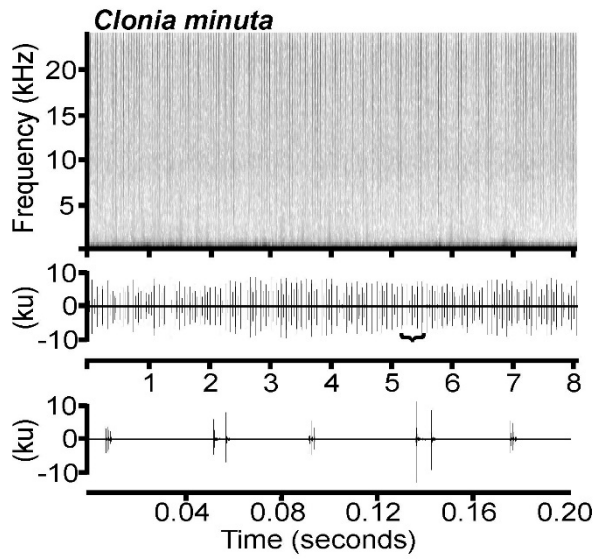
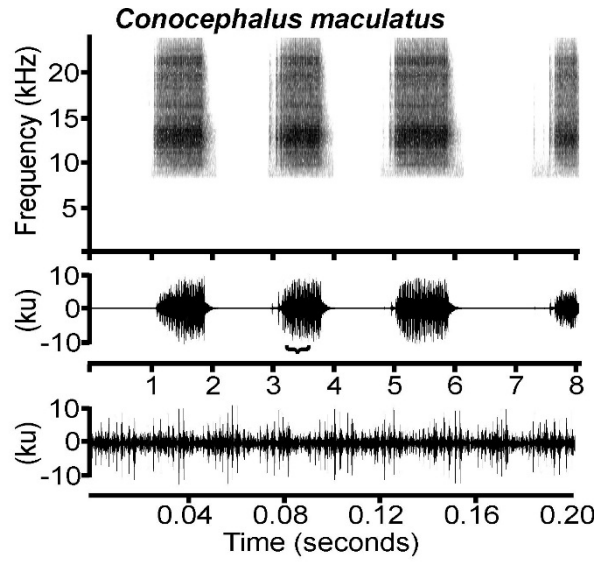
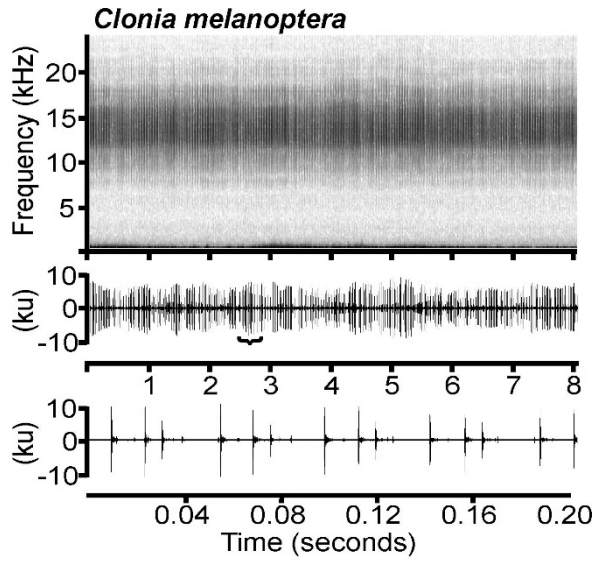


Figure 5.3. Acoustic signals of *Clonia melanoptera*, *C. minuta*, *C. vansoni*, *Conocephalus maculatus*, *C. peringueyi* and *Plangia compressa*. Spectrogram (above) displays frequency (kHz) versus time (s) with darker colours representing higher decibels (dB). Waveform associated with spectrogram (middle) displays signal structure of amplitude modulations over time (8 seconds). Marked section in middle waveform is expanded in time (0.2 seconds) to display distinct pulses within each chirp.

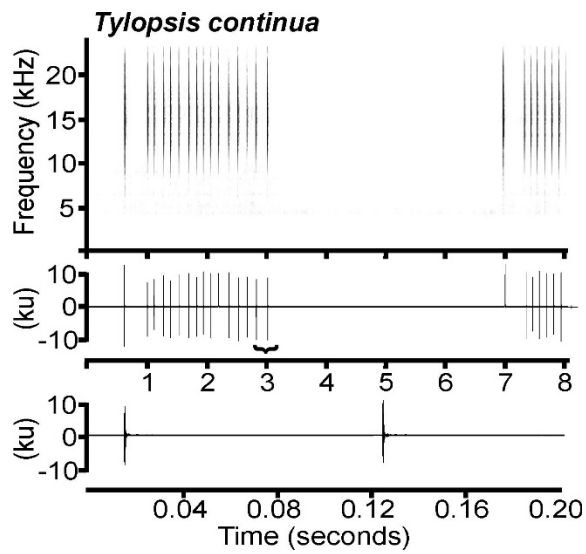


Figure 5.4. Acoustic signal of *Tylopsis continua*. Spectrogram (above) displays frequency (kHz) versus time (s) with darker colours representing higher decibels (dB). Waveform associated with spectrogram (middle) displays signal structure of amplitude modulations over time (8 seconds). Marked section in middle waveform is expanded in time (0.2 seconds) to display distinct pulses within each chirp.

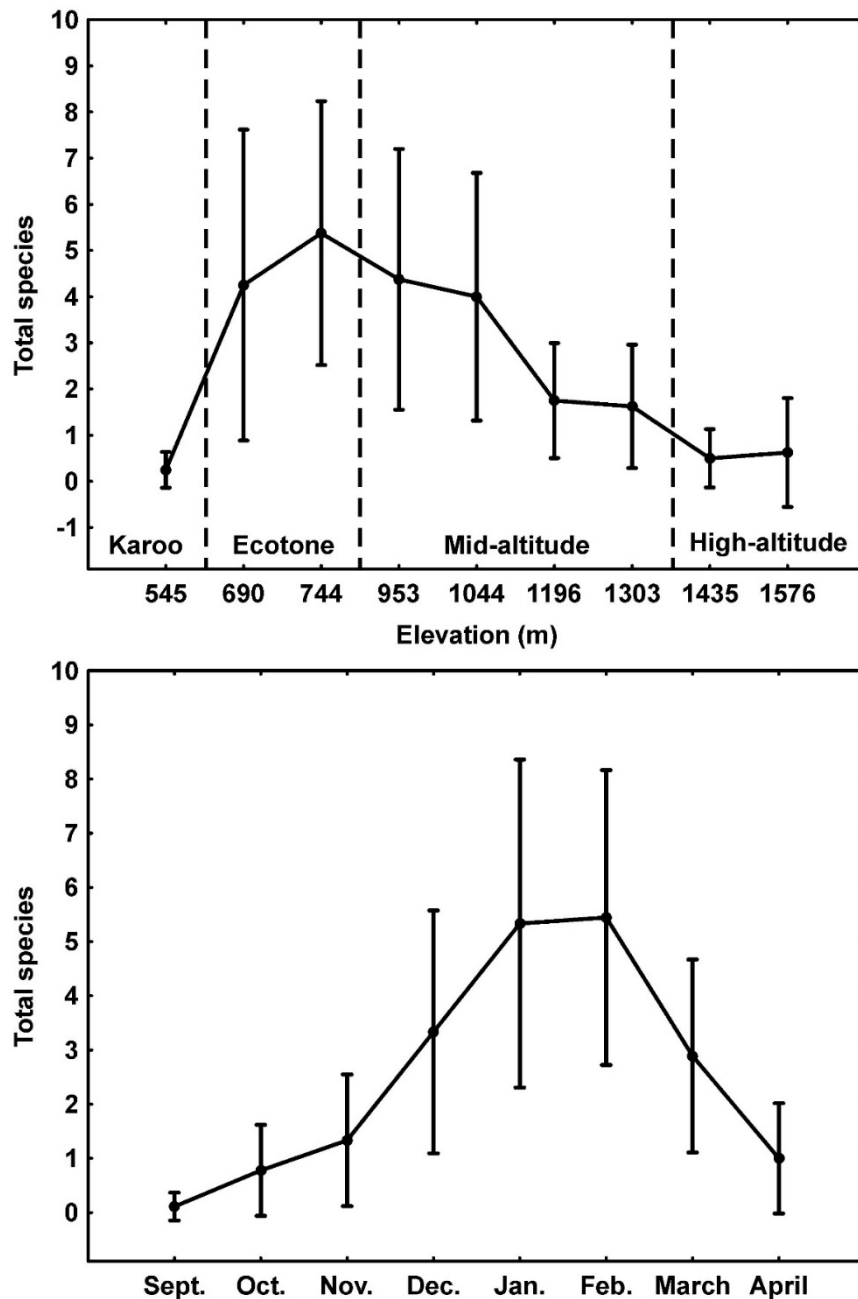


Figure 5.5. Acoustic diversity patterns of katydids (mean and standard error) across elevations (above) and seasons (below). Peak acoustic activity along the elevational gradient occurred between 690-1044 m asl. Below 690 m asl, transition to Karoo vegetation occurred, resulting in the lowest acoustic activity across the botanical and elevational gradient. Peak seasonal acoustic activity occurred in January-February. Higher acoustic diversity patterns was positively correlated with increasing temperatures.

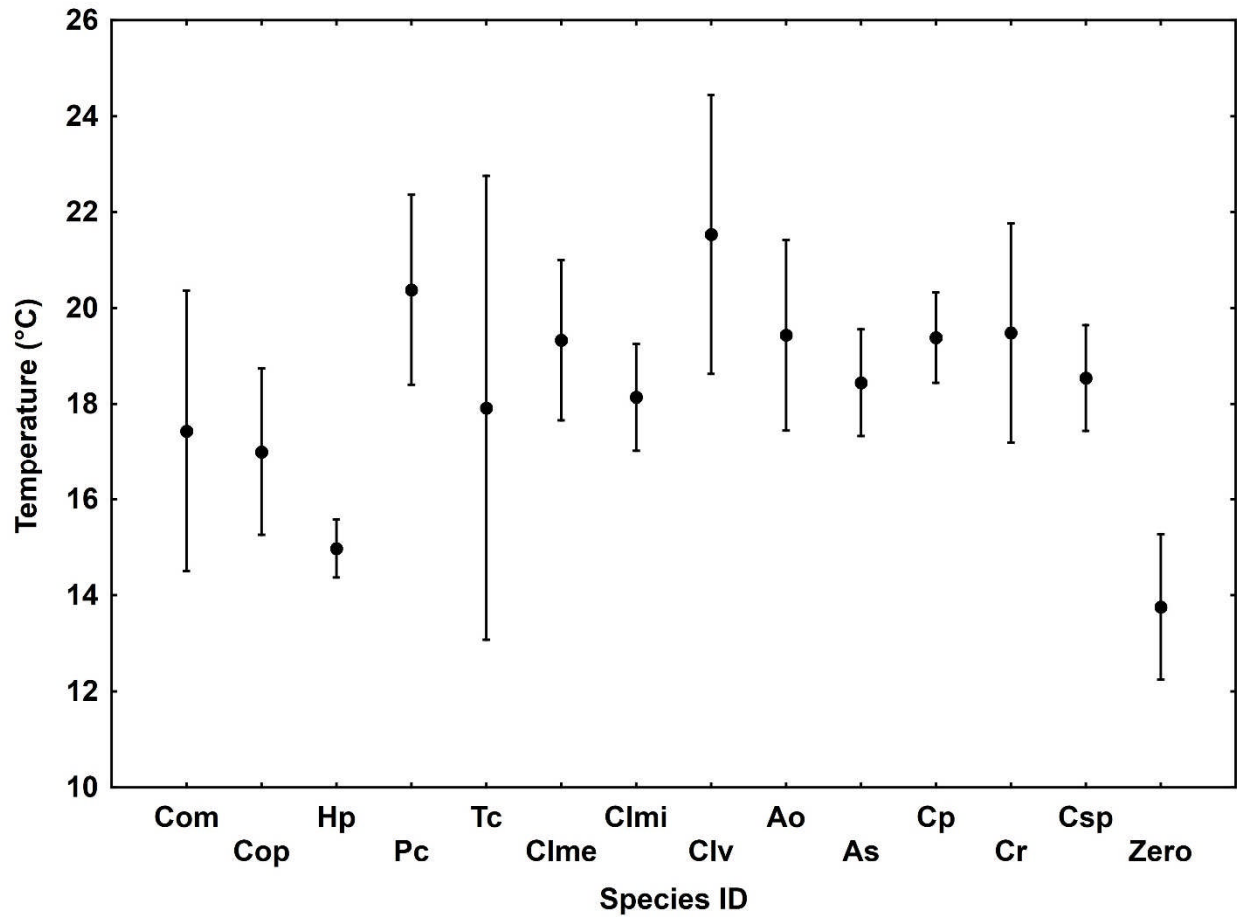


Figure 5.6. Species ID are listed in Table 5.1. Zero = no species recorded signaling. *Hetrodes pupus* was acoustically active within a lower temperature range than all other katydid species ($w = 102.79$, $p = 0.00$). At low mean temperature thresholds (Zero) species generally ceased signalling completely (mean and standard error: 13.75 ± 0.74 °C).

