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Ecological differences between rare and common species of microhylid frogs of the Wet Tropics biogeographic region

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2007

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Statement of contribution of others

Chapter Four in this thesis has been published in collaboration with my supervisors Prof. Christopher N. Johnson, Prof. Ross Alford, A/Prof Michelle Waycott and colleague A/Prof. Steve Williams. Statistic advice has been provided by my supervisors as well as A/Prof. Steve Williams, Dr Jeremy Van DerWal, Dr Rebecca Fisher and Dr Leonie Valentine. Additional data for some analysis was also provided by A/Prof Steve Williams and the Queensland museum. Species distribution maps and range sizes have been used in this thesis with permission of A/ Prof Steve Williams and microhylid species phylogeny has been presented with permission of Dr C. Hoskin. While undertaking this research, I was responsible for the project design, obtaining research funding and permits, collecting field and laboratory data, statistical analysis and interpretation, and synthesis and preparation of manuscripts for submission to peer reviewed journals.

I obtained financial support from James Cook University and the Rainforest Cooperative Research Centre. Funding to present research at conferences was obtained from James Cook University, Rainforest Cooperative Research Centre.

Declaration on ethics

All data collected adhered to the legal requirements of Australia, (Scientific Purposes Permit F1/000467/01/SAA) and the ethical guidelines for treatment of animals of James Cook University (Animal Ethics Approval A574_01).

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Dedication

I would like to dedicate this thesis to the two most significant groups of people in my life:

To my gorgeous Williams family: Steve, Anna, Kyle and Zac - who are my life and give me purpose. I feel blessed every day to be part of your lives. Thank you for supporting and joining me throughout this journey.

To my wonderful Buffett clan: Mum, Dad, Glynn and Charles - no-one could have asked for a better family or childhood. Thank you for your never ending belief in me.

I am so lucky to have you all.

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Thanks to my gorgeous mum for the sacrifices you have made, the support you have always given and the never ending belief in me; my gorgeous sister for your love, help, friendship and always standing by me and my wonderful brother for reminding me about the real world, I love you all dearly. I only wish Dad could be here to see this, for some reason I know he would think of some smart comment to sum it all up for me.

Finally to my gorgeous and wonderful husband Steve and children Anna, Kyle and Zac, my world would be nothing without you. Thank you for you constant love, the kisses and cuddles, the support and simply being the best part of my life.

Some things I have learnt along the way……

“If a short cut truly was a short cut then it would be called “the way””

Silent Bob

And……..

“In life it is important to finish stuff”

Marsha Hines

General Abstract

Why some species are rare while others are common remains a much asked question in ecology. As rare species are generally considered to be most extinction-prone, the importance of answering this question is becoming paramount in order to prioritise conservation efforts and resources to the most threatened species. The difficulty in gaining information on rare species which, by their very nature, are low in numbers and often difficult to detect, are just some of the reasons behind the apparent lack of answers regarding determinants of rarity. To further investigate why some closely related species are rare while others are common, this study examined the ecological differences between rare and common species of microhylid frogs in the Wet Tropics, North Queensland Australia. Eleven species of microhylid frog of the genus *Cophixalus* and three from the genus *Austochaperina* are endemic to the region. While some of these species occur across most of the Wet Tropics region, a majority are restricted to single mountain ranges. By comparing the ecological traits of niche breadth, dispersal ability and genetic diversity, in geographically restricted and widespread species, it has provided a more comprehensive understanding of what factors have shaped the patterns of distribution in these species.

The niche breadth of microhylid species was measured using climatic and microhabitat variables. Comparisons of climatic niche among species showed that geographically restricted species do have narrower niche than widespread species, i.e. climate variables explaining more variation in species abundance within their range than topography or vegetation. However when microhabitats of species were described in a smaller subset of six species no relationship of niche breadth and range size was found. Geographically restricted or widespread species were either microhabitat specialists or generalist with no clear trend shown.

The relationship between diet specialisation and geographic range was also investigated as a measure of species niche breath. Although macroecological theory predicts that species with broad niches should have the largest geographic ranges, I found the opposite: geographically rare species were diet generalists, widespread species were diet specialists. It is argued that this pattern is a product of extinction filtering, whereby geographically rare and therefore extinction-prone species are more likely to persist if they are diet generalists.

The dispersal ability and genetic diversity were compared in a subset of three species to determine if these traits explained restricted, intermediate or widespread distributions. Similar levels of dispersal were suggested across all species however, contra to rarity theory, genetic diversity was found to be higher in the restricted and intermediate species than in widespread. It is suggested that historical habitat stability may have maintained greater genetic diversity in restricted species than in widespread species which have recolonised areas from refugia.

The population parameters of species geographic range size, local abundance and ubiquity were used to generate a Rarity Index (RI – ranging in values between 0 - 1.7). The RI allowed for the comparison of population parameters (used as three axis of rarity) of each species in three dimensional space. No species were found to be rare on all three axis, that is, if a species is geographically restricted then it compensated by being abundant and/or ubiquitous on the other two axis. In fact no species were found to have RI values below 0.8 which suggests that species with lower values may have been more extinction prone and unable to maintain viable populations over time.

It appears that no single ecological trait explains patterns of distribution seen in microhylid frogs. While rare species may be specialist in some ecological traits they compensate by being generalists in other traits, with past history of rainforest expansion and contraction in this region placing strong selection pressure on these species or these traits being left over from previously being more widespread. This may be one of many reasons that geographically restricted and rare species, while considered to be those most prone to extinction, have been able to persist through long geological time periods.

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CHAPTER 1: GENERAL INTRODUCTION

Rarity theory attempts to understand why some species are rare and others are common and determine the consequences of rarity. Rare species are commonly characterised by combinations of the following traits; small total population size, low abundance, small geographic range size, patchy/isolated populations and specialisation in niche requirements. Because of these characteristics, rare species are often prone to extinction due to environmental and demographic stochasticity (Simberloff 1998). Single stochastic events can easily remove entire populations, and remaining populations may have slow recovery times. Despite the risk of extinction, rare species are a major component of biodiversity (Gaston 1994) often comprising 30-50 % of many assemblages (Novotny and Basset 2000). As a primary aim of conservation is to maintain biodiversity, understanding the intricacies of rarity is imperative for appropriate management of ecosystems. While it is widely accepted that rare species require improved monitoring and management, the mere fact that such species are rare, often signifies that they are difficult to study, and data on them are sparse.

Which species are rare?

As described above, rare species are commonly defined by a variety of intrinsic traits. More generally, describing a species as rare often imply that it has a small population size compared with closely-related or sympatric species. Small population size can result from three aspects of population biology:

<u>Geographic range</u>: other things being equal, a species that is narrowly distributed will have a smaller total population than a species that is widespread;

<u>Local abundance</u>: for a given geographic range, a species that occurs at low density in occupied sites will have a smaller population than one that occurs at high density; and

<u>Ubiquity</u>: for a given geographic range and local abundance, a species that is patchily distributed throughout its range (and thus has a relatively low area of occupancy and greater spatial variation (*sensu* Gaston 1994)) will have a smaller total population than one that occurs continuously, and thus occupies more sites.

In this study rare species have been initially defined as those with a restricted geographic distribution; the abundance and ubiquity of species within the geographically restricted and widespread distributions are then more closely investigated.

Small geographic range size

The geographic range size of a species is ultimately determined by interactions between limiting environmental conditions, dispersal, recolonisation and extinction dynamics, and biotic interactions such as competition and predation (Brown *et al.* 1996). Species with small geographic ranges may be at higher risk of extinction because localised catastrophic events, such as extreme weather events, anthropogenic habitat destruction or disease, can affect the entire population. Murray & Hose (2005) demonstrate that, in endemic Australian frog fauna, geographically restricted species are most likely to undergo species decline or extinction. It is generally accepted that species with larger geographic ranges, whether or not they are ubiquitous, decrease the probability per unit time to extinction (Gaston 1994) although large range size alone has rarely been demonstrated to enhance survival (McKinney 1997).

Abundance

Ecological traits that may influence species abundances are: resource availability (eg. productivity), density dependence, and biotic interactions. The relative importance of these factors varies among species, often in a seemingly unpredictable manner. The abundance of a species, or its total population size, is often the determining factor in categorising a species as vulnerable, endangered or critical on conservation lists such as the IUCN red list (Mace and Kershaw 1997). O’Grady *et al.* (2004) demonstrated that population abundance is the most important data to collect for rare and threatened species and the best predictor of a species’ relative extinction risk. Temporal fluctuations in population size become weaker as population size increases (Reed and Hobbs 2004) with larger populations more stable in space and time, thus reducing extinction risk. However, total population size is not the ultimate influencing factor and interactions between population size, population variability and population fitness (Reed and Hobbs 2004) may ultimately determine the fates of species.

Ubiquity

The third component of rarity, ubiquity or the patchiness of a species within its range, may also have strong effects on the biology of species and their extinction proneness (Gaston 2005). Ubiquity takes into account the fact that species may aggregate in their distribution for reasons other than habitat specificity, such as mating or other behavioural aggregations or in response to patchy food resources. Ecological factors that must be considered in species with low ubiquity (higher patchiness) are resource patchiness and metapopulation dynamics. Often rare species are considered habitat specialists and are thus commonly more patchy throughout their distribution than are widespread generalists (Mace and Kershaw 1997). Species with low ubiquity or patchy distributions may have an increased extinction risk due to difficulties in finding mates and/or dispersing across areas of unsuitable habitat (Gaston 1994). However, extinction risk due to patchy distributions may be ameliorated to some extent if a species is also widespread (McKinney 1997), and many patchily distributed species experience metapopulation dynamics, which may strongly affect their probability of global extinction.

Three main types of geographical distribution occur in rare species (Drury 1974): 1) A species can be widespread over a large geographical range but patchily distributed and often in low abundance in suitable habitat throughout this range (eg. Anteaters; Gaston and Kunin 1997), 2) A species can be widespread and ubiquitous over a large geographic area but occur in low abundance throughout this area (eg. Red Goshawk; Marchant & Higgins 1993), 3) A species can be restricted to a small area and consequently be considered rare even though it occurs at relatively high density within this area (eg. microhylid frogs such as *C. hosmeri*; Shoo and Williams 2004).

Ecological traits of rare species

Numerous studies have shown that patterns of species loss are seldom random and that certain life history and ecological traits make some species more vulnerable to extinction than others (McKinney 1997). These life history and ecological traits are interchangeable with those described for rare species as extinction in many cases may be the end result of rarity, whether rarity is an intrinsic trait, or the end result of anthropogenic or environmental factors (Lawton 1995). Rare species commonly exhibit seven traits including: parthenogenesis (asexual reproduction or budding off), low reproductive investment (small litter sizes and low reproductive potential), poor dispersal ability, low levels of genetic polymorphism, low competitive ability, narrow niche breadth and use of rare resources, and higher trophic level (Rabinowitz 1981, Kunin and Gaston 1997). The relative importance of these factors as determinants of rarity has been examined in many studies (Rabinowitz 1981, Thompson *et al.* 1999, Murray *et al.* 2002a, 2002b and reviewed in Gaston 1994, Kunin and Gaston 1997). However, results are often inconsistent between taxa and habitats (Rosenzweig and Lomolino 1997, Murray *et al.* 2002a). For example, Rosenzweig (1995) found no discernable relationship between rarity and trophic level, whilst Damuth (1987) observed that mammalian primary consumers have higher densities than secondary consumers.

In the present study I investigated three possible determinants of rarity in depth: a) narrow niche breadth in the forms of climatic niche (Chapter 3), microhabitat (Chapter 3) and diet (Chapter 4), b) dispersal ability (Chapter 5) and c) levels of genetic polymorphism (Chapter 5). The potential contributions of each of these factors to rarity are explored in further detail below.

Niche breadth (environmental, microhabitat and diet)

Niche breadth can be described as: the range of a resource used or the range of an environmental variable tolerated by a species (Begon *et al.* 1990), and may be described in a variety of ways including environmental characteristics, microhabitat and diet. The niche breadth of a species reflects both its physiological tolerances, and the environments in which it actually persists (Brown *et al.* 1996). Thus, the same environment can have different fitness consequences for different organisms, mediated by behaviour, morphology, physiology and life history (Kearney 2006). Geographic range size is likely to be affected by niche breadth, as a species which can exploit a wider range of conditions locally will achieve high densities and be able to survive in more places and over a larger area (Brown 1984). Rarity theory predicts that widespread species should be more abundant and have wider niches and greater environmental tolerances than rare and restricted species.

In terms of habitat specificity, common species are predicted to have more generalised habitat requirements, whereas ‘locally common’ and ‘scarce’ species are more likely to be specialised (Mace and Kershaw 1997). In some situations, as in marine gobies (*Gobiadon*), habitat specialists may have a competitive advantage over more generalist species, leading to the maintenance of high local abundances (Rosenzweig and Lomonlino 1997, Caley and Munday 2003). However, habitat specialisation can increase extinction risk as specialists will be more sensitive to perturbations than are species that occur in a variety of habitats (Arita *et al.* 1990).

Rarity may also be a product of specialisation in diet, leading to geographically restricted ranges and/or low abundances. The use of rare resources, as occurs in insects, for example the fine-scale partitioning of flower types among bee species with differing tongue lengths (Goulson *et al.* 2005), and the high host plant specificity of many butterfly larvae (Bond 1995), links the fate of consumers to the abundance and distribution of these resources. Pianka (1986) suggested that species should only become specialised on abundant and predictable resources, however, even if this is true, the abundance and predictability of resources can change, and if these changes are too rapid, species extinction may result.

Dispersal ability

Dispersal, the migration of individuals among populations, plays a key role in determining the distribution and abundance of populations in time and space (Brown *et al.* 1996). There appears to generally be a positive relationship between species’ dispersal ability and range size (Gaston and Kunin1997). Species that fly, or are large and can cover greater distances, are generally better dispersers and as a result usually have larger geographic ranges (Lowe *et al.* 2004). While the majority of studies have found that geographically rare species exhibit poorer dispersal abilities than common widespread species, extensive reviews indicate that the relationship between range size and dispersal is better described as asymmetrical (Kunin and Gaston 1993 and 1997). Good dispersers can have small, intermediate or large ranges, but poor dispersers generally only have small or intermediate ranges (Gaston 1994, Kunin and Gaston 1997).

Genetic diversity

Dispersal transports genes from one population to another (Slatkin 1985), and therefore maintains genetic diversity within populations of a species (Lowe *et al.* 2004). The ability of a species to disperse its genes also dictates local effective population size (N_e) as it is empirically measured by gene flow and total genetic diversity (Frankham *et al.* 2002). Species with smaller local effective population size have higher risks of extinction due to lower levels of adaptive genetic diversity, and are more affected by genetic drift. They are also more likely to experience inbreeding depression (Karron 1997; Kunin and Gaston 1997). Inbreeding depression poses a great threat to population persistence, with any factor that threatens species fitness and recovery after environmental perturbation making species more susceptible to extinction (Reed and Hobbs 2004). Saccheri *et al.* (1998) demonstrate that inbreeding is as important as demographic and environmental stochasticity in dictating extinction risk in metapopulations of the Fritillary butterfly (*Melitaea cinxia*). High levels of genetic diversity and gene flow may reduce the incidence of deleterious genes and inbreeding depression in populations and, therefore, increase species fitness and resilience, reducing extinction risk (Soule 1986).

How do rare species persist through time?

It is an apparent paradox that, while rare species are thought to be intrinsically prone to extinction, many have persisted throughout long periods of evolutionary time (Kunin and Schmida 1997, McKinney 1997, Rosenzweig and Lomolino1997, Simberloff 1998). Simberloff (1998) provides examples of species (e.g. Socorro Island Hawk and the Devil’s Hole pupfish) that naturally occur at small population sizes (20 pairs for the Hawk) and in very restricted geographic ranges (200m^2 for the pupfish) suggesting that rare species can and do persist even with traits that make them extinction prone. Johnson (1998) proposed that rare species that persist though time may do this by possessing ecological traits that allow them to persist despite their rarity. Thus, perhaps one of the best ways to assess how to conserve rare species is to determine what ecological traits may have conferred resilience on those rare species which have persisted through time. Johnson (1998) demonstrated, for example, that geographically restricted species may compensate by having high local abundance, thus reducing their risk of extinction. In this study I investigate traits that may increase species resilience and allow them to persist through time.

Aims of this study

The primary aim of this study was to examine how differences in specific ecological traits, including niche breadth, dispersal ability and genetic diversity, contribute towards a species rarity. Specifically, my study asked four main questions:

1. Do geographically rare species have narrower environmental, microhabitat, and dietary niches than geographically widespread species?
2. Do geographically rare species have lower dispersal ability, as indicated by gene flow between populations, than geographically widespread species?
3. Do geographically rare species have lower levels of genetic diversity than geographically widespread species?
4. When comparing species on three axes of rarity (range size, abundance and ubiquity), can a species compensate for rarity in one trait (i.e.: small range size) by being common in another (i.e.: high local abundance) and can this increase population resilience?

Study animals

To examine the influence of ecological traits on a species rarity I compared ecological differences between rare and common species of Microhylid frogs in the Australian Wet Tropics biogeographic region in northern Queensland. I investigated several aspects of their ecology to determine whether variation in those characters is related to the variation in geographic range and distribution patterns among these closely related species. Microhylid frogs from the genera *Austrochaperina* and *Cophixalus*, of which 14 species are endemic to this region, were ideal species to use for this study as they vary greatly in their geographic range sizes, and their rarity is not due to any anthropogenic factor. Microhylids frogs account for 54% of the frog diversity in this region. The microhylids are small, terrestrial breeders and mainly occur in rainforest habitats. The species in this family have deep lineages on the order of 10 million years old (Hoskin 2004) and their current patterns of distribution and species richness have been affected by geographic variation in rainforest stability during the Quaternary climate fluctuations (Graham *et al.* 2006). Investigating ecological variation among these species, which share evolutionary and historical influences but differ greatly in the degree of rarity, should provide insight into the sources of their resilience.

Study region

This study was carried out in rainforest areas of the Australian Wet Tropics biogeographic region which cover approximately 10 000km^2. This region is the most biologically rich area in Australia and was listed as a World Heritage Area primarily for its biodiversity value in terms of high regional endemism and the occurrence of primitive taxa. This area contains approximately 50% of Australia's rainforest habitat, which has persisted due to the humid climate and the orientation of the highlands and escarpment to the prevailing southeasterly tradewinds, where orographic uplift is enhanced, increasing rainfall (Nott 2005). The rainforest in this region has undergone extensive expansions and contractions during glacial-interglacial cycles over the past 10 million years (Nix 1991); these have often acted as a species filter (Moritz 2005). The vertebrate taxa of the region are well described and most rainforest areas are easily accessible.

Thesis organisation

This thesis is structured as a series of stand-alone, but conceptually interconnected, publications and is organised as follows: **Chapter 2** reviews the current knowledge of Australian microhylid frog species from the published literature to examine what is known and were gaps in knowledge for these species exist. In **Chapter 3**, I examine the niche breadth of microhylid frog at three difference scales of macro, meso and micro habitat to determine which characteristics influence geographic range size. In **Chapter 4**, the niche breadth as depicted by variation in diet among species is examined to determine the effect of resource usage on species distribution. **Chapter 5** examines the dispersal ability and genetic diversity of a subset of these species to ascertain if these characteristic effect species distribution. In **Chapter 6** the population parameters of abundance, distribution and range size are used to generate a Rarity Index to examine the mechanisms these species may have to reduce extinction risk. **Chapter 7** discusses the overall finding of this study.

CHAPTER 2: PATTERNS OF SPECIES RICHNESS, ABUNDANCE, DISTRIBUTION AND BIOLOGY IN MICROHYLID FROGS OF THE WET TROPICS, AUSTRALIA

Introduction

The anuran family Microhylidae has radiated widely throughout the tropics of Asia, Africa, South America and New Guinea, where there are more than 150 species in 20 genera, but is relatively poorly represented in the Australian fauna. Two genera occur in Australia: *Cophixalus* (Boettger 1892; 14 Australian species), and *Austrochaperina* (Zweifel 2000; 5 Australian species). Microhylids in Australia are restricted to the northern tropical east coast and the northern tip of the Northern Territory (Barker *et al* 1995). They are most diverse and abundant in the Wet Tropics Rainforest biogeographic region (Figure 1) which contains 11 species of *Cophixalus* and 3 species of *Austrochaperina*. Molecular studies (Hoskin 2004) have suggested that microhylid frogs may have radiated extensively within the Wet Tropics and speciated *in situ*. The 14 species that occur in the Wet Tropics vary greatly in their geographic ranges and abundance. Many of the species are restricted to small geographic ranges at high altitudes (above 800m), while others are found across the entirety of the region.

In Australia, tropical rainforests occur mainly near the east coast of northern Queensland, where they occupy approximately 6 300 km^2. The Wet Tropics rainforest region has the highest number of vertebrate species of any habitat in Australia, with many regionally endemic species found at higher elevations (above 600 meters; Nix 1991). This region has been described as a chain of upland isolates of tropical and subtropical rainforest, surrounded by drier and warmer environments (Moritz 2005), and is a remnant of rainforest that covered much of Australia until the mid-Miocene. Rainforest is maintained in this region by the humid climate and the orientation of the highlands and escarpment to the prevailing southeasterly tradewinds, which enhances orographic uplift and increases rainfall (Nott 2005). The rainforest in this region has undergone extensive expansions and contractions during glacial-interglacial cycles over the past 10 million years (Nix 1991). This climatic cycling has strongly affected the fauna and flora of the region, causing many extinction and speciation events (Williams and Pearson 1997, Moritz 2005, Schneider and Williams 2005). Three main periods of climatic change are thought to have shaped the biota we see today: 15mya-2mya; rapid contraction of rainforest towards the end of the late Miocene-Pliocene, 2mya- 10 000ya; periodic severe contractions of rainforest to montane refugia during glacial maxima in Pliestocene, ca. 8 000ya – Present: warm wetter conditions resulting in expansion of rainforest away from refugia (Nix 1991, Graham *et al.* 2006, Schneider and Williams 2005).

During the times of rainforest contraction to montane refugia, two main areas of rainforest are thought to have persisted in the Atherton uplands and the Thornton – Carbine uplands (Figure 1; Williams and Pearson 1997). These subregions have the highest vertebrate species richness in the Wet Tropics region today (Williams and Pearson 1997, Graham *et al* 2006). Two hypotheses (Schneider and Williams 2005) have been suggested for the composition of present assemblages of microhylid frogs: 1) species assemblages may have been “filtered” by extinction during periods of Pliestocene rainforest contractions, 2) speciation may have occurred through vicariant isolation of populations during the Miocene. Present evidence suggests that current species assemblages have been affected by both of these processes.

This chapter aims to review previous knowledge of microhylid diversity in the Wet Tropics and to present new data on the morphology, distributions, general ecology of many microhylid species. I also discuss possible threats to these species in the context of global amphibian declines and climate change.

Methods

Measurements

Snout-urostyle length, head length, head width, and length (all in mm) of the fully extended left hind limb were measured on living frogs in the field and on museum specimens, using vernier calipers. Living animals were also weighed to the nearest 0.001

g using a Gram Precision electronic balance. Means were calculated across males and females because the sexes of all species cannot be reliably distinguished except for calling males or heavily gravid females.   It is likely that females of all species are larger than males (Barker *et al.* 1995). Mean clutch sizes were taken from the literature (Barker *et al.* 1995, Hoskin 2004).

Range size estimates, distribution and species richness maps

Total range size estimates were obtained from Williams (2006), along with the distribution and species richness maps. The distribution area for *C. mcdonaldi* was estimated by counting the number of 1 km grid squares above 900 m on a topographic map of Mt Elliot because its range is outside the area for which GIS data were available.

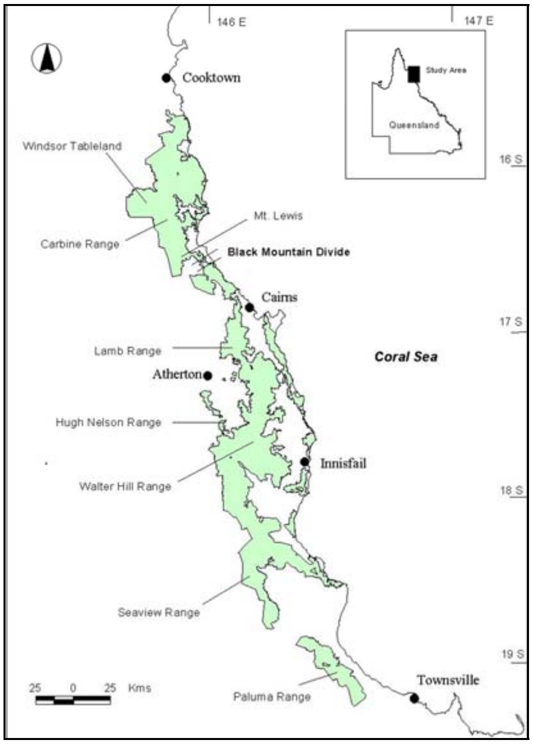


Figure 1: The rainforest area of the Wet Tropics biogeographic region spanning from Cooktown to Townsville in northern Queensland, Australia.

Results & Discussion

Morphology

All of the species are morphologically very similar (Table 1); many can only be differentiated by calls or internal anatomy. All Australian microhylids are small, ranging in size from 10 mm to 39 mm, and most are similar in colour, with the exception of *C. saxatilis* in which the males are bright yellow. The three *Austrochaperina* species are generally larger and more robust than species of *Cophixalus*. The calling ecology of these frogs has been described in many pervious studies (Zwiefel 1985; Olding 1998; Brooke *et al.* 2000; Zweifel 2000; Hauselberger and Alford 2005), and the most recent review by Hoskin (2004) has very clearly described and documented calls for all of these species and has DNA evidence to support all of the species that have been described.

The weights of most microhylids have not previously been presented because their small sizes make it difficult to weigh them accurately in the field. The weight data presented in Table 1 support the idea that the body form of *Austrochaperina* species is relatively more robust; they are heavier for their lengths than are most *Cophixalus* species. *Cophixalus* species have a wide range of weights; the smallest is *C. hosmeri,* with a mean adult mass of 0.24 grams. The largest species I measured was *C. neglectus,* with mean adult mass of 1.32 grams. It is likely that *C. saxatilis* are heavier, since they are longer and have a similar form, but I was unable to weigh any individuals of this species.

General ecology

General knowledge of the ecology of microhylid frogs has lagged behind that of the stream dwelling hylid frogs; much of this can be attributed to the difficulty of access to the restricted populations of many species on mountain tops. Most of the research on this family has been carried out on the most common species, *C. ornatus.* Only three published papers deal extensively with the behaviour or ecology of Australian microhylids (Brooke *et al.* 2000; Hauselberger and Alford 2005; Felton *et al.* 2006) while two others report the systematics (Hoskin 2004) and abundance changes over altitude in these species (Shoo and Williams 2004). Much of this research has focused on calling behaviour and mate choice, while the remainder has focused on distribution and systematics.

Correlations with calling

Brooke *et al.* (2000) found that the annual pattern of calling activity by *C. ornatus* at a series of sites along a 560 m transect was strongly correlated with the start and end of the wet season (approximately November to February). Some calling occurred almost every night within this period. Only 36% of variation among days within local sites could be explained by weather, moon or any other factor common to the entire transect. They suggested that the majority of day-to-day variation in calling activity must be due to either small-scale environmental factors or social facilitation (males responding to the calls of other males). Hauselberger and Alford (2005), using the same transect, repeated the work on *C. ornatus* with similar results but showed that calling activity by the other microhylid present, *A. robusta,* varied proportionately more among nights, and that a much higher proportion of the night-to-night variation appeared to be related to rainfall and humidity. They could not compare the timing of the onset of the breeding season between 1995-96 and 2001-02, but the breeding seasons of both species ended approximately 2 weeks earlier in the latter year.

Table 1: Morphometric measurements (mm + SE) and live weight (grams + SE) of Austrochaperina and Cophixalus species occurring in the Australian Wet Tropics. The numbers of individuals these measurements are based on are shown in parentheses.

Species	Snout-urostyle	Head width	Head length	Hind leg	Live Weight (grams)
A. fryi	26 ± 0.76 (40)	9.77 ± 0.28 (40)	7.3 ± 0.38 (24)	10.38 ± 0.27 (38)	2.02 ± 0.15 (38)
A. pluvialis	23.52 ± 0.4 (12)	9.03 ± 0.53 (12)	7.23 ± 0.27 (8)	11.13 ± 0.16 (11)	1.21 ± 0.09 (11)
A. robusta	22.49 ± 0.36 (66)	8.75 ± 0.13 (63)	7.07 ± 0.02 (30)	9.44 ± 0.13 (63)	1.32 ± 0.05 (66)
C. aenigma	19.46 ± 0.33 (46)	7.47 ± 0.13 (46)	6.16 ± 0.12 (44)	8.05 ± 0.11 (46)	0.84 ± 0.06 (20)
C. bombiens	13.97 ± 0.22 (48)	5.07 ± 0.08 (48)	4.37 ± 0.09 (36)	6.29 ± 0.08 (47)	0.29 ± 0.01 (32)
C.concinnus	19.07 ± 0.01 (6)	7.84 ± 0.77 (6)	6.08 ± 0.48 (6)	7.95 ± 0.37 (6)	N.A.
C. exiguus	14.91 ± 0.38 (23)	5.37 ± 0.17 (23)	4.31 ± 0.17 (19)	6.75 ± 0.12 (23)	0.43 ± 0.03 (4)
C. hosmeri	13.47 ± 0.17 (84)	5.36 ± 0.06 (84)	4.6 ± 0.07 (78)	5.54 ± 0.08 (84)	0.27 ± 0.01 (69)
C. infacetus	14.79 ± 0.11 (62)	5.89 ± 0.08 (62)	4.71 ± 0.05 (62)	7.36 ± 0.07 (62)	0.33 ± 0.01 (39)
C. mcdonaldi	21.1 ± 1.05 (12)	8.24 ± 0.4 (12)	6.71 ± 0.31 (12)	9.3 ± 0.37 (12)	1.14 (1)
C. monticola	20.34 ± 0.1 (4)	7.38 ± 0.55 (4)	7.55 (2)	7.82 ± 0.23 (4)	N.A.
C. neglectus	22.67 ± 0.3 (82)	8.85 ± 0.12 (82)	6.9 ± 0.09 (82)	8.34 ± 0.10 (82)	1.32 ± 0.33 (55)
C. ornatus	22.20 ± 0.49 (249)	7.78 ± 0.1 (245)	6.96 ± 0.15 (228)	9.3 ± 0.1 (223)	1.09 ± 0.19 (205)
C. saxatilis	38.58 ± 1.71 (11)	14.56 ± 0.55 (11)	11.96 ± 0.65 (11)	19.11 ± 0.78 (11)	N.A.

Mate choice by females and courtship behaviour

Brooke *et al.* (2000) and Hauselberger and Alford (2005) looked only at male calling behaviour; only Felton *et al.* (2006) have examined mate choice by females and subsequent behaviour in detail. They found that females chose males with lower dominant frequency of their calls. When females approached males, a complex series of courtship behaviours ensued. Male calls changed in character, females gave a response call, and males led females back to their nests, along paths that appeared to need to be at least a certain length. Females did not always deposit eggs; they chose to lay eggs more often in deeper nests with more solid walls and roofs, which were constructed by older males. Felton *et al.* (2006) concluded that because older males tended to produce calls with lower dominant frequencies, by choosing them females were maximising the chance that they would be led to a suitable nest site. Similar courtship behaviour has been observed in 5 other species (*A. robusta*, *C. neglectus*, *C. hosmeri*, *C. aenigma* and *C. bombiens*) and appears to be a common pattern in Australian microhylids (Hoskin 2004, Y.Williams pers obs).

Nests and clutch size

All of the Australian Wet Tropics microhylids are terrestrial breeders; they lay eggs on land and the eggs hatch out as froglets (Zweifel 1985). Therefore these species do not need water to breed, but they do require high levels of soil and litter moisture to prevent desiccation of their eggs during development. Dennis and Tennerry (1991) observed that microhylids inhabit the forest floor and trees away from creeks and place their eggs under logs, rocks and fallen debris or in cricket holes associated with high levels of soil moisture. The nest characteristics that Felton *et al.* (2006) found were favoured by females probably retains moisture better and may also reduce access to nests by predators.

Felton *et al.* (2006) also found that there was greater hatching success in nests guarded by males, presumably due to males reducing mortality from desiccation and predation, and that males spent approximately 50% of their time tending nests. Nests of all Wet Tropics species examined by Hoskin (2004) and Olding (1998) also showed a tendency to contain frogs, usually males but occasionally females, apparently guarding eggs. Nest guarding by adult frogs has been recorded in other microhylid species in New Guinea (Bickford 2002), who also attributed it to reducing predation and desiccation.

Multiple mating, i.e. individual frogs' attending egg masses of different developmental stages within the same or different nests, also appears to be present in both genera of Microhylids. Hoskin (2004) recorded multi-mating in *A. robusta* and two *Cophixalus* species however it appears to be most common in *C. ornatus*. Felton (1999) found that not only could males of *C. ornatus* have clutches of different ages within a single nest but some males had multiple nests. Hoskin (2004) also observed a captive male consuming some of the eggs and also moving eggs between nest sites; however this has not been seen in wild frogs. The information which is most important to determine the reproductive output of microhylid species is if females multi-clutch, that is, producing more than one egg mass at different times within the same breeding season. However it is still unknown if multi-clutching occurs in any of these species.

Hoskin (2004) found variation between all species in clutch size with numbers of eggs varying between 6 and 22 and averaging around 12. This was from only 29 observations across all 14 species and demonstrates just how little we know about clutch size and actual female fecundity, highlighting the need for more research in this area.

Longevity

An important life history trait which has not been well studied in these animals is their longevity. Felton *et al.* (2006) used skeletochronology (by counting lines of arrested growth, LAGs, in bones from clipped toes) to investigate the age distribution of *C. ornatus*. The oldest individual sampled was 14 years old, and males with nests were aged between 4 and 14 years. Age of adult males was not correlated to SUL. The average age of males was 5.5. Age was positively correlated with nest characteristics favoured by females; older males had nests with sizes and compositions favoured by females, and were more successful at attracting females and persuading them to lay eggs. The age distributions of females have not been determined for any species of Australian microhylids.

Diet

It has previously been thought that microhylids primarily eat ants, however Hauselberger (2002) compared the diets of *C. ornatus* and *A. robusta*, and found that the latter species had a much more diverse diet. This finding has been further confirmed in Chapter 4, which shows that *C. ornatus* is the species most specialised on ants; 7 of the other species of *Cophixalus* have much broader diets.

Local spatial distribution and site fidelity in calling males

The spatial distributions of calling male *C. ornatus* and *A. robusta* have been studied in depth. Both species show aggregation at multiple spatial scales and do not appear to exhibit territorial behaviour (Brooke *et al.* 2000; Hauselberger and Alford 2005). The benefits of these aggregations are unknown; reductions in predation, spatial variability in the availability of nest and call sites, and increases in the distance from which females are attracted to choruses have all been suggested. Both studies found within season site fidelity in male use of calling sites, and some of the *C. ornatus* initially located by Brooke *et al.* (2000) were found at the same calling sites three years after they were marked, indicating that there is site fidelity across years.

