CLIMATE CHANGE IN TROPICAL MOUNTAINS:
RESPONSE OF PLANT SPECIES TO NOVEL CLIMATIC AND BIOTIC FACTORS

by

SHAFKATUL ISLAM KHAN

(Under the Direction of JACQUELINE E MOHAN)

ABSTRACT

This dissertation research aims to examine the role of abiotic and biotic factors in tropical mountains that affect plant species distributions with climate change. My research focused on the effects of biotic and abiotic factors at the lower elevation-warmer climate boundary of high elevation tropical species. I also examined the response of localized populations of species spanning a broad elevation-climate gradient to warmer climates. Using a field transplant experiment and shade-house studies, I examined the tolerance of montane tropical tree species to novel climates, novel climatic factors such as temperature and moisture, and a novel soil microbial community. The results from the field experiment suggest that tropical high-elevation tree species cannot persist in a much warmer climate, although these high-elevation plant species may tolerate a mildly warmer climate. Local populations of species with a broad distribution perform equally well across different climates. Subsequent mesocosm studies suggest that tropical high elevation plant species may tolerate novel climatic and biotic factors such as soil temperature, moisture, and non-native soil community. Further research is needed to understand the mechanisms behind the reduced performance of high-elevation tropical species in a warmer climate and how species in high-elevation tropical forests will respond to anthropogenic climate change.

INDEX WORDS: Climate change, ecology, tropical forests, montane forests, species diversity, forest composition, global warming, soil microbial community, drought, Central America, Costa Rica

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DEDICATION

This dissertation is only possible because of the selfless love and support of my beloved parents Nurul Islam Khan and Sajeda Khan. Thank you for giving me the freedom to pursue my academic and personal interests, which I am sure, baffled you often and endlessly.

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CHAPTER 1

INTRODUCTION

Climate change is predicted to affect biodiversity via changes in species distributions (Bellard et al. 2012). Species that occupy narrow climate ranges, as the species found on the tropical mountains, are projected to experience range shifts tracking their native climates upslope (Colwell et al. 2008, Laurance et al. 2011b). Such simplistic models assume that species cannot tolerate conditions dissimilar to what they experience today (Pearson 2003). Models based on this assumption are unable to accurately predict change in species abundance and community composition with novel conditions of near future, especially if species can tolerate conditions dissimilar to what they experience currently (Buckley et al. 2010). In order to reliably predict future species abundance and community composition, we need to test the assumption of intolerance in species and understand what factors—abiotic and biotic— contribute to intolerance and limiting distribution of species across climatic regions. Tropical montane regions are composed of species limited to narrow elevation/climate bands (Janzen 1967, Ghalambor et al. 2006, Laurance et al. 2011b). With current climate change, these areas are projected to experience a high proportion of novel combinations of climate. As a result, these biologically diverse areas are projected to experience high rates of local species extinctions and species migrations (Williams and Jackson 2007). Current observed changes in tropical mountains, along with projections of high species displacement in these regions make it imperative to understand what factors limit current range distributions of tropical montane species in order to gain insight into future distributions in these forests.

In order to examine the role of different abiotic and biotic factors in determining the distribution of higher elevation species at the trailing (warm/lower elevation) edge of their range and to understand future changes in species composition on tropical mountains, I ask and examine the following questions experimentally.

1. How do tropical montane tree species respond to a warmer climate?
2. What role do belowground communities (pathogens and symbionts) play in limiting higher elevation tropical tree species range? Does this role change with change in climatic variables (such as temperature?)
3. How do higher elevation tropical tree species respond to warmer and drier conditions (i.e. increase in temperature and decrease in precipitation)?

My dissertation research aims to examine the role of abiotic and biotic drivers in tropical mountains that can affect species with limited elevation-climate ranges via affecting individual survivorship and growth. My research focuses on the biotic and abiotic factors at the lower elevation range/warmer climate boundary of high elevation tropical species and elevation generalists that span a broad elevation gradient. Using field transplant experiments and shadehouse studies, I examine the tolerance of montane tropical species to novel climatic factors such as temperature and moisture, and a novel soil microbial community. Degree of tolerance to abiotic and biotic factors at the lower edge of tropical species ranges will determine whether climate change will shift species elevation ranges and whether species will need to migrate upslope in order to avoid extinction. Persistence to climate change, on the other hand, can resist local extinction of a species and lead to resilient local community composition.

2nd chapter: SURVIVORSHIP AND GROWTH OF TROPICAL MONTANE TREE SPECIES ALONG AN ELEVATION GRADIENT IN COSTA RICA

Models predict that tropical plant species will migrate along environmental gradients to more favorable environments because of climate change, given narrow environmental requirements (e.g. temperature) for a given species (Colwell et al. 2008). These models assume that organisms, including trees, in tropical forests exist at their optimal thermal range and cannot tolerate higher temperatures, and is rooted in Janzen's hypothesis of tropical species' intolerance of broad temperature ranges (Janzen 1967). Although widely used in species distribution models, this assumption of intolerance remains largely untested, hindering a realistic understanding to near future climate change effects on tropical species distributions. A higher tolerance of temperature would result in persistence in the trailing edge of the distribution of a species translating into little change in species composition in tropical landscapes in near future (Lewis et al. 2009). However, few field experiments have tested the assumption of intolerance of novel conditions in montane tropical biota, especially whether and how tropical tree species survive and grow beyond their current environmental requirements. Utilizing an elevation gradient as proxy for climate change in Southwestern Costa Rica, we investigate tree species' survival and growth with changing climate. Lower elevation sites (600m) in the study landscape simulate predicted, near-future climate in Central American highlands, as they are warmer (on average 3-5º C), with more variable precipitation and less cloud cover, than are nearby higher elevation sites (~1400m) (cf. IPCC 2007). In three elevations, we established common garden plots of two high elevation tree species and local populations of three species of trees that span the elevation gradient. We followed these plots from 2009 to 2013 to understand how higher elevation trees within and across species respond to a novel climate warmer than their native climate.

3rd chapter: RESPONSE OF HIGH-ELEVATION TROPICAL MONTANE PLANT SPECIES TO NOVEL SOIL COMMUNITIES AND TEMPERATURE REPRESENTING POTENTIAL FUTURE CONDITIONS

Anthropogenic climate change is predicted to change species distribution and community composition in ecosystems globally (IPCC 2014). Tropical ecosystems are predicted to experience changes in species composition through changes in abiotic/climatic conditions. In Central America, by the end of 21st century, mean annual temperature is projected to increase 3-5 C with conservative emissions scenarios (IPCC 2014). On tropical mountains, this change in temperature is predicted to drive biota upslope tracking the climate the organisms are currently used to (Colwell et al. 2008). Because tropical species experience considerably less intra-annual variation in temperature and related climatic variables (Janzen 1967) which leads to proliferation of tropical high-elevation specialists (Laurance et al. 2011b), climate change may drive considerable changes in species composition in these forests. Whether these species can tolerate a climate warmer than what they currently experience is fundamental to knowing the extent to which tropical forest composition will change and tropical biota will move upslope in search of cooler climates. Recent research shows that plant soil feedback control the abundance of tropical species and pathogens may limit the local distribution of tropical trees (Mangan et al. 2010b, Bagchi et al. 2014). However, whether soil communities affect elevational distribution of species and whether effect of soil communities interact with temperature, especially soil temperature, has not been explored. In this study, I examine how abiotic (temperature) and biotic (soil community) factors in current warmer climates of lowland tropics may limit plants from cooler climates of montane tropics in order to better understand the near future effects of climate change on tropical forests. In a shadehouse experiment, I expose three species of higher elevation plants (*Quercus costaricanum, Viburnum costaricanum, Cinammomum spp.*) to native and novel/downslope soil communities and elevated soil temperature in order to understand how these species respond to novel soil communities in conjunction with novel soil temperatures.

4th chapter: RESPONSE OF HIGH-ELEVATION TROPICAL MONTANE TREES TO FUTURE TEMPERATURE AND MOISTRTURE CONDITIONS

How organisms in climatically stable (Janzen 1967, Ghalambor et al. 2006) and biologically diverse tropical mountains respond to changing climatic variables will determine how these regional ecosystems respond to climate change (Laurance et al. 2011b). This study examines how tropical tree species found in the mountains of Central America respond to elevated soil temperatures and altered moisture regimes in order to understand the range of novel conditions montane tropical trees are able to tolerate and in turn, gain insight into near future climate change effects on species distributions in tropical mountains. In testing how montane tropical trees respond to varying precipitation amount, frequency, and extreme reduction in precipitation experienced in dry season; in conjunction with elevated soil temperatures, I conduct a shadehouse experiment with seedlings of *Viburnum costaricanum* and *Quercus insignis.*

5th chapter: SPECIES DISTRIBUTIONS IN TROPICAL MOUNTAINS WITH CLIMATE CHANGE: A REVEIW

I review evidence of recent climate change induced migrations in tropical mountains and explore how abiotic and biotic factors can influence species ranges in tropical mountains. I also outline how species distribution models can incorporate current understandings of uncertainties related to species response to climate change. I discuss how changing socioeconomic factors such as deforestation and nitrogen deforestation may affect future species distributions. Finally, I lay out key research steps in improving our predictive understanding of species ranges in tropical mountains with climate change.

CHAPTER 2

SURVIVORSHIP AND GROWTH OF TROPICAL MONTANE TREE SPECIES ALONG AN ELEVATION GRADIENT IN COSTA RICA[1]

[1] Shafkat Khan, Fern Lehman, Paul Frankson, Rebecca Ostertag, Chao Song, Jacqueline Mohan.

To be submitted to *Ecology*.

Abstract:

Global climate change is predicted to affect biodiversity via changes in species distributions. With changes in local climate, species intolerant of novel conditions are predicted to experience range shifts. As regions of high biodiversity and uniquely stable climates across elevations, tropical mountains are likely to experience changes in biodiversity via biota's intolerance to novel climates. Whether tropical montane species are able to tolerate a broader range of climatic conditions than what they experience at present is pivotal to projected changes in biodiversity with climate change. In a transplant experiment along an 800-m elevation gradient, we examined the potential for tolerance to novel climates and future changes in biodiversity by exposing tropical montane tree species to warmer new climates. We exposed two species of high-elevation trees (*Viburnum costaricanum* and *Quercus insignis*) as well as local populations of three species of trees with broad elevation ranges to novel warmer climates with generally drier conditions downslope. Downslope plots also experienced less cloud cover and more intense solar radiation. The transplants were tracked for four years in common garden plots across elevations. The survivorship of both species of tropical high-elevation trees was considerably lower in the warmest climate of low (650m) elevation compared to the mid (1100m) and high (1350m) plots, while growth rates of these species were uniform across elevations. The three species of trees with broad elevation ranges did not differ in survivorship across elevations in which they were grown. Neither did the source elevation (high to low elevation) affect survivorship for these three species. The growth rates of individuals generally did not differ based on source or growth elevation. One notable exception was *Inga densiflora* sourced from low elevations and grown in low elevations that grew better than higher elevation conspecifics, thus exhibiting a "home field advantage." These results suggest that high-elevation

species may tolerate moderate increases in temperature (~1^{o}C) but not more extreme temperature enhancements (~4^{o}C). Our study illustrates the need for investigations to understand what abiotic and biotic variables contribute to intolerance of species to novel conditions leading to range limits and biogeographic shifts in tropical mountains.

Introduction:

Whether species are distributed only in the conditions they can tolerate, or occupy a subset of potential habitats, is an enduring research question in ecology (Grinnell 1917, Elton 1927, Hutchinson 1957, Grace and Wetzel 1981). With anthropogenic climate change rapidly altering conditions that species encounter in their native ranges, studies predict shifts in global and regional biodiversity via changes in species distributions (Thomas et al. 2004, Thuiller et al. 2008). How species will respond to changing conditions by altering their ranges will depend in part on whether species are able to tolerate novel abiotic and biotic conditions (Bellard et al. 2012).

Tropical mountains are biodiverse regions where species are often restricted to specific elevations and associated climates (Laurance et al. 2011b), and contain a high proportion of endemic species (Körner and M. 2002, La Sorte and Jetz 2010). Indeed, along with the rest of Mesoamerica Central American tropical mountains are deemed a global biodiversity "hotspot" (Myers et al. 2000). Tropical mountains experience relatively little intra-annual variation in climate (Janzen 1967). Thus, once a species has evolved to inhabit a temperature regime at a given elevation, it is hypothesized to be unlikely for that species to adapt and grow in other climates and elevations (Janzen 1967, Ghalambor et al. 2006). Because tropical montane species adapt and evolve to a climate with relatively little intra-annual fluctuation (compared with, for example, temperate or boreal regions), previous ecologists hypothesized that these species are less tolerant of climate change than species from other regions with more inherent climatic variability (Janzen 1967, Foster 2001, Laurance et al. 2011b, Sheldon et al. 2011). Within relatively short horizontal distance, environmental and climatic conditions change considerably in tropical mountains (Bruijnzeel et al. 2011, Bush 2011). Accordingly, with elevation gain, tropical mountains show changes in plant communities via high turnover of species from one elevation to another (Lieberman et al. 1996, Culmsee et al. 2010). The high turnover of communities along tropical mountain gradients suggests that the distributions of tropical montane species are strongly linked to their local climate (Lieberman et al. 1996, Bush 2011, Laurance et al. 2011b). Potential greater intolerance of climatic variability in the biota, coupled with high biodiversity, makes tropical mountains globally critical areas in regard to climate change impacts on biodiversity (Still et al. 1999, Myers et al. 2000, Williams and Jackson 2007, Sheldon et al. 2011). Whether species in tropical mountains are currently exclusively distributed in conditions that they can tolerate, or whether they can tolerate a broader range of conditions than they currently occupy, will be critical to how biodiversity via shifting species ranges will change in these global biodiversity hotspots (Feeley et al. 2012b). Because of unique climates across elevations within relative short distances, tropical mountains are projected to experience a high incidence of novel climates in the future (Williams and Jackson 2007, Bush 2011). Thus, montane tropical species will encounter novel climate conditions that they have not encountered in the historical or even paleo- past (Bush et al. 2004). With increases in temperature, current models predict that tropical montane species will track their native climate niche (Cayuela et al. 2009). For example, Colwell et al. 2008 predict upslope species migrations with movement of their current thermal niche (Colwell et al. 2008). Such a model is in agreement with currently observed upslope shifts in montane Costa Rican and Andean tree species (Feeley et al. 2011, Feeley et al. 2013, Duque et al. 2015). A downslope transplant study in Monteverde, Costa Rica also suggests that tropical cloud forest epiphytes are unable to persist in downslope conditions dissimilar to what these species experience in their current range (Nadkarni and Solano 2002). However, a dearth of studies examining whether species are able to persist in conditions dissimilar to what they experience today limit our understanding of how tropical montane species ranges are currently constrained by climate and how the composition of these forests may change as climate warms.

To examine whether tropical montane trees can tolerate conditions dissimilar to what they experience in their present day elevation ranges, we report on a study that transplanted seedlings of montane tropical trees and followed their survivorship and growth from 2009 to 2013. In this study we utilized two groups of species that have contrasting elevation ranges. We focus on two high-elevation tree species that are characteristic of and limited to tropical montane high elevation "cloud" forests in our study region. In addition, we utilize local populations of tree species, elevation generalists, which span a broad elevation range to examine if local populations of these species differ in their response to climate change. We were interested in examining how tolerance and growth responses vary within a species as well as across species and the functional groups of elevations generalists and specialists. We exposed these two groups of montane tropical trees to warmer climate conditions downslope to ask if tropical montane tree species are able to persist in a climate warmer than their native climate. We hypothesized that tropical tree species limited to high elevation mountains would have reduced growth and survivorship in warmer climates of lower elevations (H1). Second, we asked in species with broad elevation ranges if localized populations from cooler climates (higher elevations) differ from their warmer-climate conspecifics in their response to warmer climates. We hypothesize that within a species that is common in all elevations, individuals from warmer, downslope climates will survive and grow better in warmer climates than individuals sourced from cooler climates (H2)

Methods:

Site description

In order to test our hypotheses we conducted a common garden downslope transplant experiment along a 20-km long elevation gradient from 1350 m to 600 m near Las Cruces Biological Station (LCBS) in Coto Brus County of southwestern Costa Rica (08.785°, -082.959°). Our common gardens were established in abandoned or protected pasture areas, a common land use in Mesoamerica (Daily et al. 2001, Rickert 2005, Cole et al. 2011). The mean annual rainfall is ca. 3500-4000 mm along the elevation gradient with a distinct dry season from December to March. The soils are a mix of ultisols and andisols, and the topography of the area is mountainous with much of the former agriculture land located on steeply sloping (15–40◦) land. Our high (1300-1350 m) and mid elevation (1100 m) sites had Andept soils on top of clay rich substrates. In our low elevation site (650 m), the soil comprised of weathered Ultisols (Janzen 1983). Prior to 1950, the region was largely forested but over the last 60 years all but ~25% of the forest was cleared for agriculture (Daily et al. 2001). Typical of much of Central America, the study landscape is a highly fragmented mosaic of remnant forests, agricultural patches, pasture, and fallow land. As remnant primary forest fragments are mostly legally protected, conservation efforts in this region focus on reforestation and restoration of fallow, degraded lands (Cole et al. 2011).

Our study was designed to address our hypotheses in human-dominated landscapes, which are increasingly critical given current rates of modern day deforestation and subsequent land abandonment (Corlett 1995). Our high elevation sites were within the elevation ranges of high-elevation specialists *Viburnum costaricanum* (1000-3100 m) and *Quercus insignis* (1000-1900 m) in this region. The mid elevation sites were on the range margin of *Quercus* and slightly downslope from the currently receding edge of the range of *Viburnum*.

Species descriptions:

Elevation generalists

Croton draco Schltdl. & Cham. (Euphorbiaceae) is a medium tree growing up to 15 meters. This species is typically found in disturbed habitats, secondary forests, and in treefall gaps. This species is dispersed by ants (Hammel et al. 2005). In Costa Rica, this species is found from 100 m to 2500 m above sea level (a.s.l.) (INBIO 2015).

Inga densiflora Benth. (Fabaceae) is a medium to large tree growing up to 20 meters, with a large geographic and elevational distribution in Central America. The small, fleshy fruits are consumed and the seeds are dispersed by small mammals (Hammel et al. 2005). In Costa Rica, this species is found from near sea level (~10 m) to 1500 m a.s.l (INBIO 2015). This species is very common in secondary and mature secondary forests in the study region (personal observation) and is capable of symbiotic nitrogen fixation (Hammel et al. 2005, Condit et al. 2010).

Heliocarpus appendiculatus Turcz. (Malvaceae) is a medium to large tree growing usually around 15 m and sometimes up to 25 meters. *Heliocarpus* is common in secondary forests and aggrading landscapes. This species is an early colonizer of disturbed habitats. This species is shade intolerant and usually only present in the canopy of mid successional forests and tree fall gaps. The seeds of this species are wind dispersed (Hammel et al. 2005). In Costa Rica, this species is found from 50 m to 1670 m a.s.l. (INBIO 2015).

Higher elevation specialists

Viburnum costaricanum (Oerst) Hemsi (family Caprifoliaceae) is a small pioneer tree growing up to 10 m tall in disturbed habitats such as treefall gaps, slopes exposed to wind, and in areas undergoing secondary succession. The small fruits are important resources for avian fauna, which also disperse the seeds of this species (Hammel et al. 2005). This species is very common in disturbed areas from around 1200 m and higher in our study region (personal observation). This species is found in montane areas in Costa Rica from about 1000 m to 3100 m with a mean elevation of ~1800 m (Hammel et al. 2005). We have observed that while adult trees still occur at their lower elevation range margins around 1150-1200 m, these areas are now bereft of naturally-recruited seedlings (Khan, personal observation) suggesting recruitment limitation (Clark et al. 1999b) is shifting the habitat space for this species.

Quercus insignis M. Martens and Galeotti (Fagaceae) is an emergent, canopy dominant species found in primary and mature secondary forests, growing up to 30 m in height. Its impressively large acorns (7-8 cm) likely contain abundant seed resources for young seedlings(Mack 1998). They are dispersed by rodents of various sizes and are important wildlife forage. This species is found in montane forests in Costa Rica from 1000 m to 1900 m in elevation with a mean elevation of ~1310 m (Hammel et al. 2005).

All the elevation generalists in this study as well as *Viburnum* are shade intolerant species with wind or animal (ants, rodents, and bird) dispersal that enables these species to be very common in high elevations and, for the elevation generalists, lower elevations. Mature *Quercus* are relatively frequent in forests around 1100 m and above and can form impressive codominant canopies (Khan, personal observation). We have chosen these trees as our study species because of their high abundance in the local forests and landscapes, enabling collection of enough seedlings and making these species indicators of how these forests may respond to changes in climate. Since seedling survival and growth is critical in determining adult tree composition (Beckage and Clark 2003, Mohan et al. 2007), we used naturally-recruited, first-year seedlings with cotyledons for this study. Seedlings were generally collected from under the canopy of mature trees with root and the rhizosphere soil intact. Seedlings were kept moist and transported back to Las Cruces for overnight storage before planting in the field plots within a day or two days of collecting.