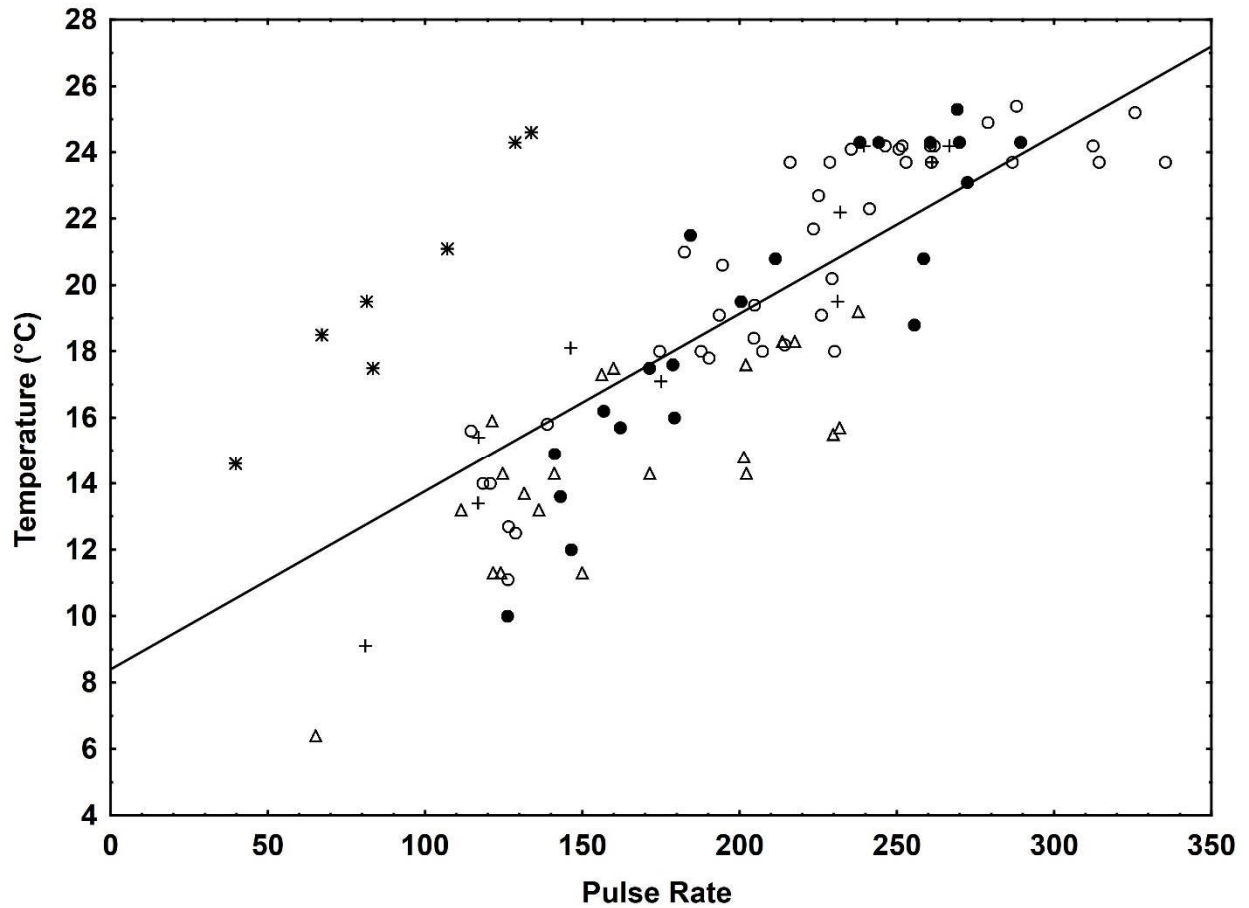


Figure 5.7. Variation in pulse rates (number of pulses per second) with temperature for *Ceresia pulchripes* (●), *C. rooi* (*), *Ceresia sp.* (○), *Alfredectes semiaeneus* (+) and *Hetrodes pupus* (Δ).

6. Acoustic prey and a listening predator: interaction between calling katydids and the bat-eared fox

Abstract

The bat-eared fox is an insectivorous, nocturnal predator that uses its characteristic large ears to detect sounds made by invertebrate prey. Behavioural observations of the bat-eared fox emphasize the significant role hearing plays in insect prey detection and localization. In turn, katydids are nocturnal insects which risk attracting predators by producing conspicuous signals for mate attraction and pair formation. To determine the interaction and potential level of predation between this listening, insectivorous predator with acoustically active katydids, behavioural observations and scat collection from bat-eared fox individuals were conducted in the Western Cape, South Africa. Acoustic surveys were also conducted to identify acoustic species within foraging areas of bat-eared foxes and assist with identifying their remains in scat. Results indicated bat-eared foxes have a broad, opportunistic diet. Despite the fox's hearing ability, and its use of sound to detect insect prey, acoustically active species were not consumed as part of the bat-eared fox diet. Instead, acoustically mute invertebrates such as most beetles and cockroaches were the dominant prey, followed by fruit and vertebrate prey, such as lizards, small mammals and nestlings. Although there was a diverse acoustic assemblage of katydids across the landscape, their absence within the bat-eared fox diet may reflect either a preference for other prey, or it suggests highly developed anti-predator behaviour found within this insect group where predation pressure has been a major evolutionary driver. It is likely that both apply, and currently bat-eared foxes find foraging on other prey more optimal.

Introduction

Katydid (Orthoptera: Ensifera: Tettigoniidae) are a remarkable group of Orthoptera, with a diverse range of species-specific calls, cryptic morphological traits and anti-predator behaviours (Greenfield 2002). This diversity has enabled them to occupy a broad range of habitats as omnivorous generalists or specialists, playing a critical role in food webs (Gwynne 2001). Yet despite being visually and behaviourally cryptic, katydids rely on acoustic signals for mate attraction, producing, propagating, receiving and reacting to acoustic sensory information (Greenfield 2002). Use of acoustic signals includes greater risk of attracting potential predators (Burk 1982; Zuk & Kolluru 1998), ranging from predatory invertebrates (Cade 1975; Burk 1982; Robert *et al.* 1992; Greenfield 2002) to a host of vertebrate predators (Walker 1964; Bell 1979; Sakaluk & Belwood 1984; Belwood & Morris 1987; Bailey & Rentz 1990; Morris *et al.* 1994) some of which may possibly have the ability recognize and locate specific acoustic signals. Predation risk has therefore been a likely important driver of camouflaged body designs and behaviour.

The bat-eared fox (Carnivora: Canidae: *Otocyon megalotis*) (Fig. 6.1) named for its distinctively large ear pinnae relative to body size, occurs across the arid, semi-arid and winter rainfall (fynbos) regions of southern Africa (Mackie & Nel 1989; Skinner & Smithers 1990; Nel & Maas 2013). Relatively small compared to other canids, its body size typically ranges from 3.0-5.3 kg, with lengths of 46-66 cm and with disproportionately large pinnae, 11.3-13.5 cm in length (Clark 2005). Although the large ears of the bat-eared fox serve a thermoregulatory function to dissipate heat (Sillero-Zubiri *et al.* 2004) and in communication (Clark 2005), their main function is to facilitate effective prey detection (Lamprecht 1979; Malcom 1986; Maas 1993; Larivière 2002; Clark 2005). The bat-eared fox has therefore frequently been observed to orientate its body and ear position relative to sounds produced by

potential prey such as invertebrates in order to locate and consume it (Lamprecht 1979; Malcolm 1986; Clark 2005). Furthermore, pinna also allows canids to rapidly pinpoint the exact location of a sound source.

Considered the only highly insectivorous member of canid family in southern Africa, the bat-eared fox, to a greater extent than other canids, has virtually given up preying on vertebrates to feed almost exclusively on insects (Nel 1978; Berry 1980; Mackie & Nel 1989; Skinner & Smithers 1990; Kuntzsch & Nel 1992; Maas 1993; Clark 2005; Nel & Maas 2013). Unlike other canids, the bat-eared fox has remarkable morphological adaptations for insectivory, lacking a carnassial shear, yet equipped with up to four pairs of extra molars capable of rapid masticatory movement (Maas 1993; MacDonald 2001; Klare *et al.* 2011a; Klare *et al.* 2011b). Their acute hearing and quick movement are also vital in insect prey capture (Maas 1993). Previous dietary studies found termites (*Hodotermes*) to be the main food item of the bat-eared fox (Bothma 1966; Nel 1978; Berry 1981; Koop & Velimirov 1982; MacDonald & Nel 1986; Skinner & Smithers 1990; Kok & Nel 1992; Maas 1993; Stuart *et al.* 2003; Klare *et al.* 2011a) corresponding to its insectivorous adaptations. However, within these same studies, an abundance of other insect prey were also recorded, including beetles (Coleoptera), grasshoppers, (Orthoptera: Acrididae) and cockroaches (Blattodea). One study in the northern savanna of South Africa also detected Heterodinae katydids (Orthoptera: Tettigoniidae) in the diet of five individuals (Berry 1981). In addition to insects, other dietary items recorded in these studies included much fruit, other plant matter, birds, rodents, lizards, snakes, snails, solifugids, scorpions, spiders, millipedes, and carrion. Geographical and seasonal shifts within the bat-eared fox diet also occurs, reflecting local prey availability (Kuntzsch & Nel 1992; Maas 1993; Klare *et al.* 2011a). For example, bat-eared fox diet in the Karoo consisted of mainly beetles and fruit which were locally abundant over winter and summer (Kuntzsch & Nel 1992). The picture that emerges within more recent studies indicates

that the bat-eared fox is not a termite specialist but an opportunistic forager with a broad dietary range consisting mostly of nocturnal insects, with this dietshifting according to prey availability (Kuntzsch & Nel 1992; Klare *et al.* 2011a; Nel & Maas 2013).

The bat-eared fox is also nocturnal and gregarious, displaying little territoriality (Nel 1978; Koop & Velimirov 1982; Nel & Bester 1983). Therefore, individuals of this species typically have overlapping ranges and forage in groups or in pairs depending on food availability (Koop & Velimirov 1982; Nel & Bester 1983; Malcolm 1986). Home range size also varies from 0.3-5.3 km², based on prey densities (Clark 2005). Breeding is seasonal and locally timed such that births coincide with peak insect densities (Malcolm 1986; Clark 2005).

Jonaskop, a plant species rich mountain within the Cape Floristic Region of South Africa, supports a substantial population of the bat-eared fox as well as a diverse and species rich assemblage of often abundant, acoustically active katydids. This situation would suggest that if sound emission by these insects were detectable by the fox, that katydids would form a major part of the fox's diet. The aim therefore, was to determine what prey the local bat-eared fox was consuming and whether katydids formed a significant part of this prey. The working hypothesis was that if katydids formed a major part of the prey, especially as they provide a substantial resource reward in terms of size, that they have not evolved an escape mechanism from fox predation. On the other hand, if katydids were absent or even formed an insignificant part of the fox's diet, it would indicate that, despite their acoustic emissions, they have become adapted to avoiding predation from the fox.

Methods

Study Area

The study was conducted on Jonaskop Mountain (33°58'00 S; 19°30'00 E; elevation 1646 m asl) within the east-west trending Riviersonderend Mountain Belt of the Cape Floristic Region, South Africa. The Jonaskop elevation gradient studied here spans 1200 m between the foothills and the summit from 446 m asl to 1646 m asl, across a distance of 6.3 km. Characterized by its rich, endemic plant diversity, Jonaskop is a protected area managed as an important catchment area for the Riviersonderend River.

Distinct vegetation types occur across the elevation gradient. Vegetation is classified as Karoo at 545 m asl, Ecotone from 690-744 m asl, Mid-altitude Sandstone Fynbos from 953-1303 m asl, and High-altitude Sandstone Dwarf Fynbos at 1576 m asl (Agenbag *et al.* 2008). The local area has a Mediterranean climate, with hot dry summers with decreasing temperatures with increasing elevation. Nocturnal summer temperatures (November-April) across the elevation gradient (mean \pm standard deviation) were (17.3 ± 4.7 °C).

Study design

Bat-eared fox scats were collected from November 2009-April 2010 by searching surroundings of observed rest sites. The bat-eared fox defecates communally in proximity to den and rest sites (Klare *et al.* 2011a), producing scats of unique cylindrical shape and size compared to other sympatric carnivores (Walker 1996; Klare *et al.* 2011a). Therefore, I am confident all scats used in analyses were from the bat-eared fox. Scats were dried at 50°C for 24 hours before being weighed. Scats were then gently rinsed through a 0.5 mm gauge sieve to retain identifiable parts of prey. Prey remains were then dried again for 24 hours, weighed, microscopically identified, and analysed for percentage of occurrence and percentage of mass.

