A quantitative assessment of arboreality in tropical amphibians across an elevation gradient: can arboreal animals find above-ground refuge from climate warming?

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DECLARATION

I hereby declare that this thesis is my original work and it has been written by me in its entirety. I have duly acknowledged all the sources of information which have been used in the thesis.

This thesis has also not been submitted for any degree in any university previously.

Brett Ryan Scheffers

22 October 2013

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SUMMARY

"For a thousand years of middle time, almost all scholars held that the earth must be flat—like the floor of a tent, held up by the canopy of the sky…"

Stephen Jay Gould –'The late birth of a flat Earth'

Climate on Earth is organized along two broad geographical gradients—latitude and altitude—along which patterns of biodiversity generally organize (Gaston 2000). Biodiversity tends to be highest in tropical regions and depreciates linearly towards the polar regions (Jenkins, Pimm & Joppa 2013). Additionally, biodiversity is structured along elevation gradients with variable patterns depending on geographic location (McCain 2010; Jenkins, Pimm & Joppa 2013). For example, lizard diversity, depending on region, may be 1) decreasing from low to high elevations, 2) exhibit a low-elevation plateau, 3) exhibit a low-elevation plateau with a mid-elevation peak, or 4) exhibit a mid-elevation peak (McCain 2009; McCain 2010). This biological organization is due to macroclimate gradients that are found within latitude and altitude and are measured from hundreds of meters to thousands of kilometers. However, climate gradients exist at smaller scales, such as from underground to above ground. These microhabitats play an important yet underappreciated role in shaping biotic communities, with different communities of organisms occupying each microhabitat (Beaulieu *et al.* 2010; Kamei *et al.* 2012).

Tropical rainforest canopies contain almost half the terrestrial biodiversity on Earth (Ozanne *et al.* 2003), in part due to the complexity of habitat arising from the multiple strata of vegetation, from the ground to the canopy. But this structural complexity might also be an important factor for not only structuring biological communities but also mitigating the future impacts of climate change. Climate warming has triggered various ecological responses

(Parmesan 2006) and perhaps the most recognized of them, is that species are on the move in response to changing climates (Chen *et al.* 2011). These movements are directly linked to animals' physiological constraints to climate (Bernardo *et al.* 2007; Calosi, Bilton & Spicer 2008). Thus, species have undergone these distributional shifts that include upward shifts in elevation, and latitudinal shifts towards the poles, to remain at physiologically optimal conditions (Maclean *et al.* 2008; Chen *et al.* 2011). But are these the only exploitable climate gradients for escaping novel climates?

To answer this question, my dissertation research first explored how biodiversity was organized along two nested climate gradients (forest height within elevation). I then explored how microhabitats within the forest's vegetative layers ameliorate abiotic conditions and promote vertical structuring of rainforest fauna. Finally, using these data, I explore the possible consequences of climate change on the biota living within the rainforest canopy and explore whether microclimates might reduce the vulnerability of arboreal communities through climatic buffering.

In Chapter 1, I reviewed the literature on missing biodiversity and the prospects for further species discoveries. Major patterns in newly discovered species are that many undiscovered species are small, difficult to find as they likely live in hard-to-access areas such as the rainforest canopy or have small geographic ranges. Cryptic species could be numerous in some taxa. Novel techniques, such as DNA barcoding, new databases, and crowd-sourcing, could greatly accelerate the rate of species discovery. Such advances are timely. Most missing species probably live in biodiversity hotspots, where habitat destruction is rife, and so current estimates of extinction rates from known species are too low. Additionally, there are habitats that are under explored such as rainforest canopies. The omission of hard-to-access habitats has likely resulted in the omission of new species and perhaps more importantly biological and ecological paradigms. In Chapter 1, I propose the rainforest canopy as one such habitat that if studied in combination with other well-studied biological systems, such as mountains, may yield new theory about how biodiversity organizes on Earth.

In Chapter 2, I explored whether frog species richness and abundance organizes along the vertical height gradient (i.e., up trees) in the same way that they do along the shallower gradients driven by elevation (i.e., up mountains) and latitude. My study was the first to explicitly examine how the climate gradient within forest height changes with the climate gradient across elevation. If vertical climate gradients are steeper than those provided by elevation, then they may play a powerful role in structuring biodiversity both at local and landscape scales. To this end, I proposed a novel “arboreality hypothesis” to explain how species’ distributions adjust vertically in the rainforest strata to compensate for broad-scale shifts in climate associated with elevation. I censused frogs from the ground to canopy levels along an elevational gradient (and therefore a temperature and moisture gradient) in Philippine (900-1900 m) and Singaporean (~10 m) rainforests, measured temperature and moisture across the height and elevation gradient, and used a biophysical model to explain how changes in temperature and moisture regimes reduced frog usage in the canopy. Lastly, using a dataset for all frogs of the Philippines, I explored and predicted how arboreality in frog assemblages was likely to increase with increasing elevation at larger spatial scales.

In Chapter 3, I explored the complex relationship between arboreal frogs and their use of a predominant microhabitat in the rainforests of the Paleotropics: epiphytic *Asplenium* bird’s nest ferns. I tested the hypothesis that bird’s nest ferns functioned as a critical canopy microhabitat for arboreal frogs, thus amplifying canopy biodiversity. I surveyed for frogs within bird’s nest ferns throughout the canopy strata to explore whether bird's nest ferns function as arboreal refuges for adult frogs, and if they serve as critical breeding habitat for these frogs. I determined whether ferns are disproportionately used by frogs compared to the surrounding rainforest environment and experimentally dried ferns to examine whether thermal buffering provided by ferns is contingent on their state of hydration. In doing so, I tested whether or not ferns functioned as a foundation species and/or keystone structures (Dayton 1972; Tews *et al.* 2004), and whether or not they expanded the biotic potential of inhospitable canopy environments.

In Chapter 4, I examined whether microhabitats within rainforests provide refuge from climate change. The vulnerability of a species to climate warming is directly linked to its sensitivity and the exposure it experiences in its habitat (Williams *et al.* 2008). Under this premise, I identified the critical thermal maxima for frog larvae from four distinct breeding habitats in order to determine sensitivity to climate change. I then identified the extent to which breeding habitats inhabited by frog larvae buffered ambient temperature in order to derive exposure. Finally, I deduced the vulnerability of specific frog life-history stages to future warming based on these two metrics.

In Chapter 5, I explored whether microhabitats within rainforests provide refuge for ectotherms from extreme weather events. In this chapter, I broaden my study organism to include lizards as well as frogs. Although a large literature exists on species (especially ectotherm) susceptibility to climate change, the degree of thermal buffering that occurs within complex microhabitats and how this might relate to the buffering of extreme events within microhabitats is not understood. I monitored how close extreme temperature events are to the thermal limits of ectotherm communities (frog and lizards), both inside and outside of buffered microhabitats and compared the vulnerability of animals under uniform and non-uniform climate change within microhabitats.

In Chapter 6, I synthesize across the chapters to find a whole picture view of how biodiversity organizes by variable scales. Small scale microclimates can strongly influence biological structuring at both small and large spatial scales. I compare the results of the previous chapters with prior studies and consider how well my work has filled the existing gaps in our knowledge. I discuss my empirical chapters in light of current conservation issues and discuss how inclusion of canopy and microhabitat science might compliment conservation practice and yield new management outcomes not previously considered.

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CHAPTER 1: General Introduction

Content within Chapter 1 is modified from: **Scheffers, B. R.,** L. P. Joppa, S. L. Pimm, and W. F. Laurance. 2012. What we know and don't know about Earth's missing biodiversity. **Trends in Ecology and Evolution** 27: 501-510

1.1 Where they live

Knowing where species live is vital for setting international priorities for conservation. Incomplete information might leave one unable to prioritize effectively where to allocate conservation efforts. For example, the 'biodiversity hotspots' (Myers *et al.* 2000) combine a measure of habitat destruction (<30% habitat remaining) with the numbers of known endemic flowering plant species (>1500). These areas have become international priorities for conservation, with large resources allocated for their preservation (Dalton 2000). The incomplete catalog of flowering plants begs our asking: Will knowing where the missing species are located alter conservation priorities? Are missing species concentrated in imperiled habitats where they are at risk of extinction? If so, can they be found before they go extinct?

Several studies identify areas of high missing biodiversity for prioritizing future conservation efforts (Medellín & Soberón 1999; Zapata & Ross Robertson 2007; Giam *et al.* 2010; Joppa *et al.* 2011). Recently, Joppa *et al.* (2011) suggest that missing plant species will concentrate in the biodiversity hotspots, places such as Central America, the northern Andes and South Africa, where, by definition, the threat of habitat loss is greatest. These predictions have limitations, obviously, because factors such as remoteness or political instability reduce the rate of species description in some regions. Expanding on Joppa *et al.* (2011), Laurance and Edwards (2011) highlighted their probable underestimate of the importance of the Asia-Pacific region, such as the Philippines and New Guinea, as centers of missing plant species. The Asia-Pacific region might also have many unknown amphibian and mammal species (Giam *et al.* 2010).

Despite such limitations, biodiversity hotspots will surely sustain large numbers of missing species and continued and equal survey effort in less biodiverse locality will be important to confirm the biological uniqueness of hotspots.

Missing species tend to have small geographical ranges. These findings bring both good and bad news. The good news is that most missing species occur in places that are already global conservation priorities. The bad news is that most of these species are in areas already under dire threat of habitat loss. By instilling an appropriate sense of urgency, focusing species-discovery efforts on hotspots would result in ‘taxonomy that matters’ (Joppa, Roberts & Pimm 2012). Discovering unknown species in hotspots would help to underscore their exceptional biological diversity and uniqueness. Invaluable insights would also be gained into the traits these species display and the services they could potentially provide.

1.2 Are missing species different?

By analogy, one may view taxonomists as ‘predators’ that exploit a continually declining ‘prey’ population (the numbers of undescribed/missing species). To this end, taxonomists are surely searching for the most obvious ‘prey’, inadvertently selecting species with traits that are most conducive for discovery. As the pool of missing species diminishes, one would expect those remaining to have traits or live in habitats that make them harder to find. For example, the unique biota of deep-sea hydrothermal vents was discovered only during the late 1970s, whereas a nocturnal stream-dwelling lizard from high in the Peruvian Andes was described in 2012 (Chávez & Vásquez 2012). This begs the question: are missing species functionally different from those already described? Certainly, the first European expeditions across the African savannahs had little trouble in finding and describing large-bodied wildebeests, giraffes, and elephants. The remaining unknown mammal species are smaller. Similarly, taxonomists have described larger-bodied species sooner in a variety of animals, including British beetles (Gaston 1991), South American songbirds (Blackburn & Gaston 1995), and Neotropical mammals (Patterson 1994). However, this trend evidently varies among taxa. Body size in most animal groups is highly right skewed (Blackburn & Gaston 1994; Blackburn & Gaston 1998) and, thus, the tendency for newly described species to be small bodied might simply reflect a random sample of the overall size distribution, rather than small-bodied animals being harder to find or describe (Gaston & Blackburn 1994). Body size and year of description strongly correlate in insects, but this phenomenon varies considerably among different insect taxa (Gaston 1991; Gaston, Blackburn & Loder 1995). However, scientists still find larger-bodied species in remote or poorly studied parts of the world. Many islands in the Philippines, for instance, remain unexplored. Recent discoveries there include a 2-m long monitor lizard (*Varanus olivaceus*) (Welton *et al.* 2010) and a large-bodied fruit-bat (*Styloctenium mindorensis*) (Esselstyn 2007). Local communities hunt both. Along with small body size, geographical remoteness affects the rate at which taxonomists discover species. Unknown species might also be less colorful or obvious than their described brethren. I hypothesize, for instance, that taxonomists will describe brightly colored bird species earlier than drab, earth-toned bird species. Species with cryptic behaviors also tend to be discovered later. For instance, as-yet-undescribed shore fish are likely to be those that hide in deeper waters (Zapata & Ross Robertson 2007), whereas researchers recently discovered a fossorial caecilian, representing an entirely new family (Chikilidae), only after 1100 hours of digging holes in the ground (Kamei *et al.* 2012). Animals with elusive life histories can be discovered even in the best-studied parts of the world. A recently described fossorial salamander in the southeastern USA not only represents a new genus (Urspelerpes), but is also among the smallest salamander species ever found (Camp *et al.* 2009).

As I discuss below many undescribed species may exist in the rainforest canopy. For example, the best-known hyper-estimate of species on Earth was Erwin (1982) astounding conjecture of 30 million species. His approach started with the number of arboreal beetle species associated uniquely with a single species of tropical rainforest tree in Panama. This generated criticism, primarily from those concerned about the assumptions underlying such a ‘small to large’ extrapolation, but spawned considerable interest and research. Fundamental was the degree of host specificity of herbivorous insects on their food plants, which Erwin assumed to be high. ØDegaard (2000), Novotny *et al.* (2007), among others found considerably lower host specificity, perhaps by a factor of four or five. The resulting global estimate of insect species richness has accordingly dropped sharply. The important element here however is the consideration of arboreal biodiversity, which is seldom accounted for in traditional sampling techniques. Yet, when canopy sampling is employed in the field, new discoveries of canopy dwelling species become frequent. For example, two new species of frog were discovered from the lowland rainforest canopy of Yasuni Nationa Park, Amazonian Ecuador (Guayasamin *et al.* 2006; McCracken, Forstner & Dixon 2007) and a new arboreal mammal species named the Olinguito was recently discovered in Ecuador and Colombia (Helgen *et al.* 2013). Zozaya *et al.* (2013), surveyed by myself and using similar canopy survey techniques as those outlined in Chapter 2, documented a significant 110 km range extension of a skink species (*Eulamprus frerei*) that was thought to be endemic to a single mountain in the Australian wet tropics (AWT). *Eulamprus frerei* has historically been found on the ground or low hanging vegetation in boulder fields, yet it was discovered in the upper canopy of a montane rainforest from an entirely different mountain range. The AWT is arguably one of the most studied tropical biomes on Earth and the exact locality in which the arboreal skink was discovered was regularly sampled for reptiles via ground transects for over 20 years. Thus, including canopy surveys in biological inventories may yield new biological insights and discoveries.

Finally, taxonomists describe small-ranged species later than more widely distributed ones (Gaston & Blackburn 1994; Gaston, Blackburn & Loder 1995; Gibbons *et al.* 2005). Such trends are evident in holozooplankton (Gibbons *et al.* 2005), fleas (Krasnov *et al.* 2005), leaf beetles (Baselga *et al.* 2007), Palaearctic dung beetles (Cabrero-SaÑudo & Lobo 2003), South American oscine songbirds (Blackburn & Gaston 1995), and Neotropical mammals (Patterson 1994). Missing species will typically be more vulnerable than are described species. Typically, two key factors combine to determine the threat level for a species under the IUCN Red List criteria: its geographical range size and the amount of its habitat loss. We have already emphasized that missing species are generally concentrated in the places where habitat loss is greatest. In showing that missing species are also typically those with small ranges, we can be certain that many will eventually be listed as ‘threatened’; that is, if they do not become extinct first. The high vulnerability of missing species is evident in Brazil, which has the largest number of amphibian species globally. Although local amphibian diversity is especially high in the western Brazilian Amazon, the greatest concentration of species with small geographic ranges is in the coastal hotspot of the Atlantic forest (Pimm & Jenkins 2010). Taxonomists described most of these small-ranged species only within the past two decades, a pattern similar to that for mammals in Brazil (Pimm *et al.* 2010). Missing species, such as those only recently discovered, will probably also be in such vulnerable areas. Only approximately 7% of the original Brazilian Atlantic forest remains (Pimm & Jenkins 2010). All this signals that researchers are underestimating the magnitude of the current extinction crisis, because many undiscovered species will both have small ranges and occur in threatened hotspots (Giam *et al.* 2011).

Including estimates of missing species increases the percentage of threatened plants to 27–33% of all plant species (Joppa *et al.* 2011). If many species are morphological and behaviorally cryptic, the figure could be even higher.

1.3 Prospects

Relative to the task at hand, taxonomists are describing species slowly. Although the catalog of flowering plants should be compete in a few decades (Joppa *et al.* 2011), recent estimates suggest another 480 years is needed to describe all the species on Earth (May 2011), or possibly 1000 years just to describe all fungi (Blackwell 2011). Yet, the outlook is considerably brighter than one might suppose, for several reasons. Herbaria and museums might harbor many of the missing species. For example, Bebber *et al.* (2010) found that existing herbarium material typically took decades to describe. They estimated that perhaps half of all missing plant species were already in herbaria. Recent advances in DNA barcoding make it easier to discriminate similar species (Smith *et al.* 2006), thereby accelerating species descriptions and generally aiding better taxonomy. Barcoding is also inherently a quantitative technique, allowing statistical sampling methods to estimate what fraction of samples are missing species and how species turn over geographically. Potentially, barcoding can address many of the methodological concerns we have highlighted here. Nonetheless, the use of ‘floating barcodes’ (ones without associated morphological descriptions of organisms) generates considerable debate. The genetic methods used to detect fungi discussed above are rapidly expanding knowledge of what could be an extremely diverse group, but one poorly sampled by traditional morphological approaches. Many communities of taxonomists are now addressing the tedious but vital issue of synonymy and placing their lists and taxonomic decisions into the public domain. These include websites for flowering plants (http://www.kew.org/wcsp/), spiders (http://research.amnh.org/oonopidae/catalog/), amphibians (http://research.amnh.org/herpetology/amphibia/ index.php), birds (http://www.birdlife.org/datazone/info/taxonomy), and mammals (http://www.bucknell.edu/msw3/). Global efforts to catalogue all species, such as All-Species (http://www.allspecies.org), GBIF (http://www.gbif.org), Species 2000 (www.sp2000.org), and Tree of Life (http://www.tolweb.org/tree/phylogeny.html), are also now readily available online. Efforts to map where species occur are progressing. The most obvious advance is using smart phones and software website applications such as iNaturalist (http://www.inaturalist.org) that link data directly into the IUCN Red Lists, the Global Biodiversity Information Facility, and other pre-existing databases. Crowd-sourcing of species mapping could greatly expand these databases, which are major contributions to knowledge of where species live. Such databases are already promoting the discovery of missing species, revealing those that do not fit known descriptions. Finally, even if it might not be practical or even desirable to describe every species, cataloguing carefully selected taxa, locations, or regions might generate important insights (Joppa, Roberts & Pimm 2012). Better quantification of the number and locations of known species afford a fighting chance to set effective conservation priorities, even if the taxonomic catalog is incomplete.

1.4 Unknown biological dimensions

Although there have been serious examinations to decipher where unknown biodiversity might occur and what it might look like, my thesis research explores whether there might be unknown dimensions to how biodiversity is organized on Earth. Similar to identifying new localities and traits of unknown biodiversity (as mentioned above), uncovering new patterns and biological dimensions to biodiversity might also uncover patterns that are essential to conservation.

Biodiversity is patchily distributed across the Earth with some areas having high concentrations of species while others are almost entirely devoid of life. Much of this biodiversity is concentrated in the tropics, with a gradual reduction of biodiversity as one approaches the polar regions (Gaston 2000).

Although the tropics are generalized as having high biodiversity, life in the tropics still remains patchily distributed (thus, patches within patches) with some areas having noticeably higher species richness than others. This mosaic of species richness is attributed to the distribution of abiotic and structural factors that support life such as temperature, precipitation, habitat structure, among many others.

Quantifying biological patterns is contingent on scale and results are typically highly nested with small scale patterns expressed within larger scale patterns (Levin 1992; Gaston 2000; Scheffers, Whiting & Paszkowski 2012). As mentioned, biodiversity is broadly patterned at latitudinal scales (from the poles to the tropics). However, closer examinations of species diversity at smaller scales within the tropics reveal that biodiversity also changes along altitudinal and structural gradients. Thus, broad biological patterns of species richness are derived from the collective organization of species richness at small scales. Species respond to temperature and habitat at the scale of millimeters to kilometers and as such, small scale microhabitats and the collective distribution of essential resources play an important role in maintaining population persistence and shaping species distributions (Suggitt *et al.* 2011).

Tropical rainforests harbor major proportions of Earth's terrestrial biodiversity (Dirzo & Raven 2003), in part, because of diverse structures and habitats that span from ground to canopy.

Since the early 1990s, vertical stratification (distribution of fauna from ground to canopy) has become a well-studied paradigm throughout the tropics (Lowman & Nadkarni 1995). It is now known that tropical fruit-eating bats frequently occupy sub-canopy heights in lowland dipterocarp rainforests (Francis 1994), a substantial portion of mite fauna occurs above the forest floor (Beaulieu *et al.* 2010), and stratification of bird communities reflects the stratification of fruit availability in rainforests (Shanahan & Compton 2001). Furthermore, vertical stratification of animal populations may depend on physiology (Graham & Andrade 2004), habitat type (Hodgkison *et al.* 2004), resource availability (Beaulieu *et al.* 2010), environmental gradients (e.g., elevation; (Russell-Smith & Stork 1994)) and taxonomic group. Additionally, there are numerous accounts documenting the vertical distribution of bats (Francis 1994), birds (Shanahan & Compton 2001), terrestrial mammals (Monteiro Vieira & Monteiro-Filho 2003), epiphytes (Graham & Andrade 2004) and invertebrates (Roisin *et al.* 2006).

These are a select number of studies from an extensive literature on ecology and conservation in the tropics. As such, only a fraction of the total structure within biologically rich canopies are studied in ecology and conservation science—likely due to the difficulty in accessing and sampling canopy habitats (Kays & Allison 2001; Ozanne *et al.* 2003). This is especially true for studies that quantify the amount of above-ground habitat used by animals, particularly highly cryptic animals such as amphibians.

Amphibians are a diverse vertebrate group and are expected to be ubiquitous in rainforest canopies. Yet, they are one of the least studied vertebrate groups (Brito 2008) and the least studied arboreal vertebrate in tropical forests (Kays & Allison 2001; Brito 2008). Amphibians are also one of the most threatened terrestrial taxa on Earth (Beebee & Griffiths 2005) largely due to habitat loss and disease (Sodhi *et al.* 2008). Future research on the ecology and conservation of amphibians is paramount, especially in the canopy where they are likely abundant.

The overlooked vertical dimension to local distributions and the biogeography of amphibians could have serious consequences for 96% of past studies on the ecology and conservation of frogs (Kays & Allison 2001) as their data were derived solely from the ground. For example, in Chapter 2, I study amphibians in the Philippine archipelago and show that 88% of frogs were found above 1m in height. Frogs occurred higher up in rainforest strata with increasing altitude such that the lowlands were dominated by rich ground-dwelling communities and the uplands comprised rich arboreal communities. Furthermore, vertical habitat use can also vary over time between day and night or in response to extreme climatic events. Bickford (2005) monitored amphibians through El Niño induced drought and documented an increase in the number of frogs in leaf litter plots giving the impression that populations had become healthier and more robust over time. However, careful examination revealed that abundances were inflated by a downward shift in the arboreal component of the frog community presumably in response to stressful climate conditions in the canopy.

Arboreal frogs have flexible vertical distributions as a result of seeking optimal microclimates from the ground up to the canopy (Tracy, Christian & Tracy 2010; Scheffers *et al.* 2013c). Traditional ground-based surveys may adequately account for species richness because a proportion of the vertical distribution of frogs is almost always near ground (Scheffers *et al.* 2013c). However, these same studies might miss important aspects of their ecologies that are essential to the functioning of these systems as the bulk of the distribution is unobservable from the ground.

Even though there have been advances in the knowledge of canopy environment since the 1990's, the difficulty of accessing canopy trees has left arboreal communities largely neglected compared to other areas of ecological study (Kays & Allison 2001). My thesis research is the first ever examination of vertical stratification across an elevation gradient. In this thesis, I coin a novel and previously unknown dimension to biodiversity ("arboreality") (Chapter 2). I further examine the role that microhabitats play in amplifying arboreal biodiversity (Chapter 3). These fine-scale habitats provide microclimates that ameliorate physical stress within the hot and dry rainforest canopy (Scheffers *et al.* 2013a; Scheffers *et al.* 2013b).

Because species richness organizes along climate gradients, scientists use these gradients as natural laboratories to examine the potential effects of climate change on species persistence and distribution. Along these gradients, the colder regions serve as "current" climate whereas the warmer regions along this gradient serve as "future" climate. Climate is predicted to change in varying ways depending on region however; annual temperatures might warm by up to 6 C by 2100 (IPCC 2007). Climate extremes and altered precipitation regimes are expected (McCain & Colwell 2011; Watson, Iwamura & Butt 2013). Climate extremes are likely one of the most important considerations for future climate change impacts on biodiversity because the rate of change in climate occurs much faster than the time required for populations to respond. Thus, instead of gradual shifts in populations that track suitable climate through space and time, climate extremes can cause widespread and unabated mortality. Thus, in Chapter 4 (Scheffers *et al.* 2013a) and 5 (Scheffers *et al.* 2013b), I examine the potential of local microhabitats in buffering species from climate change and extreme weather events.

Chapter 2: Increasing arboreality with altitude: a novel biogeographic dimension

A modified version of this chapter is published:

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2.1 Introduction

Changing distributions of species richness and abundance across environmental gradients such as elevation and latitude are fundamental features of life on Earth (Gaston 2000). Mechanisms behind these patterns are largely attributed to gradients of temperature and moisture (McCain 2009). But large-scale elevational and latitudinal gradients are not the only ones evident. In tropical rainforest, strong gradients in temperature and moisture occur from the forest floor to the canopy (Johansson 1974; Fetcher, Oberbauer & Strain 1985). Patterns of species richness and abundance may organize along this vertical gradient in the same way that they do along the shallower gradients driven by elevation and latitude. If so, then vertical climate gradients may play a powerful role in structuring biodiversity (Schulze, Linsenmair & Fiedler 2001).

Tropical rainforests are the most biodiverse communities on Earth (Gaston 2000), and one reason for this high diversity is the great number and variety of niches afforded by the complex vertical structure of rainforest environments (Ozanne *et al.* 2003). In rainforests, the three major climatic gradients (across latitude, elevation, and height) may interact to drive species' distributions. For example, a species that is highly arboreal at cooler high elevations may be much less so at warmer low elevations. Most rainforest animals are ectotherms and are thought to behaviorally exploit microclimatic mosaics within these complex forests to optimize temperature and water balance (Kearney, Shine & Porter 2009; Tracy, Christian & Tracy 2010; Huey *et al.* 2012), but data on the vertical structuring of ectotherm communities, especially over large spatial gradients, are extremely limited (Kays & Allison 2001). This is due to the difficulty in accessing and studying canopy habitats as well as the overall cryptic nature of ectothermic vertebrates (Kays & Allison 2001). As a consequence, the interaction among these three major environmental gradients in the structuring of rainforest communities has remained a relatively unexplored dimension in biodiversity science.