In July 2009, individuals of *Viburnum* were collected from naturally-recruited populations (minimum 500 m apart) and planted in three plots at each elevation at 1350 meters (high elevation), 1100 meters (mid elevation), and 650 meters (low elevation). Four individuals were planted in each plot, for a total of 36 seedlings per species. In addition, four individuals per elevation of *Heliocarpus, Croton,* and *Inga* were downslope transplanted in each plot. Hence, a given plot at high elevation would get four seedlings of *Heliocarpus* from high elevation, whereas a given plot in low elevation would get four seedlings each of *Heliocarpus* sourced from high, mid, and low elevations. During summer 2010, we established 3 more plots each in middle and high elevations and 2 more plots in low elevation. The imbalance in design was due to lack of availability of another low-elevation site. The new plots in 2010 were added to complement the initially established plots in their land use history. In July 2010, we planted 5-7 seedlings each of *Viburnum* and *Quercus* in the six high-elevation plots, six middle elevation plots, and five low-elevation plots. We also transplanted 5 individuals of *Croton, Heliocarpus, and Inga* from each source elevations to a given plot downslope. In both years, each seedling was assigned a random 1-m^2 spot within a plot. All plots had a 1-m buffer in order to eliminate potential edge effects. As competition with non-native pasture grasses in this region has been documented to be a major barrier to individual tree recruitment (Holl et al. 2000), we cut grasses down every three to six months from 2009-2012.

Plant censuses

After initial planting, we tracked the growth and survivorship of all the transplanted individuals from 2009 through 2012. We conducted one additional census for *Quercus* and *Viburnum* in July 2013. At each census period, we recorded the survival status of the individual, height, and diameter at 5-cm height.

Statistical analysis

Survival analysis

In order to model survival probability for individuals, we used the survival package BaSTA to fit recorded survivorship data in R (Colchero et al. 2012, R Development Core Team 2013). BaSTA is able to incorporate individuals with unknown death data and account for irregular census intervals. BaSTA is also able to include multiple cohorts entering the analysis at different census dates, which is appropriate for the survivorship data for this study. BaSTA models birth intervals, in this case, the time of planting into the plots, and death intervals, the time interval when the death of an individual was recorded, as latent variables, and thus draws inference on age-specific mortality given the covariate of interest. In our study, the plants were assumed to be born in the interval preceding the interval they were first recorded in the censuses. Death for an individual was recorded at the earliest interval when an individual was recorded missing for a year, which constitutes two censuses for 2009 July-2011 July and yearly censuses for 2012 June-2013 July. For both elevation generalists and high elevation specialists, growth elevation was modeled as a categorical covariate. In addition, for elevation generalists the source elevation of individuals was modeled as a categorical covariate. Survivorship was modeled as a two parameter Gompertz model, which consists of an initial mortality parameter (b_0) and an exponential increase in mortality parameter (b_1). For each of the species, four BaSTA simulation chains were run simultaneously for 11,000 iterations with 1000 burn-ins and thinning at every 20 iterations. Convergence was assessed both visually ensuring the mixing of the chains and formally within the model with potential scale reduction $\hat{R}$. For any given variable and group of plants that did not reach convergence (i.e. $\hat{R}<1.1$), simulation plots of survival trajectories from multiple runs were visually assessed to see if there remained any potential difference in predicted survivorship trajectories. This is applicable for the simulations of the elevation generalist species. For all simulations, we used an uninformative prior of (-3, 0.01) for (b_0, b_1) variables with BaSTA option "updateJumps" to improve Markov Chain Monte Carlo (MCMC) search. The covariates in the survival model were assessed upon reaching convergence using projected survival trajectories and associated credible intervals (CI). For elevation specialists, the Kullback-Leibler discrepancies calibrated to reduce asymmetry (KLDC) provided by BaSTA were assessed to see the extent of overlap between posterior parameter estimates. KLDC value of 0.5 indicates identical distribution, whereas KLDC value of 1 indicates no overlap.

Plant growth

Relative growth rates (RGR) or the intrinsic rate of growth (*r*) of individual plants over census intervals were calculated using plant height and diameter at 5-cm height. Assuming exponential growth for early life stages of trees, monthly relative growth rates (RGR) were calculated for each individual using the equation:

Equation (1) $\text{Biomass}_{T2} = \text{Biomass}_{T1} \times e^{r(T2-T1)}$, where T_1 and T_2 represent time 1 and time 2, respectively. Here, T_2 is the current census time and T_1 refers to the initial census time.

Equation (1) is reduced to:

Equation (2) RGR = (LNH2-LNH1)/(T2-T1),

where RGR is the rate of increment, H2 and H1 are any growth variable (height or diameter) at times T2 and T1, and T2-T1 corresponded to the number of months between census intervals.

Individual RGR was analyzed using a Monte Carlo Markov chain (MCMC) generalized linear mixed models framework with the R package MCMCglmm (Hadfield 2010). MCMCglmm is an MCMC sampler for multivariate mixed models that enabled us to model RGR as a variable dependent on multiple predictor variables with fixed and random effects on RGR. Growth elevation for both groups of species as well as source elevation for elevation generalists were modeled as fixed effects with uninformative normal priors. In addition, plot location within an elevation, the census interval when the RGR was measured, and associated plant ID were used as random effects with uninformative parameter-expanded inverse-wishart priors (V=1, nu=0.02) (Hadfield 2015). Plot random effect was added in the model to account for plot-level variation on RGR. Time (i.e., census interval) random effects were added in the model to account for correlation resulting from growth measurements at a given census interval. Individual ID random effect was added in the model to account for correlations resulting from measuring the same plant multiple times. MCMC chains were run for 100,000 iterations, with 3000 burn-ins and thinning intervals of 100. Trace plots of the variance-covariance matrix were visually assessed for plant growth models to ensure that the parameter space was adequately searched by the MCMC algorithm and that the MCMC simulations were not dependent on specified prior values. Competing models of individual growth rates were compared to test hypotheses about growth of the study species in different elevations using the Deviance Information Criterion (DIC) value provided in the MCMCglmm output (Spiegelhalter et al. 2002).

Results

Survivorship

Elevation specialists

Quercus insignis planted in high and middle elevations survived considerably longer than at low-elevation plots, with 100% mortality reached in 5.5-6.5 years compared to low-elevation individuals planted reaching 100% mortality in four years (*Figure 2.1*). The KLDC index for *Quercus* planted in low elevation was dissimilar to the individuals planted in middle and high elevations (**Table 2.1**). *Viburnum costaricanum* experienced a similar survival trajectory with individuals planted in middle and high elevation reaching 100% mortality in 4.5-5 years compared to individuals planted in low elevation reaching 100% mortality by year 2 (*Figure 2.2*). The KDLC indices for low elevation transplants were also dissimilar to mid and high elevation transplants (**Table 2.1**).

Elevation generalists

The three elevation generalist species in this study exhibited neither source nor growth elevation effects on demography. *Heliocarpus apendiculata* survivorship did not depend on either growth or source elevation. The range of survivorship across different sources and growth elevations was 3.25-5 years, with lower elevation plots having higher mortality than mid or high-elevation plots (*Figure 2.3*). Similar to *Heliocarpus, Croton draco* survivorship did not depend on either growth or source elevation, with the credible interval for survivorship trajectories overlapping considerably. The range of survivorship across different sources and growth elevations was 4-5.5 years (*Figure 2.4*). Growth elevation and source also did not affect *Inga densiflora* individuals planted in different elevations. The range of survivorship across different sources and growth elevations was 4-5.5 years (*Figure 2.5*). Visually we assessed multiple runs of the simulations for these three species and the survivorship trajectories were similar in each run.

Both the elevation generalists and high-elevation specialists reach 100% mortality within 6-7 years in all the simulations. This suggests that all of the study species experience very high juvenile mortality in general and only a few adults reach reproductive age (Solbrig 1980). This 'tail-end' survivorship probability is not well represented in our data, although we planted >100 individuals per species.

Growth

Elevation specialists

For *Quercus*, the model without elevation as an explanatory variable was a better fit for the monthly growth rate than the model that included elevation as a factor (**Table 2.2**). This suggests that the monthly growth rate of *Quercus* did not depend on the elevation at which seedlings were planted (*Figure 2.6*). *Viburnum* also showed a similar response to climate, with the model without elevation as a factor being a better fit for the monthly growth data than the model that included elevation (**Table 2.2**), showing no important effect of growing elevation on the monthly growth rate (*Figure 2.7*).

Elevation generalists

For *Heliocarpus* and *Croton*, the models without elevation and source were better models to explain the monthly growth rate data for each species than the models that included the source and growth elevation (**Table 2.2**). Both these species have similar monthly growth rates across growth elevations and source (*Figures 2.8* and *2.9*). Contrasting with these two species, monthly growth rate of *Inga* was best explained by the model that included growth elevation and source elevation as additive effects (**Table 2.2**). *Inga* individuals that were collected from low elevation and planted in their native elevation grew more than conspecific individuals that were sourced from higher elevations (*Figure 2.10*).

Discussion

Our hypothesis that high-elevation species growth and survivorship would be reduced in lower elevations (H1) was partially supported by the results from our lowest elevation plots. The high-elevation species, *Viburnum* and *Quercus* had reduced survivorship in the warmest climate of low elevation, but perhaps surprisingly survivorship among mid and high elevation did not differ. For the short duration that the individuals of the two species persisted in the low elevation, the growth rates did not vary across elevations. However, the finding that these 'cloud forest' specialists did not survive to grow at the lower elevation plots suggests grim predictions for their persistence in a rapidly warming world. Our hypothesis regarding elevation generalist species survivorship was not supported for the survivorship of *Croton or Heliocarpus.* Contrasting with our hypothesis (H2), the individuals of these three species did not differentially survive based on the source or elevation they were grown in. H2 was also not supported with regard to the growth rate of *Croton* and *Heliocarpus.* Individuals of these two species grew equally well across elevations and among sources. Contrasting with these two species, *Inga* individuals sourced from and planted in low elevation had a higher growth rate than conspecifics planted in low elevation.

Individuals of the three elevation generalist species sourced from cooler, higher elevation climates did not have reduced survivorship and growth in the warmer climates of lower elevations. These results suggest that local, spatially distinct populations of these species are not considerably different in their phenotypic response to a changing climate. These results contrast with studies of alpine and tundra herbs from northern latitudes that differ in their survivorship and growth to different climate (Doak and Morris 2010, Anderson et al. 2015). However, plant species response to climate depending on their source varies among a number of phenotypic performance measures besides survivorship and growth. For example, Anderson et al. 2015 showed that *Boechera stricta* populations from different sources varied in their trait heritability, susceptibility to foliar herbivores, germination, and fecundity that ultimately have an effect on fitness. Plants also may respond to variation in atmospheric CO_2 concentrations depending on their geographical source (Mohan et al. 2004). Accordingly, besides survivorship and growth, local populations of the elevation generalist species in this study may vary in their responses to anthropogenic climate change and associated conditions.

The high-elevation species in this study showed that their response to a warmer climate is mediated via difference survivorship and not a change in their growth rate for the short period of time that they persist in the warm climate. A downslope transplant study of cloud forest epiphytes in Monteverde, Costa Rica documented an increase in mortality of epiphytes when they were exposed to a warmer, drier climate in lower elevations (Nadkarni and Solano 2002). A similar pattern of high elevation epiphyte mortality in warmer and drier climates was also seen in a transplant study in the Peruvian Andes (Rapp and Silman 2014). It is worth noting, however, that both high-elevation species *Viburnum* and *Quercus* survived and grew equally well in mid elevations as in their native high elevations, an elevation change of about 200 m. The mid elevations in this study are downslope from current range margins of *Viburnum* and near the warmer range margins of *Quercus.* This suggests that some tropical montane species may be able to persist in a climate mildly warmer of ~1^{o}C temperature increase, but not in a climate much warmer climate of ~4^{o}C increase.

The decline in performance of high-elevation species in this study suggests that these species are absent from lower elevations because of intolerance to warmer climates particularly affecting survivorship. Climate warming has been attributed to changes in species distributions observed in northern Costa Rican mountains, Northern Andean, and Peruvian Andean Mountains. In these locations, montane tree species currently are tracking their optimal climate upslope via truncated lower edge boundaries with increased mortalities (Feeley et al. 2011, Feeley et al. 2013, Duque et al. 2015). In general, experiments transplanting plants outside of their current geographic distributions also show a high mortality in the novel range (Hargreaves et al. 2014). Our results, combined with these studies, suggest that current distribution of plant species closely correspond to their abiotic tolerance.

Along the elevation gradient, a number of climatic variables may influence the high-elevation species survivorship and growth. Plants from cooler biomes generally grow best at temperatures they experience in their current range (Cunningham and Read 2003), suggesting that intolerance to novel temperatures may play a role in limiting distribution of species across climates (Criddle et al. 1994). Clouds also play a key role in the hydrology of tropical montane forests with cloud-borne precipitation delivering a considerable portion of total precipitation (Still et al. 1999, Foster 2001). Cloud cover also creates unique light conditions that may enable montane species to occupy their current location and alleviate drought stress (Hölscher 2008). The unique hydrology of tropical montane forests has likely led to species in these forests being drought intolerant and potentially vulnerable to a warmer, drier climates (Foster 2001, Hölscher 2008, Rapp and Silman 2014). A combination of the changes in these abiotic variables along the elevation gradient may contribute to the reduced survivorship seen in lower elevation plots.

Besides abiotic variables, a number of biotic variables could also affect the survivorship of *Quercus* and *Viburnum* planted in low elevations. Lower elevations may have plant antagonists such as insect and other invertebrate herbivores and fungal pathogens that may contribute to the high mortality of high-elevation species. Insect foliar herbivores are known to vary along elevation gradients and are known to affect plants from different environments disproportionately (Rasmann et al. 2014, Anderson et al. 2015). However, whether herbivores exert a strong enough influence to limit range sizes needs to be examined with experimental studies (Maron and Crone 2006). Similarly, soil communities, especially fungal pathogens, are known to affect plant relative abundance in tropical forests (Mangan et al. 2010b, Bagchi et al. 2014). Plants also benefit from the presence of a soil fungal mutualists such as mycorrhizae (Mangan et al. 2010a, Mohan et al. 2014). Taken together, a combination of potential absence of best adapted soil mutualists and presence of novel fungal pathogens in lower elevations may contribute to the high-elevation species' absence from lower elevations.

Conclusions

Our results support the recent observations of increased mortality of higher elevation species resulting in communities comprised of a higher proportion of warm-climate associated species. Our results, lending support to the observations of species migrations upslope, show that a warmer climate results in higher mortality for higher elevation/colder climate associated species at considerably warmer (~4^{o}C) temperatures. Studies also suggest along with cool climate ward retreat of some species, other species are expanding their range both in tropical mountains and in northern latitudes (Mohan et al. 2009, Woodall et al. 2009, Feeley 2012). Interestingly, while growth of *Viburnum,* a high elevation species, did not depend upon the elevation where they were planted, the species survived equally well in ~1˚C warmer mid-elevation plots as they did in their native high-elevation plots. This suggests that perhaps with a climate moderately warmer than found at current high elevation locations, the high elevation species in this study may persist at their current location.

The elevation generalists in this study survived equally well across elevations and origins. Similarly their survivorship was not negatively affected by warmer climate conditions. And low-elevation sourced Inga grew better when planted at warmer low-elevation plots than at the cooler plots in our study. In our landscape, it is possible that with upslope retreat of higher elevation plants, the generalist species adapted to a wider range of conditions and with higher dispersal ability may become more abundant with climate change. In order to understand future changes in high-elevation species distribution and forest composition, we need more manipulative studies lending mechanistic understanding of the distributions of high-elevation species.

Table 2.1: Mean Kullback-Leibler discrepancy calibration (KLDC) for high-elevation species

Comparision between elevations	*Viburnum costaricanum*		*Quercus insignis*	
	b_o	b_1	b_o	b_1
Low-High	1	1	0.58	0.97
Mid-High	0.59	0.66	0.59	0.68
Mid-Low	0.99	1	0.5	0.85

Table 2.2: Competing models with DIC values for relative growth rate (RGR) of species. DIC values for the best model are in bold.

Species	Model	DIC
High-elevation species		
Q. insignis	~Elevation, random=~Plot+time+ID	-151.7326
	~1, random=~Plot+time+ID	**-154.5034**
V. costaricanum	~Elevation, random=~Plot+Time+ID	-117.6015
	~1, random=~Plot+Time+ID	**-119.9721**
Elevation generalist species		
H. appendiculata	~Elevation*Source, random=~Plot+Time+ID	-335.3438
	~Elevation, random=~Plot+Time+ID	**-339.9005**
	~Source, random=~Plot+Time+ID	-328.4224
	~Elevation+Source, random=~Plot+Time+ID	-337.18
C. draco	~Elevation*Source, random=~Plot+time+ID	-610.0716
	~Elevation, random=~Plot+time+ID	**-615.3571**
	~Source, random=~Plot+time+ID	-614.6681
	~Elevation+Source, random=~Plot+time+ID	-611.6027
I. densiflora	~Elev*Source, random=~plot+Time+ID	-1075.385
	~Elev, random=~plot+Time+ID	-1072.84
	~Elev, random=~plot+Time+ID	-1072.84
	~Elev+Source, random=~plot+Time+ID	**-1075.845**

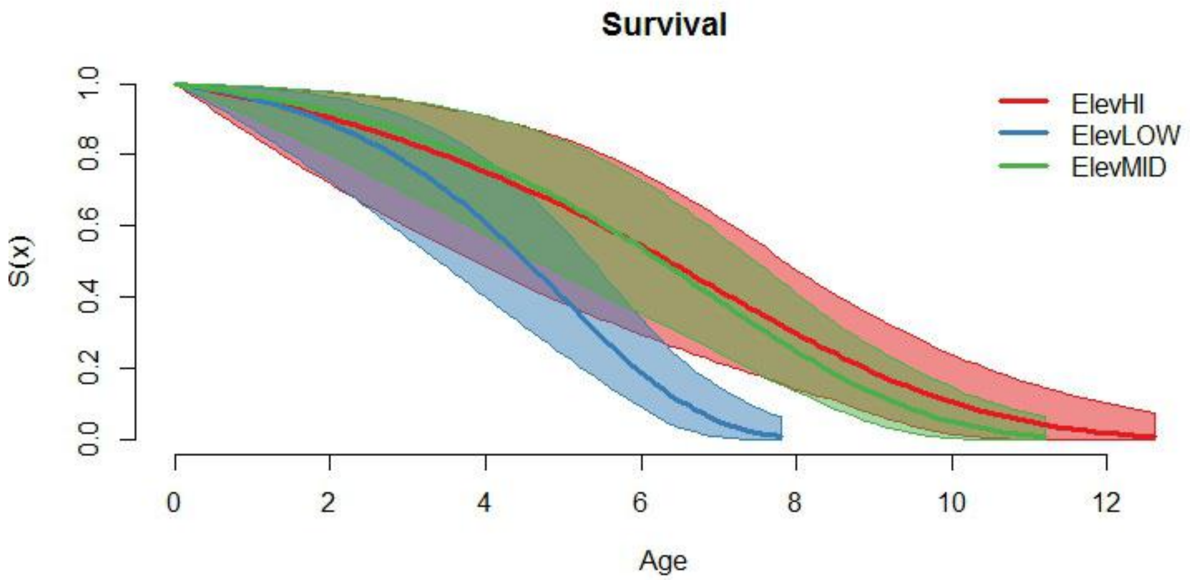

Figure 2.1: Survivorship of *Quercus insignis*, a high elevation specialist, planted in low, middle and high elevations. X axis denotes census intervals, two census intervals constitutes a calendar year. Y axis denotes survival probability at any given time. Survivorship at high and middle elevations was higher than survivorship in low elevations. Shaded areas represent 95% credible intervals.