While the frequency of occurrence method weighs the presence of small and large prey equally, it contributes useful information on presence of rare food items (Klare *et al.* 2011a). This provides a greater understanding of bat-eared fox behavior and its role as a dietary specialist or generalist (Klare *et al.* 2011b). Use of mass of prey items is recommended to provide additional information on prey intake (Klare *et al.* 2011b). Vertebrates were classified to order level, and arthropods were also classified to order, but when possible, to family or sub-family level. Seeds were identified by comparison with reference material collected in the study area. The small amount of unidentified organic matter was ignored as not being relevant to this study. Bat-eared fox surveys were also conducted to record foraging behaviour. Alternating nocturnal and diurnal surveys were conducted weekly for ± 8 hours across the elevation gradient to make behavioural observations and assess scat dispersion. This was done to include as many scats from as many individuals as possible across the range of vegetation types.

Acoustic sampling

Nocturnal acoustic sampling determined katydid species diversity. Sampling was conducted from early spring of September 2009 to early winter of April 2010, corresponding to start and end of katydid acoustic activity over the period of bat-eared fox scat collection. Acoustic surveys were conducted weekly for the duration of the study within three permanent 100 m² sites along the elevational gradient at 545, 690, 744, 953, 1044, 1196, 1303, 1435 and 1576 m asl. Acoustic sampling was done after dusk and before dawn, 20:00-05:00 hrs. Katydid signals were located through their signals (both infra- and ultrasonic), recorded, collected and identified. Voucher specimens of species were retained to confirm species identity and for identification of prey remains in bat-eared fox scat. Recordings were made of acoustic species using a Sennheiser ME 67 long gun microphone (Sennheiser, Germany) in conjunction with a Marantz PD660 solid state digital recorder (Marantz, USA). The Sennheiser microphone has a

frequency response sensitivity of <20 kHz and is highly directional, preventing sound colouration from off-axis sources, making it ideal for recording call structure with minimal background noise. The Marantz PD660 recording parameters were set to a sampling rate of 48 kHz with an uncompressed file format (.wav). A Pettersson D230 Ultrasound Detector (Pettersson, Sweden) was also utilized to help detect and locate katydids with high frequency signals. Acoustic recordings were analyzed using Raven Pro 1.5 (Cornel Laboratories, USA). As katydids utilize various frequency ranges to communicate, their center frequency, or the smallest discrete frequency which contains 50% of their total energy, was measured.

Results

Nocturnal katydid surveys recorded in 13 species in five subfamilies within Tettigoniidae (Table 6.1). Within half an hour after sunset, all katydid species signalled continuously for the duration of the evening hours. Spectrograms of nocturnal recordings were generally fairly quiet, punctuated with acoustic signals from katydids (Fig. 6.2). Center frequency (mean \pm standard deviation) for katydid signals was 17 ± 5.4 kHz, with species-specific center frequencies listed (Table 6.1). In addition to katydids, acoustic signals from crickets (Orthoptera: Ensifera: Gryllidae) (3.5-7.5 kHz), bladder grasshoppers (Orthoptera: Caelifera: Pneumoroidea) (1.5-3.1 kHz), beetles (Coleoptera: Carabidae: *Gonogenia tabida*) (3.5-75 kHz) and frogs (Anura: Brevicipitidae) (<4 kHz) were also detected. Acoustic signals were detected across the whole of the elevation gradient, and all acoustic species were detected within areas that the bat-eared fox was foraging.

Bat-eared fox individuals were only observed at night during diurnal and nocturnal surveys. During surveys, two pairs of bat-eared foxes were observed simultaneously, indicating a minimum of four individuals but an unknown maximum number of individuals. Behavior of

all individuals was generally skittish and they avoided human presence, limiting detailed behavioural observations. Nevertheless, on six separate occasions, they were briefly observed foraging in what appeared to be acoustic orientation by shifting pinnae, head and body towards sound source, tracking it and consuming the unidentified prey.

The number of scats examined was a good representation of the diet of the bat-eared fox on Jonaskop (Fig. 6.3). Diet consisted mainly of invertebrates (68%), fruit (24%) and vertebrate prey (8%) based on percentage of occurrence for all 34 scat samples (Fig. 6.4). Vertebrate prey included small mammals (4%), lizards (2%), and nestlings (2%). Fruit was identified as *Rhus* sp. Invertebrate prey items included cockroaches (Blaberidae) (21.3%) and beetles (Curculionidae (18.2%), Tenebrionidae (11.5%), Carabidae (7.5%), Scarabaeidae (3.1%), and Chrysomelidae (0.96%)). Orthoptera prey items included Acrididae (1.5%), Gryllacrididae (0.91%), and Stenopelmatidae (0.09%). Additionally, ants (2.6%) and termites (*Amitermes*) (0.38%) were also included in the diet.

Percentage of total dry mass of fragments produced similar results to percentage of occurrence (Fig. 7.5). In terms of dry mass, invertebrate prey was 64%, fruit 20%, and vertebrate prey 16%. Based on percentage of total mass, there were minor shifts in rank within some invertebrate prey items, with Curculionidae (22.7%) and Tenebrionidae (12.7%) becoming the dominant invertebrate prey items, followed by Blaberidae (9.3%).

Invertebrates from Blaberidae, Curculionidae and Tenebrionidae were overall the dominant prey items based on both percentage of occurrence (51% of total occurrence) and mass (44.7% of total mass). In contrast, Orthoptera species were a minor part of the bat-eared fox diet. Only species of Acrididae, Gryllacrididae and Stenopelmatidae (most of which are acoustically mute) were recorded in the fox's diet but not a single fragment from any species of the acoustically active Tettigoniidae was found in any bat-eared fox scat.

Discussion

Assessing bat-eared fox diet is essential for evaluating the species' role in the ecosystem and potential impact on prey populations. Results of this study emphasize that the bat-eared fox is not a termite specialist but has a broad opportunistic diet (Kok & Nel 1992; Kuntzsch & Nel 1992; Maas 1993; Berry 1981; Clark 2005; Klare *et al.* 2011a). Within the Cape Floristic Region, bat-eared fox diet reflects opportunistic nocturnal foraging on certain insect groups that are active at night, especially certain beetles and cockroaches. In addition, fruit and vertebrate prey were also consumed. Both frequency of occurrence and mass of prey items gave similar results, although mass likely overemphasizes the importance of insects, such as weevils with heavily armoured exoskeletons, and underemphasizes insects with light exoskeletons, such as cockroaches. While previous studies demonstrate high proportion of termites in the bat-eared fox diet, the low proportion of only *Amitermes* recorded here probably reflects the poor availability of this prey item, as termites in general are relatively scarce at these southern latitudes. The large proportion of fruit, mostly *Rhus* species, in the diet is well known (Berry 1981; Koop & Velimirov 1982; Nel & Mackie 1990; Kok & Nel 1992), and this food item even actively sought out (Kuntzsch & Nel 1992). The high abundance of *Rhus* trees at the study site likely provides an opportunistic food source during summer months. Predation on nestlings, lizards and small mammals, also has been previously reported (Berry 1981; Nel & Mackie 1990; Kok & Nel 1992) and further emphasizes the broad dietary range of this fox.

Here this fox was distinctly nocturnal and used acoustic orientation to locate prey. These observations are supported by previous research which emphasizes the importance of hearing in this fox for effective prey localization and capture (Lamprecht 1979; Malcom 1986; Maas 1993; Larivière 2002; Clark 2005). Bat-eared fox diet also reflects opportunistic foraging

on nocturnally active insect groups, which is consistent with their morphological adaptations for insectivory and previous dietary studies (Nel 1978; Berry 1981; Mackie & Nel 1989; Skinner & Smithers 1990; Kuntzsch & Nel 1992; Maas 1993; Clark 2005; Nel & Maas 2013).

Yet this nocturnal, insectivorous predator which uses sound to detect prey did not consume katydids, which announce their location acoustically and continually during nocturnal hours. Furthermore, bat-eared fox diet did not contain any other acoustically active species such as species of gryllids, bladder grasshoppers or frogs. This indicates that despite conspicuous proclamation songs, acoustic species were not consumed by this fox. The possible exception to this could be a carabid beetle (*Gonogenia tabida*) which produces acoustic signals (Grant *et al.* 2013). Beetle remains could only be identified to family level, making confirmation of the presence or absence of this species in the fox scat impossible. However, even if this species was consumed, it only a very small portion of the diet, as carabids in general were not a major food item.

For acoustic communication to be effective, signals need to reach the receiver with minimal loss of information (Greenfield 2002). To minimize acoustic interference and increase signal broadcast range, acoustic taxa often utilize different frequency ranges to communicate (Greenfield 2002). Signal perception therefore varies considerably across taxa (Greenfield 2002; Heffner & Heffner 2007). Hearing range for a related canid (*Canis lupis*) was determined to be 0.067-45 kHz (Heffner 1983; Heffner & Heffner 2007), suggesting that the communication frequencies that katydids and other acoustic species use are within the hearing range of the bat-eared fox. Furthermore, this fox foraged exactly where the acoustic species here were signalling. It is therefore reasonable to assume that this fox detected these acoustic signals, yet found foraging on non-acoustic species more optimal.

The nocturnal habits of moving vertebrate predators produces sound, and these acoustic species have hearing that in many cases may enable them to detect approaching predators. In the case of the European katydid *Platycleis intermedia*, it is so sensitive that it is able to detect the transient wave front produced even by the breaking of a single dry grass stem (Samways 1976a). What this means is that while certain katydid species at least broadcast their songs to their potential disadvantage in terms of predation, they also have good hearing to their advantage (in both male and female), with a particular sensitivity to the transients emanating from disturbance produced by vegetation or the ground as a vertebrate predator approaches. Nevertheless, while some katydids are visually and behaviourally cryptic, their acoustic signals for mate attraction are known to attract unwanted invertebrate and vertebrate predators (Walker 1964; Cade 1975; Bell 1979; Burk 1982; Sakaluk & Belwood 1984; Belwood & Morris 1987; Bailey & Rentz 1990; Robert *et al.* 1992; Morris *et al.* 1994; Zuk & Kolluru 1998; Greenfield 2002). But the point here is about proximity. A predator may approach but it must get close, especially at night, before it can lunge at its prey. To combat predators, katydids employ a range of defensive strategies including camouflage to blend into their background, protective spines or body armour, distasteful chemicals, and escape behaviour (Greenfield 2002). Response behavior takes place within 50 msec (Samways 1976b), making a safe getaway highly feasible, which appears to be case and honed by natural selection: move fast or die. Many katydids utilize high perch heights within dense vegetation, which not only helps propagate their acoustic signal but keeps them relatively safe from ground predators and provides dense foliage into which to jump when startled. However, there was also an abundance of large, ground dwelling katydids such as *Hetrodes pupus*. These katydids have heavy body armour and spikes to deter predators. Additionally, they are quick to terminate signals when disturbed, and then remain silent and motionless. This indicates that although katydids emit acoustic signals which may direct predators directly to them, through predation

pressure, they have evolved morphological and behavioural characteristics which provide protection from being eaten by the bat-eared fox.

Katydids in the Cape Floristic Region therefore either have effective strategies for avoiding predation from bat-eared fox predation and/or the fox simply prefers other prey items. It is likely that both have and/or do apply as they are not mutually exclusive. In short, it seems that some sort of equilibrium has been reached whereby the katydids are now virtually immune from predation from this fox, and that the fox finds foraging on other prey more optimal.

References

- Agenbag, L., Esler, K. J., Midgley, G. F. & Boucher, C. 2008. Diversity and species turnover on an altitudinal gradient in Western Cape, South Africa: base line data for monitoring range shifts in response to climate change. *Bothalia* 38:161–191.
- Bailey, W. J. & Rentz, D. C. F. 1990. The Tettigoniidae – their diversity and importance in biological research. In: Bailey, W. J. & Rentz, D. C. F. (eds.). *The Tettigoniidae: biology, systematics and evolution*. Crawford House Press, Australia.
- Bell, P. D. 1979. Acoustic attraction of herons by crickets. *Journal of the New York Entomology Society* 87:126–127.
- Belwood, J. J. & Morris, G. K. 1987. Bat predation and its influence on calling behavior in neotropical katydids. *Science* 238:64–7.
- Berry, M. P. S. 1981. Stomach contents of bat-eared foxes, *Otocyon megalotis*, from the northern Transvaal. *South African Journal of Wildlife Research* 11:28–30.
- Bothma, J. 1966. Notes on the stomach contents of certain Carnivora Mammalia from the Kalahari Gemsbok Park. *Koedoe* 9:37–39.
- Burk, T. E. 1982. Evolutionary significance of predation on sexually signalling males. *The Florida Entomologist* 65:90–104.
- Cade, W. H. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* 190:1312–1313.
- Clark, H. O. 2005. Mammalian species, *Otocyon megalotis*. *American Society of Mammalogists* 766:1–5.
- Grant, P. B. C., Roets, F., Samways, M. J. 2013. Sound characterization and structure of the stridulatory organ in *Gonogenia tabida* (Coleoptera: Carabidae). *Bioacoustics* (Accepted 2013).