If vertical stratification of species assemblages changes across elevation, it suggests that patterns of diversity are indeed subject to the interaction of the vertical climatic gradient (height) with the much shallower one of elevation. Incorporating the impact of this underappreciated spatial dimension (height) on community structure could uncover important relationships that help explain (in concert with other biogeographical principles such as mid-domain effects; Colwell, Rahbek and Gotelli (2004)) distributional patterns of richness and abundance (McCain 2010) and possibly reveal important patterns, not only in space but also in time. For example, as climate change progresses (i.e., time), plant and animal species alter their distributions as they track suitable climates through space (Patrick *et al.* 2008). Because the Earth is warming and in some areas becoming drier (Lewis *et al.* 2011), species' distributions are generally moving uphill or toward the poles, following thermal and moisture gradients associated with latitude and/or elevation (Parmesan 2006; Colwell *et al.* 2008; Raxworthy *et al.* 2008). The vertical partitioning of species in rainforest driven by a steep microclimatic gradient may provide some level of compensation against changing microclimates, by allowing species to shift vertically within the forest. If so then climate change will likely trigger small-scale downward shifts in height that precede distributional shifts poleward or to higher elevations.

Herein, I propose an “arboreality hypothesis” which suggests that species’ distributions may adjust vertically in the rainforest strata to compensate for broad-scale shifts in climate associated with elevation. I explored these ideas by censusing frogs from the ground to canopy levels along an elevational gradient (and therefore a temperature and moisture gradient) in Philippine (900-1900 m) and Singaporean (~10 m) rainforests. Along this gradient I sampled frogs during both day and night within 67 individual trees, using ascenders to climb from ground level to nearly the uppermost canopy (Methods). I also placed 60 data loggers within the forest canopy and understory to measure temperature and moisture across the height and elevation gradient. To further explore how physical conditions might affect frog usage in the canopy, I used a biophysical WETAIR model (Tracy, Christian & Tracy 2010) to show the effect of body mass, moisture, and temperature on frog water loss. Lastly, I compiled a dataset for all frogs of the Philippines to explore how arboreality in frog assemblages might respond to changing climate across elevation at larger spatial scales.

2.2 Methods

2.2.1 Study areas

In the Philippines, I surveyed a community of largely endemic frog species on Mt. Banahaw in southern Luzon. The site is characterized by lowland dipterocarp forest up to 800 m elevation, dipterocarp and montane forest from 900-1700 m elevation, and mossy and *Pinus* forest above 1700 m elevation. My study was not conducted below 900 m because at lower elevations (<800 m) agriculture has replaced forest (Peh *et al.* 2011). I allowed 100 metres of elevation to buffer any potential effects from these disturbances. The climate is marked by the absence of a distinct dry season with annual rainfall of around 3100 mm yr^{-1} and 85% relative humidity on average

(Banaticla & Buot 2005). I observed that rainfall and cloud cover for our Philippine study site varied with elevation, both of which increased at higher elevations.

In Singapore, my study area consisted of primary and older-secondary lowland dipterocarp forest. Most areas on the island receive more than 2000 mm rainfall yr^{-1} with no apparent dry season. The average high temperature year round is around 30 ˚C (Chia & Foong 1991).

2.2.2 Vertical stratification of frogs across an elevation gradient

In the Philippines, from May – October 2011, I conducted 118 ground-to-canopy surveys across a gradient of elevation at 900, 1100, 1300, 1500, 1700, 1900, and 2100 m above sea level. Each survey was centered on a single canopy tree. Tree selection was randomized at each elevation; however, each tree had to meet safety standards for arborist single-rope climbing (Jepson 2000). Selected trees were at least 100 m apart at each elevation. I surveyed a total of 59 trees for adult frogs (14 trees at 900 m, 5 at 1100 m, 13 at 1300 m, 5 at 1500 m, 11 at 1700 m, 5 at 1900 m and 6 at 2100 m elevation).

Tree surveys lasted for one hour and were conducted during the day and repeated at night to account for species with diurnal and nocturnal activity. I alternated surveys along the elevation gradient (low to high to low elevations) to avoid temporal bias in sampling. I recorded the maximum height climbed and tree height for each survey. Following each canopy survey, I used a laser distance meter (Leica Geosystems, Leica Disto D2; http://www.leica-geosystems.ca) to record tree height from the top of tree to the base of tree. Climbing to the top of trees is dependent on suitable branches that allow for safe access. Thus, I could not always ascend to 100% of the total tree height. I accounted for this in our analyses (see below).

I conducted “canopy surveys” for adult frogs—a single 10-minute visual survey for the ground (base of tree), sub-canopy (approximately half the maximum height climbed), and canopy (maximum height climbed). Ten-minute ground surveys were confined to a randomly selected 4 x 4 m plot, and consisted of thoroughly searching leaf litter, logs, and other microhabitats that may harbor animals. Visual-encounter surveys were expected to be most comprehensive when attempting to locate both ground and arboreal animals (Doan 2003). Both the middle and canopy surveys were confined to approximately four vertical metres of above-ground habitat. Thus, I attempted to standardize the search area across my three survey locations. Because of limited above-ground surface area, I consider my sub-canopy and canopy surveys to be conservative, as I likely surveyed more area on the ground than above-ground. For above-ground surveys, I searched for arboreal frogs in tree holes, moss, epiphytes, and other microhabitat structures. I conducted ground surveys first to account for the potential bias of having frogs jump out of the tree while conducting arboreal surveys, and thereby inflating ground-survey abundances.

2.2.3 Surveys in Singapore

In February, 2011, I surveyed eight trees from ground to upper canopy for amphibians, using identical canopy-survey methods described above. Surveys were conducted within the primary lowland dipterocarp forests of Nee Soon Swamp (1 tree) and Bukit Timah Nature Preserve (2 trees), and within the mature second-growth forest of Kent Ridge (2 trees), Bukit Batok (1 tree), and Labrador Park (2 trees) preserves.

2.2.4 Environmental temperatures

From May – September 2011, I used temperature and moisture loggers (Maxim Hygrochron ibutton Model DS1923; http://www.maxim-ic.com/) to determine the thermal and moisture profiles of forests in the Philippines. To identify the maximum potential ambient-air temperature as well as minimum moisture for my study area, I placed data loggers in the upper canopy of five trees per elevation (900-1900 m elevation), each paired with an identical logger suspended 1 m above-ground. I chose to record maximum temperature and minimum moisture as these two variables are important to frog survival (e.g., high temperature and low moisture can negatively affect frog survival). Data were recorded every 15 minutes. Canopy and near-surface loggers were suspended under a plastic funnel and were thereby sheltered from direct solar radiation and precipitation. I used box-and-whisker plots to display maximum daily temperature and minimum daily moisture (figure. 1).

2.2.5 Elevation gradient of species richness and arboreality in the Philippines

I compiled a database of frog distributions across elevation, taken from Diesmos & Brown 2011. For each of the 107 species, I recorded it as occupying either one of two possible habitat niches: arboreal or ground-dwelling. A species was defined as arboreal if it is capable of climbing and using above-ground habitats. By contrast, non-arboreal species were those that lacked grasping toe-pads and are thus less likely to exploit aboveground habitats. Alternatively, a species was considered ground-dwelling if it is confined to the ground 100% over the course of its life. I examined patterns of arboreal richness across elevation by 1) plotting total species richness for each 100 m elevation band and 2) plotting the proportion of species that are arboreal and ground dwelling across 100 m elevation bands. Lastly, I plotted total arboreal and ground dwelling species richness by genus to explore taxonomic relationships across the elevation gradient.

2.2.6 Data Analysis and Kernel-density estimation

I used univariate kernel density to estimate the distributions of amphibians across vertical forest strata (Silverman 1986; Venables & Ripley 2002). Kernel-density estimation is a procedure for generating a smoothed histogram of data, with the advantage that the area under the smoothed histogram integrates to one. Thus, the smoothed line represents the probability density of the data. In my study, I estimated the probability density of the height at which frogs were observed. Although not an absolute density of animals, the absolute density of animals should scale directly with the probability density (assuming animal detectability is invariant with height), so the probability density I calculated here can be thought of as the relative density of animals with height.

I attempted to estimate the true probability density of animals with height by integrating my results across the distribution of tree heights in the forest (estimated using our data on climb height for each tree). Thus, I estimated a kernel bandwidth (using Silverman's rule of thumb; see Silverman (1986)) for my total dataset, but then executed a kernel-density estimate, using this bandwidth independently for each tree in my dataset. I then combined these tree-wise kernels using a weighted mean, where the weighting for each tree was taken from the kernel describing the distribution of tree heights. Because no animals can be observed at negative height, I used a modified version of the density function in the R (v. 2.12.2) statistical package to generate left-bounded univariate kernel-density estimates by reflecting the density falling below zero back into the positive domain of our estimated kernel (Silverman 1986).

I generated a composite distribution based on data collected from ground, sub-canopy, and canopy surveys to reflect an aggregate distribution for amphibians. To explore the presence of an upward shift in vertical positioning across elevation, I generated distributions for all arboreal frogs for three elevational zones (900-1100, 1300-1500, and 1700-1900 m). I examined only the arboreal frogs in this analysis as non-arboreal species that lack grasping toe-pads are incapable of exploiting aboveground habitats. Finally, I compared these trends to arboreal frog distributions in Singapore.

To identify the potential impacts of arboreal frogs shifting downwards towards ground communities, I quantified the proportion of the total community (both ground and arboreal frogs) that was found above-ground. Specifically, as the total area under the curve equals one, I identified the cumulative distribution of all frogs found above 1 m height (i.e., the area occurring above 1 m on the curve) across all elevations in the Philippines.

2.2.7 Dehydration and arboreality

Frogs that exploit canopy habitats are often away from water for extended periods of time, making them vulnerable to desiccation. Body mass, moisture, and temperature are all factors that affect the rates at which an individual loses water and thus its ability to use canopy habitats (Tracy, Christian & Tracy 2010). To further explore whether there is support for decreased arboreality by elevation in frogs, I used a biophysical WETAIR model (Tracy, Christian & Tracy 2010) to show the effect of body mass, moisture, and temperature on frog water loss. In this theoretical exercise, all parameters but body mass were held constant whereas mass (ranging from 0.1 to 10 g) and temperature were allowed to increase. This analysis was repeated with increasing mass and moisture. Mass selection from 1 to 10 g was based on a range of masses representative of species found in my study area. The smaller masses (i.e., 0.1 and 0.5 g) are indicative of young-of-the-year/metamorphs for species in my study area. The output for models was time (h) to 30% desiccation. Specifically, the variables held constant were cutaneous resistance (R_c) at 1.64 (averaged from Wygoda (1984)), relative humidity at 72%, and elevation at 450 m elevation (the mid-point of the elevational difference between Singapore and the Philippines). I then repeated this exercise for the same range of body masses as above but used temperature, moisture, and elevation derived from my study area to determine the time to 30% desiccation specifically for our study areas. Lastly, I used the WETAIR models to display desiccation under three climate scenarios across elevation to identify climate scenarios that are favorable and unfavorable for arboreality: 1) high temperature (35 ˚C to 28 ˚C) and high moisture (95% to 100%), 2) low temperature (22 ˚C to 15 ˚C) and low moisture (42% to 47 %) and 3) high temperature (35 ˚C to 28 ˚C) and low moisture (42% to 47 %).

2.2.8 Alternative hypotheses

I considered three additional variables that represent structural components of the forest that may affect arboreality in frogs across elevation. It is possible that tree height influences patterns of frog arboreality as taller trees may offer greater height for frogs to use. Tree density and basal area (cross-sectional area of all stems per transect) are indicative of structure and habitat for frogs. Therefore, frog arboreality may correlate with increasing tree height, stem density, and basal area of the local environment across elevation.

To examine this relationship, I documented tree height, stem density, and basal area in order to characterize the local environment surrounding our tree surveys. I counted all trees (i.e., density), greater than 4 cm diameter-at-breast-height (dbh), along a 2 m wide and 20 m long transect. The direction of each transect was chosen at random and each transect was centered on a survey tree. Height and dbh was recorded for each tree recorded. I determined basal area by multiplying 0.00007854 by dbh to the power of 2 (Husch, Miller & Beers 1972). For each transect, basal area was summed for all trees and divided by the transect area (40 m^2).

2.2.9 Linear models

I explored temperature and moisture across my elevation gradient. I modeled temperature across elevation by running an Analysis of Covariance (ANCOVA) with temperature as a response variable and elevation and position (ground or canopy) as predictors. A second ANCOVA was performed with the same predictors but moisture was used instead of temperature as the response variable.

I examined whether the proportion of frog arboreality changed with elevation in the Philippines. To do this, I used linear regression with the proportionate of total frogs that are arboreal as my response variable and elevation as our predictor variable.

To explore the relationship between animal height and elevation I performed an (ANCOVA) with my response variable as height (m) and predictor variables as elevation and species. To properly assess animal height by elevation, I only used species for which I had occurrence data at three or more elevations. Therefore, *Platymantis luzonensis* was not included in this analyses as it only occurred at 900 m and 1100 m elevation. Lastly, to determine whether height in canopy predicts body mass I used a second ANCOVA with two covariates. My response variable was mass (g) and the predictor variables were height in forest stratum, elevation, and species. Both body mass and height were log-transformed to normalize data. In both cases, I initially tested for first-order interactions between height and elevation, but removed the term because it was not statistically significant.

I explored tree height, tree density and total basal area as alternative predictors of arboreality across elevation. I performed three linear regressions with tree height, tree density, and total basal area as response variables and elevation as a predictor variable. Data were log-transformed to achieve normality.

All models were checked for heteroscedasticity via the studentized Breusch-Pagan test. My mass and height and height and elevation models were both non-heteroscedastic. Of my three alternative hypotheses models, the basal area and elevation and tree density and elevation models were both non-heteroscedastic. I did not log-transform data in my ANCOVA analyses of temperature and moisture, as these analyses were primarily conducted to derive a slope for temperature and moisture across elevation. I corrected for heteroscedasticity using White's robust standard errors (MacKinnon & White 1985).

2.2.10 Diagram of height and elevation shifts

To display the options an animal may have to remain at an optimum temperature and moisture under climate warming, I created a temperature-by-height-by-elevation contour figure derived from my temperature data and a moisture-by-height-by-elevation contour figure derived from my moisture data.

2.3 Results

Microclimatic gradients in temperature and moisture are significantly steeper than elevational gradients. In the rainforests, temperature decreased by 1.4 ˚C with every ~200 m increase in elevation but varied by 2.2 ˚C over just ~20 m between the forest canopy and ground level ($F_{2,1421}$=559.9, P<0.001; ANCOVA) (figure 2.1; table 2.1). Similarly, moisture increased by 1%

with every ~200 m increase in elevation but differed by 11% over the ~20 m gradient between canopy and ground ($F_{2,1421}=107.8$, $P<0.001$; ANCOVA) (figure. 2.1; table 2.1).

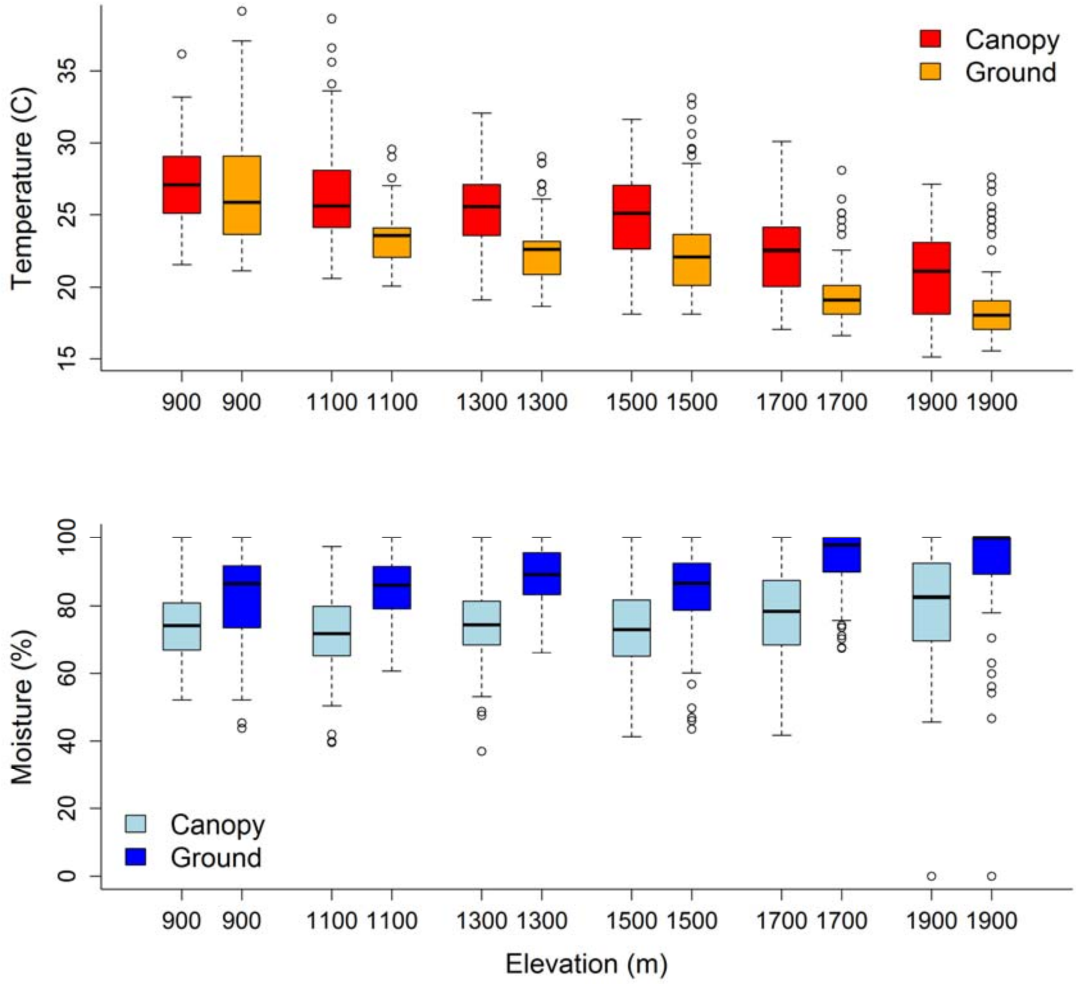

Figure 2.1 Temperature and moisture differ between canopy and ground as well as across elevation. Canopy and ground daily maximum temperature and minimum moisture profiles from sub-montane to montane rainforests in the Philippines. Temperature and moisture were collected from May – September, 2011.

Table 2.1. Analysis of Covariance models suggest maximum temperature and minimum moisture significantly change between canopy and ground (i.e., position) and from 900 to 1900 m elevation. Bold values are significant at *P*<0.05.

Model	Estimate	S.E.	*P*
maximum temperature model			
elevation	-1.39	0.048	**<0.001**
position (ground)	-2.24	0.158	**<0.001**

minimum moisture model			
elevation	0.997	0.288	**<0.001**
position (ground)	11.326	0.804	**<0.001**

My data show that, with increasing elevation, total species richness generally decreased and the degree of assemblage arboreality increased (figure. 2.2). Specifically, ground-dwelling species richness decreased from low to high elevations and arboreal species richness peaked between 600 and 800 m. My linear regression model suggests that the proportion of all frogs that are arboreal increases with elevation ($F_{1,28}$=112, R^2=0.793, P<0.001)—a 10% increase in assemblage arboreality for every 500-m rise in elevation. Assemblages above 300 m are comprised of more than 50% arboreal species, whereas they are 100% arboreal above 2300 m (figure. 2.2). The number of arboreal species is lower in the lowlands, with ~42% of the total assemblage being arboreal at sea level. Multiple genera are present across the elevation gradient for both ground and arboreal species suggesting that a single genus is not driving the observed biogeographical trends (figure 2.3 and 2.4).

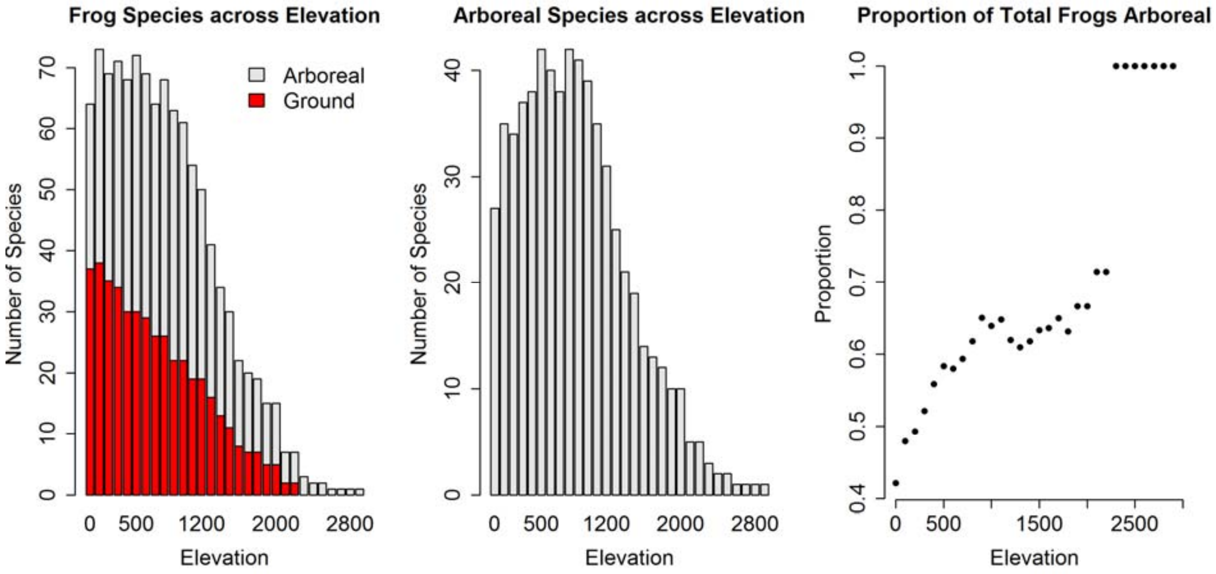

Figure 2.2 (left) Changes in frog species richness across elevation in the Philippines (N=107) separated by ground-dwelling and arboreal species. (right) Frog assemblages become increasingly arboreal with elevation. Assemblages above 300 m are more than 50% arboreal. Above 2300 m, species richness is low, so our percentages in these altitudinal bands are derived from only 1-3 frog species.

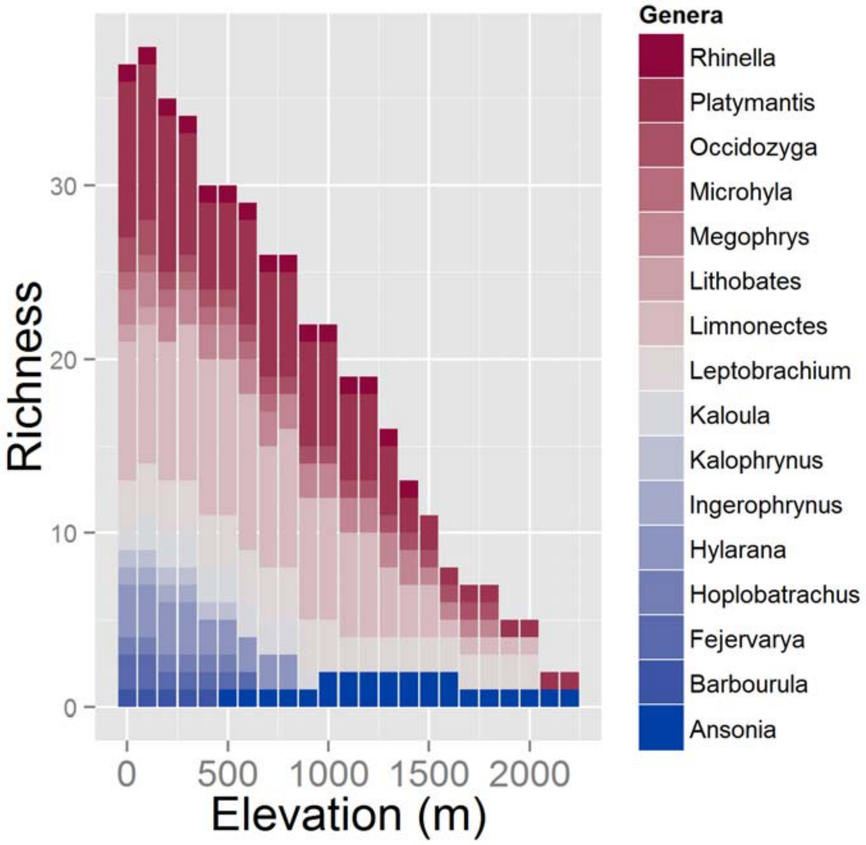

Figure 2.3. Stacked histograms showing patterns of ground species richness separated by genus across elevation. Ground-dwelling species from multiple genera are present from low to high elevations.

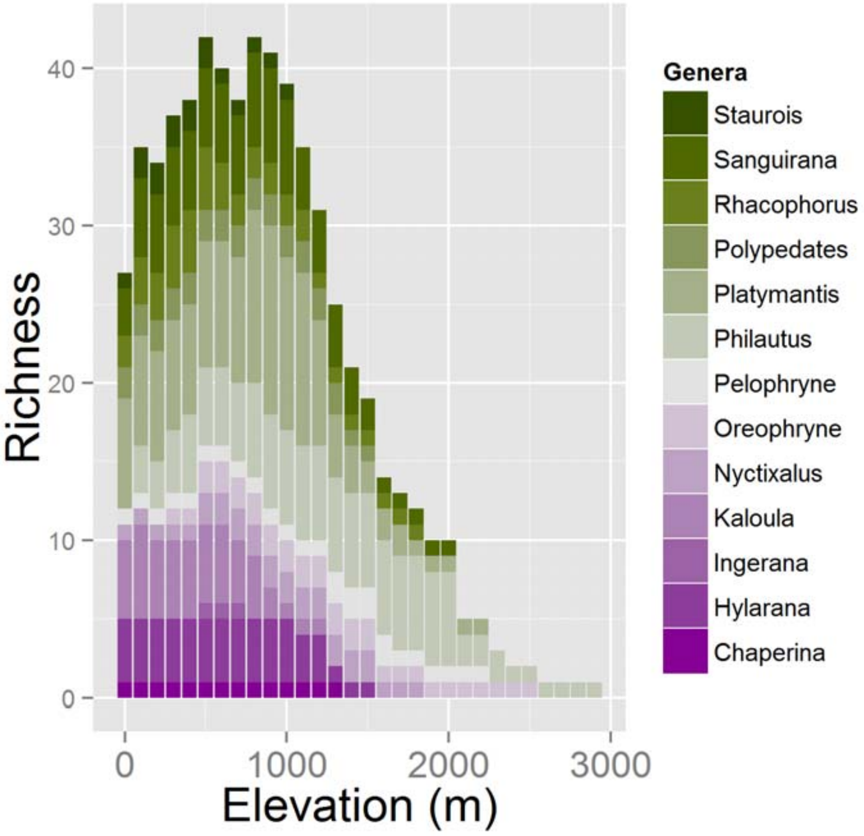

Figure 2.4 Stacked histograms showing patterns of arboreal species richness separated by genus across elevation. Arboreal species from multiple genera are present from low to high elevations.

I documented three ground and five arboreal species in the Philippines and seven ground and four arboreal species in Singapore (table 2.2). There was a significant relationship between elevation and height of frogs in forest canopies across our Philippine landscape ($F_{4,51}$=4.50, P=0.003; ANCOVA) (figure. 2.5, figure. 2.6 and table 2.3); a trend that was consistent across all species for which I had sufficient data (interaction terms were not found to be significant (p>0.29 for all factor levels), and so were dropped from the final reported model). In the lowland forests of Singapore, all frogs were located either on the ground or below 3.5 m in height (figure. 2.3). Increased arboreality in frogs is evidenced by the second hump in the kernel-density estimate distribution (figure. 2.3), which is missing at 900-1100 m elevation but becomes more apparent at higher elevations. Across the entire elevational range (900 – 1900 m) in the Philippines, 88% of all frogs are found above 1 m in height (figure. 2.7).