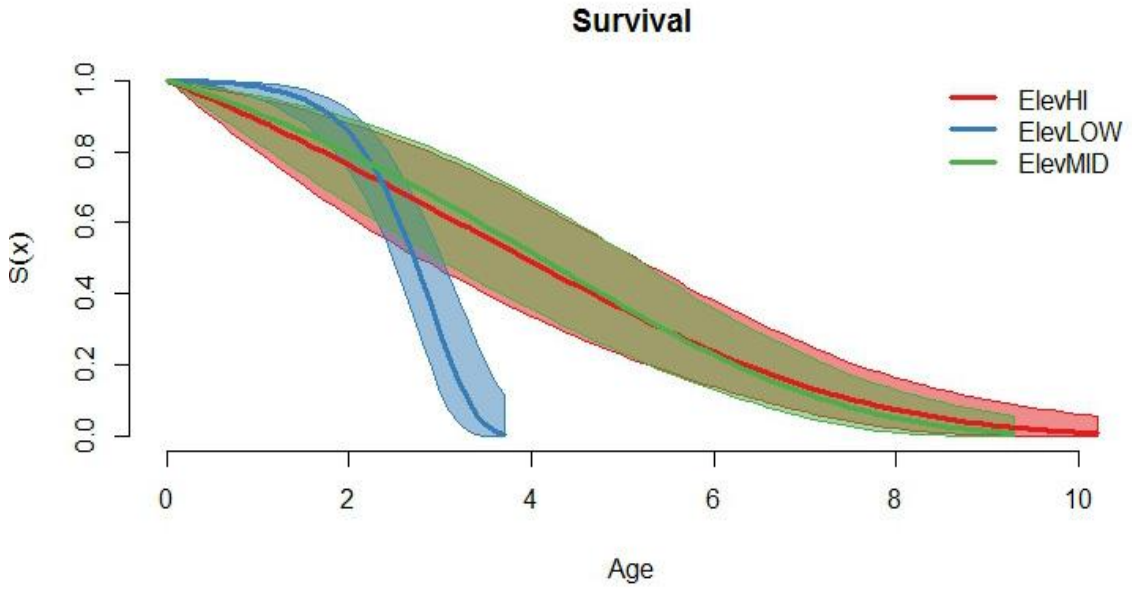

Figure 2.2: Survivorship of *Viburnum costaricanum,* a high elevation specialist, planted in low, middle and high elevations. X axis denotes census intervals, two census intervals constitutes a calendar year. Y axis denotes survival probability at any given time. Survivorship at high and middle elevations was higher than survivorship in low elevations. Shaded areas represent 95% credible intervals.

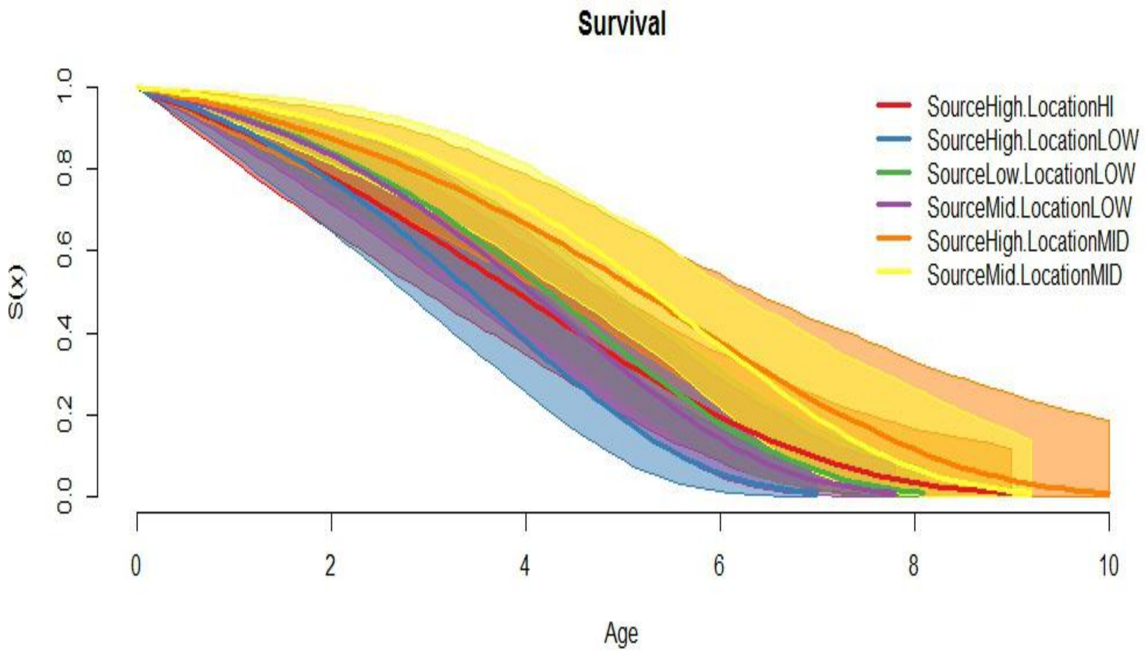

Figure 2.3: Survivorship of different source populations of *Heliocarpus apendiculata*, an elevation generalist, downslope transplanted in low, middle and high elevations. X axis denotes census intervals, two census intervals constitutes a calendar year. Y axis denotes survival probability at any given time. The different source populations grown at different elevations did not show appreciably different survivorship. Shaded areas represent 95% credible intervals.

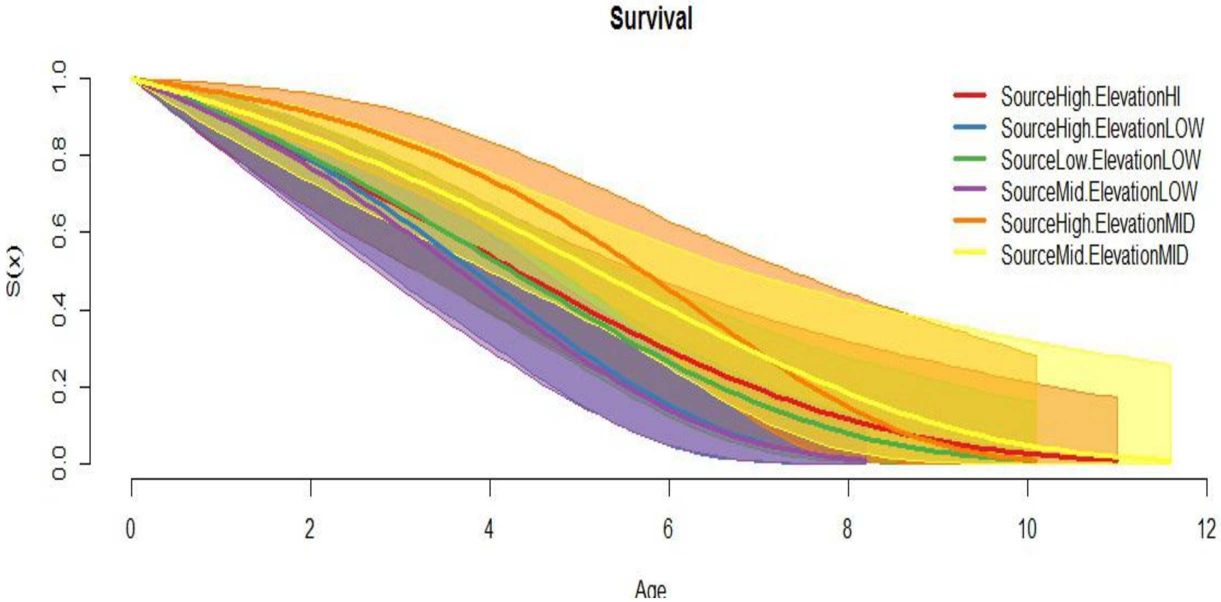

Figure 2.4: Survivorship of different source populations of *Croton draco,* an elevation generalist, downslope transplanted in low, middle and high elevations. X axis denotes census intervals, two census intervals constitutes a calendar year. Y axis denotes survival probability at any given time. The different source populations grown at different elevations did not show appreciably different survivorship. Shaded areas represent 95% credible intervals.

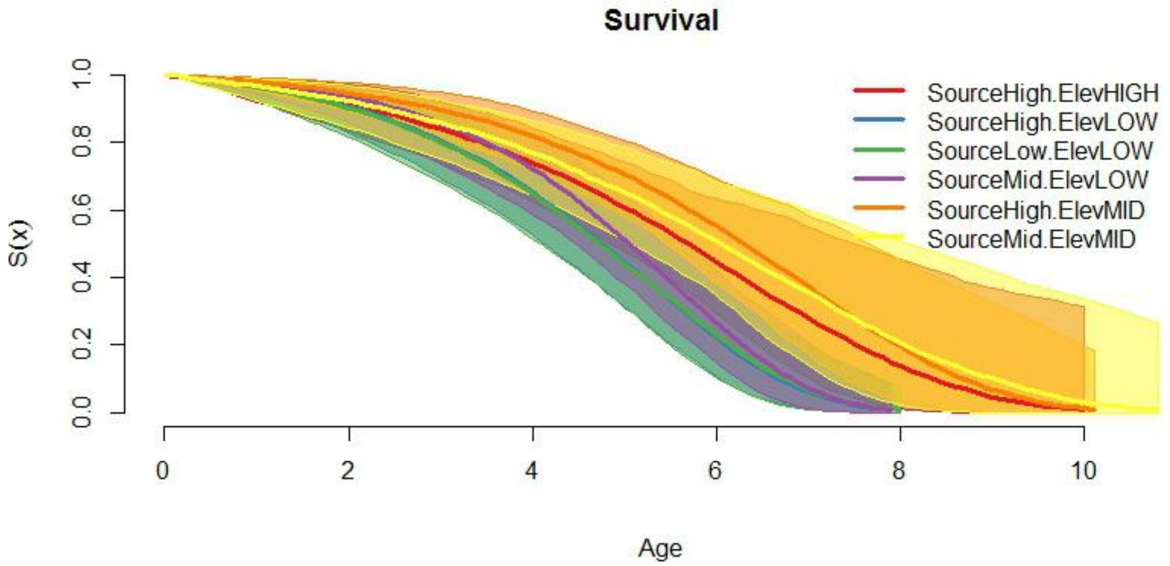

Figure 2.5: Survivorship of different source populations of *Inga densiflora,* an elevation generalist, downslope transplanted in low, middle and high elevations. X axis denotes census intervals, two census intervals constitutes a calendar year. Y axis denotes survival probability at any given time. The different source populations grown at different elevations did not show appreciably different survivorship. Shaded areas represent 95% credible intervals.

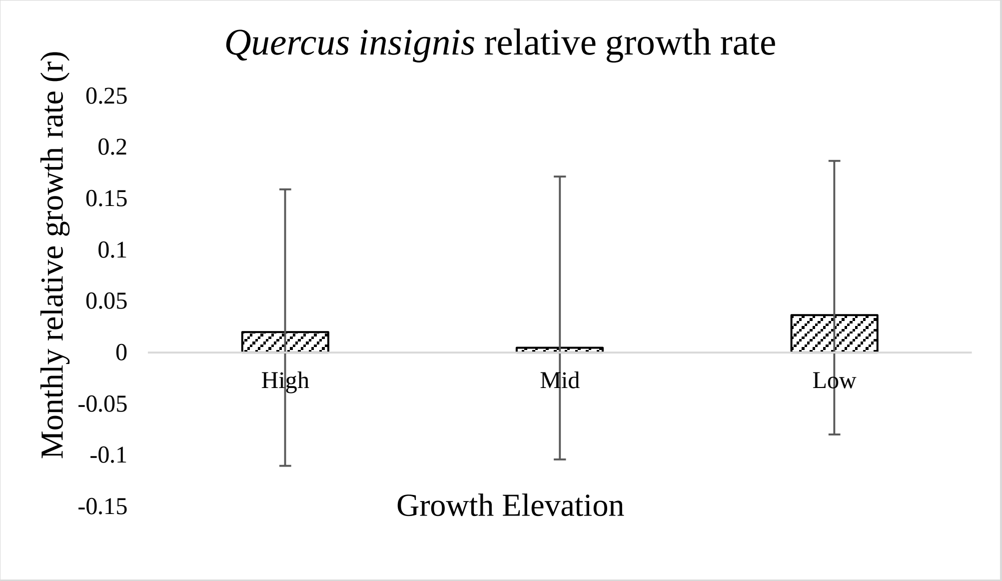

Figure 2.6: Monthly relative growth rate (RGR) of *Quercus insignis* growing at high, mid and low elevations. Growth elevations are plotted on the X axis and RGR plotted on the Y axis. Error bars show 95% credible intervals.

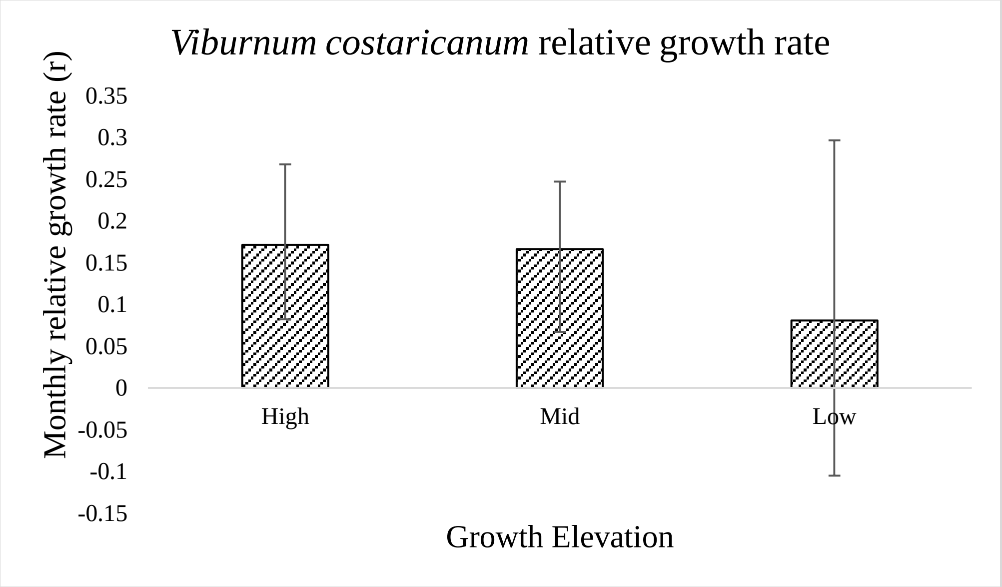

Figure 2.7: Monthly relative growth rate (RGR) of *Viburnum costaricanum* growing at high, mid and low elevations. Growth elevations are plotted on the X axis and RGR plotted on the Y axis. Error bars show 95% credible intervals.

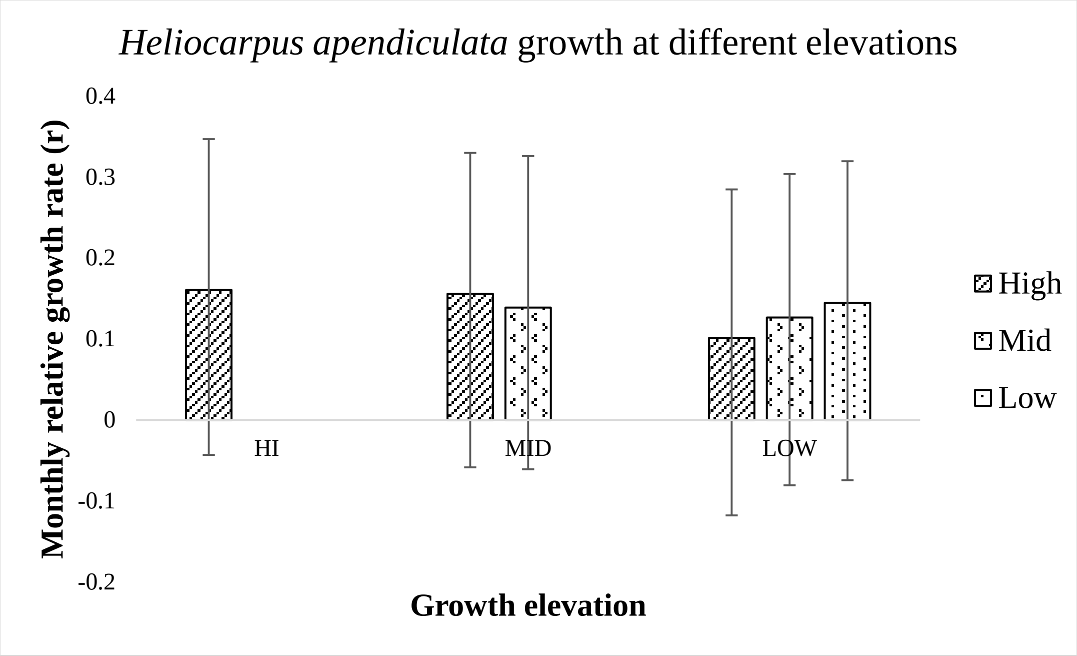

Figure 2.8: Monthly relative growth rate (RGR) of *Heliocarpus appendiculata* growing at high, mid and low elevations. Growth elevations are plotted on the X axis and RGR plotted on the Y axis. Individual bars denote elevation of origin. Error bars show 95% credible intervals.

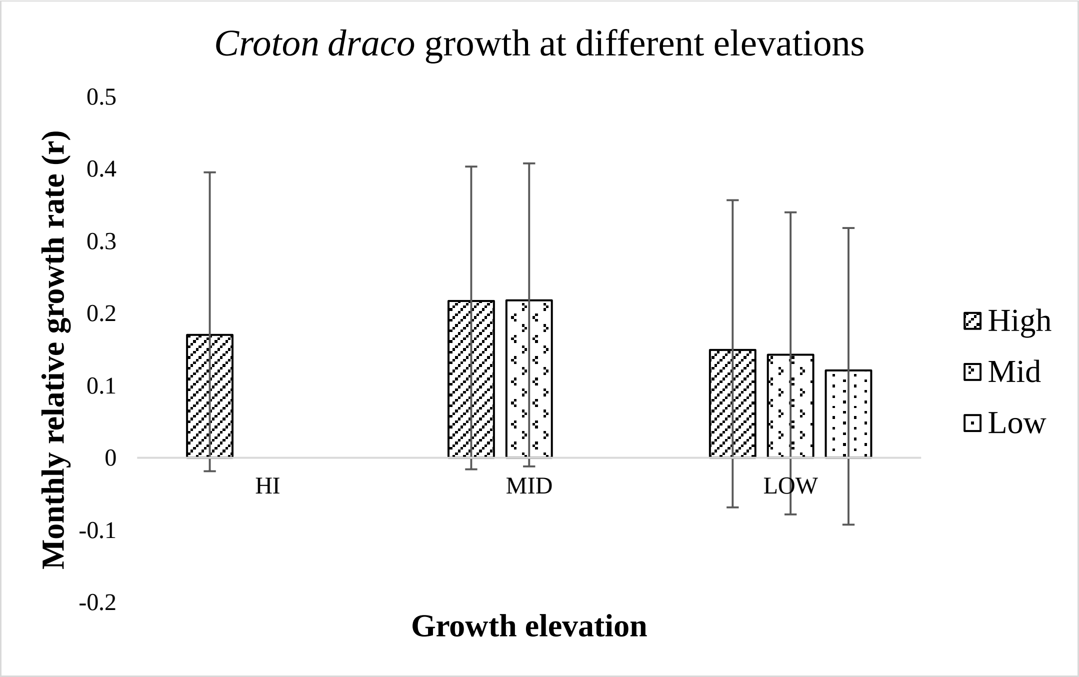

Figure 2.9: Monthly relative growth rate (RGR) of *Croton draco* growing at high, mid and low elevations. Growth elevations are plotted on the X axis and RGR plotted on the Y axis. Individual bars denote elevation of origin. Error bars show 95% credible intervals.

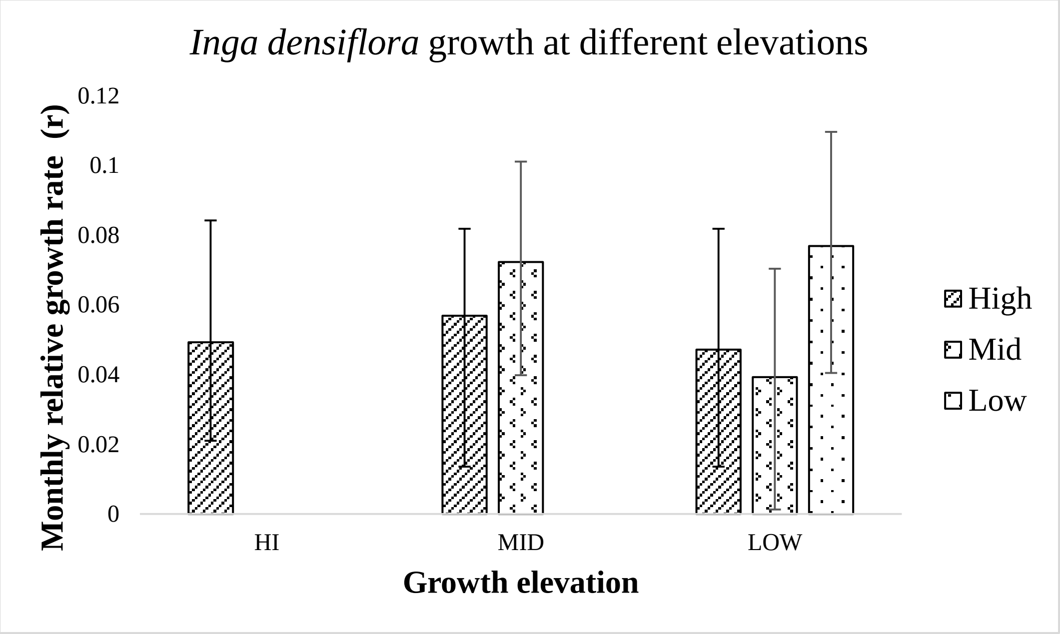

Figure 2.10: Monthly relative growth rate (RGR) of *Inga densiflora* growing at high, mid and low elevations. Growth elevations are plotted on the X axis and RGR plotted on the Y axis. Individual bars denote elevation of origin. Error bars show 95% credible intervals.