- Greenfield, M. D. 2002. *Signalers and receivers. Mechanisms and evolution of arthropod communication*. Oxford University Press, Oxford.
- Gwynne, D. T. 2001. *Katydid and bush-crickets. Reproductive behavior and evolution of the Tettigoniidae*. Cornell University Press, London.
- Heffner, H. E. 1983. Hearing in large and small dogs: absolute thresholds and size of the tympanic membrane. *Behavioral Neuroscience* 97:310–318.
- Heffner, H. E. & Heffner, R. S. 2007. Hearing ranges of laboratory animals. *Journal of the American Association for Laboratory Animal Science* 46:21–23.
- Klare, U., Kamler, J. F. & MacDonald, D. W. 2011a. The bat-eared fox: A dietary specialist? *Mammalian Biology* 76:646–650.
- Klare, U., Kamler, J. F. & MacDonald, D. W. 2011b. A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review* 41:294–391.
- Kok, O. B. & Nel, J. A. J. 1992. Diet of the bat-eared fox in the Orange Free State and northern Cape Province. *South African Journal of Wildlife Research* 22:36–39.
- Koop, K. & Velimirov, B. 1982. Field observations on activity and feeding of bat-eared foxes. (*Otocyon megalotis*) at Nxai Pan, Botswana. *African Journal of Ecology* 20:23–27.
- Kuntzsch, V. & Nel, J. A. J. 1992. Diet of bat-eared foxes *Otocyon megalotis* in the Karoo. *Koedoe* 35:37–48.
- Lamprecht, J. 1979. Field observations on the behaviour and social system of the bat-eared fox *Otocyon megalotis* Desmarest. *Zeitschrift für Tierpsychologie* 49:260–284.
- Larivière, S. 2004. Mammalian species, *Vulpes zerda*. *American Society of Mammalogists* 714:1–5.
- Maas, B. 1993. *Behavioural ecology and social organisation of the bat-eared fox in the Serengeti National Park, Tanzania*. Ph.D thesis, University of Cambridge. UK.
- MacDonald, D. 2001. *The encyclopedia of mammals*. Andromeda Oxford, Oxfordshire. UK.

- MacDonald, J. T. & Nel, J. A. J. 1986. Comparative diets of sympatric small carnivores. *South African Journal of Wildlife Research* 16:115–121.
- Mackie, A. J. & Nel, J. A. J. 1989. Habitat selection, home range use, and group size of bat-eared foxes in the Orange Free State. *South African Journal of Wildlife Research* 19:135–139.
- Malcom, J. R. 1986. Socio-ecology of bat-eared foxes (*Otocyon megalotis*). *Journal of Zoology* 208:457–469.
- Morris, G. K., Mason, A. C., Wall, P. & Belwood, J. J. 1994. High ultrasonic and tremulation signals in neotropical katydids (Orthoptera: Tettigoniidae). *Journal of Zoology* 233:129–163.
- Nel, J. A. J. & Bester, M. H. 1983. Communication in the southern bat-eared fox *Otocyon megalotis megalotis* (Desmarest) in the Kruger National Park. *Koedoe* 13:23–27.
- Nel, J. A. J. & Maas, B. 2008. *Otocyon megalotis*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Accessed 31 October 2013.
- Nel, J. A. J. & Mackie, A. J. 1990. Food and foraging behaviour of bat-eared foxes in the south-eastern Orange Free State. *South African Journal of Wildlife Research* 20:162–166.
- Nel, J. A. J. 1978. Notes on the food and foraging behaviour of the bat-eared fox *Otocyon megalotis*. *Bulletin of the Carnegie Museum of Natural History* 6:132–137.
- Robert, D., Amoroso, J. & Hoy, R. R. 1992. The evolutionary convergence of hearing in a parasitoid fly and its cricket host. *Science* 258:1135–1137.
- Sakaluk, S. K. & Belwood, J. J. 1984. Gecko phonotaxis to cricket calling song: a case of satellite predation. *Animal Behaviour* 32:659–662.
- Samways, M. J. 1976a. Effect of vegetation noise on the song behaviour of *Platypleis intermedia* (Orthoptera, Tettigoniidae). *Biophon* 4:4–8.

- Samways, M. J. 1976b. Song modification in the Orthoptera. I. Proclamation songs of *Platycleis* spp. (Tettigoniidae). *Physiological Entomology* 1:131–149.
- Sillero-Zubiri, C., Hoffmann, M. & MacDonald, D. C. 2004. *Candida: foxes, wolves, jackals and dogs. Status survey and conservation action plan*. IUCN/SSC Canid Specialist Group, IUCN, Gland.
- Skinner, J. D. & Smithers, R. H. N. 1990. *The mammals of the southern african subregion*. University of Pretoria, Pretoria, South Africa.
- Stuart, C. T., Stuart, T. & Pereboom, V. 2003. Diet of the bat-eared fox *Otocyon megalotis*, based on scat analysis, on the western escarpment, South Africa. *Canid News* 6:1–5.
- Walker, T. J. 1964. Experimental demonstration of a cat locating orthopteran prey by the prey's calling song. *The Florida Entomologist* 47:163–165.
- Zuk, M. & Kolluru, G. 1998. Exploitation of sexual signals by predators and parasitoids. *Quarterly Review of Biology* 73:415–438.

Table 6.1. Katydid (Orthoptera: Ensifera: Tettigoniidae) species recorded at the study site. Center frequency (kHz) is listed for all species.

	subfamily	species	authority	kHz
1	Conocephalinae	<i>Conocephalus maculatus</i>	Le Guillou, 1841	20.0
2	Conocephalinae	<i>Conocephalus peringueyi</i>	Uvarov, 1928	20.0
3	Hetrodinae	<i>Hetrodes pupus</i>	(Linné, 1758)	10.9
4	Phaneropterinae	<i>Plangia compressa</i>	(Walker, 1869)	10.5
5	Phaneropterinae	<i>Tylopsis continua</i>	(Walker, 1869)	15.4
6	Saginae	<i>Clonia melanoptora</i>	(Linné, 1758)	12.0
7	Saginae	<i>Clonia minuta</i>	(Haan, 1842)	21.0
8	Saginae	<i>Clonia vansoni</i>	Kaltenbach, 1971	20.3
9	Tettigoniinae	<i>Aprosphyllus olszanowskii</i>	Naskrecki, 1994	18.1
10	Tettigoniinae	<i>Alfredectes semiaeneus</i>	(Serville, 1838)	13.0
11	Tettigoniinae	<i>Ceresia pulchripes</i>	(Péringuey, 1916)	17.2
12	Tettigoniinae	<i>Ceresia rooi</i>	Grant, 2013	31.1
13	Tettigoniinae	<i>Ceresia</i> sp.	Grant, 2013	14.7

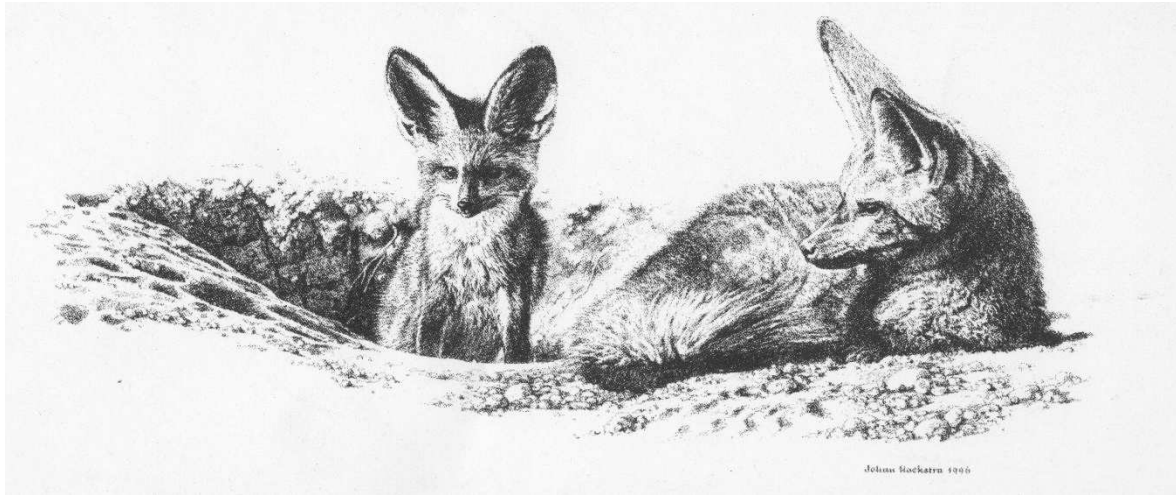


Figure 6.1. The bat-eared fox by Johan Hoekstra, 1996.

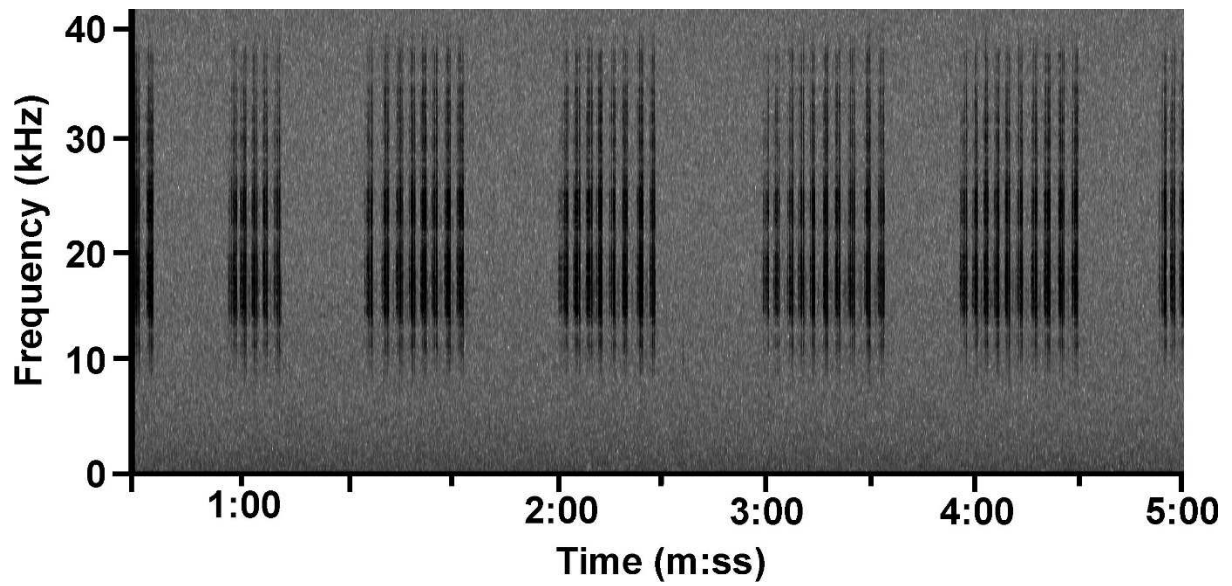


Figure 6.2. This spectrogram (above) displays frequency versus time with darker colour representing higher decibels (dB). It represents a typical nocturnal soundscape at the study site i.e. generally fairly quiet, punctuated with acoustic signals from katydids, in this case *Ceresia pulchripes*.