Phylogeny

Microhylids almost certainly originated in Gondwanaland (Savage, 1973) however it is unclear whether the Austropapuan microhylids initially radiated in New Guinea and dispersed into Australia or vice versa. The first modern revision of the taxonomy of Australian species was undertaken by Zweifel (1985), who described 12 new species. Since then 2 additional species have been described: *C. monticola* (Richards *et al.* 1994) and *C. aenigma* Hoskin (2004). Zweifel (2000) split the genus *Austrochaperina* from *Sphenophryne* based on a thorough analysis of morphological characters. Recently Hoskin (2004) carried out a comprehensive analysis of the genetics and call structure of Australian microhylids. He determined that there are 14 species of *Cophixalus* and 5 species of *Austrochaperina* within Australia. All but one of these species is endemic to Australia; only *A. gracilipes* which occurs in Cape York Peninsula in Australia, is shared with New Guinea.

Hoskin (2004) constructed the first near-comprehensive molecular phylogeny of the Australian microhylids (Figure 2). It includes all but two of the Australian species (*C. peninsularis* and *A. adelphe)*, which were excluded because he could not obtain samples. He found that the Australian *Cophixalus* form a monophyletic clade which is the sister taxon to the genus *Austrochaperina*. He found good support for the species level divergence in the clade, but was not able to resolve all of the ambiguity in the deeper resolution of the tree, e.g. the relationships among the four major *Cophixalus* clades.

Hoskins' genetic analysis of the genus *Cophixalus* indicates that it is a very old taxon with speciation events occurring at around 8-10 mya during the late Miocene (Hoskin 1996). Hoskin also found substantial genetic structure within some species (particularly *C. ornatus*, *C. neglectus* and *C. aenigma*). This structure is likely to reflect the expansion and contraction of rainforest in this region during the Pleistocene, when connectivity between populations of these frogs was limited by cool, dry conditions (Hoskin 1996). This is in accordance with the suggestion by Williams and Pearson (1997) that patterns of vertebrate species diversity across the Wet Tropics are due to species filters - the extinction of species due to climatic changes which resulted in rainforest contraction in the Pleistocene.

The distributions of many microhylids were first presented by Zweifel (1985) and later were revised by McDonald (1992). Using his genetic data, Hoskin (2004) further modified the known distributions. Following this, the ranges of some species expanded substantially (e.g. *C. bombiens*), while those of other species were found to be much smaller than previously thought (e.g. *C. exiguus* and *C. concinnus*). Hoskin's (2004) data, with additional data on distributions from Williams *et al.* (1993) and Shoo and Williams (2004), were used to generate the distribution maps (Figure 3a to 3l).

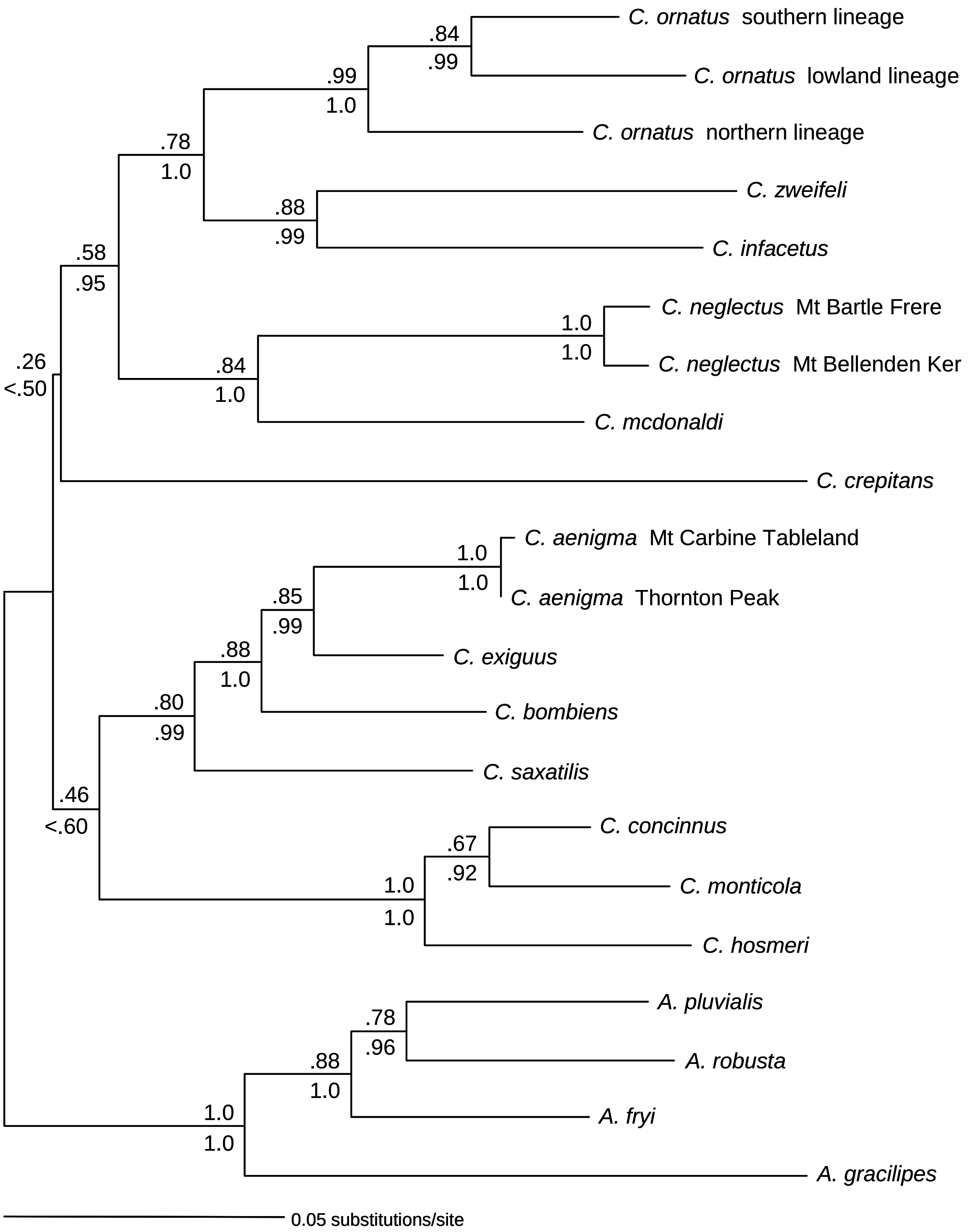


Figure 2: Phylogeny of Cophixalus and Austrochaperina in Australia based on mitrochondral DNA (from Hoskin, 2004).

Species distribution maps

The distributions of microhylid species has just been revised by Williams (2006). Prior to this publication and Hoskins (2004), there was some confusion regarding the distributions of many microhylid species. However the distribution of Australian microhylids has now been clarified, with only a few species (e.g. *C. exiguus*) remaining uncertain. Further studies in the field will be required to confirm the extent of the ranges of these species. The maps presented here (reproduced with permission from Williams, 2006) for 13 of the 14 microhylid species found within the Wet Tropics region are the most accurate maps available. The distribution of *C. mcdonaldi* has not currently been fully determined as this species occurs outside the Wet Tropics region proper although is closely related to other species in the region.

The three species of *Austrochaperina* have some of the largest distributions among the Australian microhylids. One species (*A. pluvialis*) occurs across much of the Wet Tropics, while the other two species (*A. fryi* and *A. robusta*) appear to be allopatric with only a very small area of contact between them. The distributions of these species are shown in Figure 3a to 3c:

Austrochaperina fryi: Occurs from Lake Barrine on the Atherton Tablelands (inland from Cairns) to just south of Cooktown over an area of approximately 4660km^2 (Figure 3a). Its altitudinal range appears to be from around 600 to 1300 m and was found to be more of an upland species than previously recorded.

Austrochaperina pluvialis*:* Occurs from the Seaview range (inland from Ingham) to rainforest areas just south of Cooktown over a range approximately 5970 km^2 (Figure 3 b). The altitudinal range of this species is from 0 to 900 m and it generally appears to be a lowland species. While there are records of this species at higher altitudes, some of these records may be due to confusion because of the similarity between species if they are not calling.

Austrochaperina robusta: Occurs from Paluma range north of Townsville to around the Atherton Tablelands near Lake Eacham over a range of 5211km^2 (Figure 3c). The species occurs from 400 to 1590m although is most abundant at elevations near 1000m and is considered an upland species.

The species in the genus *Cophixalus* vary greatly in distributional ranges, from single mountain top endemics to species that inhabit the entire region. The distributions of these species are shown in Figure 3d to Figure 3l.

Cophixalus aenigma: This species has only recently been described (Hoskin 2004); it had previously been included in the species *C. concinnus*. This species occurs from Mount Lewis on the Carbine Uplands (inland from Mossman) to just south of Cooktown in the Finnigan Uplands over an area of 930km^2 (Figure 3d). It generally occurs above 750m but has been found to occur in small numbers at lower altitudes on Thornton Peak.

Cophixalus bombiens: This species was long considered to be endemic only to the Windsor Uplands however further field surveys and genetic analysis by Hoskin (2004) have shown it to occur from Cape Tribulation to Mt Finnigan south of Cooktown, an area of 695km^2 (Figure 3e) . It occurs over a wide range of elevations, from 20 to 1200m, within rainforest areas.

Cophixalus concinnus: This single mountain top endemic has the smallest geographic range of any vertebrate in the Wet Tropics region of just 3km^2 and is restricted to above 1100m on Thornton Peak (Figure 3f). It is generally found in boulder outcrops on which rainforest vegetation is present (Hoskin and Higgie 2005).

Cophixalus exiguus: Previously considered to be a widely distributed species, genetic and field sampling has shown that this species is restricted to Big Tableland, Mt Harley and Gap Creek just south of Cooktown over an area of 318km^2 (Figure 3g). The confusion arose because it is very morphologically similar to *C. bombiens* and has a call similar to that of *C. aenigma.* More surveys are required to determine the full extent of the range of this species.

Cophixalus hosmeri: This species is limited in distribution to the Carbine Uplands subregion (inland from Mossman), mainly occurring at Mt Lewis and Mt Spurgeon over an area of 300km^2 (Figure 3h). It occurs at elevations between 900 and 1250m with peak abundance at around 1000 to 1200m (Shoo and Williams 2004).

Cophixalus infacetus: This is the second most widespread species of *Cophixalus,* however it appears to be very patchily distributed within its range from Broadwater (inland from Ingham) to Crystal Cascades (just north of Cairns), covering a total area of 3120 km^2 (Figure 3i). It has an elevational range from 0 to 800m, with greatest abundance at about 600m, however it generally only occurs on the eastern side of the range and is only found on the western side at Kirrima Uplands.

Cophixalus monticola: A single mountain top endemic of Mt Lewis in the Carbine Uplands. It occurs in an area of 208km^2, and only above 1100m. It is generally found in palms and appears to be quite patchy in its distribution.

Cophixalus neglectus: This species is found only on the two highest mountain tops in North Queensland, Mt Bellenden Ker and Mt Bartle Frere, where it occupies an area of approximately 37 km^2 (Figure 3j). It has a disjunct distribution, with an area of lower elevation rainforest between the two populations potentially being a barrier to dispersal. Recent surveys by Shoo and Williams (2004) and Hoskin (2004) only found this species above 1150m however there have been previous reports of it as low as 900m.

Cophixalus ornatus: The most widespread of all Australian microhylid species. It occurs from the Bluewater range inland of Townsville to the Carbine Uplands (north of Mossman), ranging over an area of 6550 km^2 (Figure 3 k). It is by far the most general in habitat preferences; it occurs outside of rainforest in Wet Sclerophyll and over the widest elevational spread, 0 to 1590m. However it occurs at the greatest abundance from 400 to 1000m. There is one gap in this species otherwise continuous range at the Seaview Range, where there may have been no refugial areas during Pleistocene rainforest contractions; even today this area appears to be too dry and thus suboptimal habitat.

Cophixalus saxatilis: Found only in the rocky outcrop of Black Mountain just south of Cooktown, it has a very restricted distribution of 5 km^2 (Figure 3l). It occurs outside of rainforest although the boulder fields may offer some buffering from the warm and dry environment. This is the largest microhylid species in the region. Very little ecological data exists for this species due to the boulder fields making it very hard to access and find the frogs.

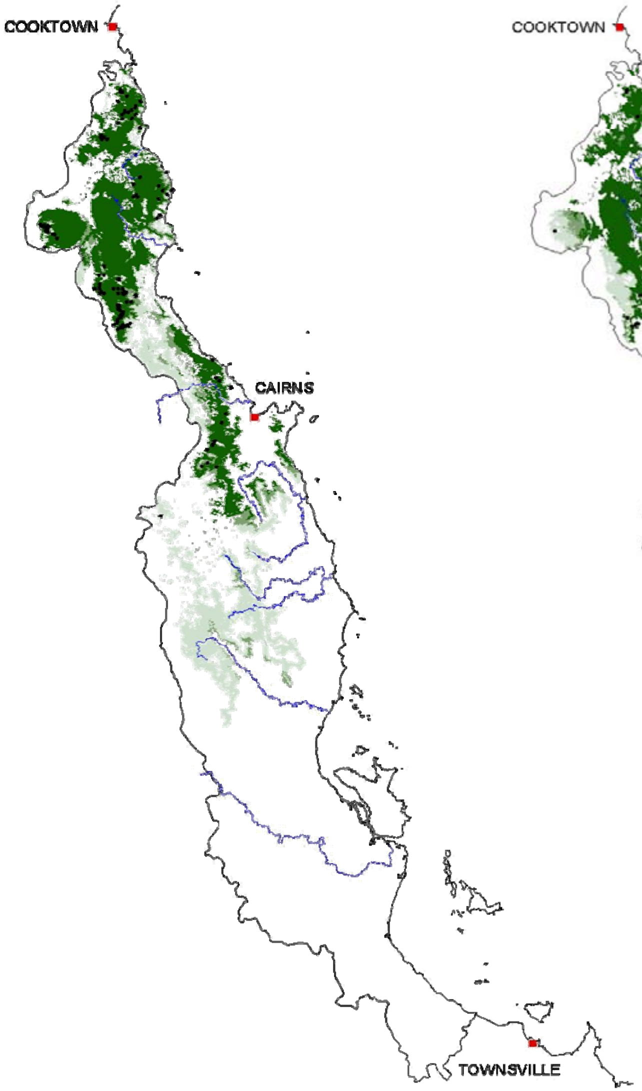
Abundance

Shoo and Williams (2004) carried out standardised sampling of many species over much of their ranges. These data have clarified the picture of the abundances of many species and their elevational distributions. Shoo and Williams (2004) also estimated density per hectare for many species, and found that it varies greatly within and among species (Table 2).

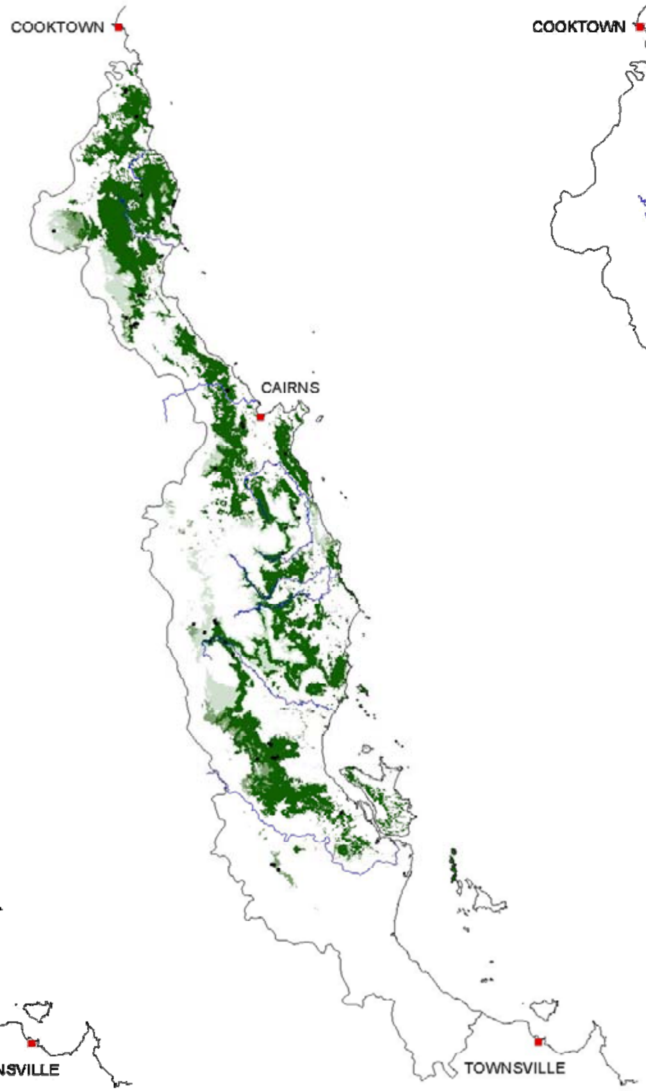
Table 2: The ranges and abundances per hectare of 14 microhylid species.

Species	Species range (km^2)	Abundance per hectare (number of surveys)
A. fryi	4660	6 (132)
A. pluvialis	5970	1 (328)
A. robusta	5211	13 (258)
C. aenigma	930	17 (78)
C. bombiens	695	30 (51)
C. concinnus	3	78 (8)
C. exiguus	318	10 (6)
C. hosmeri	300	42 (46)
C. infacetus	3120	6 (184)
C. mcdonaldi	28	N.A
C. monticola	208	31 (21)
C. neglectus	37	18 (38)
C. ornatus	6550	28 (328)
C. saxatilis	5	N.A

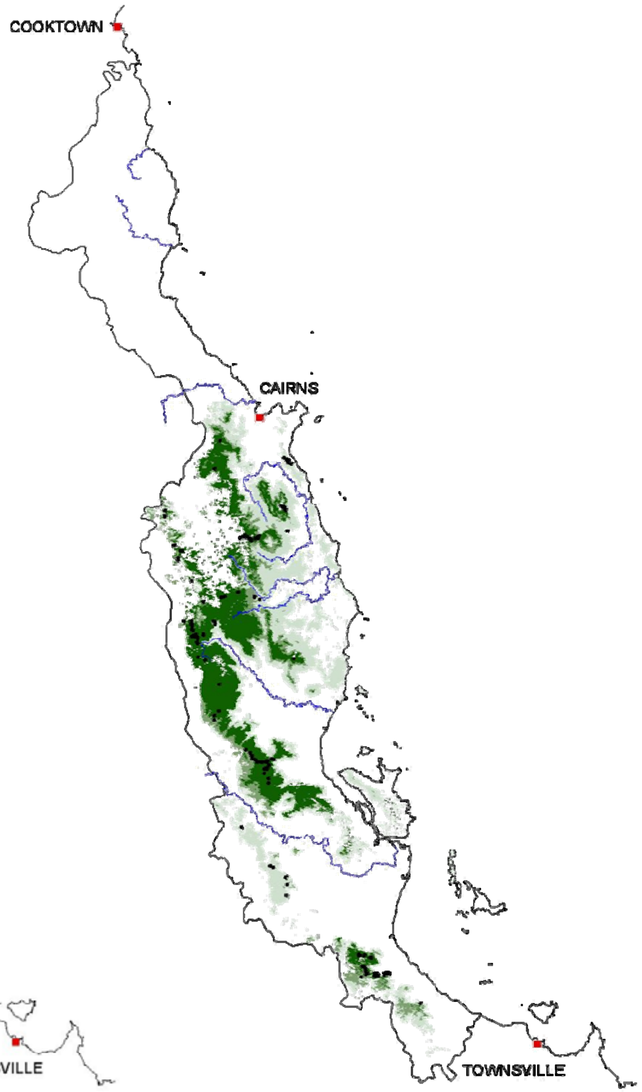
a) *Austrochaperina fryi*



b) *Austrochaperina pluvialis*



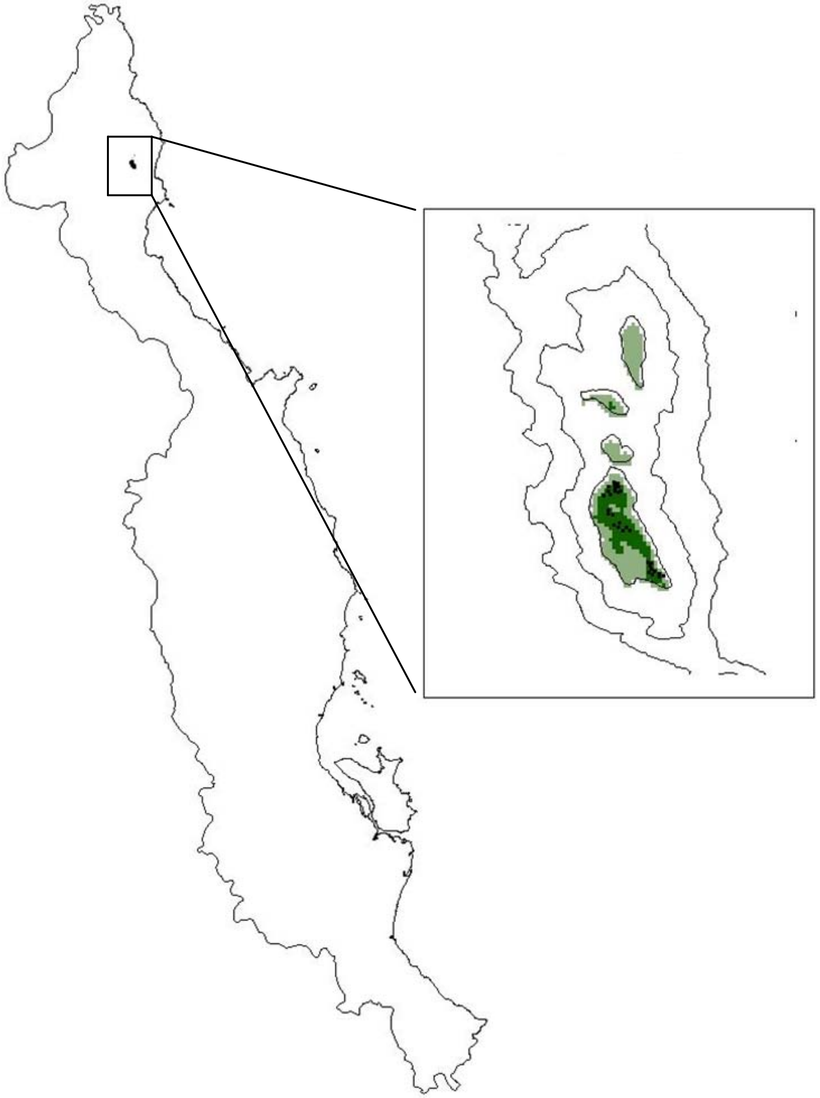
c) *Austrochaperina robusta*



d) *Cophixalus aenigma*

e) *Cophixalus bombiens*

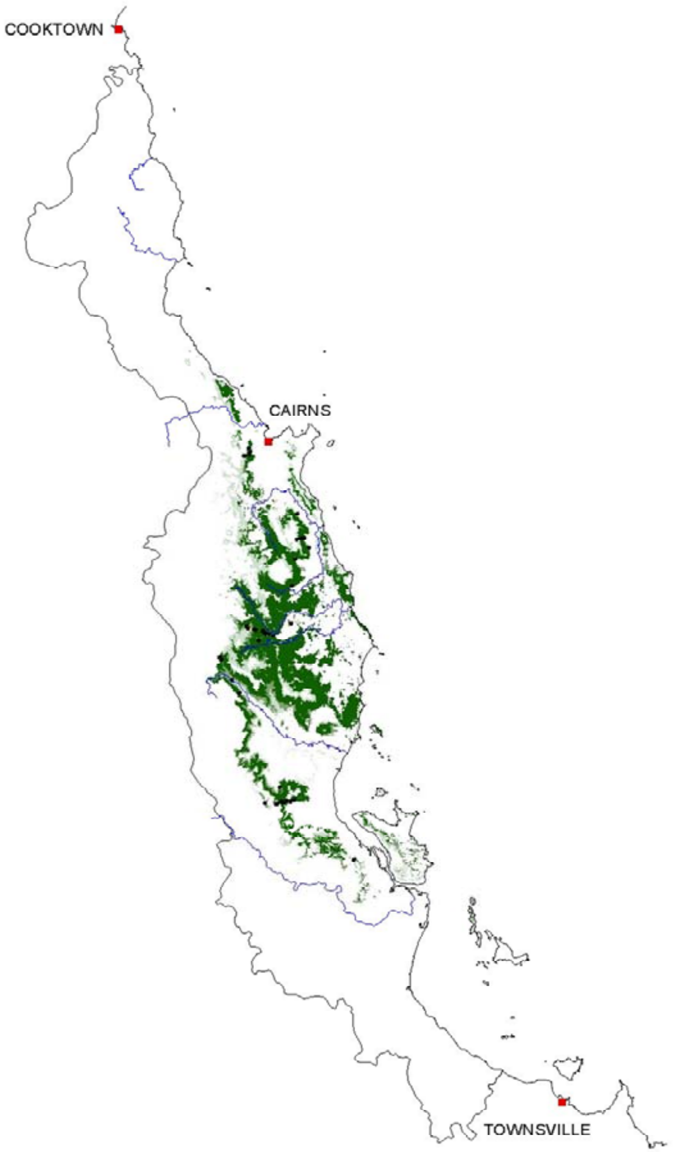
f) *Cophixalus concinnus*



g) *Cophixalus exiguus*

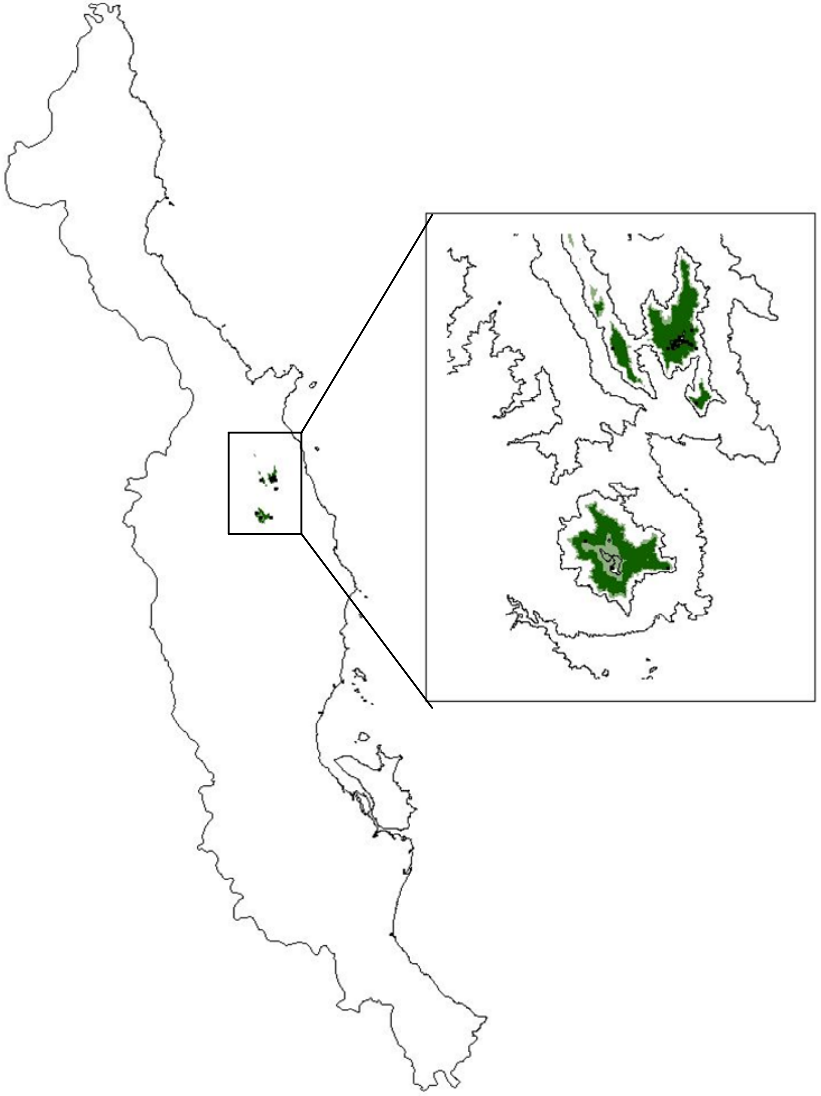
h) *Cophixalus hosmeri*

i) *Cophixalus infacetus*

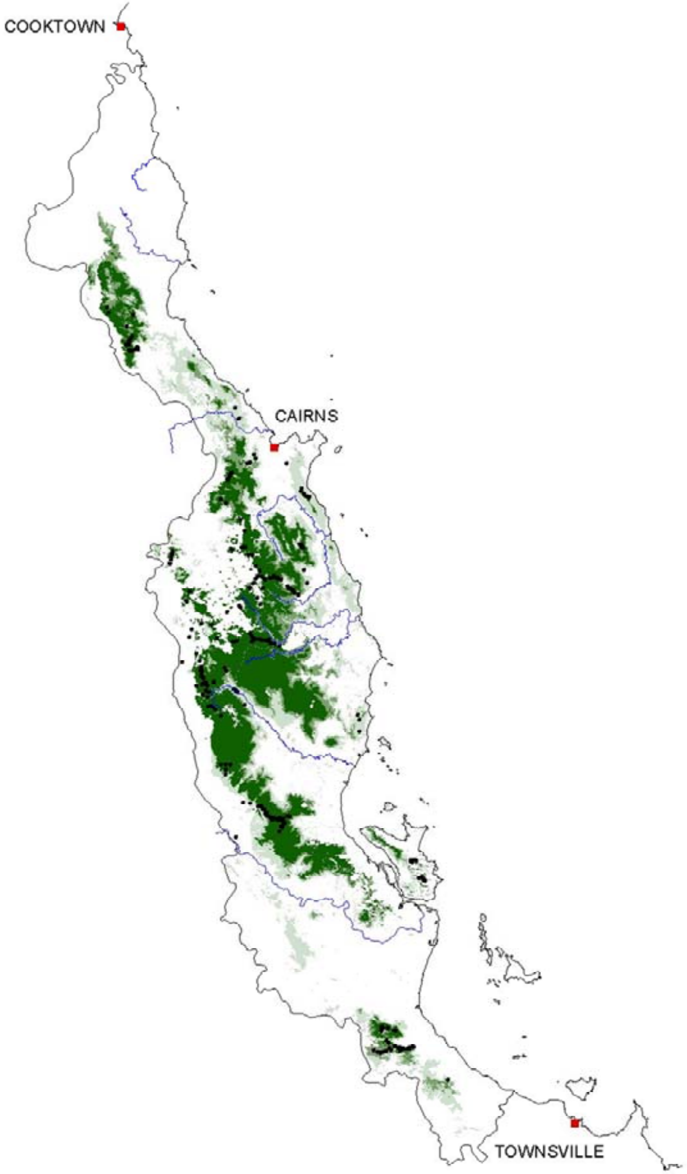


j) *Cophixalus monticola*

k) *Cophixalus neglectus*



k) *Cophixalus ornatus*



l) *Cophixalus saxatilis*

Figure 3a to 3l. The distribution of each microhylid species that occurs within the Wet Tropic region (presented with permission of Williams 2006).

Species richness

Williams and Hero (2001) observed that the strongest correlate of species richness for microhylids was the consistency of rainfall throughout the year. Given the breeding biology of these frogs, and their reliance on moisture to maintain eggs in leaf litter, this is unsurprising. Temperature (as a surrogate for elevation) was also strongly negatively correlated with microhylid species richness, indicating that microhylids generally occur at higher elevations, where temperatures are lower.

This study also found that species richness was not related to area of rainforest and thus concluded that the species – area relationship should be examined at a finer scale. Williams and Hero (2001) suggest that vicariant speciation and limited dispersal may be the most important influences in microhylid diversity patterns. This suggestion is backed up by genetic analysis carried out by Hoskin (2004) which found very deep species branches in this genus suggesting much older diverges than previously thought.

A more recent paper by Graham *et al.* (2006) examined in depth the predictors of species richness of all vertebrates in the Wet Tropics. This paper compares the power of historical patterns of rainforest expansion and contraction with that of present day shapes and areas of extant rainforest patches (which could explain patterns of species diversity; Williams and Pearson 1997) to see which best explain species richness patterns. Although the present shape and area of rainforest patches explains patterns in most vertebrate groups with high dispersal, it does not explain patterns in some taxa, including microhylid frogs (Williams and Pearson 1997). Instead patterns of species richness in microhylids are best explained by the long-term habitat stability of a region (Graham *et al.* 2006). Microhylids species are found in high numbers only in regions in which rainforest has been continually available over very long time periods, persisting through historical expansions and contractions of rainforest. The most species rich areas for Microhylids are the Carbine Upland (this includes Mt Lewis) with 6 species and the Atherton Tablelands with 5 to 6 species (see Figure 4). Graham *et al.* (2006) suggested that the major refugial areas for microhylids have been Bellenden Ker and the Carbine, Thornthon, and Finnigan Uplands (Figure 1). This finding is supported by the greater species richness found on these mountain tops and the presence and persistence of single mountain top endemics thought time.

The species of *C. mcdonaldi* is not represented on this map of species richness as it occurs only in rainforest on the top of Mt Elliot (above 900m) just south of Townsville outside of what is considered the Wet Tropics biogeographic region. This species while it occurs on its own on the top of Mt Elliot is however closely related to *C. neglectus* (only found on Mt Bartle Frere and Mt Bellenden Ker) and considered as an important species thus included in this review.

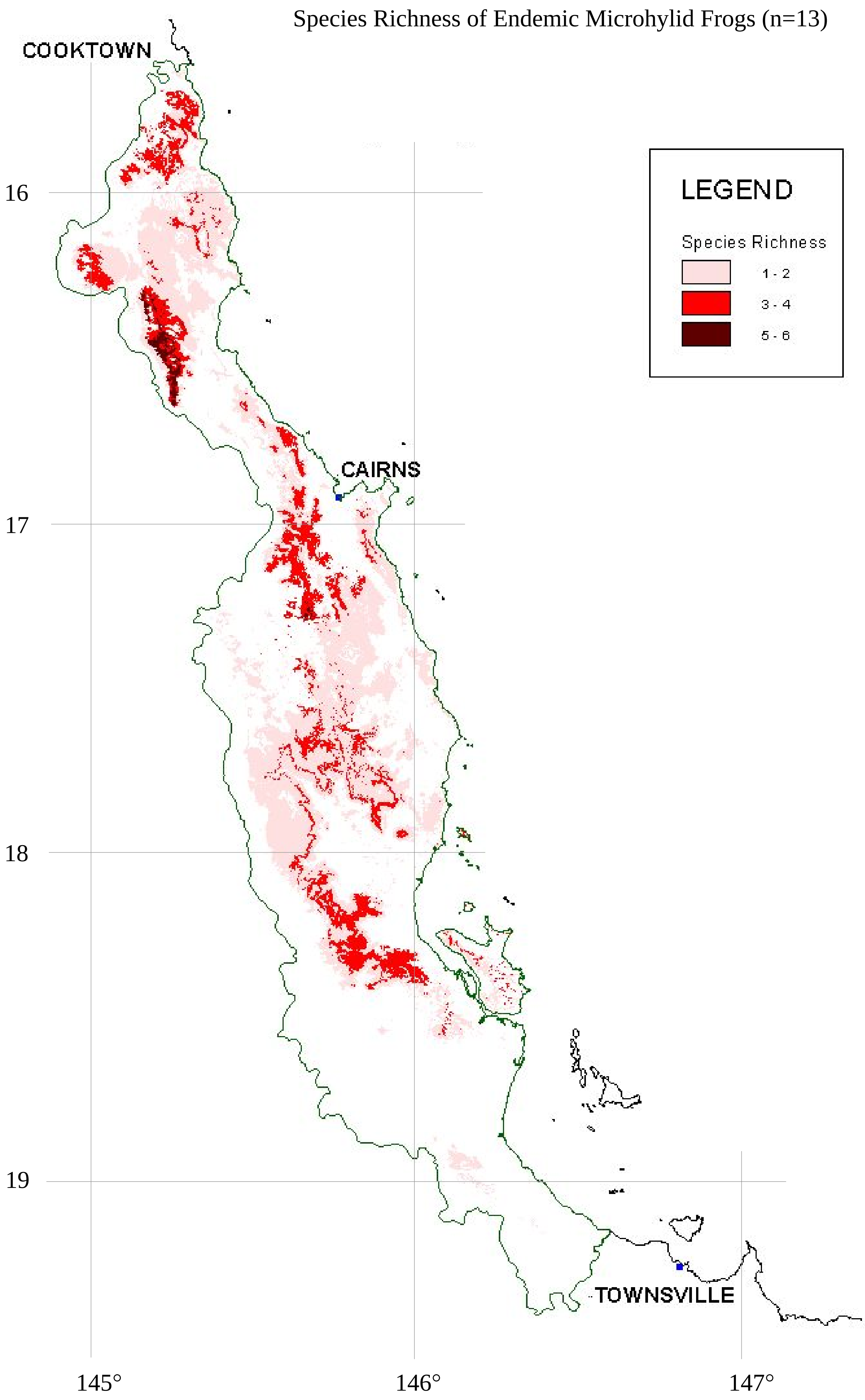

Species Richness of Endemic Microhylid Frogs (n=13)
COOKTOWN
CAIRNS
TOWNSVILLE
LEGEND
Species Richness
1 - 2
3 - 4
5 - 6
16
17
18
19
145°
146°
147°

Figure 4. The species richness of Microhylid frogs within the Wet Tropics region. Darker colours of red denote areas of higher species richness than lighter colours (Figure from Williams 2006).