Chapter 3

RESPONSE OF HIGH-ELEVATION TROPICAL MONTANE PLANT SPECIES TO NOVEL SOIL COMMUNITIES AND TEMPERATURES REPRESENTING POTENTIAL FUTURE CONDITIONS[1]

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[1] Shafkat Khan, Paul Frankson, Jacqueline Mohan. To be submitted to *Global Change Biology*.

Abstract

How biotic and abiotic variables affect the growth and distribution of a species is a classic research question in ecology. The response of plant species in biologically diverse tropical mountains to novel soil microbial communities and new abiotic conditions with climate change will determine which species will be most likely present in the future. Soil communities exert strong influence on local distributions of tropical tree species and may contribute to elevational range limits of tropical montane plants by interacting with soil temperature to limit growth of individual trees. In this study we investigated how soil communities downslope from a species' current distribution interact with elevated soil temperature to affect the growth of tropical montane plant species. We report on a threemonth shadehouse experiment with seedlings of three tropical montane tree species *Quercus costaricensis* (Fagaceae), *Viburnum costaricanum* (Caprifloiaceae), *Cinnamomum costaricanum* (Lauraceae), and a tropical vine *Passiflora edulis* (Passifloraceae) exposed to soil communities from within and downslope of their elevation in combination with elevated soil temperature. None of the species showed reduced growth when grown with soil communities from downslope of their range. However, all the species grew more with ambient and elevated soil temperature. Taken together, the species in this study may be able to tolerate novel temperatures and non-native soil communities to an extent, pointing to the need to understand other potential factors determining the lower elevation range limits of these species.

Introduction

How tropical forest diversity is determined over space and time is an enduring research theme in ecology (Wallace 1878, Janzen 1967, Connell 1978). The pursuit of understanding of the drivers of tropical diversity has received renewed attention because of predictions of loss of tropical diversity resulting from current anthropogenic climate change (Thomas et al. 2004, Williams and Jackson 2007, Colwell et al. 2008). Understanding how tropical species distributions are constrained by abiotic and biotic factors enables us to examine whether tropical species can exist in conditions dissimilar to what they experience today. This question has been traditionally formulated as whether species currently occupy their fundamental niche, the range of abiotic conditions that species are able to tolerate, or their realized niche, a subset of the fundamental niche, limited by biotic interactions, sensu Hutchinson 1967 (but see (Grinnell 1917, Elton 1927). Is the current distribution of a species mainly determined by the species' response to the abiotic environment or is the distribution of the species also constrained by ecological interactions? If species currently occupy their full fundamental niche, then their current distributions represent the species' individualistic response to the environment and species are intolerant of dissimilar and/or novel conditions. In this case, climate change may cause significant range shifts and range contractions leading to local extirpations and possibly extinction of sensitive tropical species (Williams and Jackson 2007, Laurance et al. 2011b). On the other hand, if species currently occupy their realized niche, i.e., ecological interactions such as competition, dispersal limitation, mutualists, and pathogens limit their current distribution, then tropical communities may be more resilient to climate change. This resilience will be manifest if species can tolerate a broader range of abiotic conditions -- including novel conditions -- than their current distribution would suggest (Hannah 2011), and/or if species benefit from novel biotic interactions in their current or new temperature range.

Simple species distribution models (e.g., Colwell 2008) tend to focus on the fundamental niche concept, assuming that species' current range corresponds to abiotic, typically temperature,tolerance limits, and that species are unable to persist in conditions found beyond their current spatial range. Based on such assumptions, studies in tropical regions, especially mountains, have yielded dire predictions of species range contractions and local extinctions (Thomas et al. 2004, Colwell et al. 2008, Laurance et al. 2011b). However, in other terrestrial biomes, similar assumptions of intolerance have led to potentially inaccurate predictions (Pearson 2003, Buckley et al. 2010). Moreover, these conceptual models also assume that tropical species' response to abiotic conditions are primarily driven by temperature, which reflects historical bias in thinking about species distributions along elevation gradients in tropical mountains (Janzen 1967, Ghalambor et al. 2006).

Soil communities as a biotic factor may have important influence on plant species abundance and distributions. Recent evidence from tropical forests suggests that tropical forest composition is influenced by specific soil fungal pathogens that influence species composition via mortality at seedling stages and reducing species abundance and promoting species coexistence via negative density dependence (Mangan et al. 2010b, Bagchi et al. 2014). Soil pathogens may reduce the growth of a species outside a species' range, resulting in species being limited to their current location. Whether the net effect of soil communities is positive or negative across a species' range, particularly at distribution limits, may constrain the current range of a species. Hence, in temperate grasslands and forests plant-soil feedbacks limit plant abundance at local levels (Packer and Clay 2000).

At a regional level, plant-soil interactions play a role in facilitating invasion and range expansions. Introduced species from Costa Rica invading Hawaiian forests are able to proliferate with release from fungal pathogens (DeWalt et al. 2004). In the case of climate change-induced range expansion, studies from temperate forests suggest that range expanding species experience less pathogen pressure enabling them to successfully invade new areas (Engelkes et al. 2008, McCarthy-Neumann and Ibanez 2012). Colonization and subsequent growth of a species can also be inhibited by absence of symbionts, especially with obligate relationships such as some ectomycorrhizal interactions and orchid-fungal symbiosis (Smith 2009). Although less studied, there is evidence that plants can modify their soil symbiont community to elicit positive plant-soil feedbacks resulting in increased conspecific plant growth (Mangan et al. 2010a). Positive plant-soil feedbacks may lead to competitive advantage via increased growth resulting in persistence in a species' native range. Conversely, loss of competitive advantage via lack of a best-adapted soil community outside of the species' range may limit the range of the species.

The effect of soil communities on plant growth may depend on temperature. Climate change is thought to interact with plants' vulnerability to pathogens (Pautasso et al. 2012), and potentially have important consequences for community composition and diversity (Garrett et al. 2011). For example, *Phytopthora cinnamomi*, a root fungal pathogen, have increased rates of infection on *Quercus suber* and *Quercus ilex* in the Mediterranean with increased temperature (Brasier 1996). Warmer temperatures can also decrease plant resistance to fungal pathogens (Harvell et al. 2002). Evidence from agricultural studies also suggests that plant vulnerability to pathogen effects may increase with temperature (Garrett et al. 2006). Given the difference in soil temperatures along tropical elevation gradients, the soil temperatures at lower elevations may promote pathogenic fungal growth on higher elevation plant species, ultimately limiting the species to their current elevation range.

Projections and simulations in accordance with the near future climate predictions suggest that tropical montane species are going to experience no-analog climates and coexist in novel species combinations in novel communities (Williams and Jackson 2007). If soil communities downslope from species' current ranges are able to disperse to the trailing edge of tree species, the potential negative effect of incoming fungal pathogens may exacerbate range migrations and contractions by limiting recruitment. How species respond to novel soil communities outside of their range in conjunction with novel soil temperatures can explain whether soil biota interact with soil temperature to limit the warmer range limit of tropical montane trees and may indicate how these species will respond to novel conditions of elevated soil temperature and novel soil communities. In this study, we examine the potential role of soil communities, as a biotic factor, in limiting tropical montane species range distributions across native and elevated soil temperatures in order to understand whether the species are currently occupying their fundamental temperature niche and how soil communities may constrain their realized, actual distribution.

This project examined tropical high elevation tree seedling performance with their native soil communities and with novel, out-of-range soil communities across two soil temperature regimes (ambient temperature at 1200 m elevation and 3˚C elevated) to ascertain how soil communities across different soil temperatures may influence growth of seedlings of montane tropical plants. We manipulated soil communities from different elevations as a whole, instead of manipulating pathogens and symbionts individually, because plants experience both pathogens and symbionts together in their environment. We focus on the seedling stage of the focal species in this study as tree seedlings' responses determine, via recruitment into forests of the future, which species will most likely be present in the forests of future altered conditions (Mohan et al. 2007).

We hypothesize that individual plant growth will be lower with lower elevation/out-of-range soil inoculum compared to native/within range inoculum (H1). We also asked how elevated soil temperature affects higher elevation tree species' growth to explore if differential growth in elevated soil temperature contributes to limiting species elevation ranges. If temperature poses an abiotic limitation at the lower elevation range limit of a species, we hypothesize those plants grown at higher than ambient/native temperatures have reduced growth (H2). Lastly, we asked whether soil inocula from within and outside ranges and different soil temperatures interact to limit growth of tropical montane tree species. If the effect of soil microbial communities from within and outside a species' range change with elevated soil temperature, we hypothesize that plants may have reduced growth even in temperatures that they can tolerate (H3) (see *Figure 3.1* for a schematic of the hypotheses). In other words, if plant performance varies with different soil inocula across temperatures, a species may be absent from temperatures and elevations that they can tolerate and be limited to their current temperatures and elevations because of interactions with the soil community.

Methods

To test these hypotheses, we conducted a shadehouse experiment at Las Cruces Biological Station (LCBS), San Vito, costa Rica in September 2012-December 2012. LCBS is on a mountain gradient in Southwestern Costa Rica and situated at 1200 meters above sea level. The location of LCBS enabled us to conduct our experiment at the warmer range limit and lower elevation limit (trailing edge) for *Viburnum costaricanum* and *Cinnamomum costaricanum* and downslope from current distribution of *Quercus costaricensis* (see **Table 3.1** for elevation distributions of study species). The experiment took place in open shadehouses (i.e. not climate controlled) in order to expose the seedlings to ambient conditions and light regimes. Ambient rain was usedwater the experimental plants. In this study, we chose to manipulate belowground organisms as a whole because introducing whole soil communities to plants is a more realistic treatment than introducing isolated individual pathogen and mutualist strains as treatments.

Species descriptions

Viburnum costaricanum (Oerst) Hemsi (family Caprifoliaceae) is a small tree growing up to 15 m tall in disturbed habitats such as treefall gaps, slopes exposed to wind, and in areas undergoing secondary succession. The small fruits are important resources for avian fauna, which also disperse the seeds of this species. This species is thought to be arbuscular mycorrhizal associated. This species is very common in disturbed areas from around 1200 meters and above. *Cinnamomum costaricanum* (Mez & Pittier) Kosterm (family Lauraceae) is a canopy species that are found in mature forests in montane tropical forests from around 1200 meters and above. This species is thought to be arbuscular mycorrhizal associated. This species has a fleshy fruit that is avian dispersed and an important avian food source. *Quercus costaricensis* Liebm (family Fagaceace) is a tropical montane oak species characteristic of upper montane tropical forests in Central America that forms monodominant canopies. The large seed of this species attracts rodents and rodent like mammals that disperse the seeds. This species is ectomycorrhizal associated, but possibly also arbuscular mycorrhizal at seedling stage (Dickie et al. 2001). *Passiflora edulis* Sims (family Passifloraceae) is a tropical vine found in Costa Rica above 1000m. However, we collected the seeds of this species from local commercial fruits and the distribution of the cultivar may be more widespread elevationally than the elevations documented at the INBIO website (www.inbio.ac.cr/bims/PLANTAE.html). As such, we include this species in our final analysis with caution. The three tree species in this study are limited to higher elevation forests, above 1000 meters for *Viburnum* and *Cinnamomum*, and above 2500 m for *Quercus* (Hammel et al. 2005, INBIO 2015{, 2005 #276) and were chosen as representative higher elevation species for this study. We collected the seeds of these species from naturally occurring stands in their native elevations (see **Table 3.1** for species elevation distributions and see below for sources of the seeds for the three tree species). These species are ecologically important as foundational species in these forests because of their abundance and dominance (personal observation), and can be indicators to how higher elevation tropical forests will respond to climate change.

Experimental details

Soil inocula were collected from multiple lower elevation sites (100-600 m elevations) in regions near the villages of Florida and Brunca, in Southern Costa Rica. Soil inocula were collected from microsites in low elevations similar in slope to where adults of the species were usually found in higher elevations. Higher (native) elevation soil inocula for *Viburnum and Cinnamomum,* were collected from areas around Las Cruces Biological Station near San Vito and Las Alturas Biological Station, Coto Brus near parent trees (1200-1350 m). We used the same soil inocula for *Passiflora* as used for *Viburnum* and *Cinnamomum*. Soils for *Quercus* were collected from near parent trees in the Cerro de la Muerte region around 3200 m. Soils were homogenized within elevation to create composite elevation specific soil inocula, except for the high (native) elevation soil inocula for *Quercus*. 200 ml of live soil from either high or low elevation were added to 3.5 L pots containing 3 L of sterilized soil (a 1:1:1 mixture of sterilized lower elevation soil: sterilized higher elevation soil: fungicide treated sand). For the control group, 200 ml of sterilized soil were added to the 3 L potting soil. To treat sand for fungicides, commercially available Chlorothaionil was used. Treated sand was actively washed with water several times, followed by rainwater percolation through the sand for two weeks prior to using the sand in the potting mix, to reduce fungicide load in the potting sand. Seeds were collected from three distinct sources for *Viburnum costaricanum* around 1300 meters near LCBS and two each for *Cinnamomum* from 1200 m at Finca Las Alturas (08.94°, -082.83°) and *Quercus costaricanum* from 3200 m at Cerro de la Muerte (09.59°, -083.91°).

Using a CR10X data logger (Campbell Scientific, Logan, Utah) that controlled circuits of electric resistance heating cables running through the plant pots, we applied the elevated soil temperature treatment. Similar technology has been used to conduct field soil warming experiments in temperate forests (Butler et al. 2012).

Seeds were surface sterilized by soaking in 10% bleach solution for 10 minutes and germinated in sterile soil. Soil inocula were mixed in the rhizosphere of the newly planted seedlings prior to initiating warming of the pots. Soil heating commenced when seedlings were approximately three-four weeks old.

Plants were grown for three months (September 12-December 12, 2012) before final harvest of above ground and belowground mass took place. We chose the length of this study with similar tropical studies (Mangan et al. 2010a, Mangan et al. 2010b) in consideration. During harvest, no plant roots were found to be pot-bound. The harvested plant mass was dried at 60 C for 48 hours before dry mass were recorded.

We analyzed the experimental data for each species separately as a two-way analysis of variance (ANOVA) in R (R Development Core Team 2013). The biomass for each species was normally distributed. We modeled plant biomass as the variable dependent on soil temperature and soil inoculum source, with an interaction term. We used Tukey's Honestly Significant Difference (Tukey's HSD) tests to compare pair-wise difference in means of all of the treatment combinations (i.e., temperature-inocula combinations) for each species.

Results

Elevated soil temperature significantly affected growth of *Cinnamomum* seedlings, with consistently higher growth at elevated temperature ($p<.01$). Soil inocula also significantly affected growth ($P<0.01$), with reduced growth in the native/high elevation inoculum treatment, compared to the other soil inocula treatments. There was no significant interaction effect between the soil inocula and soil temperature treatments (*Figure 3.2*, **Table 3.3**).

Elevated soil temperature resulted in greater growth of *Viburnum seedlings,* ($p<0.01$). Soil inocula also significantly affected growth ($p<0.01$), but there was no significant interaction between the effects of treatment and inoculum source (*Figure 3.3*, **Table 3.3**). Pairwise comparisons with Tukey's HSD showed that at ambient temperature, growth did not differ significantly between inoculum sources. At elevated temperature, growth in both inoculum treatments was significantly greater than in the sterile soil, with no difference between low elevation and high elevation/native soil inocula grown plants (*Figure 3.3*). Using pairwise comparisons to evaluate the temperature effects within each soil inoculum treatment, we found that increased temperature positively affected growth in the low elevation and high elevation inoculum treatments, but temperature did not affect growth of plants grown in sterile soil.

While *Quercus* seedlings showed slightly higher growth at elevated temperatures in each inoculum treatment, neither temperature nor inoculum significantly influenced growth of *Quercus* seedlings, and there was no significant interaction between the elevated soil temperature and soil inocula treatments (*Figure 3.4*, **Table 3.3**).

Similar to the response seen in *Viburnum,* elevated soil temperature increased *Passiflora* biomass ($p<.01$). Soil inocula affected growth of *Passiflora* seedlings ($p<.01$, *Figure 3.5*, **Table 3.3**). Pairwise comparisons (Tukey's HSD) showed that the seedlings grew more when they were inoculated with soil inocula. However, there was no difference between high and low, compared to plants grown in sterile soil. There was no significant interaction between the soil temperature and soil inoculum treatments. Despite no significant interaction, *Passiflora* grown in the elevated temperature and inoculated soil grew more than plants grown in sterile soil inocula or inoculated plants grown in ambient soil temperature.

Taken together, the results do not support H1 regarding the soil inocula that soil communities outside a species' range limit the range boundary of the species by reducing growth of the species. Two of the three tree species (*Viburnum costaricanum* and *Cinnamomum costaricanum*) used in this study and *Passiflora,* a vine, showed positive growth to 3˚ C elevated soil temperature. A similar, but not statistically significant, trend of positive growth (mediated via growth in shoots, not significant) with elevated soil temperature was observed for *Quercus costaricensis*. These results did not support H2 that plants grown at higher than ambient/native temperatures have reduced growth. Moreover, the evidence of increased growth with elevated soil temperature does not support our hypothesis H3 of elevated soil temperature interacting with out-of-range soil inocula to limit range of high elevation tree species by limiting growth of individual plants.

Discussion

Our study shows that it is possible, especially for montane tropical tree species, that plants increase their biomass when soil temperature is above their ambient soil temperature. This effect is only seen when soil microbial community was present. The increase in biomass in the plants in this study can be possibly explained as a fertilization effect from increased plant available soil nitrogen and possible mobilization of other nutrients resulting from elevated soil temperature. Similar increases in plant biomass, especially from increased plant-available nitrogen, have been documented in field warming experiments in tundra environments and temperate forests (Bret-Harte et al. 2001, van Wijk et al. 2004, Butler et al. 2012). Other nutrients such as phosphorus can also be mobilized with higher uptake by mycorrhizae under elevated temperature (Gavito et al. 2003). Given tropical montane forests are thought to be limited by nitrogen and phosphorus (Tanner et al. 1998), potential mobilization of soil nutrients because of higher temperatures may promote high elevation tropical plant growth. However, other environmental factors such as altered moisture availability may counteract any potential growth gain from elevated soil temperature.

The observed increase in plant biomass in the presence of soil microbial inocula for two of the species with elevated soil temperature suggests that the presence of soil microbial communities can mediate the response of plants when faced with novel conditions. This increase in plant biomass with elevated temperature in the presence of a soil community supports the idea that soil microbial communities may mediate plant responses to novel conditions and associated stressors (Van der Putten et al. 2010b, Bardgett et al. 2013) and may play a key role in determining species distributions on tropical mountains with climate change. *Cinnamomum*'s response of increased growth to out-of-range soil inoculum compared to within range soil inoculum may be due to presence of species specific fungal pathogen being limited to *Cinnamomum's* native range. Similar patterns manifest in temperate grasslands where native soils result in reduced growth via negative plant-soil feedbacks (Mills and Bever 1998, Klironomos 2002) and increased growth of *Clidemia hirta* in its novel range in Hawaii compared to its native range in Costa Rica because of absence of pathogenic fungi in its introduced range (DeWalt et al. 2004). *Quercus* did not show an effect of soil inocula, possibly due to its large seed size providing stored energy and nutrients buffering the plants against adverse growing conditions (Mack 1998, Barberis and Dalling 2008).

The results suggest that the three tropical montane tree species used in this study, at the seedling stage, can tolerate abiotic and biotic conditions dissimilar to what they experience in their current location today. Novel climatic conditions are projected to become common in tropical regions, especially in tropical mountains with climate change (Williams and Jackson 2007). The tolerance of non-native, novel conditions indicates that these species may be able to persist in their current location because their current distribution may not be tightly constrained with the range of abiotic conditions they can tolerate, i.e. their fundamental niche. We note with caution that our study examined the response of the four species at seedling stages and response to novel conditions at other life stages may vary. However, documented current migration of tropical trees suggests that montane species are sensitive to ongoing abiotic and possibly biotic changes resulting from anthropogenic climate change (Feeley et al. 2011, Feeley 2012, Feeley et al. 2013). Our study underscores the need to examine how species respond to novel conditions in greater detail, than afforded by bioclimate envelope models and by observational censuses, in order to gain mechanistic understanding of how species are currently distributed with respect to abiotic and biotic variables and how these species will respond to near future climate change.

This study showed that high-elevation plants were growing faster at higher soil temperature, contrasting with long-held notions that tropical montane species only occur at their optimum temperature conditions (Janzen 1967, Colwell et al. 2008). It is important to note, however, that while plants did not grow in competition in the current study, past work demonstrated that plant species distributions could be constrained by competition even when abiotic conditions alone would have been tolerated (Bertness 1991). Microcosm studies show that tropical lowland tree seedlings grow more when exposed to elevated temperatures in growth chambers (Cunningham and Read 2003, Cheesman and Winter 2013a, Heinrich Krause et al. 2013). Our study and previous work suggest tropical species, may be able to tolerate warmer temperature conditions. These results also suggest, if growth increases can correspond to positive or neutral response in other aspects of life history (such as fecundity and recruitment), that species may grow optimally in non-ambient, elevated temperatures and that growth limitation or inhibition by elevated temperature may not be the driver that limits current species distribution as posited by Janzen (1967).