Table 2.2. Total frog abundance for each documented species (both ground and arboreal) from 59 tree surveys in the Philippines and eight tree surveys in Singapore.

		Singapore	The Philippines			
	Ground/Arboreal	0	900&1100	1300&1500	1700&1900	Total
Kaloula kalengensis	Arboreal	--	2	2	0	4
Philautus surdus	Arboreal	--	2	6	0	8
Platymantis banahao	Arboreal	--	2	14	2	18
Platymantis luzonensis	Arboreal	--	11	3	0	14
Platymantis montanus	Arboreal	--	0	8	18	26
Platymantis corrugatus	Ground	--	4	0	0	4
Platymantis dorsalis	Ground	--	5	1	0	6
Platymantis naomi	Ground	--	0	3	4	7
TOTAL		--	26	37	24	87
Hydrophylax raniceps	Arboreal	2	--	--	--	2
Kaloula pulchra	Arboreal	1	--	--	--	1

Nyctixalus pictus	Arboreal	1	--	--	--	1
Polypedates leucomystax	Arboreal	1	--	--	--	1
Kaliphrynus pleurostigma	Ground	1	--	--	--	1
Leptobrachium nigrops	Ground	3	--	--	--	3
Limnonectes malesianus	Ground	1	--	--	--	1
Limnonectes paramacrodon	Ground	1	--	--	--	1
Microhyla butleri	Ground	2	--	--	--	2
Pulchrana laterimaculata	Ground	1	--	--	--	1
TOTAL		14	--	--	--	14

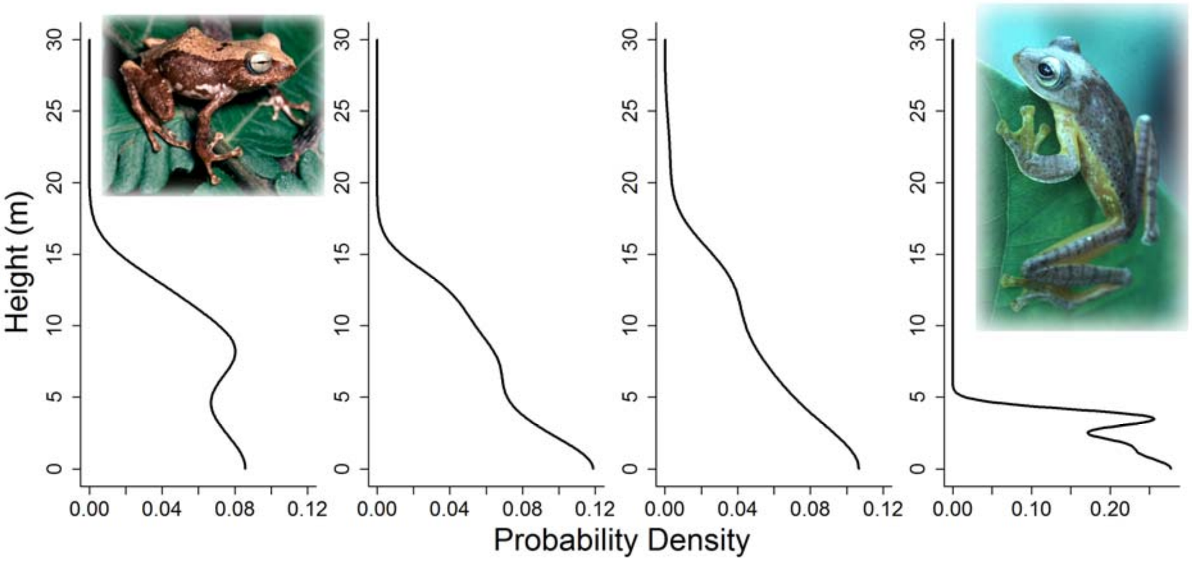

Figure 2.5 Vertical stratification of arboreal frogs from higher (left) to lower (right) elevations (N=20 at 1900 & 1700 m; N=33 at 1500 &1300 m; N=17 at 1100 & 900 m and N=5 at 0 m; respectively). These data show a clear decrease in arboreality from cooler/moister (high elevation) to warmer/drier (low elevation) climate. Curves are derived from kernel-density-estimation techniques and can be interpreted as the relative density of animals with height (Silverman 1986) (see Methods). (Photos of *Platymantis montanus* and *Rhacophorus pardalis* in the Philippines by Rafe Brown).

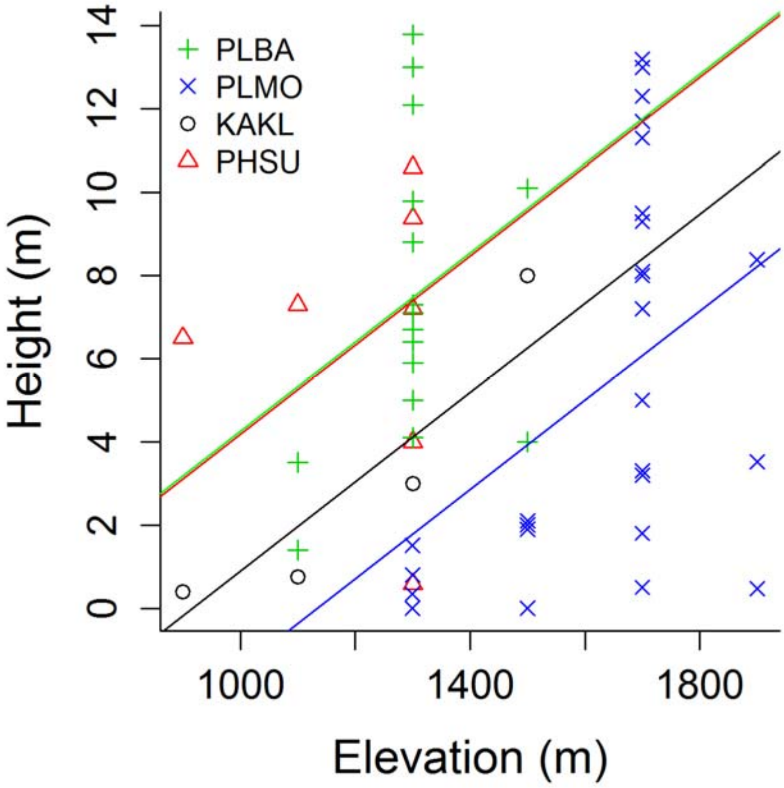

Figure 2.6 Height in forest stratum increases with elevation for arboreal frog species. According to Analysis of Covariance models, elevation significantly predicts height in forest canopy at which frogs were observed (N=56; table S3). PLBA: *Platymantis banahao*; PLMO: *Platymantis montanus*; KAKL: *Kaloula kalengensis*; PHSU: *Philautus surdus*.

Table 2.3. Analysis of Covariance models suggest elevation significantly predicts height in rainforest canopy of frogs (N=56). Bold values are significant at $P<0.05$.

Model	Estimate	S.E.	*P*
elevation+species model			
elevation	0.011	0.003	**0.002**
species *P. surdus*	3.290	2.232	0.147
species *P. banahao*	3.362	2.039	0.105
species *P. montanus*	-2.329	2.389	0.334

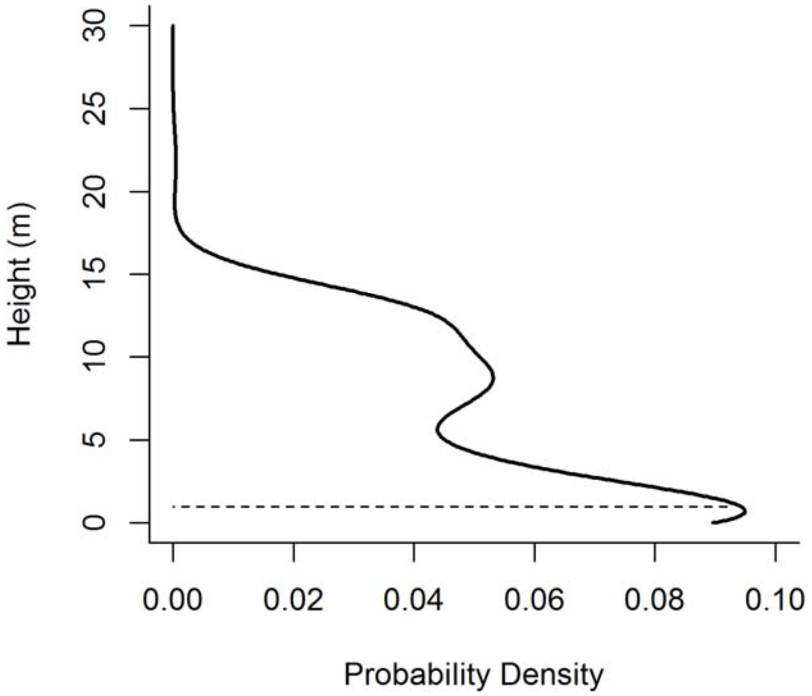

Figure 2.7 Approximately 88% of all individuals occur above 1 m in Philippine rainforests. Kernel density estimate of the distribution for all frogs (ground to canopy; N=87) across all elevations. The dotted line indicates 1 m above-ground.

Larger frogs were found higher in the canopy. That frog body size varies significantly with height in the forest ($F_{6,51}$=8.27, P<0.001; ANCOVA) (figure. 2.8, table 2.4) supports the notion that temperature and moisture are key drivers of frog arboreality. Biophysical WETAIR models reveal that frogs desiccate faster with higher temperatures, lower moisture, and when they are smaller-bodied (figure. 2.9a-c). The WETAIR models, which include environmental parameters of my study sites, suggest a frog of 3 g can remain in the canopy at the highest elevations during the hottest hours of the day for ~8 hours before reaching lethal dehydration, whereas an equivalent frog in the lowland forest canopy of Singapore has about half as much time. To that end, I also modeled three climate scenarios using WETAIR models: (1) high temperature and high moisture, (2) low temperature and low moisture, and (3) high temperature and low moisture. Desiccation rates for high temperature and low moisture were 3-4 times greater than for low temperature and low moisture and 6-7 times greater than for high temperature and high moisture (figure. 9d).

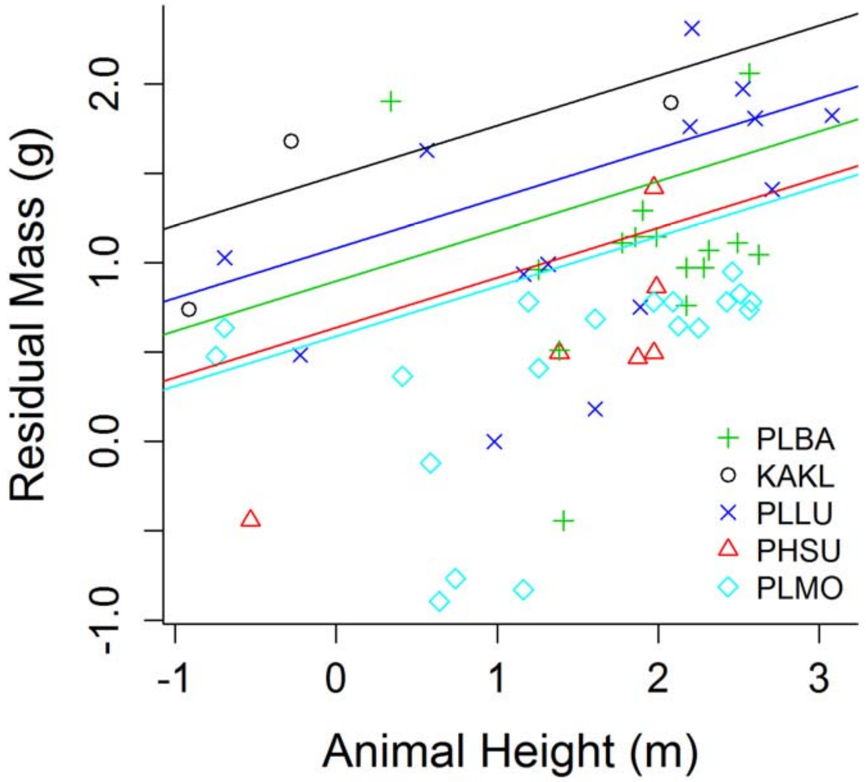

Figure 2.8 Larger arboreal frogs occur higher in forest stratum that smaller frogs. According to linear regression analysis, animal height in forest significantly predicts body mass (N=58; table 2.4). Residual mass is mass corrected for the influence of elevation. Mass and height were log transformed. PLBA: *Platymantis banahao*; KAKL: *Kaloula kalengensis*; PLLU: *Platymantis luzonensis*; PHSU: *Philautus surdus;* PLMO: *Platymantis montanus*.

Table 2.4. Analysis of Covariance models suggest height in rainforest canopy significantly predicts mass of frogs (N=58). Bold values are significant at *P*<0.05.

Model	Estimate	S.E.	*P*
height+elevation+species model			
Height	0.279	0.490	**0.004**
Elevation	-.0001	0.070	0.780
species *P. surdus*	-0.851	0.267	**0.002**
species *P. banahao*	-0.589	0.247	**0.021**
species *P. luzonensis*	-0.407	0.263	0.127
species *P. montanus*	-0.898	0.300	**0.004**

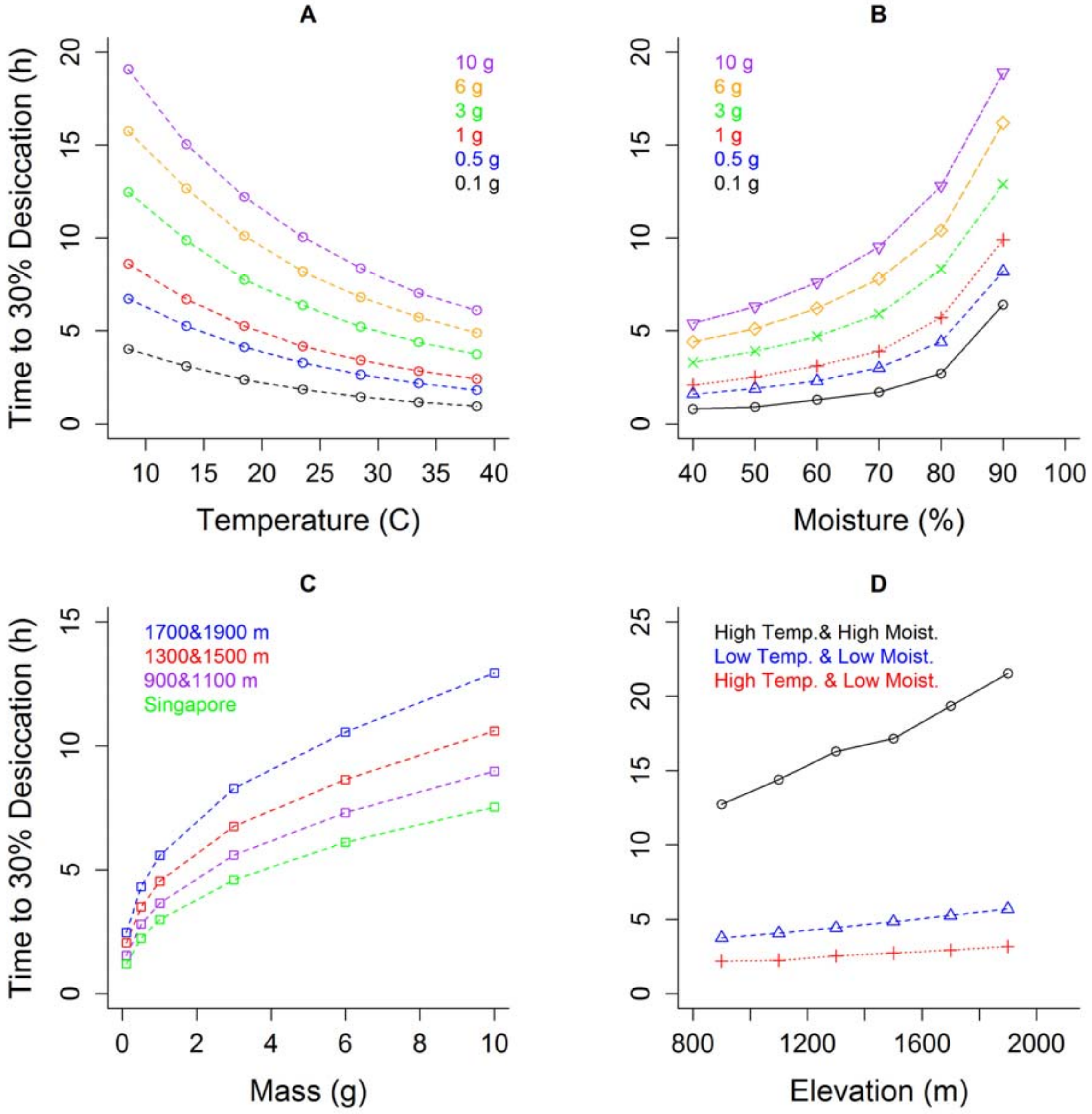

Figure 2.9 The time to 30% desiccation varies by temperature (A) and moisture (B) when all other variables are held constant. Under each mass scenario frogs in hotter-drier environments will ultimately desiccate faster than frogs in cooler-wetter environments. The top dashed line represents a frog weighing 10 g and bottom line represents a frog weighing 0.1 g. (C) Using actual site-specific temperature and moisture data recorded at canopy and ground heights across elevations, time to 30% dehydration increases with body mass across elevations. (D) Based on three temperature-moisture scenarios across our elevation gradient, high temperatures in combination with high moisture causes minimal desiccation. However, combinations of low temperature and low moisture or high temperature and low moisture can cause severe and rapid desiccation.

I considered three alternative hypotheses in which elevation-related changes in forest structure might cause the observed changes in arboreality, but none was supported. Specifically, linear regression models suggest that neither tree height ($F_{1,469}$=1.06, R^2=0.00, P=0.31), basal area ($F_{1,48}$=0.25, R^2= -0.02, P=0.62), nor tree density ($F_{1,48}$=0.35, R^2= -0.01, P=0.56) significantly change from 900 to 1900 m elevation (table 2.5 and 2.6).

Table 2.5. Linear regression models suggest that neither tree height, basal area, nor tree density significantly change from 900 to 1900 m elevation. Values are significant at *P*<0.05.

Model	Estimate	S.E.	*P*
tree height model			
Elevation	0.00007	0.00007	0.316
basal area model			
Elevation	0.0000009	0.000002	0.324
tree density model			
Elevation	0.00009	0.0002	0.558

Table 2.6. Mean (±SD) tree height, diameter-at-breast-height (DBH) and basal area for survey trees. In order to characterize the environment surrounding survey trees, stem density (tree abundance per 40m² transect), tree height, DBH, and basal area was measured. Height climbed indicates the mean percentage of survey tree height that was climbed.

		Survey Tree				Surrounding Trees			
Elevation (m)	N	tree height	height climbed (%)	DBH	basal area	stem density	tree height	DBH	basal area
0	8	28.8 (10.1)	80	--	--	--	--	--	--
900 & 1100	18	18.8 (3.9)	77	72.4 (21.6)	0.4 (0.2)	8.5 (3.8)	8.1 (6.0)	19.7 (23.9)	0.1 (0.2)
1300&1500	17	15.7 (3.5)	75	74.1 (31.1)	0.5 (0.5)	9.9 (3.8)	7.0 (4.3)	19.1 (23.4)	0.1 (0.2)
1700&1900	16	15.1 (1.6)	82	69.6 (19.2)	0.4 (0.2)	8.9 (2.3)	7.6 (4.0)	20.3 (22.5)	0.1 (0.2)

2.4 Discussion

My study shows conclusively that arboreality (or ‘vertical stratification’) plays a role in determining patterns of rainforest species richness and abundance, especially for ectothermic and hydrophilic species. Specifically, the vertical distributions of frogs shift upwards into the forest strata with increasing elevation. The distribution of animals with height (their ‘vertical distribution’) is rarely examined relative to the large body of research on animal distributions across elevation and latitude (Parmesan 2006; Colwell *et al.* 2008; Raxworthy *et al.* 2008; Williams *et al.* 2010). Moreover, given the logistical difficulties of ascending to upper forest strata, species’ vertical distributions, when examined, are rarely studied at multiple sites, as I have done here. To my knowledge, mine is the first study to examine comprehensively how the vertical dimension of faunal distributions changes with elevation. From these observations, my proposed “arboreality hypothesis” suggests that arboreality offers flexibility in finding optimal micro-climatic conditions across a wider range of macro-climates. Thus, I propose that species would have a narrower geographic range in the absence of their ability to exploit micro-climates offered by vertical habitat structure.

I propose that adult frogs that use two key habitat niches—arboreal and terrestrial—are physiologically constrained on opposite ends of the elevation gradient. Specifically, arboreality is constrained in the lowlands from conditions that are excessively hot and dry in the canopy, whereas terrestriality is constrained in the uplands because ground temperatures are too cold. My data support this proposition. First, my canopy surveys show that frogs become more arboreal as canopy conditions improve with increasing elevation. Second, my Philippines-wide dataset shows that species richness of ground-dwelling frogs decreases linearly with increased elevation (as ground conditions become too cold) whereas the proportion of the total frog assemblage that is arboreal increases with elevation (as canopy conditions become more favorable, transitioning from being hot in the lowlands to being warm or cool in the uplands).

These patterns suggest that species richness of frogs and other temperature- and desiccation-sensitive fauna should be highest at some intermediate elevation where both canopy and ground level temperatures are most optimal. My data show a peak in frog species richness at around 600 to 800 m elevation (well below the 1400 m mid-domain in this system) and a linear decrease in the proportion of ground-dwelling species as elevation increases. Mid-elevation peaks of richness and abundance are found across various taxonomic groups (McCain 2009; McCain 2010; Williams *et al.* 2010) and are generally thought to be driven by temperature and moisture (McCain & Colwell 2011) as well as the mid-domain effect (Colwell, Rahbek & Gotelli 2004; McCain 2010). Although it is difficult to disentangle mid-domain effects from other potential drivers, the strong shift from ground-dwelling to arboreal life-histories with elevation argues strongly that the interaction between the climatic gradients of height and elevation is a powerful mechanism driving patterns of richness in this system.

The inference that high temperatures and lower moisture greatly constrain frog arboreality (Stewart 1995) is supported by my observation that frog mass increased with height above-ground (figure. 4), a pattern predicted by my WETAIR models. These models indicate that larger frogs are substantially more resistant to evaporative water loss (Tracy, Christian & Tracy 2010), which is an increasing problem in the warmer and drier upper forest strata (Bohlman, Matelson & Nadkarni 1995) as well as at lower elevations (figure. 2.9a-c).

My novel height dimension to biogeography may broadly apply to other taxonomic groups. For example, some species of ground carabid beetles from Southeast Asia appear to increase in arboreality with elevation (Stork 1988; Stork & Brendell 1990). My findings, however, may not apply to non-ectothermic communities. The general applicability of my hypothesis to other non-anuran animal groups with variable physiological requirements should be further tested.

Interestingly, the vertical stratification of body size in my study is opposite to that expected under Bergmann's rule (Bergmann 1847; Sears & Angilletta 2004), in which large-bodied animals are generally found in cooler habitats. Opposing patterns to Bergmann's rule are, however, routinely observed in ectotherms, possibly because of the effects of body size on thermal inertia and water loss as captured by my WETAIR model (Sears & Angilletta 2004). Indeed, ants and other arthropods are closely tied to temperature and energy within ecosystems (Kaspari, Ward & Yuan 2004) and therefore may mirror the same stratification patterns as we found with frogs (Stork & Blackburn 1993). Similar non-Bergmann 'body size' clines have also been observed in *Asplenium* bird's nest ferns in Malaysia, where individual plant biomass of ferns increases with height in forest canopy (Fayle *et al.* 2009) and in arthropods in Indonesia and Australia where mean arthropod body size decreased from treetop down to soil (Stork & Blackburn 1993; Grimbacher & Stork 2007). In short, the mechanisms driving the vertical distribution of frogs in my study might well apply to a broad suite of taxa.

In the frogs I studied, 8 of every 10 individuals were found above-ground (figure 2.7), echoing patterns of species abundance in other taxa, such as insects (Stork 1991). Yet, these patterns seem to be highly dependent on locality and taxa under consideration: beetle assemblages from the Australian wet tropics are equally abundant and diverse in both canopy and ground habitats (Grimbacher & Stork 2007), whereas arthropod densities in a Cameroon rainforest were approximately three times higher in the canopy than understory shrub layers (Basset, Aberlenc & Delvare 1992). Future research should also consider the role that keystone micro-habitats play in vertical stratification. For example, a single *Asplenium* bird's nest fern in

Bornean rainforests contains twice the invertebrate biomass as its entire host tree (Ellwood & Foster 2004). Thus, the distribution of select keystone micro-habitats across elevation may be an important feature governing vertical stratification of select animal communities.

2.4.1 Research Caveats and Future Prospects

I highlight the following possible caveats to my study and research prospects for further exploration of the arboreality hypothesis:

1. A limitation to my study as well as many previous studies on canopy communities is sample size (Kays & Allison 2001). Although we conducted over 120 ground-to-canopy surveys over several months, I documented only 87 individual frogs. I suggest testing the "arboreality hypothesis" with a more abundant study organism such as beetles, spiders and/or ants as a priority.
2. My study is confined to Southeast Asia. Are patterns of frog arboreality also prevalent in other tropical regions such as the Neotropics? Currently, no other research has explored my hypothesis (although see Stork (1988); Stork and Brendell (1990)) so until such work is undertaken, caution should be used when generalizing my trends to other habitats and geographic regions.
3. Cloud cover was not examined in my study area but may vary by topography and location and its presence could intensify moisture over small spatial scales (Cavelier, Solis & Jaramillo 1996), therefore, cloud cover may interact with the degree of change in arboreality with elevation.
4. Arboreality may vary by season. For example, vertical stratification of some arthropod species varies in areas with strong seasonal variation in climate (Wagner 2001). Interestingly, the impacts of future climate change on arboreal communities might be deduced from examining seasonal variation in arboreality (see below for further discussion).

5. At my local Philippine site, I observed that frogs at 1900 m were primarily arboreal whereas no frogs were observed at my highest elevation of 2100 m. One plausible explanation for these trends is that the climate in the canopy at 1900 m was marginally suitable for frogs and thus even canopy habitats may be rendered unsuitable at colder and wetter elevations.

6. Frogs are one of the most threatened animal groups on Earth largely as a result of the fungal disease, Chytridiomycosis (Puschendorf *et al.* 2011). Some species believed to have gone extinct have recently been rediscovered (Scheffers *et al.* 2011), but in hotter and drier habitats than normal (Puschendorf *et al.* 2011). Hot habitats dry frog's skin making them more resilient to fungal infection. Therefore, chytrid fungus may be less prevalent in arboreal than ground-dwelling frog species, especially those at higher elevations, as canopy frogs are exposed to warmer and drier conditions than the ground.