Threatening processes

Amphibian declines

In the late 1980's it was recognised that a global decline in amphibian species was occurring (Barinaga, 1990). In 1993 Richards *et al.* recorded widespread losses of stream dwelling frogs, with three species disappearing from much of the Wet Tropics (*Taudactylus rheophilus, Litoria lorica* and *L. nyakalensis*) and rapid declines of upland populations of three other species (*L.nannotis, L. rheocola* and *Nyctimystes dayi*). Unfortunately this survey did not include microhylids, but subsequent data collection strongly suggests that microhylids have not been affected by whatever agent caused the declines in other Wet Tropics species, since their abundance and presence in all Wet Tropic regions are still very high.

Alford and Richards (1999) reviewed the extent and possible causes of global amphibian declines. They suggested that some declines have reasonably clear anthropogenic causes, but that the causes of many others were unknown. More recently, Stuart *et al.* (2004) reviewed the data in light of many recent studies, and suggested that many amphibian declines in apparently undisturbed habitats have been caused by the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*). It is not clear why this disease has had no detectable affect on microhylids. However it is possible that this fungus can infect and kill microhylids held in captivity (Hoskin pers comm.). However, it has not been found infecting microhylids in the field (Hauselberger, 2002 – 42 *A. robusta* tested negative, Williams- 36 animals across all species tested negative, unpublished). Williams and Hero (1998) showed that frog species which had suffered the greatest declines were regionally endemic specialists that had low fecundity, a high degree of habitat specialisation and reproduced in flowing streams. In an MDS analysis the fact that microhylids were terrestrial breeders seems to remove them from the effects which caused declines in stream dwelling frogs. Williams and Hero (1998) suggested that by having terrestrial eggs microhylids not only used the entire rainforest habitat available but removed themselves from stream habitats where factors causing global decline in frog species seem to be associated.

Climate change

Models of global climate change indicate that temperature increases of 1^{o} to 6^{o} C in the dry season and reductions in orographic cloud layer are likely to occur in the Wet Tropics within this century (Williams *et al.* 2003). Williams *et al.* (2003) predicted that much of the fauna, including microhylid frogs, will be strongly affected by these changes. GIS modelling of the effects of increased temperature on range sizes indicated that there would be a total loss of the core habitat of regionally endemic rainforest species with 7^{o}C of warming. Of the 21 most vulnerable species (i.e. those species which are expected to lose 50% of core habitat with 1^{o}C of warming), five are microhylid frogs (*C. concinnus*, *C. hosmeri*, *C. neglectus*, *C. exiguus* and *C. monticola* in order of vulnerability; Williams and Hilbert 2006). All of these species are restricted to mountain tops. This is a problem, because climate change should cause species to shift their latitudinal or altitudinal ranges, moving to cooler habitats. Species on mountain tops would need to shift latitudinally, since they are already at the limits of their potential elevational ranges. This is likely to pose a problem for microhylid frogs, as changes in latitudinal range would require dispersal over long distances through unsuitable habitat, and they appear to have limited dispersal ability. Given this, the greatest threat to the survival of microhylids at present is the impacts of climate change. The family Microhylidae contains the greatest diversity of rainforest endemic frogs in the Wet Tropics (Williams and Hero 1998), and there have already been substantial losses in diversity in other families because of amphibian declines, so major losses in this family will severely affect the remaining amphibian biodiversity of the region.

Conclusion

While knowledge of the biology of microhylids still lags behind that of other frog taxa, recent advances in research on the group have filled in many of the gaps, including knowledge of their general biology and ecology. However, there is still a paucity of information on the reproductive output and longevity (and thus lifetime reproductive success) of all species, and also on their physiological tolerances. Most information on behaviour and population density is biased toward males because of the difficulty of locating females. The looming threat of global warming makes it imperative to gain a superior understanding of the behaviour and ecology of these species so that effects on them can be predicted and ameliorated.

CHAPTER 3: NICHE BREADTH IN RARE AND COMMON SPECIES OF MICROHYLID FROGS: EFFECTS OF ENVIRONMENT AND HABITAT SELECTION

Introduction

Geographically common species often have broad niches while the niche breadth of geographically rare species are comparatively narrow (Brown 1984). Furthermore a wider niche breadth may confer greater longevity upon species (McKinney 1997). Brown (1984) suggested in "the jack of all trades is master of all" hypothesis that a species which can exploit a wider range of conditions locally and thus also achieve high densities will be able to survive in more places and over a larger area. The niche breadth of a species may reflect the resources (habitat or diet) utilised and / or the environmental conditions in which the species can reproduce, grow and survive (Hutchinson 1957). However, since niche space may not be directly related to geographic space, it is feasible that some geographically common species may have limited niche breadth while geographically rare species may have relatively broad niche breadth.

Ambiguity and misuse of terminology is frequent with respect to the usage of habitat, niche and environment. Kearney (2006) emphasised this and proposed the following definitions, which are used throughout this chapter. Habitat is defined as a description of a physical place where an organism either actually or potentially lives; Environment is the biotic and abiotic phenomena surrounding and potentially interacting with an organism; and the Niche is a subset of those environmental conditions which affect a particular organism, where the average absolute fitness of individuals in a population is greater or equal to one. The definition of niche includes the fundamental and realised niches (*sensu* Hutchinson 1957). The fundamental niche can be thought of as the n-dimensional hypervolume representing the physiological limits of the species in the environment, excluding any biotic interactions (e.g., competition or predation), whereas the realised niche is a smaller region, a subset of the fundamental niche that is actually utilised when accounting for biotic interactions.

The abundance and distribution of a species is limited by the combination of physical and biotic environmental variables that determine its niche (Brown 1984). Brown *et al.* (1996) showed that combinations of 5 to 10 environmental variables could be used to explain the distribution and abundance of most species. The environment in which a species occurs is a reflection on one hand of its physiological tolerances and on the other the biological stresses in which it can persist (Brown *et al.* 1996). That is, an organisms' realised niche typically represents a smaller subset of the theoretically available environment that can be occupied. However, the environmental variables which affect a species' distribution are often species-specific with no *a priori* set of variables recognised. The spatial distribution of species within their ranges is also rarely uniform. Rather there is a tendency for species to be more abundant at the centre of their ranges than at the boundaries (Brown 1984, Brown *et al.* 1995). Patterns of abundance within species' ranges may be explored by examining habitat specificity, species physiological tolerances and population dynamics. Rarity theory predicts that widespread species should be more abundant and have a greater niche breadth (Gaston 1994).

Species with low habitat specificity occupy a broad range of habitats, whereas habitat specialists are restricted to a few specialised habitats in a few sites (Rabinowitz *et al.* 1986). Thus, habitat specificity is a measure of the breadth of habitat preferred by a species. Based on these definitions, species that are habitat specialists may have a competitive advantage over generalist species, where increased resource availability may lead to increased fitness and high local abundances (Rosenzweig and Lomonlino 1997). While widespread species may be competitively subordinate in many areas, they are able to use a wider range of habitats and thus may have greater resilience to factors which cause extinction. Common species are more likely to be habitat generalists, whereas 'locally common,' 'scarce,' and endemic species are more likely to be specialised (Mace and Kershaw 1997). However, specialisation can increase extinction risk as habitat specialists should be more sensitive to perturbations than species that occur in a variety of habitats (Arita *et al.* 1990).

Endemic microhylid frogs of the Wet Tropics in northern Queensland vary in their distribution from geographically restricted (entire distribution being a single mountain top) to geographically widespread across the entire region. In this chapter, I quantitatively describe the niche of 13 microhylid frog species. First, I compare geographic breadth (distribution relative to available geographic space) with niche breadth (niche volume in n-dimensional space [*sensu* Hutchinson 1957]) relative to available niche space. Then I examine environmental correlates of species abundance within each species' distribution, identifying common environmental determinants of abundance for rare and common species. Finally I examine the abundance and microhabitat use for a subset of these species.

Methods

Study organisms

This study used 13 of the 14 species of microhylid frogs found in the Australian Wet Tropics biogeographic region in northeastern Queensland (Figure 1). *Cophixalus mcdonaldi* was excluded due to limited information. These frogs are small (14 - 35mm) terrestrial breeders, generally occurring in rainforest habitats. The species in this genus have deep lineages of the order of 10 million years old (Hoskin 2004), and current patterns of distribution and species richness in the group are related to geographic variation in rainforest stability during Quaternary climate fluctuations (Graham *et al.* 2006). Microhylids are the only group in the region that do not exhibit a significant species-area relationship (Williams and Hero 2001) and their distribution patterns suggest a complex interaction between *in-situ* survival in isolated mountaintops and non-random patterns of local extinction (Williams and Pearson 1997; Williams and Hero 2001; Hoskin 2004; Graham *et al.* 2006). These species have high local abundance and are easily located and identified by male calls.

Records of species presence in the Australian Wet Tropics region were obtained from three main sources: standardised surveys conducted in this study; the Queensland Museum and Williams (2006). Abundance estimates were obtained from standardised surveys. The standardised surveys were carried out for 12 species of microhylid frogs (excluding *C. mcdonaldi* and *C. saxatilis* due to insufficient data) in the Wet Tropics Biogeographic region. Surveys were carried out across the entire geographic range of all species as in Shoo and Williams (2004). A standardised survey consisted of a 50 m long by 20 m wide transect in which all calling frogs were counted over approximately a 30 minute period. Transects were carried out at every 50 meter change in altitude and only on nights in which good frog calling was likely (see sampling condition criteria in Chapter 6). Standardised surveys for *C. exiguus* and *C. concinnus* were conducted by C. Hoskin and S. Williams (pers comm.) and data from Hoskin and Higgie (2005) were also used in this study as similar sampling methodologies were employed. The number of transects used in the analysis for each species were: *Austrochaperina fryi* -132, *A. pluvialis* – 328, *A. robusta* – 258, *Cophixalus aenigma* – 78, *C. bombiens* – 51, *C. concinnus* – 8, *C. exiguus* – 6, *C. hosmeri* – 46, *C. infacetus* – 184, *C. monticola* – 21, *C. neglectus* – 38, *C. ornatus* – 328.

Geographic area and niche breadth

Relative geographic area and niche volumes were estimated for each of the 13 species of microhylid frogs. The relative geographic area of a species' distribution was estimated as the proportion of the available area in the Wet Tropics (some 19800 km^2). Species distributions were based on the bioclimatic models of Williams *et al.* (2003) and Williams (2006). Climatic variables were based on Bioclim (Houlder *et al* 2000) climate information created for the Wet Tropics by Rochester (2003).

Macro-habitat: environmental correlates of species occurrence

Estimates of a species niche (macro habitat) were created using two methods. The first method defined the available niche as the minimum concave hull that encloses all combinations of mean annual temperature and precipitation found in the Wet Tropics buffered by 0.1 ^{o}C in the temperature axis and 50 mm precipitation on the precipitation axis. The niche of each species was estimated as the minimum convex hull (polygon containing all combinations of temperature and precipitation representing species occurrences) clipped by the concave hull of the Wet Tropics. From this, the proportion of available niche utilised by each species was then estimated.

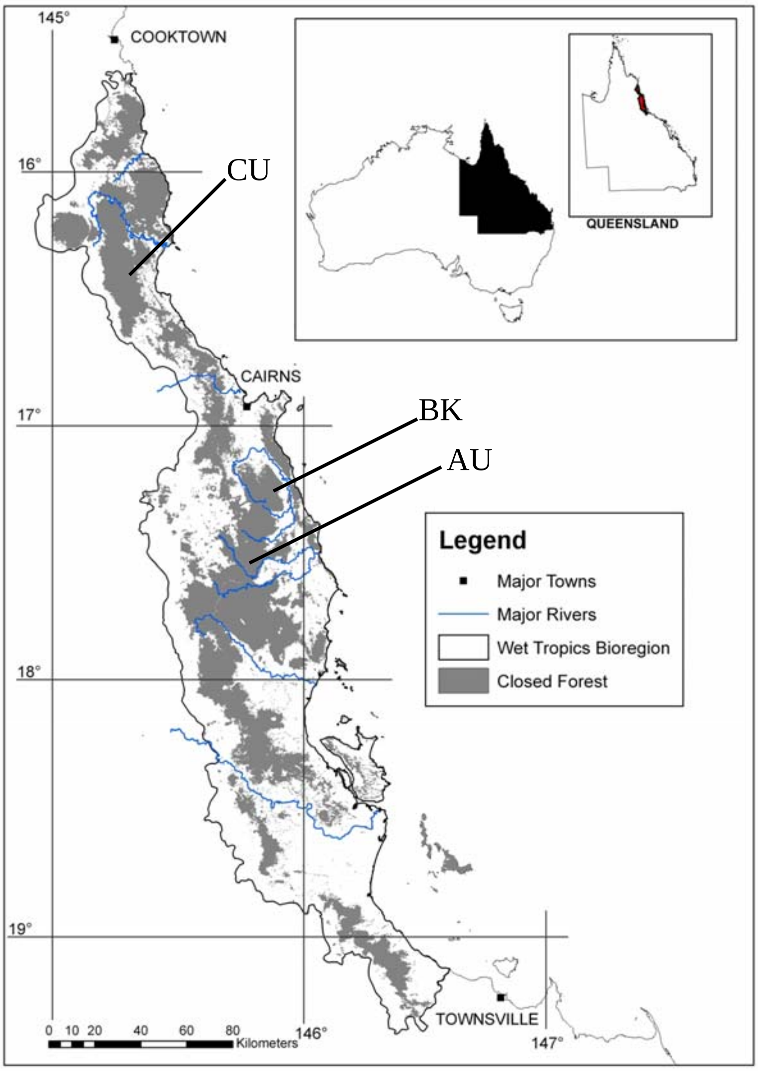


Figure 1: The Wet Tropics Bioregion with rainforest shown as the shaded area. The three permanent sites used in this study to examine species microhabitat use are indicated: CU- Mt Lewis in the Carbine Uplands, BK – Bellenden Ker, and AU –Atherton Uplands.

The second method estimates the n-dimensional hypervolume (*sensu* Hutchinson 1967) that describes the niche of a species in 2, 4 and 8 dimensions. Species occurrences represent points with the position of each point being described in 2, 4 or 8 dimensions (its environmental attributes). The size of the n-dimensional hypervolume was estimated using Qhull (Barber *et al.* 1996) to first compute the minimum convex hull encapsulating all occurrence points, and then estimating its volume. For any set of points S, a minimum convex hull is the smallest convex set of points containing all points within S. In 2 dimensional space, the convex hull can be can be visualised as a rubber band stretched and released around all points in S. The length of the rubber band is the minimum polygon perimeter required to surround all points in S. The available niche (volume estimated for the entire Wet Tropics) was estimated as the mean volume of 10 replicates of 10,000 randomly selected locations within the Wet Tropics. It was found that only 7500 random locations were needed to accurately characterise the volume of the available niche (via accumulation curves, see appendix 1). The species-specific niche volumes were estimated using environmental data for all occurrences of the species. The reliability of the estimates was determined by examining accumulation curves using subsets of available occurrence information (Appendix 1). This method allowed for the comparisons of the niche in 2, 4 and 8 dimensions. The 2D volumes were based on mean annual temperature and precipitation; the 4D volumes also included temperature and precipitation seasonality; and the 8D volumes added temperature during the warmest and coolest quarter and precipitation during the wettest and driest quarter.

Meso-habitat: environmental correlates of species abundance within distributions

Linear multiple regressions were used to examine how much variance in microhylid abundances could be explained using macro- and meso-scale habitat variables. Three sets of predictor variables were examined (Table 1), including vegetation (Stanton vegetation class 4; Stanton and Stanton 2005), topographic and climatic variables (Rochester 2003) (Table 1).

Table 1. The three sets of predictor variables used in the multiple regression analysis to examine the influence of broad-scale habitat characteristics on microhylid abundances. Vegetation variables are for Stanton vegetation class 4 (Stanton and Stanton 2005) and the topographic and climatic variables were created by Rochester (2003).

	Code	Description	Units	Range
Vegetation	MeVF	Mesophyll vine forest	Yes/No	0-1
	MiFT	Microphyll fern thicket	Yes/No	0-1
	MiVF	Microphyll vine forest	Yes/No	0-1
	NVF	Notophyll vine forest	Yes/No	0-1
Topography	alt	Altitude (meters above sea level)	meters	26-1540
	slope	Slope of the landscape	Deg C	0-43.4
	N-S	North-South component of the aspect, North=0 and South=180	Deg C	0-180
	E-W	East-West component of the aspect, East=0 and West=180	Deg C	0-180
Climate	bc01	Annual mean temperature	Deg C	15.7-23.9
	bc02	Mean diurnal temperature range	Deg C	7.1-10.3
	bc04	Temperature seasonality	NA	0.83-1.13
	bc07	Temperature annual range	Deg C	14.3-19
	bc10	Mean temperature of the warmest quarter	Deg C	19-26.7
	bc11	Mean temperature of the coldest quarter	Deg C	11.8-20.5
	bc12	Annual mean precipitation	mm	1351-7417
	bc15	Precipitation seasonality	NA	63-103
	bc16	Precipitation of the wettest quarter	mm	880-3564
	bc17	Precipitation of the driest quarter	mm	60-738
	bc23	Radiation seasonality	NA	17-20
	bc28	Annual mean moisture index	NA	0.6-1
	bc31	Moisture index seasonality	NA	0-60
	bc34	Mean moisture index of the warmest quarter	NA	0.78-1

The square root of the maximum abundance of each species (standardised for transect size) at each unique location was used as the dependant variable in a best-subsets multiple regression. To discover the environmental determinants of abundance within a species' range, only surveys conducted within the geographic distribution and altitudinal range of each species were included in each analysis. Analyses were only conducted on species for which data were collected at more than 20 locations within their range. Four species were excluded from this analysis due to a lack of abundance estimates including *C. concinnus*, *C. exiguus*, *C. mcdonaldi* and *C. saxatilis*.

Least-squares linear regressions were performed using R (R Development Core Team 2006), using a best-subsets procedure implemented using the regsubsets function from the leaps package (written by Lumlet using Fortran code by Alan Miller, see Miller (1990)), and specifying the method as an exhaustive search. This procedure was used to determine the best possible regression model (highest R^2) of all potential model sizes. The Swartz criterion (SIC, McQuarrie and Tsai 2006) and "Swartz weights" were used to evaluate and select the best model with the smallest number of variables. This was selected over AIC because it has a stronger penalty against larger model sizes and therefore provides greater protection against over-fitting. Standardised regression coefficients were calculated for the variables included in the best model, following Bring (1994). As the vegetation type was categorical, this was included in the analysis as dummy variables. Because many of the categories were very rare within the geographic range of some species, vegetation dummy variables were only included if they made up more than 5% of the sample size for a species.

Along with the best model, a full model (including all variables) was fitted, to determine the maximum variance in abundance that could be explained by broad-scale habitat characteristics. In addition, models were fitted using each dependant variable type (vegetation, topography and climate) separately. The unique variance of each variable type was calculated as the difference in R^2 between the full model and a model fitted excluding all variables of that type.

Micro-habitat:

Field sites and species

Permanent 400 m transects were established within three subregions, Henrietta Creek (subregion AU), Mt Bellenden Ker (subregion BK), and Mt Lewis (subregion CU) within the Wet Tropics (Figure 1). Sites were established in core areas of species distribution for six microhylid species, including both rare and common species. The species that were present at each site were *Cophixalus infacetus* and *C. ornatus* at Henrietta Creek (AU), *C. negelectus* at Mt Bellenden Ker (BK) and *C. hosmeri*, *C. aenigma* and *C. monticola* at Mt Lewis (CU). For this study geographically rare and restricted species are *C. neglectus* and *C. monticola*, intermediate restricted and rare species are *C. hosmeri* and *C. aenigma* and geographically widespread and common species are *C. ornatus* and *C. infacetus*. Other microhylids were encountered at these sites but not in high enough abundances to be used in these analyses.

Within each subregion, three transects at each of two sites differing in altitude were established. The sites which were established at 400 m and 600 m for Henrietta Creek, 1000 m and 1500 m for Mt Bellenden Ker and 1000m and 1200m for Mt Lewis. Each of these sites were sampled throughout the wet season (November to March) monthly for 4 years (1999, 2001,2002,2003) with the exception of 1000m sites at Mt Bellenden Ker and Mt Lewis, where sampling was stopped after 2 years (1999, 2001)due to unusually dry conditions. Each transect was walked at night using a hip chain spool to measure the distance traversed along the transect. The positions of males of each species within 10 m either side of the transect were recorded. The analysis of microhabitat preferences of the six species, only used transects / sampling periods in which the highest abundance of frogs were encountered. This was to ensure that habitat preferences were not biased by bad calling nights and thus false absences in the data. The analysis was carried out for each subregion as very few species overlapped between subregions or were not found in high enough abundance to include in this analysis. Abundance of each species was pooled for every 20 m section of a transect to allow for comparison on the same scale as the vegetation and microhabitat variables collected.

Vegetation and microhabitat surveys were carried out at every 20 m point along each 400m transect. Microhabitat and vegetation structure were collected using a 20 m long x 20 m wide area. Microhabitat variables surveyed included rock size, rock abundance, litter cover, litter depth, canopy density < 1m, canopy density 1-2 m, canopy density 2-5m, canopy density > 5m, canopy density, total canopy cover, canopy connectiveness, log fall, palm cover and slope as categorical (ordinal scale) data, and number of tree stems and slope as continuous data.

Non-metric multidimensional scaling (NMDS; Kruskal 1964) was used to investigate the microhabitat structure of each 20 m point for all transects within each subregion. NMDS was used because of its lack of assumptions about linear relationships among the variables, as initial exploration of the microhabitat data showed few strong linear relationships. The sixteen microhabitat variables were ordinated using a Sorensen distance matrix in the statistical package PC-ORD (McCune and Mefford 1999). Two variables, tree stem counts and canopy height, were square-root transformed. Scree plots and Monte Carlo tests were used to determine dimensionality, and I display the first two axes that represented the greatest amount of variation. Frog abundance and species presence/absence were overlayed on the NMDS graphs to explore the relationship between microhabitat variables and each species.

A Multiple Response Permutation Procedure (MRPP; Mielke 1984) was used on the same similarity matrix where there were differences in the presence and absence of frog species to examine significance (given as an A statistic and an associated p-value). Spearman correlations (rho) were used to further examine relationships between frog abundance, NMDS axes and microhabitat variables.

Results

Macro-habitat

The geographic range sizes of the 13 species ranged from 0.02 % (*C. concinnus*) to some 33% (*C. ornatus*) of the available geographic space in the Wet Tropics (Table 2). The niche volumes as estimated from either the concave hull of temperature and precipitation or from the 2D or 4D Qhull convex volumes were significantly correlated with range size (Pearson correlation coefficients, r = 0.965, 0.953 and

0.954 respectively, $p < 0.001$). In general, geographically restricted species had smaller niche volumes while geographically common species had larger niche volumes. However this relationship is not significant when comparing geographic range size with the 8D Qhull niche volumes ($r = 0.226$, $p = 0.481$).

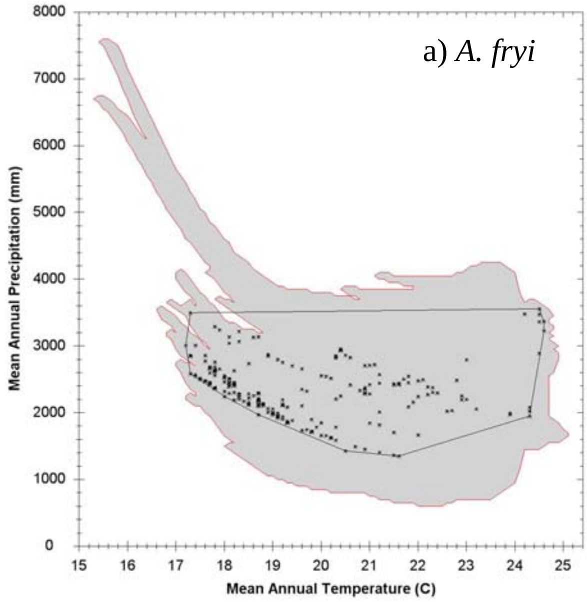
While differing in magnitudes of the estimates, the different methods of estimating the niche volumes did not differ much in relative size. The concave hull, 2D Qhull and 4D Qhull niche volume estimates were also significantly correlated ($r > 0.953$, $p < 0.001$ for all possible combinations). The 8D Qhull estimates deviated from this trend being most correlated with the 4D Qhull ($r = 0.378$, $p = 0.319$).

Table 2: The percentage of geographic space, percentage of environmental space occupied, and the results for calculation of 2 D, 4 D and 8 D hyper-niche volume for 13 species of microhylids.

Species	% of available				
	Geographic space	Niche space			
		concave hull	2D Qhull	4D Qhull	8D Qhull
Austrochaperina fryi	23.5	54.7	19.8	0.03	0.03
A. pluvialis	30.1	58.5	41.7	0.04	0.05
A. robusta	26.3	74.3	49.1	0.06	2.3
Cophixalus aenigma	4.7	18.9	8.9	0.007	0.00006
C. bombiens	3.5	25.9	9.8	0.004	0.00007
C. concinnus	0.02	0.3	0.3	5.8E-05	3E-10
C. exiguus	1.6	0.4	0.6	3.2E-05	1E-10
C. hosmeri	1.5	2.6	1.5	0.00036	1E-07
C. infacetus	15.7	48.6	29.6	0.029	0.08
C. monticola	1.05	0.1	0.04	NA	NA
C. neglectus	0.2	8.2	3.5	0.001	4.8
C. ornatus	32.9	78.9	48.4	0.07	3.5
C. saxatilis	0.03	0.1	0.2	1.3E-05	1E-10

The concave hull estimates of niche volume have been visualised in Figure 2a to 2m. These plots show that *C. ornatus* and *A. robusta* had the greatest environmental space occurring in temperatures ranging from 16 to 24 degrees and mean precipitation levels of 1000 to over 7000 mm per year. While the other three widespread species (*A. fryi, A. pluvialis* and *C. infacetus*) occur over areas of large temperature variation (17 to 24.5 degrees), their ranges of mean annual precipitation are more restricted, to 1000 to 4000mm per year. The rare and restricted species *C. neglectus* only occurs in environmental space that combines cool (16 to 20 degrees) temperatures and very high mean precipitation (3500 to 8000mm). The rare and restricted species *C.*

concinnus and *C. monticola* occupy very small areas of the available environmental space, requiring moderate precipitation (2500 to 3500mm) and cooler temperatures (17 to 19 degrees). The species with intermediate distributions occur over moderate precipitation and temperature ranges: *C. aenigma*, 17 to 22^{0}C, 1500 to 3500mm, *C. bombiens* 18 to 24^{0}C, 1500 to 3500mm. Two species that are rare and restricted, however, occur in higher temperature and lower precipitation niches; these are *C. exiguus* (20^{0}C to 23^{0}C, 2000 to 3000mm) and *C. saxatilis* (23^{0}C to 24^{0}C, 1500 to 2000mm).


a) *A. fryi*
Mean Annual Precipitation (mm)
8000
7000
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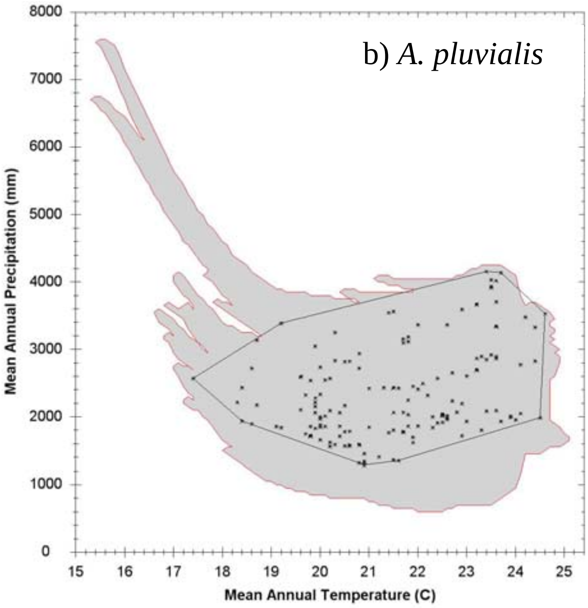
25
Mean Annual Temperature (C)


b) *A. pluvialis*
Mean Annual Precipitation (mm)
8000
7000
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22
23
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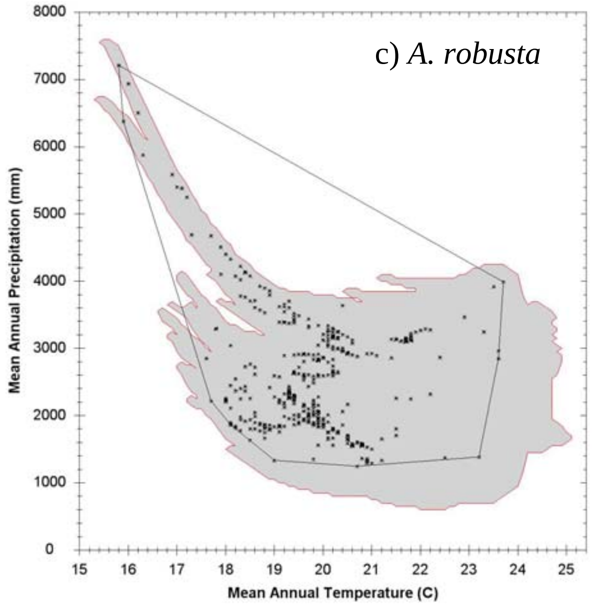
25
Mean Annual Temperature (C)


c) *A. robusta*
Mean Annual Precipitation (mm)
8000
7000
6000
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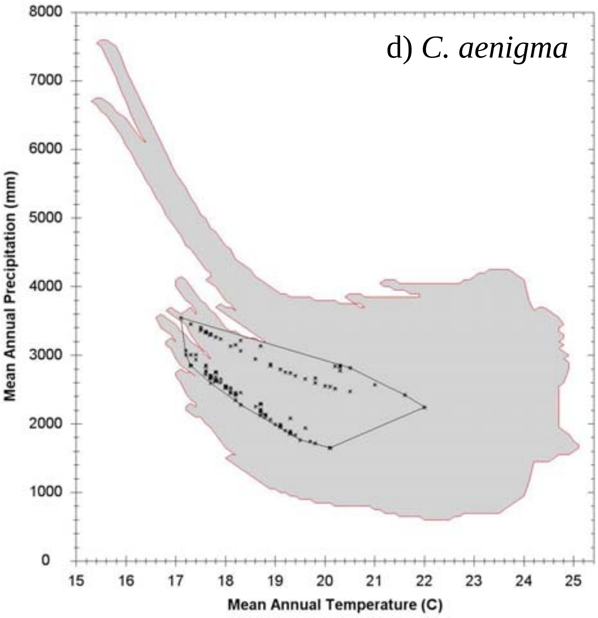
20
21
22
23
24
25
Mean Annual Temperature (C)


d) *C. aenigma*
Mean Annual Precipitation (mm)
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7000
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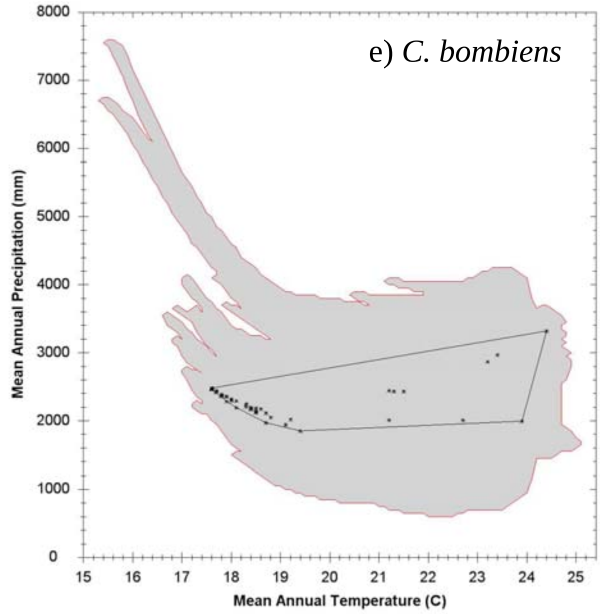
25
Mean Annual Temperature (C)


e) *C. bombiens*
Mean Annual Precipitation (mm)
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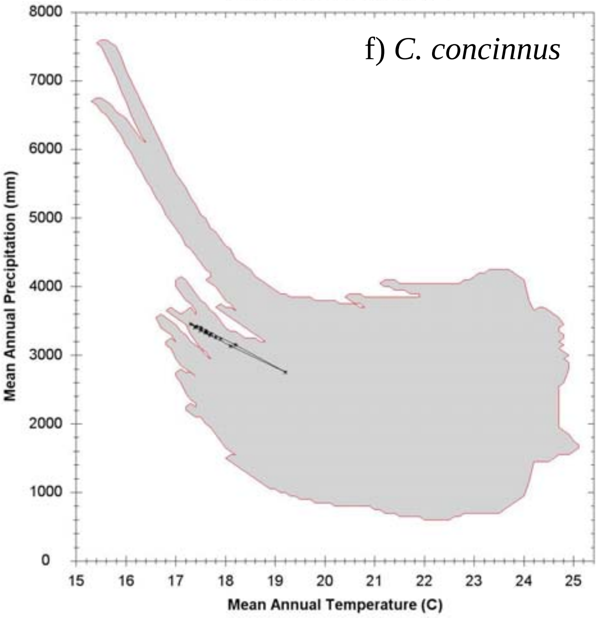
Mean Annual Temperature (C)


f) *C. concinnus*
Mean Annual Precipitation (mm)
8000
7000
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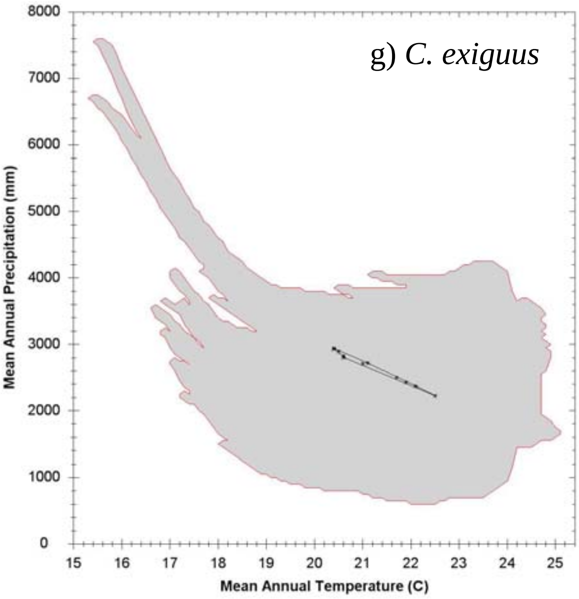
Mean Annual Temperature (C)