It is likely that plant pathogens experience dispersal limitations and are concentrated around populations of a plant host. It is possible that these pathogens can be host-specific and unable to proliferate without their host and as a result absent from outside of the species range (Gilbert 2002). While soil communities play a key role in affecting plant community composition at local scales (Mangan et al. 2010b, Bagchi et al. 2014), based on this study, soil communities from outside of the plant's range, potentially inclusive of non-native soil pathogens, do not seem to have a more negative effect compared to soil communities found within a species' range and do not seem to play a role in limiting elevation distributions of tropical montane tree species. Effects of soil microbial communities on higher elevation plant growth may interact with effects of other environmental variables that change across elevation and climate gradients, such as moisture availability and soil saturation (Pautasso et al. 2012). Studies examining tropical montane plant growth with different soil microbial communities across environmental gradients are needed to have a predictive understanding of how tropical tree species are distributed across climates currently and how these species will respond to future changes in climate.

The tree seedlings in this study were grown in individual pots and were not competing with seedlings of the same or other species. Competitive interactions with heterospecific trees from lower elevations may affect higher elevation plant performance and ultimately, species ranges (Van der Putten et al. 2010a). Competitive interactions with ecologically similar heterospecifics that occupy similar niche space and are better competitors in warmer climates are likely to limit species ranges along abiotic gradients such as elevation gradients (Sexton et al. 2009). For tropical montane species, as our study suggests, if soil temperature and soil communities do not affect species distributions along elevation gradients, other abiotic factors such as moisture stress may play a key role. Besides abiotic variables such as moisture availability, competition among closely related species may limit species distribution and can result in spatially more limited realized niche than the species' fundamental niche. Studies with multiple tree species and soil inocula collected from multiple sources can answer whether competitive interactions alter plant growth with different abiotic variables such as temperature and moisture, and biotic variables such as different soil microbial communities.

One of the more unexpected consequences of climate change is novel contact between previously geographically separated host and pathogens (Davis and Shaw 2001). In the context of climate change effects on tropical mountains, our results suggest that soil communities containing pathogens from lower elevations, moving into the trailing edge of higher elevation species, which are potential hosts, will not accelerate upslope migration via decreased growth or increased mortality of these higher elevation tree species. However, consequences of current anthropogenic climate change on tropical montane biodiversity remain poorly understood and remain a key research priority to understand effects of climate change on biodiversity.

Conclusions

Our study finds that with novel, increased soil temperature and novel, out-of-range soil microbial communities do not negatively affect tropical montane tree species. The results from this study suggest that tropical montane trees in our study region are able to tolerate abiotic and biotic variables different from what they experience in their current range. These results contrast with predictions of range contractions of tropical montane species in novel conditions and assemblages. These results are also unable offer up any explanation for the current observed changes in Neotropical mountains where tree species are currently migrating upslope. This research underscores the need for experiments and carefully designed field studies to gain a clear understanding of the factors that constrain current species distributions in tropical mountains and elsewhere in order for better predictions of changes in species diversity with anthropogenic climate change, especially in tropical forests.

Table 3.1: Species elevation ranges (INBIO 2015) and source of soil inocula

Species	Species minimum, maximum, and mean (± se) elevation	Low elevation inoculum		High elevation inoculum	
		inoculum source elevation	relation to species range	inoculum source elevation	relation to species range
Q. costaricensis	2400-3600, 3016 ± 90	100-600m	below range	3200 m	Native/within range
C. costaricanum	700-2000, 1368 ± 66	100-600m	below range	1200-1350 m	Native/within range
V. costaricanum	845-3400, 1762 ± 83	100-600m	below range	1200-1350 m	Native/within range
P. edulis	850-2900, 1581 ± 202	100-600m	below range	1200-1350 m	Native/within range

Table 3.2: Summary of experimental design
6 treatment combinations*10 seedlings*4 species, N=60 per species

Soil community	**X**	**Temperature**
Control (sterilized soil)		Ambient (of Las Cruces ~1250 m)
Inoculum from higher (native) elevation (~1350 m in general; ~3200 for *Quercus*)		Elevated (+3-4^{o} C, differential between higher and lower end of the elevation Gradient)
Inoculum from lower elevation (~100-600 m)		

Table 3.3: ANOVA table for biomass (g) of the four species

Effect	*Viburnum*			*Cinnamomum*			*Quercus*			*Passiflora*		
	df	F	p	df	F	p	df	F	p	df	F	p
Soil temp	1	15.35	<.01	1	9.45	<.01	1	2.72	0.10	1	21.24	<.01
Inoculum	2	6.68	<.01	2	5.23	<.01	2	.3	0.74	2	6.65	<.01
Temp x Inoculum	2	2.38	0.1	2	0.18	.84	2	.008	0.99	2	1.02	0.36
Residuals	52			53			54			53		

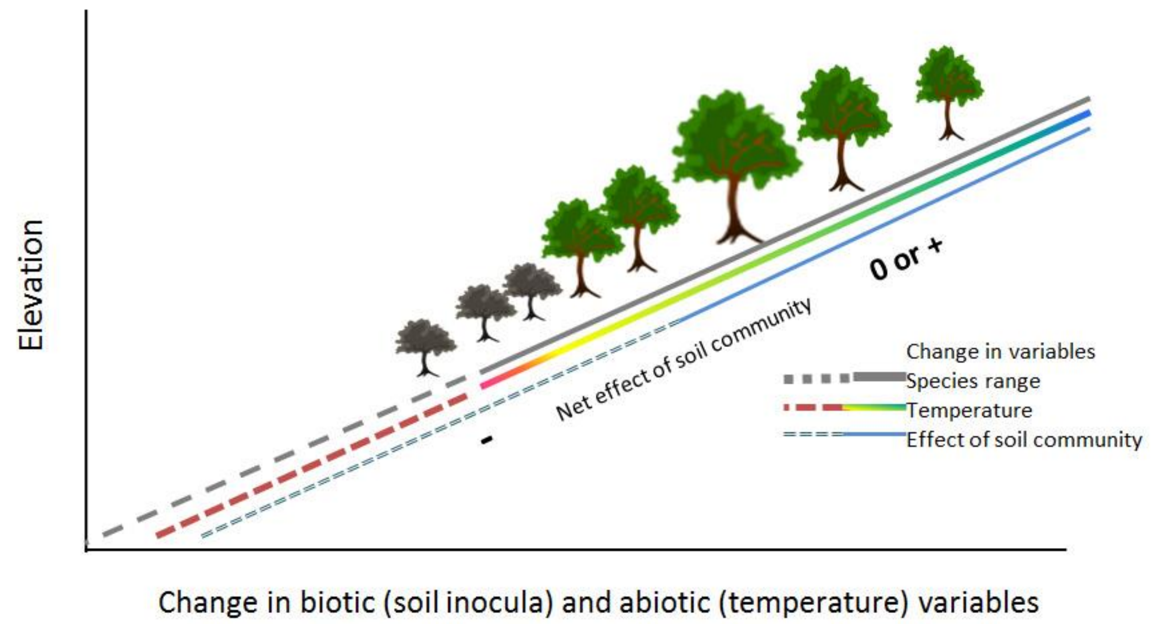

Figure 3.1: The schematic shows hypothetical changes in the effects of soil temperature and soil microbial communities on the growth of individual plants along a species' elevation distribution. The X axis shows changes in soil microbial community and soil temperature; and the Y axis denotes elevation. The top, grey line shows the elevation distribution of a species. The solid portion shows the species current elevation distribution and the dotted portion shows the elevation below the species' range. The bottom line denotes the net effect of the soil community on the growth of the species. This effect, within the species' range, is neutral or positive; and at and outside the range margin is negative (shown with diminished growth of individuals). The middle, multicolored line denotes the temperature across and outside the elevation range of the species. We hypothesize the current elevation distribution of a species follows its temperature tolerance (i.e., the species only exists in soil temperatures it can tolerate and not outside, i.e., the species fundamental niche). The species is best adapted to the temperature within its range, resulting in most optimal growth. As the species encounters novel temperatures, its growth diminishes. Furthermore, the negative effect of the outside of the range soil community may interact with the warmer temperatures to further diminish the growth of the species outside the range to maintain the current distribution (realized niche).

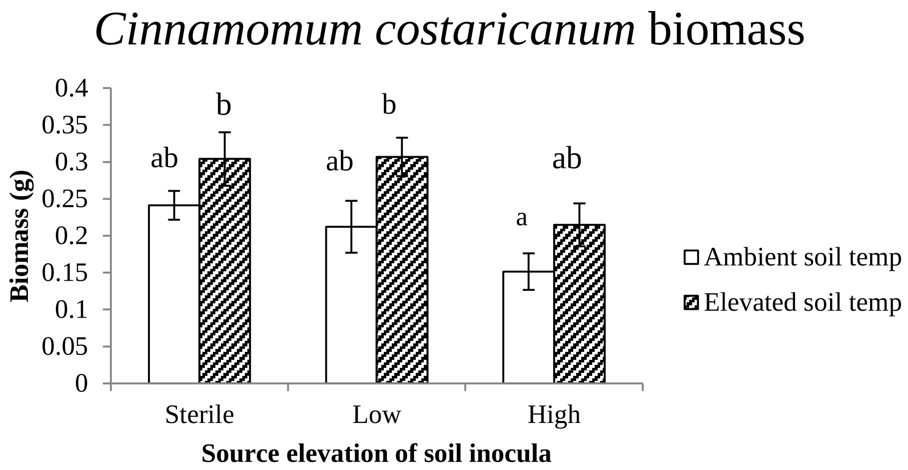

Figure 3.2: Dry biomass (average ± standard error) of *Cinnamomum costaricanum*, a higher elevation tropical tree species is plotted on the Y axis. X axis denotes soil inocula treatments (Sterile, inocula from low elevation (100-500 m) and high elevation (1100-1300 m)). The plain and the striated bars correspond to plants grown in ambient and 3° C elevated soil temperatures. Soil temperature ($p<.01$) and inocula ($p<.01$) were both significant as main effects. The letters denote statistically significant differences at $\propto < 0.05$

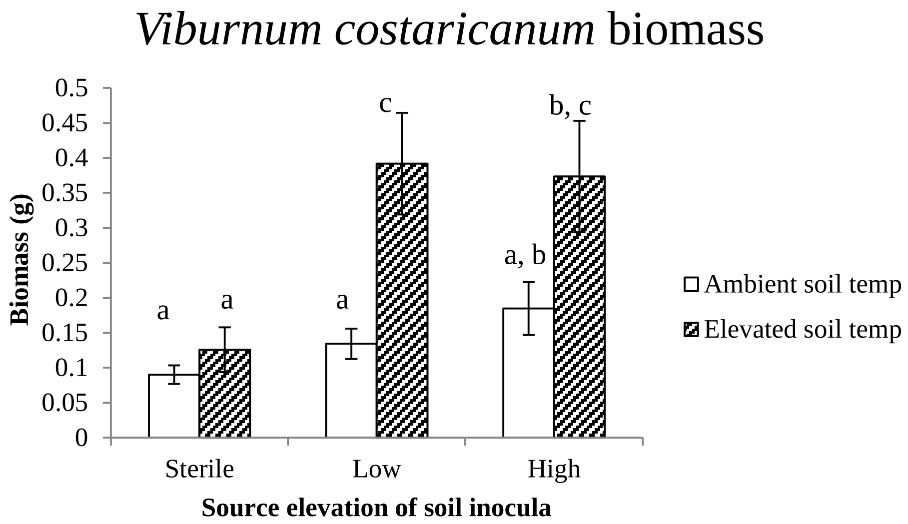

Figure 3.3: Dry biomass (average ± standard error) of *Viburnum costaricanum*, a higher elevation tropical tree species is plotted on the Y axis. X axis denotes soil inocula treatments (Sterile, inocula from low elevation (100-500 m) and high elevation (1100-1300 m)) on the X axis. The plain and the striated bars correspond to plants grown in ambient and 3˚ C elevated soil temperatures. Soil inocula ($p<0.01$) and soil temperature ($p<0.001$) were significant main effects. The letters denote statistically significant differences at $\propto < 0.05$

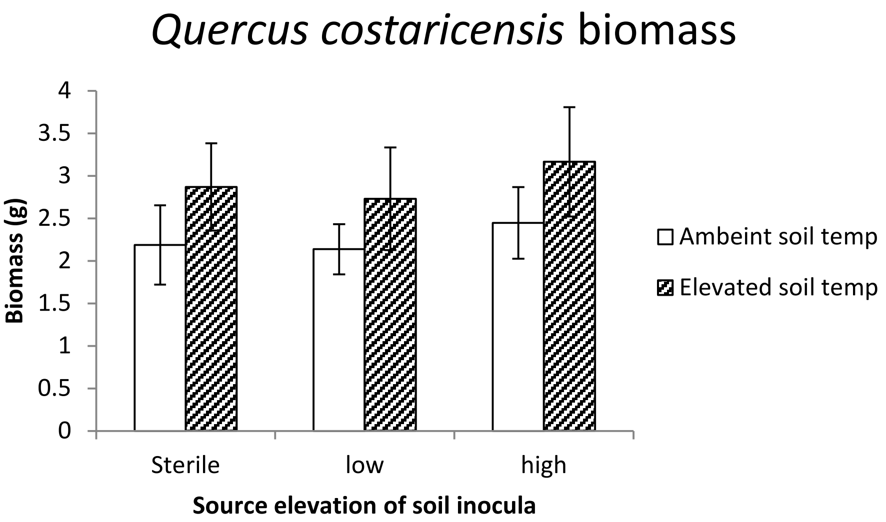

Figure 3.4: Dry biomass (average ± standard error) of *Quercus costaricensis*, a higher elevation tropical tree species is plotted on the Y axis. X axis denotes soil inocula treatments (Sterile, inocula from low elevation (100-500 m) and high elevation (~3000 m)) on the X axis. The plain and the striated bars correspond to plants grown in ambient and 3˚ C elevated soil temperatures. None of the treatment effects was statistically significant.

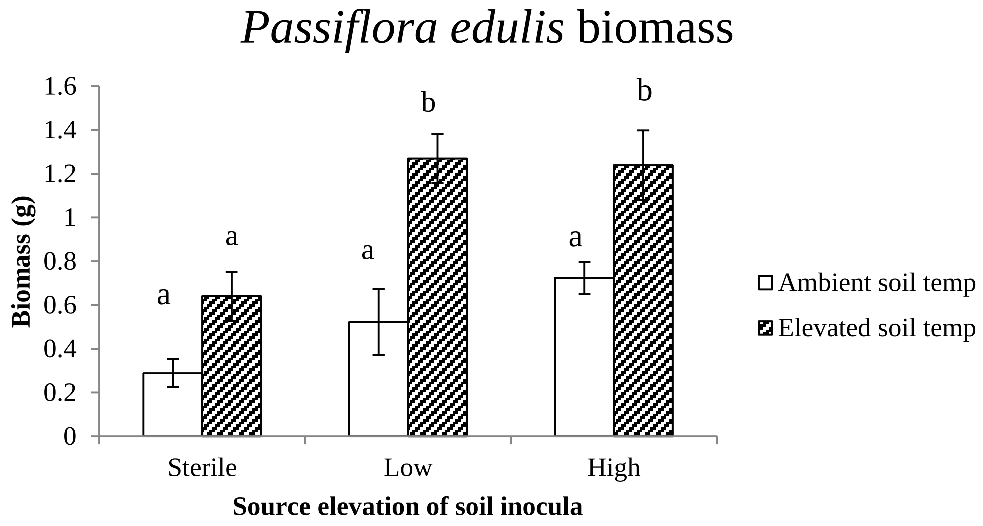

Figure 3.5: Dry biomass (average ± standard error) of *Passiflora edulis*, a higher elevation tropical vine species is plotted on the Y axis. X axis denotes soil inocula treatments (Sterile, inocula from low elevation (100-500 m) and high elevation (1100-1300 m)) on the X axis. The plain and the striated bars correspond to plants grown in ambient and 3˚ C elevated soil temperatures. Soil inocula ($p<0.01$) and soil temperature ($p<0.001$) were significant main effects. The letters denote statistically significant differences at $\propto< 0.05$

Chapter 4

RESPONSE OF HIGH-ELEVATION TROPICAL MONTANE TREES TO FUTURE TEMPERATURE AND MOISTURE CONDITIONS[1]

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[1] Shafkat Khan, Paul Frankson, Andrea Westerband, Jacqueline Mohan. To be submitted to *Global Change Biology*.

Abstract

Understanding how abiotic and biotic variables affect the growth and distribution of species is a classical research pursuit in ecology. How species in biologically diverse tropical forests respond to changing abiotic and biotic conditions with climate change will determine which species will remain in these forests. In this study we seek to understand how changes in temperature and precipitation affect the growth and survivorship of tropical montane tree species. We conducted a three-month shade house study on seedlings of two high-elevation tropical montane tree species, *Quercus insignis* (Fagaceae) and *Viburnum costaricanum* (Caprifloiaceae), exposed to 5°C elevated soil temperatures and novel soil moistures from altered watering regimes.

Neither species showed changes in biomass from altered soil moistures generated by reduced amounts and/or frequencies of watering compared to ambient watering regimes. However, *Quercus* obtained a greater final biomass when grown in elevated soil temperature. Maximum photosynthetic capacity of *Quercus* also increased with higher temperature, while the photosynthetic capacity of *Viburnum* did not differ between temperature treatments. Under the warmest and driest conditions *Viburnum* reached the same size as under current temperature and moisture regimes. Taken together, these two species may be able to tolerate novel temperatures and soil moisture. Further investigations are needed to understand how species in tropical mountains may respond to new abiotic conditions with climate change.

Introduction

Climate in tropical mountains is thought to be stable, with relatively little intra-annual variation in temperature and relatively constant precipitation regimes (Janzen 1967, Foster

2001). Species in tropical mountains are thought to specialize in narrow climate and elevation niches, leading to high biodiversity in these regions (Janzen 1967, Ghalambor et al. 2006, Sheldon et al. 2011). Climate change in this region is projected to decouple and recombine climatic variables such as temperature and precipitation in novel combinations, with increased climatic variability (Williams and Jackson 2007, IPCC 2014). Whether organisms on tropical mountains and elsewhere can tolerate ranges of climatic conditions wider than the conditions they experience today will be key to determining whether species can persist at their current locations with climate change, or whether organisms will need to migrate in order to track suitable climatic conditions. Recent evidence of upslope migration of tropical montane biota (Feeley et al. 2011, Feeley 2012, Feeley et al. 2013, Freeman and Freeman 2014) suggest that these communities are responding to current climate change, but whether intrinsic intolerance to climate or higher dispersal triggered by climate change are driving this pattern is unclear (Rehm 2014).

The question of whether organisms occupy the entire niche space of conditions they can tolerate or whether they occupy a subset of conditions that they can tolerate, i.e. whether species occupy their fundamental niche or their realized niche, is a classic question in ecology (Grinnell 1917, Elton 1927, Hutchinson 1957, Silvertown 2004). With anthropogenic climate change, understanding the spatial and temporal distribution of species with respect to their fundamental and/or realized niches has gained a renewed impetus (Thomas et al. 2004, Hannah 2011, Bellard et al. 2012). Recent efforts have focused on understanding how species are distributed with respect to climate (Sexton et al. 2009, Lavergne et al. 2010). Species distribution models assume that current species distributions represent their fundamental niche, and they are unable to tolerate conditions dissimilar to what is found in their range today (Pearson 2003, Buckley et al.

2010). However, if current distributions are constrained by biotic interactions or are not indicative of the species' fundamental niche, future distributions may not simply depend on where current climatic conditions are located in the future.

Currently, bioclimate envelope models and related predictions, especially for tropical mountains, tend to simplify the current and future species distributions as driven mainly by temperature (Colwell et al. 2008, Sheldon et al. 2011, Freeman and Freeman 2014). This leaning reflects the historical bias in thinking of tropical montane species' distributions being influenced mainly by temperature (Janzen 1967). Combined with the paucity of species distribution data in tropical regions (Feeley and Silman 2011a), the assumption of species distributions tracking a certain temperature inhibits our understanding of how these forests will undergo changes in composition with multiple dimensions of climate change. Other climatic and abiotic variables, such as precipitation and edaphic conditions, strongly influence species' distributions, especially in tropical regions (Clark et al. 1998, Clark et al. 1999a, Engelbrecht et al. 2007, Laurance et al. 2010). For example, precipitation seems to be a strong driver of species composition in tropical lowland forests of Panama and in Amazonia (Engelbrecht et al. 2005, Engelbrecht et al. 2007, Nepstad et al. 2007). When coupled with temperature change, increased precipitation variability is projected to influence tropical biodiversity adversely (Bonebrake and Mastrandrea 2010). As a result, modeling species distribution in relation to temperature only has limited utility in understanding how these species are distributed in space currently or how these species will be distributed in the future.