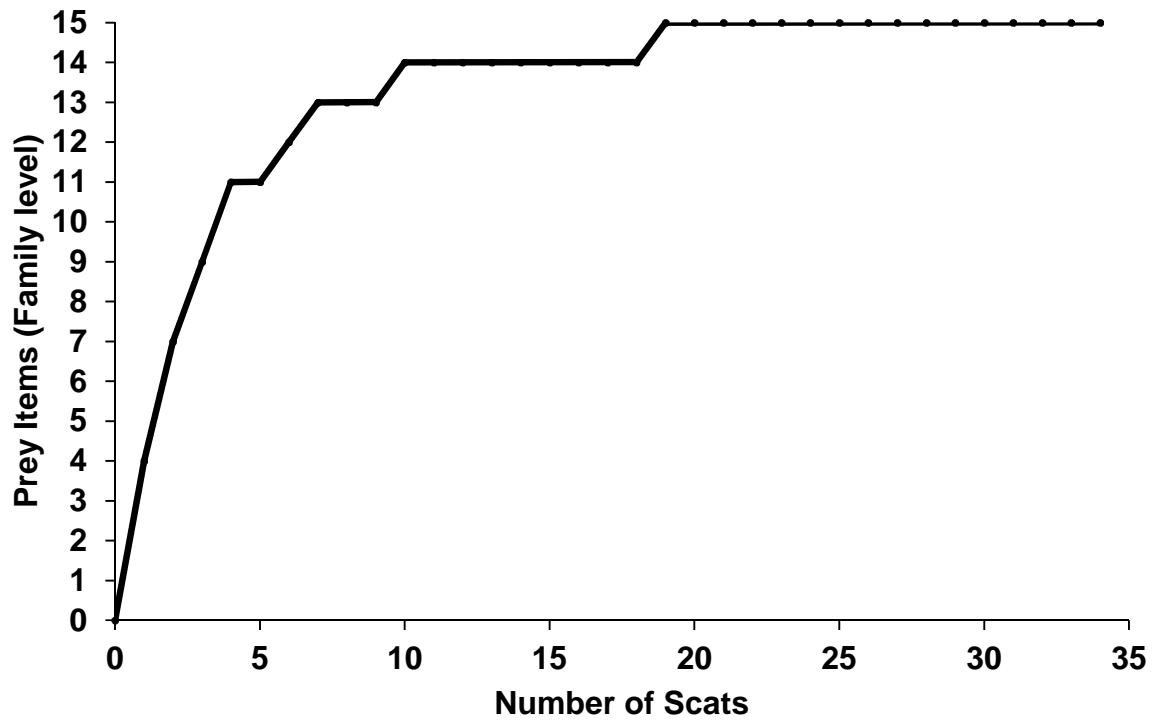


Figure 6.3. Cumulative diversity of prey items against the number of scats.

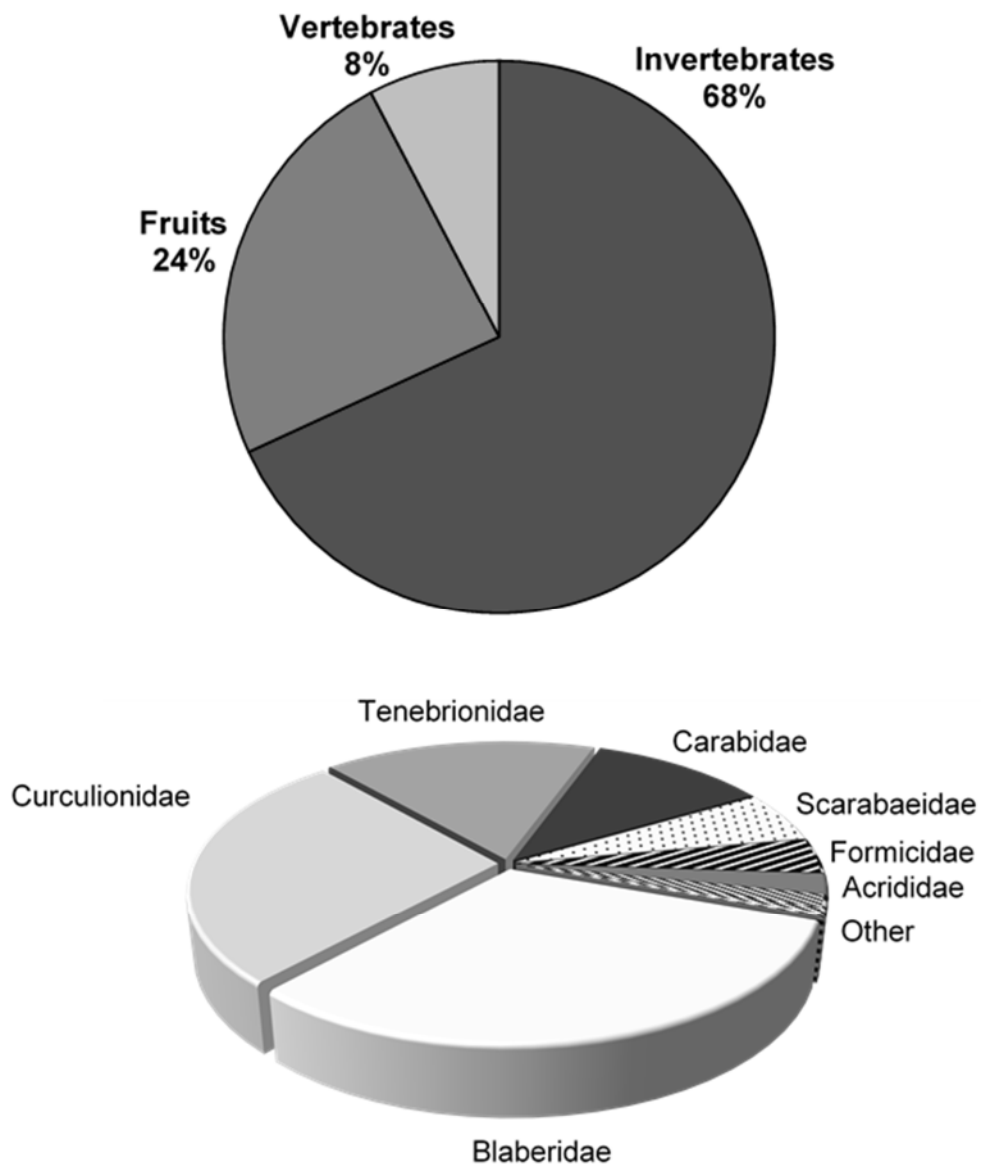


Figure 6.4. Diet of the bat-eared fox based on percentage of occurrence of food items. Total diet above. Breakdown of the 68% invertebrate diet below. 'Other' comprises Gryllacrididae, Termitidae, Chrysomelidae and Stenopelmatidae.

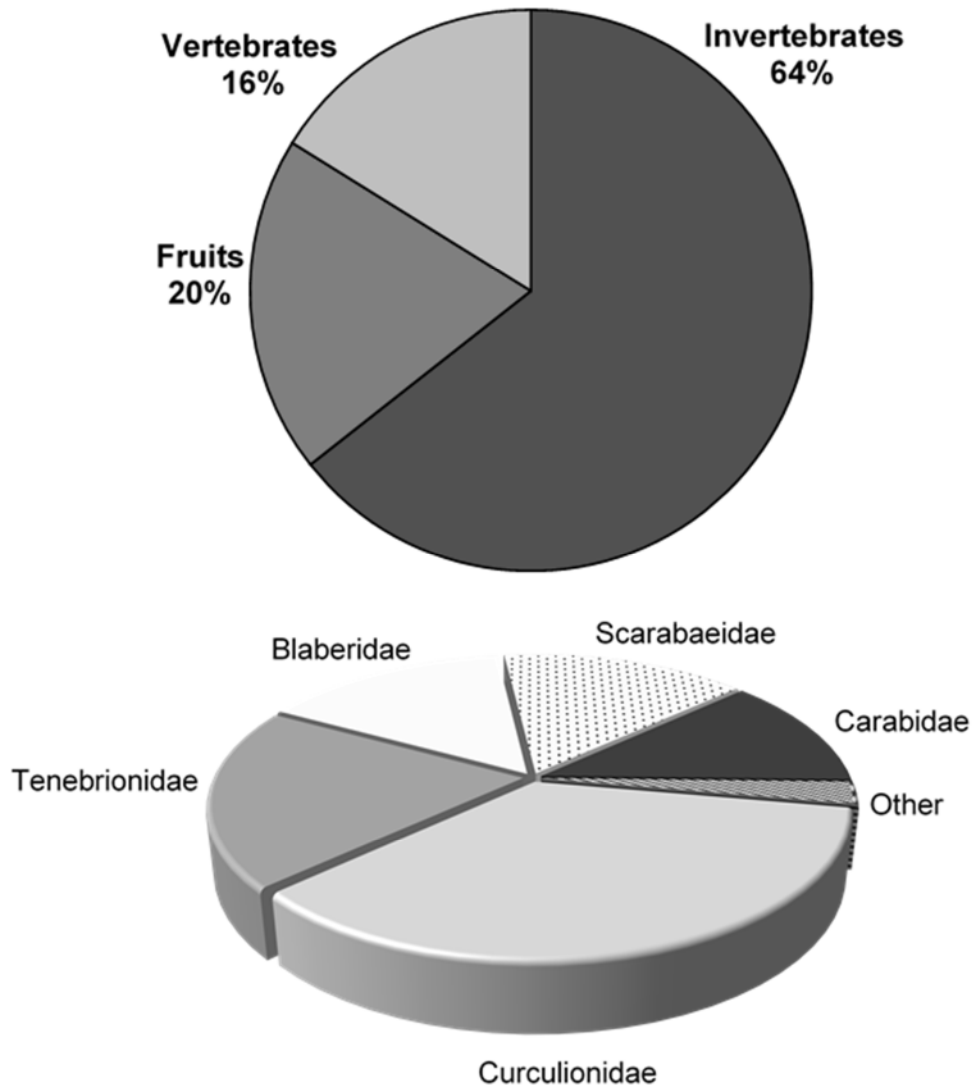


Figure 6.5. Diet of the bat-eared fox based on mass of the food items. Total diet above. Breakdown of the 64% invertebrate diet below. 'Other' comprises Acrididae, Gryllacrididae, Termitidae, Formicidae, Stenopelmatidae, and Chrysomelidae.

**7. Sound characterization and structure of the stridulatory organ in *Gonogenia tabida*
(Coleoptera: Carabidae)**

Abstract

A new stridulatory structure for the Carabidae, based on morphology and acoustics of the Southern Hemisphere genus *Gonogenia*, is described. Sound is produced by abdomino-elytral movement between the surfaces of two projections on the inner lateral surface of the elytra (*pars stridens*) against the surfaces of two opposing projections from the outer edges of the first abdominal sternite (*plectrum*). While both males and females had stridulatory organs, only males were recorded producing signals. Signals were broad spectrum extending into ultrasound frequency ranges (3.5-75 kHz). Signals were produced continually by male *G. tabida* individuals while mobile in a localized area and likely represent a form of intraspecific communication, due to absence of observed potential disturbance stimuli.

Introduction

Sound and the ability to detect sound waves are evolutionary adaptations allowing organisms to propagate and receive acoustic sensory information invisibly within their environment. Although not without inherent risks and constraints, the advantages have driven development of acoustic communication in a diversity of forms in many aquatic and terrestrial organisms.

Among insects, acoustic signals are a major mode of communication (Alexander *et al.* 1963; Bailey 1991; Hirschberger 2001; Greenfield 2002). Within insects, beetles (Coleoptera) have the greatest diversity of stridulatory sound producing organs containing at least 14 types with multiple convergent origins ranging across and within 30 families located on the cephalic, thoracic, abdominal, leg, or elytra regions (Arrow 1904; Arrow 1942; Dumortier 1963; Barr 1969; Aiken 1985; Lyal & King 1996; Hirschberger 2001; Kasper & Hirschberger 2005; Wessel 2006). Within the Carabidae, stridulatory organs have been described on the abdominal, leg and elytra regions (Wessel 2006). Due to the diversity of forms within stridulatory structures, labelling specific structures based on morphology can sometimes be subjective. Structures are therefore often described based on their function, where the *plectrum* is considered the mobile portion of the system or excitatory structure that rubs against the *pars stridens*, causing the *pars stridens* to vibrate and produce sound (Barr 1969; Panneton *et al.* 2005). Within this study stridulatory organs consist of mobile parallel ridges (*plectrum*) that move across non-mobile, sclerotic lamellae projections with sharp tips, defined as the *pars stridens*, producing mechanical signals (Wessel 2006). Sound production in carabid beetles is known to extend over a wide range of frequencies up to 80 kHz, with a diverse range of temporal amplitude modulations (Wessel 2006).

Although a large amount of morphological knowledge on beetle stridulatory organs exists, less is known about its function and ethological context (Wessel 2006). Across beetle

families a great deal of variability also exists between which gender produces signals and the associated behavioural roles of these signals (Barr 1969; Lyal & King 1996; Fleming *et al.* 2013; Mankin *et al.* 2013). Presence of the same structure in both males and females does not necessarily mean identical use (Hirschberger 2001; Greenfield 2002). In most acoustically active insects males are observed to be the dominant callers. Calling involves higher energy consumption and increased risk of predation, features that are assumed to select against elaborate acoustic emissions in females (Bailey 1991). While females generally signal less frequently (Mini & Prabhu 1990), they do often answer or even duet with the male, showing a call-response behaviour (von Helversen & von Helversen 1983; Claridge 1985; Hirschberger 2001). It is therefore believed that the dominant function of acoustic communication is sexual advertising and pair formation (Rudinsky & Michael 1972; Mini & Prabhu 1990; Hirschberger 2001; Greenfield 2002; Yack 2004; Kasper & Hirschberger 2005). Sound production in beetles has long been stressed as an important component of mating behaviour, shaped by sexual selection (Darwin 1877; Hirschberger 2001; Wessel 2006) and serves as an efficient species-specific mate recognition system preventing interspecific matings (Kasper & Hirschberger 2005; Wessel 2006).