7. Variation in thermal tolerances (i.e., the minimum and maximum temperatures lethal to an individual) by forest height is unknown and only a few studies have examined ecotypic variation in thermal tolerances along elevation gradients (e.g., see Miller and Packard (1974)). Lowland frogs are assumed to only operate within a narrow thermal range whereas high elevation frogs are assumed to operate over a much larger range of temperature (Navas 1997). Despite different thermal ranges, all species will have a thermal optimum, and we would expect abundances to track this optimum. Thus, although the ground at high elevations may not be "as cold" for montane frogs (with broad tolerances) as they might be for lowland frogs (with narrower tolerance), I would still expect abundances to track gradients in temperature across height and altitude.

2.4.2 Arboreality Under Climate Change

That the vertical distributions of arboreal species shift with elevation is important not only for understanding biogeographic patterns, but for projecting how rainforest biodiversity might respond to future climatic change. Under a changing climate, shifts in both temperature and moisture could strongly influence species distributions (figure. 2.10) (McCain & Colwell 2011). Mean temperatures and moisture in rainforests followed a steep gradient from the upper canopy to the forest floor, spanning more than 2˚ C and 11% relative humidity over a distance of just ~20 m (figure. 2.1). Similar changes in temperature and moisture across elevation require movements of over 300 m and 2000 m, respectively. Thus, these vertical temperature and moisture gradients are orders of magnitude steeper than those associated with elevation or latitude. This steep climate-height gradient is the principle driver of stratification patterns in my study and suggests that, in a warming and sporadically drier world, amphibians and perhaps other temperature-sensitive ectotherms will likely adjust their vertical distributions downward within the forest (figure. 2.5 and 2.10). The steepness of the vertical gradient suggests that this will happen long before they shift to cooler and wetter conditions at higher elevations or latitudes (Chen *et al.* 2011). Indeed, this downward shift might be the only one available to arboreal species in the world's vast lowland rainforests, such as the Amazon and Congo Basins, where elevational gradients are virtually absent. If patterns of arboreality in frogs are globally coherent, climate change may exacerbate the vulnerability of this critically threatened animal group (Sodhi *et al.* 2008).

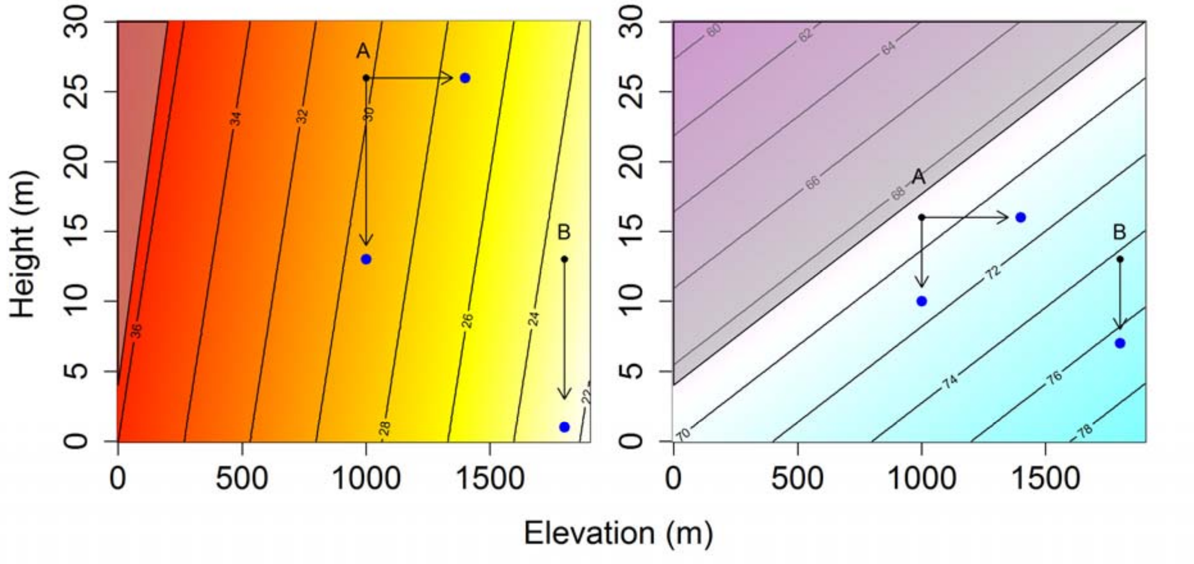

Figure 2.10 Modeled effects of elevation and canopy height on maximum temperature (left) and on moisture (the 25% lower quartile) (right). The ground and upper canopy differ by ~2 ˚C, which corresponds to an elevational increase of ~350 m. Similarly, moisture between the ground and canopy differs by 11%, which corresponds to an elevational increase of 2200 m. Point A shows movements of mid-elevational animals under a hypothetical 1 ˚C temperature increase (left) or a 1% moisture decrease (right), in which they shift 13 m down in height or migrate 200 m upward in elevation to remain at 26 ˚C or shift 6 m down in height or migrate 400 m upward in elevation to remain at ~71 %. Point B shows a mountain-top animal, under the same temperature increase and moisture decrease, that can only shift downwards in height. The shaded "extinction zone" will expand downwards in height and upwards in elevation as mean temperature rises or moisture falls.

Most alarmingly, my findings suggest that rising temperatures and severe drying events, such as the major Amazonian droughts in 2005 and 2010 (Lewis *et al.* 2011), could create an "extinction zone" for ectotherms in rainforests that progressively widens (figure. 2.10) as one moves toward the ground and uphill into mountain habitats. Species will be pushed off the top of mountains, but they will also be pushed to the ground. A downward shift in arboreal communities would squeeze together species that normally avoid interacting via vertical niche partitioning (Bickford 2005). For example, during hot, dry El Niño events in Papua New Guinea, significantly more frogs were encountered on the ground of which 78% of individuals were arboreal species (Bickford 2005). Thus, this effect could be dramatic; in our Philippines sample, for example, 88% of frogs were found more than 1 m above the ground (figure. 2.7). If these individuals were compressed downward (figure. 2.10), it would inflate ground densities of animals and potentially promote an array of negative interactions for affected species (Parmesan 2006) such as intensified interspecific and intraspecific competition (Jankowski, Robinson & Levey 2010; Gifford & Kozak 2012), and increased density-dependent mortality from predators, pathogens, and parasites (Patrick *et al.* 2008). Thermal stress and altered community interactions might interact synergistically, increasing extinction risk for vulnerable species (Brook, Sodhi & Bradshaw 2008; Laurance & Useche 2009).

Hence, my findings suggest the downward movement of many arboreal species in rainforests could be a rapid response to warming climates, and should be carefully monitored in the future. Such movements could serve as an early warning that rich arboreal communities in rainforests are in danger of reorganization or collapse.

Chapter 3: Epiphytic bird's nest ferns are climate-contingent keystone species; they amplify biodiversity as long as they stay wet

A modified version of this chapter is *in review* at Journal of Animal Ecology:

Scheffers, B. R., B. Phillips and L.P. Shoo. *In review*. Bird's nest ferns amplify biodiversity: as long as they stay wet.

3.1 Introduction

Tropical rainforests harbor most of the world's terrestrial biodiversity, in part because they are structurally complex, providing niches that span from canopy down to the understory (Ozanne *et al.* 2003). Many of these niches are physical structures derived from plants and therefore are keystone species that serve to promote species diversity through fine-scale habitat creation and amelioration of physical stress (Angelini *et al.* 2011). Unfortunately, the altered climate due to climate change may render these foundational niches uninhabitable through the direct death of living keystone species or through the loss of their ecophysiological functionality. Foundational species are synonymous to keystone species in that they create complex habitat niches in which associated organisms find refuge from biological and physical stress (Angelini *et al.* 2011). The interplay between keystone species, their abiotic environment that they create, and the communities dependent on this abiotic environment is an underappreciated aspect of climate change science (Koh *et al.* 2004).

Epiphytes are plants that grow on other plants; ranging from lichen and moss, to orchid, ferns, vines, and lianas. Given this range of species diversity and the habitat they create, epiphytes comprise a non-trivial component of forest structural complexity, especially in wetter forests. Epiphytes represent a prominent above-ground structure in rainforests and appear to provide shelter for a significant proportion of the invertebrate biodiversity in rainforest canopies (Hietz 1999; Ellwood & Foster 2004; Díaz *et al.* 2012; Fayle *et al.* 2012). One widespread and abundant epiphyte in the Paleotropics of particular note is the *Asplenium* spp. bird's nest fern (BNF) (Holttum 1976). It is the suspended-soil habitats in the BNFs that appears to be so important, with above-ground biodiversity strongly associated with this type of habitat (Ellwood & Foster 2004; Beaulieu *et al.* 2010; Gonçalves-Souza *et al.* 2010; Díaz *et al.* 2012). Indeed, bird's nest ferns may support species in over 27 orders of Arthropods (Ellwood & Foster 2004) and have distinct suspended-soil invertebrate communities from those on the ground (Beaulieu *et al.* 2010). Impressively, a single fern in Bornean rainforests contained twice the invertebrate biomass as its entire host tree (Ellwood & Foster 2004). Thus, these ferns likely represent one of the most important epiphyte groups and above-ground habitats throughout the Paleotropics (Ellwood & Foster 2004).

Although a modest body of research has highlighted the importance of *Asplenium* ferns to arboreal invertebrates and local canopy microclimate, only post-hoc hypotheses have been proposed to explain the mechanisms underlining these patterns. These hypotheses propose that ferns expand canopy space for retreat and nesting, buffer climate, and absorb and therefore serve as a source of moisture (Ellwood, Jones & Foster 2002; Freiberg & Turton 2007; Fayle *et al.* 2012; Scheffers *et al.* 2013a; Scheffers *et al.* in press). For example, ferns in one hectare of forest can contain over one ton of dry biomass (Ellwood, Jones & Foster 2002), invertebrate biomass is related to fern size (Ellwood & Foster 2004), and ferns are consistently moister than the air that surrounds them (Freiberg & Turton 2007), respectively. For the exception of bats (*Cynopterus horsfieldi*), which use ferns as roosting sites (Tan, Akbar & Kunz 1999), not a single study we know of examines whether ferns are used by vertebrates (a fundamental question posed by

Ellwood and Foster (2004)) and none explicitly examine why these ferns are the real estate of choice in tropical rainforest canopies.

Here, I demonstrate that bird's nest ferns also appear to function as a critical canopy microhabitat for a vertebrate group – arboreal frogs. Little is known about this group as they are highly cryptic, nocturnal, and located in the hard-to-access rainforest canopy (Kays & Allison 2001). I surveyed frogs within bird's nest ferns throughout the canopy in a Philippine montane rainforest to explore whether bird's nest ferns function as arboreal refuges for adult frogs, and if they serve as critical breeding habitat for these frogs. I compare fern usage to the surrounding rainforest environment to determine whether ferns are disproportionately used by frogs and therefore may function as a foundation species and/or keystone structures (Dayton 1972; Tews *et al.* 2004). I further examined which fern and surrounding habitat characteristics best predict frog occurrence and abundance within ferns. Last, I test whether ferns provide a more consistent climate than the surrounding rainforest and therefore expand the biotic potential of inhospitable canopy environments. In total, my data suggest that *Asplenium* provide strong protection from temperature extremes and act as critical sources of moisture in the canopy. Further, experimental drying of ferns indicates that the thermal buffering they provide is strongly contingent on their state of hydration, a state that can change very rapidly in the absence of rain.

3.2 Methods

3.2.1 Study area

I surveyed bird's nest ferns on Mt. Banahaw in southern Luzon, Philippines. The site is characterized by lowland dipterocarp forest up to 800 m elevation, dipterocarp and montane forest from 900-1700 m elevation, and mossy and *Pinus* forest above 1700 m elevation. My study was not conducted below 900 m because at lower elevations (<800 m) agriculture has replaced forest. I allowed 100 meters of elevation to buffer any potential effects from these disturbances. The climate is marked by the absence of a distinct dry season with annual rainfall of around 3100 mm yr^{-1} and 85% relative humidity on average (Banaticla & Buot 2005).

3.2.2 Bird's nest fern and paired sampling surveys

I established two 100 m transects at 900, 1100, 1300, 1500, 1700 m (across the altitudinal distribution of bird's nest ferns; Figure 3.1) and recorded each fern observed from my transect line. I used canopy access techniques to access and survey canopy ferns (Jepson 2000).

Each fern was surveyed for frogs and eggs four times during the day starting from May - September, 2011. I sampled during the day as frogs were found in ferns more often during the day than at night. Some ferns were located in dead trees, over cliffs, and/or on dead or thin branches and were therefore too dangerous to survey. These ferns were omitted from my surveys. During each survey, I thoroughly searched each fern, starting at the bottom, working up along its sides, and lastly searching the debris filled bowl located at the top of each fern. During surveys, I also had an observer on the ground watching for frogs that may jump out during our searches.

For each fern surveyed for frogs, I also sampled for frogs in other near-by microhabitats. Paired samples occurred on the same day as ferns surveys. Paired samples varied from two to five locations, and sample size area was always, at a minimum, of equal size to the associated fern. The number of samples varied due to availability of suitable habitats for paired samples.

Paired samples consisted of ground, leaf-litter plots, the trunks of adjacent trees, tree branches and hollows, non-*Asplenium* fern species, vines, moss and epiphytic mats, decaying logs, and *Pandanus* palms, among others. For each paired survey, I sampled the closest available habitat type of similar size and structure.

3.2.3 Ground to canopy tree surveys—frog occurrence in rainforest canopies

I conducted tree canopy surveys for frogs to examine whether they use alternative arboreal habitats. From May – October 2011, I conducted 74 ground-to-canopy tree surveys at each elevation band where populations of *Asplenium* ferns occur. I surveyed a total of 37 trees for amphibians (14 trees at 900 m, 5 at 1100 m, 13 at 1300 m, and 5 at 1500 m elevation). I searched for arboreal frogs in tree holes, moss, epiphytes, and other microhabitat structures and for each frog captured I recorded the microhabitat it used. I recorded the habitat type for each frog as well as if they were exposed or sheltered (within the habitat). Each survey was centered on a single canopy tree. Tree selection was randomized at each elevation; however, each tree had to meet safety standards for arborist single-rope climbing (Jepsen 2000). Tree surveys lasted for one hour and were conducted during the day and repeated at night to account for species with diurnal and nocturnal activity. I alternated surveys along the elevation gradient (low to high to low elevations) to avoid temporal bias in sampling. I recorded the maximum height climbed and tree height for each survey. Climbing to the top of trees is dependent on suitable branches that allow for safe access. Thus, I could not always ascend to 100% of the total tree height. I sampled approximately 75% ± 9 SD of the total tree height across elevations.

3.2.4 Bird's nest fern characteristics

For each fern I collected fern and local habitat characteristics that may affect frog use of ferns. Fern size may influence its ability to stay cool and wet and has been linked to increased richness and abundance of invertebrates (Ellwood & Foster 2004). I measured two metrics that are indicative of a fern's size 1) I determined its area by multiplying the width of the organic mass by its height and 2) I measured the length of the five longest fronds (LL). I quantified local habitat characteristics that may influence frog usage of ferns. I measured the canopy cover above each fern using a spherical densitometer (CC). For each bird's nest fern located within a tree, I recorded tree height and its diameter-at-breast-height (DBH). I also recorded the total epiphyte cover (EPI) for each tree by assigning a score from 0-4 (0: 0%, 1: 1-25%, 2: 26-50%, 3: 51-75%, and 4: 76% and above). I recorded the average moss cover (MOSS) at breast height by recording percent cover within a square, averaged from measurements taken on three sides of the fern's host tree. Justification for the inclusion of fern variables and descriptive statistics are provided in Table 3.1 and 3.2.

Table 3.1. **Definition of seven variables and a justification for their inclusion in this study.**

CODE	Variable definition	Justification
AREA	The height of root mass multiplied by the width of root mass	Size of fern may influence the micro-climate of each fern. Frogs may use large ferns more than small ferns if they remain wetter and cooler.
LL	The leaf/frond length—averaged from five fronds on each fern.	There is a strong positive relationship between fern area and leaf length. Frogs may use large ferns more than small ferns if they remain wetter and cooler.
BNF HGHT	The height of fern above ground	Ferns higher in the forest canopy may be used more than ferns near the ground. The climate outside of micro-habitats is warmer and drier in the canopy and therefore less suitable for frogs.
CC	Index for the amount of leaf cover above	Ferns with more canopy cover may be cooler than ferns with less canopy cover.

	each fern	
TREE DBH	The diameter at breast height of the tree the fern is located in	Tree DBH is used as a proxy for tree size. Larger trees may have more frogs than small trees and therefore might influence the occupancy and abundance of frogs in ferns.
EPI	Epiphyte cover of tree the fern is located in	Epiphytes influence the overall structure and micro-climate of the surrounding environment and may therefore influence the occurrence and abundance of frogs
TREE HGHT	The height of tree the fern is located in	Tree height is used as a proxy for tree size. Tall trees may have more frogs than shorter trees and therefore might influence the occupancy and abundance of frogs in ferns.

Table 3.2. **Summary of habitat and bird's nest fern characteristics. Data are presented as mean (± SD).** AREA is the area of fern (height x width), LL is average leaf length, BNF HGHT is the height of each fern in the canopy, CC is canopy cover directly above each fern, EPI is the epiphyte cover for the tree the fern is attached to, MOSS is the moss cover on each tree the fern is attached to, TREE HGHT is the height of each fern's tree, and DBH is the diameter at breast height of each fern's tree. Values for EPI, MOSS, TREE HGHT, and DBH exclude all ferns located on the ground.

Variable	Mean (SD)
AREA (cm^2)	832 (1161)
LL (cm)	52 (24)
BNF HGHT (m)	3.1 (3.5)
CC (%)	71 (15)
EPI (1-4)	2.5 (1.2)
MOSS (%)	44 (35)
TREE HGHT (m)	7.4 (3.8)
DBH (cm)	25 (23)

3.2.5 Garden Experiments—link between temperature buffering and precipitation

I assessed the relationship between thermal buffering and precipitation in bird's nest ferns through drying experiments. I removed nine ferns of varying sizes, from small to large, and wrapped the root mass in nylon mesh (to retain all roots, humus, and other debris) and suspended the ferns approximately 1.5 m above the ground with rope. I derived dry mass for each fern by drying them until mass was no longer lost. I then continuously watered each fern until water leaked through the sides and bottom of the root mass. Ferns were protected with a clear plastic tarpaulin that was elevated a few meters above the ferns to allow normal transpiration and drying, and to prevent rain from re-wetting the ferns. Ferns were weighed three times daily for 20 days. The dry mass was subtracted from wet mass recorded on each day to determine the total volume of water in each fern. I considered the total mass lost since initial wetting to be equal to the total volume of water lost from each fern, by assuming the weight change due to photosynthesis and respiration during the experiment to be negligible.

During the drying experiment, I also examined within-fern temperatures relative to ambient temperature directly above the fern. I did so by placing a single temperature logger (Maxim Hygrochron ibutton Model DS1923; http://www.maxim-ic.com/) in the central bowl of each fern. Paired loggers were placed approximately 0.5 m above each fern and suspended under a plastic funnel to shelter them from direct solar radiation.

3.2.6 Analysis—predictors of abundance

I derived a total abundance metric by summing the total number of frogs with the total number of egg masses and dividing by the total number of surveys. Path analysis was used as I was interested in the relationships among predictor variables and total abundance. I designated bird’s nest fern area (BNF AREA), height of fern (BNF HGHT), canopy cover above fern (CC), diameter at breast height of fern’s tree (TREE DBH), tree height (Tree HGHT) and epiphyte cover of fern’s tree (EPI) as predictors of abundance. Prior to analysis, I standardized all variables to a mean of zero and standard deviation of approximately 1. I created a four “layer” multiple regression analysis; “layer 1” had DBH, CC, EPI, and TREE HGHT as predictors and BNF HGHT as the response variable; “layer 2” had BNF HGHT predicting AREA; “layer 3” had AREA predicting total abundance and “layer 4” had AREA, BNF HGHT, CC, DBH, EPI, and TREE HGHT as predictors and total abundances as the response variable. Leaf length (LL) and moss cover (MOSS) were removed from analysis due to their correlation with other variables (Table 3.3). Lastly, I provide a summary of variables that best predict occurrence in Table 3.1.

Table 3.3. **A split plot correlation table among 10 variables sampled at 150 bird's nest ferns in the Philippines.** Spearman rho statistics are displayed above the dotted diagonal and p-values are displayed below the dotted diagonal. Spearman rho r > 0.4 are considered significant with corresponding p-values ≤ 0.001 in bold. All variables are defined in Tables 3.1 except for 'Leaf Num' which represents the number of leaves for each fern.

	CC	AREA	LFNUM	LL	BNF HGHT	MOSS	EPI	DBH	TREE HGHT
CC	*****	-0.388	-0.268	-0.273	-0.455	-0.085	-0.276	-0.331	-0.393
AREA	**<0.001**	*****	0.583	0.839	0.443	0.205	0.273	0.399	0.413
LFNUM	0.001	**<0.001**	*****	0.714	0.326	0.067	0.144	0.07	0.179
LL	0.001	**<0.001**	**<0.001**	*****	0.303	0.086	0.172	0.229	0.276
BNF HGHT	**<0.001**	**<0.001**	**<0.001**	**<0.001**	*****	0.333	0.309	0.433	0.617
MOSS	0.304	0.012	0.418	0.293	**<0.001**	*****	0.482	0.397	0.377
EPI	0.001	0.001	0.078	0.035	**<0.001**	**<0.001**	*****	0.55	0.453
DBH	**<0.001**	**<0.001**	0.392	0.005	**<0.001**	**<0.001**	**<0.001**	*****	0.675
TREE HGHT	**<0.001**	**<0.001**	0.029	0.001	**<0.001**	**<0.001**	**<0.001**	**<0.001**	*****

3.2.7 Predictors of occurrence

I used random forest to examine which variables best predict frog occurrence. The relative importance of each variable in predicting occurrence (frog and egg occurrence combined) was determined using regression tree analysis. I used Breiman's random forest algorithm from the package *randomForest* in R stats version 2.15.1 (R Project for Statistical Computing, http://www.r-project.org). I chose random forest analysis because it is robust to interactions and correlations among variables, and does not over fit the data (Ranganathan & Borges 2009). For random forest analysis, the prediction error on the out-of-bag portion of the data was determined and then repeated for each predictor variable. The difference between the two were then averaged over all trees, and normalized by the standard deviation of the differences. The node impurity was measured by the Gini index. I designated bird's nest fern area (AREA), height of fern (BNF HGHT), canopy cover above fern (CC), diameter at breast height of fern's tree (TREE DBH), and epiphyte cover of fern's tree (EPI) as predictors of occurrence (justification and statistics for each variable is provided in Table 3.1 and 3.2).

3.2.8 Temperature buffering and precipitation between fern and ambient

For all nine ferns I plotted the total water remaining and the proportion of water remaining for each day. Water remaining is derived by subtracting fern dry weight from total weight (wet and dry). For six of the nine ferns, I determined the difference in maximum temperature and difference in the coefficient of variation in temperature from the paired ambient loggers. Coefficient of variation (CV) is a normalized measure of dispersion that is calculated as the ratio of the standard deviation to the mean. When subtracting the ambient CV from fern CV, positive numbers indicate a more stable temperature within the fern relative to ambient. I used analysis of covariance (ANCOVA) to model differences in temperature maximums and CV with fern as a factor and days since watering as a covariate. Lastly, I used pairwise comparisons of means via Tukey contrasts on the variables in order to determine which groups of ferns differ from each other.

3.3 Results

3.3.1 Distribution of BNFs by elevation

The distribution of BNFs followed a left skewed distribution with highest abundance at 1500 m. The abundance of BNFs declined sharply above 1500 m as only two BNFs were found at 1700 m and no ferns were found at 1900 and 2100 m (Fig 3.1).

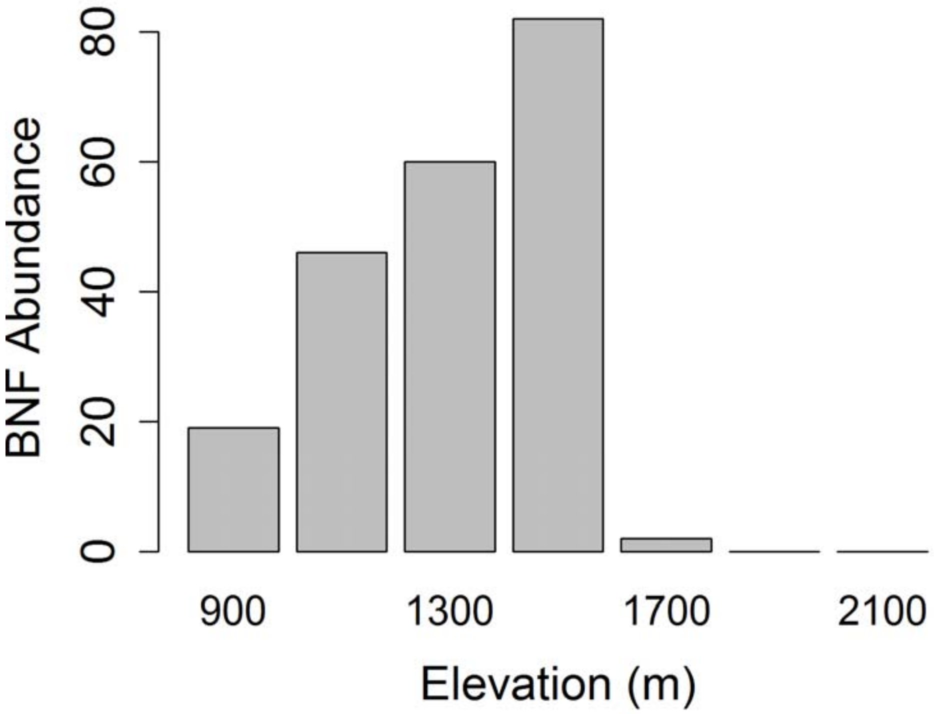

Figure. 3.1. **The abundance of BNFs by elevation is left skewed with a steep drop in abundance at 1700 m.** Data are compiled from two 100 m long transects surveyed at each elevation on Mt. Banahaw, the Philippines..

3.3.2 Frog abundance and richness in bird's nest ferns

Adult frogs used ferns as microhabitats and breeding habitats (Figure 3.2 and Table 3.4). Of the 150 ferns surveyed, five frog species, *Philautus surdus*, *Platymantis luzonensis*, *P. banahao*, *P. montanus*, and *Polypedates leucomystax,* were found within ferns. Ferns were occupied by *P. luzonensis* at 900 m, *P. luzonensis* and *P. surdus* at 1100 m, *P. surdus* and *P. banahao*, and at 1300 m, *P. banahao*, and *P. montanus*, at 1500 m, and *P. montanus*, at 1700 m. Abundance ranged from 0 to 5 and 0 to 6 for adults and egg clutches, respectively. One bird's nest fern surveyed prior to the start of my study contained 9 adults and 12 clutches of eggs. I also observed an individual *P. luzonensis* reside in a large bird's nest fern, checked multiple times a day, over four days in succession.