Anthropogenic climate change is projected to reduce precipitation amount and frequency globally with Central America projected to undergo up to 25% reduction in summer precipitation (Rauscher et al. 2008). Associated with changes in precipitation amount, models also project an increase in the frequency of intense precipitation events (Rauscher et al. 2008, IPCC 2014). Despite projected changes in precipitation in Central America, and elsewhere in the tropics, the effects of future reductions in precipitation are poorly understood (Weltzin et al. 2003). Soil moisture deficit and drought can change the species composition of tropical forests by increasing mortality of drought intolerant species (Engelbrecht et al. 2007, Nepstad et al. 2007, Phillips et al. 2010). Tropical montane forests may be exceptionally sensitive to drought, because they depend on relatively constant precipitation (Foster 2001). A downslope transplant study in montane Costa Rica suggests that reduced cloud cover, via reduced moisture, can increase mortality and possibly limit current elevation ranges of cloud forest epiphytes (Nadkarni and Solano 2002). In the mountains of Central America, however, temperatures are projected to increase and precipitation projected to decrease (Rauscher et al. 2008, IPCC 2014). As a result, species may be more susceptible to local extinctions than can be predicted from temperature increase alone.

The performance of early life stages such as seedlings and juvenile plants are important determinants of future forest composition because how juvenile plants respond to changing conditions determine what species will be most likely be present in future communities (Beckage and Clark 2003, Mohan et al. 2007). How novel climate conditions in tropical mountains affect juvenile trees of different species can tell us how these species will respond to climate change in the near future. The dearth of precipitation studies in tropical systems, especially in the montane tropical forests, hinders our understanding of compositional changes in these forests. These systems are ripe for exploring questions related to the effects of climate change-induced moisture regimen shifts on the composition and function of montane tropical forests.

In order to understand how changes in temperature and moisture may affect growth of tropical montane species, we report on an experiment conducted in southwestern Costa Rica. For this study, we focused on the effects of changing precipitation, mediated via soil moisture, and elevated soil temperature. We asked the following questions in this study:

1) How does change in precipitation, via changes in soil moisture, affect individual growth of tropical higher elevation tree species?

2) How does elevated soil temperature affect individual growth of tropical higher elevation tree species?

3) How do elevated soil temperature and change in precipitation interact to affect individual growth of tropical higher elevation tree species?

4) How do a combination of elevated soil temperature and altered precipitation regimes affect maximum photosynthetic capacity (A_{max})?

Methods

We conducted a shadehouse experiment at Las Cruces Biological Station (LCBS) in southwestern Costa Rica (08.785°, -082.958°). LCBS is on a mountain gradient, with shadehouse facilities situated at 1200 meters above sea level, enabling us to conduct our experiment near the lower edge of the high elevation species range used in this study. The mean annual temperature in this region is between 19 and 21˚ C. The average rainfall in this region is around 4000mm per year (meteorological data for LCBs can be accessed at http://www.ots.ac.cr).

Plants in the shadehouse were exposed to ambient relative humidity and grown in partially sunny conditions (approximately one-third of full sun). We measured photosynthetically active radiation (PAR) using a PAR meter on two separate days during the experiment, which gave a peak value of around 1000 µmol $m^{-2}s^{-1}$ around midday in the shadehouse.

Species description

We selected *Quercus insignis* (Fagaceae) and *Viburnum costaricanum* (Caprifoliaceae) as representative montane trees of this region. The mean elevation (average±s.e.) for *Quercus insignis* is 1310 (±72) m and for *Viburnum costaricanum* is 1810 (±80) m (INBIO 2015). Both these species are ecologically important, characteristic species of montane forests in Central American mountains. *Quercus insignis* is an emergent, canopy dominant species found in primary and mature secondary forests. Its large acorns are dispersed by rodents of various sizes and are important wildlife forage, and contain relatively abundant seed resources. *Viburnum costaricanum* is a medium sized, shade intolerant tree found in open areas such as forest edges, tree fall gaps, and abandoned pastures. The small fruits of *Viburnum* are dispersed by birds and are important avian forage.

Seeds of *Quercus insignis* and *Viburnum costaricanum* were collected from local trees at 1200 m above sea level for *Q. insignis,* and 1300 m for *V. costaricanum* near Las Cruces Biological Station. We collected additional seeds of *Quercus insignis* from trees around 1300 m near Finca Las Alturas (08.945°, -082.833°). Seedlings were grown from seeds in native soil before being transferred to the experimental pots. We randomly allocated 2-3 month old seedlings into the experimental containers. Potting soil was a mix of 2:1 local soil and coarse sand. The soil was collected from local sources near forests within the Las Cruces Biological Station and used unsterilized in the pots. The sand was mixed in to prevent waterlogging in pots.

Experimental design

Our experimental design consisted of two levels of soil temperature (ambient and +5˚C elevated above ambient) and four levels of precipitation treatments (**Table 4.1**). The ambient precipitation amount and frequency of rainy season precipitation were determined in the following manner. First, precipitation frequency during the early rainy season months (April-September) of 2009-2012 was calculated based on the meteorological data of Las Cruces Biological Station (accessible at http://www.ots.ac.cr/meteoro/default.php?pestacion=3). During April-September, the average precipitation frequency is about once daily (ambient frequency). Soil moisture data from 2011 logged at 1350 m elevation near Las Cruces (Khan et al, unpublished) suggested that field soil, during the early rainy season, retains on average around 30% volumetric soil moisture at 10 cm depth. We conducted a preliminary trial to determine the appropriate amount of water to add per day to achieve 30% volumetric soil moisture for ambient amount and ambient frequency treatment (control). Precipitation projections for end-of-century climate in Central America are 20-30% reduction in rainy season precipitation amount (Rauscher et al. 2008). Therefore, in the second treatment, we administered 20% less water per day than the control (ambient) treatment. One of the predictions of future precipitation with warmer climate is intense, more episodic and less frequent precipitation (IPCC 2014). Therefore, in the third precipitation treatment we again administered 20% less precipitation in total, but at 1/3 frequency as the second treatment. Lastly, in the dry season (January-March), precipitation is ca. one third the amount of the early rainy season months and the frequency is also approximately one third. Therefore, the last precipitation treatment we administered was a 66% reduction of the amount of water applied for ambient treatment, applied every third day.

The watering treatments were factored with two levels of soil temperature treatments: ambient (control) air temperature of Las Cruces Biological Station and 5˚C elevated above ambient (warmed treatment). Warming treatment was administered by passing high resistance heating cables through the containers and using CR10X data logger as a thermostat (Campbell Scientific, Logan, Utah), similar to the soil warming technology used by Melillo et al. (2011).

For each treatment combination, we used 15 shadehouse germinated seedlings each of *Viburnum costaricanum* (Caprifoliaceae) and *Quercus insignis* (Fagaceae). *Viburnum* seedlings were grown in 3.5 L pots and *Quercus* seedlings were grown in 5 L pots. The two pot sizes were chosen to accommodate the different seedling sizes of *Quercus* and *Viburnum*, with *Quercus* seedlings being larger and with longer tap root system than *Viburnum* seedlings. During the course of the study, daily measurements of volumetric soil moisture in all the pots were conducted using a 10-cm double pronged TDR probe (Hydrosense, Campbell scientific, Logan, Utah) prior to daily watering.

At the end of the study (85 days), we harvested total plant biomass. Plants were checked during and at the end of the study for pathogen damage and no visible effects were observed in any of the treatments. During harvest, we inspected plants for evidence of root binding and found none. Root biomass of *Viburnum* is estimated from shoot height using allometric equations based on a dataset from a previous study (Khan et al, unpublished), as *Viburnum* roots were saved for a future study. Plants were dried in the drying oven at 50˚ C for 48 hours before dry biomass were recorded.

Photosynthesis measurements

Photosynthetic performance was assessed in the shadehouse based on rates of gas exchange, using a portable gas exchange system (LI-6400 XT; Li-Cor, Lincoln, NE, USA). After

79 days in the shadehouse, we measured net photosynthesis on one leaf per individual, for two random individuals per species. For preliminary assessment of PAR levels to use for subsequent survey measurements, we constructed a light response curve using estimates of photosynthesis taken between 0900 and 1100 hours, to minimize any confounding effects of sampling during the hottest hours of the day. Only mature leaves were used, and were selected to have little or no damage (evidence of senescence or herbivory), and maximum exposure to sunlight. Leaves were exposed to a gradient of eight light levels from 0 to 1000 μmol PAR m^{-2} s^{-1} (starting at high light and decreasing to zero) and we measured the rate of exchange of CO_2 and H_2O from the leaf at each light level to construct a light curve. Once the light curve was constructed, we visually assessed at what level of PAR photosynthetic rates were saturated (A_{max}).

Following the light curves, we randomly selected one undamaged, fully grown new upper leaf per plant on each individual and exposed the leaf surface to 1000 μmol PAR m^{-2} s^{-1} for up to five minutes, or when the photosynthetic rate became stable (whichever occurred first). Across all survey measurements, CO_2 concentration was 400 μmol m^{-2} s^{-1}, leaf temperature was 25°C±2, and average relative humidity was 58%±8. These measurements were conducted between 0900 and 1300 hours on July 4th and July 7th 2013. On July 4th, a total of 45 *Viburnum* seedlings sufficiently large enough were selected across treatments for photosynthesis, as a majority of *Viburnum* seedlings were too small for the leaf chamber of the Li-COR. On July 7th, 2013, we estimated A_{max} for all 120 *Quercus insignis* seedlings.

Effects of water input on soil moisture

For both ambient and elevated temperatures, soil moisture with ambient amount and frequency of watering successfully maintained moisture near 30% field capacity for both *Quercus* and *Viburnum* plants (Supplementary *Figure B1* & *B2*). Similarly, at both ambient and elevated temperatures, and for both species, a 20% reduction in watering amount at daily frequency resulted in only small decreases in soil moisture (ca. 29% for *Quercus*, and 27% for *Viburnum*). A 20% reduction in watering amount applied only every third day further reduced soil moisture to ca. 27% and 25% for ambient and elevated temperatures, respectively, for both tree species. Finally, the combination of a 66% reduction in watering amount applied at 1/3 frequency, emulating current dry-season precipitation conditions with infrequent rainfall, resulted in the greatest reductions in soil moisture, particularly under elevated temperature. Whereas ambient temperature *Quercus* maintained 25% soil moisture under these watering treatments, heated *Quercus* had moisture readings averaging 13%. *Viburnum* had moisture levels averaging 20% and 12%, respectively, at ambient and elevated temperatures at this driest watering treatment.

Statistical analyses

Analyses of total biomass as a function of temperature and watering regimes were done separately for each tree species, using a linear model with temperature and watering as main additive effects in R (R Development Core Team 2013). Temperature-by-Watering interaction terms were initially included in the statistical models, but final analyses excluded interactions as interactions did not explain significant variation in the data. *Quercus* shoot and root biomass were analyzed as linear models, with temperature and watering as the main additive effects. Total biomass of *Quercus* and *Viburnum* were also regressed against actual soil moisture (SM) and the coefficient of variation (CV) in soil moisture as predictor variables (**Supplementary Table B1)**. However, both SM and CV(SM) were weak predictors of biomass for both species and these analyses are excluded from the main results and presented in the supplementary information.

Survey measurements of A_{max} for both species were analyzed as linear models, with temperature and watering treatments as additive factors. Photosynthesis data for *Viburnum* were square root transformed for normality.

Results

Watering and temperature effects on plant biomass

Viburnum and *Quercus* responded to the treatments differently. For *Viburnum* seedlings, the main effects of watering and temperature did not significantly affect biomass (p=0.4 and 0.56, respectively, *Figure 4.1*). The interaction between watering and temperature also did not significantly influence biomass (p=0.4). For *Quercus* seedlings, elevated temperature tended to increase total seedling biomass (p=0.06) across all watering treatments, but there was no significant effect of watering on total biomass (p=0.18, *Figure 4.2*). The interaction between watering and temperature levels were also not significant for *Quercus* (p=0.58). Analyzing shoot and root biomass of *Quercus* seedlings separately, we found that increased temperature significantly increased shoot biomass (p=0.02, *Figure 4.3*), but not root biomass (p=0.3, *Figure 4.4*) of *Quercus* seedlings, and the shoot-to-root ratios did not significantly change (Supplementary *Figure A2.5*). Similar to total biomass, neither shoot nor root biomass of *Quercus* differed between watering treatments, nor were the interaction between soil temperature and watering treatments significant (**Table 2**).

Watering and temperature effects on Photosynthesis

Similar to the growth results A_{max} of *Viburnum* seedlings did not respond to either the temperature treatment (p=0.98) or the moisture treatments (p=0.28, *Figure 4.5*). Also similar to the growth responses of the species, A_{max} of *Quercus* responded positively to elevated temperature (p=0.02), but did not differ among the watering treatments (p=0.56, *Figure 4.6*, **Table 3**).

Discussion

During the course of the study period, *Quercus* seedlings grew more when soil temperature was elevated by 5˚C, but were not influenced by variations in watering quantity or frequency. *Viburnum* grew equally well among the treatments. Taken together, these results suggest that, at the seedling stage, *Quercus* and *Viburnum* are able to tolerate the novel soil moisture and temperature regimes tested in this study representing climate conditions in near-future scenarios. It is, however, possible that the soil moistures were not sufficiently low to negatively affect plant growth. It is also possible that regular application of less frequent watering regime is not a realistic reflection of how climate change will cause stochastic changes in moisture regimes and in weather patterns in general (Knapp et al. 2015). Besides the less frequent watering regime tested in this study, extended dry periods during the rainy season or increased aridity during dry season may be detrimental to plant growth in tropical mountains (Still et al. 1999, Weltzin et al. 2003).

At least initially, seedlings of the montane tree species used in this study were not negatively affected by elevated soil temperatures. *Quercus* grew better with elevated soil temperature, similar to what has been documented for tree species in the lowland tropics, in response to increased temperature (Cunningham and Read 2003, Cheesman and Winter 2013a). Similar to the trend seen in *Quercus*, in two Australian *Eucalyptus* species, cool origin provenances positively responded to a 3.5˚ C warming, suggesting that cooler elevation plants may benefit from increased temperature (Drake et al. 2015). Evidence from microcosm studies in the lowland tropical forests of Panama also suggest that lowland tropical forest tree species are able to grow equally well at temperatures several degrees above the current temperatures they experience up to 35°C (Cheesman and Winter 2013b, Heinrich Krause et al. 2013).

The increase in aboveground biomass that we observed may be attributed to warming-induced increases in nitrogen (N) availability (Melillo et al. 2011), along with potential mobilization of other soil nutrients. An increase in plant available N was observed in an N-limited Arctic tundra system, where *Betula nana* increased in aboveground biomass when nitrogen availability increased from soil warming (van Wijk et al. 2004). A similar mechanism of increase in plant available nitrogen and possibly other limiting nutrients could explain the increased growth of *Quercus* grown under elevated temperature. In the N-limited montane tropics, in the short term, an increase in N availability from warmer soils may increase shoot growth, and could counter the potentially negative effects of drought.

Photosynthesis of *Quercus*, similar to its growth, increased with elevated soil temperature. In contrast, increased temperature did not increase photosynthesis rates of *Viburnum*, although the small sample size for *Viburnum* likely contributed to the high variability in the data. Plants grown at a higher temperature have a higher optimal temperature of photosynthesis rate as long as growth temperature is not too high or low (Berry and Bjorkman 1980). This acclimation of photosynthesis likely contributed to the positive response of photosynthesis rate of *Quercus* grown in elevated temperature. The different response of photosynthetic rates for the two species in this study can be attributed to the individualistic ways photosynthetic processes and machinery of a given plant species respond to temperature (Hikosaka et al. 2006) Surprisingly, drought treatments did not affect photosynthesis for either species, suggesting that these two species are highly water use efficient (Chaves et al. 2003). As an early successional pioneer species, *Viburnum* may be more susceptible to extended droughts in the field, because early successional species are often drought intolerant (Bazzaz 1996).

Do these species currently occupy only a subset of conditions they can tolerate?

Our results suggest that in terms of elevated soil temperature and variable soil moisture regimes, these two tropical montane tree species, at least at the seedling stage, can tolerate conditions dissimilar to their current native conditions. These species and the forest communities they comprise may thus be resilient to climate change due to plasticity of their growth and physiology, rather than simply migrating upslope to track the climate they currently occupy (Morris et al. 2008). Based on this study, the response of higher elevation tropical species appears to be more nuanced than model predictions, posited by Colwell et al (2008).

Assuming no ontogenetic shifts in response and that overall recruitment shows the same response as growth at the seedling stage, the results suggest that these higher elevation tropical species may currently occupy their realized climate niche and may persist in their current distributions as climate warms. Such persistence may translate to resilience of forest communities in tropical mountains (Ibanez et al. 2006, Morris et al. 2008, Feeley et al. 2012b). We note with caution, however, that performance at the seedling stage may not reflect the full spectrum of responses in the life history of species and that plant performance across different life history stages may vary with climate. For example, two species of North American tundra plants show that warm climate-edge populations of the species have higher mortality and lower recruitment into larger size classes although individual growth increased at the warm climate-edge (Doak and Morris 2010). Recruitment at range margins may limit plant distributions although individuals of a species may be able to persist at a warmer climate-edge (Hargreaves et al. 2014). The idea that recruitment rather than tolerance of established individuals may limit warm climate-edge of a species is supported by our observation that the relic adults of *Viburnum* in our study region are present around 1100 m but with no seedlings at this elevation, and that younger size classes of *Viburnum* are present starting around 1250 m (Khan, personal observation).

Although our results show the two study species are tolerant of altered moisture regimes, a growing body of information underscores the importance of relatively consistent moisture regimes for species in tropical mountains. Epiphyte transplant studies in Costa Rican and Andean montane forests suggest that transplanted communities shift towards drought tolerant species with higher mortality of drought sensitive species (Nadkarni and Solano 2002, Rapp and Silman 2014). Paleoecological pollen data from lake sediment cores suggest that montane forests respond to changes in moisture availability by switching from tree-dominated forest communities to a grassland-dominated community with reduced precipitation (Bush et al. 2011). A similar phenomenon has been observed in montane Hawaiian forests, where extreme drought associated with strong El Nino events determined the upper range limit of montane forests (Crausbay et al. 2014). These studies point to the pressing need to understand how climate change induced precipitation change will affect species distributions and composition in tropical mountains.

Competition and other biotic interactions may be a key piece of the puzzle in trying to understand what factors determine the trailing edge of a higher elevation species' distribution (Hargreaves et al. 2014). If tropical montane species can tolerate novel climate conditions, then the current trailing edge at the warmer limit of the species' distribution is likely due to competition with better-adapted species from lower/warmer elevations (Sexton et al. 2009). If the current range margins are maintained by competition rather than climatic intolerance, then upslope retreat of the trailing edge with current climate change may be slow, and communities are likely to be resilient via persistence of long-lived adults of the species (Morris et al. 2008, Bellard et al. 2012). On the other hand, if the species in this study are only occupying their fundamental climate niche, i.e., these species are unable to persist in conditions outside of their current range boundaries, their occupied ranges may at beast contract upslope concurrently with novel climate conditions moving upslope. Other biotic factors such as dispersal and the role of soil communities in establishing in a new location were not examined in this study. These biotic factors may also contribute to the species' absence from warmer locations.

Conclusions

Overall, both high-elevation tree species performed equally well or better under novel climate change scenarios representing future conditions as they did under their current soil temperature and moisture conditions. These results are encouraging for the future status of these and potentially other montane tropical tree species. However, by growing these seedlings in individual pots under shadehouse conditions, we excluded potential effects of competition, herbivory, or extreme climatic events such as droughts lasting longer than several days in duration, which may have important consequences for these species during seedling stages and at other life stages in actual field settings. In order to better predict future forest composition in tropical mountains, in addition to temperature and moisture change, effects of clouds, UV insolation, and competitive interactions need to be considered. Next generation bioclimate envelop models could also use more mechanistic inputs from longer term empirical studies examining combined effects of these environmental factors on plant growth and survivorship.