Acoustic signals in beetles may also function in aggression or aggregation behaviour for environmental resources (Claridge 1974; Lewis & Cane 1990; Greenfield 2002; Wessel 2006; Howard *et al.* 2008). Resource partitioning patterns have also been described in several studies in which competition for food or resources is used to explain distribution (Niemela 1993; Lovei & Sunderland 1996). How conspecifics perceive intraspecific communication is still poorly understood in general. Furthermore, while tympanal hearing has been described for a few species within two families, our knowledge on mechanisms and extent of hearing across beetle groups is also severely limited (Spangler 1988; Forrest *et al.* 1997; Yager 1999; Yager *et al.* 2000; Wessel 2006). Interspecific disturbance stridulation as a startle mechanism has also

been demonstrated to deter potential beetle predators (Freitag & Lee 1972; Claridge 1974; Masters 1979; Buchler *et al.* 1981; Forrest *et al.* 1995; Forrest *et al.* 1997; Lovei & Sunderland 1996). Stridulation temporarily startles predators, eliciting prey release allowing stridulating beetles to escape predators more readily than non-stridulating beetles (Lewis & Cane 1990).

During recent nocturnal recording and identification of katydid (Tettigoniidae) acoustic signals associated with endemic vegetation of the Cape Floristic Region (CFR) of South Africa, a characteristic sound that could not be assigned to any of the study organisms was commonly encountered. In follow-up surveys it was determined that individuals of a Carabidae beetle (*Gonogenia tabida* Fabricius) were responsible for producing these acoustic signals. Sound production in the Carabidae is fairly well categorised for members of the family from the Northern Hemisphere, but are largely unknown from the Southern Hemisphere (Wessel 2006). Within Africa, sound production by carabid beetles was thought to be restricted to Tiger beetles (*Mantichora*) (Cincindelinae) (Pearson 1988).

The genus *Gonogenia* Chaudoir contains six species that are confined to southern Africa. Individuals are fairly common throughout the drier regions of South Africa and Namibia. *Gonogenia* species are nocturnal, apterous carabids, with the most commonly encountered western CFR species being *G. tabida* (Fig 7.1 A). *Gonogenia rugosopunctata* Thunberg is also fairly commonly occurs in the eastern regions of the CFR.

In the present study, sound producing organs of *G. tabida* based on morphology are described. Additionally, the sound made by these beetles was characterized under natural field conditions where beetles were not harassed.

Methods

Morphological characterization

Ten individuals of *G. tabida* were collected from Jonaskop, Villiersdorp, South Africa (33°58'00 S; 19°30'00 E; elevation 1646 m asl) on 9 February 2011, from 21:00 to 02:00 hrs. Individuals were located within a 50,000 m² quadrant through their acoustic signals, with the exception of three individuals which were encountered visually. After capture, individuals were kept separately in glass tanks (20 cm x 30 cm) with vegetation and substrate taken from the site of capture to simulate natural conditions. These individuals were visually observed and acoustically monitored for sound production for a period of two weeks under similar environmental and temporal settings as the field conditions in which they were acoustically active. After which, they were killed by freezing for sex determination via dissection and morphological evaluation of stridulatory organs. The position of the stridulatory organs was determined with a dissection microscope and studied in detail using a Leo 1430VP Scanning Electron Microscope (SEM). For the SEM studies, the dried arthropods were dissected and mounted onto stubs using double-sided carbon tape and sputter coated with gold-palladium using standard methods.

Acoustic characterisation

Acoustic signals from 4 of the 10 *G. tabida* individuals were recorded under natural field conditions before capture. Individuals were detected and located through their acoustic signals and recorded approximately 2 m away to avoid disturbance. A series of three recordings were made of approximately 1 min in duration for each individual. Temperature was recorded with each acoustic recording. Recordings were made using a Sennheiser (Sennheiser, Germany) ME 67 long gun microphone in conjunction with a Marantz PD660 (Marantz, USA) solid state

digital recorder. The Sennheiser microphone has a frequency response sensitivity of up to 20 kHz and prevents sound colouration from off-axis sources, making it ideal for recording call structure with minimal background noise. The Marantz PD660 recording parameters were the same for all recordings, set to a sampling rate of 48 kHz with an uncompressed file format (.wav). Due to the limited response frequency of the Sennheiser microphone, a Pettersson D230 Ultrasound Detector (Pettersson, Sweden) was also utilized to determine upper frequency limits of signals. The Pettersson D230 contains an electret microphone with a frequency response sensitivity up to 120 kHz. Acoustic recordings were analysed using Raven Pro (Cornel Laboratories, USA). No filtering of acoustic recordings was carried out. Bioacoustic signals are comprised of several of elements. Pulses are the smallest discrete amplitude modulations within signals and can form discrete groups known as chirps (Greenfield 2002). Chirps, comprised of multiple pulses, can occur singularly or within groups known as trills (Greenfield 2002). The gaps between pulses, chirps and trills are referred to as intervals. For each recording, the number of trills within 30 seconds were counted along with the number of chirps per trill and the number of pulses per chirp. Pulse, chirp and trill durations and interval durations, were also measured. Minimum, maximum and center frequency, the smallest discrete frequency which contains 50% of total energy, were calculated by Raven Pro, for each recording. Waveforms, spectrograms were produced to measure and visually display acoustic signals of *G. tabida*.

Results

Morphological characterization

The ten collected individuals consisted of 8 males and 2 females. The three individuals located and collected by visual encounter consisted of 2 females and 1 male. Unlike the other seven individuals, which were located by their acoustic signals, these individuals were not observed producing acoustic signals. The seven male individuals were observed producing sound in the field by protracting abdominal segments against fused elytra. Yet in captivity, none of the 10 individuals produced acoustic signals. Dead males and females both produced a distinct sound resembling normal stridulation when physically manipulated, by pressing gently on elytra and abdomen. Further examination revealed both male and female *G. tabida* had identical stridulatory organs. The sound produced can be heard as a series of ‘chirping’ sounds. Sound is produced mechanically through abdomino-elytral movement by rubbing together two projections – one from abdomen (*plectrum*) and another from elytra (*pars stridens*) (Fig. 7.1 B). The structure on the elytra was labelled as the *pars stridens* as it is non-mobile and has distinctive tooth like structures, commonly associated with this type of sound producing structure (Wessel 2006). Comparatively, the structure on the abdomen was mobile, moving across the non-mobile structures on the elytra, containing distinctive parallel ridges, a feature more characteristic of *plectrum*, and was therefore labelled as such. The fused elytra has two small concave projections on the ventral side, just below the lateral edge (C, E). The convex projects of the *plectrum* on the abdominal side (D, F) are formed by the outer edge of the first abdominal sternite and fit into these concave projections and move against them. The concave projections of the *pars stridens* curve over the dorsal side of the abdomen underneath the elytra between the first and second abdominal spiracles.

Scanning electron micrographs at low magnification revealed that the stridulatory surface on the elytra (*pars stridens*) seems to be covered with small scale-like structures (G). Under high magnification these scale-like structures can be seen as a series of sclerotic lamellae projections with sharp tips (I). Each projection is ca. 5 μm long and ca. 2 μm wide at base. These are arranged in rows that are ca. 2 μm apart and with ca. 4 μm interspacing. Directly opposite and opposing this surface is the abdominal projection that seems to be covered with a series of very fine, parallel lines (*plectrum*) under medium magnification (H). Under high magnification these can be identified as a series of ridges ca. 2 μm apart (J). Each ridge is incised at a regular interval of ca. 8 microns, with the incised angle at 45 degrees. This arrangement results in a series of sharp points. The positions of these alternate between each row to form rows of incisions over the entire surface (at a right angle to the ridges) at ca. 4 μm spacing.

Acoustic characterisation

Male individuals of *G. tabida* were prolific signallers, continually producing sound when mobile, constantly moving in random directions within a small area of a few square meters. Care was taken not to disturb individuals and no sign of predators or other potential disturbance were observed. No other *G. tabida* individuals were observed or heard in the immediate area surrounding the signalling individuals. Temperature did not vary greatly and had a mean and standard deviation (SD) of $24.3 \pm 0.7^\circ\text{C}$. Across all acoustic recordings ($n = 12$; four individuals), there was a mean and standard deviation (SD) of 7.2 ± 3.05 trills or group of chirps within each 30 second (s) time period ($n = 63$ trills; four individuals). Trills were 1.51 ± 0.93 s in duration with intervals between them of 1.88 ± 0.16 s ($n = 63$ trills; four individuals). The number of chirps per trill ranged from 1 to 11 with a mean and SD of 4.9 ± 2.2 ($n = 182$ chirps; four individuals). Duration of chirps were 0.16 ± 0.02 s, with intervals of 0.09 ± 0.01 s ($n = 182$

chirps; four individuals). The number of pulses comprising each chirp was 66.5 ± 11.7 with durations of 0.0001 ± 0.0003 s and intervals of 0.0012 ± 0.0008 s ($n = 292$ pulses; four individuals). Frequency analysis across all recordings ($n = 12$; four individuals) showed *G. tabida* produced broad spectrum acoustic signals ranging from 3.5 to 23.9 kHz, with center frequencies of 8.9 ± 1.3 kHz. However, the frequency response of the Sennheiser microphone limits the ability to record frequency ranges over 20 kHz. Therefore the measured center frequency of 8.9 ± 1.3 kHz, only provides information of the smallest discrete frequency containing 50% of the total energy within the <20 kHz range and does not reflect the center frequency of signal across its entire frequency range. In order to determine upper extent of *G. tabida* signals, frequencies >20 kHz were measured by the Pettersson D230. It was determined that *G. tabida* produced broadband signals extending into ultrasound frequencies of 75 kHz. Waveform and spectrogram were created to visually display a typical acoustic signal of *G. tabida* (Fig. 7.2).

Discussion

Acoustic communication can function in sexual advertisement, courtship, aggression, aggregation and defence (Greenfield 2002; Wessel 2006). However, the ecological context of the acoustic signals produced by *G. tabida* individuals remains unknown. While interspecific disturbance stridulation cannot be ruled out, individuals were located by their signals, and no potential predators or other disturbances were observed. Furthermore, individuals signalled continuously while moving within a localized area. Therefore, it is likely that their acoustic signals have an intraspecific context such as sexual advertisement, or agnostic behaviour such territorial defence. It is common for only males to signal in sexual advertisement due to higher energy demands and risk of predation, while females often signal in response or even duet with

males (Hirschberger 2001; Greenfield 2002). Although females were not recorded or observed producing acoustic signals, as they have identical stridulatory structures as males, it is possible they are capable of stridulation within certain contexts. What those contexts might be and their potential influence on conspecifics remains unclear. Based on conspecific signal detection, crickets and other orthopterans also space themselves across the landscape within suitable habitat (Howard *et al.* 2008). This type of agnostic behaviour could also explain male signalling within localized areas by *G. tabida* individuals. Therefore their acoustic signals may function in agnostic territorial defence of environmental resources (Clarridge 1974; Greenfield 2002; Wessel 2006). While a large amount of morphological knowledge on beetle stridulatory organs and tympanal hearing organs exist, the ethological context of intraspecific communication, is still poorly understood (Wessel 2006).

In the field, male individuals were prolific signallers, all recorded under similar temperature ranges. As it is commonly accepted that weather conditions and temperature affect calling rates in other insect groups (Edes 1899; Franklin *et al.* 2009), recording individuals under consistent conditions allows for unbiased signal analysis. Unfortunately, while in captivity, none of the individuals produced acoustic signals, limiting further understanding of the ethological context of signals. As they utilize audible broad spectrum acoustic signals, it is unlikely signals were produced unnoticed. It is more likely that captive conditions failed to match natural field conditions, altering behaviour and preventing acoustic communication to occur.

Various beetle species, including carabids have signals which contain ultrasound frequencies, even up to 80 kHz (Claridge 1974; Fleming *et al.* 2013) and the ability to detect ultrasound (Yager *et al.* 2000; Forrest *et al.* 1997; Hirschberger 2001). Yet the true extent of sound production and hearing across beetle families is poorly described. Typically, the

spectrum of the conspecific signals generally matches the best sensitivity of the receiver (Stumpner & von Helversen 2001). However, detection of ultrasound has also been attributed to predator avoidance, especially for flying beetles to evade capture by echolocating bats (Yager *et al.* 2000). As ground dwelling beetles, *G. tabida* individuals use of broadband signals (3.5-75 kHz) likely contributes to signal propagation and reception by conspecifics as they are less affected by attenuation from habitat structure, particularly at higher frequencies (Greenfield 2002).