Table 3.4. The occurrence of frog adults and eggs (combined) in BNFs was 53%. Conversely, the occurrence of frog adults and eggs (combined) in paired random samples was 9%. BNF and paired habitats were sampled from 900 to 1700 m on Mt. Banahaw the Philippines from May to September, 2011. For each BNF, areas of equal size (minimum) to the associated fern were sampled at two to five locations. Paired samples consisted of ground leaf litter, tree branches and hollows, non-*Asplenium* fern species, vines, moss and epiphytic mats, decaying logs, and *Pandanus* palms, among others. Adult and egg abundance are the total number of individuals observed across all samples. Occupied indicates the habitats (i.e., fern or pair) which were occupied after four surveys. Total occupied was the total number of sampled habitats that had frogs and/or eggs present.

Variable	BNF total	Pair total
Total sampled	**150**	**953**
Adult Abundance	**39**	**9**
Egg Clutch Abundance	**62**	**0**
Occupied (Adults)	**30**	**9**
Occupied (Egg Clutches)	**35**	**0**
Total Occupied	**53**	**9**
	(avg.)	(avg.)
Adult Proportion	(0.20)	(0.006)
Egg Proportion	(0.23)	0
Combined Proportion	(0.35)	(0.006)

Figure 3.2 (A) A pair of bird's nest ferns in the rainforest canopy on Mt. Banahaw, the Philippines; (B) an exposed male *Platymantis luzonensis* sitting on the frond of a fern; (C) a sheltered female and male *Platymantis banahao* in amplexus within a bird's nest fern; and (D) a clutch of eggs (marked by the arrow) within a bird's nest fern (subset photo shows a single egg).

Assuming that frog detectability was constant across survey locations, my data suggested that BNFs were on average 58 times more likely to have frogs and/or their eggs present during the day than a random sample of equivalent area from the forest (Table 3.4). BNFs served as habitat for adults but also serve as breeding habitat for arboreal frogs. Of the two species of frogs for which eggs could be located, *P. luzonensis* (distribution below 1100 m) and *P. banahao* (distribution from 1100 to ~1600 m), I found that eggs were present in approximately one in five ferns, whereas no eggs were found in randomly sampled microhabitats adjacent to BNFs (i.e. were exclusively laid within BNFs, Table 3.4).

3.3.3 Predictors of frog abundance

The path analysis suggested that canopy cover was negatively related to abundance, even after accounting for its negative impact on BNF height and area (Figure. 3.3). BNF area positively predicted abundance with tree and BNF height influencing frog abundance indirectly through its positive effect on BNF area (Figure. 3.3). Tree diameter-at-breast height (Tree DBH) and surrounding epiphyte cover (EPI) had no effect on frog abundance or fern size (Figure. 3.3). Fern size, canopy cover and fern height were all correlated (Table 3.3). Larger BNFs are found higher up in the forest stratum and under sparser canopy cover (Table 3.3).

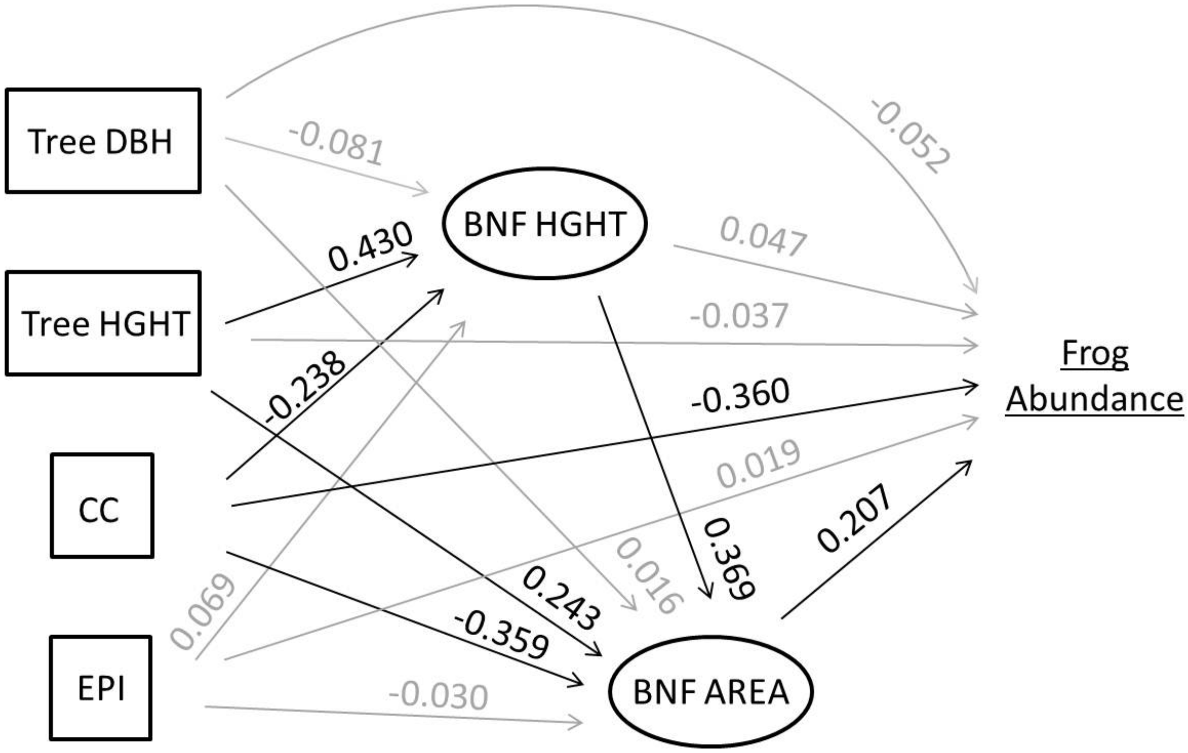

Figure 3.3 Path analysis showing relationships between habitat variables and total frog abundance (eggs and adults) within bird's nest ferns. Variables are defined in Table 3.1. Dark arrows indicate significant relationships (p-value < 0.5) and grey arrows indicate non-significant relationships. Numbers along arrows represent the coefficients and the direction of the relationship.

3.3.4 Predictors of frog occurrence

I examined six predictors of frog and egg occurrence (combined) within BNFs using randomforests models. My analyses suggested that fern size and height in the forest stratum positively predicted frog occurrence whereas canopy cover negatively predicted frog occurrence (Figure. 3.4). Epiphyte cover had a small effect on frog occurrence within ferns (Figure. 3.4).

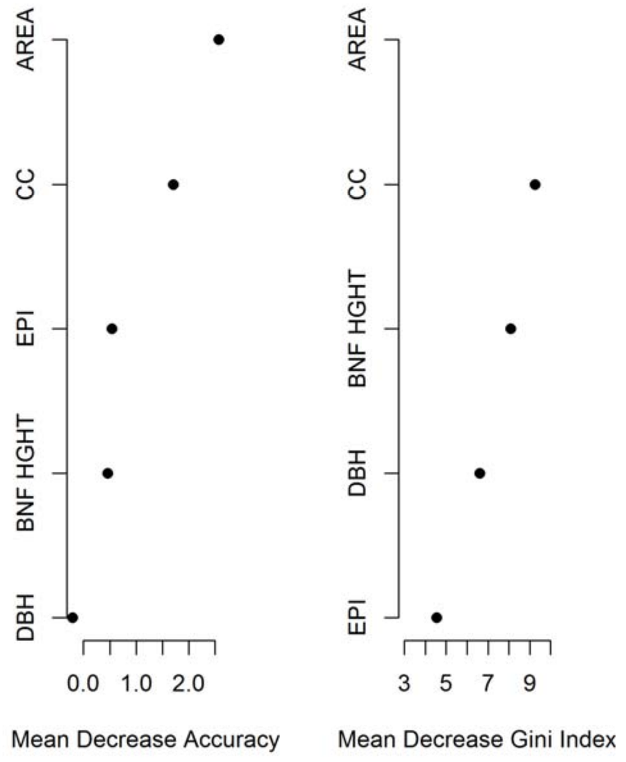

Figure. 3.4 Variable importance values in predicting the occurrence of frogs in BNFs using Random Forests classification. The best predictors of occurrence based on the mean decrease in accuracy of each model (after removing each variable) (left) and the mean decrease in Gini index (right) for all surveyed bird's nest ferns. Values are arranged in increasing importance from left to right along the x-axis. For random forest analysis, the prediction error on the out-of-bag portion of the data is determined and then repeated for each predictor variable. The difference between the two are then averaged over all trees, and normalized by the standard deviation of the differences. Variables on Y-axis are defined in Table 3.1.

3.3.5 Complimentary arboreal surveys

To explore whether frogs use other habitats in the rainforest canopy, I conducted canopy day and night surveys for adult frogs across the elevation range of bird's nest ferns . During these extensive broad area surveys, I found 51 frogs in the forest canopy of which 10 (20%) were found during daytime surveys. Of 41 frogs found at night, 34 were found in exposed habitats and four (11%) were found in sheltered habitats (Table 3.5). Three individuals did not have habitat data recorded. Conversely, 10 frogs were found during the day, all of which were in sheltered habitats (Table 3.5). Two (5%) frogs from night surveys were sheltered within BNFs compared to six during the day (60%). The remaining frogs were found on broad leaves, within or on moss and epiphytic mats, crevices and organic detritus, among others (Table 3.5).

Table 3.5. **The number of adults found during canopy surveys (day and night) in 37 trees from 900 to 1500 m (14 trees at 900 m, 5 at 1100 m, 13 at 1300 m, 5 at 1500 m elevation).** Sheltered indicates that individuals were found within the habitat and therefore not exposed to ambient air.

Habitat Type	Night	Night Sheltered	Day	Day Sheltered
Broad leaf	14	0	0	0
Vine	7	0	0	0
Tree bark	5	0	0	0
Other epiphyte	4	0	0	0
BNF	3	2	6	6
Crevice with Detritus	2	2	3	3
Branch	1	0	0	0
Moss	1	0	1	1
Pandanus	1	0	0	0
NA	3	0	0	0
Total	41	4	10	10

3.3.6 Garden Experiments

Bird's nest ferns had a large capacity to absorb water: water increased fern weight by around 52 % (± 7 SD) across all fern sizes. Ferns retained over 30% of their water for 8-13 days

(Figure 3.5). The ability of ferns to buffer maximum temperatures and reduce variability in temperatures is directly linked to their hydration (Figure 3.5). The slope of the relationship between delta Tmax or delta CV and days since watering was similar among ferns despite their varying weight (delta Tmax: df=5, *F*=1.074, *P* =0.379; delta CV: df=5, *F*=1.498, *P* =0.197). Removal of the interaction term did not significantly affect the fit of either model (*F*=1.0729, *P* =0.3791 and *F*=1.498, *P* =0.1967 for delta Tmax and delta CV, respectively). The more parsimonious models with the interaction term removed revealed a significant effect of days since watering and fern on both delta Tmax and delta CV (in both cases, days since water *P* <0.001 and fern *P* <0.001). Post-hoc Tukey tests indicated that the main difference was between two of the three largest ferns (>4000g) and all other ferns, the former approaching ambient conditions more slowly.

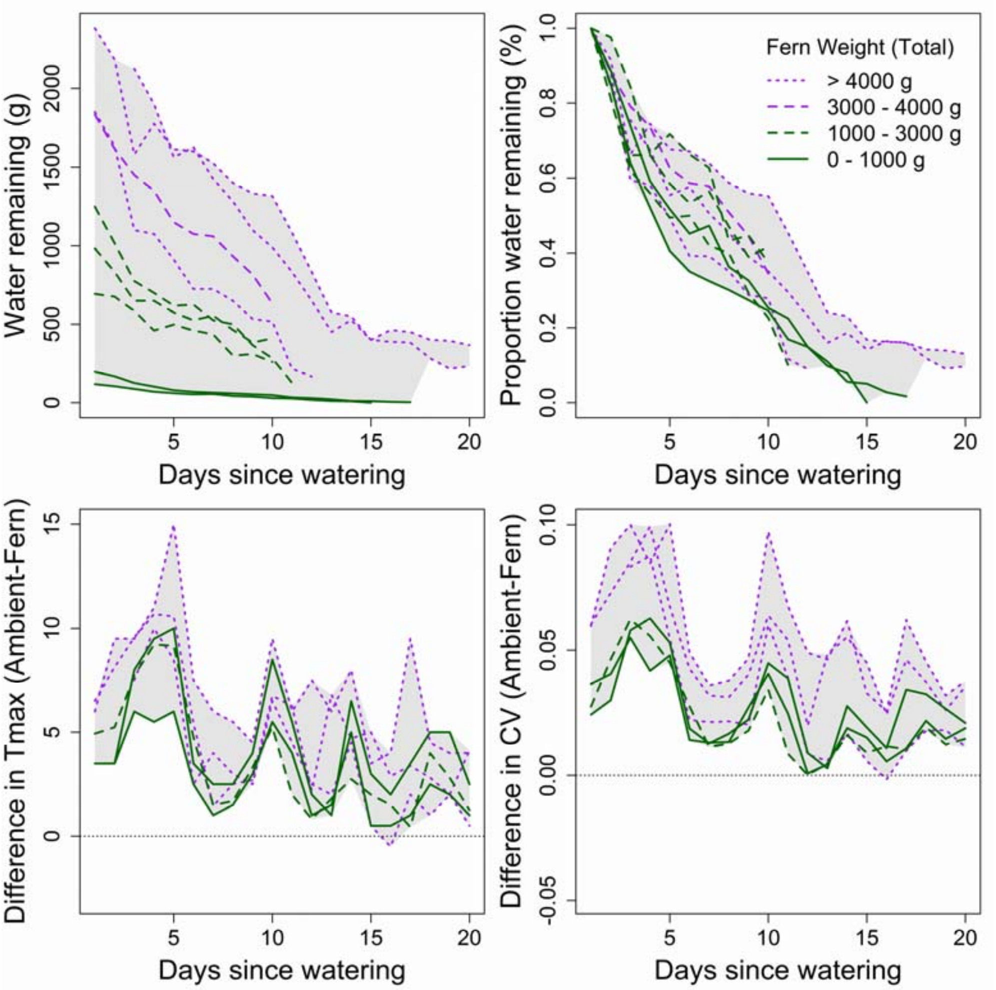

Figure 3.5 The total water weight (top left), proportion of water remaining (top right) and thermal buffering of bird's nest ferns (lower left and right). Water weight was monitored in ten ferns over a 20 day period of no exposure to rain following complete saturation. Temperature was monitored in six of the ten ferns. Difference in maximum temperature and in coefficient of variation from ferns and paired ambient are shown as ferns dry. Positive differences in maximum temperature and the coefficient of variation (y-axis) indicate that ferns had cooler and less variable temperature than ambient. The bigger the difference in coefficient of variance the greater the fern's capacity to buffer temperature. Ferns are grouped and colored by total fern weight (dry and wet).

3.4 Discussion

3.4.1 Frogs and ferns in the rainforest canopy

Bird's nest ferns are one of the most widely distributed and ecologically important epiphytes in the Paleotropics (Ellwood & Foster 2004). Yet, much of their importance is understood from only a few key studies that are focused on invertebrate communities. My study has documented a novel frog-fern relationship: bird's nest ferns serve as an important above-ground refuge and a critical breeding habitat for arboreal frogs in my study site. Whether these ferns serve as important habitats for frogs elsewhere in the Philippines and throughout the Paleotropics remains unknown. My study does provide evidence that *Asplenium* ferns are used by a broader range of animals than previously documented. The results of my study compliment a growing literature that points to ferns as biodiversity and biomass amplifiers. My study shows strong dependence of *Asplenium* ferns across frog life-history stages and it is likely that many species have a critical reliance on these aerial structures, and that, without them, would not persist (Angelini *et al.* 2011). This is particularly true for a large suite of canopy dwelling ectothermic animals (e.g., invertebrates; Ellwood and Foster (2004); Karasawa (2008); Beaulieu *et al.* (2010)) that partition space in the hot and dry canopy to remain at optimal climates (Huey *et al.* 2012).

Knowledge of arboreal habitat use by frogs is limited due to the cryptic nature of frogs as well as the difficulty in accessing canopy habitats (Kays & Allison 2001). Canopy surveys in my study area show that almost 80% of all frogs in my study site are found above-ground (Scheffers *et al.* 2013c). Yet, frogs are temperature sensitive and hydrophilic which begs the question: how are such high abundances maintained in the relatively hot, dry canopy environment?

The most likely mechanism for this frog-fern relationship and for why ferns promote diversity in rainforest canopies is that they create small-scale temperature and moisture refuges and so buffer sensitive ectotherms from excesses of heat and desiccation (Chapters 4 and 5). In my study, this micro-refugia interpretation was supported in three ways: 1) patterns of occupancy in day versus night surveys (see Table 3.4 in Supporting Information); 2) through the environmental characteristics that best predict occupancy and abundance of frogs in BNFs, and 3) by direct observation and experimental data on the microclimates fostered by BNFs.

3.4.2 Day versus night

This is the first study for any taxon to examine the use of *Asplenium* between night and day, and the results are revealing. My day/night comparisons clearly show that ferns function as diurnal retreat sites in the canopy: 60% of all frogs found in day ground to canopy surveys were located within ferns with the remainder located in crevices with detritus or moss. When I further examined daytime use of ferns using a paired sampling design, ferns surveyed along transects during the day were on average 58 times more likely to be used by frogs than a paired random sample in the forest. Moreover, all five arboreal frog species from my study area used ferns as diurnal retreats and two of these (*P. luzonensis and P. banahao*) species may be obligate bird's nest fern breeders: I did not locate a single clutch of eggs outside of BNFs during my fern transect surveys nor during canopy surveys. Despite this high fern usage in the day, adult frogs clearly move out of BNFs at night: only 5 % of frogs in the night surveys were found in ferns. Given that the extremes of heat and desiccation occur mostly during the day, these observations suggest that the disproportionate use of BNFs by adult frogs during the day provides strong circumstantial evidence in support for my microhabitat hypothesis. This evidence is strengthened further when I examine the microhabitat characteristics that predict frog usage.

3.4.3 Fern characteristics that best predict frog usage

Ferns occurring at greater heights tend to be larger and occur under less canopy cover. Bigger ferns had the highest abundances of frogs. These results mirror those of Ellwood and

Foster (2004) who show a strong positive relationship between the number of leaves on a fern (i.e., indicative of size) and invertebrate biomass. As canopy cover above ferns increased, frog abundance decreased. This pattern remains applicable even after accounting for canopy cover's negative impact on BNF area. A similar pattern was observed in Brazil, where epiphytic bromeliads located in habitats exposed to the sun were more frequently occupied by frogs than habitats located in the shade (Silva, Carvalho & Bittencourt-Silva 2011). Higher canopy cover may lower temperature and evaporation, thereby diminishing dependence on the buffering effect afforded by BNFs. Alternatively, places that are warmer in the afternoon and evening (i.e., places with low canopy cover) may be favorable, but these places, without the buffering provided by ferns may also be inhospitable during the middle of the day. I also examined other possible factors that might impact the abundance of frogs within ferns, such as surrounding epiphyte cover and tree diameter size, but none of these were found to play a significant role.

3.4.4 Micro-climatic environment within ferns

By monitoring fern climate within the rainforest canopy as well as directly manipulating ferns' abiotic conditions, I show that BNFs reduce temperature variation (also see Turner and Foster (2006); Scheffers *et al.* (2013a)) and that BNFs within my study area can store water for almost two weeks. These results are consistent with those of others: bird's nest ferns in Australia and Singapore have also been shown to retain water (see Kluge (1989); Freiberg and Turton (2007)). Importantly, however, my experiment shows that this capacity to retain water is strongly contingent on the size of the fern (in turn, the major predictor of frog occupancy and abundance). Thus, I suspect frogs developed a proclivity for laying eggs in ferns because they not only provide ample above-ground space (Fayle *et al.* 2012) for laying eggs but also provide a climate controlled environment for development that is more stable than external conditions. In this respect, bigger ferns provide a better buffer than their smaller conspecifics.

Further, my experiment clearly demonstrated that the temperature buffering ability of ferns is strongly contingent on their hydration status, and that big ferns dry out more slowly than small ferns. But ferns in my study area likely remain moist almost constantly (the longest consecutive time without precipitation in our study area was 9 days over the course of 7 months: Scheffers, unpub. data). Thus while temperature buffering and shelter from desiccation serve as the most likely explanations for why ferns harbor significant biodiversity in the canopy, these capacities are strongly dependent on regular rainfall.

3.5 Conclusion

3.5.1 The role of bird's nest ferns in thermal ecology, arboreality and species distributions

My work identifies a direct link between fern size (the primary predictor of frog abundance) and temperature and moisture. This link suggests that the presence of smaller scale climate controlled epiphytes collectively expand the availability of useable space in the harsh rainforest canopy. The relatively hot and dry canopy is unsuitable for most species of frog unless they are behaviorally or physiologically well-adapted (Tracy, Christian & Tracy 2010). I show that the use of BNFs by frogs as daytime refuges is one such adaptation: frogs that utilize BNFs can evade the daytime canopy environment while minimizing the energetic costs of daily movements between suitable daytime refuges and optimal night time foraging areas (Stewart 1995; Vickers, Manicom & Schwarzkopf 2011). Levels of arboreality in many organisms may prove to be strongly linked to the presence of suitable arboreal habitats such as bird's nest ferns.

The strong dependence on ferns by multiple life-history stages of *P. luzonensis* and *P. banahao* in my study area suggest that microhabitats may play an important role in determining distribution both within and across the rainforest landscape. Ferns in the rainforest canopy expand vertical height distributions of frogs but may also play an important role in determining species' distributions across a broader geographic range as has been found for other microhabitats (Monasterio *et al.* 2011). This is especially true when there is strong dependence on ferns for egg and larval development. The loss of a single life-history stage may threaten the long-term persistence of populations—consequently influencing landscape scale distributions. For example, the distribution of at least one of the species, *P. banahao*, exactly mirrors the upper distribution of bird's nest ferns: both stop at 1650 m asl. Thus, this frog-fern relationship operates along both vertical (e.g., forest height) and horizontal (e.g., landscape and elevational) planes. This multidimensional habitat usage complicates predictions of species distributions and inference made from modeled projections of future climate.

3.5.2 Bird's nest ferns as climate refuges

My study shows a link between precipitation and temperature buffering in arboreal microhabitats. The buffering capacity of ferns expands the thermal habitat tolerances of fern-obligate frogs in my study area by 8.5 ˚C (Scheffers *et al.* 2013a) and reduces their exposure to climate extremes by over 30 fold (Scheffers *et al.* in press), yet my study suggests that this expansion in tolerance and reduction in vulnerability will largely be dependent on precipitation. This link indicates that warming is not required to threaten canopy communities because changes in precipitation alone can remove the buffering capacity of canopy ferns making even contemporary temperatures inhospitable in the rainforest canopy. This is an important consideration because current climate models project extreme warming as well as strong reductions in or increased stochasticity of rainfall in some areas (Meehl & Tebaldi 2004; Fischer & Knutti 2013). Changes in precipitation can increase extirpation risk of montane species by 10-fold (McCain & Colwell 2011). Therefore, although ferns effectively serve as thermal buffers, these buffering properties are only applicable if minimum inputs from precipitation are maintained. Two possible scenarios might occur if extreme changes occur in weather: 1) the ferns themselves die (periods longer than eight weeks of no rain can kill ferns: Freiberg and Turton (2007)); or 2) the ferns survive but lose their buffering capabilities from sporadic small drought events. The loss of these biotic amplifiers would result in an overall attrition in canopy biodiversity as organisms would likely need to shift towards the ground (Scheffers *et al.* 2013c) as has been observed for frog communities during El Niño events in Papua New Guinea (Bickford 2005). This increased density at ground levels may lead to local population decline across animal communities from competition and density-dependent mortality (Patrick *et al.* 2008; Green & Middleton 2013).

Bird's nest ferns effectively buffer contemporary climate and thus serve as a keystone species in rainforest canopies. The strong link between climate buffering and precipitation however suggests that fern dependent communities might be especially vulnerable under extreme weather events.

Chapter 4: Thermal buffering of microhabitats is a critical factor mediating warming vulnerability of frogs in the Philippine biodiversity hotspot

A modified version of this chapter is published:

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4.1 Introduction

Global climate change will undoubtedly threaten biodiversity (Williams, Bolitho & Fox 2003; Thomas *et al.* 2004). Climate warming has triggered numerous ecological responses (Parmesan 2006) that include species range shifts (Chen *et al.* 2011), decreased fitness in adults and offspring (Derocher *et al.* 2004), and even a global reduction in species' body size (Sheridan & Bickford 2011). Also relevant are animals' physiological constraints to temperature (Bernardo *et al.* 2007; Calosi, Bilton & Spicer 2008). Many species have highly defined thermal optima with limited potential to acclimate to elevated temperatures (Tewksbury, Huey & Deutsch 2008; Huey *et al.* 2009). If temperatures continue to rise as predicted (Sokolov *et al.* 2009), many species, particularly ectotherms, will experience detrimental, if not fatal, physiological responses (Sinervo *et al.* 2010).

Physiological upper thermal limits are expected to increase at a slower rate than environmental temperatures (Compton *et al.* 2007; Deutsch *et al.* 2008; Huey & Tewksbury 2009). As such, many ectothermic species from tropical areas face high risks of extinction due to climate change (Compton *et al.* 2007; Deutsch *et al.* 2008; Tewksbury, Huey & Deutsch 2008;

Sinervo *et al.* 2010), especially if they are unable to find refuge from extreme temperatures (Shoo *et al.* 2011b). Cool refugia serve as thermal buffers, and may allow species with relatively low thermal tolerances living in hot habitats to evade exposure to life-threatening temperatures (Kearney, Shine & Porter 2009; Shoo *et al.* 2010) [thermal tolerances are calculated by subtracting the maximum environmental temperature that a species experiences (T_{max}) from the temperature at which an individual loses normal motor functions *i.e.,* critical thermal maximum (CT_{max})]. Whether or not habitats effectively buffer against hot temperatures remains relatively unknown, and a better understanding will provide important implications for conservation management and climate change mitigation strategies.

Under an integrated framework for assessing the vulnerability of species to climate change, factors that determine exposure and govern sensitivity must be identified (Williams *et al.* 2008; Shoo *et al.* 2011a). Traits that are intrinsic to a species (*e.g.,* CT_{max}) and factors that are extrinsic to a species (*e.g.,* T_{max}) are strong determinants of its sensitivity to climate warming. Under this premise, understanding both sensitivity and exposure in unison is critical for evaluating future warming tolerance and prioritizing conservation actions under climate change (Williams *et al.* 2008; Shoo *et al.* 2011a). To date, however, little research exists in way of identifying these two key components for assessing vulnerability to climate warming, especially in the understudied tropics of SE Asia.

Under the premise that the vulnerability of a species to climate warming is directly tied to its sensitivity and the exposure it experiences in its habitat (Williams *et al.* 2008), I derived two primary goals for my study: (1) identify the critical thermal maximum of frog larvae from four distinct breeding habitats (*i.e.,* sensitivity), and (2) identify the extent to which breeding habitats used by frogs (specifically the larval life-history stage) buffer ambient temperature (*i.e.,* exposure). Based on these two metrics, I can deduce the vulnerability of specific life-history stages to future warming, which I hereafter term ‘warming vulnerability’. I conducted my study in the Philippines—an archipelago with some of the highest species richness and endemism per area on earth (Myers *et al.* 2000). I chose an isolated mountain site, Mt. Banahaw (approximately 10,000 ha) in Luzon, to examine the thermal tolerance of larvae for five endemic frog species. No study to date, however, has examined potential sensitivities of amphibians to climate warming in the Philippines. My study location is completely isolated from other contiguous mountain ranges (*e.g.,* Sierra Madres in the northern Philippines). Consequently, species at this mountain site have limited options for evading climate warming via dispersal.