g) *C. exiguus*
Mean Annual Precipitation (mm)
Mean Annual Temperature (C)
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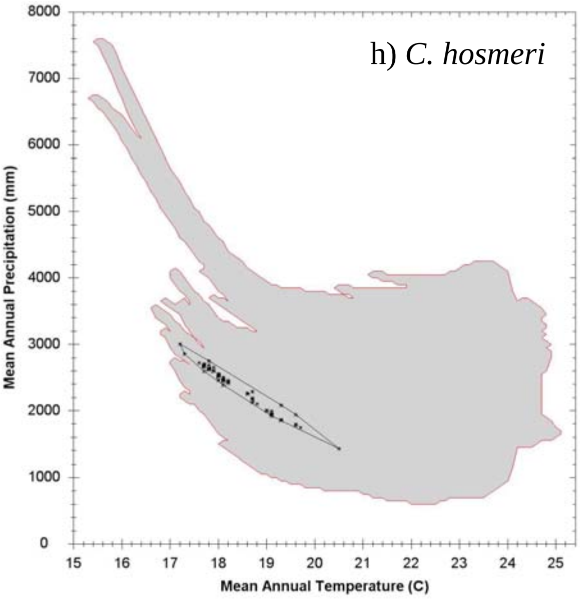
h) *C. hosmeri*
Mean Annual Precipitation (mm)
Mean Annual Temperature (C)
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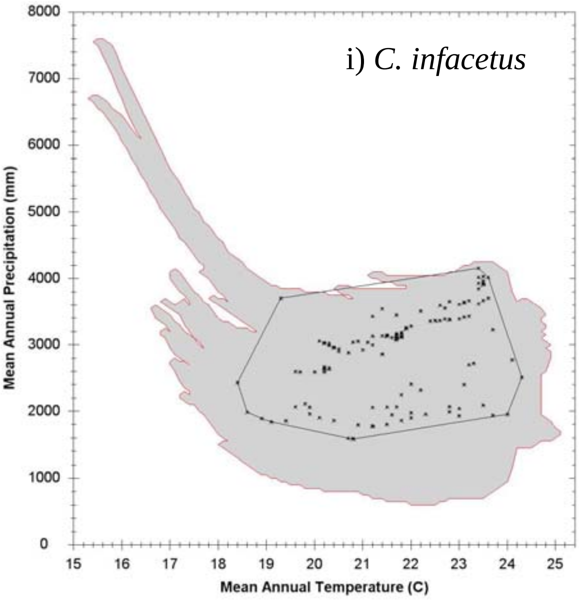
i) *C. infacetus*
Mean Annual Precipitation (mm)
Mean Annual Temperature (C)
0
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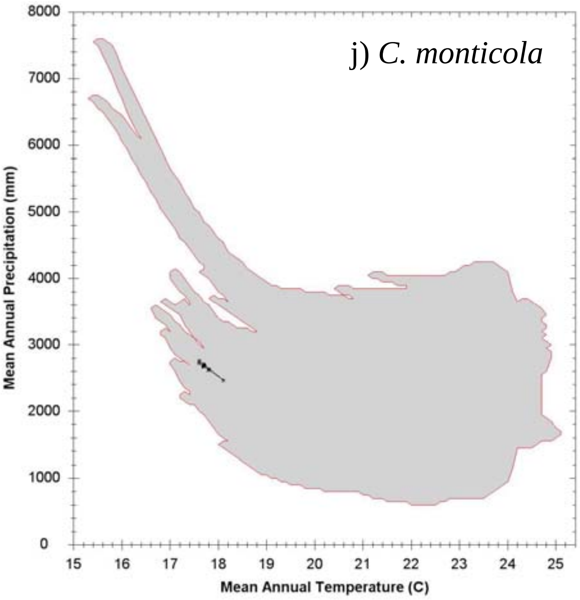
j) *C. monticola*
Mean Annual Precipitation (mm)
Mean Annual Temperature (C)
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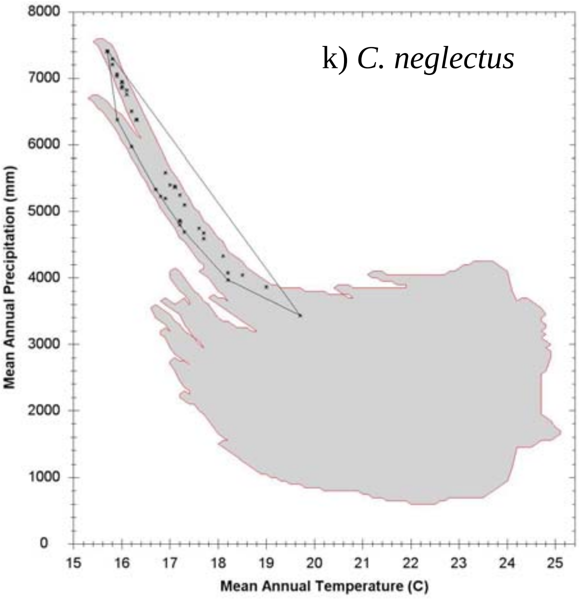
k) *C. neglectus*
Mean Annual Precipitation (mm)
Mean Annual Temperature (C)
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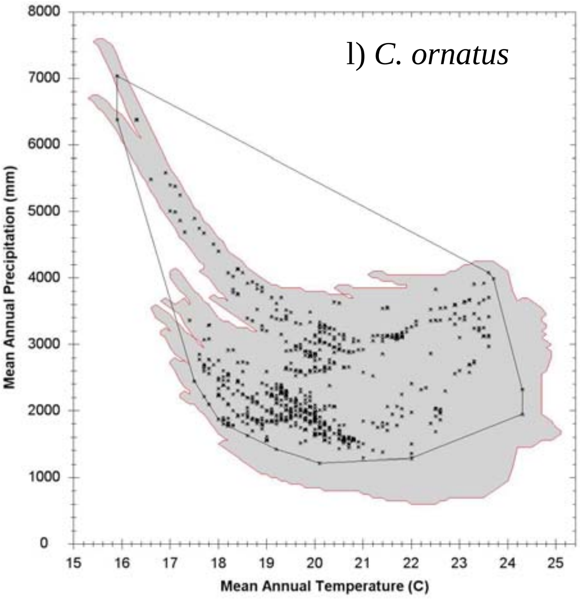
l) *C. ornatus*
Mean Annual Precipitation (mm)
Mean Annual Temperature (C)
0
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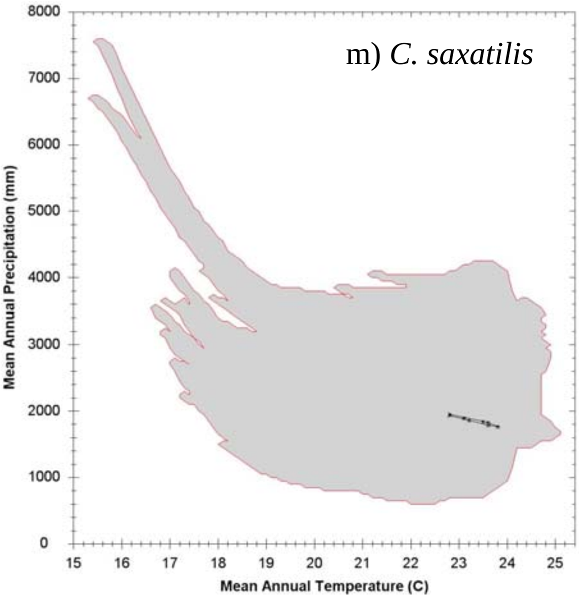

Figure 2: The plot of annual mean temperature and annual mean precipitation for 13 species of microhylid frogs shown as points for their environmental space in which they occupy. Shaded area is the outline of all available environmental space within the Wet Tropics Biogeographic region.

Meso-habitat

Regression models were constructed to explain the abundance of microhylids within their geographic ranges using vegetation, topographic and climatic broad-scale habitat variables. Only 10 species, those that occurred at enough locations for analysis, were included in regression models. The amount of variance explained by broad-scale habitat characteristics varied considerably among the species, with the best selected model explaining as little as 18% of the variance (*A. robusta*) and as high as 91% (*C. neglectus*; Table 3). The variables included in the best model for each species varied considerably, and the response of the microhylids to their broad-scale environmental envelope appear to be species-specific (Table 3).

The importance of broad-scale habitat variables (vegetation, topographic and climate) varied among species. The climatic variables appeared to be the best predictors of the abundance of microhylids, explaining from 15 to 89 % of the variance. For four species (*C. neglectus, C. hosmeri, C. bombiens* and *C. monticola*) over 50% of the variance was explained by climatic variables. The variables that explained each best fit model for each species are listed at the bottom of table 4. The variables that occurred most commonly in the models were annual mean moisture index (bc28) and its associated seasonality (bc31), precipitation of the wettest quarter (bc16), occurrence in mesophyll vine forest (MeVF), slope (slope) and the East-West component of aspect (E-W). Topographic variables provided very little unique explanatory power for many species, with R^2 values ranging from 3 to 15% (Table 3). Alone, topography was able to explain substantial variance in the abundance of five species: *C. aenigma, A. pluvialis* and *C. infacetus*, *C. monticola* and *C. neglectus* (Table 3). In general, vegetation type appeared to have the least influence, explaining from 3 to 47 % of the variance (Table 3). The only two species for which vegetation alone could explain substantial variance in abundance were *C. aenigma* and *C. monticola*, which occurred in greater abundances in microphyll vine thicket and notophyll vine forest respectively. Despite this, vegetation variables were included in the best models for several species, with both positive and negative regression coefficients.

Table 3: The variance explained using linear multiple regression models on the abundance data within species ranges for10 microhylid frog species in the wet tropics. Values are the adjusted R^2 and are shown for the best model (as determined by a best-subsets multiple regression and selected using the Swartz Criterion), the full model (including all variables), and for the three different categories of predictor variables including vegetation (Stanton vegetation type 4), topographic variables and climate variables (extracted using the Bioclim model). Adjusted R^{2}'s for the three different types of predictor variables are shown both as the unique component of the variance explained (unique), as well as the maximum variance they can explain on their own (alone). Values are the same as given in Table 2. The variables included in the best model are also shown, and are listed in order of the magnitude of their standardised regression coefficient. Codes for the included variables can be found in Table 1.

		Austrochaperina fryi	*A. pluvialis*	*A. robusta*	*Cophixalus aenigma*	*C. bombiens*	*C. hosmeri*	*C. infacetus*	*C. ornatus*	*C. monticola*	*C. neglectus*
Best model		0.37	0.39	0.18	0.64	0.72	0.78	0.31	0.37	0.71	0.91
Full		0.37	0.38	0.23	0.63	0.75	0.74	0.31	0.37	0.43	0.86
Veg	unique	0.02	0.00	0.01	0.09	0.00	0.04	0.01	0.08	0.28	0.02
	alone	0.09	0.03	0.08	0.34	0.15	0.04	0.16	0.08	0.47	0.05
Topo	unique	0.08	0.03	0.00	0.07	0.00	0.04	0.11	0.03	0.15	0.03
	alone	0.14	0.24	0.04	0.35	0.04	0.11	0.26	0.03	0.52	0.78
Clim	unique	0.21	0.13	0.06	0.14	0.58	0.53	0.03	0.30	0.2	0.13
	alone	0.26	0.36	0.17	0.48	0.73	0.75	0.15	0.30	0.57	0.89
Variables included in the best model	Positive coefficients	bc31 bc28 MiFT E-W slope MoVF	bc11 slope	bc23 bc15 MeVF bc28 NoVF	bc02 MiFT bc17 E-W slope	bc31 bc16 bc34	bc07 bc17	bc10 slope bc23	bc04	bc04 NoVF	bc11 bc31
	Negative coefficients		bc16 bc02 bc31		alt bc15 bc16	bc02 bc11 bc17	alt bc15 bc16 bc28	E-W MeVF	bc12 alt bc10 NoVF MeVF E-W		bc10 bc23 bc28

Micro habitat

Bellenden Ker site

Of the 60 points in which surveys were conducted, *C. neglectus,* a rare and restricted species, occurred at 88% of survey points indicating that this species was almost ubiquitous through the habitats. Indeed, MRPP did not detect any differences in habitat types between the presence and absence of this species (MRPP: A = -0.00086, *P* = 0.460). NMDS ordination found a stable 3-dimensional solution representing 84% of the habitat variation, with the first two axes representing 64% of variance (Figure 3a). Variation in habitat structure was mostly explained along axis 1 and sites with low canopy density (< 1m) separating from sites with higher canopy density (> 5m). When *C. neglectus* abundance was overlayed with habitat NMDS no patterns were detected (Figure 3b).

Atherton Tableland sites

Of the 120 points sampled at Atherton Tableland sites for the two common and widespread species, *C. infacetus* was present at only 46 % while *C. ornatus* was present at 71 %. An NMDS ordination of the habitat structure for these sites found a stable 3-dimensional solution that represented 78% variance of sites with axis 1 representing 30% and axis 2 displaying 21% of the variation (Figure 4c). Variation in habitat structure of sites along axis 1 was mostly described by rock size and abundance, slope and the number of trees (Figure 4c). The occurrence of *C. infacetus* at sites also separated along axis 1, and there was a significant difference in habitat structure of sites in which *C. infacetus* was present and absent (MRPP: A = 0.057, P = 0.000; Figure 4b). *C. infacetus* tended to occur more often in sites that had greater rock size, abundance and more slope. Furthermore, abundance of *C. infacetus* was significantly positively correlated with axis 1 (r_s = 0.395, p = 0.000), rock size (r_s = 0.301, p = 0.001) and rock abundance (r_s = 0.348, p = 0.000) and was negatively correlated with axis 2 (r_s = -0.215, p = 0.018), canopy connectiveness (r_s = - 0.274, p = 0.002) and the number of tree stems (r_s = -0.267, p = 0.003). However, these variables still only explained a little variation in abundance of *C. infacetus* between sites, as shown by the small Spearman rho values. In contrast to *C. infacetus*, *C. ornatus* was ubiquitous throughout sites and there was no difference in habitat between sites where *C. ornatus* was present and absent (MRPP: A= -0.006, *P* = 0.884). In addition, none of the habitat variables were correlated with *C. ornatus* abundance (Figure 4b).

Mt Lewis site

The species *C. aenigma* and C. *hosmeri*, of intermediate geographic rarity, were found consistently throughout the habitat occurring at 72 % and 90 % respectively of the sampled habitat sites (Figure 5a and 5b). In contrast, the rare and geographically restricted species, *C. monticola* was present in only 55% of sites sampled indicating a patchy distribution. An NMDS ordination of the habitat structure of sites gave a stable 3 dimensional solution that representing 82% of the variance; axis 1 and axis 2 explained 37% and 22 % respectively (Figure 5). The variation in habitat structure for these sites is mostly explained by differences in the occurrence of palms, logfall and canopy cover at 1, 2 and 5 m of sample sites (Figure 5d). There was no significant difference in habitat structure of sites with any of the species present and absent (MRPP: *C. aenigma* A = 0.001, *P* = 0.392; *C. hosmeri* A = -0.019, *P* = 0.975; *C. monticola* A = 0.005, *P* = 0.264). However abundance of *C. aenigma* was significantly correlated with abundance of *C. hosmeri* (r_s = 0.344, p = 0.008) and negatively correlated with abundance of *C. monticola* (r_s = -0.273, p = 0.037). In addition, abundance of *C. monticola* was negatively correlated with that of rocks (r_s = -0.327, p = 0.011). Once again, the small Spearman rho values indicate that the correlations did not explain a great deal of variation in frog species abundance.

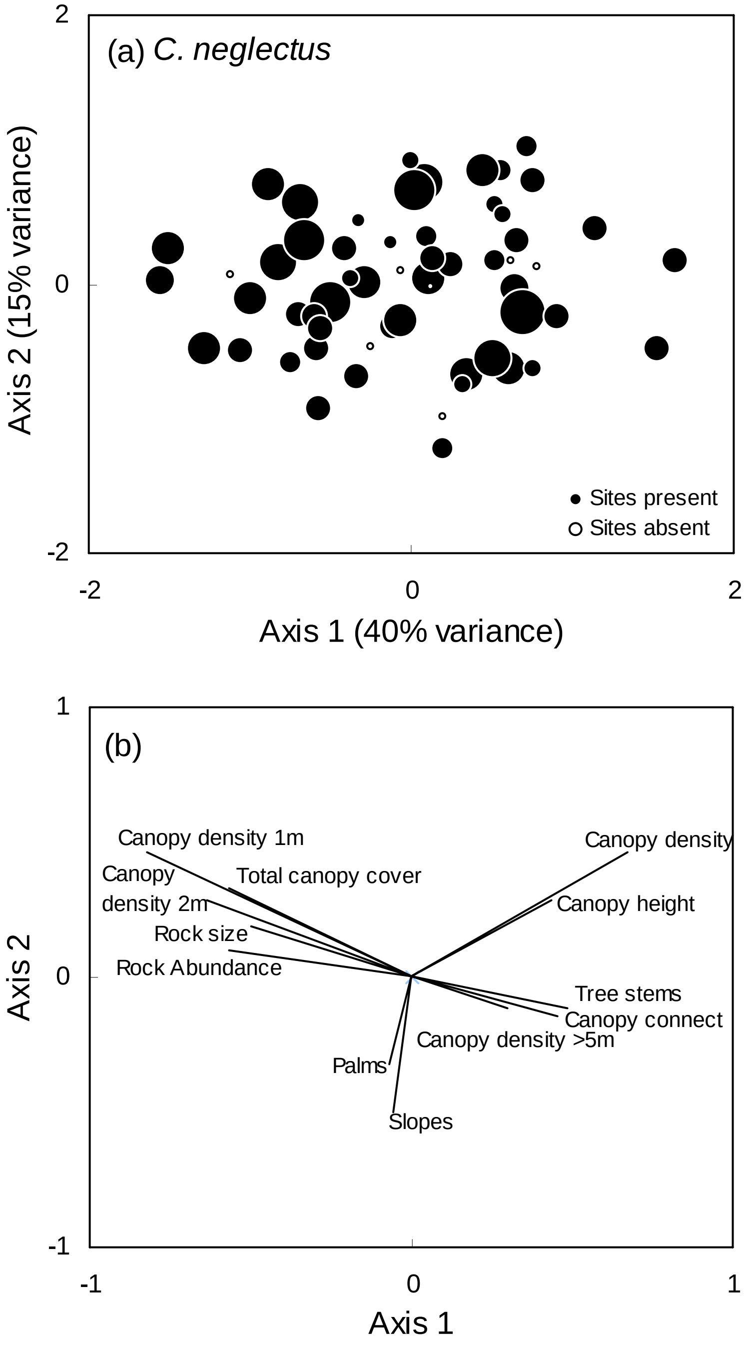

Figure 3: Plots of the variance explained by axis 1 and axis 2 from NMDS and presence / absence and abundance for a) *C. neglectus* from sites at BK- Bellenden Ker. Size of the black circle indicates the relative abundance of this species at each site. b) Correlations of environmental variables with NMDS ordination.

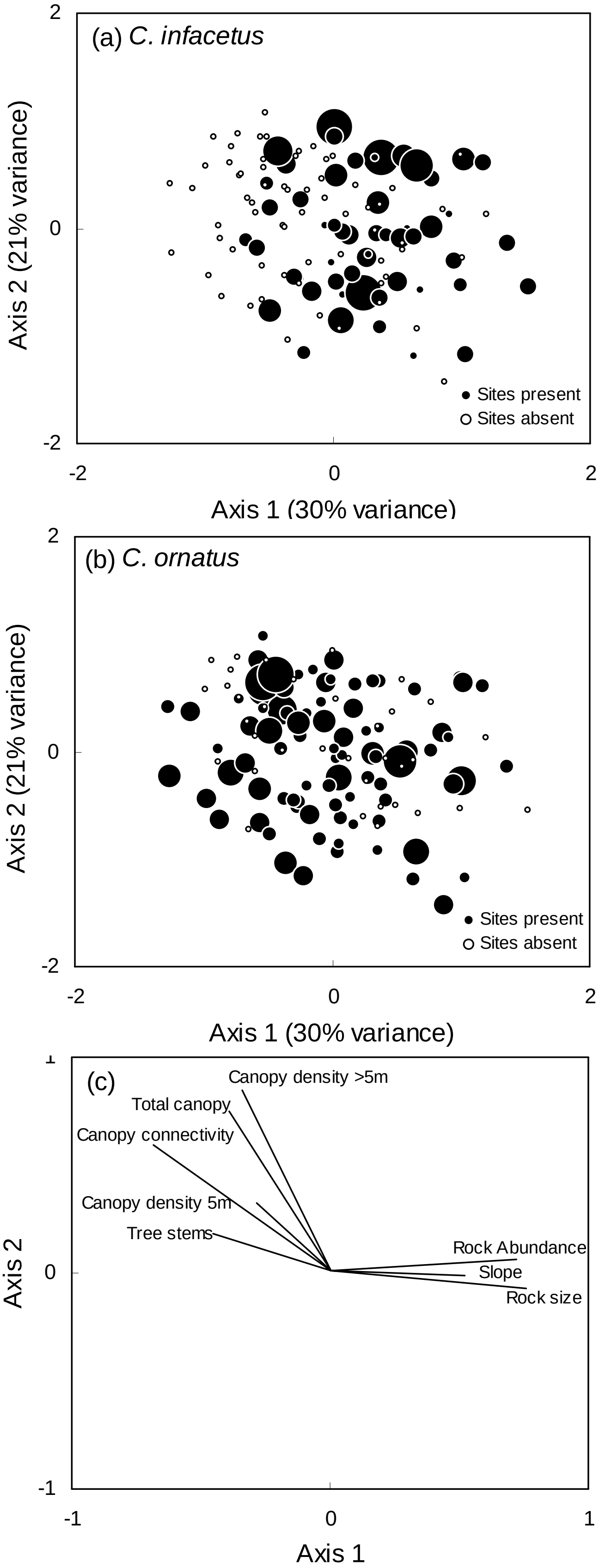

Figure 4. Plots of the variance explained by axis 1 and axis 2 from NMDS and presence / absence and abundance for a) *C. infacetus* and b) *C. ornatus* from sites at AU – Atherton Uplands. Size of the black circle indicates the relative abundance of each species at sites. c) Correlations of environmental variables with NMDS ordination.

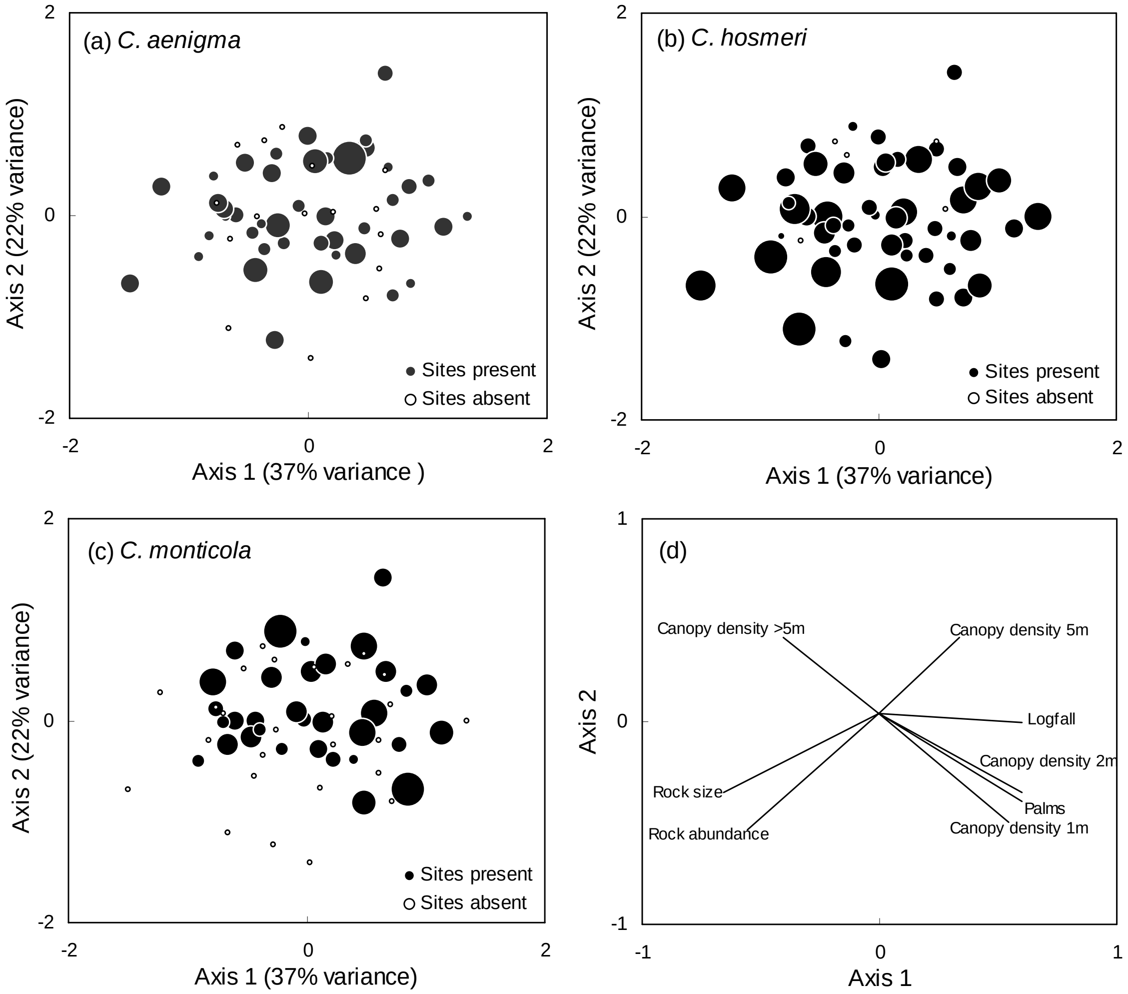

Figure 5. Plots of the variance explained by axis 1 and axis 2 of the NMDS and the presence / absence and abundance of microhylids species a) *C. aenigma*, b) *C. hosmeri* and c) *C. monticola* from sites at CU - Mt Lewis. Size of the black circle indicates the relative abundance of this species at each site. d) Correlations of environmental variables with NMDS ordination.

Discussion

Macro-habitat

When examining environmental niches (macro-habitat) of microhylid frogs in the Wet Tropics, Brown's (1984) hypothesis, that geographically rare species have narrower niches than widespread species, seems to apply. All niche volume estimates were strongly correlated with geographic range size of microhylid species ($r > 0.95$), with the exception of the 8D Qhull niche volume. Indeed, my results illustrate that widespread species occurred over a much greater range of environmental variables, including mean annual precipitation and temperature, and seasonality of moisture and temperature, than the rare and restricted species. Similarly, species of European carabid beetles (Carabidae) with broader environmental tolerances and niches were also more widely distributed (Kotze *et al.* 2003). Gaston and Spicer (2001) also provided evidence that amphipod (*Gammarus*) species with larger geographic ranges were the most environmentally tolerant.

As the distribution of frogs may be constrained by a species' physiologically dependence on sufficient moisture for reproduction and survival (Blaustein *et al.* 1994), it is unsurprising that my results imply that the occurrence of microhylid frogs may be limited by their environmental tolerances. Further, *in situ*- speciation of sister taxon on adjoining mountain tops infers that species may have been more widespread in cooler and wetter times (Hoskin 2004). Indeed, the physiological tolerances (which reflects a species' fundamental niche) of widespread microhylid frogs may be broader than rare species, and, thus, provide a mechanism by which the widespread species can inhabit more areas. However, this concept requires confirmation by experimentally testing each species' physiological tolerances, as well as examining other potentially important biotic interactions, such as competition.

Meso-habitat

In my study, the overall patterns of abundance within the rare species distributions (at the meso-habitat level) were generally best explained by climatic variables, and to a lesser extent topographic variables, rather than broader scale vegetation type.

However, the proportion of variation explained, and the relative importance of these meso-environmental variables (vegetation, topography and climate), differed among species. The geographically and altitudinally restricted species *C. neglectus*, *C. monticola*, *C. hosmeri,* and the geographically restricted *C. bombiens,* all had abundances that were largely correlated with climatic variables, indicating that these species will be most susceptible to changes in climatic conditions. Similarly, other studies of amphibians have shown a variety of climatic and topographic variables are the most important aspects determining species richness and abundances (Toft 1980, Giaretta *et al.* 1999, Vonesh 2001). For microhylid frogs of the Wet Tropics, species with a small macro-habitat niche (i.e. species with a narrow range of tolerance of macro-environmental variables) may be more severely affected by climatic variables at a local scale.

In contrast, meso-environmental variables explained far less variation in the abundance of widespread microhylids with broader macro-habitat niches. For example, *C. ornatus* had the broadest macro-habitat niche of any microhylid species examined, however, only a small amount of the abundance and distribution within its range (meso-habitat) was explained by climatic variables. Indeed, the occurrence and abundance of *C. ornatus* appears fairly unrestricted throughout the Wet Tropics, occurring in all rainforest habitats, and even non-core rainforest areas, such as wet sclerophyll. Similarly, the best predictor of widespread English herbaceous plants was a high diversity of habitats exploited (Thompson *et al.* 1999). Likewise, all three *Austrochaperina* microhylid species (*A. fryi*, *A. pluvialis* and *A. robusta*) had broad macro-habitat niches, with little variation of abundance within range explained by meso-environmental variables (climate, topography or vegetation). For widespread species that are habitat generalists with broader macro-habitat niches, local scale climatic and environmental variables may be far less important in describing within-range distribution and abundance patterns. Instead, the within-range patterns of species occurrence and abundance may perhaps be described by other ecological factors, such as metapopulation dynamics. However, of the many factors previously investigated, which may account for abundance / geographic range relationships, neither niche breadth or metapopulation dynamics have conclusively explained differences among rare species (Gaston *et al.* 1997).

Micro-habitat

The breadth of microhabitat niche varied among species, regardless of geographic range size, and there was no tendency for rare species to be more specialised in microhabitat use, or to occupy narrower microhabitat niches, than common species. Microhabitat preferences of six species of microhylids, which varied greatly in their geographic distribution, showed very little habitat specialisation in any species. Only the widespread species, *C. infacetus* and the rare and restricted species, *C. monticola*, displayed microhabitat preferences. *C. infacetus* was positively associated with rocks and greater slope, while *C. monticola* was negatively correlated with the abundance of rocks, suggesting a degree of microhabitat specialisation within these species. In contrast to the other microhylid species examined, both *C. infacetus* and *C. monticola* display a patchy distribution within their range. Previous studies have shown that patchily distributed species, regardless of geographic range size, have a tendency to be habitat specialists (Futuyma and Moreno 1988; Mace and Kershaw 1997; Munday 2004). For example, water voles (*Arvicola terrestris*), have a wide geographic distribution in England, but are very patchily distributed throughout their range, probably due to the patchiness of essential environmental factors, including the presence of freshwater, adequate food and shelter (Bonesi *et al.* 2002). Given that the level of ubiquity within a species range may contribute to whether or not a species has specialised microhabitat requirements, it is unsurprising that the ubiquitously distributed species *C. ornatus*, *C. aenigma*, *C. hosmeri* and *C. neglectus* were microhabitat generalists.

Within their preferred environment, habitat specialists may out compete generalist species (Rosenzweig and Lomolino 1997; Caley and Munday 2003), as may be the case with *C. monticola*, which, in its very restricted range, is extremely abundant within palms (Chapter 6) and may exclude *C. aenigma*. In addition, habitat specialists may display faster growth and have higher juvenile survival rates, leading to a competitive dominance within their specialised habitats (Caley and Munday 2003). Indeed, the phenomenon of a patchy distribution has been shown in many widespread species (see Rabinowitz *et al.* 1986; Rosenzweig and Lomolino 1997). While such species may be rare across their range, in comparison to geographically restricted species, they are more resilient to extinction due to the low risk of extinction from localised stochastic events. However, species that are both geographically restricted and patchily distributed, such as *C. monticola*, are at a high risk of extinction, as local stochastic events may affect the entire population.

Environmental niche breadths – a question of scale

The influence of environmental variables on microhylid frogs varied among species and the scale at which the variables were measured. Here, I summarise and compare differences in habitat associations of six microhylid frogs, with varying geographic ranges, that were examined on all three habitat scales (macro, meso and micro; Table 4).

Table 4. Summary table of the macro-, meso-, and micro-habitats of the six microhylid species for which all these scales were measured. For macro-habitat the codes are B – broad niche, I – intermediate niche, N - narrow niche; for meso-habitat, the variables which were most important for explaining patterns of abundance within ranges are listed, including C - climate, T – topography, V – vegetation; and for micro-habitat, factors that significantly relate to species distribution are given, or, where no factors are significant, 0 – no correlates. The within-range ubiquity of the each species (U – ubiquitous, P – patchy) is also listed.

	C. ornatus	*C. infacetus*	*C. aenigma*	*C. hosmeri*	*C.monticola*	*C. neglectus*
Range	6550	3120	930	300	208	37
Macro	B	B	I	I	N	N
Meso	C (30%)	T (26%)	C (48%) T (35%) V (34%)	C (75%)	C (57%) T (52%) V (47%)	C (89%) T (78%)
Micro	0	(rocks/slope)	0	0	(no rocks)	0
Ubiquity	U	P	U	U	P	U

The distribution and abundance of both widespread species who also occupied broad macro-habitats, *C. infacetus* and *C. ornatus,* were not well explained by any of the meso-environmental variables (Table 4). Similarly, no microhabitat variables were associated with the abundance of *C. ornatus*, suggesting that this species is a habitat generalist at several scales. However, the abundance of *C. infacetus* was positively correlated with a number of microhabitat variables, including slope, and rock abundance and size, indicating that *C. infacetus*, while being a habitat generalist in the broad sense, is more specialised at a microhabitat scale. Although only speculation, the association of calling males with rocky microhabitat suggests there may be some benefits of rocky perches, such as greater protection from predators, increased call volume (Felton 1999), or a higher rate of water retention on soil covered rocks, which may protect frogs (and eggs) from desiccation. Furthermore, the patchy occurrence of dense rocky habitat on high incline slopes could well explain the localised patchy distribution of *C. infacetus* in this otherwise, widespread species.

Compared to the widespread species, meso-habitat variables explained substantially more variation in the distribution and abundance of the two intermediately-distributed species, *C. aenigma* and *C. hosmeri* (Table 4). For both of these species, climate variables explained the highest proportion of variability in abundance, although *C. aenigma* abundance also varied with topographic variables and vegetation type. However, neither species showed microhabitat preferences, and were ubiquitous throughout their ranges.

Both rare and restricted species, *C. monticola* and *C. neglectus*, displayed very narrow macro-habitat niche breadths, with substantial amounts of variation in their abundance and distribution explained by meso-habitat variables, particularly climate and topography (Table 4). However, both species varied in their specialisation of microhabitat features. In contrary to predictions that species with restricted macro-environmental distributions should also have restricted microhabitat preferences (Brown 1984, Gaston and Kunin 1997, Rosenzweig and Lomolino 1997), *C. neglectus*, the species with the most restricted macro-habitat, was non selective in microhabitat preference (Table 4). Although *C. neglectus* only occurred in a very limited macro-environmental space (limited to combinations of very wet and cool environments), at the micro-habitat level, *C. neglectus* occurred ubiquitously throughout the sampled habitat. Furthermore, even though climate limits the distribution of *C. neglectus*, within their range, resource availability may have facilitated the observed high abundances. Given this, Fretwell’s theory, that habitat selectivity of a species will decrease as population density increases (Rosenzweig 1985), may be more applicable for this species.