Within other carabid beetles, adults have been known to stridulate actively when disturbed or handled (Claridge 1974). Dead males and females both produced a distinct sound resembling natural stridulation when physically manipulated, by pressing gently on elytra and abdomen. Sound produced by physical manipulation of dead beetles was similar to sound produced by live beetles in natural settings. Observations in the field show sound emission associated with protraction of apical abdominal segments, against fused elytra (Claridge 1974). It has been theorized that within carabid beetles with similar stridulatory organs that each tooth strike of the *pars stridens* across the *plectrum* results in a single acoustic pulse and one full movement of the *plectrum* across the entire *pars stridens* results in a full chirp consisting of multiple pulses (Claridge 1974). Furthermore, fused elytra, common in carabid beetles, may act as an acoustic resonating and amplifying device (Claridge 1974).

While the stridulatory structures within *Gonogenia* are novel, the surface structure of the *plectrum* and *pars stridens* bare similarities to other sound producing Carabidae (Claridge 1974; Forsythe 1978). This variation in surface structure allows for species-specific signals. That novel stridulatory structures also exist within the same family is not surprising as sound producing organs have multiple convergent origins across and within groups (Wessel 2006). This diversity of sound producing organs in beetles is unmatched by any other order of insects,

yet despite the variety of morphological structures and variety of sounds, the ethological context of these signals is still relatively poorly understood (Wessel 2006) and warrants further investigation.

References

- Aiken, R. B. 1985. Sound production by aquatic insects. *Biological Reviews* 65:163–211.
- Alexander, R. D., Moore, T. E. & Woodruff, R. E. 1963. The evolutionary differentiation of stridulatory signals in beetles (Insecta: Coleoptera). *Animal Behaviour* 11:111–115.
- Arrow, G. J. 1904. Sound-production in the lamellicorn beetles. *Transactions of the Entomological Society of London* 52:709–750.
- Arrow, G. J. 1942. The origin of stridulation in beetles. *Proceedings of the Royal Entomological Society of London* 17:83–86.
- Bailey, W. J. 1991. *Acoustic behaviour of insects. An evolutionary perspective*. Chapman and Hall. London and New York.
- Barr, B. A. 1969. Sound production in Scolytidae (Coleoptera) with emphasis on the genus *Ips*. *The Canadian Entomologist* 101:636–672.
- Buchler, E. R. T., Wright, B. & Brown, E. D. 1981. On the functions of stridulation by the passalid beetle *Odontotaenius disjunctus* (Coleoptera: Passalidae). *Animal Behaviour* 29:483–486.
- Claridge, M. F. 1974. Stridulation and defensive behavior in ground beetle, *Cychrus caraboides* (L.), *Journal of Entomology Series A - Physiology & Behaviour* 49:7–15.
- Claridge, M. F. 1985. Acoustic signals in the Homopetera: Behavior, taxonomy, and evolution. *Annual Review of Entomology* 30:297–317.
- Darwin, C. R. 1877. *The descent of man, selection in relation to sex*. 2nd ed. Murray, London.
- Dumortier, B. 1963. Morphology of sound emission apparatus in Arthropoda. In: Busnel, R. G. (ed.). *Acoustic Behaviour of Animals*. Elsevier. Amsterdam.
- Edes, R. 1899. Relation of the chirping of the tree cricket (*Oecanthus niveus*) to temperature. *The American Naturalist* 33:935–938.

- Fleming, A. J., Lindeman, A. A., Carroll, A. L. & Yack, J. E. 2013. Acoustics of the mountain pine beetle (*Dendroctonus ponderosae*) characteristics. *Canadian Journal of Zoology* 91:235–244.
- Forrest, T. G., Farris, H. E. & Hoy, R. R. 1995. Ultrasound acoustic startle response in scarab beetles. *Journal of Experimental Biology* 198:2593–2598.
- Forrest, T. G., Read, M. P., Farris, H. E. & Hoy, R. R. 1997. A tympanal hearing organ in scarab beetles. *The Journal of Experimental Biology* 200:601–606.
- Forsythe, T. G. 1978. Preliminary investigation into the stridulation mechanisms of the genus *Elaphrus* (Coleoptera: Carabidae) *Elaphrus cupreus* Duftschmid. *Coleopterists Bulletin* 32:41–46.
- Franklin, M., Droege, S., Dawson, D. & Royle, J. 2009. Nightly and seasonal patterns of calling in common true katydids (Orthoptera: Tettigoniidae: *Pterophylla camellifolia*). *Journal of Orthoptera Research* 18:15–18.
- Freitag, R. & Lee, S. K. 1972. Sound producing structures in adult *Cicindela tranquebarica* (Coleoptera: Cicindelidae) including a list of tiger beetles and ground beetles with flight wing files. *The Canadian Entomologist* 104:851–57.
- Greenfield, M. D. 2002. *Signalers and Receivers: Mechanisms and evolution of arthropod communication*. Oxford University Press. Oxford.
- Hirschberger, P. 2001. Stridulation in *Aphodius* dung beetles: Behavioral context and intraspecific variability of song patterns in *Aphodius ater* (Scarabaeidae). *Journal of Insect Behavior* 14:69–88.
- Howard, D. R., Mason, A.C., Hill, P. S. M. 2008. Hearing and spatial behavior in *Gryllotalpa major* Saussure (Orthoptera: Gryllotalpidae). *The Journal of Experimental Biology* 211:3613–8.

- Kasper, J. & Hirschberger, P. 2005. Stridulation in *Aphodius* dung beetles: Songs and morphology of stridulatory organs in North American *Aphodius* species (Scarabaeidae). *Journal of Natural History* 39:91–99.
- Lewis, E. E. & Cane, J. H. 1990. Stridulation as a primary anti-predator defence of a beetle. *Animal Behaviour* 40:1003–1004.
- Lovei, G. & Sunderland, K. D. 1996. Ecology and behavior of ground beetles. *Annual Review of Entomology* 41:231–256.
- Lyal, C. H. C. & King, T. 1996. Elytro-tergal stridulation in weevils (Insecta: Coleoptera: Curculionoidea). *Journal of Natural History* 30:703–773.
- Mankin, A. R. W., Moore, A., Samson, P. R. & Chandler, K. J. 2013. Acoustic characteristics of dynastid beetle stridulations. *The Florida Entomologist* 92:123–133.
- Masters, W. M. 1979. Insect disturbance stridulation: Its defensive role. *Behavioural Ecology and Sociobiology* 5:187–200.
- Mini, A. & Prabhu, V. K. K. 1990. Stridulation in the coconut rhinoceros beetle *Oryctes rhinoceros* (Coleoptera: Scarabaeidae). *Proceedings of the Indian Academy of Science* 99:447–455.
- Niemela, J. 1993. Interspecific competition in ground-beetle assemblages (Carabidae) - what have we learned. *Oikos* 66:325–35.
- Panneton, B. E., Sprague, M. W., Kalmus, G. W., Charles, T. M. & Daniel, H. J. 2005. Stridulatory organs in the scarab beetle *Polyphylla occidentalis* (Scarabaeidae: Coleoptera): an SEM and acoustic study. *Journal of the North Carolina Academy of Science* 121:131–144.
- Pearson, D. L. 1988. Biology of tiger beetles. *Annual Review of Entomology* 33:123–147.
- Rudinsky, J. A. & Michael, R. R. 1972. Sound production in Scolytidae: Chemostimulus of sonic signal by the douglas-fir beetle. *Science* 175:1386–1390.

- Spangler, H. G. 1988. Hearing in tiger beetles (Cicindelidae). *Physiological Entomology* 13:447–452.
- Stumpner, A. & von Helversen, D. 2001. Evolution and function of auditory systems in insects. *Naturwissenschaften* 88:159–170.
- von Helversen, D. & von Helversen, O. 1983. Species recognition and acoustic localization in acridid grasshoppers: A behavioral approach. In: Huber, F. & Markl, H. (eds.). *Neuroethology and behavioral physiology*. Springer-Verlag, Berlin.
- Wessel, A. 2006. Stridulation in the Coleoptera - an overview. In: Drosopoulos, S. & Claridge, M. F. (eds.). *Insect sounds and communication. physiology, behaviour, ecology and evolution*. Taylor and Francis Group, Florida.
- Yack, J. E. 2004. The structure and function of auditory chordotonal organs in insects. *Microscopy Research and Technique* 63:315–37.
- Yager, D. D. 1999. Structure, development, and evolution of insect auditory systems. *Microscopy Research and Technique* 47:380–400.
- Yager, D. D., Cook, A. P., Pearson, D. L. & Spangler, H. G. 2000. A comparative study of ultrasound-triggered behaviour in tiger beetles (Cicindelidae). *Journal of Zoology* 251:355–368.

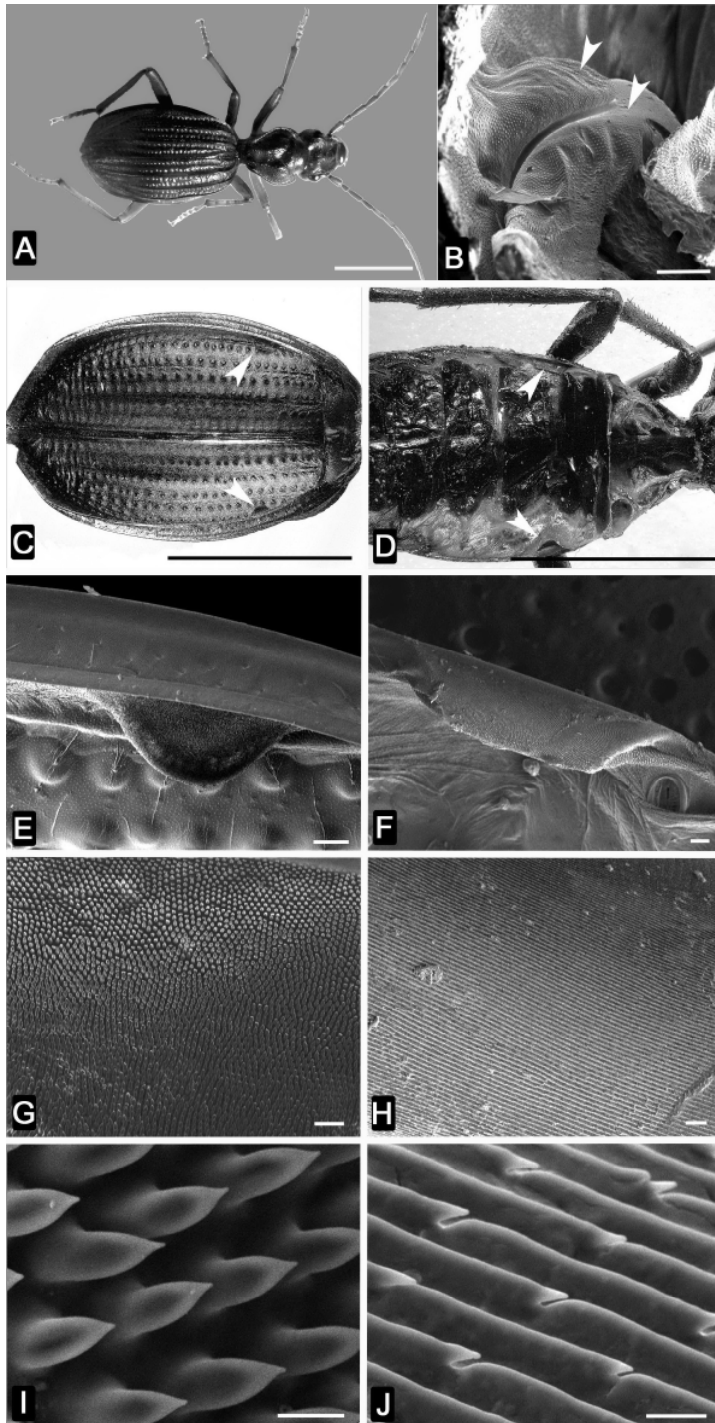


Figure 7.1. A) *Gonogenia tabida*; B) Cross section through abdomen and elytra of *G. tabida* showing the stridulatory structure and how the *pars stridens* and *plectrum* fit together; C, E) tooth like *pars stridens* on ventral side of elytra; D, F) ridge like *plectrum* on first abdominal sternite; G, I) fine stridulatory surface of the *pars stridens*; H, J) stridulatory surface of the *plectrum*. Scale bars: A, C, D = 5 mm; B, E, F = 100 μm ; G, H = 10 μm ; I, J = 2 μm .