Table 4.1: Summary of precipitation treatments

Label (Amount, frequency)	Amount for *Quercus* (5 L pots)	Amount for *Viburnum* (3.5 L pots)	Frequency of watering
Ambient, Ambient	65 ml	50 ml	Daily
-20% amount, Ambient	50 ml	40 ml	Daily
-20%, reduced	150 ml	120 ml	Every 3rd day
-66%, reduced	60 ml	50 ml	Every 3rd day

Table 4.2: ANOVA table for analysis of biomass			
***Viburnum* total biomass**			
	df	F statistic	p value
Soil temperature	1	0.33	0.56
Watering treatments	3	0.98	0.40
Interaction	3	0.97	0.41
Residuals	103		
***Quercus* total biomass**			
Soil temperature	1	3.51	*0.06*
Watering treatments	3	1.64	0.18
Interaction	3	0.6565	0.58
Residuals	106		
***Quercus* shoot biomass**			
Soil temperature	1	5.28	**0.02**
Watering treatments	3	1.66	0.18
Interaction	3	0.76	0.51
Residuals	106		
***Quercus* root biomass**			
Soil temperature	1	1.08	0.29
Watering treatments	3	1.48	0.22
Interaction	3	0.6373	0.59
Residuals	106		

Table 4.3: ANOVA table for A_{max}

Viburnum	df	F statistic	p value
Soil Temperature	1	0.0006	0.98
Watering treatments	3	0.93	0.43
Interaction	3	0.52	0.66
Residuals	33		
Quercus			
Soil Temperature	1	5.09	**0.02**
Watering treatments	3	0.82	0.48
Interaction	3	0.98	0.41
Residuals	108		

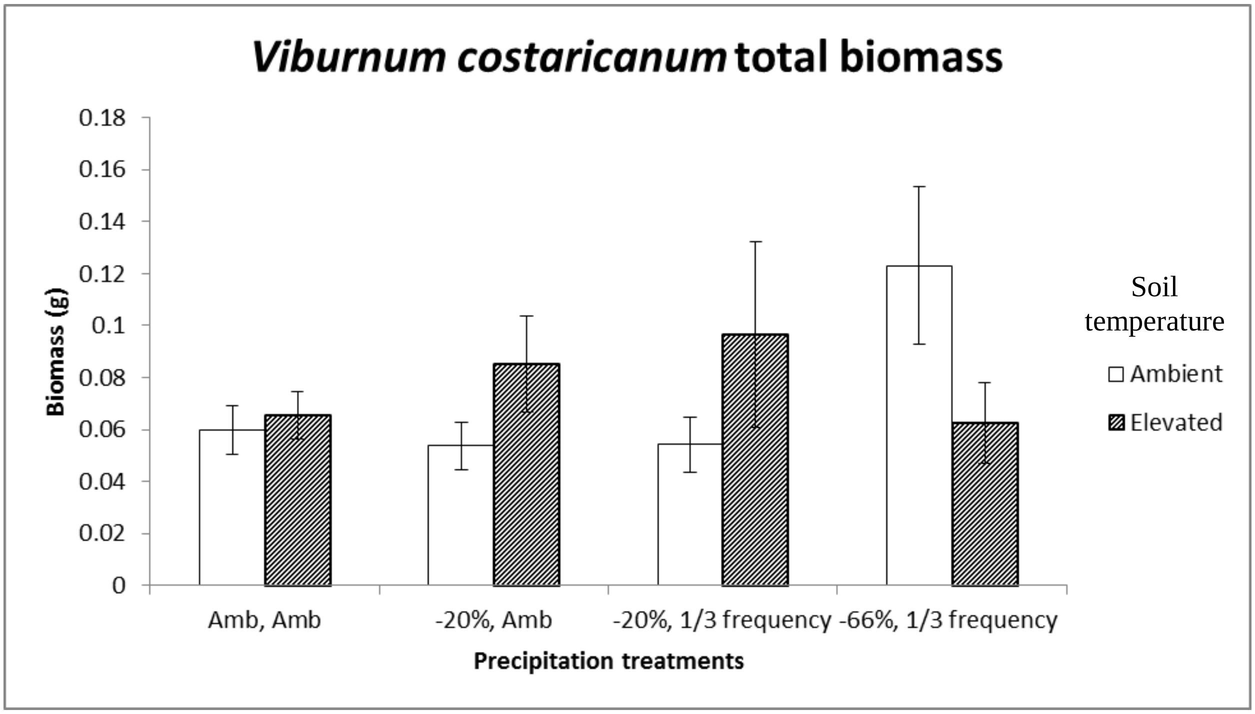

Figure 4.1: *Viburnum costaricanum* total biomass harvested at the end of the 85 day study period. Moisture treatments with two levels of soil temperature are on the X axis and dry biomass in grams is on the Y axis. Pale columns represent ambient temperature condition, and shaded columns connote +5^{o}C elevated temperatures. Error bars denote standard errors. Total biomass did not show any statistically significant response to the treatments. N=111

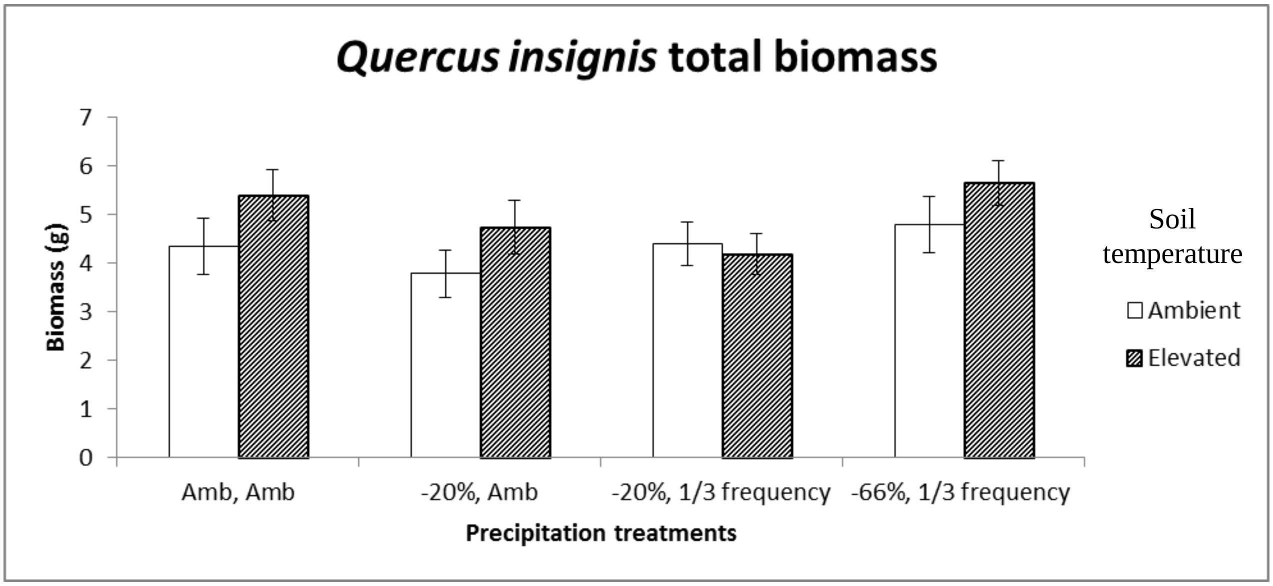

Figure 4.2: *Quercus insignis* total biomass harvested at the end of the 85 day study period. Watering treatment names indicate ambient or reduced volume, and ambient or reduced frequency. Pale columns represent ambient temperature condition, and shaded columns connote +5^{o}C elevated temperatures. Biomass, in general, tended to increase with elevated soil temperature (p=0.06), although none of the pairwise comparisons were significant. Error bars denote standard errors. N=115

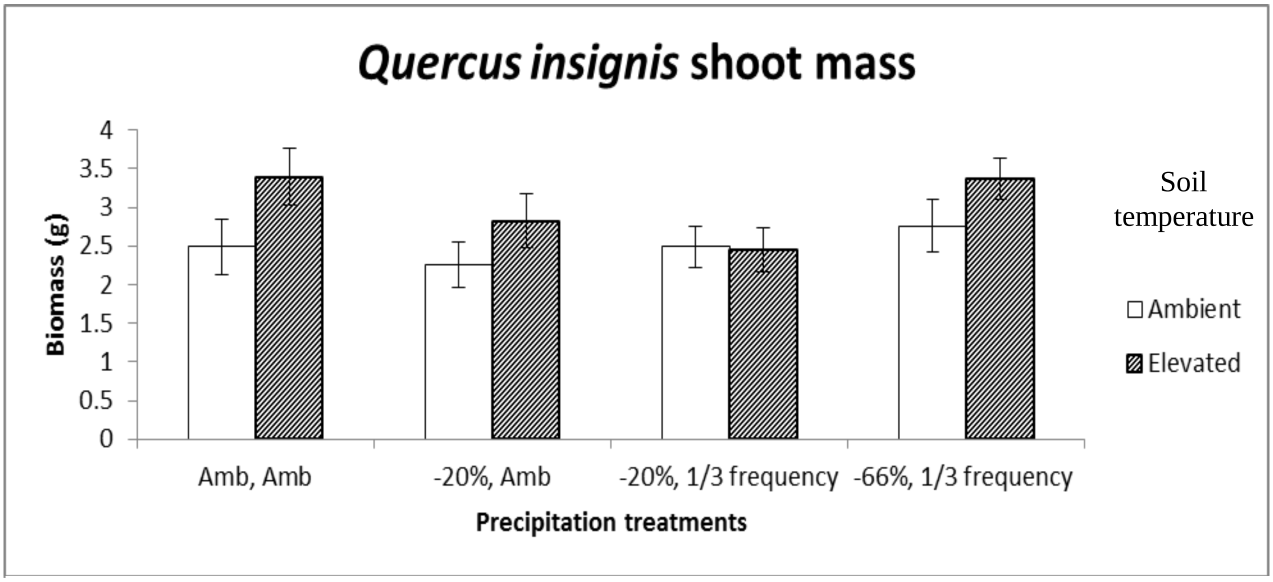

Figure 4.3: *Quercus insignis* shoot biomass harvested at the end of the 85 day study period. Moisture treatments with two levels of soil temperature are on the X axis and dry biomass in grams is on the Y axis. Shoot biomass increased in response to elevated soil temperature (p=0.02). Pale columns represent ambient temperature condition, and shaded columns connote +5oC elevated temperatures. Error bars denote standard errors. N=115.

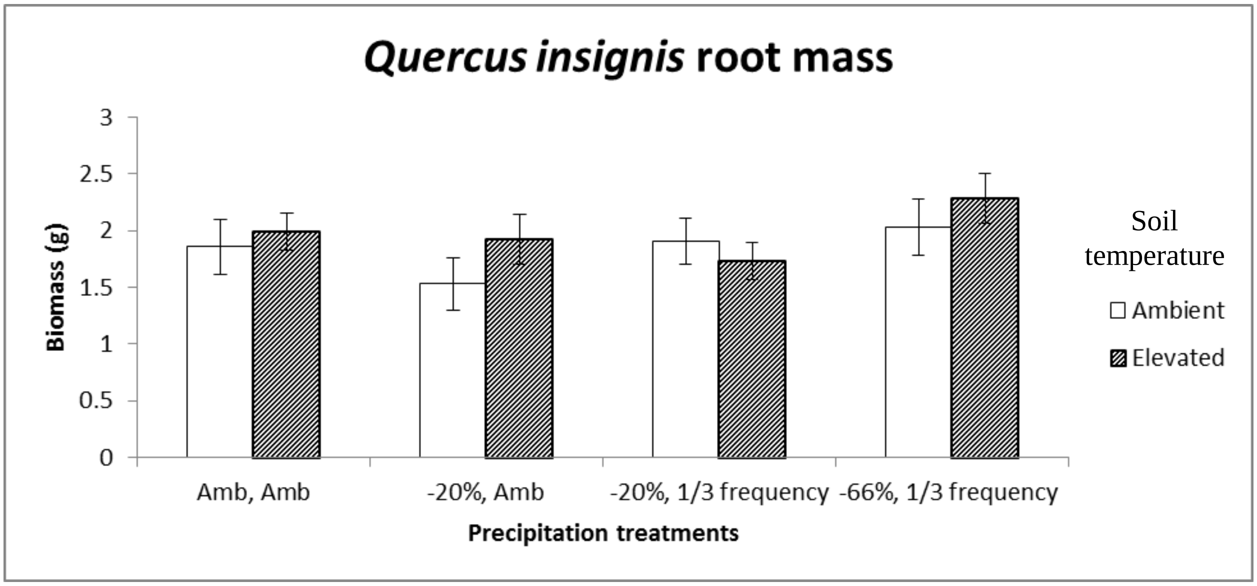

Figure 4.4: *Quercus insignis* root biomass harvested at the end of the 85 day study period. Moisture treatments with two levels of soil temperature are on the X axis and dry biomass in grams is on the Y axis. Root biomass did not show any response to the treatments. Error bars denote standard errors. N=115.

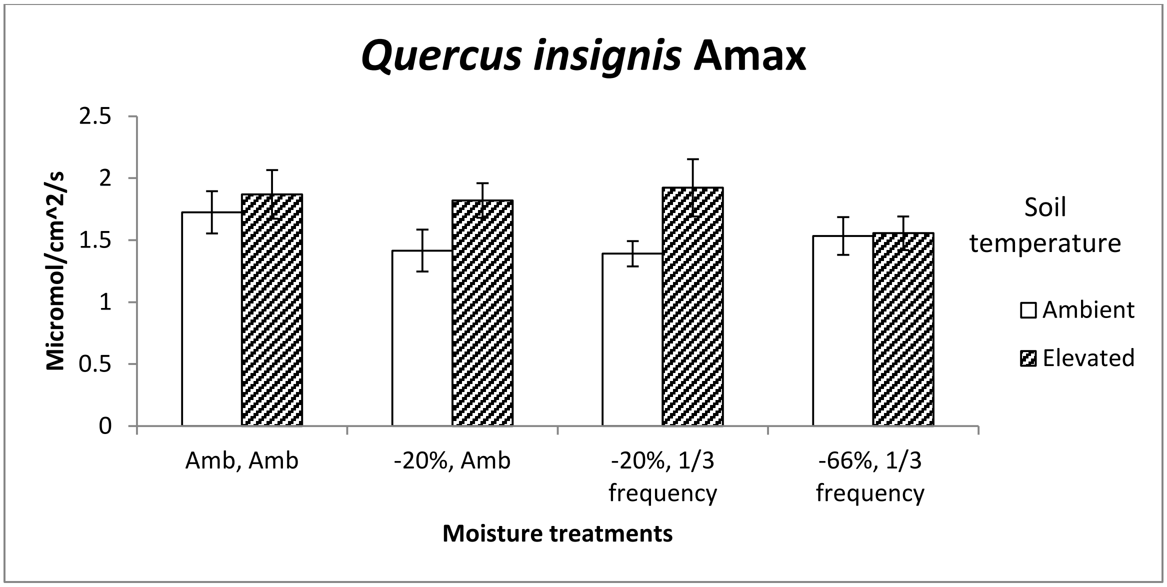

Figure 4.5: *Quercus insignis* maximum photosynthesis rates measured on day 84. Moisture treatments with two levels of soil temperature are on the X axis and rate of maximum photosynthesis is on the Y axis. Similar to growth, elevated soil temperature resulted in increased photosynthesis rates. Error bars denote standard errors. N=116.

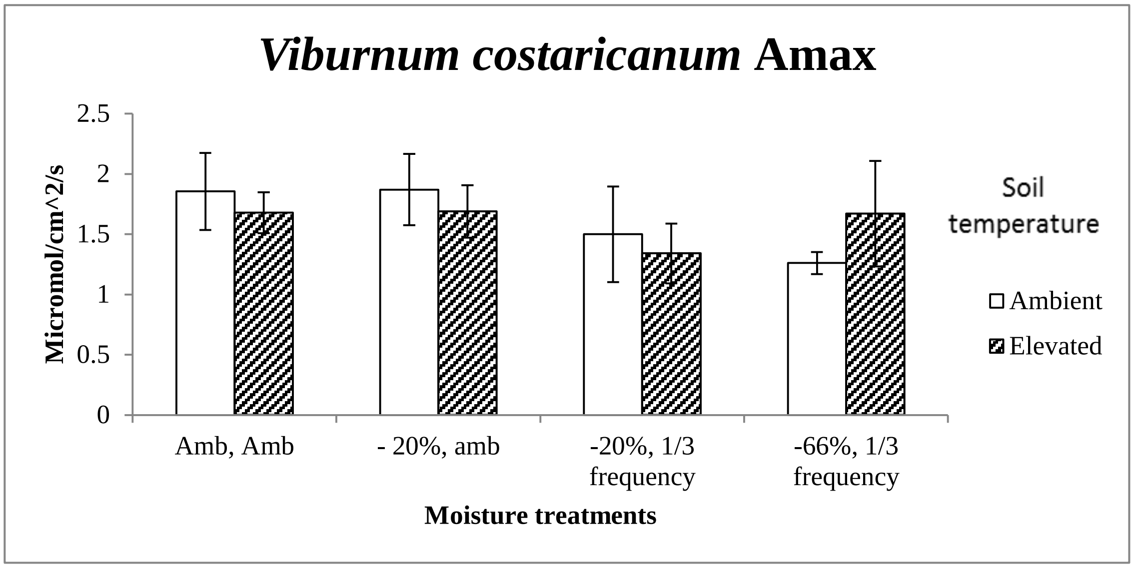

Figure 4.6: *Viburnum costaricanum* maximum photosynthesis rates measured on day 81. Data were square root transformed. Moisture treatments with two levels of soil temperature are on the X axis and rate of maximum photosynthesis is on the Y axis. *Viburnum* photosynthesis rates did not respond to any of the treatments. Error bars denote standard errors. N=41; individual treatment combinations had n= 5 or 6.

CHAPTER 5

SPECIES DISTRIBUTIONS IN TROPICAL MOUNTAINS WITH CLIMATE CHANGE: A REVIEW

[1]Shafkat Khan, Paul Frankson, Jacqueline Mohan. To be submitted to *Biological Reviews.*

Abstract

Understanding distributions of species over space and time is an enduring and important research goal in ecology (Grinnell 1917, Elton 1927, Hutchinson 1957, Silvertown 2004, Colwell and Rangel 2009). Anthropogenic climate change has made understanding current and future species distributions a research imperative. How individual species are spatially and temporally distributed determines overall patterns of species diversity (Connell 1978). Examining factors determining species distributions, enables us to understand species diversity patterns and ultimately predict distributions of species with current and future climate change. Our understanding of climate change effects on terrestrial diversity are region-specific, with tropical ecosystems receiving less attention than higher-latitude systems (Bellard et al. 2012, Wood 2012). Focusing on tropical montane ecosystems, this review explores the challenges and current uncertainties in gaining a predictive understanding of species' distributions with respect to changing abiotic and biotic variables as well as important anthropogenic factors that are driven by social and economic dynamics such as nitrogen (N) deposition and deforestation. We highlight ways in which species distribution models (SDM) can incorporate understandings and uncertainties to provide predictions of changing biodiversity patterns in tropical mountains with current and future climate change.

Background

Understanding distributions of species in space and time is a classical pursuit of ecology (Silvertown 2004). Original efforts included understanding the distribution of species in space; these efforts assumed that conditions outside of a species' range are intolerable to a species and therefore drew a boundary of the ecological distribution or niche for the given species (Grinnell

1917). Another concurrent view sought to understand the distribution and abundance of species as determined by interactions with other organisms in a given community (the trophic niche). In this view, distributions were dependent on the biotic interactions such as competition and symbiosis (Elton 1927). Hutchinson synthesized these two concepts to define the “fundamental” and “realized” niches. In a Hutchinsonian view of the ecological distribution of a species, abiotic limitations determined the potential distribution or fundamental niche, and biotic limitations determined the actual distribution, the realized niche of a species (Hutchinson 1957). Subsequent research has focused on understanding the complex interactions of abiotic factors and biotic factors such competition that can determine, at least in part, the distributions of species and possibly promote coexistence (Silvertown 2004, Colwell and Rangel 2009). Anthropogenic climate change has provided a recent impetus to understand the distributions of organisms and how these distributions are changing with climate change (Thomas et al. 2004, Thuiller et al. 2008). In this review, we focus on biologically diverse tropical mountains, reviewing the current evidence of climate change affecting plant species composition, and exploring the challenges in predicting future species distributions in these regions.

Tropical montane areas are uniquely biodiverse regions and contain a high proportion of endemic species (Körner and M. 2002, La Sorte and Jetz 2010) that often are limited to specific elevations and associated climates (Laurance et al. 2011b). Tropical mountains are environmentally heterogeneous regions with a range of climatic conditions within a short horizontal distance (Bush 2011). Along elevation gradients, tropical mountains show changes in plant communities via high turnover of species from one elevation to another (Lieberman et al. 1996, Culmsee et al. 2010). The high turnover of communities along tropical mountain gradients suggests that the distribution species can be strongly linked to their climate (Lieberman et al.

1996) Bush chapter 2. A specific elevation on tropical mountains experiences relatively little variation in intra-annual temperature (Ghalambor et al. 2006). Thus, once a species has evolved to inhabit a given temperature regime, it is hypothesized to be suboptimal for that species to adapt and grow in other climates/elevations (Janzen 1967). Because tropical montane species adapt and evolve to a climate with relatively little annual fluctuation (compared with, for example, temperate or boreal regions), previous ecologists hypothesized that these species are less tolerant of climate change than species from other regions with more inherent climatic variability (Janzen 1967, Foster 2001, Laurance et al. 2011b, Sheldon et al. 2011). Potential greater intolerance of climatic variability in the biota, coupled with high biodiversity, makes tropical mountains globally critical areas in regard to climate change impacts on biodiversity (Still et al. 1999, Williams and Jackson 2007, Sheldon et al. 2011).