In contrast, *C. monticola* had significant associations with meso-scale vegetation type, and a negative association with the microhabitat, rock abundance. Although *C. monticola* is usually found in endemic limnospadic palms (Richards *et al.* 1994), which only occur at high abundance in higher altitude (above 1100m) rainforest habitat on Mt Lewis (Chapter 6), a significant association between palms and this microhylid was not detected. This is probably an artefact of sampling, as all *C. monticola* observed during surveys occurred in palm clumps, but there were many surveyed palm clumps where this species was absent. Furthermore, the negative association with rocks may merely reflect a high density of palms that were obscuring rocks from view. As *C. monticola* breeds in limnospadic palm apices, where decaying leaf litter gathers and forms a protected environment for eggs and froglets, the patchy distribution of *C. monticola* may be caused by aggregations of calling males on palms. In addition, the abundance of *C. monticola* was also negatively associated with *C. aenigma*, and may be caused by interspecific competition between these two species, with *C. monticola* being competitively dominant in palms.

In summary, despite examining a number of microhylid species with different biological and ecological traits, few clear-cut patterns between geographic range size and habitat requirements were detected. However, some broad generalisations can be drawn. Geographically widespread species had broad macro-habitat niches, with little dependence on meso-habitat variables. In contrast, meso-habitat variables explained substantially more variation in the distribution and abundance of less widespread species. In particular, species with intermediate or narrow macro-habitat niches were greatly influenced by climatic variables. Finally, the degree of microhabitat specialisation appears unrelated to geographic range size in microhylid frogs, as both widespread and restricted species could be either microhabitat specialist or generalists.

CHAPTER 4: NICHE BREADTH IN RARE AND COMMON SPECIES OF MICROHYLID FROGS: EFFECTS OF DIET

Publication: **Williams, YM**, Williams, SE, Alford, RA, Waycott, M, Johnson, CN (2006) Niche breadth and geographic range: ecological compensation for geographic rarity in rainforest frogs. *Biology Letters* **2**: 532-535.

Introduction

Brown (1984) argued that species with broad ecological niches should be geographically widespread as well as being locally abundant. This is because a broad niche allows a species to persist in a wide range of different habitat types, while a narrow niche restricts a species to the few places where its niche requirements are met (Gaston, 1994; Kunin and Gaston 1997). Generalists have more areas available to them as suitable habitat and have a correspondingly large potential geographic range (Lawton 1995).

There are two other reasons why I expect geographic range and niche breadth to be positively correlated. First, in geographically restricted species, there is a higher chance that selection will produce ecological specialisation as a result of adaptation to local conditions, whereas in widespread species local adaptation is more likely to be frustrated by gene flow from different environments with different selective regimes (Kirkpatrick and Barton 1997). Second, a positive relationship could arise simply as a sampling effect. Widespread species are likely to have access to a more diverse resource base (Gaston *et al.* 1997). Therefore, measurements of niche breadth should be broader than in geographically restricted species.

However, there is an alternative hypothesis that predicts the opposite pattern. Species with small geographic ranges should have elevated extinction risk, because small ranges make them highly vulnerable to effects of environmental stochasticity and localised catastrophes (Lawton 1995, Simberloff 1998). Specialists should also be extinction prone because they are sensitive to environmental changes, while generalists are resilient to such changes (Lawton *et al.* 1994, Johnson 1998). Therefore, the extinction risk due to small geographic range should be compounded in specialists, but compensated in generalists. If geographically rare specialists have high extinction risk, I should find few examples of them, while rare generalists should be better represented in living communities. With increasing geographic range, the risk of extinction declines, so widespread species should persist longer and have more opportunity to evolve specialised adaptations. In this way, selective extinction may create a negative relationship between niche breadth and geographic range. I examined these relationships in microhylid frogs in the genus *Cophixalus,* from the Wet Tropics of northeast Australia. These species have deep lineages of the order of 10 million years old (Hoskin 2004), with the patterns of distribution and species richness a result of non-random local extinctions related to geographic variation in rainforest stability during the Quaternary climate fluctuations (Williams and Pearson 1997, Graham *et al.* 2006).

Among living *Cophixalus* species there are some with extremely narrow geographic ranges, typically mountaintop endemics with ranges as small as 3 km^2, compared with 6 550 km^2 for the most widespread species. They share similar life histories, morphologies and ecologies: all are restricted to rainforest and breed terrestrially, with direct-developing eggs (Hoskin 2004). I suggest that these geographically-restricted species have ecological traits that confer resistance to extinction, and here I test if they have broader diets than widespread species.

Methods

Stomach samples from 86 animals in the collection of the Queensland museum were examined. Of the 11 species of *Cophixalus* that occur in this region, adequate samples were obtained for 10. Stomach contents were placed on a gridded sorting tray, viewed under a dissecting microscope, and the abundance of each taxonomic prey group scored to order level. Vegetable matter and rock were recorded in the stomach contents, but not included in the dietary analysis as they were considered to be incidentally ingested. Wherever possible, samples where taken from across the species range, however no significant difference was found between sites ($p = 0.2$) for dietary evenness. The number of stomach samples used, the number of prey taxa eaten and the geographic range size for each species can be found in Table 1. Geographic range size for each species is taken from Williams (2006).

Table 1. The number of stomach samples examined, the number of invertebrate orders observed in the diet of each species of *Cophixalus*, the total geographic range of each species in km and the % of available rainforest occupied by each species.

Species	# samples	# taxa eaten	Range size (km^2)	Percentage of rainforest in region occupied
C. ornatus	31	10	6550	66
C. infacetus	*8*	6	3120	31
C. aenigma	23	11	930	9
C. bombiens	12	9	695	7
C. exiguus	8	7	318	3
C. hosmeri	8	8	300	3
C. neglectus	8	10	37	<1
C. concinnus	4	9	3	<1

For each frog species, a randomised cumulative curve was constructed for the number of invertebrate taxa occurring against number of individual stomachs sampled, using the program Species Diversity and Richness V2.1 (Henderson and Sealy 1998). Only frog species in which the curve plateaued were used in this analysis; two species (*C. saxatilis* and *C. mcdonaldi*) had very few samples for accurate depiction of their diets and were removed. Diet similarity among species was compared using a multidimensional scaling ordination (MDS) based on the mean abundance of each dietary category across individuals for each species. I calculated two measures of dietary specialisation for each species: 1. an estimate of total dietary richness (Michaelis-Menton estimate of total richness, (Raaijmakers 1987) was calculated to account for unequal sample sizes; and, 2. a dietary evenness index (Equitability J; Henderson and Sealy 1998) was calculated from the relative abundance of each invertebrate taxonomic group. Regression analyses were performed to examine the relationships between geographic range size and both measures of dietary specialisation. I re-tested the relationships with phylogenetically independent contrasts, using the program CAIC (Purvis and Rambaut 1995) and the phylogeny from Hoskins (2004) to control for effects of phylogeny.

Results

A total of 11 invertebrate taxa were eaten by the eight species of *Cophixalus* (Table 1). Ants represented over 50% of the stomach contents of five species (Figure 1). Patterns of similarity and difference in diets were driven primarily by the abundance of ants in the diet (Figure 2) with almost all of this variation (98%) being represented in the first axis of the ordination. The second MDS axis (Figure 2) related to the proportion of Arachnida and Amphipoda in the diet, however, very little additional variation was explained by this. The species with the most distinctive diet (*C. ornatus*) was also the only species whose distribution overlapped substantially with a number of other species (*C. infacetus, C. hosmeri C. neglectus* and *C. aenigma*) (Hoskin 2004, Williams 2006).

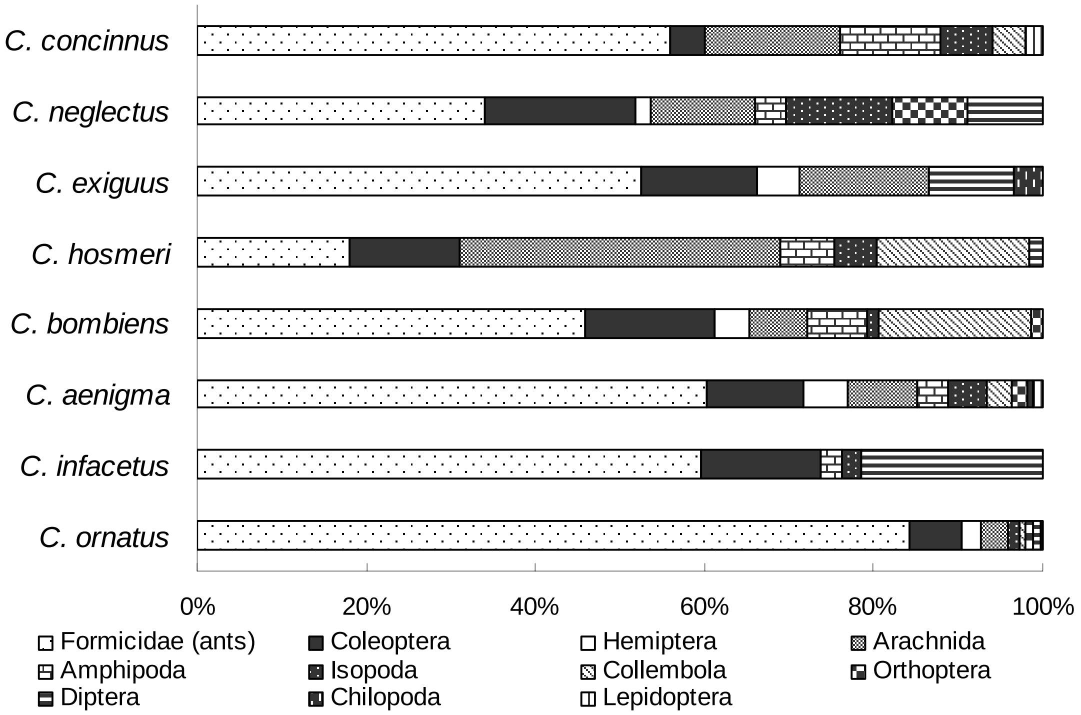

Figure 1: The proportions of each invertebrate taxon consumed by each species of microhylid frog.

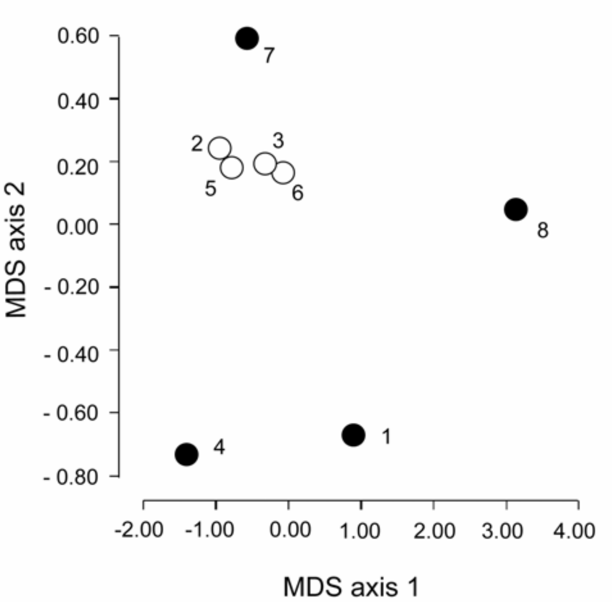

Figure 2: Ordination (multidimensional scaling) using the abundance of different invertebrate taxa in stomach contents of microhylid frogs, to show patterns of similarity in diets. Open circles identify species that rarely overlap in geographic ranges with one other species, filled circles represent species that overlap ranges with at least one other species. Species are identified by number, as follows: **1** *C. concinnus*; **2** *C. neglectus*; **3** *C. bombiens*; **4** *C. hosmeri*; **5** *C. exiguus*; **6** *C. aenigma*; **7** *C. infacetus*; **8** *C. ornatus*.

The total estimated dietary richness was similar across species, with each consuming between 6 and 10 different invertebrate taxa. There was no relationship between range size and dietary richness ($r^2 = 0.12$, $p = 0.41$). However, there was a strong negative relationship between range size and the evenness of the diet (Figure 3; $r^2 = 0.87$, $p < 0.005$; phylogenetically constrained $r^2 = 0.63$, $p < 0.05$). In other words, the geographically restricted species had diets that sampled most broadly from the total range of invertebrate orders eaten by microhylid frogs and with increasing range size, there was an increasing tendency to specialise on one or a few invertebrate orders, in particular, ants (Figure 1).

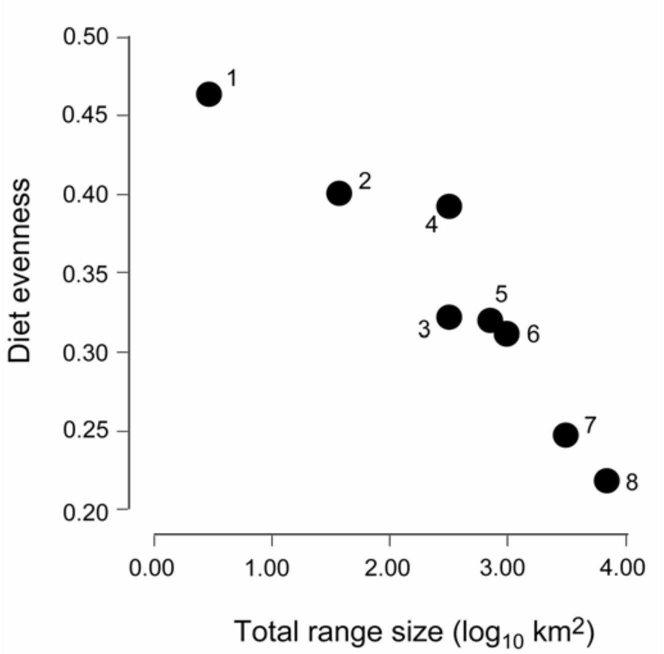

Figure 3: Relationship between dietary specialisation (evenness in the relative abundance of invertebrate taxa in stomach contents) and range size for the eight microhylid frog species examined. Species are numbered as in Figure 2.

Discussion

The analyses showed that in this lineage of rainforest frogs, geographically restricted species have the most generalised diets, and widespread species are more specialised. While Gaston *et al.* (1997) recognised that negative relationships between species range size and niche breadth might occur, he suggested they would arise because of sampling in atypical areas. In this study, diets were described from frog samples across the entire range for both restricted and widespread species. Most studies of the relationship of niche breadth to range size have supported “Brown’s hypothesis” (Brown 1984), i.e. species with large range size also have the largest niche or resource breadth. Studies of geographically rare species typically conclude that they are ecologically specialised (Futuyma and Moreno 1988).

The microhylid frogs of the Wet Tropics have persisted for around 10 million years (Hoskin 2004), passing through a series of extreme fluctuations in climate (Graham *et al.* 2006). Widespread species might have persisted through these fluctuations by virtue of their ability to reverse local extinctions by recolonisation. However, species restricted to high elevations on a single mountaintop do not have this option, and can persist only by virtue of high resilience of local populations. Species that sample broadly from the available range of food should be less susceptible to fluctuations in any particular food type than species that forage in a more specialised way. Pianka (1986) suggested that in low-productivity environments, such as these mountain tops, the low abundance of prey items encourages generalisation of diet to maximise returns per unit effort. This may be the mechanism that forces these geographically-restricted species to be dietary generalists in order to survive.

The most widespread species, *C. ornatus* and *C. infacetus,* specialised on ants in particular. The reason for specialisation on ants is unknown, although they undoubtedly represent a widespread and abundant food source (Anderson and Majer 2000). Optimal foraging theory (Pyke 1984) suggests that dietary specialisation can occur when a reliable and abundant food source is consistently available. It seems plausible that the reliability of ants as a food source across the region has facilitated this level of dietary specialisation.

The species with the most geographic overlap with other species was the one with the most distinctive diet, and there was a trend in our data for diet differentiation between species to increase with range overlap. This phenomenon occurs in many taxa (Schoener 1974) including ground-dwelling frogs in Peru, where Toft (1980) showed diet partitioning among thirteen sympatric species with overlapping geographic ranges. In the case of Australian rainforest microhylids, the degree of dietary overlap requires further examination in order to determine if diet partitioning is a significant mechanism driving competition and thereby distribution patterns. Dietary partitioning in co-occurring species may also be one of the mechanisms that allow the sympatric species to occur in such high abundances.

In conclusion, our study indicates that “Brown’s hypothesis” is not universally true. In systems where species richness has been shaped by extinction risk, rare and common species may differ greatly in traits that confer ecological resilience on local populations. In the genus *Cophixalus,* I found that geographically-restricted species, which should be at higher risk of extinction, have broad diets, consistent with the hypothesis that broad niche breadth has conferred high ecological resilience on local populations and allowed them to persist. This implies that other more specialised, species may once have existed, but that those that combined dietary specialisation with small geographic range size have gone extinct.

CHAPTER 5: COMPARISON OF POPULATION GENETIC STRUCTURE AMONG GEOGRAPHICALLY RESTRICTED AND WIDESPREAD MICROHYLID FROGS IN THE WET TROPICS

Introduction

Why some species are geographically restricted and rare while others are widespread and common has long been contemplated by ecologists (Darwin 1859, Brown 1984, Gaston 1994). Rarity theory proposes that dispersal ability and genetic diversity may explain observed patterns of rare and widespread species in nature, with rare species predicted to have lower dispersal ability and lower genetic diversity compared to more widespread species (Gaston and Kunin 1997).

Dispersal, or the migration of individuals among populations, plays a key role in determining the distribution and abundance of populations in time and space (Brown *et al.* 1996). Species which can fly or are large, and are able to cover greater distances are generally predicted to be better dispersers and often have greater geographic ranges (Lowe *et al.* 2004). As a result, positive relationships often occur between species' dispersal ability and range sizes (Kunin and Gaston 1997). While the majority of studies have found that geographically rare species exhibit poorer dispersal abilities than common, geographically widespread species, extensive reviews have shown that the relationship between range size and dispersal is better described as asymmetrical (Kunin and Gaston 1993 and 1997). That is, good dispersers can have small, intermediate or large ranges but poor dispersers only have small or intermediate ranges (Gaston 1994, Kunin and Gaston 1997).

Dispersal moves genes from one population to another (Slatkin 1985), and leads to the maintenance of genetic diversity both within and among populations of a species (Lowe *et al.* 2005). The ability of a species to disperse its genes also dictates local effective population size (N_e), as it is empirically measured by gene flow and total genetic diversity (Frankham *et al.* 2002). Species with smaller N_e have a greater risk of extinction due to lower levels of adaptive genetic diversity, and are more affected by genetic drift. Species that have small population sizes are also more likely to experience inbreeding depression or impoverished genes due to reduced genetic variability (Karron 1997; Kunin and Gaston 1996). Saccheri *et al.* (1998) have shown that inbreeding is just as important in determining extinction risk in natural metapopulations of the Fritillary butterfly (*Melitaea cinxia*) as are demographic parameters and environmental stochasticity. Greater dispersal ability should lead to higher levels of genetic diversity and gene flow, therefore reducing the expression of deleterious alleles, or inbreeding depression in populations (Soule 1986).

To test the predictions of rarity theory, this study compares dispersal ability, gene flow and genetic diversity among three species from the microhylid genus *Cophixalus* to determine if these factors could explain differences in species geographic ranges. These three species vary greatly in their geographic range size, from the most geographically widespread (6550km^2) species *C. ornatus*, through the intermediate range size of *C. hosmeri* (300km^2), to the most restricted species *C. neglectus* (37km^2), which is only found on two mountain tops. The geographic ranges of these species are not restricted by anthropogenic factors and they occur in high abundances within their ranges (Shoo and Williams 2004). *Cophixalus ornatus*, *C. hosmeri* and *C. neglectus* are all terrestrial-breeding frog species endemic to the tropical rainforest of North Eastern Australia. Previous studies have shown the importance of consistent rainfall (Williams and Hero 2001) and habitat stability (Graham *et al.* 2006) for microhylid persistence in rainforest habitats. Williams and Hilbert (2006) also demonstrate that five species of this genus (two considered in this study) are the most vulnerable to climate change within the Wet Tropics biogeographic region. However, it is unknown whether low dispersal ability is the cause of restricted distribution in these species or they are physiologically constrained by their need for sufficient moisture for reproduction and survival.

The aim of this study is therefore to compare genetic measures of dispersal ability (gene flow, genetic diversity and population structure) in these three closely related frogs, to evaluate whether dispersal ability influences range size. I predict that, if these species follow the rarity theory model, there will be lower genetic diversity and gene flow in the geographically restricted species (*C. neglectus*) than in the more geographically widespread species (*C. ornatus*).

Methods

Sample collection

Samples for population genetic analysis were collected in the Wet Tropics biogeographic region, northern Queensland, Australia, at three locations (Figure 1). Genetic samples were collected from *Cophixalus ornatus* at Tully Falls Rd, Atherton Tablelands (Lat; Long -17.75; 145.53), from *C. neglectus* at Mt Bellenden Ker (Lat; Long –17.26; 145.85) and from *C. hosmeri* from Mt Lewis, Carbine Uplands (Lat; Long –16.52; 145.27) in December 2002, February 2003 and March 2003 respectively.

Sample locations were at 0, 50, 100, 200, 500 and 1000 m along 1km transects in core habitat in areas of continuous rainforest and high frog abundance for all three species. For two species, samples were also collected from single locations on additional mountaintops; these were Lamb Range (Lat; Long -17.02; 145.63) for *C. ornatus* and Mt Bartle Frere - BF (Lat; Long -17.38; 145.80) for *C. neglectus*. These increased maximum distances between samples to 16km for *C. neglectus* and 80km for *C. ornatus*, to give some idea of larger scale dispersal capacity.

Seven to 19 samples were collected at each location (Table 1). Samples were collected at each site over three consecutive days and nights. This effort allowed most individuals from each location to be captured, as after this time I mainly encountered recaptured animals. Frogs were measured, toe tissue samples were taken and stored in 100% ethanol, and frogs were then released at their point of capture.

A total of 211 individuals was sampled along the 1 km transects: 82 *C. ornatus*, 61 *C. hosmeri*; 78 *C. neglectus* (Table 1). Nine additional samples were obtained from *C. ornatus* at Lamb Range, and eight were obtained from *C. neglectus* at Bartle Frere.

DNA Extraction and Inter Simple Sequence Repeats (ISSR) amplification

DNA was extracted from frog toe tissue samples using ammonium acetate/ ethanol precipitation (Nicholls *et al.* 2000), and was resuspended in 50µl of 10 mM Tris 1 mM EDTA buffer (TE). It was then quantified using a GeneQuant spectrophotometer

(GE Health) and diluted in TE to 5ng/µl. Additional purification of DNA from *C. ornatus* to remove inhibitors from DNA extracts of this species that were preventing polymerase chain reaction (PCR) amplification was conducted using a MoBio gel purification kit (MoBio™ catMB5830).

Genetic analysis was conducted using Inter-Simple Sequence Repeats (ISSR's) which are generated by single primer amplification from genomic DNA; they are based in simple sequence repeats (SSRs) but anchored in the flanking sequences, and exhibit a relatively high level of polymorphism (Bussell *et al.* 2005). ISSR's are a highly reproducible class of genetic marker making them a very effective tool for gathering genetic information from natural populations (Zietchiewicz *et al.* 1994). They were used because of a paucity of fast evolving, species specific, nuclear makers for species in this genus. ISSR's are dominant markers, and thus only the presence or absence of a banding position can be determined, similar to AFLP's and RAPD's. However, anchoring of the PCR primer prevents amplification of long SSR repeat regions and reduces the number of fragments produced. Data on dominant markers such as this cannot be used in many standard analyses, including Hardy-Weinberg equilibrium tests. Hardy-Weinberg equilibrium was therefore assumed when carrying out all analyses.

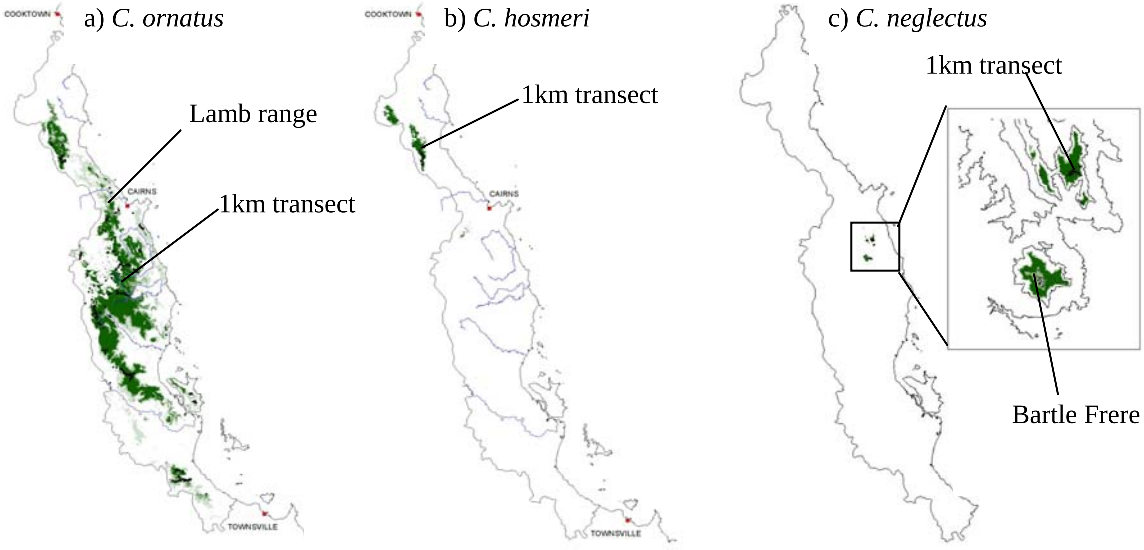

Figure 1: The distribution maps for a) *C. ornatus* , b) *C. hosmeri* and c) *C. neglectus* show the sites in which DNA was obtained for the 1 km transect and sites Bartle Frere (BF) and Lamb Range (LR).

Thirty three Universal ISSR primers from the University of British Columbia SSR primer set 9 were initially screened and six primers that consistently amplified across all three species were used in subsequent population screening. Final genetic analysis was conduced using fluorescently labelled primers: 818-$(CA)_8$ G, 836-$(AG)_7$ AAT, 841-$(GA)_8$ YC, 844-$(CT)_8$ RC, 859-(TG)8 RC, and 864-$(ATG)_6$. PCR reactions were carried out in a total volume of 25 µl consisting of 25 ng of template DNA, 1 x PCR buffer (Qiagen), including 1.5 mM of $MgCl_2$, 0.16 mM dNTP's , 20 pmol primer and 1 unit of *Taq* DNA Polymerase (Qiagen). ISSR's were amplified on a thermocycler (Eppendorf) using a PCR amplification profile consisting of 5 mins at 94°C, then 35 cycles of 94°C for 1 min, 50°C for 30 secs, 72°C for 1 min and a final 10 min extension at 72°C.

For ISSR primers 818, 844 and 859 band presence / absence was detected by running 10µL of product on 2% agarose gels buffered with Tris-Borate-EDTA (0.15 M Tris, 0.15 M Boric acid, 0.003 M $EDTANa_2$) and stained with ethidium bromide after being run for 120 mins at 80 volts with 1kb DNA ladder (Generuler) as a size marker. For ISSR Primers 836, 864 and 841, fluorescently labelled (HEX) PCR product were separated on 4% denaturing acrylamide gels run on a Gelscan 2000 machine (Corbett) for 60 min. The 1kb DNA ladder (Generuler) was used as a size marker. ISSR bands were binary coded as present (1) or absent (0) and concatenated among primers. Any smeared or very weak banding positions were excluded. The number of polymorphic loci scored varied between species. The total number of loci scored for each species was 61 for *C. ornatus*, 46 for *C. hosmeri* and 66 for *C. neglectus*.

Data analysis

The presence/absence data matrix was analysed in ALFP-Surv 1 (Vekemans *et al.* 2002) to gain estimates of gene flow and genetic diversity using the Lynch and Milligan (1994) methods. AFLP-Surv was used as it accounts for dominant data (i.e. not knowing if the population is in Hardy-Weinberg equilibrium (Lowe *et al.* 2004). Population genetic diversity was analysed in AFLP-Surv 1 and statistics analogous to those for co-dominant data are given in Table 2. The analogous statistics are within population diversity $\boldsymbol{H_j}$ (comparable to $\boldsymbol{H_e}$, Figure 2), total heterozygosity $\boldsymbol{H_t}$, and mean heterozygosity across populations $\boldsymbol{H_w}$ (comparable to $\boldsymbol{H_s}$). Parameters for genetic diversity were given as Nei's total genetic diversity $\boldsymbol{H_t}$ and Nei's genetic diversity within populations $\boldsymbol{H_w}$ (Lynch and Milligan 1994) and between population differentiation is given as $\mathbf{F_{st}}$ values.

To determine the amount of gene flow between populations the number of effective migrates per generation was calculated using the Stepping Stone Model of gene flow: $N_em = ([1-F_{ST}]\ [-\ln 2\ \mu])/4\ \mu\ F_{ST}$, where N_em is the average number of migrants per generation and µ is the mutation rate (Crow and Aoki 1982) and Wright's Island model where $Nm = (1-F_{st})/\ 4\ F_{st}$ (Wright 1951). A published estimate of vertebrate nuclear mutation rate of 10^{-6} for vertebrates was taken from the literature as pervious publications have suggested very slow rates of mutation for frog species (Crawford 2003).

Isolation by distance analysis comparing the genetic distance matrix to the known geographic distance for each species (Mantel's test) was carried out in GenAlex version 6 (Peakall *et al.* 2006), using the Nei's genetic distance matrix, generated by AFLP-Surv (Vekemans *et al.* 2002). These analyses were run including and excluding the Bartle Frere (BF) and Lamb Range (LR) sites for *C. ornatus* and *C. neglectus* respectively, to investigate isolation by distance over both the larger and smaller scales for these species.

To look for cryptic genetic population structuring within the 1 km transect for each species the Bayesian clustering method developed by Pritchard *et al.* (2000), and implemented in the software STRUCTURE V.2 (Flaush *et al.* 2003), was used. STRUCTURE determines the log likelihood that an individual sample (in this case any given frog) belongs to a “population” with the number of sub-populations (*k*) defined for each run. In total five iterations for each predicted value of *k* (the number of subpopulations) were carried out with admixture models run for *k* values between 1 and 7 populations. Burn in periods of 10 000 replications and MCMC (Markov chain Monte Carlo) of 10 000 iterations were carried out for each run (as recommended by Evanno *et al.* 2005). Testing of additional burn-in (up to 100 000) and iterations (up to 250 000) did not reveal an improved likelihood outcome. For each species additional analysis was carried out on the output from STRUCTURE as per Evanno *et al.* (2005) to determine correct values for *k*.

Table 1: Sites in which samples were taken, central latitudinal and longitudinal position of sites, the number of samples from each population and the overall species estimate of density and range size.

Species	Density / Range size	Site	Lat; Long	No. of samples at 0m, 50m, 100m, 200m, 500m, 1000m
C. neglectus	18 per Ha	BF	-17.38; 145.80	8 (from one location)
	37 km^2	1km	-17.7418; 145.5356	9, 13, 14, 19, 9,14
C. hosmeri	42 per Ha	1km	-16.5155; 145.2696	7, 6, 8, 12, 8, 10
	300 km^2			
C. ornatus	28 per Ha	LR	-17.02; 145.63	9 (from one location)
	6550 km^2	500m	-17.2636; 145.8538	11, 9, 19, 15, 14, 14

Results

The genetic differentiation among populations over the 1km transects (F_{st}, Table 2) did not vary greatly between the restricted-range *C. neglectus* ($F_{st} = 0.08$), the intermediate-range *C. hosmeri* ($F_{st} = 0.11$) and the widespread *C. ornatus* ($F_{st} = 0.11$). These values were used to generate estimates of the number of migrants exchanged between populations using both Wright's island model and the Stepping Stone model (values presented consecutively). For the one km transect 3 to 12 migrants are estimated per generation for *C. neglectus* and 2 to 8 migrants per generation for the more widespread species *C. ornatus* and *C. hosmeri*.

The genetic differentiation among populations (F_{st}) for the two species (common - *C. ornatus* and rare - *C. neglectus*) suggests very restricted gene flow between the different mountain ranges (BF and LR) sampled (Table 2). Estimates for migrants per generation (Wright's island model and Stepping stone model) for the widespread species, *C. ornatus*, over a distance of approximately 80 km between the 2 mountain ranges with no observable geographic barriers and continuous population was less than 1 suggesting restricted dispersal between populations. The amount of gene flow between the two mountain ranges, over approximately 16 km, for the geographically restricted species, *C. neglectus* is approximately 4 to 2 migrants per generation.

The expected heterozygosity (H_j) or genetic diversity within populations of the restricted species *C. neglectus* did not differ significantly among populations across the 1 km transect (populations 0 m, 50 m, 100 m, 200 m, 500 m and 1000 m) or from the total genetic diversity (H_t) (Figure 2a). However, the population from BF had significantly lower levels of genetic diversity than the populations on Bellenden Ker from the main study site. For the intermediate, *C. hosmeri*, (Figure 2b) and widespread species, *C. ornatus*, (Figure 2c) genetic diversity did not differ significantly among populations along the 1 km transect or between those populations and the isolated mountain population. Populations of *C. neglectus* and *C. hosmeri* tended to have overall higher levels of genetic diversity within population compared to that of *C. ornatus*. The genetic diversity across populations (H_w) was higher in *C. neglectus* ($H_w = 0.28 \pm 0.02$) and in *C. hosmeri* ($H_w = 0.23 \pm 0.02$) than in *C. ornatus* ($H_w = 0.16 \pm 0.02$). Genetic diversity across sites decrease slightly when other sites

(BK and LR) were include for *C. neglectus* (H_w = 0.26 ± 0.02) and *C. ornatus* (H_w = 0.15 ± 0.02).

The highest total genetic diversity (H_t) within a 1km transect occurred in the range-restricted species *C. neglectus* , which occupies an area of 37 km^2 on the two highest mountain tops in northern Queensland (H_t = 0.30). The other, more widespread species both had lower levels of genetic diversity within transects, *C. hosmeri* (H_t = 0.26) and *C. ornatus* (H_t = 0.18; Table 2). The genetic diversity for both *C. ornatus* (H_t = 0.27) and *C. neglectus* (H_t = 0.32) increased when the extra mountain top samples were included (Table 2).

Table 2: Genetic diversity within populations H_w, total genetic diversity H_t and Wright's F_{st} (* means significantly different at 0.05 level) for all species across the 1 km transect and including extra sites (BF and LR) stated separately.