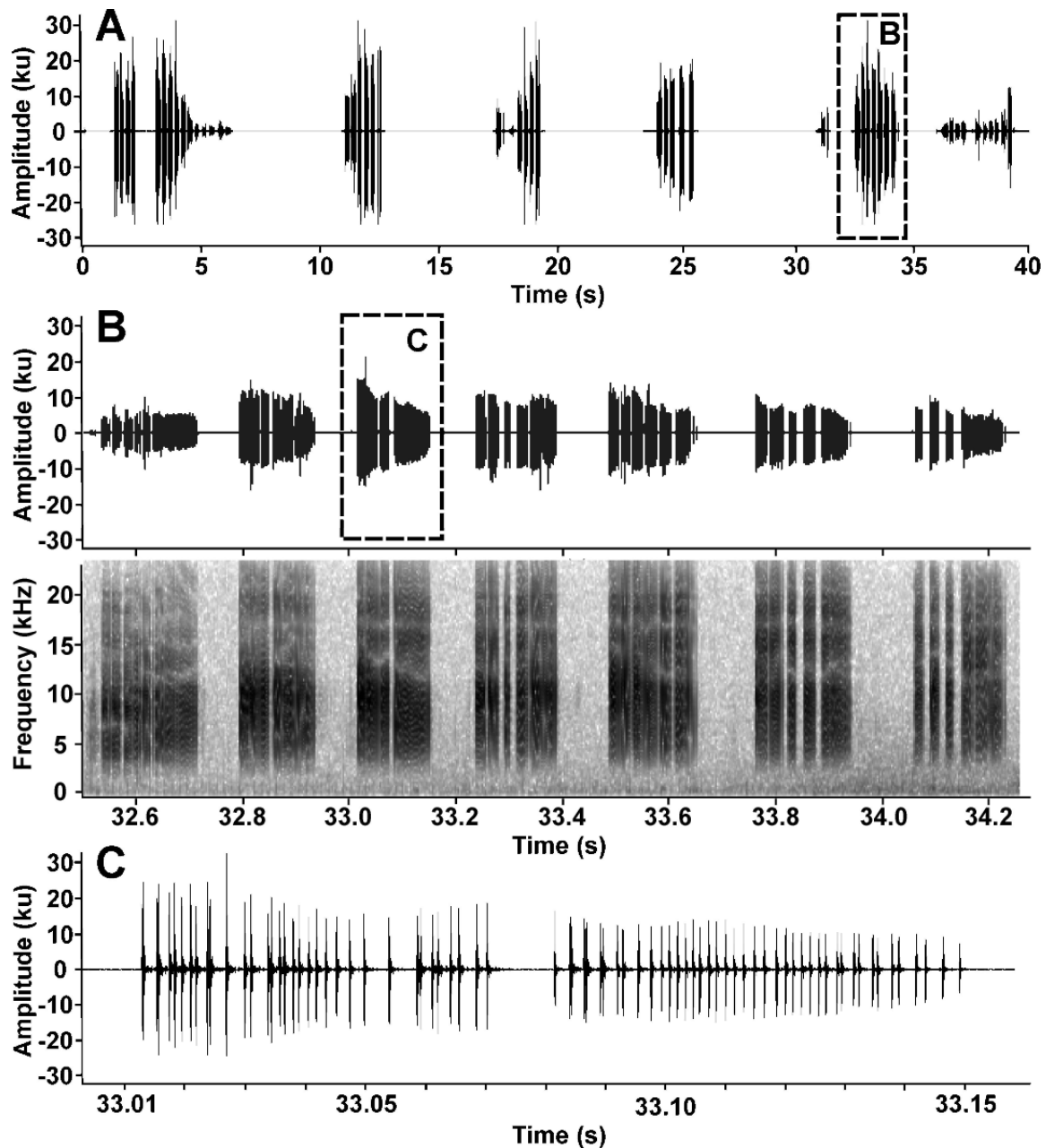


Figure 7.2. Acoustic signal of *Gonogenia tabida* at different temporal resolutions. Waveforms A, B and C display amplitude of signal over time. Spectrogram (below waveform B) displays frequency of signal over time, with darker colour representing higher decibels (dB). Waveform A) displays the temporal pattern of trills over a time period of approximately 40 seconds (s). Waveform B) displays the temporal expansion of a single trill and the discrete chirps that compose it. The associated spectrogram of waveform B displays the broad frequency range of *G. tabida* signals. Waveform C) displays the temporal expansion a single chirp and the discrete pulses which compose it.

8. General discussion

Acoustic communication: windows to cryptic diversity

The evolutionary drivers and constraints of katydid communication have resulted in a remarkable diversity of songs, occurring across a range of environments (Gwynne 2001). From a katydid perspective, songs are a critical communication channel necessary for mate attraction and therefore dependent on transfer of detectable clear signals that can be accurately interpreted (Greenfield 2002). Within this communication channel, local abiotic and biotic influences cause katydids to utilize acoustic niches, signalling within specific frequency ranges, places or times to reduce acoustic interference and increase communication ranges (Samways 1977a; Samways 1977b; Samways 1977c; Riede 1993; Riede 1997; Greenfield 2002; Gerhardt & Huber 2002; Diwakar & Balakrishnan 2007; Schmidt *et al.* 2012; Jain *et al.* 2013).

How acoustic species partition their acoustic environment, has direct implications for monitoring species and environments. This is highlighted by both diurnal and nocturnal Bornean acoustic species using spectral and spatial (vertical and elevation) partitioning to avoid acoustic interference. Yet, only diurnal species relied on temporal partitioning, showing extremely low temporal overlap, while nocturnal species did not. Lack of nocturnal temporal partitioning suggests other mechanisms of acoustic avoidance are sufficient to avoid acoustic overlap, or that there are insufficient cues to partition nocturnal acoustic environments. For acoustic surveys across multiple sites, this implies nocturnal surveys have flexibility in terms of time sampled, whereas diurnal surveys need to be sampled within consistent time periods.

From a human perspective, katydid songs not only create ambient acoustic orchestras that are aesthetically appealing, but the signals themselves provide an acoustic window to cryptic diversity patterns across ecological gradients and over time (Riede 1998). Acoustic

inventorying and monitoring can reflect the environmental status of dynamic systems, therefore determining the relationship between natural and anthropogenic, abiotic and biotic sounds with corresponding environmental processes (Riede 1998; Depaetere *et al.* 2011). In contrast to traditional survey techniques, sound recording is a non-invasive method that allows for the detection and classification of highly cryptic, yet insightful indicators of environmental health (Riede 1998). Importantly, species-specific acoustic parameters such frequency and pulse rate allow the definition of recognizable taxonomic units, overcoming taxonomic impediments due to declining expert knowledge and lack of adequate species descriptions (Riede 1998). Consequently, acoustic profiling is highly adaptable and effective, even within signal rich environments where signalers have not been taxonomically identified.

The effectiveness of acoustical profiling of the landscape is shown within this project, and highlighted by the discovery of new species based on their acoustic signals. Furthermore, irrespective of the geographic location, the complexity of the acoustic environment or the ecological gradients, acoustic signals were readily recorded, identified and classified, providing an excellent means to measure acoustic diversity of focal taxa (katydids) as well as numerous other species which broadcast signals in the same acoustic space and time. As taxa can have diverse reactions to various changes in the environment, acoustic surveys using entire acoustic guilds incorporate this variation and therefore provide an extremely robust and powerful assessment tool (Riede 1998). Current anthropogenic influences on the natural world and associated environmental changes highlight the need for robust, rapid and cost effective acoustic assessment tools to monitor species and environments. Long term monitoring of entire soundscapes also enables insight into changes in acoustic diversity through landscape alteration or climate change (Dumyahn & Pijanowski 2011; Pijanowski *et al.* 2011a). This type of analysis also allows for habitat assessment and monitoring to determine the level of restoration or deterioration from anthropogenic or environmental landscape change.

Acoustic profiling of landscapes not only shows patterns of diversity but can reveal the associated ecological influences which drive them. This was shown across the plantation forestry landscape mosaic in KwaZulu-Natal, South Africa. This landscape contained diverse ecological gradients, in which diversity patterns and associated ecological influences needed to be identified to develop effective conservation strategies to ensure continued sustainable management. Acoustic profiling revealed the influence of invasive vegetation, patch size, heterogeneity and management practices on acoustic diversity patterns. Identification of these drivers in addition to diversity patterns enables implementation of informed management practices to reduce the contrast of transformed landscape with surrounding natural areas and maintain functional ecosystem integrity.

Influences and drivers of acoustic diversity patterns can also shift geographically based on local abiotic and biotic factors. Within the Cape Floristic Region, South Africa, wind influences katydid communication channels shifting them to higher frequency ranges to avoid acoustic interference. Temperature was also a significant driver of acoustic diversity patterns across gradients of elevation and season. Here, identification of species-specific acoustic signals, diversity patterns and ecological influences contribute towards effective monitoring of species within local environments.

Incorporation of acoustic diversity patterns within conservation strategies not only preserves local acoustic environments, but the biodiversity and function of ecological systems (Farina 2009; Dumyahn & Pijanowski 2011). Currently, management policies have been established elsewhere to monitor soundscapes and take action to prevent or minimize all noise through frequency, magnitude or duration which adversely affects the natural soundscape (National Park Service 2006; Hults & Burson 2006; Miller 2008; Dumyahn & Pijanowski 2011). Katydids and their high frequency songs have been directly identified within these

conservation strategies (National Park Service 2006), highlighting their importance in nocturnal soundscapes. Keeping the acoustic perspective in mind when developing conservation or monitoring strategies is therefore an invaluable step forward towards protecting soundscapes and conserving biodiversity within.

Conclusion

Acoustic profiling of the landscape provides an acoustic window to cryptic diversity patterns across ecological gradients and over time. It is a highly effective, robust, non-invasive technique, capable of detection and classification of highly cryptic acoustic species difficult to detect through traditional methods. Implemented on a species-level scale it reveals strategies utilized in niche partition of the acoustic spectrum. On a landscape-level scale it reveals acoustic diversity patterns across ecological gradients and time, and the associated ecological influences which drive them. As technology develops, conservation strategies turn towards incorporating and preserving soundscapes, and with an increasing need to effectively monitor species and environments, acoustic profiling is developing into an incredibly powerful, tool and continues to gain traction.

References

- Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S. & Sueur J. 2011. Monitoring animal diversity using acoustic indices: Implementation in a temperate woodland. *Ecological Indicators* 13:46–54.
- Diwakar, S. & Balakrishnan, R. 2007b. Vertical stratification in an acoustically communicating ensiferan assemblage of a tropical evergreen forest in southern India. *Journal of Tropical Ecology* 23:479–486.
- Dumyahn, S. L. & Pijanowski, B. C. 2011. Soundscape conservation. *Landscape Ecology* 26:1327–1344.
- Farina, A. 2009. *Ecology, cognition and landscape: linking natural and social systems*. Springer, New York.
- Gerhardt, C. H. & Huber, F. 2002. *Acoustic communication in insects and anurans: Common problems and diverse solutions*. The University of Chicago Press, Chicago.
- Greenfield, M. D. 2002. *Signalers and receivers. Mechanisms and evolution of arthropod communication*. Oxford University Press, Oxford.
- Gwynne, D. T. 2001. *Katydid and bush-crickets: reproductive behavior and evolution of the Tettigoniidae*. Cornell University Press, Ithaca.
- Hults, C. & Burson, S. 2006. Soundscapes of Denali National Park and Preserve. *Alaska Park Science* 5:20–22.
- Jain, M., Diwakar, S., Bahuleyan, J., Deb, R. & Balakrishnan, R. 2013. A rain forest dusk chorus: cacophony or sounds of silence? *Evolutionary Ecology* doi:10.1007/s10682-013-9658-7.
- Miller, N. P. 2008. US National Parks and management of park soundscapes: A review. *Applied Acoustics* 69:77–92.

- National Park Service. 2006. *Management policies 2006*. U.S. Department of Interior, National Park Service, Washington, DC.
- Pijanowski, B. C., Farina, A., Gage, S. H., Dumyahn, S. L. & Krause, B. L. 2011a. What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology* 26:1213–1232.
- Riede, K. 1993. Monitoring biodiversity: analysis of Amazonian rainforest sounds. *Ambio* 22:546–548.
- Riede, K. 1997. Bioacoustic diversity and resource partitioning in tropical calling communities. In: Ulrich, H. (ed.). *Tropical biodiversity and systematics. Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems*, Bonn 1994. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.
- Riede, K. 1998. Acoustic monitoring of Orthoptera and its potential for conservation. *Journal of Insect Conservation* 2:217–223.
- Samways, M. J. 1977a. Song modification in the Orthoptera. IV. The *Platypleis intermedia*/*P. affinis* interaction quantified. *Physiological Entomology* 2:301–315.
- Samways, M. J. 1977b. Bush cricket interspecific acoustic interactions in the field (Orthoptera, Tettigoniidae). *Journal of Natural History* 11:155–168.
- Samways, M. J. 1977c. Effect of farming on population movements and acoustic behaviour of two bush crickets (Orthoptera, Tettigoniidae). *Bulletin of Entomological Research* 67:471–481.
- Sanborn, A. F. 2006. Acoustic signals and temperature. In: Drosopoulos, S. & Claridge, M. F. (eds.). *Insect sounds and communication. Physiology, behaviour, ecology and evolution*. Taylor and Francis Group, Florida.