Lastly, the majority of literature regarding thermal tolerances of ectotherms is derived from adult life-history stages. Since amphibians undergo multiple life-history stages, threats (*e.g.,* hot temperatures) that may not threaten one life-history stage may dramatically affect another (Becker *et al.* 2007). Thus, I also fill an important gap in the literature on tropical ectotherms by considering multiple life-history stages for two locally endemic frogs in my study (Duarte *et al.* 2012).

4.2 METHODS

4.2.1 Study region

The Philippines is recognized as an important global biodiversity hotspot, due to its exceptionally rich endemic fauna (Diesmos & Brown 2011). Almost 80% of its amphibians and reptiles are found nowhere else in the world. However, because the majority of these species are forest-dependent, they are highly threatened by loss of primary forest cover, which has been reduced by 63% during the 20th century (Heaney & Ragalado 1998). Due to extensive clearing of lowland forest, the little forested habitat that remains is confined to mountains (Peh *et al.* 2011).

I conducted my study on Mt. Banahaw in southern Luzon, the largest island in the Philippines. The site is characterized by lowland dipterocarp forest up to 800 m, dipterocarp and montane forest from 900-1700 m and mossy and *Pinus* forest above 1700 m (Mallari *et al.* 2001). The topography of my study area in the Philippines is characterized by moderate to steep terrain and sandy clay loam soil (Banaticla & Buot 2005). The climate is marked by the absence of a distinct dry season with annual rainfall around 3100 mm and 85% relative humidity (Banaticla & Buot 2005).

4.2.2 Study species and larvae type

Amphibians undergo varying modes of reproduction (Duellman & Lizana 1994); depending on the species, one mode may be more or less susceptible to climate warming. The two dominant modes of development in my study area are reproduction via eggs deposited in water that develop through multiple tadpole stages (*e.g.,* see Gosner (1960)) and direct development, whereby frogs lay eggs in terrestrial jelly-like clutches with no free-living larval stage (*e.g.,* see Townsend and Stewart (1985)). In my study area, nine stream and two phytotelm ("tree hole") breeding frog species reproduce via aquatic tadpoles, and six terrestrial frog species reproduce via direct-developing eggs. Of the seventeen species available, I chose to use five species that used the four unique breeding habitats, represented both reproductive methods and were reliably encountered in my study area.

For this study, I identified the CT_{max} for larvae of these five species of frogs collected in tropical montane forest (900-1300 m asl) between the months of May and September, 2011. I identified four unique breeding habitats and chose one or more species that utilize each habitat: (1) Bird's nest fern (BNF) breeders: direct-developing eggs laid by *Platymantis banahao* in *Asplenium* bird's nest ferns. BNFs collect canopy debris due to their circular frond orientation and thus serve as a large area of above-ground humic soil. This fern-dependent frog species is endemic to Mt. Banahaw and occurs from 1100 m to a maximum of 1600 m asl within my study area; (2) Leaf breeders: direct-developing eggs laid on exposed leaves by *P. montanus*. This is a parental care species whereby males guard and incubate eggs at night. Clutches are typically laid on the surface of a broad-leaf at approximately 1 m above-ground. This species is endemic to Mt. Banahaw and occurs from 1250 m to 1900 m asl; (3) Phytotelm breeders: *Kaloula kalingensis* tadpoles found in phytotelmata. The phytotelm environment is typically a tree hole that forms a small pocket of water of varying depths, ranging from almost dry to several centimeters deep, depending on rainfall. This species is endemic to the Philippines and occurs from 50 m to 1600 m asl; and (4) Stream breeders: tadpoles of two species (*Sanguirana luzonensis* and *Kaloula walteri*). The stream environment is characterized by aquatic pools that vary greatly in depth (from 12 cm to >200 cm), size (from 0.5 m to ~8 m wide), and flow depending on recent rainfall. Deep pools maintain relatively constant water depths throughout the year. *Sanguirana luzonensis* occurs from 0 m to 2000 m and *Kaloula walteri* occurs from 50 m to 900 m; both species are endemic to the Philippines (Diesmos & Brown 2011). I collected larvae of each species from six birdnest ferns, two phytotelmata, two exposed leaves, and four stream pools.

4.2.3 Critical thermal maximums

In order to stabilize CT_{max}, all field sampled tadpoles and direct-developer eggs were acclimated to a constant 22˚C at my field base camp at 1100 m for a minimum of four days. This was a conservative time period for stabilizing CT_{max} (Hutchison 1961; Brattstrom 1968). Because CT_{max} estimates may vary as a function of methodology, I standardized CT_{max} estimates for all species experimented on in this study. Tadpoles were housed in an aquarium and fed lettuce leaf and crickets *ad libitum*. I maintained eggs by separating them in shared containers by clutch and sprayed eggs with water on a daily basis to avoid desiccation.

The critical thermal maxima of ectothermic vertebrates provides a useful index for the thermal constraints of animals (Hutchison 1961; Hutchinson & Dupré 1992). I obtained upper critical thermal tolerances via Hutchinson dynamic methods (Lutterschmidt & Hutchison 1997b), whereby each individual was exposed to a constant temperature increase of 0.5˚C/min until muscular spasms were observed. A spasm was defined as the combination of head over tail movement and/or lateral rotations while swimming or suspended in the egg. Heating experiments were conducted using a generator-run incubator.

Tadpoles were placed in individual containers filled with 60 ml of water and were gradually heated inside the incubator. I ended the experiment as soon as I observed muscular spasms. A k-type thermocouple temperature sensor (Extech, model #421502) was placed inside the container to record water temperature. Tadpoles were placed in a water-filled container at ambient temperature immediately following CT_{max} in order to recover. Placed in individual containers, direct-developing eggs were gradually heated in the incubator until the onset of spasms. A k-type thermocouple temperature sensor was placed just beneath the jelly coating of the egg to record temperature. Following muscular spasms, I removed eggs from the incubator, sprayed them with water and allowed them cool at ambient temperature. Mass was recorded for all tadpoles and eggs prior to each experiment. I only included tadpoles between Gosner stages 26 and 38 (with the only variation being slight differences in limb development) (Gosner 1960) and direct-developer eggs between stage 9 and 12 (Townsend & Stewart 1985). Our staging criteria were equivalent for tadpoles and direct-developer eggs. Each individual was tested only once, and data from individuals that died (N = 7) during experimentation were not included in analyses. Following heating experiments, all individuals were housed in a holding tank for 1-2 days and released.

4.2.4 Metamorph and adult life-history stages

In order to determine whether warming vulnerability varies by life-history stage, I repeated my heating experiments for metamorph and adult individuals for the two direct-developer species, *P. banahao* and *P. montanus*, as: (1) they are locally endemic to Mt. Banahaw and their ranges are therefore constrained to high elevations, (2) I observed that these two species were likely most vulnerable to increased temperature based on initial observations, and (3) behaviors such as parental care in direct-developer species may help circumvent high temperatures (*e.g.,* reduce ambient air temperature by sitting on eggs). Thus, in order to determine if the adults will be able to provide such care for their eggs as temperatures increase, I needed to better understand their vulnerability in conjunction with their larvae. I applied the same heating and response criteria to both metamorph and adult life-history stages; each individual was exposed to a temperature increase of 0.5˚C/min until muscular spasms were observed. I defined a spasm as the combination of erratic and uncontrolled body spasms. Onset of body spasms is an accurate method for identifying a definitive CT_{max} in terrestrial amphibians (Lutterschmidt & Hutchison 1997a).

4.2.5 Environmental temperatures

I used Maxim ibutton (http://www.maxim-ic.com/) temperature loggers to determine the thermal profiles of each breeding habitat. I deployed temperature loggers (1) under the fronds of four birdnest ferns, (2) suspended approximately one meter from the ground at two locations for leaf breeders, (3) at the deepest bottom of two stream pools where tadpoles were collected, and (4) at the bottom of two phytotelm tree holes where tadpoles were collected. Loggers recorded temperature data every 20 min. Duration of sampling temperature varied by breeding habitat: approximately two months for birdnest ferns (6/29-8/25), approximately two and a half months for leaf habitats (7/5-9/23), and approximately one month for phytotelm and stream habitats (8/27-9/25). In order to identify the maximum potential ambient air temperature for my study area, I placed data loggers in the upper canopy of five trees at 1100 m (specific to phytotelm, stream and BNF habitats) and five trees at 1300 m (specific to leaf breeders). The locations of canopy loggers were randomly selected within our study area. I suspended canopy loggers and leaf habitat loggers under a plastic funnel to shelter them from direct solar radiation and precipitation.

4.2.6 Analysis

I examined the relationship between habitat-specific temperatures and ambient air temperatures taken from the forest canopy. To achieve this objective, I created two scatter plots to compare: (1) the minimum temperature recorded daily in each habitat (e.g. minimum recorded of all 20 minute observations) to the daily minimum ambient air temperature recorded from the adjacent forest canopy, and (2) the maximum temperature recorded daily in each habitat to the daily maximum ambient air temperature recorded from the adjacent forest canopy. If habitats fail to buffer temperature, points will align along a line of equivalency between the x and y axis—a line with a y-intercept of 0 and a slope of 1 (herein “equivalency line”). If habitats reduce temperature, points will occur below the equivalency line; if they are warmer than air temperature, they will occur above the equivalency line.

I calculated warming tolerance (WT) of a species by subtracting the maximum environmental temperature that it experiences (T_{max}) from its CT_{max}. A positive thermal tolerance indicates the number of degrees in temperature that the climate must warm before a species begins to fail physiologically. A negative thermal tolerance indicates that the environmental temperature has surpassed a species’ CT_{max} and should cause physiological failure and/or death. In other words, a small WT predicts a low tolerance for warming; a large WT predicts a high tolerance.

I calculated a single overall naïve thermal tolerance for each species. Naïve warming tolerance (WT_n) reveals the thermal tolerance of animals in the absence of habitat that buffers ambient air temperatures, while habitat-specific thermal tolerance (WT_h) indicates realized thermal tolerance. Naïve thermal tolerances were derived by subtracting the average maximum temperature from the average CT_{max} for each species. The average maximum temperature was derived from loggers placed in five local canopy trees at 1100 m (to correspond to phytotelm, stream, and BNF breeders), and in five canopy trees at 1300 m (to correspond with leaf breeders). I derived a habitat-specific thermal tolerance by subtracting the average maximum temperature across loggers in species-specific breeding habitats from the average CT_{max} for each species (see Table 4.1). I conducted four sets of analyses of variance (ANOVA) models to test for statistical differences in CT_{max} among species and among life-history stages, thermal tolerance derived from naïve air temperatures, and thermal tolerances derived from habitat-specific temperatures among the four breeding habitats. I used the single highest value averaged across data loggers to determine thermal tolerances for each individual. To further explore differences in CT_{max}, naïve thermal tolerance, and habitat-specifc thermal tolerances among breeding habitats, I used a Tukey's 'Honestly Significant Difference' (HSD) method to conduct pairwise comparisons among breeding habitats in R (v. 2.12.2). This method accounts for potential inflated probabilities caused by multiple comparisons, which can cause spurious error in determining statistical significance.

To explore the relationship between animal body mass and $CT_{max,}$ I performed a linear regression analysis with our response variable as CT_{max} and predictor variable as body mass. I conducted this analysis for each breeding habitat. Both CT_{max} and body mass were log-transformed to normalize data. I checked all models for heteroscedasticity via the studentized Breusch-Pagan test. All models were non-heteroscedastic.

4.3 RESULTS

4.3.1 Sensitivity

Species from stream and phytotelm habitats had higher CT_{max} than species from BNF and leaf habitats (stream: 37.8 ˚C ± 0.8 (SD throughout), phytotelm: 38.3 ˚C ± 0.8, BNF: 34.8 ˚C ± 1.9, and leaf: 33.5 ˚C ± 0.3).

According to analysis of variance, CT_{max} differed for species that breed in each of the four habitats ($F_{3,58} = 33.10$, $P < 0.001$; see Table 4.1 for means and Table 4.2 for pairwise comparisons). Specifically, my Tukey's HSD test indicates that CT_{max} differed among all breeding habitats, except between leaf and BNF breeders and between phytotelm and stream breeders (Table 4.2).

Table 4.1. Critical Thermal Maximum (CT_{max}) of five frog species (egg/tadpole life-history stage) from a sub-montane rainforest in the Philippines. T_{max} indicates the maximum averaged temperature observed for each species' habitat. Overall naïve and habitat specific warming tolerance is $CT_{max} – T_{max}$ of air (WT_n) and habitat (WT_h). T_{max} for naïve air temperature at 1100 m is 31.1˚C and at 1300 is 30.0 ˚C.

Strategy	Breeding Habitat	Species	N	Mass (SD) (g)	CT_{max} (SD)	T_{max}	WT_n	WT_h
Direct Dev.	BNF	*P. banahao*	23	0.44 (0.2)	34.8 (2.0)	22.3	3.7	12.2
Direct Dev.	Leaf	*P. montanus*	6	0.13 (0.02)	33.5 (0.3)	27.8	3.5	5.7
Aquatic Tadpole	Phytotelm	*K. kalingensis*	8	0.10 (0.2)	38.3 (0.8)	22.8	7.2	15.5
		S. luzonensis	23	0.31 (0.37)	37.8 (0.8)	20	6.7	17.8
Aquatic Tadpole	Stream	*K. walteri*	2	0.03 (0)	38.5 (1.3)	20	7.4	18.5
		All Species (stream)	25	0.29 (0.4)	37.8 (0.8)	20	6.7	17.8

Table 4.2. Multiple comparisons among critical thermal maximums, naïve thermal tolerances, and habitat-specific tolerances for individuals found in four breeding habitat types (egg/tadpole life-history stage). Provided are the upper and lower confidence intervals on the differences between the means of the levels of each factor with the specified family-wise probability of coverage. The intervals are based on the Studentized range statistic, Tukey's 'Honest Significant Difference' method. P-values of < 0.05 are significant.

Variable	Comparison	Difference	Lower	Upper	p-value adjusted
CT_{max}	Leaf – BNF	-1.27	-2.96	0.42	0.202
	Phyto – BNF	3.57	2.06	5.08	< **0.001**
	Stream – BNF	3.06	1.99	4.12	< **0.001**
	Phyto – Leaf	4.84	2.82	6.83	< **0.001**
	Stream – Leaf	4.33	2.66	6.01	< **0.001**
	Stream – Phyto	-0.51	-2.01	0.99	0.805
Naïve	Leaf – BNF	-0.17	-1.86	1.52	0.993
	Phyto – BNF	3.57	2.06	5.08	< **0.001**
	Stream – BNF	3.06	1.99	4.12	< **0.001**
	Phyto – Leaf	3.74	1.72	5.73	< **0.001**
	Stream – Leaf	3.23	1.56	4.91	< **0.001**
	Stream – Phyto	-0.51	-2.01	0.99	0.805
Habitat Specific	Leaf – BNF	-6.77	-8.46	-5.08	< **0.001**
	Phyto – BNF	3.12	1.61	4.63	< **0.001**
	Stream – BNF	5.36	4.29	6.42	< **0.001**
	Phyto – Leaf	9.89	7.90	11.88	< **0.001**
	Stream – Leaf	12.13	10.46	13.81	< **0.001**
	Stream – Phyto	2.24	0.75	3.74	**0.001**

I explored whether body mass of eggs/tadpoles predicts CT_{max} in each habitat type using linear regression models. There were no significant relationships between body mass and CT_{max} for any of the species within each breeding habitat type: BNF ($F_{1,21}$=1.969, R^2= 0.042, P=0.175; Regression), leaf ($F_{1,4}$=1.709, R^2= 0.124, P=0.261), phytotelm ($F_{1,6}$=0.091, R^2= -0.149, P=0.773; Regression), or stream ($F_{1,23}$=1.712, R^2= 0.029, P=0.204; Regression).

4.3.2 Exposure

Temperatures for all four breeding habitats were lower than the ambient air temperatures derived from the forest canopy (Figure 4.1). I compared daily habitat-specific temperatures to ambient temperatures—BNF, leaf, pytotelm, and stream habitats were cooler than minimum ambient temperatures 73%, 60%, 93%, and 93% of the time, respectively, and were cooler than maximum ambient temperatures 100%, 98%, 100%, and 100% of the time, respectively (*i.e.,* below the equivalency line of Figure 4.2). On average, all four habitats were cooler than the minimum temperature: BNF habitats by 0.37 (±0.8) ˚C, leaf habitats by 0.2 (±0.4) ˚C, phytotelm habitats by 0.7 (±0.6) ˚C, and stream habitats by 0.7 (±0.6) ˚C. In comparison, on average, all four habitats were cooler than the maximum temperature: BNF habitats by 5.1 (±3.4) ˚C, leaf habitats by 3.2 (±2.2) ˚C, phytotelm habitats by 3.7 (±1.0) ˚C, and stream habitats by 5.9 (±1.4) ˚C.

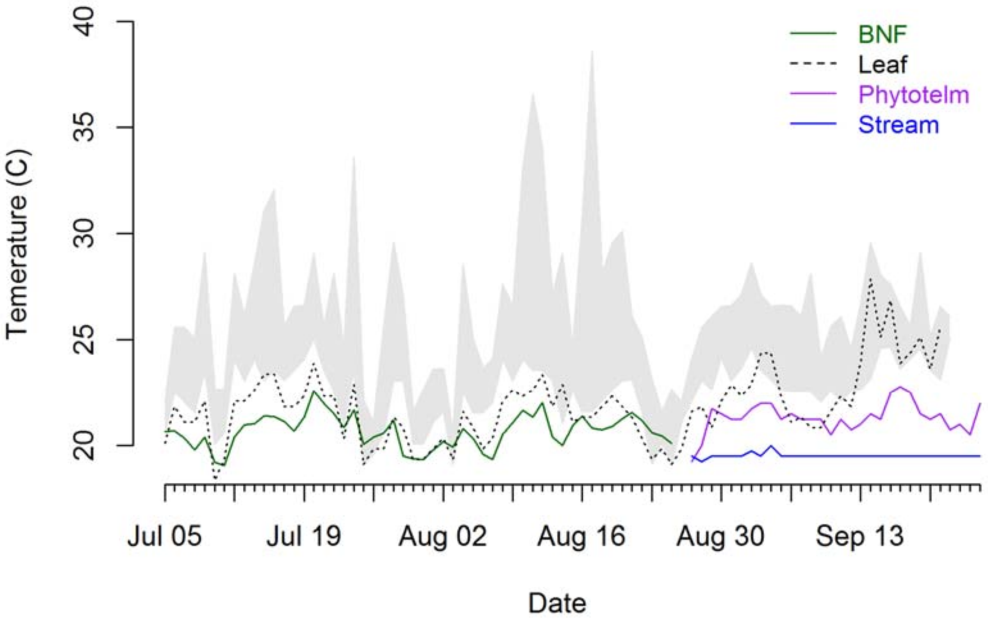

Figure 4.1. The relationship between non-buffered ambient and habitat-specific temperatures. The shaded area indicates the minimum and maximum range in daily ambient temperature taken from the canopy of ten rainforest canopy trees at 1100 m and 1300 m asl. Lines indicate habitat-specific temperatures for BNF, leaf, phytotelm, and stream habitats. Habitat specific temperatures were derived from daily maximum temperatures averaged across locations.

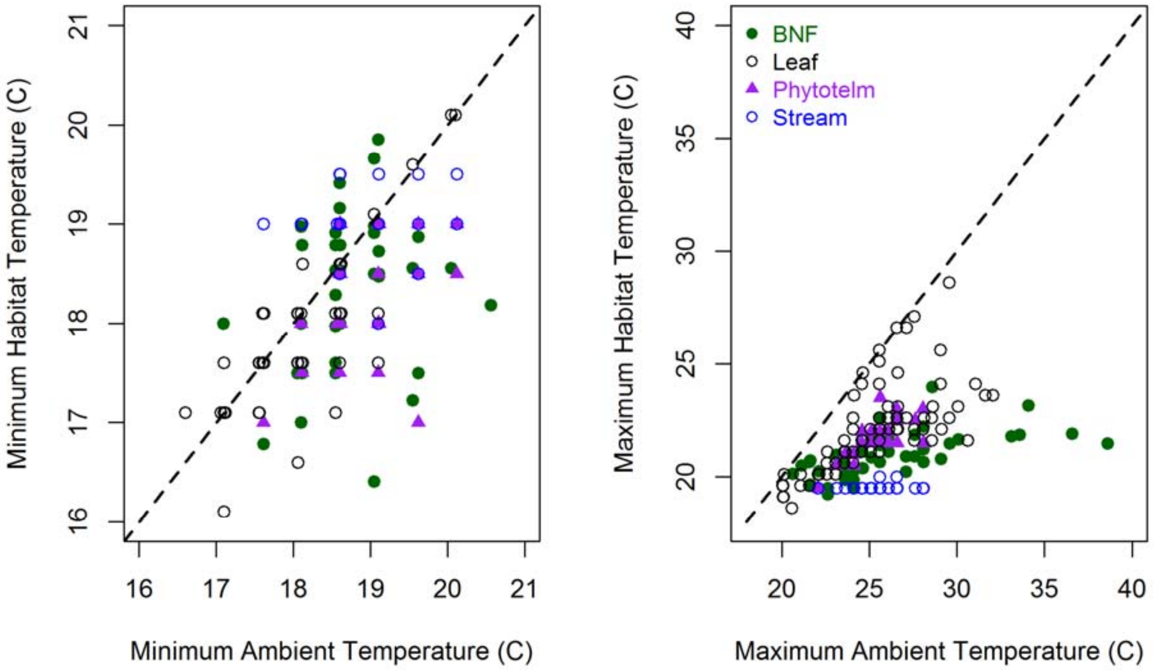

Figure 4.2. Relative difference in daily temperature extremes between ambient air temperature (macroclimate) and habitat specific temperatures (microclimate). Daily minimums and maximums were derived from 20 min temperature readings. Ambient temperatures are derived from loggers placed in the canopy (*i.e.,* amibent air temperature) of ten rainforest trees at 1100 and 1300 m asl. Habitat-specific temperatures are derived for bird's nest fern (BNF), leaf, phytotelm, and stream habitats. The dashed line indicates temperature equivalency between ambient and habitat specific temperatures.

4.3.3 Warming vulnerability

I compared the thermal tolerance of frogs, derived from habitat-specific temperatures (thermal tolerance = CT_{max} - T_{max} of habitat), to naïve thermal tolerances, derived from ambient air temperature recorded in the rainforest canopy (thermal tolerance = CT_{max} - T_{max} of ambient). The naïve thermal tolerances derived from ambient air temperatures in the forest canopy were lower than tolerances derived from habitat-specific temperatures (Figure 4.3). According to my ANOVAs, WT_n and WT_h significantly differed for species that breed in the four breeding habitats ($F_{3,58} = 27.77$, $P < 0.001$; $F_{3,58} = 145.27$, $P < 0.001$; respectively; see Table 4.1 for means and Table 4.2 for pairwise comparisons) (Figure 4.3). Based on Tukey's HSD test, naïve thermal tolerance differed among breeding habitats, except between leaf and BNF breeders and between phytotelm and stream breeders (Table 4.2). Comparisons among habitat-specific tolerances revealed that warming tolerances differed among breeding habitats, except between phytotelm and stream breeders.

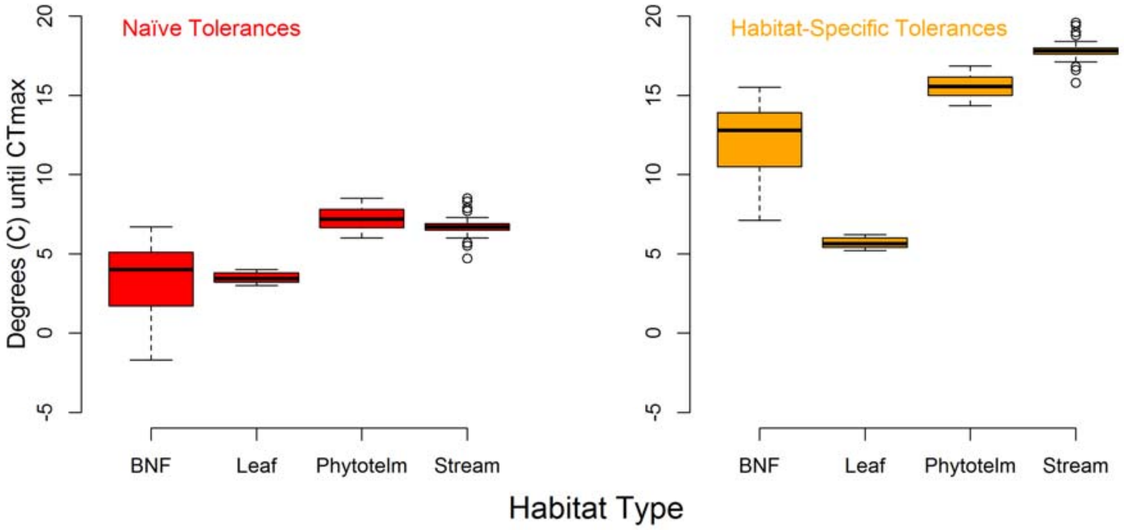

Figure 4.3. **A boxplot for naïve warming tolerances (left) and habitat specific warming tolerances (right) for frog species that breed in four different breeding habitats found on Mt. Banahaw in the Philippines.** Dark horizontal lines represent the median for each habitat, boxes with dotted hashes indicate the sample minimum, lower quartile, median, upper quartile and sample maximum. Open circles indicate outliers.

4.3.4 Life-history stages

CT_{max} varied by life-history stage for the two direct-developer species. Notably, CT_{max} for the egg stage was lowest for both species. The CT_{max} of *P. montanus*, the leaf-breeding species, increased with each subsequent life-history stage (*i.e.,* adults had the highest CT_{max}), whereas the metamorph stage had the highest CT_{max} for *P. banahao*, the BNF-breeding species (Table 4.3).

The CT_{max} significantly differed among life-history stages for *P. banahao* and *P. montanus* ($F_{1,48} = 22.1$, $P < 0.001$; $F_{1,30} = 15.42$, $P < 0.001$; respectively).

Table 4.3. Critical Thermal Maximum (CT_{max}) for multiple life-history stages of two direct-developer frog species (BNF and Leaf habitat) collected from a sub-montane rainforest in the Philippines. CT_{max} is derived from first observation of body spasms.