	H_w (± 95%CI)	**H_t**	**F_{st}** (± 95%CI)
C. neglectus 1 km	0.28 ± 0.02	0.30	0.08*± 0.03
C. neglectus with BF	0.26 ± 0.04	0.32	0.19*± 0.02
C. hosmeri 1 km	0.23 ± 0.02	0.26	0.11*± 0.02
C. ornatus 1 km	0.16 ± 0.02	0.18	0.11* ± 0.01
C. ornatus with LR	0.15 ± 0.02	0.27	0.53* ± 0.01

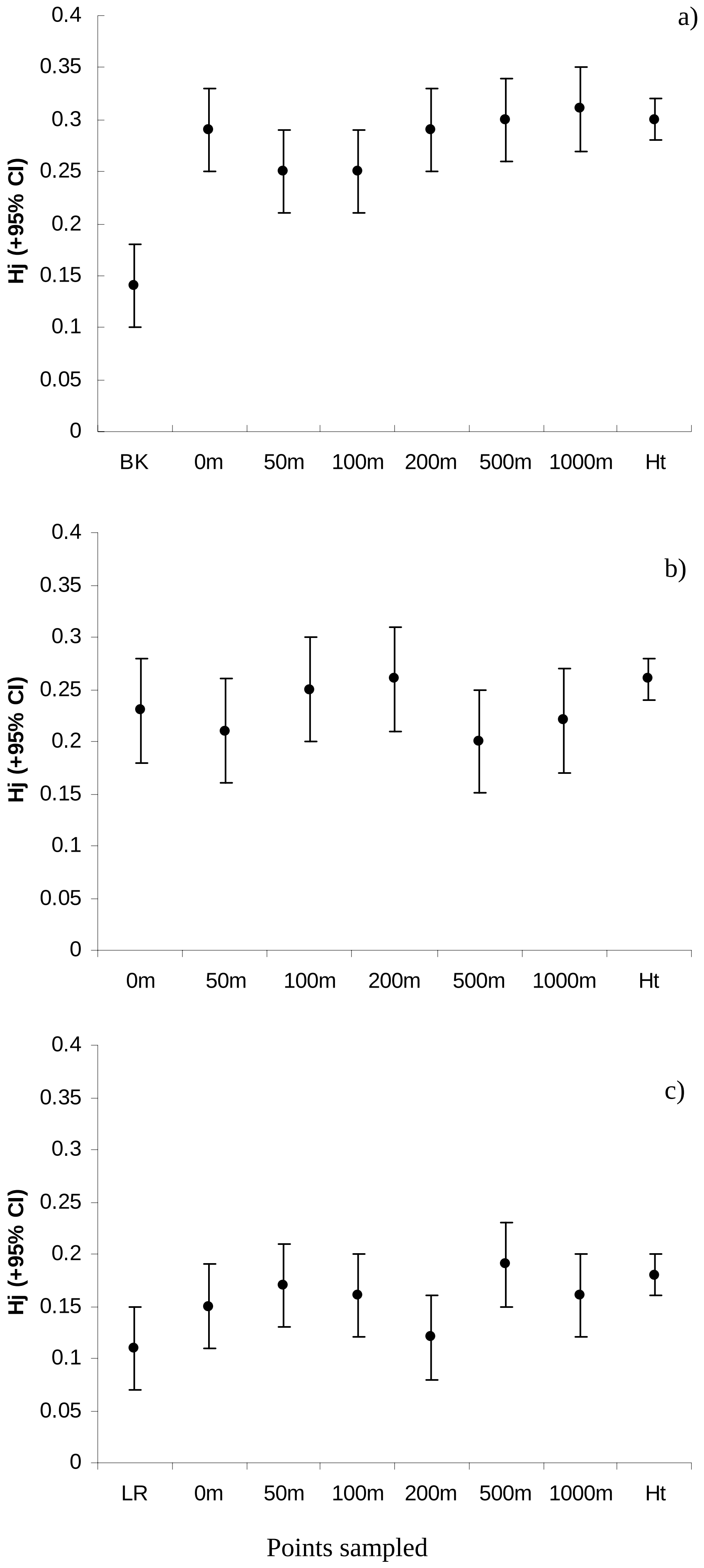
a)
Hj (+95% CI)
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
BK
0m
50m
100m
200m
500m
1000m
Ht
b)
Hj (+95% CI)
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
0m
50m
100m
200m
500m
1000m
Ht
c)
Hj (+95% CI)
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
LR
0m
50m
100m
200m
500m
1000m
Ht
Points sampled

Figure 2. Genetic diversity within populations compared across populations along the 1km transects, at other sites, and in total for all species a) *C. neglectus,* b) *C. hosmeri* and c) *C. ornatus*. Abbreviations for BK = Bellenden Ker, LR = Lamb range and H_t = total genetic diversity.

Genetic population structuring

A comparison of Nei's genetic distance with geographic distance (Mantel's test) including the data for all populations of *C. neglectus* demonstrates significant isolation by distance in this range-restricted species (r = 0.908, p = 0.000; y = 0.0895x + -0.1819) (Figure 3a). The widespread species *C. ornatus* also showed significant isolation by distance (Figure 3b, r = 0.994 p = 0.000; y = 0.1977x + -0.4441) between the 1km transect and the Lamb Range site over 80km away (Figure 3b).
Isolation by distance analyses were also carried out over the 1 km transects for all three species to look at fine scale genetic structure. The widespread species, *C. ornatus*, and the intermediate-range species, *C. hosmeri*, showed significant isolation by distance along transects (r = 0.728, p= 0.003; y = 0.00003x + 0.0121, Figure 4c and r = 0.663, p = 0.02; y = 0.00005x + 0.0252; Figure 4b, respectively). For *C. neglectus*, the most restricted species, there was no significant isolation by distance over the 1km transect (r = 0.348, p = 0.115; y = 0.0895x +-0.1819, Figure 4a). This suggests that over a distance of 1 km there is more population differentiation within the widespread and intermediate-range species than in the restricted species.

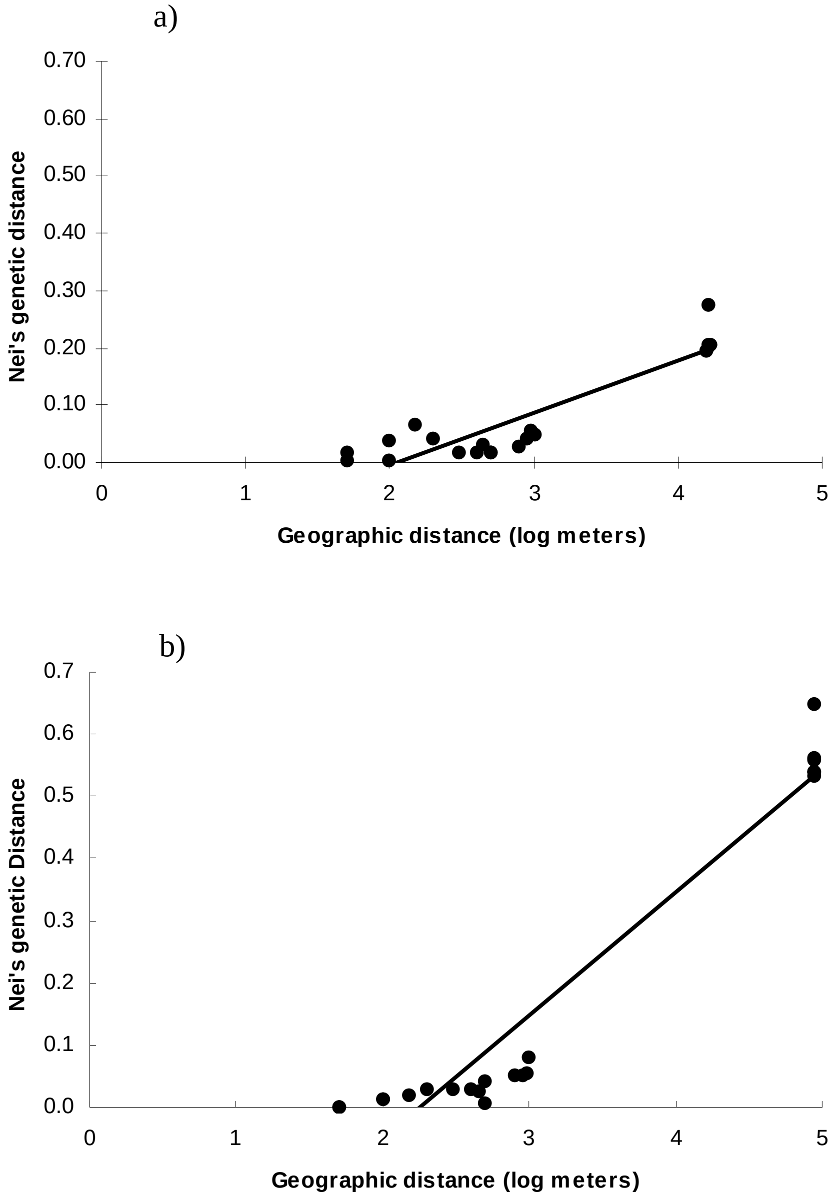

Figure 3: Plots of isolation by distance for a) *C. neglectus* including the population BF from 16 km apart and b) *C. ornatus* including the population of LR from 80 km apart, line slopes and intercepts are in text.

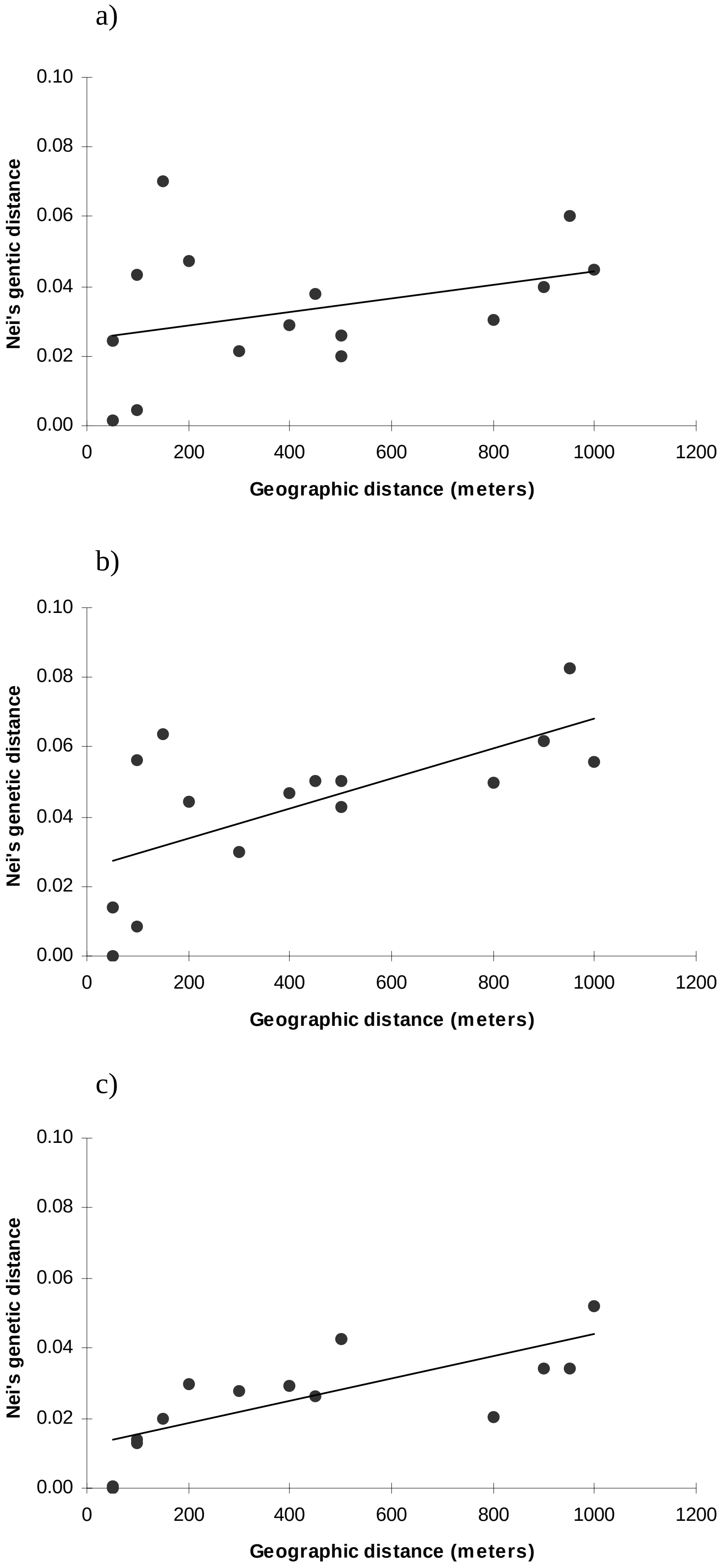

Figure 4: Plots of isolation by distance across the 1 km transect for a) *C. neglectus,* b) *C. hosmeri* and c) *C. ornatus* using Nei's genetic distance, with regression lines.

Slopes and intercepts presented in text.

Bayesian analysis of population genetic differentiation using STRUCTURE within each 1 km transect by the allocation of genetically similar individuals to subpopulations revealed a difference between the population structures of the two wider ranging species and that of the more restricted species, *C. neglectus*. The number of sub populations (*k* value) that best explained the allocation of individuals within the 1 km transect for the most widespread species, *C. ornatus* was *k*=2. The split into distinct sub populations occurred at 200 m along the 1 km transect. For the intermediate-range species, *C. hosmeri, k* = 2 subpopulations were also suggested, with the turn over of individuals again occurring at around 200 m from the start of the transect. For the most restricted species, *C. neglectus k* = 3 subpopulations were indicated. Individuals from the 200 m sample were found to be related to individuals from both the 0 to 100 m samples and the 500 to 1000 m samples.

Discussion

Rarity theory suggests that species may be rare due to loss of genetic diversity and lower levels of gene flow (Gaston and Kunin 1997). This study demonstrates that levels of genetic diversity are very similar among three species with sidely varying range sizes, indicating that the loss of genetic diversity does not explain their patterns of distribution. All three of the species studied have relatively high levels of genetic diversity on the local (1km in this study) scale (*C. neglectus* H_t = 0.30, *C. hosmeri* H_t = 0.26 and *C. ornatus* H_t = 0.18) as compared to other amphibians (H_t = 0.109 across 116 species, Lowe *et al.* 2004). Across the complete ranges I studied (including additional mountain top populations), all three species had similar levels of diversity (H_t ca. 0.30). The highest H_t occurred in the most restricted species, suggesting that this species is not genetically impoverished as has been suggested for species with small range sizes (Gaston and Kunin, 1997). High levels of genetic diversity have been found in rare species in other comparative studies, such as rare and common plant congeners in America (Gitzendanner and Soltis 2000) and rare and common plants of the genus *Boronia* in Queensland Australia (Shapcott *et al.* 2005).

Hewitt (1996) suggested that long term demographic stability of populations can lead to high genetic diversity. The core distributions of both *C. neglectus* and *C. hosmeri* within the Wet Tropics are in "rainforest refugia" which are thought to have been the most stable rainforest areas over geological time (Graham *et al.* 2006). This may explain the maintenance of genetic diversity observed in these species. In contrast, the recolonisation and expansion of *C. ornatus* from refugial areas within rainforest may explain lower levels of local genetic diversity seen in this species (Hoskin 1996). The range expansion of frog species such as yellow-bellied toads (*Bombina pachypus*) in Italy show similar patterns of reduced genetic diversity (Canestrelli *et al.* 2006); populations of this frog that have recolonised northern environments have lower genetic diversity compared to populations of the same species that have maintained higher diversity in refugial southern environments. I found relatively lower levels of local genetic diversity in the intermediate (*C. hosmeri)* and widespread (*C. ornatus*) species. Both species have relatively high levels of local genetic diversity compared to the amphibian average; this may be due to the high abundance and population density of these species within their restricted range (Shoo and Williams 2004). Other studies show that restricted species can still have substantial genetic diversity, with the number of individuals contributing to the gene pool being more important than geographic range size (Xiao *et al* 2005; Simberloff 1998). Differences in life history between frog genera such as terrestrial-breeding in microhylid frogs, which typically lay fewer eggs and have greater parental care, than stream or pond breeding frogs such as toads may also explain higher genetic diversity seen here due to variation in reproductive success among individuals.

All calculated F_{ST} values except that comparing the transect populations of *C. ornatus* with the Lamb range populations of that species were below 0.2, suggesting that at least some gene flow was occurring. There was, however, significant isolation by distance within the 1 km transects for *C. ornatus* and *C. hosmeri*, the species with the broadest and intermediate geographic ranges. Isolation by distance was not significant at this scale for *C. neglectus*, the species with the narrowest range. This suggests that at this scale gene flow is highest in *C. neglectus*, indicating that the limited geographic range of this species is not a consequence of lower local dispersal rates by individuals. Frogs are generally poor dispersers when compared to other tetrapods (Blaustein *et al.* 1994, Frankham *et al.* 2002, Lowe *et al.* 2004), this is reinforced by a comparison of gene flow from other vertebrate taxa that also occur within the Wet Tropics biogeographic region (Birds $F_{st} = 0.07$ across entire Wet

Tropics region, Anderson 2002; Skinks F_{st} = 0.008 to 0.046 over 7 km Philips *et al.* 2004). However, when comparing gene flow in Microhylid frogs over 1 km to other small rare amphibians from other studies (Larson *et al.* 1984, Driscoll 1998), microhylids do appear to have good levels of gene flow. Driscoll (1998) looked at genetic structure in ecologically similar frogs, *Geocrinia rosea* complex, in Western Australia and found large amounts of genetic differentiation between populations (*G. rosea* F_{st} = 0.69 & *G. lutea* F_{st} = 0.64) over very small distances of 1 to 4 km. Comparisons of gene flow in the ecologically very different Columbian spotted frog, *Rana luteiventris* showed much higher levels of gene flow between populations (results from 2 different populations were Fst = 0.064 + 0.011 & Fst = 0.016 + 0.002) and juvenile dispersal events of up to 5km were recorded (Funk *et al.* 2005). Rates of gene flow differ strongly among frog taxa, probably due to differences in the behavioural ecology and life histories of species.

Although rates of gene flow were relatively high across the 1 km transects for all species, the significant evidence for isolation by distance at this scale among populations of the two more widely distributed species indicates that genetic differentiation can occur over relatively small spatial scales in these species. This result is supported by the results of subpopulation assignment using STRUCTURE, which showed that all three species have population structuring along the 1 km transects. In *C. ornatus*, and to a lesser extent in *C. hosmeri*, breeding males form small, discrete calling aggregations, and in *C. ornatus*, they are known to return to the same calling sites across years (Brooke *et al.* 2000). Limited male dispersal, combined with unknown but possible relatively low dispersal by females and subadults, could lead to sub-structuring on the scale observed.

Only minimal genetic differentiation was detected across 1km in the most range-restricted species, *C. neglectus*. This result is somewhat contradictory to rarity theory which suggests more differentiation should occur in restricted species (Brouat *et al.* 2004, Kunin and Gaston 1997, Lowe *et al.* 2005). However STRUCTURE analysis suggested that three sub populations of *C. neglectus* existed (while not detectable over geographic distance in the isolation by distance analysis) with these aggregations of individuals more closely related than by random over the 1km transect. This suggests that dispersal between sub populations in *C. neglectus* may occur across greater distances then just neighbouring populations, as is suggested by the stepping stone model or than separation of individuals over geographic distance (Kimura 1953).

The two species for which samples were available from another mountain range (*C. ornatus, C. neglectus),* showed no gene flow for *C. ornatus* occurring over these larger distances and only limited gene flow for *C. neglectus*. Although there are no physiological barriers to dispersal or lack of suitable habitat available, the population structuring seen over the 80 km between the two sites suggested limited dispersal rates for *C. ornatus*. This widespread species shows population structure across the entirety of its range, and in fact mitochondrial analysis suggests that there are distinct northern and southern lineages in this species (Hoskin 2004). In the restricted-range species, *C. neglectus,* limited gene flow apparently occurs over the 16 km between the two isolated populations. Although the rainforest cover between these two populations is continuous, this species presently occurs only at altitudes above 1000 m. The populations are separated by elevations as low as 300 m, which should be a barrier to dispersal between the sites. These populations would have been continuous in wetter, cooler times, but may been separated by habitat for as long as 18 000 years since the last cool wet period in the region (Moritz 2005).

The calculated F_{ST} between the populations of *C. neglectus* suggests that they exchange between two and four migrants per generation. If this is occurring, the dispersing individuals are passing through an extensive region that is outside the normal range of the species. This suggests that the species is capable of tolerating the physical conditions occurring outside its normal range for periods long enough to move through the unoccupied habitat. It is possible that factors other than the physical environment, such as competition or resource availability, restrict this species, and to a lesser extent *C. hosmeri,* to mountain tops. It is also possible that conditions at lower elevations during part of the year, perhaps during the winter, are within the environmental tolerances of *C. neglectus,* but that conditions during another season are not, so that the species can migrate through these habitats but cannot establish populations within them. Other studies have shown that the abundance and species richness of microhylids are strongly correlated with the rainfall consistency (Williams and Hero 1998) and with the long term persistence and stability of high quality rainforest (Graham *et al.* 2006). Further investigation is required to determine if this gene flow between mountain top populations is occurring.

The actual factors limiting the distributions of all of these species require further investigation, but their apparent ability to disperse through habitat they cannot permanently occupy suggests that the limitations on reproductive habitat may be important. Observations made during this study determined that *C. neglectus* lays eggs in nests covered only by 2 to 5 cm of humus, compared to *C. ornatus* and *C. hosmeri*, the nests of which were most commonly found under logs and rocks or in cricket holes (Y. Williams, personal observations), which should provide a more buffered climate. Felton *et al.* (2006) demonstrated that female *C. ornatus* actively choose males that provide deeper, more protected nests. Hoskin and Higgie (2005) suggested that habitat suitable for *C. concinnus*, the microhylid with the most restricted range, occurs at lower altitudes where no frogs were recorded. This was also the case for *C. neglectus* within this study, where no observable change occurred in the rainforest structure but frogs were not recorded below 1000 m altitude.

The species with an intermediate geographic range, *C. hosmeri,* has levels of local gene flow very similar to those of *C. ornatus,* which has a much greater range. *Cophixalus hosmeri* is limited to areas above 900 m in continuous rainforest habitat. As with *C. neglectus*, the genetic data do not suggest that the limited range of this species is caused by limited dispersal. Physiological tolerances, resource availability, and species interactions need to be investigated as possible limiting factors. The most widespread species, *C.ornatus,* which genetic data suggest has similar dispersal rates, occurs in more habitat types, such as wet sclerophyll forest at the edge of rainforest, rather than just core rainforest. This suggests that is has a wider range of physiological tolerance (Chapter 3) which may be a more important factor than dispersal ability. In times of historical rainforest contraction, a greater area of habitat suitable for *C. ornatus* would have persisted, allowing the species to persist over a wider area and recolonise its wide range rapidly when the climate became more favourable.

In conclusion, the results of my study strongly suggest that differences in the geographic distributions of three microhylid frog species may not be caused by differential dispersal ability or limitations in gene flow or genetic diversity. Local rates of gene flow appear to be higher in the species with the most restricted range, and overall levels of genetic diversity appear to be similar across all three species. It appears that habitat stability may have allowed these species to maintain moderate levels of genetic diversity and gene flow. These species appear to be limited by climate, resources, or species interactions rather than dispersal, however more testing of these hypotheses are needed.

CHAPTER 6: EXTINCTION FILTERING SHAPES PATTERNS OF COMMONNESS AND RARITY IN AUSTRALIAN RAINFOREST FROGS

Introduction

In many ecological communities, the majority of species are rare (MacArther and Wilson 1967) and therefore rare species contribute disproportionately to species richness. Rare species are also important because rarity is a trait that is generally considered to predispose species to extinction (Simberloff 1998). Rare species are thus commonly given high priority in conservation planning.

The attributes that cause a species to be rare can be difficult to resolve. Most generally, to say that a species is rare is to imply that it has a small population size, compared with closely-related or sympatric species. Small population size can be the result of three fundamental aspects of population biology, as follows:

Geographic range: other things being equal, a species that is narrowly-distributed will have a smaller total population than a species that is widespread;

Local abundance: for a given geographic range, a species that occurs at low density in occupied sites will have a smaller population than one that occurs at high density; and

Ubiquity: for a given geographic range and local abundance, a species that is patchily distributed throughout its range (and thus has a relatively low area of occupancy and greater spatial variation *sensu* Gaston 1994) will have a smaller total population than one that occurs continuously, and thus occupies more sites.

These three attributes can therefore represent distinct axes of rarity and the combination of all three determines the global commonness or rarity of a species. Clearly, a species that has a small range, occurs at low density, and is patchily distributed within its range, is very rare, while a widespread and ubiquitous species that occurs at high density is very common (Rabinowitz *et al.* 1986; Gaston 1994). Between these extremes there are many different combinations of high or low range size, local abundance and ubiquity that make up a continuum from very rare to very common species.

The way in which species in an assemblage are distributed along this continuum of rarity will be shaped by patterns of correlation between range size, local abundance and ubiquity within that assemblage. Understanding these correlations is one of the major goals of macroecology, and a great deal of theoretical and empirical work has been devoted to this problem (reviewed in Gaston *et al.* 2000; Gaston *et al.* 1997). For example, it is frequently observed that range size and local abundance are positively correlated among species (Lawton 1995; Gaston and Blackburn1996). This correlation means that species tend either to be very rare (because they are both locally uncommon and narrowly distributed) or very common (if they have the opposite characteristics). Similarly, metapopulation theory predicts that species that are locally abundant will also occupy more habitat patches within a region, and so have relatively high ubiquity (occupancy), and this positive correlation has been demonstrated frequently in a variety of systems (Warren and Gaston 1997; Gaston *et al.* 2000). A more recent paper has also shown positive relationships between abundance, occupancy and spatial variation (He and Gaston 2003; Gaston *et al.* 2006) for arthropod species which can be used to describe much of their spatial distributions.

The fact that rare species are thought to have high extinction risk suggests that they should tend to be filtered out of communities over time (Johnson 1998). However, each of the three axes of rarity described above makes an independent contribution to total extinction risk. Species that have small ranges are at risk from localised environmental changes that remove all of their habitat; species with low population densities are at risk from stochastic effects that cause fluctuations in density (Simberloff 1998); and species that are very patchily distributed are vulnerable to the effects of local genetic depletion and dispersal failure (Saccheri *et al.* 1998). Therefore, species that are rare on all three axes should be at especially high risk, and we might expect to find few such species in groups that are evolutionarily ancient (Johnson 1998). On the other hand, the extinction risk conferred by rarity on one axis may be at least partly compensated in species that are ‘common’ on one or two of the other axes. In this way, extinction filtering may eliminate species with some combinations of values of the three axes, and allow the persistence of other combinations, thus shaping patterns of geographic rarity, local abundance and ubiquity in assemblages of living species. Niche conservation (Wiens and Graham 2005) may also mean these species maintain ecological traits from when they were once more widespread (e.g. being abundant and ubiquitous) which gives them resilience during times of contracted geographic range (which makes them rare in present times).

In this study I examine relationships among geographic range, local abundance and ubiquity in an ancient lineage of rainforest microhylid frogs in the genus *Cophixalus,* from the Wet Tropics in north Queensland Australia. I determine the way that interactions among these three axes of rarity shape patterns of overall commonness and rarity in the assemblage. The species in this genus have deep lineages on the order of 10 million years old (Hoskin 2004) and current patterns of distribution and species richness in the group are related to geographic variation in rainforest stability during the Quaternary climate fluctuations (Graham *et al.* 2006). Microhylids are the only group in the region that do not exhibit a significant species-area relationship (Williams and Hero 2001) and their distribution patterns suggest a complex interaction between in-situ survival in isolated mountain-tops and non-random patterns of local extinction (Williams and Pearson 1997; Williams and Hero 2001; Hoskin 2004; Graham *et al.* 2006). There are large differences among species in geographic range, varying from some species that are mountaintop endemics with ranges as small as three square kilometres, up to 6 550 km^2 (most of the Wet Tropics bioregion) for the most widespread species (see chapter 2). All species have similar life histories, morphologies and ecologies: they are small terrestrial frogs that are restricted to rainforest and have direct-developing eggs (Hoskin 2004). I suggest that these geographically-restricted species have ecological traits that confer resistance to extinction, and here I test if compensation of rarity on any three axes of rarity has allowed these species to persist through time.

I test for non-random associations among these three axes of rarity, and go on to demonstrate how these associations shape the distribution of species along a continuum from rare to common species. To take this second step, I develop a single measure of rarity that is a composite value of the three axes of rarity just discussed.

A new measure of rarity

I derive a measure of the rarity or commonness of a species in the following way; first, each of the three quantities that contribute to overall rarity – range size, local abundance and ubiquity – is measured for the species, and each measure is then standardised to a range between zero and one by dividing all values by the largest value; secondly, I define a 3-dimensional space using the orthogonal axes of range size, local abundance and ubiquity (see Figure 1). The location of any species in this space defines the contributions of each of the three axes to its final degree of rarity or commonness. A single measure of overall rarity is derived as the Euclidean distance of that location from the origin – I refer to this as the 'RI' value of a species (Rarity Index). This number is a composite measure of rarity for a species that reflects the combined influences of range size, local abundance and ubiquity, with each of these sub-variables given equal weight.

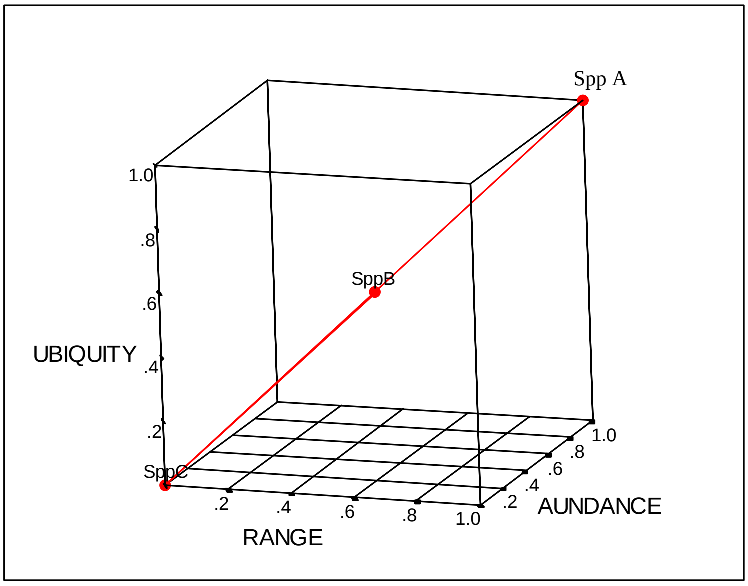

Figure 1. Species A, B and C plotted in three dimensional space showing how rarity indices were generated from the point of origin to each species' position in 3D space when values were plotted for all three axis of ubiquity, abundance and range size. Sp. A would be very common on all three axis, Sp. B would be intermediate on all three axis, while Sp. C would be extremely rare and restricted and have a low RI value.

Methods

Sampling conditions

Preliminary sampling of microhylid frog populations was conducted to determine the environmental conditions under which the highest frog calling occurs, and thus in which the best sampling would be carried out. Initial regression tree analysis (S-Plus) on optimal conditions for microhylid frog calling determined that calling rates were highest when sampling was carried out if moisture was above an index of 2 (meaning all leaf litter and vegetation are wet), temperature was above 20^{o}C and humidity was above 80%. Samples were not included that did not meet these criteria. All species abundance counts were from calling males; detectability of males in these frogs is very high as calls are loud and easily distinguished between species. Transect width was limited to 20 metres (10 meters either side of central line) to minimise the effects of vegetation density on calling detectability. This distance was initially determined to allow all calls to be detected. It was established that beyond a distance of 10 meters calls may become too faint to reliably count. Sampling within a subregion was always carried out on the same night so that inter-night variation did not confound abundance counts.

Population density

Standardised surveys where carried out for 12 of the 14 Microhylid frog species in the Wet Tropics (excluding *C. saxatilis* and *C. mcdonaldi* due to poor sampling conditions). A survey consisted of a 50 m long by 20 m wide transect in which all calling frogs were counted over approximately a ten minute period. Transects were surveyed at every 50 meter change in elevation and only on nights in which good frog calling was likely to occur (see sampling conditions). Surveys were carried out across the entire geographic range of all species. For more details see Shoo and Williams (2004). For *C. exiguus* and *C. concinnus* counts were also used from surveys carried out by C. Hoskin and S. Williams (pers comm.) and Hoskin and Higgie (2005) that used similar criteria to those sampling methods described here. The number of transects used in the analysis for each species were: *Austrochaperina fryi* -132, *A. pluvialis* – 328, *A. robusta* – 258, *Cophixalus aenigma* – 78, *C. bombiens* – 51, *C. concinnus* – 8, *C. exiguus* – 6, *C. hosmeri* – 46, *C. infacetus* – 184, *C. monticola* – 21, *C. neglectus* – 38, *C. ornatus* – 328.

Geographic range size

Total geographic range size (the sum of core and marginal habitat inhabited by each species) for each species was taken from Williams (2006). These distributions were obtained using a combination of bioclimatic modelling, known habitat preferences and biogeographic constraints on distributions (see Williams 2006 for full details of methodology).

Ubiquity

Ubiquity was measured in two different ways. First, I calculated the coefficient of variation (CV) of measures of abundance (including zero values) at all surveyed sites within a species' geographic range. High values of the CV indicate species with uneven distributions of abundance among sites. I measured ubiquity as 1 – CV: species with values close to one on this index had continuous and uniform distributions throughout their geographic ranges. Second, I calculated for each species the proportion of surveyed sites within its geographic at which it was recorded as present. This is a direct measure of the proportion of the total geographic range that was occupied, irrespective of variation in abundance at occupied sites. These two measures of ubiquity were highly correlated among species (r = 0.80). I used the first measure ($1 - CV_{abundance}$) in all subsequent analyses because it contained more information on variability in abundance among sites.

Measures of abundance were square-root transformed, and measures of range size were double square-root transformed, to normalise values. The transformed data were then standardised to maximum values of one. The ubiquity measure did not require transformation.

Phylogenetic analysis

Rather than simply assuming an effect of phylogeny on extinction risk, possibly resulting in erroneous conclusions (see Putland 2005) and increasing the chance of making a type II error, I used the program PHYSIG in MATLAB v6.5 to check for a phylogenetic signal in the three traits of interest. A phylogeny was created in PDTREE (PDAP, Garland *et al.* 2003) by pruning the microhylid phylogeny of Hoskin (2004). There was no significant phylogenetic signal in any of the traits (Abundance, p = 0.18; Range size, p = 0.27; Ubiquity, p = 0.14). Therefore I did not correct for phylogeny in further analysis. Phylogenetic independence contrasts was also not tested for in this analysis as it could not be used to plot species in three dimensional space.

Random distribution of RI values

To determine if the RI values were significantly different from random, 5000 randomly generated RI values were obtained. These values were obtained by resorting the actual values which I had measured for each of the 12 frog species on each axis, re-allocating these values randomly, and recalculating RI indices for the new combinations of values. I compared the actual values to the frequency distribution of randomly generated values. To test if the randomly generated common index (RI) values were significantly different from the actual RI values, a one sample t-test and F- test was used.

Results

There was a significant positive correlation among species between ubiquity and abundance ($r = 0.76$, $p = 0.004$, Figure 2), and a significant negative correlation between range size and abundance ($r = -0.68$, $p = 0.02$, Figure 3). That is, species that were more abundant at occupied sites were also more evenly distributed throughout their ranges, and also had smaller geographic ranges. These relationships imply a negative trend between ubiquity and geographic range, but were found to be non-significant ($r = -0.54$, $p = 0.07$, Figure 4).

I calculated partial correlations to test the strength of the association between each pair of variables, independent of the influence of the third variable. This revealed a significant independent relationship between abundance and ubiquity ($r = 0.64$, $p = 0.03$), but partial correlations for the other two variables were not significant (range size – abundance: $r = -0.49$, $p = 0.12$; ubiquity-range size: $r = -0.04$, $p = 0.90$). Figure 5 plots the location of each species in the 3-dimensional range-abundance-ubiquity space. This plot reveals a tendency for species to be clustered towards the middle of the space, with few species in that region close to the origin which is defined by small range, low abundance and low ubiquity. Species tend to be equidistant from the origin as a result of the tendency for those that score low on one axis to score highly on one or both of the others, as described above. The effect of these compensatory relationships is made even more clear in Figure 6. This shows the distribution of RI values for all species (Figure 6), where R is the distance of each species from the origin of the 3-d plot of Figure 5. RI values for these frog species varied from 0.8 to 1.3. This is a narrower range of values than would be expected from a random association of the observed values of range, abundance and ubiquity in this set of species (t_{11} = 5.26, p = 0.0001; $F_{4999,11}$ = 3.50, p = 0.01).