	P. montanus			*P. banahao*		
	egg	metamorph	adult	egg	metamorph	adult
N	3	9	17	12	8	17
CT_{max} (SD)	33.5 (0.3)	36.2 (3.2)	37.4 (3.4)	34.8 (2.0)	41.7 (0.6)	36.2 (2.2)

4.4 DISCUSSION

I showed that breeding habitats buffer ambient air temperature, expanding the warming tolerances of frogs by ~ 2 - 11 ˚C. Without the buffering capacity of specific habitats, direct-developer eggs laid in BNF and leaf habitats may experience temperatures close to their critical thermal maxima, with low margins for tolerating future elevated temperatures. Few studies of climate warming distinguish between temperatures derived at microhabitat scales (Duarte *et al.* 2012) and temperatures derived from macroclimatic ambient air (Deutsch *et al.* 2008), even though habitat driven microclimates play an enormous role in mediating air temperature (Shoo *et al.* 2010; Shoo *et al.* 2011a). My findings prompt the inclusion of microclimatic (habitat-specific) variables in assessing thermal tolerances of animals when developing predictive models of climate warming (Williams *et al.* 2008).

4.4.1 Sensitivity and exposure

I considered two metrics indicative of warming vulnerability in our study—sensitivity (*i.e.,* CT_{max}) and exposure (*i.e.,* temperature) (Williams *et al.* 2008). In my study area, sensitive species were exposed to the warmest temperatures (high sensitivity with high exposure) and less sensitive species were exposed to the coolest temperatures (low sensitivity with low exposure). Sensitivity of frog larvae differed by species—CT_{max} was highest for stream breeding species (range: 37.8 – 38.5 ˚C) and lowest for direct-developer species (range: 33.5 - 34.8 ˚C). A comparison of mass and CT_{max} for larvae of each species showed no statistical significance, suggesting that observed differences in sensitivity may be more influenced by physiological differences among species rather than morphology alone.

Canopy temperatures (*i.e.,* macroclimate) were almost exclusively warmer than associated habitat-specific temperatures suggesting that habitats buffer temperature and exposure based on macroclimate (*e.g.,* see Deutsch *et al.* (2008)) alone may provide a misleading impression of vulnerability. For example, naïve tolerances (derived from canopy temperatures) between BNF and leaf breeders and between phytotelm and stream breeders did not differ. However, after accounting for habitat-specific exposure, WT_h (*i.e.,* warming vulnerability) of BNF breeders was significantly greater than WT_h of leaf breeders. Likewise, WT_h of stream breeders was significantly greater than for phytotelm breeders. Naïve thermal tolerances for the two direct-developer species only differed by 0.6 ˚C, but when comparing habitat-specific thermal tolerances, the difference was much greater (6.5 ˚C).

4.4.2 Warming vulnerability and its caveats in the context of climate change

Although thermal tolerances for some species in my study appear to be quite large, I must consider a few factors to properly assess “true” climate vulnerability: (1) I considered temperature as the primary driver of warming vulnerability in my study; however, I recognize that “true” vulnerability can only be determined by complex interactions among numerous variables (Brook, Sodhi & Bradshaw 2008). For example, water, in addition to temperature, strongly influence the physiology (*e.g.,* evaporative water and energy loss) of animals (Tracy, Christian & Tracy 2010) and therefore when considered in combination may provide a more holistic assessment of vulnerability (McCain & Colwell 2011). (2) The estimates in my study are conservative. Frogs may be negatively affected by environmental temperatures well before CT_{max} is realized. Animals will alter their behavior under suboptimum temperatures and attempt to seek alternative habitats that are optimum (Vickers, Manicom & Schwarzkopf 2011). This behavioral response occurs before temperatures reach CT_{max} (as discussed below, behavioral mitigation is not an option for some species in our study) and can severely impact populations (Huey & Tewksbury 2009). (3) Climate warming projections are typically based on mean temperatures. Extreme, above-average temperatures are capable of causing rapid population declines (Welbergen *et al.* 2008). Thus, extreme weather events may substantially increase the vulnerability of all species in our study area.

Vulnerability to future warming is highly dependent on a species’ behavior (Huey & Tewksbury 2009). Free swimming tadpoles, especially stream tadpoles, are able to seek deeper, cooler temperatures within stream pools. Unlike tadpoles, direct-developing larvae are confined within eggs and habitat preferences are likely fixed as extensive surveys in our study area suggest that *P. banahao* and *P. montanus* are obligate BNF and leaf breeders (Chapter 3). Parental care of the leaf breeding species, *P. montanus*, may circumvent hostile temperatures via covering and watering the eggs (Bickford 2004). However, daytime mitigation of hot temperatures is also unlikely, as adult frogs only guard eggs at night. The elimination of a single life-history stage from climate warming may cause substantial population declines.

Behavior aside, eggs of this direct developing species begin body spasms at 34˚C, only a few degrees above ambient T_{max}. Thus, larvae of *P. banahao* live close to their physiological limits, with little opportunity for behavioral mitigation. This suggests that the CT_{max} of larvae may be an important determinant of range limits (Sunday, Bates & Dulvy 2012), especially considering the limited scope for behavioral or evolutionary adaptation to alter the status quo (Monasterio *et al.* 2011).

According to my study, the egg life-history stage is most sensitive to hot temperatures for direct developer species. Literature regarding thermal tolerances of ectotherms is confined to the adult life-stage even though susceptibility to threats may vary by life-history stage (Becker *et al.* 2007). Thus, without considering all life-history stages, the true vulnerability of ectotherms to climate warming may be difficult to discern.

The species in my study are globally and locally limited in distribution. All are endemic to the Philippines, and two species are endemic to Mt. Banahaw. Species with restricted geographic ranges have limited capacity to adjust physiologically (Brattstrom 1968). Furthermore, Mt. Banahaw is an isolated mountain completely surrounded by deforested lowlands (below 700 m asl.), thus limiting the dispersal potential of these species. Microhabitat temperatures should be a critical component when considering the impacts of climate change, as alternative habitats are extremely limited for range-restricted species—particularly montane species (Ohlemüller *et al.* 2008).

Chapter 5: Microhabitats reduce animal's exposure to climate extremes

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5.1 Introduction

Climate change is forcing species to undergo a series of multidimensional shifts, including combinations of groundward shifts within forests, upward shifts in elevation, and latitudinal shifts towards the poles, to remain at physiologically optimal conditions (Maclean *et al.* 2008; Chen *et al.* 2011; Scheffers *et al.* 2013c). The magnitude of species shifts will depend on the severity of changes in climate within niche space relative to the physiological tolerances of impacted species (Sunday, Bates & Dulvy 2012; Scheffers *et al.* 2013a). This interaction is of particular importance in the context of extreme weather events, which are expected to increase in severity and frequency under climate change (Meehl & Tebaldi 2004; Fischer & Knutti 2013).

Weather extremes are predicted to accelerate the negative impacts of climate change on species populations, excaerbating those already derived from changes to mean rainfall and temperature (Meehl & Tebaldi 2004; McCain & Colwell 2011). For instance, in Australia, extreme temperature events kill entire colonies of Australian flying-foxes (*Pteropus alecto* and *P. poliocephalus*) (Welbergen *et al.* 2008). Extreme events threaten species because the rate of change in climate is far faster than species' ability to physiologically adjust (e.g., Stillman and Somero (2000), Compton *et al.* (2007)) or to disperse to new localities with optimal conditions

(Parmesan, Root & Willig 2000; Chen *et al.* 2011). Thus, the fate of species exposed to extreme events will depend on whether or not they can find locally abundant climate refuges that buffer against life-threatening conditions (Sears, Raskin & Angilletta 2011; Suggitt *et al.* 2011).

Understanding acute climate exposure within microhabitats relative to the physiological sensitivities and limits of species that use them is critical in identifying species vulnerability to novel climates (Williams *et al.* 2008; Duarte *et al.* 2012; Scheffers *et al.* 2013a). A key research objective is understanding the role habitats will play in moderating the ecophysiological impacts of climate change on ectotherm communities (Huey & Tewksbury 2009). Many studies that examine species vulnerability to climate derive their temperatures from macroclimate sampling, for example, from satellites and regional weather stations that measure ambient air temperatures (Warren & Chick 2013). As a result, these studies do not incorporate habitat complexity into deriving estimates of species vulnerability to climate change (Williams *et al.* 2008; Suggitt *et al.* 2011). For instance, a study by Warren and Chick (2013) makes predictions of vulnerability to climate change for over 50,000 species globally. Yet, all temperature data incorporated in this study are derived from satellite macroclimatic temperature measurements and, in doing so, ignore a fundamental outcome of habitat complexity—climate buffering (Evans 1939; Johansson 1974).

This is an important consideration for species that reside in structurally complex ecosystems, such as rainforests, which contain numerous structures that span from ground to canopy, any of which may reduce ambient temperature by several degrees (Shoo *et al.* 2010; Scheffers *et al.* 2013a; Scheffers *et al.* 2013c). Further, microclimates within structures might adjust at a similar rate (herein uniformly) to temperature changes in ambient macroclimates, or alternatively they could adjust at a higher or lower rate (herein non-uniformly). Whether changes in microclimates within structures are uniform or non-uniform with changes in ambient macroclimates is likely one of the most important considerations in predicting the impacts of novel climates on species and ecosystems. Yet, to my knowledge, all macroecological studies ignore this potential and simply assume that shifts in temperature are uniform.

Although there is a growing literature on species susceptibility to climate change (reviewed by Huey *et al.* (2012)), there is limited understanding as to 1) the degree of thermal buffering that occurs within complex microhabitats, 2) how this might relate to the buffering of extreme events within microhabitats, 3) how close extreme temperature events are to the thermal limits of ectotherm communities, both inside and outside of buffered microhabitats, and 4) how predictions of vulnerability vary under uniform and non-uniform climate change within microhabitats. Herein, I assess how *in situ* climate microrefuges (as defined by Keppel *et al.* (2012)) buffer extreme temperature relative to the thermal physiology of inhabiting frog and lizard species, which are two of the most threatened taxa to climate change (Huey *et al.* 2009; Sinervo *et al.* 2010). To do this, I monitored temperature exposure from microhabitats distributed across the vertical strata (soil, tree-hole phytotelmata, arboreal epiphytes, and ground vegetation) of a Philippine montane rainforest and identified the temperature sensitivity via critical thermal maximas (CT_{max}) of frog and lizard species that occupy these microhabitats. Lastly, I relate these thermal limits to the frequency of extreme climate events to deduce species' vulnerability to uniform and non-uniform changes within microhabitats under contemporary scenarios of future climates.

5.2 Materials and methods

5.2.1 Study site and taxa

My study site is Mt. Banahaw in southern Luzon (14.094895 N, 121.489634 E), the Philippines, Southeast Asia. The site is characterized by agriculture that has replaced lowland dipterocarp forest to 800 m a.s.l., dipterocarp and montane forest from 800-1700 m a.s.l., and mossy and *Pinus* forest above 1700 m a.s.l. The climate is marked by the absence of a distinct dry season with annual rainfall of around 3100 mm yr^{-1} and 85% relative humidity on average (Banaticla & Buot 2005).

I considered 15 species of frogs and lizards from my study area that utilize four dominant microhabitats: 1) soil, 2) phytotelmata (hollows in tree trunks and branches that fill with water), 3) bird's nest ferns and 4) ground vegetation (Figure 5.1). I chose these microhabitats because they likely encompass a large proportion of niche space from ground to forest canopy. Habitat usage by each species was observed over the course of nine months and includes 118 ground to canopy surveys and surveys of 150 bird's nest ferns paired with over 900 samples of additional microhabitats from the surrounding forest (e.g., soil, logs, tree holes, and surrounding vegetation; Scheffers *et al.* (2013a); Scheffers *et al.* (2013c)).

Figure 5.1. Four dominant microhabitats (soil, phytotelm, bird's nest fern and ground vegetation; left to right) that are located from ground to canopy within a Philippine rainforest. Photos courtesy of BR Scheffers and S Zozaya.

5.2.2 Temperature data

To assess how various microhabitats buffer temperature, at 1100 m a.s.l. I placed a temperature logger (Maxim Thermochron (model: DS1921G) and Hygrochron (model: DS1923) iButton; http://www.maxim-ic.com/) in the canopy of five trees at 17 - 20 m above the ground and in the ground vegetation directly below the five canopy loggers at approximately 1 m above the ground. In the same localities as my canopy and ground vegetation loggers, I also placed a single data logger in 16 bird's nest ferns growing from 0.5 m to 11 m above-ground. I compared temperature data from ferns and ground vegetation to temperature data from the five canopy trees. Additionally, I placed one logger within and one logger ca. 50 cm above two tree-hole phytotelmata located 2 m above the ground; and one logger 5 cm deep in the soil, paired with a logger approximately 1 m above-ground at three locations. Data were recorded from May - September 2011 for canopy, June - August 2011 for fern, and August - September 2011 for phytotem and soil habitats. I suspended a plastic funnel above all exposed data loggers to shelter them from direct solar radiation and precipitation (as per Shoo *et al.* (2010).

5.2.3 Buffering climate extremes across microhabitat types

I examined the ability of each microhabitat to buffer extreme weather events, using box and whisker plots to display the temperature profile of each habitat in comparison to ambient conditions (our macrohabitat measures). I used Crawley (2007) definition of extreme outlier events (hereafter "extreme events"), which was all temperature measurements from ambient samples that exceeded the lowest datum above 1.5 times the interquartile range of the upper quartile. For each microhabitat pair, I then quantified the number of hours spent at these extreme temperatures.

5.2.4 Critical Thermal Maxima

The critical thermal maxima (CT_{max}) of ectothermic vertebrates provides a useful index for the thermal constraints of animals (Hutchison 1961; Hutchinson & Dupré 1992). I determined CT_{max} of frog and lizard species that use soil, phytotelmatum, and bird's nest fern and ground vegetation microhabitats. I stabilized CT_{max} for all field-sampled individuals by acclimating them to a constant 22˚C at my field base camp at 1100 m a.s.l. for a minimum of four days. This was a conservative time period for stabilizing CT_{max} (Hutchison 1961; Brattstrom 1968). Because CT_{max} estimates may vary as a function of methodology, I standardized CT_{max} estimates for all species experimented on in this study. I housed individuals in an aquarium and fed them forest invertebrates *ad libitum*.

I obtained upper critical thermal tolerances via Hutchinson dynamic methods (Lutterschmidt & Hutchison 1997a), whereby each individual was exposed to a constant temperature increase of 0.5˚C min^{-1} until muscular spasms were observed. I defined a spasm as the combination of erratic and uncontrolled rapid movements of the body. I recorded body temperature at the time of spasms by inserting a k-type thermocouple temperature sensor (Extech, model #421502) into the cloacal.

5.2.5 Exposure to Death Zone

I derived a 'death zone' for all frog and lizard species in each microhabitat. Death zones were based on the CT_{max} of each species that occupy each microhabitat. Thus, the breadth of the death zone for each microhabitat will vary based on the species that use them. The minimum end of the death zone for each microhabitat is defined by the lowest CT_{max} value of the frog and lizard community and the maximum end of the death zone is defined by the highest CT_{max} value of the community. This zone represents environmental temperatures at or near the CT_{max}, and thus will cause mortality. This is a conservative approach as these species will experience physiological stress at temperatures lower than CT_{max}, which may cause behavioural changes leading to higher mortality (Huey & Tewksbury 2009). I recorded the number of contemporary outlier temperature events that intersect with the death zone for each microhabitat.

Additionally, I project this death zone under a 6˚C increase in global temperatures as documented in the fourth assessment of climate change by the Intergovernmental Panel on Climate Change (IPCC 2007). This scenario represents the upper margin of climate change under business-as-usual carbon emissions. Macroecological models often project changes in mean daily temperature (ambient) with the implicit assumption that microclimates will increase in temperature to an equal degree under climate change as macroclimate (i.e., a uniform increase of 6˚C in both macro- and micro-habitats). To explore this assumption, I used the slopes derived from regression analysis of micro- and macro-habitat temperature to adjust the uniform 6˚C increase to a non-uniform increase that accounted for variation in the rate of change in temperature between micro- and macro-habitats. To do this, I scaled the 6˚C temperature increase by a regression coefficient derived from linear regression models in R v. 2.15.1 (R Project for Statistical Computing, http://www.r-project.org), in which my response variable was microhabitat temperature and my predictor variable was the paired macrohabitat ambient temperature. This coefficient indicated whether microhabitat temperatures uniformly changed with increased macrohabitat temperature (i.e., a slope of 1) or whether microhabitat temperatures non-uniformly changed with increased macrohabitat temperature (i.e., a slope of less than or greater than 1). For each scenario, I quantified the number of outlier temperature events that intersect with the death zone for each microhabitat following uniform and non-uniform increases in temperature.

5.3 Results

My data suggested that microhabitats from soil to the rainforest canopy strongly influenced microclimate (Table 5.1). The temperatures within microhabitats were on average cooler than surrounding ambient air (19.6°C compared to 20.3°C for phytotelms, 19.5°C compared to 21.1°C for ferns, and 20.5°C compared to 21.1°C for ground vegetation). Soil temperatures were warmer than ambient (21.2°C in soil compared to 20.8°C for soil ambient). Relative to macrohabitats, extreme events in microhabitats were reduced, on average, by a magnitude of 22 (Table 5.1). For example, soil buffered extreme temperature events by a factor of 14 whereas bird’s nest ferns buffered extreme temperature events by a factor of 31. Variances of microhabitat temperatures were always lower than variances of ambient temperatures (Table 5.1).

Table 5.1. The rate at which microhabitat temperatures change with a 1˚C increase in ambient temperature, and the ratio of time spent at extreme temperatures in each microhabitat compared to ambient. We studied four of the dominant microhabitats (soil, phytotelm, bird's nest fern and ground vegetation; left to right in Figure 5.1) within a Philippine rainforest, and these microhabitats all reduce extreme weather events and serve as critical habitat for rainforest fauna. The rate of change is the coefficient derived from regression analysis comparing macro temperatures (predictor variable) to micro temperatures (response variable). The variance in temperature is provided for each microhabitat type. Soil and phytotelms were compared to adjacent ambient air whereas ferns and ground vegetation were compared to ambient air within the rainforest canopy.

Microhabitat types : Ambient	Rate of Change (˚C) (microhabitat : ambient)	Hours at Extreme (microhabitat : ambient)	Microhabitat variance (σ^2)	Ambient variance (σ^2)
Soil : Ambient	0.11 : 1	1 : 14	0.3	5.7
Phytotelm : Ambient	0.66 : 1	1 : 23	1.1	1.6
Fern : Canopy Ambient	0.30 : 1	1 : 31	1.1	2.6
Ground Vegetation : Canopy Ambient	0.64 : 1	1 : 21	1.5	2.6

5.3.1 Uniformity in temperature extremes and Death zone

Microhabitats increased in temperature at a slower rate than temperature increases within paired macrohabitats suggesting that contemporary fluctuations between macro- and micro-habitats were non-uniform (Table 5.1). Specifically, for every 1°C increase in ambient macrohabitat temperatures, temperatures in soils increased by 0.11°C (R^2=0.19, $p < 0.001$; 0.11x

+ 18.8), in phytotelms increased by 0.66°C ($R^2=0.63$, $p < 0.001$; 0.66x + 6.2), in ferns increased by 0.30°C ($R^2=0.36$, $p < 0.001$; 0.30x+13.9) and in ground vegetation increased by 0.64°C ($R^2=0.71$, $p < 0.001$; 0.64x+7.0) (Table 5.1).

The mean critical thermal maxima of 10 frog species ranged from 32.9 to 35.9°C and of five lizard species from 32.9 to 37.0°C (Figure 5.2). Except for two extreme temperature events (~40 minutes in total) for fern microhabitats, all microhabitats buffered contemporary temperatures below these physiological limits. Considering increases of 6°C in ambient temperature, exposure to lethal temperatures increased for all but phytotelm communities (Figure 5.3). Although exposure to extreme events increased under both uniform and non-uniform temperature changes, microhabitat climates were still between 16 to 108 times more buffered and less exposed to lethal conditions than ambient macroclimates (Tables 5.2 and Figure 5.3). Consequently, uniform changes in microhabitat temperature intersected with the death zone on average 3 times more often than under non-uniform changes (Table 5.2).

Table 5.2. The ratio of time (hours) spent above the CT_{max} of frog and lizard communities in each microhabitat (soil, phytotelm, fern and understory vegetation) compared to ambient. The ratio of time (hours) spent above the CT_{max} under a uniform +6 ˚C increase and a non-uniform increase in temperatures are also provided. Uniform +6˚C increases are based on business-as-usual carbon emissions whereas the non-uniform increases are derived from the +6˚C increase after adjusting for the rate of change between paired macroclimate and microclimate (rates are provided in Table 1).

Microhabitats : Ambient	Hours above CT_{max} (contemporary)	Temperature increase (uniform)	Hours above CT_{max} (+6˚C Uniform)	Temperature increase (non-uniform)	Hours above CT_{max} (non-uniform micro : +6˚C uniform macro)	Hours above CT_{max} (mico non-uniform : mico uniform)
Soil : Ambient	1 : 1*	+6 ˚C	1 : 32*	+0.66 ˚C	1 : 32*	1 : 1
Phytotelm : Ambient	1 : 1*	+6 ˚C	1 : 1*	+3.96 ˚C	1 : 1*	1 : 1
Fern : Canopy Ambient	1 : 5	+6 ˚C	1 : 16	+1.8 ˚C	1 : 63	1 : 4
Ground Vegetation : Canopy Ambient	1 : 10*	+6 ˚C	1 : 18	+3.84 ˚C	1 : 108	1 : 6
average	1 : 4		1 : 17		1 : 51	1 : 3

*denotes values that were zero but inflated to 1 in order to derive a ratio.

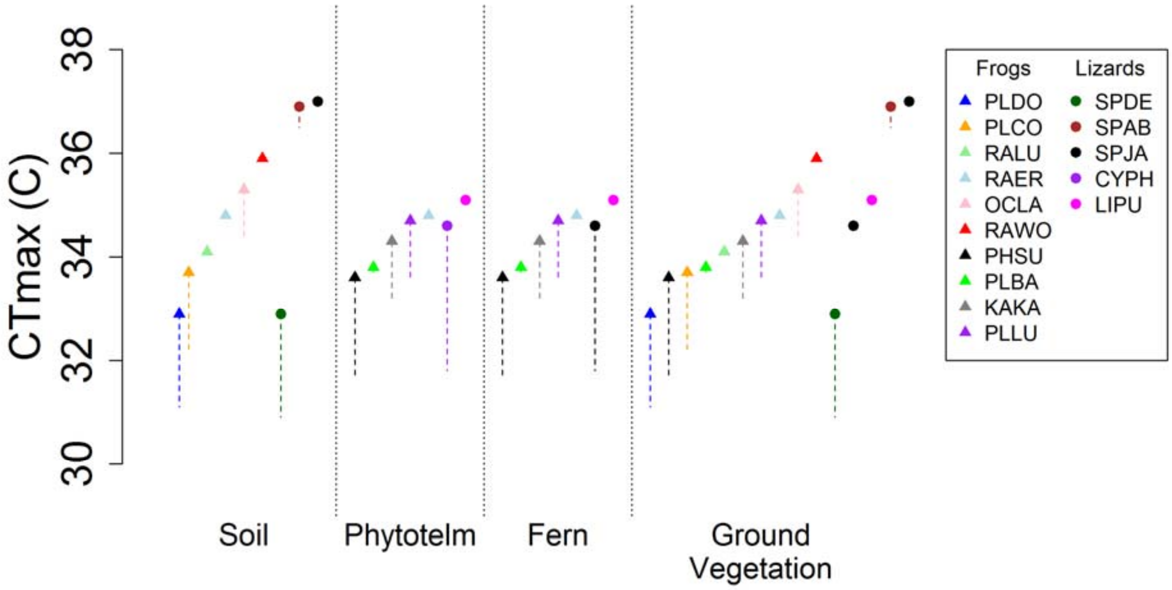

Figure 5.2. The critical thermal maximum (CT$_{max}$) of the frog and lizard communities that use four habitat types. The dashed tails indicate standard deviations from the mean.

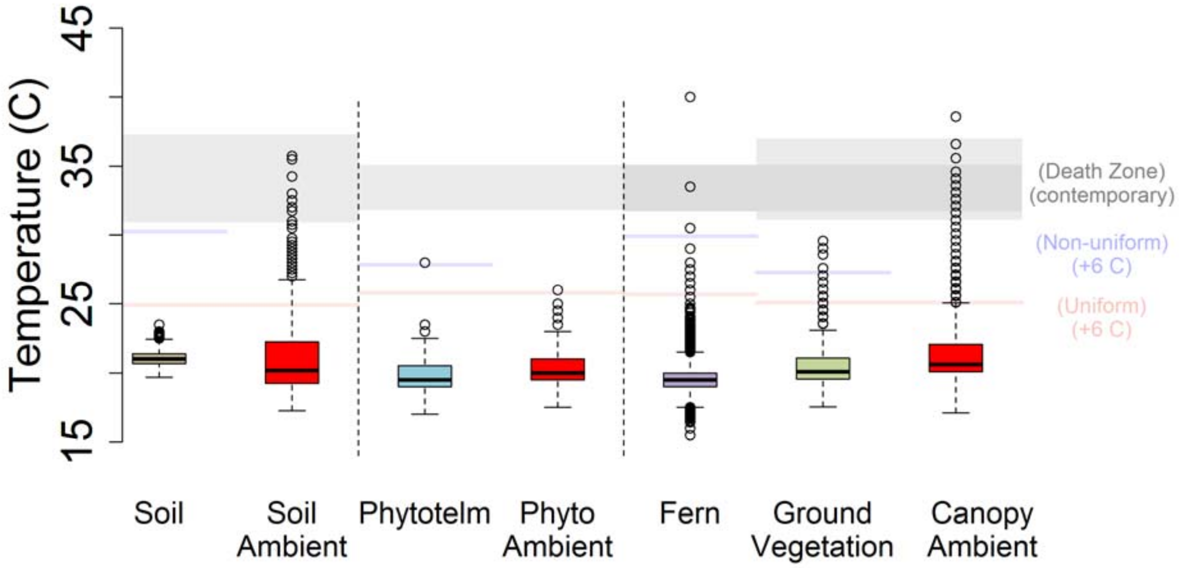

Figure 5.3. The relationship between temperature within each habitat type and the contemporary death zone (shaded area) of frog and lizard communities that utilize these habitats. The red lines were based on a uniform increase of 6˚C (thus the contemporary shaded death zone shifts downward by 6˚C), which was based on the upper threshold of a business-as-usual carbon emission scenario. The blue lines were based on a non-uniform increase in microhabitat temperature (after adjustment by the regression coefficient outlined in Table 5.1) at a 6˚C increase in ambient temperature. The contemporary death zone was derived from the critical thermal maximums (CT_{max}) of each species that use each habitat type and thus represents the current range of temperatures that are lethal to frogs and lizards. The CT_{max} of each species is provided in Figure 5.2.

5.4 Discussion

5.4.1 The value of rainforest microhabitats under future climate change

My findings agree with other studies globally (e.g., rainforest of Costa Rica, Amazonia, New Caledonia, and West Africa) that show microhabitats can stabilize and reduce local ambient temperatures by between 2-5°C (Johansson 1974; Fetcher, Oberbauer & Strain 1985; Freiberg 2001; Ibanez, Hély & Gaucherel 2013). Thus, as suggested by Huey and Tewksbury (2009), microhabitats may play an important role in moderating the ecophysiological impacts of climate change on ectotherm communities. Indeed, my data suggest that non-buffered ambient temperatures at times approach lethal levels that spanned the entire breadth of the death zone for the herpetofauna community, whereas microhabitats effectively buffer extreme temperature conditions to well below the physiological limits of the frog and lizard species that utilize them. Overall, microhabitats were cooler and less variable in temperature than non-buffered ambient conditions, and pivotally they reduced exposure to lethal temperatures, suggesting that microhabitats from canopy to ground may serve as key climate refuges.