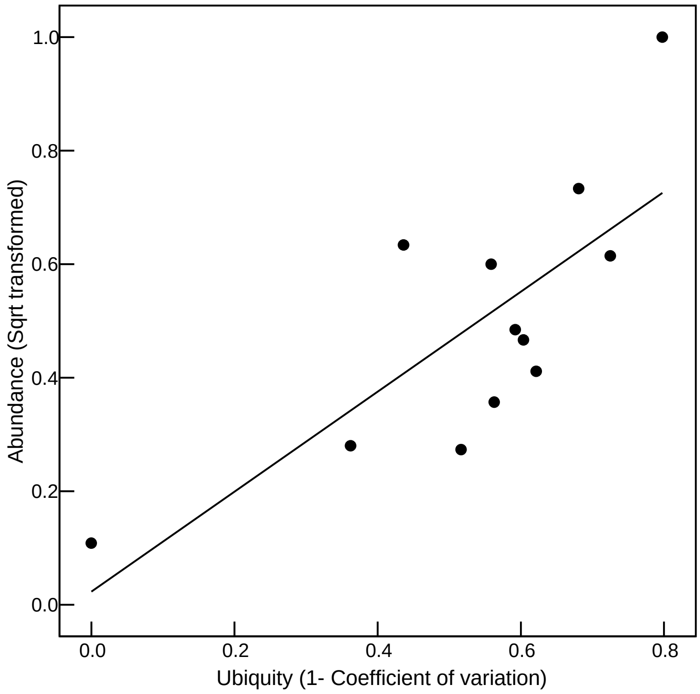

Figure 2: Correlation of abundance (square root transformed) with ubiquity for 12 species of microhylid frogs with a fitted linear trend line.

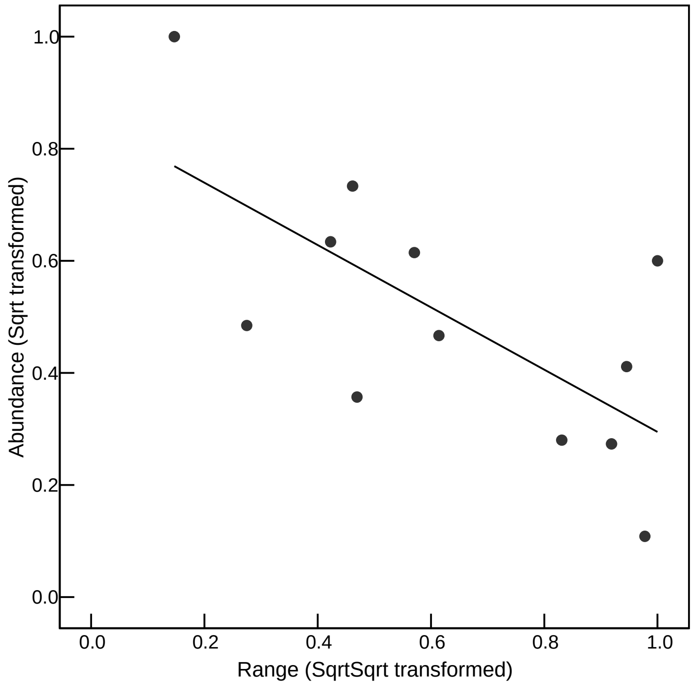

Figure 3: Correlation of abundance and range size (4th root transformed) for 12 species of microhylid frogs with a linear trend line fitted.

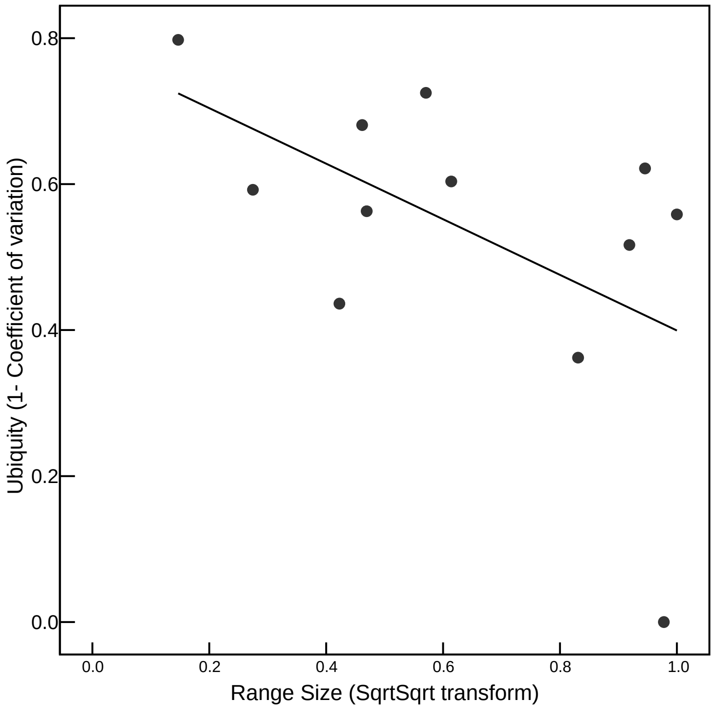

Figure 4: Correlation of ubiquity and range size for 12 species of microhylid frogs with linear trend line fitted.

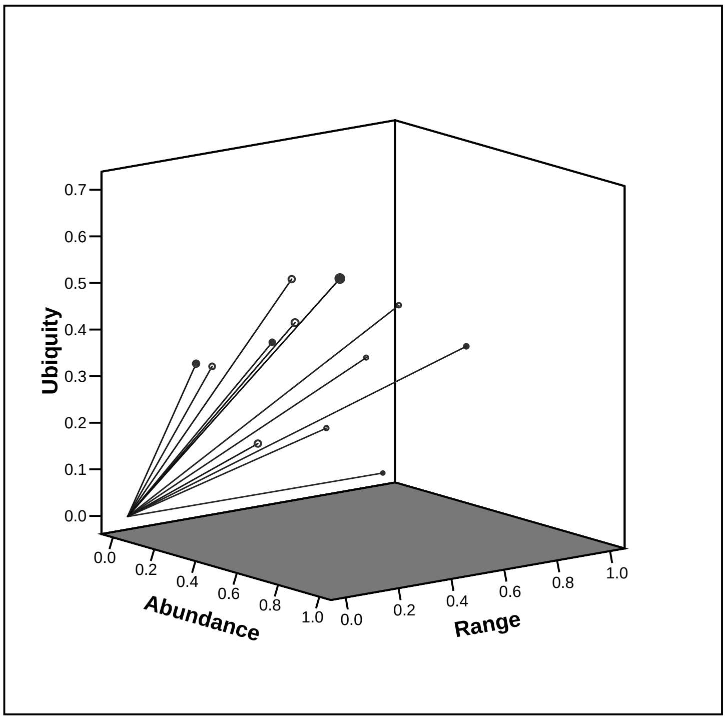

Figure 5: Rarity indices for all 12 species of *Cophixalus*.

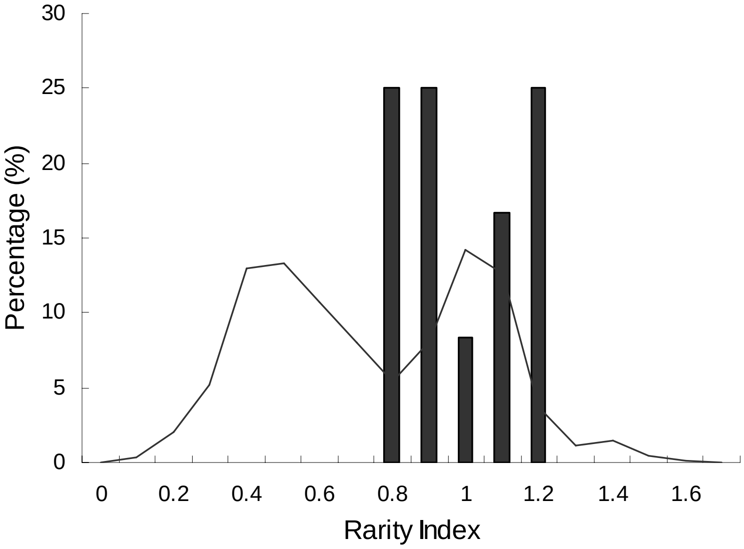

Figure 6: The distribution of 5000 randomly generated rarity index values (line) compared to those values calculated for microhylid species (solid bars).

Discussion

Comparison of all species shows that no species are rare on all three axes of rarity. Species are clustered in space indicating that while a species may be rare on one axis, this is compensated by being ‘common’ on another axis. Results show that no species has a rarity value of below 0.8, suggesting that a species cannot be rare on all three axes and persist through time. It is possible that species which may have been rare on all three axes in the past have gone extinct as their populations became non-viable under changing environmental conditions. I thus propose that while some species are rare on one axis, this is ameliorated by being common on another axis and it is this compensation that has allowed them to persist through time.

The Wet Tropics bioregion has undergone many previous extinction events due to the expansion and contraction of rainforest habitats (Williams and Pearson 1997, Graham *et al.* 2006) and thus my results indicate that, in these microhylid frogs, the compensation I observed among the three axes of rarity confers resilience, as these species have persisted while many other species may have become extinct. Extant species may simply be an extinction-resilient group which have previously passed through many extinction filters and have ecological traits that have allowed them to persist. With few exceptions (*C. saxatilis, C. exiguus* – limited information) all of the rare and restricted species are confined to high mountain tops above 900m and appear to be geographically limited by environmental tolerances. There may be of two possible explanations for the compensation of species on the three axes of rarity: 1) They are simply leftover traits from once being more widespread (niche conservatism - Wiens and Graham 2005). Peterson *et al.* 1999 showed that very little niche differentiation occurred over evolutionary time scales (several millions of years) in sister-taxa of birds, mammals and butterflies. However, they found little niche conservatism at the family level. Within the family Microhylidae, niche conservatism may have resulted in the retention of traits usually associated with widespread species, such as high abundance and ubiquity, in species that are now geographically restricted; 2) although many of these species are geographically rare, they tend to have ecological traits that are more generalist than specialist. Generalised diets and microhabitat preferences (Chapters 4 & 3) in combination with the high productivity of tropical rainforest, may allow these species to be abundant and ubiquitous within their range as they are only resource limited at high population sizes.

My study found a strong association between species abundance and ubiquity; as species became more abundant they also become more ubiquitous throughout their habitat. Theory would predict that as a species becomes more abundant it would be more evenly spaced throughout the available habitat. While positive abundance – occupancy and positive abundance- occupancy – spatial variation relationships have been documented widely in the literature (reviewed in Gaston *et al.* 2000, Gaston *et al.* 2006), the mechanisms driving these relationships remain unresolved. It has been suggested that these relationships result from sampling bias, range position, resource availability and /or population dynamics (Gaston *et al.* 2000); however, no single answer has been found. In the present study, samples were taken across species' entire ranges and most species had high-intensity efforts, thus I consider resource availability and/or population dynamics as more likely explanations of the observed relationship. Warren and Gaston (1997) found that only a combination of these factors could explain positive abundance occupancy patterns found in protists. The fact that the more abundant species also have the most generalised diet (Williams *et al.* 2006; Chapter 4), are habitat generalists (Chapter 3) and are comparable to common species in their dispersal ability (Chapter 5) may allow them to be non-selective in space due to their broader niches and thus abundant and ubiquitous throughout their ranges.

My results are converse to those predicted by most macro-ecological theory, in that species with small range size have the highest local abundance. A study by Murray *et al.* (1998) showed a positive relationship between abundance and range size across all Australian frogs. Although my negative abundance-range size relationship became non-significant when we controlled for ubiquity this may be due to the limited number of species in the analysis. However, Johnson (1998) found a comparable result which showed that ancient lineages that had experienced much extinction may have resulted from species surviving through compensation of small range size by being very abundance in this range. Lawton *et al.* (1994) also reviewed cases of negative abundance - distribution relationship across a variety of taxa. Other studies have shown as populations increase in size there is a decrease in population fluctuations over time, increasing overall population resilience to stochastic events

(Reed and Hobbs 2004). This may also be occurring in microhylid frogs in the Wet Tropics meaning that while a species has a small range size it may be more abundant and thus resilient to population fluctuations due to stochastic events (Simberloff 1998). Certainly in my study there was a tendency for geographically rare species to be both more abundant and ubiquitous within small ranges, which I suggest confers resilience on what would otherwise be considered extinction-prone species.

Finally, my study also compared ubiquity and range size and found a trend for species with small range sizes to be more ubiquitous. While rare microhylid frogs in the Wet Tropics are often limited to a very small geographic range size, they are also habitat and diet generalists (Chapter 3 & 4). It is thus not surprising that within their range they can occur ubiquitously. It is commonly found that species will increase in abundance within their area of occupancy before they will disperse (Gaston *et al.* 2000). Perhaps because the geographic ranges of Wet Tropics microhylids are more limited by physiological tolerances they are not able to disperse and thus have become abundant and ubiquitous within their available environmental niches. This use of the entire habitat within their range means that microhylid frogs are can be very abundant and have large population sizes even within small geographic ranges.

In conclusion, my study suggests that species that are rare on any of the three axes of rarity compensate on at least one of the other axes, and that it is this ecological compensation that infers resilience to this species through time.

CHAPTER 7: GENERAL DISCUSSION

The results of this thesis clearly demonstrate that no single ecological trait can explain restricted geographic range size in this group of closely related species of microhylid frogs. The investigation of niche breadth (climatic, microhabitat and diet), dispersal ability, genetic diversity and population parameters (abundance, ubiquity and range) have resulted in conflicting support for rarity theory, with some ecological characteristics providing support and some suggesting that other factors, such as historical biogeography and environmental change, must be invoked to explain variation in geographic range size of this group.

Summary of major findings

Niche breadth - habitat

The scale at which niche breadth is described in terms of habitat (macro, meso and micro) greatly influences the amount of specialisation which can be detected across species, and the extent to which species conform to rarity predictions. The observed broader environmental niche breadth in geographically widespread species, compared to a narrow niche breadth in geographically restricted species suggests that “Brown’s hypothesis” can be applied when comparing macro-habitat climatic niches’ in microhylid frogs. Species with intermediate or narrow macro-habitat niches were greatly influenced by climatic variables. A combination of physiological tolerances, biotic interactions and resource requirements of these species may dictate their geographic range. This is supported by anecdotal evidence that some species die when taken to lower altitudes. Climatic variables had the greatest influence on the abundance of species within their ranges which also supports the suggestion that these frogs may be limited by their dependence on a high level of consistent rainfall. Finally, the degree of microhabitat specialisation appears unrelated to geographic range size in microhylid frogs, as both widespread and restricted species could be either microhabitat specialist or generalists.

Niche breadth - dietary

In systems where species richness has been shaped by extinction risk, rare and common species may differ greatly in traits that confer ecological resilience on local populations. In the genus *Cophixalus*, I found that geographically restricted species, which should be at a higher risk of extinction, have broad diets, indicating that broad niche breadth may have conferred higher ecological resilience on local populations, allowing them to persist. This implies that other, more specialised, species may once have existed, but that those that combined dietary specialisation with small geographic range size have gone extinct.

Dispersal ability and genetic diversity

Rare species are predicted to have poor dispersal ability and low genetic diversity. Contrary to this prediction, I demonstrated that a restricted geographic distribution is not explained by limited gene flow and lower genetic diversity in rare microhylid species. It appears that habitat stability may have allowed these species to maintain moderate levels of genetic diversity and gene flow, which has resulted in these species not being affected by inbreeding depression. Population structure occurred across small geographic scales (1km) for all species. However, analysis suggests that different types of population dynamics (such as dispersal modes and behavioural aggregation) may be occurring that effects the structuring seen within these populations. Testing of all species is needed, however, to determine how consistent the patterns seen here are across the entire Wet Tropics microhylid taxa.

Extinction filtering

Rare species are predicted to be extinction prone, yet they still persist. Here, I suggested that species compensate for rarity in any one of three population parameters of range size, abundance and ubiquity, and this infers resilience from extinction in microhylid frogs. Past extinction events may mean that the microhylid taxa still present today are an extinction resilient group. Resilience may be due to niche conservatism in this taxon in which the retention of traits from once being more widespread or perhaps selection pressure on species for generalised traits to persist through time.

Variation of ecological traits across species

This study emphasises the fact that there are no universal rules or taxa wide determinants of rarity that can explain why some species are rare and others are common. This phenomenon has also been demonstrated in other taxa such as plants (Edwards and Westoby 2000; Murray et al 2002a, 2002b), frogs (Murray & Hose

2005), birds (Blackburn and Gaston 2002) and moths (Mattila *et al.* 2005). Certainly, a comprehensive study by Murray & Hose (2005) demonstrates that while small geographic range size is a major predictor of species decline and extinction in endemic Australian frog fauna, factors such as life history, introduced species and habitat loss must also be considered. Further studies over a broader geographic and taxonomic range may assist in a more comprehensive understanding of how life history trait relate to rarity in some groups (Murray *et al* 2002b, Murray & Hose 2005). However, this is not possible for Australian microhylid frogs because I have already sampled much of the available geographic and taxonomic diversity. Given that the most widespread species of this group (*C. ornatus*) can be considered rare relative to many other taxa, the inability to find consistent patterns may simply be because microhylids do not show a broad enough geographic range to start with. Within such a generally rare group, compensation in key ecological traits may be pivotal to their resilience and long term persistence.

The ecological traits which could be examined for each species in this study varied depending on the availability of data. For the three species for which the most data are available (*C. ornatus*, *C. hosmeri* and *C. neglectus*), there are no clear trends or unifying patterns in their ecological traits which could be attributed to the rarity of microhylid species (Table 1; Rabinowitz 1981; Kunin and Gaston 1997). For example, it would be expected that rare species (e.g. *C. neglectus*) should be habitat specialists while widespread species (e.g. *C. ornatus*) should generalise in habitat selection. However, few distinct differences were found among these species in the type of variables important to their abundance within their range (meso-scale habitat effects), or their degree of specialisation at a micro-habitat scale (Chapter 3, Table 1). In contrast, for some ecological traits, such as environmental niche (macro-habitat), these species do exhibit traits that are consistent with rarity theory, with widespread species having larger niche breadth than geographically restricted species (Chapter 3, Table 1). To complicate matters further, some ecological traits, such as resource use (diet, Chapter 4), for these microhylid species showed the opposite trends to rarity theory predictions, with widespread species being diet specialists and restricted species being diet generalists (Table 1).

So why are such a closely related group of frogs so variable in ecological traits with no consistent trend among rare and common species? Microhylid frogs are the only vertebrate taxa to have radiated in the Wet Tropics region, with patterns of species diversity the result of both vicariant speciation among historical refugia and persistence within these refugia (Graham *et al.* 2006). The lower dispersal ability of microhylid frogs, compared to other vertebrate taxa, means that the microhylid fauna have strong selection pressure over geological time due to the expansion and contraction of the rainforest habitat in this region (Graham *et al.* 2006). This selection pressure has resulted in a resilient fauna with traits which could be assumed to have helped them to persist through time. The ability of these microhylid species to persist in small refugial areas (Williams 2006) may mean that they are also influenced by niche conservatism (Wiens and Graham 2005), in that species have conserved traits from historically being more widespread and retained these traits even as their range size decreased during rainforest contracts. This combination of historical biogeography and environmental change in this region has resulted in species which compensate among key ecological traits and species which are resilient to extinction (Chapter 6).

Table 1. Summary of the ecological traits investigated throughout this thesis for three species of Microhylid frogs of varying geographic range size. Parameters examined included: habitat characteristics at various spatial scales (Chapter 3), diet (Chapter 4), Genetic diversity and gene flow (Chapter 5) and abundance and ubiquity (Chapter 6). The abbreviations in the table stand for B= board, I = intermediate, N = narrow, G = generalist, M= moderate and S = specialist.

		Chapter 3			Chapter 4	Chapter 5		Chapter 6	
		Habitat							
Species	Geographic range	Macro	Meso	Micro	Diet	Geneflow	Genetic diversity	Ubiquity	Abundance
A. fryi	B	B	Climate					Patchy	Low
A. pluvialis	B	B	Climate					Patchy	Low
A. robusta	B	B	Climate					Patchy	
C. aenigma	I	I	Climate	G	G			Ubiq	Mod
C. bombiens	I	I	Climate		G			Ubiq	Mod
C. concinnus	N	N			M			Ubiq	
C. exiguus	I	N			M			Mod	Low
C. hosmeri	**I**	**N**	**Climate**	**G**	**G**	**Mod**	**Mod**	**Ubiq**	**High**
C. infacetus	B	B	Topo	S	S			Patchy	Low
C. mcdonaldi	N								
C. monticola	N	N	Climate, Veg	S				Patchy	High
C. neglectus	**N**	**N**	**Climate**	**G**	**G**	**Mod**	**Mod**	**Ubiq**	**Mod**
C. ornatus	**B**	**B**	**Climate**	**G**	**S**	**Mod**	**Low**	**Ubiq**	**Mod**
C. saxatilis	N	N							

Present threats to microhylid frog persistence

Microhylids occur in rainforest habitats of the Wet Tropics which are protected from current human induced threats, such as fragmentation and habitat clearing, by the World Heritage Listing of this area in the early 1980's. This frog family also seems to be one of the few that have not been affected by Chytrid fungus which has decimated other stream frog populations. However in current face of climate change, the long term persistence of geographically restricted species is in question. Climate change modelling carried out by Williams and Hilbert (2006) suggests that five species of *Cophixalus* would lose more than 50% of their core habitat with just a 1^{o}C increase in temperature. However an increase by 3^{o}C to 5^{o}C is considered more likely in the next 50 years. *C. concinnus*, *C. hosmeri*, *C. neglectus*, *C. exiguus* and *C. monticola* were ranked 1st, 2nd, 7th, 15th and 17th respectively on a list of the twenty most vulnerable vertebrate species to climate change in the Wet Tropics (Williams and Hilbert 2006). As microhylid frogs make up 54% of the frog taxa in the Wet Tropics region (Williams and Hero 1998), climate change is a significant threat to the frog biota of this region. It been suggested that vulnerable species may be able to disperse to other areas of suitable habitat to overcome climate change. While these species may have the capacity to disperse they may be physiologically incapable of achieving this, or be able to adapt to changing conditions in time to avoid extinction.

Future directions

While this study has increased our current knowledge of the ecological traits which influence geographic range size, large knowledge gaps still remain regarding factors restricting species distribution. The three most obvious knowledge gaps are those of species fundamental niche as determined by their physiological tolerances, and the biotic interactions of competition and predation, species longevity and reproductive output. The most important consideration for these studies would be to ensure that comparison are made between a number of species which vary in their geographic range and to incorporate phylogenetic independent contrasts were possible. Further investigation of the recommended ecological traits are essential if we are to make predictions about the future of these species and their ability to adapt in the face of climate change and other threatening processes such as amphibian disease. However, the biology of these species, including detectability of females, access to remote mountain tops and reliance on rain to detect males, greatly hinders the ability to acquire such information.

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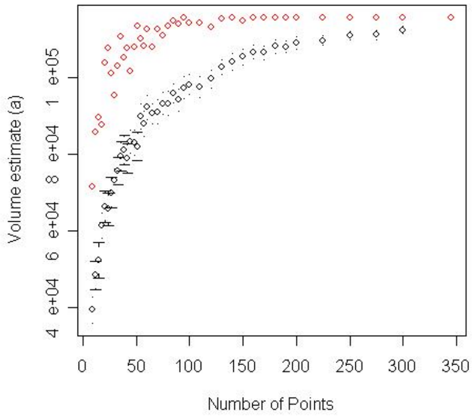
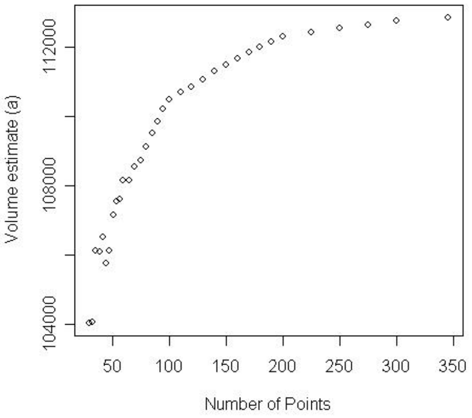
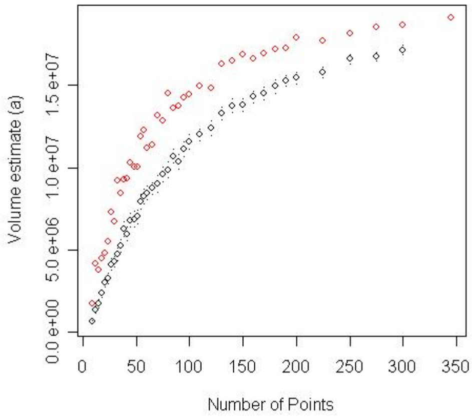
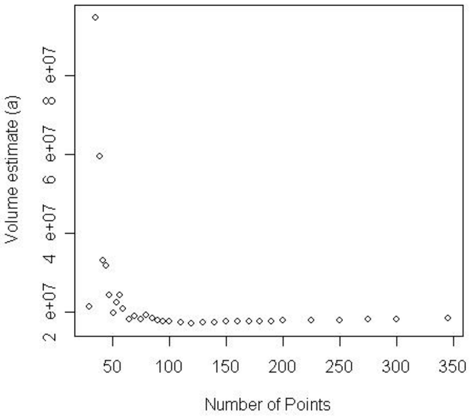
APPENDICES

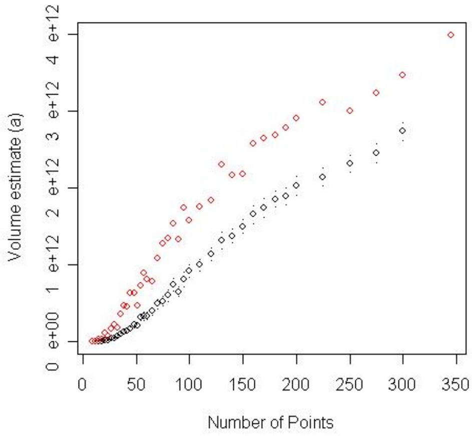
Appendix 1. QHull results for microhylid frog species











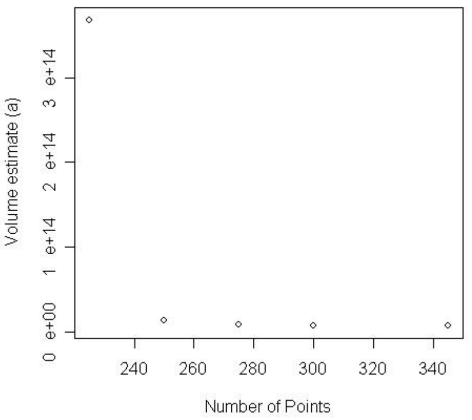


Figure 1. Qhull results for *Austrochaperina fryi* at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and the bottom row is for 8 variables (the 4 previous plus precipitation during the wettest and driest quarters and mean temp during warmest and driest quarters).

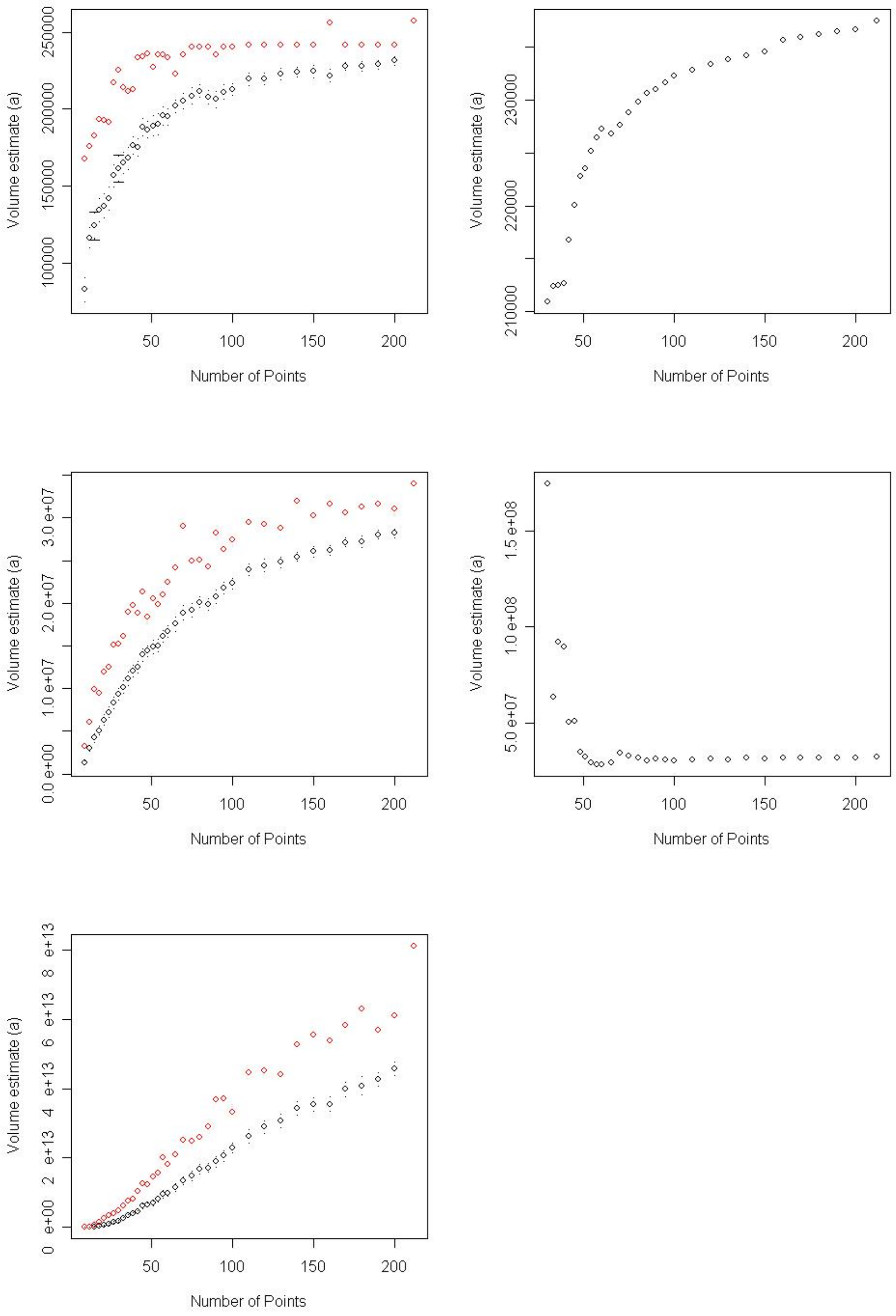


Figure 2. Qhull results for *Austrochaperina pluvialis* at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and the bottom row is for 8 variables (the 4 previous plus precip during the wettest and driest quarters and mean temp during warmest and driest quarters).

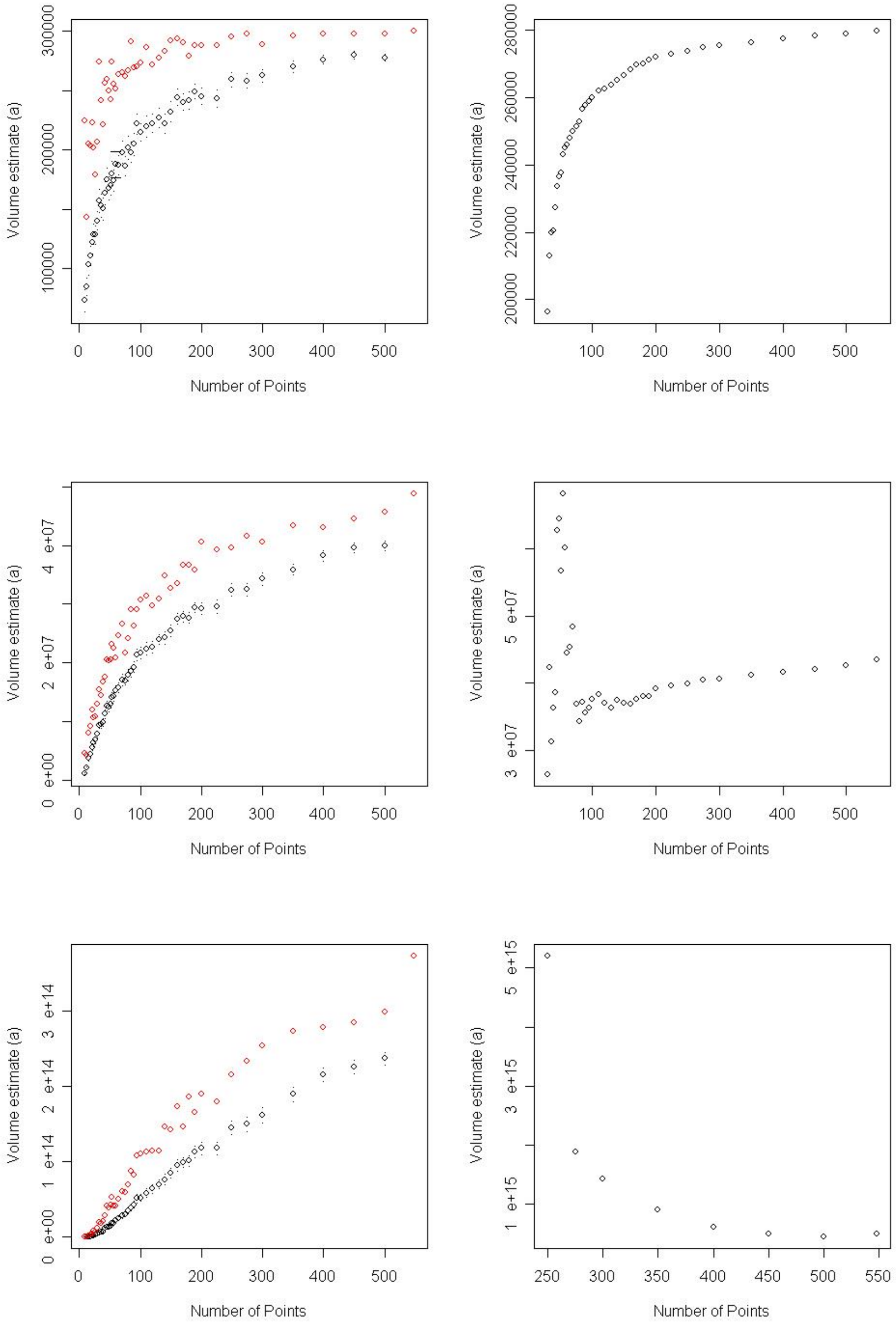


Figure 3. Qhull results for *Austrochaperina robusta* at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and the bottom row is for 8 variables (the 4 previous plus precip during the wettest and driest quarters and mean temp during warmest and driest quarters).