I considered abundant microhabitats that span the entire rainforest stratum. The microhabitats in my study had negligible extreme temperature events whereas non-buffered ambient temperatures more frequently contained events that exceeded the CT_{max} of their dependent animal communities. Under a 6°C increase as projected by the IPCC (2007), exposure to thermal extremes could increase by several orders of magnitude, which would undoubtedly have severe effects on population persistence (Welbergen *et al.* 2008). For example, in 1932, several days of extreme heat caused the death of tens of thousands of birds at Rumbalara, central Australia (Finlayson 1932) and a 2010 heat wave caused the death of 208 endangered Carnaby's Black Cockatoo (*Calyptorhynchus latirostris*) along the south coast of western Australia (Saunders). The only microhabitat in my study that experienced limited to no exposure based on both contemporary and future temperature increases are phytotelm microhabitats. There are large phytotelm dependent vertebrate and invertebrate communities throughout the tropics (Malkmus & Dehling 2008; Silva, Carvalho & Bittencourt-Silva 2011; Marino, Srivastava & Farjalla 2013) and my study suggests that the buffering capacity of phytotelm habitats may reduce the vulnerability of these communities to future climate change (Scheffers *et al.* 2013a).

I show that animals exposed to fine scale temperatures within microhabitats are less vulnerable to extreme events than those exposed to ambient temperatures. This, however, is highly dependent on whether microclimate temperature changes at a uniform or a non-uniform rate versus macroclimates. My study provides support for non-uniform changes in microhabitat temperatures (Table 5.1). I show that the rates of warming in microhabitats are lower than the rates of warming in macrohabitats, such that as microhabitats warm they will remain 34 to 89% cooler than macrohabitats. This non-uniformity in microhabitat versus macrohabitat temperatures results in fewer events (a 3-fold reduction) that intersect with the death zone than with uniform changes in microclimate.

An animal's vulnerability to extreme climate events may depend on several important factors not considered in this study:

Scale of time – Although my study clearly demonstrates non-uniform buffering of temperature within microhabitats, the temperature fluctuations we document occur over a time scale of hours to days. If at longer time scales (e.g., multiple decades) mean temperature in microhabitats uniformly track with mean increases in macrohabitat temperatures, I suspect that microhabitats will continue to provide non-uniform buffering at the shorter time scales of hours to days. However, as mean ambient temperatures increase, the thermal safety margin between buffered microhabitat temperature and CT_{max} will decrease. Thus, the only way to prevent this safety margin from shrinking is via a total reduction in annual mean temperatures.

Severity of extreme events – I used outlier events derived from the distribution of temperature data as an indicator of extreme weather. Changes in future climate may be more severe than has been documented under contemporary climate and, therefore, my extrapolations may underestimate the severity of extremes. My assumption is that buffering by microhabitats will persist and thus represents the only avenue for species to escape lethal conditions.

Behavior – Behavior is a critical factor in deciphering the vulnerability of animals to extreme climate events (Hassall *et al.* 2010). For example, Welbergen *et al.* (2008) documented a 10% die-off in some Australian flying-fox populations following a single day of exposure to extreme temperatures. The lack of behavioural plasticity was an important driver in deaths, because bats were likely not able to adjust habitat selection to utilize more buffered microhabitats (for example, low hung branches in the understory). Consequently, not all species will have the behavioral repertoire to exploit microhabitats. Disrupted behavior may also reduce foraging and/or reproductive opportunities (Parmesan, Root & Willig 2000). As such, while climate refuges may allow species to persist under extreme events, reduced fitness and interrupted habitat and metapopulation dynamics may ultimately increase the risk of extinction (Huey & Tewksbury 2009).

Body size – Large-bodied organisms may persist under extreme conditions better than small-bodied organisms due to lower dehydration and increased thermal inertia (Tracy, Christian & Tracy 2010; Huey *et al.* 2012). However, small-bodied animals have greater availability of buffered microhabitats than large bodied animals (e.g., a mouse versus an elephant) (Huey *et al.* 2012).

Thermal Acclimation – The frequency of extreme temperature events relative to the rate of overall warming will directly impact vulnerability because many species are capable of expanding their thermal limits when exposed to gradual increases in temperature (i.e., acclimation;). However, species that have evolved the greatest tolerance to high temperatures have done so at the expense of acclimation capacity to maximum temperatures (Stillman 2003). Species from my study that define the upper area of the death zone may thus be most susceptible to increases in average temperature.

Precipitation – Climate models project extreme warming combined with strong reductions in moisture (Meehl & Tebaldi 2004; Fischer & Knutti 2013). Changes in precipitaiton can cause severe population decline. For example, a drought lasting from 1975-77 caused the extinction of 5 out of 21 surveyed populations of Edith's Checkerspot butterfly (*Euphydrayas editha*) in California, USA (Ehrlich *et al.* 1980). In addition to the direct effects of drought, the buffering properties of microhabitats are likely directly linked to rain, as less water results in less capacity to absorb heat. For example, by experimentally manipulating water concentrations in ferns from my study area, I observed that both a reduction and variability in maximum temperatures was directly linked to rainfall (Chapter 3). Thus, in times of severe drought or in areas with seasonal variation in precipitation, microhabitats may periodically lose their buffering capacity as thermal refuges.

Plant-Animal Interactions – When microhabitats are living they too may be impacted by novel climates, resulting in population declines and reduced refuge availability. Several species are already highly dependent upon microhabitats to complete their life-history stages, including direct-developing frogs that are obligate *Asplenium* fern breeders (see Chapter 3 and Scheffers *et* *al.* (2013a)). This link indicates that declines in plant habitats could have severe cascading impacts on animal communities.

5.4.2 Biological Importance of Microhabitats Under Climate Change

My study offers a possible mechanism for why canopy environments are biologically rich. Rainforest canopies are hot, dry environments yet these habitats are unparalleled in their terrestrial biodiversity (Ozanne *et al.* 2003). For example, a single epiphytic bird's nest fern in the lowland rainforest canopy of Borneo may contain double the invertebrate biomass of the entire host tree (Ellwood & Foster 2004). Similarly, bromeliads in the Neotropics, which are functionally equivalent to phytotelms and *Asplenium* bird's nest ferns, increase spider richness by 41% (Gonçalves-Souza *et al.* 2010), increase the suitability of hot and dry habitats for frogs (Silva, Carvalho & Bittencourt-Silva 2011) and serve as foraging habitats that amplify the richness and abundance of resident birds (Nadkarni & Matelson 1989; Cruz-Angón & Greenberg 2005). Entire frog communities on Mt. Banahaw are obligate breeders within bird's nest ferns, phytotelm and vegetative habitats and, therefore, their persistence is directly linked to microhabitat conditions (Scheffers *et al.* 2013a). The harshness of canopy environments means that much of the world's arboreal organisms must either be well adapted for these conditions (Tracy, Christian & Tracy 2010) or be able to find refuge in arboreal microhabitats. My study provides empirical support for the latter microhabitat hypothesis—microhabitats promote species coexistence through fine-scale habitat creation and amelioration of physical stress.

Above-ground microhabitats will also serve as key refuges for transient wildlife in a changing climate (Hole *et al.* 2009; Shoo *et al.* 2010). As mentioned, many of the microhabitats within rainforests are living and therefore may too be susceptible to changes in climate. The loss of local microhabitats and their associated microclimates may lead to the acceleration in groundward shifts in arboreal animal distributions (Nadkarni & Solano 2002; Scheffers *et al.* 2013c). For example, Bickford (2005) observed a 78% increase in arboreal frog abundances on the ground following extreme weather caused by erratic El Niña events in Papua New Guinea. Specific to my study area, downward shifts in arboreal species could cause ground densities to inflate by 88% (Scheffers *et al.* 2013c). This new dimension to species response to climate change, in addition to altitudinal and poleward shifts (Parmesan 2006; Colwell *et al.* 2008), has not been considered in other study areas but may largely be driven by the availability of above-ground refuges. My data suggest we need a next generation of predictive models that account for species' ability to move within microhabitats to exploit favorable buffered microclimates. Models may be improved by including both specific physiological limitations of a species (Kearney, Shine & Porter 2009; Rodriguez-Sanchez, De Frenne & Hampe 2012; Walters, Blanckenhorn & Berger 2012), detailed information about extreme conditions at the microhabitat scale (Williams *et al.* 2008; Walters, Blanckenhorn & Berger 2012) and an adjustment for non-uniform shifts in microhabitat temperature. My data suggest that consideration of microhabitats provides a more realistic assessment of exposure within rainforests, possibly reducing exposure to extreme events by an order of 22. Inclusion of microhabitat buffering within models is therefore fundamental to making accurate assessments of vulnerability under future conditions.

Chapter 6: Discussion

6.1 The “arboreality hypothesis”

Biodiversity is spatially organized by climatic gradients across elevation and latitude (Gaston 2000). But do other gradients exist that might drive biogeographical patterns? In chapter 2, I show that rainforest’s vertical strata provide climatic gradients much steeper than those offered by elevation and latitude, and biodiversity of arboreal species is organized along this gradient. In Philippine rainforests, I demonstrate that rainforest frogs tend to shift up in the rainforest strata as altitude increases. Moreover, a Philippine-wide dataset of frog distributions shows that frog assemblages become increasingly arboreal at higher elevations. Thus, increased arboreality with elevation at broad biogeographical scales mirrors patterns I observed at local scales. My proposed “arboreality hypothesis” suggests that the ability to exploit arboreal habitats confers the potential for larger geographic distributions because species can shift their location in the rainforest strata to compensate for shifts in temperature associated with elevation and latitude. This novel finding may help explain patterns of species richness and abundance wherever vegetation produces a vertical micro-climatic gradient. My results further suggested that global warming will likely ‘flatten’ the biodiversity in rainforests by pushing arboreal species toward the cooler and wetter ground. This ‘flattening’ could potentially have serious impacts on forest functioning and species survival.

Frog communities have discordant distributions based on whether or not they are arboreal and whether or not they are found in the lowlands or the uplands. This overlooked dimension to local distributions and the biogeography of amphibians could have serious consequences for 96% of past studies on the ecology and conservation of frogs (Kays and Allison 2001) as their data were derived solely from the ground. For example, Deichmann *et al.* (2010) documented stable and increasing populations of lowland Amazonian frogs over a 22 year period, however the historical and contemporary studies never accounted for the individuals that occupy above-ground habitats. Applying my discovery to Deichmann et al.'s (2010) study suggests an alternative explanation to a stable population: instead above-ground populations may have shifted downwards towards the ground due to stress induced by climate change. The alternative explanation, due to the lack of above ground data, thus makes populations appear to be healthier and more robust (as was documented by Bickford (2005)).

My "arboreality hypothesis" may have wider application in conservation science in the early detection of climate stressed ecosystems. A major field in climate change science is climate driven shifts across altitude and latitude. Changes in climate have already triggered range shifts in montane species (Raxworthy *et al.* 2008; Chen *et al.* 2011). A major challenge for climate change science is the detection of such shifts, and there are few long term species distribution datasets across altitude and latitude. However, my results from Chapter 2 have shown that abundance of frogs in rainforest is largely arboreal and is organized by climate gradients that span from canopy to ground (Chapter 2). I suggest from these results that novel climates could cause an increase in abundance on the forest floor, perhaps up to a maximum of 88% if all arboreal frogs survived and shifted down to the forest floor. Therefore, my "arboreality hypothesis" from Chapter 2 may be usefully applied in conservation science, with canopy surveys across elevation gradients used as an early detection system for communities under stress as groundward shifts by arboreal species will likely precede shifts in altitude (Bickford 2005).

6.2 Biological amplification and climate buffering

Epiphytes are important above-ground habitats for canopy dwelling organisms because they provide a cool and moist microhabitat in the relatively hot and dry canopy. These functional roles may be altered by a changing climate. *Asplenium* (“bird’s nest”) ferns are known to be one of the most important above-ground habitats for Paleotropical invertebrates (Ellwood & Foster 2004), yet little is known regarding their functional roles for canopy vertebrates. In Chapter 3, I presented *Asplenium* fern survey data from the Philippines and examined whether ferns act as keystone species for arboreal frogs. I conducted extensive day and night *Asplenium* fern, habitat and ground-to-canopy surveys for frogs at a montane rainforest site. I examined fern and surrounding habitat characteristics (e.g., fern size, canopy cover) that best predicted frog usage and abundance. I found ferns to be the preferred microhabitat for arboreal frogs, and their use by frogs is strongly diurnal. Moreover, *Asplenium* serve as the preferred breeding site for this arboreal frog community. A strong positive relationship exists between fern size and frog usage and abundance.

I de- and re-hydrated ferns in order to identify relationships between water and temperature buffering. The ability of ferns to buffer maximum temperatures and reduce variability in temperatures was directly linked to their size and thus also their level of hydration. These results supported the buffered microhabitat hypothesis, and suggested that frogs are using large ferns for their moist, cool, environments for breeding and daytime retreat. Temperature and drying experiments suggest that ferns assume this role because they provide buffered microclimates, but this buffering must be contingent on regular rainfall. Thus, altered rainfall regimes from climate change, such as longer periods without rain (Lewis *et al.* 2011) could lead to the unexpected loss of the functional capacity of these keystone ferns. Clearly, this situation would rapidly affect the rich arboreal frog community, likely to push populations downwards to the ground, with consequences as discussed above (section 6.1). My research from Chapter 3 also has implications for species-area relationships. The species-area (habitat) relationship is a fundamental tenant of biogeography. In Chapter 3, I show that (1) frogs use bird's nest ferns more than the surrounding forest, especially during the day, (2) that most frogs (or eggs) are found in large ferns under low canopy, (3) large ferns dry out more slowly and have lower temperature variability than small ferns and 4) temperature buffering is strongly linked to precipitation.

The following pathways for identifying a link between climate and biological amplification collectively provide anecdotal evidence that supports microenvironment buffering as a novel attribute that compliments habitat (patch) size and complexity in shaping patterns of biodiversity. As I show in Chapter 2, small scale gradients from canopy to ground strongly affect the vertical distributions of frogs, which affect large-scale distributions of community structuring. Bird's nest ferns are yet another structure component but even at a smaller scale that influence biodiversity patterns (Chapter 3-4).

A well-studied facet of amphibian conservation in North America is habitat loss that disconnects terrestrial from aquatic life-history stages (Semlitsch 1998). This is because many amphibian species display life histories that straddle both aquatic and terrestrial environments and populations can decline due to degradation of either habitat. The vulnerability of amphibians as a result of their biphasic life-cycle has seldom been explored in terms of climate change and habitat disturbance, especially for direct-developing frogs that live in the rainforest canopy of Southeast Asia. *Asplenium* ferns are 58 times more used by frogs than other randomly selected microhabitats on Mt. Banahaw suggesting that some of the arboreal frogs on Mt. Banahaw are obligate fern breeders. Thus, the ferns are critically important as they are used by all life-history stages of frogs to complete their life cycle. Variable breeding strategies may make one species (e.g., direct-developing) or life-history stage (e.g., metamorph) more vulnerable than another. In this regard, bird's nest ferns are equivalent to breeding wetlands and the rainforest canopy is synonymous with surrounding terrestrial habitat. Alterations to either the breeding habitat (fern) or the habitat that surrounds it (canopy) will affect different life-history stages.

Species may circumvent the impacts of climate warming if the habitats they use reduce their exposure to (higher) ambient temperatures. In Chapter 4, I identified which frog species from a tropical montane rainforest in the Philippines may be vulnerable to climate warming. To do so, I selected five frog species that utilize four breeding habitats (including *Asplenium* ferns) and identified the sensitivity and exposure of tadpoles and direct-developer eggs to heat by measuring their critical thermal maxima (CT_{max}) and the habitat-specific temperatures they experience. My study species included two direct-developer frogs—one species that lays its eggs on exposed leaves, and another that lays its eggs in ferns—and three species that produce aquatic free-swimming tadpoles—two stream breeders, and one phytotelm (tree hole) breeder. I compared thermal tolerances derived from microclimates of breeding habitats to tolerances derived from macroclimate (i.e. non-buffered air temperature taken from the rainforest canopy). I also examined whether differences in CT_{max} existed across life-history stages (egg, metamorph/young-of-year, and adult) for the two direct-developer frog species. Habitats buffered ambient temperature and expanded thermal tolerances of all frog species. However, I found that direct-developers were more vulnerable to increased temperatures than aquatic breeders, due to their high sensitivity to increased temperature, and greater exposure to higher macroclimate (ambient air) temperatures. Direct-developer eggs were more sensitive to warming than both metamorph and adult life-history stages. Thermally buffered microhabitats may represent the only protection against current and impending climate warming. My data highlight the importance of considering sensitivity and exposure in unison when deciphering warming vulnerability of frogs.

Finally, as discussed above, in order for species to survive in the relatively hotter and drier rainforest canopy, they have to either have special physiological adaptations or be able to seek refuge that buffer inhospitable conditions. In Chapter 4 and 5, I explored whether a variety of microhabitat distributed from the ground to canopy can buffer climate and expand the biological niche space for canopy-dwelling frogs. Additionally, I explored how climate change might affect amphibians that require different habitat types for breeding and for supporting multiple life-history stages. I showed that all these microhabitats (leaf, bird's nest ferns, streams and phytotelmata) provide climate buffering for frogs. This expanded the range of habitats with buffered microclimates from the single one (*Asplenium* bird's nest ferns) explored in Chapter 3. In some cases, climate buffering expands the thermal tolerance of frogs by over 10 degrees Celsius.

Extreme weather events, such as unusually hot or dry conditions, can cause death by exceeding physiological limits, and so cause population decline. Survival will depend on whether or not susceptible organisms can find refuges that buffer extreme conditions. Microhabitats offer different microclimates to those found within the wider ecosystem, but do these microhabitats effectively buffer extreme climate events relative to the physiological requirements of the animals that frequent them? I collected temperature data from four common microhabitats (soil, tree holes, epiphytes and vegetation) located from the ground to canopy in primary rainforests in the Philippines. Ambient temperatures were monitored from outside of each microhabitat and from the upper forest canopy, which represent the macrohabitat controls. I measured the critical thermal maxima (CT_{max}) of frog and lizard species, which are thermally sensitive and inhabit my microhabitats. Microhabitats reduced mean temperature by 1-2˚C and reduced the duration of extreme temperature exposure by 14 to 31 times. Microhabitat temperatures were below the CT_{max} of inhabitant frogs and lizards, whereas macrohabitats consistently contained lethal temperatures. Microhabitat temperatures increased by 0.11 to 0.66˚C for every 1˚C increase in macrohabitat temperature, and this non-uniformity in temperature change influenced my forecasts of vulnerability for animal communities under climate change. Assuming uniform increases of 6˚C, microhabitats decreased the vulnerability of communities by up to 32-fold, whereas under non-uniform increases of 0.66 to 3.96˚C, microhabitats decreased the vulnerability of communities by up to 108-fold. Microhabitats have extraordinary potential to buffer climate and likely reduce mortality during extreme climate events. These results suggest that predicted changes in distribution due to mortality and habitat shifts that are derived from macroclimatic samples and that assume uniform changes in microclimates relative to macroclimates may be overly pessimistic. Nevertheless, my data suggest that even non-uniform temperature increases within buffered microhabitats would still threaten the frogs and lizards that utilize these microhabitats.

Perhaps my most important finding from Chapter 5 was that refuges non-uniformly buffer climate and in doing so significantly reduce threat from climate change. This finding ought to be included in assessing species threat from climate change, not simply assuming temperature will rise uniformly (as I had done in Chapter 4). I improved upon my predictions made in Chapter 4 by expanding my prediction to reptiles as well as frogs, and also incorporating non-uniform shifts in microclimate relative to macroclimate. This new facet, non-uniformity, to microclimate buffering has important implications for assessing species vulnerability under extreme weather events. Weather extremes are important as they are indicative of the hottest times of the day. As I show in Chapter 3, frogs seek refuge in *Asplenium* ferns during the day and move out of the ferns at night. In Chapter 3 and 4, I show that ferns and other microhabitats used for breeding by frogs reduce temperature maximums and variance in temperature and in Chapter 5 I found that terrestrial microhabitats provide refuge for adult frogs and lizards from extreme events. Importantly, non-uniform shifts in microclimate (relative to macroclimate) substantially expand the thermal safety margin for frogs and lizards as compared to assuming a uniform shift. However, as I show in Chapter 3, this buffering is likely contingent on the availability of rain. Thus, altered rainfall regimes may not only affect the hydric state of rainforest animals but could lead to the unexpected loss microhabitat buffering and subsequent exposure to thermal extremes.

6.3 The ecological importance of Biomass and Abundance

I have shown that a major portion of amphibians occur in the upper tiers of the rainforest canopy and are thus unobservable from ground. High frog densities in the forest canopy suggest that they may play an underappreciated role in the functionality of tropical rainforest canopies, especially those of SE Asia. In some terrestrial and aquatic systems, amphibians significantly contribute to the overall biomass of a system (Gibbons *et al.* 2006). Amphibian biomass can surpass that of avifauna and is estimated to be about equal to that of mice and shrews (Burton & Likens 1975). As such, amphibians may alter food web dynamics and nutrient cycling in terrestrial systems (Dial & Roughgarden 1995; Wyman 1998) and may even significantly contribute to pollination and seed dispersal (Silva, Britto-Pereira & Caramaschi 1989; Olesen & Valido 2003). I did not document predation in my research; however I consider it reasonable to speculate about the level and effects of frog predation, based on previous studies. Frogs are predators, and as such are expected to provide direct and indirect biotic control of species diversity and ecosystem processes along herbivore and detritus pathways. Rainforests canopies are typically nutrient poor and I suspect frogs in Mt. Banahaw may transfer energy and matter as they move from ground to canopy (and visa versa) (Romero *et al.* 2010).

The arboreal frog assemblage in Mt. Banahaw is largely dependent on epiphytic *Asplenium* bird's nest ferns at various life history stages (e.g., reproduction, climate refuges, and adult retreat sites). Bird's nest ferns contain considerable invertebrate biomass (Ellwood, Jones & Foster 2002). Through the predation of invertebrates it is plausible that frogs play a role in nutrient cycling within epiphytic systems (Hunter 2001; Romero *et al.* 2010).

6.4 Chytrid fungus

Leaf litter frogs are significantly less vulnerable to chytrid than other frog guilds such as stream species that live in or near aquatic systems (Williams & Hero 1998). This suggests that infection by chytrid may be closely linked to habitat. Chytrid may be less prevalent in arboreal than ground-dwelling species due to warmer and drier conditions in the canopy (similar to that found by Puschendorf *et al.* (2011)). The relationship between arboreality and susceptibility to disease warrants future research.

6.5 Climate Change and Habitat Disturbance

Habitat disturbance in the form of selective logging and clear cutting likely parallels climate change's impacts on the physiology of frogs because warming of the understory layers from tree and vegetation removal is synonymous with human-induced climate warming (Larsen 2012). Threats such as forest loss and climate change may disproportionately affect species that occupy specialized habitats or habitats that are highly susceptible to disturbance (e.g., drying due to increased temperature) such as forest canopies (Walter *et al.* 1998; Floren *et al.* 2001; Briant, Gond & Laurance 2010). Prior assessments that omitted canopy surveys may have documented inflated abundances on the ground due to the downward movement of canopy species to escape hot conditions in thinned or disturbed canopies. In this regard, omitting canopy surveys from studies of habitat disturbance and fragmentation may have led overly optimistic conclusions. This 'data vacuum' (Gardner *et al.* 2007) could have serious implications when assessing and comparing the value of primary (lower richness and abundance due to more animals in the canopy) to secondary (higher richness and abundance due to the downward shifting of animals towards the ground) rainforest. Thus, secondary rainforests may appear to have higher or equivalent conservation value even though researchers on the ground are merely documenting a community under considerable stress.

My data show that limited field data on canopy abundance hinders our ability to objectively assess the impacts of human disturbance (current or future) for biodiversity. In the absence of a thorough empirical foundation that includes canopy environments we are in jeopardy of formulating poor and potentially highly biased predictions that could lead to inappropriate ecological conclusions, or poorly supported management and policy recommendations.

Canopy trees host epiphytes, such as ferns and orchids, and contain tree holes and other microhabitats, all of which serve as arboreal habitats for vertebrates and invertebrates (Ellwood & Foster 2004; Malkmus & Dehling 2008). The removal of these micro-habitats (e.g., as a consequence of the loss of epiphytes) can result in radical compositional changes of canopy communities (Nadkarni & Solano 2002). Degradation of primary rainforests structure is happening at a rapid pace (Asner *et al.* 2005). Even canopy gaps created by single tree cutting increases local temperatures compared to the adjacent primary rainforest (Vitt *et al.* 2008), causing declines in soil fauna biomass (Martius *et al.* 2004). In fact, rainforest understory and epiphyte species across the tropics are harvested for international demand for ornamental plants, essential oils and traditional medicines (Iqbal 1993; Flores-Palacios & Valencia-Díaz 2007), plus local demand for fuel wood (Jenkins & Oldfield 1992; Arnold *et al.* 2003). For example, a single Mexican vendor had over 7500 illegally collected epiphytic plants consisting of 207 species (Flores-Palacios & Valencia-Díaz 2007). Between 1993-1995 it is estimated that Guatemala exported ~14.5 million epiphytic plants annually (Véliz-Pérez 1997) of which approximately 75% were collected from the wild (Rauh 1992). Collection of this magnitude can cause drastic declines in epiphyte and plant populations (Porembski & Biedinger 2001). Importantly, illegal collection and use within protected areas is an understudied area of conservation and climate change science begging the question: How will such degradation impact upon the ability of tropical rainforests to serve as climatic refuges?

Far more heed must be given to the illegal collection and harvesting of plants within pristine rainforest areas. Protected areas are projected to provide refuge from climate change—assuming they remain healthy and intact (Hole *et al.* 2009). Illegal felling and plant collection are poking holes in the world's rainforests, which will have far reaching consequences for rainforest communities in a continuously warmer and drier climate (Nadkarni & Solano 2002; Vitt *et al.* 2008; Lewis *et al.* 2011). For example, the loss of local micro-habitats and their associated micro-climates may lead to the acceleration in downward (for arboreal species), altitudinal or poleward shifts in distributions as animals will need to adjust their distributions, perhaps at a faster rate than if protected areas were left undisturbed, to remain at a thermal optimum (Parmesan 2006; Colwell *et al.* 2008; Scheffers *et al.* 2013c). Thus, incorporating local scale features within macro-scale predictions of climate change and how illegal activities threaten long term potential of these areas to protect against future warming is essential. The fate of temperature sensitive animals will depend on whether these climatically buffered habitats remain intact and thus whether they can continue to reduce ambient temperatures and retain moisture under climate warming (Huey & Tewksbury 2009). This suggests that we urgently need to re-assess the importance of preventing small-scale disturbances within biologically important areas to ensure that our climate refugia are fit for purpose.

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