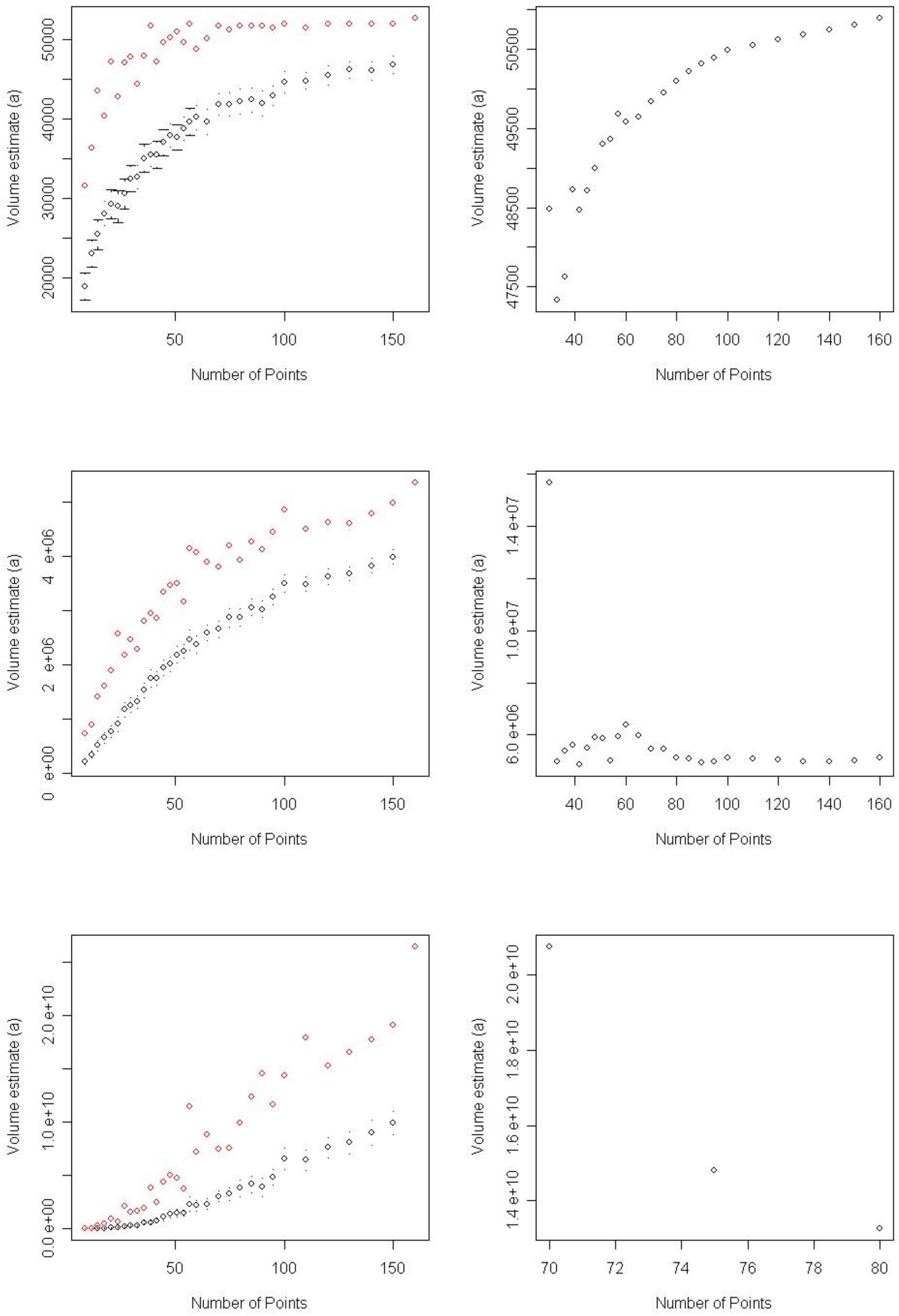


Figure 4. Qhull results for *Cophixalus aenigma* at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and the bottom row is for 8 variables (the 4 previous plus precip during the wettest and driest quarters and mean temp during warmest and driest quarters).

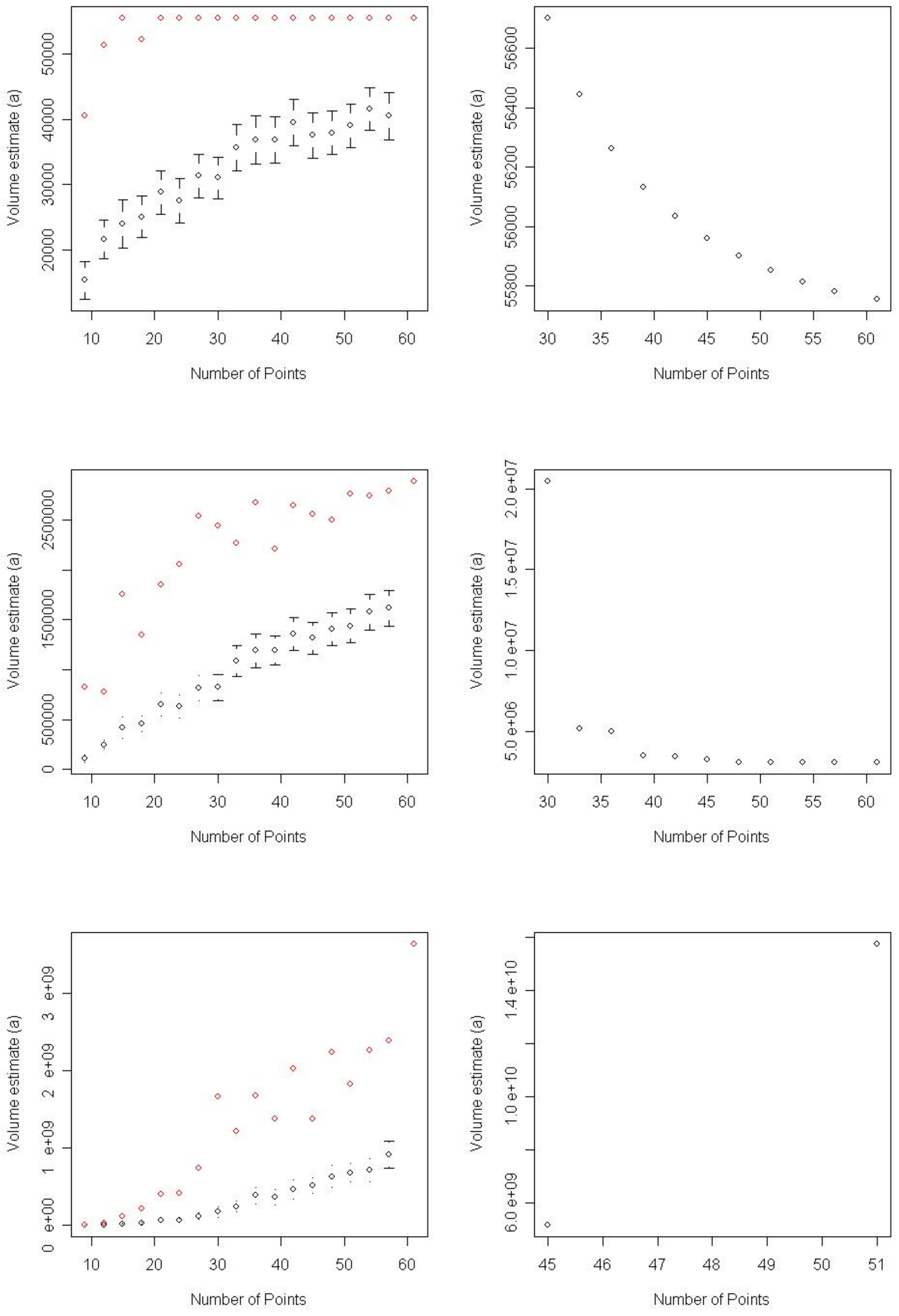


Figure 5. Qhull results for *Cophixalus bombiens* at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and the bottom row is for 8 variables (the 4 previous plus precip during the wettest and driest quarters and mean temp during warmest and driest quarters).

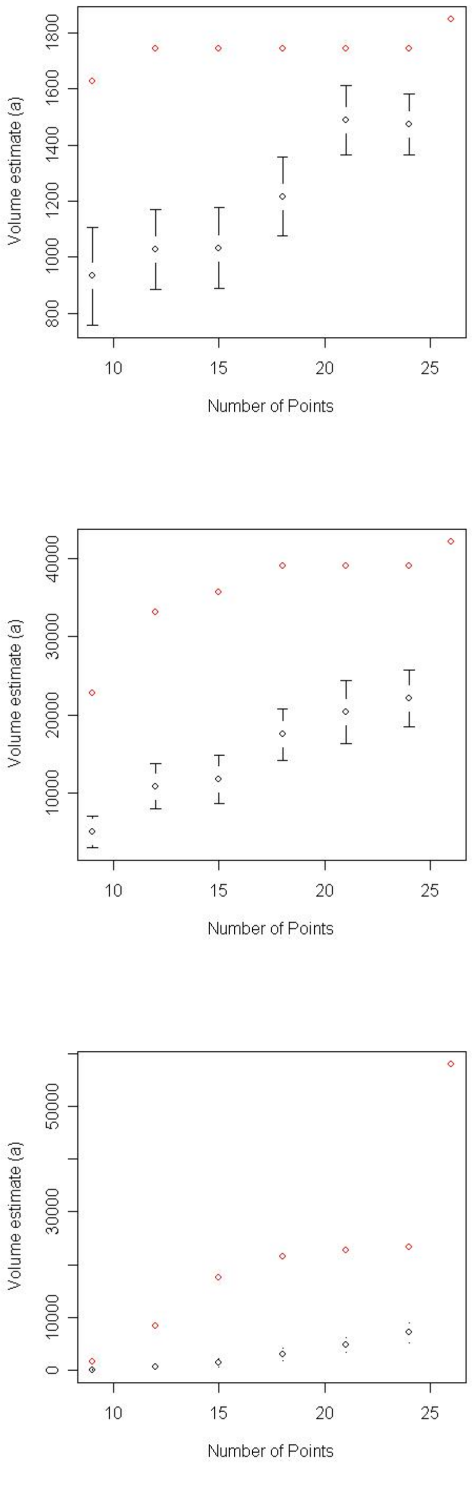


Figure 6. Qhull results for *Cophixalus concinnus* at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and the bottom row is for 8 variables (the 4 previous plus precip during the wettest and driest quarters and mean temp during warmest and driest quarters).

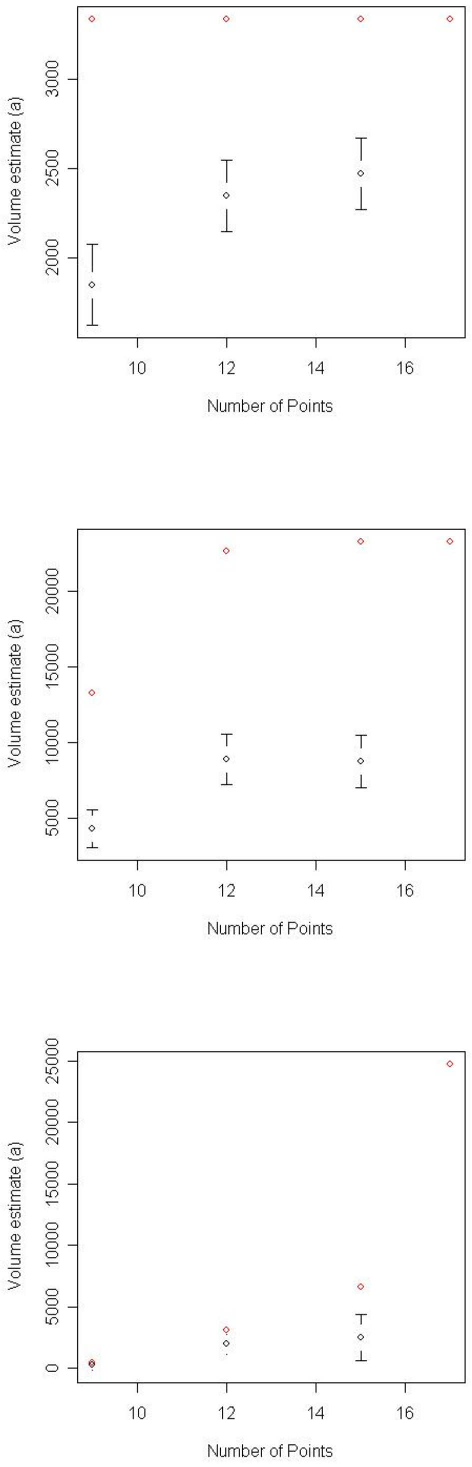


Figure 7. Qhull results for *Cophixalus exiguus* at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and the bottom row is for 8 variables (the 4 previous plus precip during the wettest and driest quarters and mean temp during warmest and driest quarters).

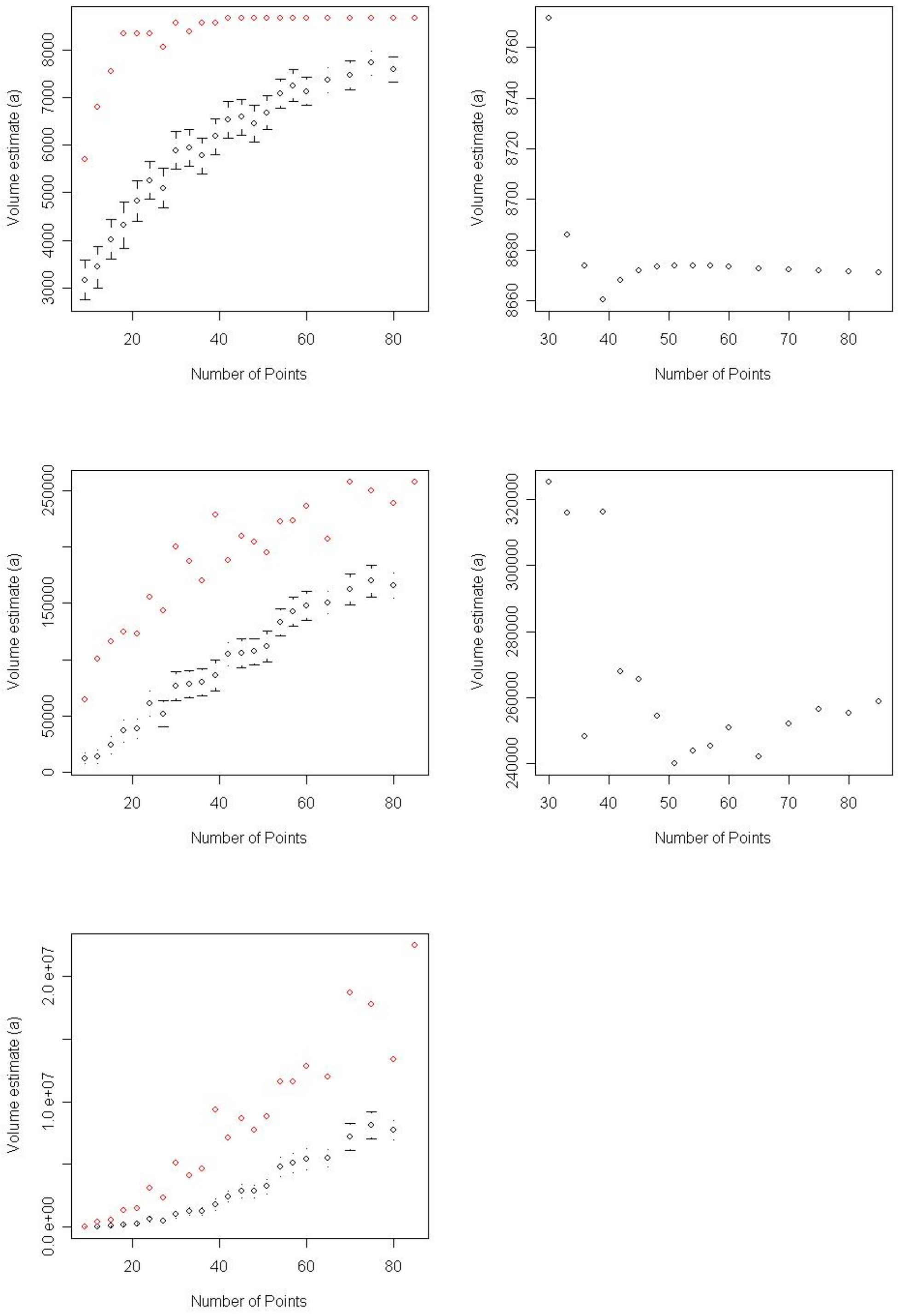


Figure 8. Qhull results for *Cophixalus hosmeri* at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and the bottom row is for 8 variables (the 4 previous plus precip during the wettest and driest quarters and mean temp during warmest and driest quarters).

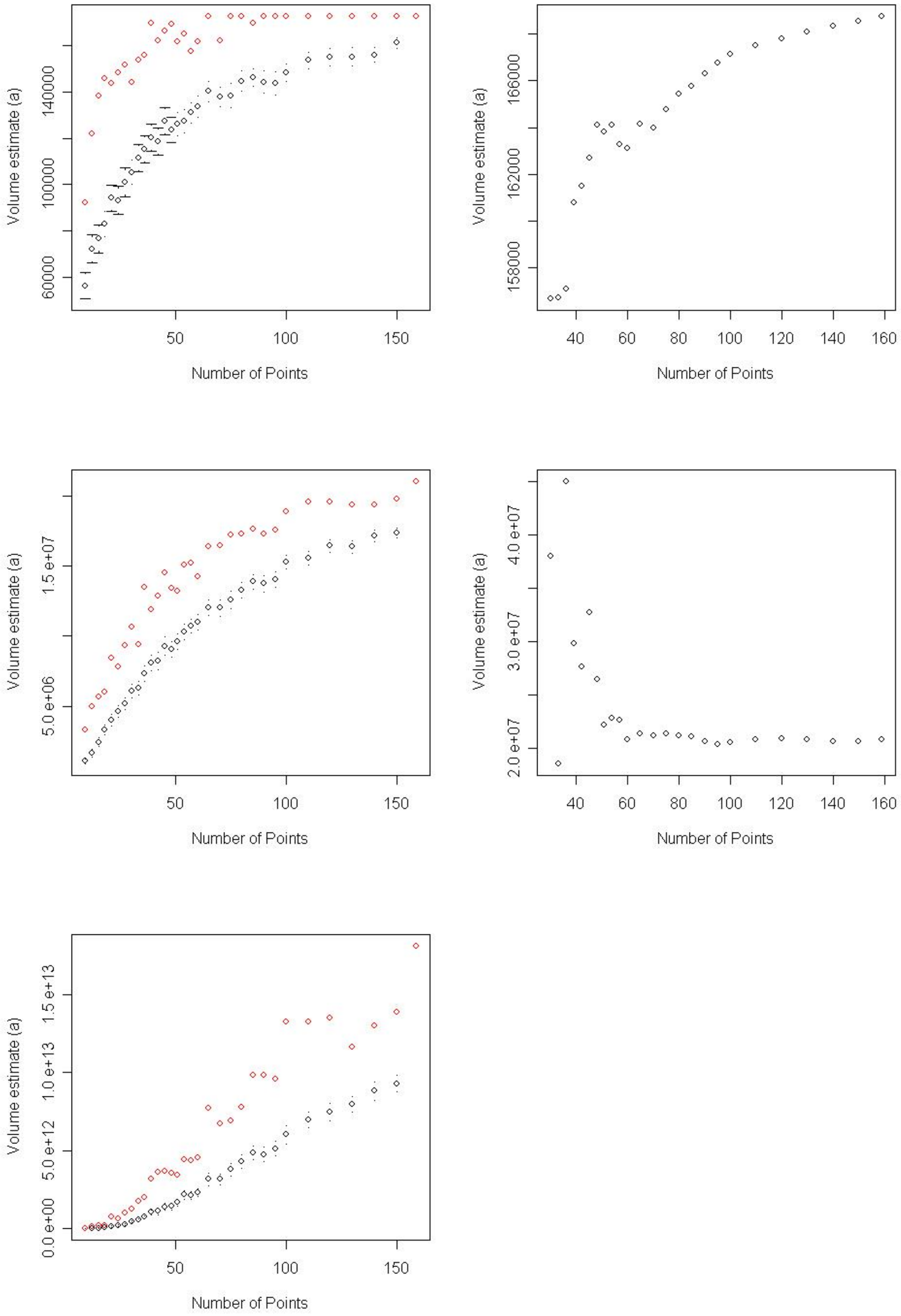


Figure 9. Qhull results for *Cophixalus infacetus* at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and the bottom row is for 8 variables (the 4 previous plus precip during the wettest and driest quarters and mean temp during warmest and driest quarters).

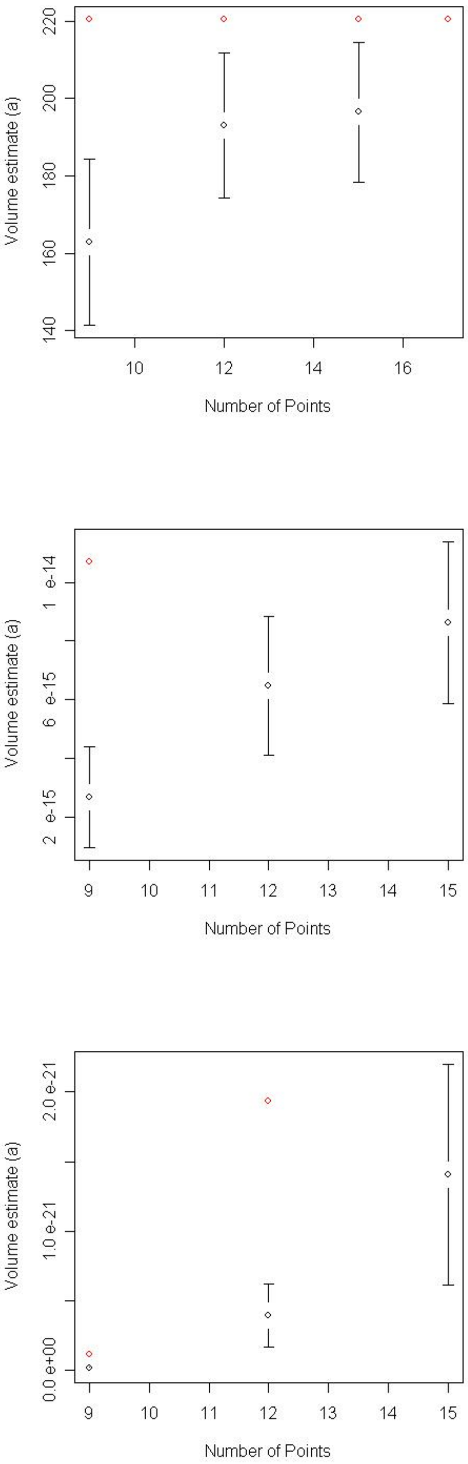


Figure 10. Qhull results for *Cophixalus monticola* at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and the bottom row is for 8 variables (the 4 previous plus precip during the wettest and driest quarters and mean temp during warmest and driest quarters).

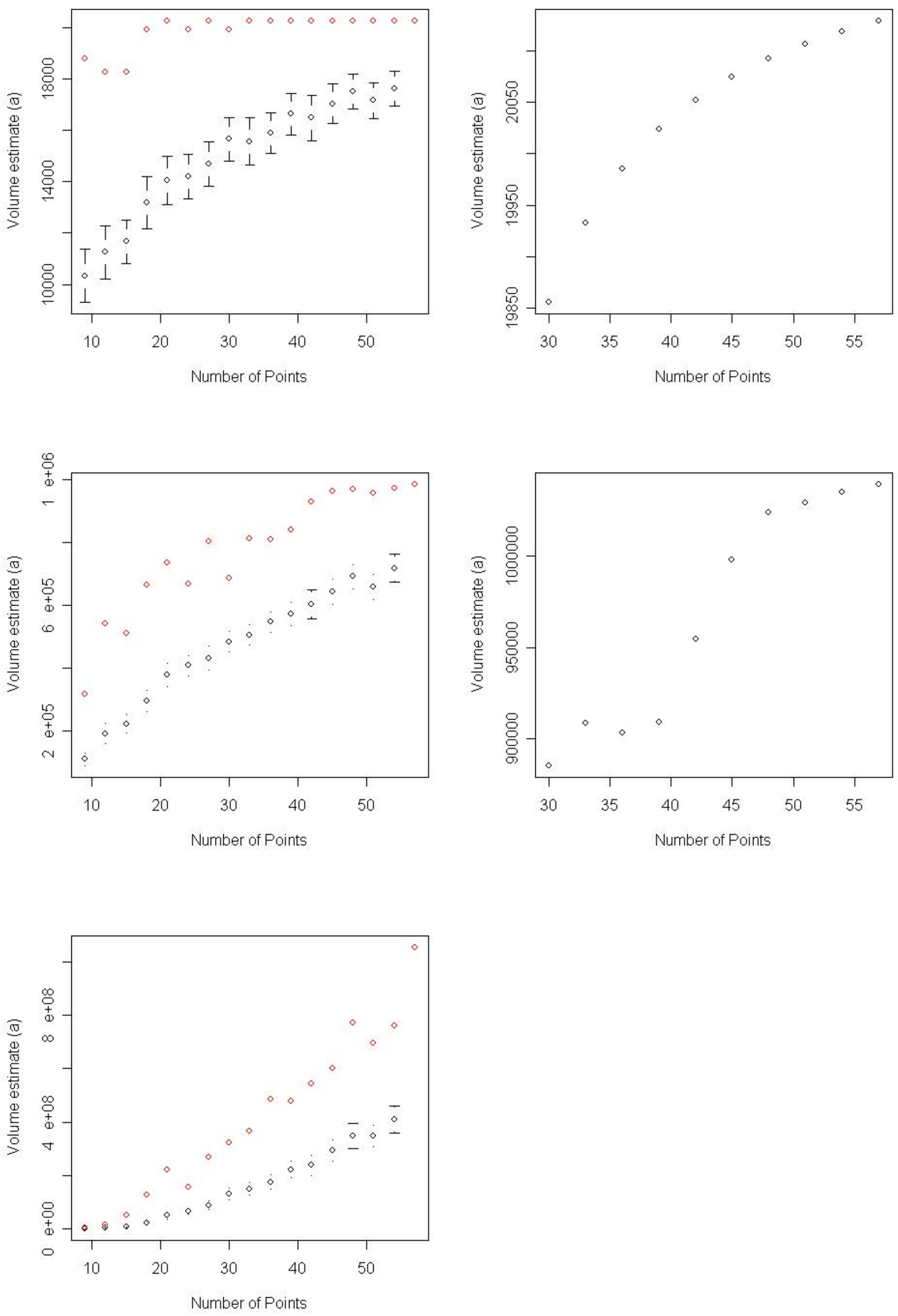


Figure 11. Qhull results for *Cophixalus neglectus* at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and the bottom row is for 8 variables (the 4 previous plus precip during the wettest and driest quarters and mean temp during warmest and driest quarters).

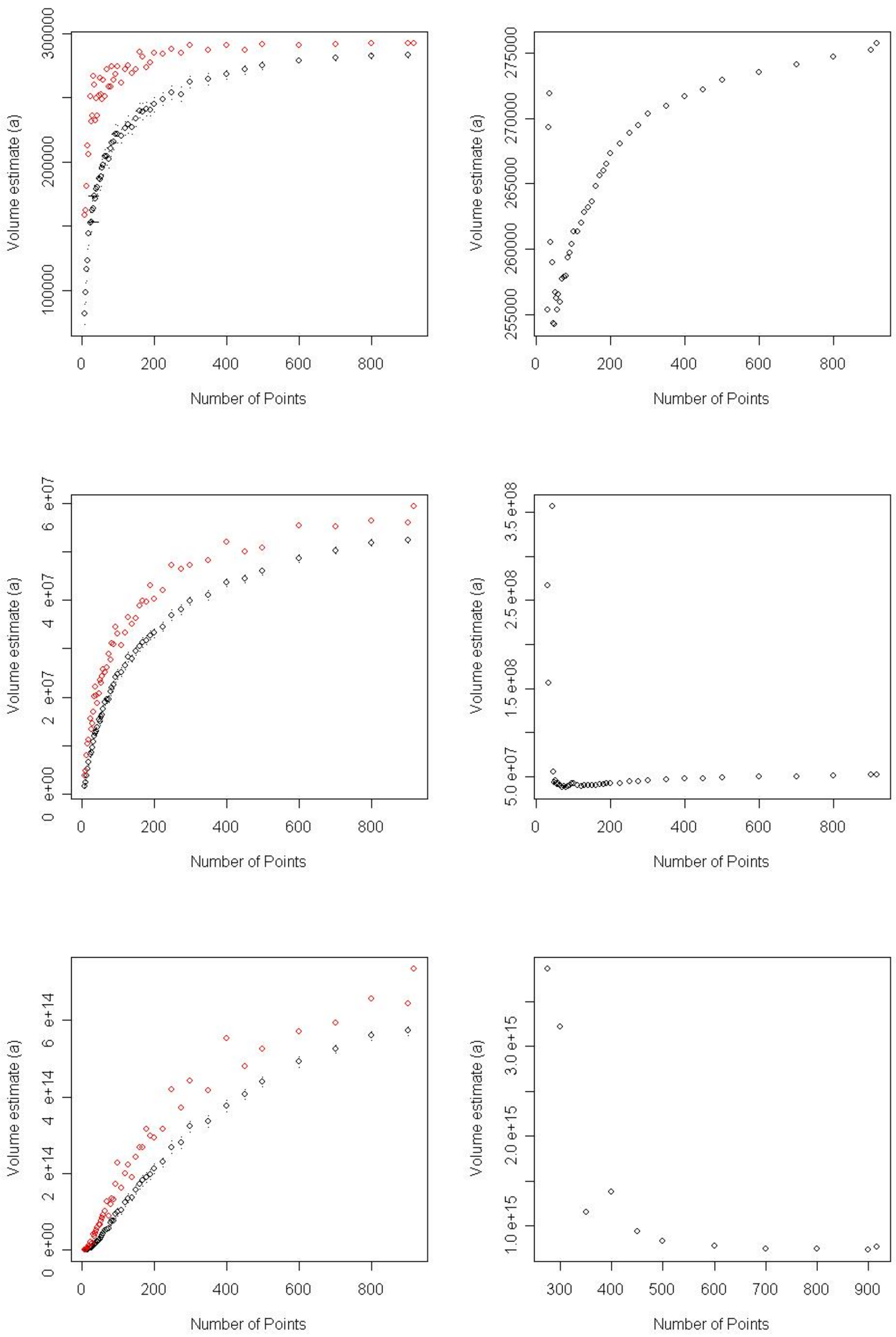
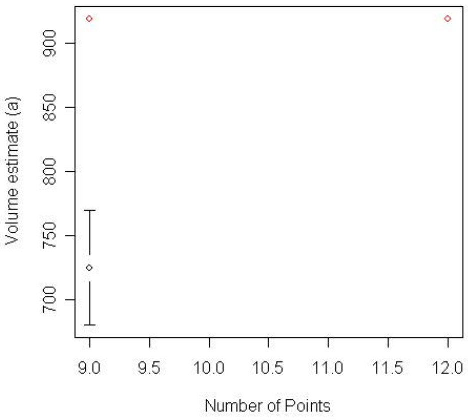


Figure 12. Qhull results for *Cophixalus ornatus* at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and the bottom row is for 8 variables (the 4 previous plus precip during the wettest and driest quarters and mean temp during warmest and driest quarters).



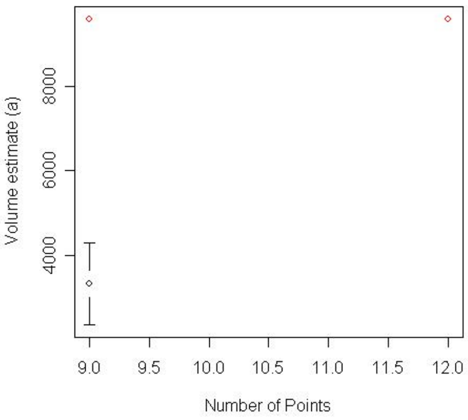


Figure 13. Qhull results for *Cophixalus saxatilis* at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and there was insufficient numbers to run the 8 variable model.

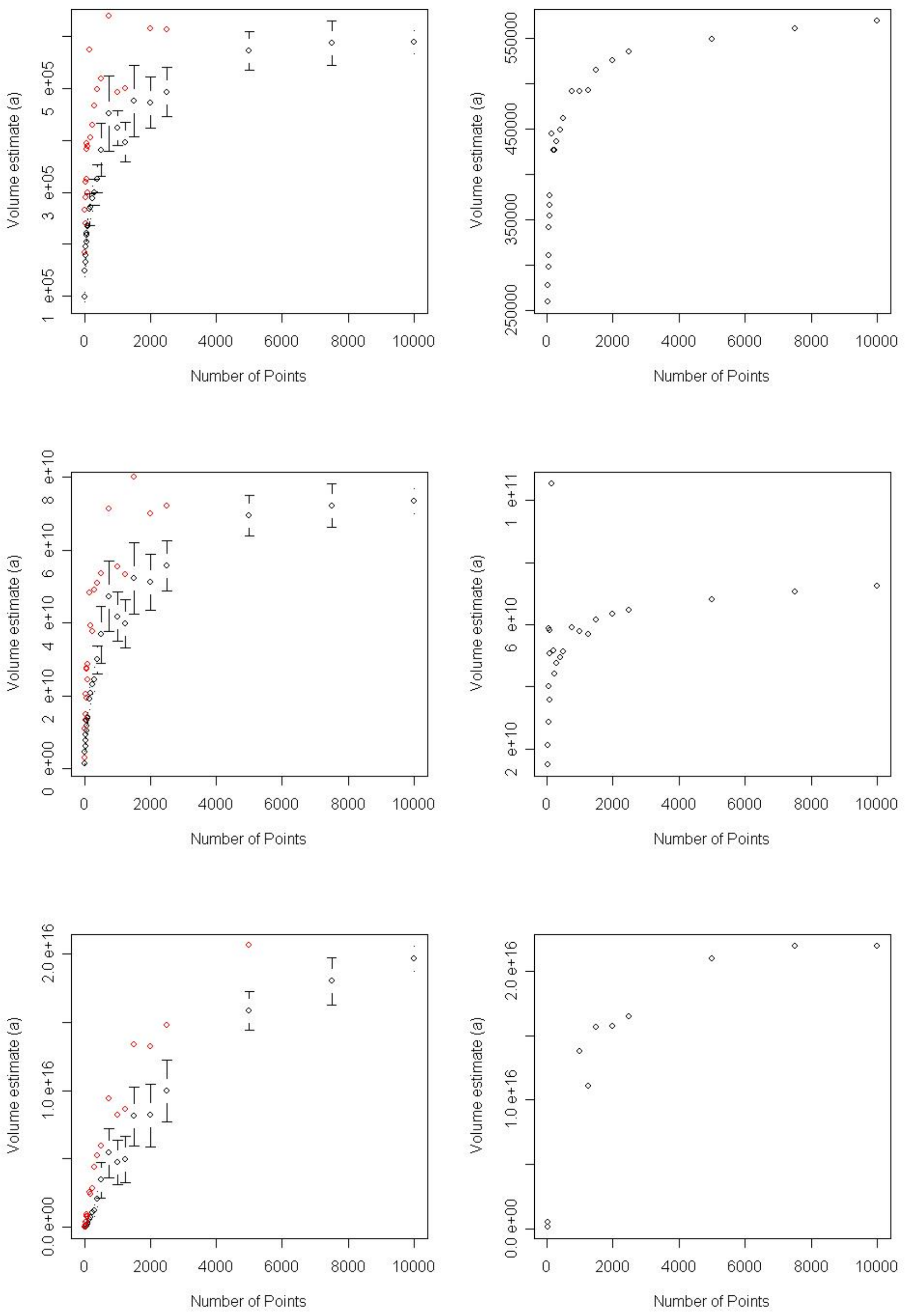


Figure 14. Qhull results for **background** niche space for the AWT at 2-, 4-, and 8-dimensions. Top row is for 2 variables (mean annual temperature and precipitation); second row is for 4 variables (the 2 previous and each of their seasonality); and the bottom row is for 8 variables (the 4 previous plus precip during the wettest and driest quarters and mean temp during warmest and driest quarters).