The unique biotic communities in tropical mountains are intricately linked to the climatic conditions found on tropical mountains. Several characteristics distinguish tropical montane forests from other terrestrial biomes. Tropical montane forests greatly vary in their mean annual temperature and precipitation (Scatena et al. 2011). In general, tropical mountains are cooler than the lowlands, with adiabatic lapse rate generally around 5-6˚ C per 1000 m of elevation gain (Colwell et al. 2008, Bush 2011). Montane plant taxa replace lowland taxa and start attaining dominance when minimum daily temperature drops below 18 ˚ C (Scatena et al. 2011).These regions also experience relatively little intra-annual variation in temperature compared to extra-tropical biomes (Janzen 1967, Ghalambor et al. 2006). Mean annual precipitation also vary across regions, but in general are above 1000-1200 mm (Bush 2011) (Bush, second chapter). While precipitation patterns are variable and local in tropical mountains, clouds play a moderating effect on tropical mountains (Hölscher 2008) (Still et al. 1999). In some regions, the precipitation derived from cloud condensation droplets can exceed precipitation from rain events, especially during dry periods (Hölscher 2008, Scatena et al. 2011).

Because of unique climates across elevations, tropical mountains are projected to experience a high incidence of novel climates in the future (Williams and Jackson 2007). Novel climates are projected climate conditions that are not currently found regionally or even globally, depending on the spatial scale of comparison. As a result, montane tropical species will encounter novel climate conditions that they have not encountered in the recent past. In these climate conditions, different climate variables, such as mean temperature, precipitation variability and frequency, cloud cover and duration, and others, will become decoupled locally (Cramer et al. 2007). This decoupling of climate variables in novel climates will expose species to sub-optimal conditions that may reduce their fitness over time (Thuiller et al. 2008, Sheldon et al. 2011). A mechanistic understanding of these species' responses to different combinations of these climate variables can yield important insight into the near-future composition and diversity in montane tropics with climate change.

Climatic variables exert control over species distributions on tropical mountains

Temperature as a predictor for tropical montane species distributions

Current models for tropical species diversity along elevation gradients usually have considered temperature as the main driver for species composition or a suitable proxy for effects of climate on species composition. For example, Colwell et al. 2008 predict species migrations with shift of their current thermal niche (Colwell et al. 2008). Species distribution models are not widely available for tropical species, especially montane species, because of lack of data (Feeley and Silman 2011a). However, more general, global models tend to use temperature or species/biomes' thermal niche/distribution for making predictions of near future diversity especially for tropical regions (Thomas et al. 2004, Cayuela et al. 2009). Similarly, recent work documenting species migrations along elevation gradients in tropical mountains have related change in temperature as the main factor driving the observed change in species composition (see (Feeley et al. 2011, Feeley et al. 2013, Freeman and Freeman 2014) for examples). While temperature is a major driver of distribution of biomes and species globally, the predominance of temperature as a critical variable for predicting tropical montane species diversity reflects a historical bias (see Janzen 1967 for an early example) that influences current thinking (see Colwell et al. 2008, Laurance et al 2011). In smaller spatial scales relevant to a species, or even within a biome, other abiotic variables such as rainfall patterns, fog, soils and other edaphic factors exert a strong influence on species distributions (Clark et al. 1999a, Crimmins et al. 2011, Feeley et al. 2012a). Understanding of how other abiotic variables affect species' distribution is a research challenge for much of tropical biomes, but especially more so for montane tropics.

Along with temperature, several other climate variables are projected to change with near future climate change (Still et al. 1999) and can influence species distributions and community composition. Other climate and abiotic variables, such as precipitation and edaphic conditions, strongly influence species composition at local to regional scales (Clark et al. 1999a, Engelbrecht et al. 2007). Although evidence of how moisture and other abiotic factors affect species diversity in tropical mountains is not aplenty, studies from other tropical biomes such as the lowlands enable us to infer the importance of other abiotic factors besides temperature in shaping montane communities. For example, precipitation seems to be a strong driver of species composition in tropical wet systems (Engelbrecht et al. 2005, Engelbrecht et al. 2007, Nepstad et al. 2007, Baltzer et al. 2008) . When coupled with temperature change, moisture variability and change is projected to adversely affect tropical montane biodiversity more than these factors changing individually (Bonebrake and Mastrandrea 2010), underscoring the need to expand our understanding of effects on species diversity and community composition with changes in other climatic factors beyond temperature.

How does moisture/precipitation affect montane tropical composition and diversity?

Palaeoecological pollen data from lake sediment cores suggest that with reduced precipitation, montane communities respond to changes in moisture, at least by switching from a tree- dominated community to a grassland-dominated community (Bush et al. 2011). Current anthropogenic climate change is projected to alter precipitation regimes in tropical mountains, with projected increase or decrease is dependent on the specific region (IPCC 2014). In a warmer world, precipitation events are projected to be more intense and less frequent (Rauscher et al. 2008, IPCC 2014). Tropical montane forests—forests that experience constant input of less intense precipitation are likely to respond to these projected precipitation changes.

Direct contemporary evidence of effects of moisture regimes on species composition in tropical mountains is scarce. In examining the effects of reduced mist and cloud cover, downslope transplant experiments in a cloud forest of Costa Rica demonstrate high mortality in cloud forest epiphytes and a change in canopy species composition from epiphyte to gap colonizing plants when epiphyte mats were exposed to warmer and drier lower elevations (Nadkarni and Solano 2002). As epiphytes are important carbon sinks in tropical montane forests (Nadkarni et al. 2004, Comita and Engelbrecht 2014) and provide important ecological niches to a whole host of species, including diverse invertebrate assemblages (Richardson et al. 2000), the changes cascading from local extinction or reduction of montane epiphytes can be profound and needs to be investigated urgently(Nadkarni and Solano 2002). Despite the prescient research needs to understand the effects of precipitation on montane forests in the tropics and tropical forests as a whole, empirical data, especially from controlled experiments, are scarce. There exists, however, a growing body of literature on how tropical lowland forests are influenced by precipitation and moisture availability. From these studies, we can attempt to infer how such factors would shape montane tropical communities.

Evidence from lowland Amazonia shows that stand-scale drought can increase liana and tree mortality, with a concurrent increase in smaller stemmed individuals (Nepstad et al. 2007). Lowland forest species seedlings in Panama respond strongly to precipitation change, with an increase in drought intolerant plants with increased watering (Engelbrecht et al. 2005). On a regional scale, in Panama, more drought tolerant species occupy drier areas whereas less drought tolerant species were found in high rainfall areas (Engelbrecht et al. 2007). Similarly, species distributions along a climatic gradient in Malay-Thai peninsula respond to desiccation tolerance, a measure of drought tolerance (Baltzer et al. 2008). One may hypothesize that, as with other precipitation gradients, shift in species composition along elevation gradients currently are influenced by the precipitation patterns experienced going upslope, especially the typical constant cool and moist environment of the montane forests. We can also expect that as warmer climates with more moisture deficit move upslope with climate change, species used to current moisture regimes of tropical mountains will respond negatively, as evidenced in the downslope transplant study by Nadkarni et al. (2002).

Interaction between temperature, precipitation and soil moisture

With elevation gain and transition from lowland forests to montane forests, tropical elevation gradients in general experience increased soil moisture and increased water logging in the soil (Bruijnzeel and Veneklaas 1998, Richter 2008). With elevation gain, Hawaiian tropical forests gain in 14 Mg of carbon per hectare soil carbon for 1˚C loss by retaining coarse woody debris and standing litter (Selmants et al. 2014). Tropical montane forests show a similar increase in standing litter and organic layer with elevation gain (Richter 2008, Scatena et al. 2011), which, from a plant's perspective, can alleviate water logging in fine rooting zone. Indeed, local topographic factors such as slope can affect oxygen content in soils (Silver et al. 1999). Canopy and forest floor soil temperature remain within 1˚C of each other in a tropical montane cloud forest in Monteverde, Costa Rica. Soil moisture at these two different levels remained similar in the wet season (over 70% mass water content) but varied considerably during the dry season when canopy soils experienced rapid drying events (20-40% mass content) while forest floor soils remained constantly wet with 60-70% mass water content (Bohlman et al. 1995). These lines of evidence suggest that tropical montane plants may be tolerant of water logged conditions and canopy plants may be tolerant of seasonal dryness. However, to what extent changes in these conditions with climate change will affect tropical montane plants is not well understood.

A downslope transplant study in Monteverde, Costa Rica showed that canopy epiphytes are sensitive to drier conditions and experience high mortality below cloud levels (Nadkarni and Solano 2002). Contrastingly, a shadehouse study done in montane southern Costa Rica suggests that montane tree species may not, at least in the short term, respond to a combination of reduced total precipitation, a lower frequency but higher intensity of precipitation and a drought resulting from an increase in soil temperature during the dry season (Khan, in prep). The same study finds that dry season precipitation treatment, even in combination with elevated soil temperature causing 10% volumetric soil moisture (contrasting with 30% soil moisture of the control) did not result in reduced growth for *Viburnum costaricabum* and *Quercus insignis*, suggesting that some tropical montane tree species may not respond negatively to dry season precipitation even when the soil temperature is representative of a warmer climate. To our knowledge, there are no other published studies currently that examine the effect of different moisture regimes on tropical montane plants. These contrasting results and the dearth of precipitation studies in montane tropical systems hinders our understanding of compositional changes in these forests and these systems remain ripe for exploring questions related to the effects of climate change-induced moisture regimen shifts on the composition and function of montane tropical forests.

Other abiotic factors important for tropical montane diversity

Much of climate change research focuses on temperature and precipitation regime changes in the montane tropics and in the tropics in general (Cunningham and Read 2003, Engelbrecht et al. 2005, Engelbrecht et al. 2007, Bush et al. 2011, Wood 2012, Cheesman and Winter 2013b, a, Heinrich Krause et al. 2013). However, associated changes in abiotic conditions can result in important consequences for montane diversity by affecting different species differentially. Base height of cloud formation has important ecological consequences for the species composition of montane tropics. Cloud cover affects the quantity and quality, including UV insolation, of light reaching the canopy and is likely to have important consequences for species composition in these forests (Lawton 1990). Cloud cover also affects the relative humidity and delivers a substantial amount of precipitation in montane forests via cloud immersion (Foster 2001, Bush et al. 2011, Scatena et al. 2011). In montane cloud forests, precipitation via cloud immersion is an important source of moisture (Foster 2001). Cloud forest upper limit is defined by strong el Nino induced drought events in Hawaiian mountains (Crausbay et al. 2014). At this ecotone, high vapor pressure deficit negatively affects stomatal conductance and transpiration of *Metrosideros polymorpha*, the foundational tree species in this system (Gotsch et al. 2014), and drives the transition from cloud forests to sub-alpine shrubland communities (Crausbay et al. 2014). Similarly, cloud borne moisture is important for defining the lower boundary of montane cloud forest communities. Canopy epiphytes planted below the cloud line experienced higher mortality compared to ones transplanted above the cloud line. This likely happened because of decrease in cloud cover and cloud-borne moisture (Nadkarni and Solano 2002). However, little other work has explored the role cloud cover plays in determining species composition in these forests. As a result, how near future montane tropical diversity will be influenced by increased height of cloud formation and reduced cloud cover is unclear.

Flenley et al. (2011) hypothesize that UV insolation, especially reflected by clouds onto montane forests above the base height of cloud formations in addition to the UV insolation from the sun, acts as a filter for recruiting into tropical mountain plant communities. For example, tropical montane species above cloud levels have thicker, waxy leaves arguably resulting from exposure to elevated levels of UV exposure (Flenley 2011). The species that are able to tolerate high levels of UV are the ones that recruit into the montane forests. Depending on the elevation of base height of cloud formation, in near future climates of where current montane cloud forests are located, montane species may experience altered competitiveness and lower elevation species that are inferior competitors with cloud cover may become better competitors with lack of cloud cover.

How species will track their preferred climate:

Dispersal is key to presence in communities of the future

Recent evidence suggests that tree species in tropical mountains are moving upslope in response to climate change (Feeley et al. 2011, Feeley 2012, Feeley et al. 2013). However the rate of species migration is slower than current climate velocity on tropical mountains (Feeley et al. 2011). Montane Costa Rican plots show an increase in warmer climate associated plants mostly by mortality of cooler climate associated plants, i.e., composition change is not driven by new arrivals/dispersal but by mortality of existing higher elevation associated plants (Feeley et al. 2013). If species are to persist with climate change, dispersal of these species to suitable cooler climate upslope will be key, and change in composition need to be mediated via increased dispersal to cooler climates/elevations and not via increased local mortality. Dispersal limits plant abundance and diversity in temperate and tropical forests and dispersal is seen as a key limiting factor for species to recruit in a community (Primack and Miao 1992, Clark et al. 1999c). The inability for species to disperse to a suitable climate makes predictions of future species distribution tricky as there may be suitable climate present in the region but a species may not be able to migrate to the location (Angert et al 2011). This means that even if the plants are given adequate landscape corridor to move, they may not still colonize a new area because of dispersal limitation (Dullinger et al. 2004).

Dispersal ability will be key for species to disperse to novel locations/communities upslope. Species with high dispersal ability, typically wind/insect/bird dispersed may have an advantage over species that have shorter dispersal ranges, typically species with mechanical dispersal and with large seeds (Howe and Smallwood 1982). As species are found to be unable to adequately move upslope with current climate velocity, ease of local to regional dispersal may accentuate species recruitment in novel communities. Species with high dispersal ability tend to be early successional species, whereas species with low dispersal ability tend to be later successional species. In keeping with climate envelopes moving upslope, we can hypothesize that a majority of the arrivals to a given elevation will be early to mid-successional species that have high dispersal ability. On the other hand, later successional species that can persist with suboptimal growing conditions may continue to persist in their current locations. A global survey in response to the 2005 el-Nino induced droughts show that species with high wood density were able to persist in drought/dry/warm conditions while species with lower wood density perished with drought (Phillips et al. 2010). Species with higher wood density tend to be late successional (Plourde et al. 2015). If this pattern of mortality in the face of drought manifests along elevation gradients, then persistent, albeit dispersal limited, later successional species will lag at the trailing edge of their climate distribution long after the optimal climate band has moved upslope (i.e., remnant populations) and make up the forest communities with newly arrived species from down the slope. Forest fragmentation and landscape corridors will also affect dispersal of species to a novel location. We discuss the effect of landscape barriers in along with other socio-economic factors.

Will a lack of mutualists or presence of novel antagonists affect future species composition?

Challenges in colonization outside of native ranges

Beyond dispersing to a novel location, colonization and establishment in that location may act as a filter for novel community compositions. Colonization and establishment in the new location may be affected by success of mutualistic partnerships, such as soil microbial symbiosis, pollinators, etc. Tropical forests contain highly evolved and specific symbiotic relationships such as specialist pollinators, specialist mycorrhizal relationships (especially among orchids) that require presence of one mutualistic partner’s presence for the other mutualist to thrive. Similarly, though less explored, parasitic and pathogenic (insect or plant) relationships, when specific, will also require the presence of the host. Tropical forests have a disproportionately high number of mutualistic obligate relationships that may break down due to climatic intolerance and/or lack of dispersal of one of the mutualistic partners (Bazzaz 1998). Similarly, a pathogen or a parasite may face local extinction and/or lack of establishment in a new location if the host experience climatic intolerance locally or at the new location or if the pathogen is unable to disperse to the new location.

Even if a plant species is able to disperse to a new climate location, the mutualistic relationships may break down if one of the mutualists is not able to disperse to or survive in a different climate location. Such mismatch may result in decline in recruitment, survivorship and growth of these species in the new location over time although the species themselves may be tolerant of the climate in the new location (Van der Putten 2012). In the same vein, hypothetically, fitness for a species may be lower in a novel community because of the presence of novel pathogens, although pathogens may actually facilitate recruitment by negatively affecting residents and thereby benefiting the newly colonizing species. Pathogens play a key role in the relative abundance of tropical tree species and controlling their abundance locally (Mangan et al. 2010b, Bagchi et al. 2014) and may also play a key role in the regional abundance of a species. Despite tolerance of climate conditions, the presence of pathogens may keep the species from establishing in a new climate-location. However, evidence from temperate zone studies suggests that novel plant-soil microbe associations may boost establishment via escape from plant species specific pathogens (Engelkes et al. 2008, McCarthy-Neumann and Ibanez 2012, Van der Putten 2012). If this is true for tropical montane species, soil microbial interactions may facilitate rather than inhibit establishing in a new location.

With current climate velocity, species may need to continually move upslope until global climate reaches a steady state. Studies suggest that tropical montane species take several decades to reach maturity (Foster 2001) and communities, especially epiphytes, recover from disturbance on a multi-decadal scale (Nadkarni 2000). With current climate velocity, even if species are able to disperse to a new location initially, the subsequent time needed for a given species to establish and reproduce in order for maintaining propagule pressure upslope may determine the long-term survival of species with climate change.

Will species evolve or adapt in situ?

Authors raise the possibility that species may evolve in-situ to novel climate conditions (Lavergne et al. 2010), which may impart resilience to montane forest communities with species adapting to changing conditions (Feeley et al. 2012b) rather than tracking suitable climate upslope. However, montane species have retreated and expanded during previous ice ages/glacial-interglacial cycles, as evidenced by pollen in sediment cores from Andean lakes (Bush et al. 2011, Feeley et al. 2012b) instead of evolving in situ. The majority of present taxa have responded to past climate change by tracking their suitable climate/habitat (Bush et al. 2011). As many tropical plant species have long and complex life cycles, the rate of current climate change that is unprecedented in the species' evolutionary past/quaternary past makes it difficult for these species to rapidly evolve with current climate change. While the range of temperatures may be within a species' evolutionary history/their quaternary experience, the current rate of change is probably something the species have not experienced (Bush 2004). However, the range of intrinsic tolerance to changing conditions may buffer species against going extinct locally (Thuiller et al. 2008). Evidence so far suggests that rather than evolving in situ, species are shifting ranges, upslope in montane tropics and towards suitable climates elsewhere (Feeley et al. 2011, Feeley et al. 2013); see (Woodall et al. 2009) for a temperate example). Despite climate change driven migrations among a range of taxa, current climate velocity is faster than these species can migrate (Feeley et al. 2011, Zhu et al. 2012). Given that current rate of climate change is faster than the changes most species have experienced in their evolutionary history (Bush et al. 2011, Feeley et al. 2012b), this potential compensation of biodiversity via rapid evolution in the face of anthropogenic climate change is unlikely. Species, then, face a choice of acclimating via plastic responses to in situ climate or moving to a different location with favorable climate. This makes the need to experimentally test and understand physiological limits in these species paramount in order to predict near future composition in these speciose forests.

Responses of tropical montane diversity/composition to recent climate change

While tropical montane forests are relatively understudied regarding climate change effects, recent evidence suggests the species in this biome are responding to climate change by changing their altitudinal distributions. An examination of herbarium records going back to 1970 by Feeley (2012) show South American tropical plants have experienced an upward movement of their warmer range boundaries but not a corresponding change in their colder range margins, thus resulting in general range contractions. A majority of the herbarium samples (59%) showed some cold-ward range shifts, with 35% of the species showed cold-ward movement of their warm range limits. Thirty percent of total species showed range contractions by not shifting their cold range limits. Twenty five percent of the examined species showed cold-ward range movements, with 20 % of the species showing no corresponding change in their warm range limits and experiencing range expansions (Feeley 2012). Censuses in a montane gradient in northwestern Costa Rica documented an increase in relative abundance of lowland species when modern censuses were compared with herbarium records. This change towards a warm climate associated community resulted from increases in mortality of species associated with higher elevations and cooler climates (Feeley et al. 2013). A study using an elevation gradient in Peruvian Andes documented a shift in tree genera elevation ranges and that average rate of upslope migration was 2.0 ± 0.9 m·y −1 (Feeley et al. 2011). Similar migrations rates were reported for Costa Rican mountains ((1.2 ± 0.9 m·y −1) (Feeley et al. 2013) and in Northern Andes (∼2.0 m·y −1) (Duque et al. 2015). Despite the migration upslope, the rate of migration was not enough to stay on par with current or projected change in temperature on the Andean slopes (Feeley et al. 2011, Duque et al. 2015). Similar to the upslope migratory response of trees documented in plants neotropics, tropical birds in Papua New Guinea showed upslope movement with climate change (Freeman and Freeman 2014). A similar increase in warm climate associated birds have been documented in Costa Rican mountains (Pounds et al. 1999). Freeman and Freeman (2014) observed that tropical species show a greater sensitivity to change in climate compared to temperate montane species, which is consistent with Janzen's idea of tropical species being sensitive to climatic variability, although the extent to which this statement is accurate has been called into question (Rehm 2014). However, there is general agreement that tropical montane forests and the communities/species therein remain poorly studied, especially with in the context of climate change.

Despite the high biodiversity, a high concentration of biodiversity hotspots (Myers et al. 2000) and the projected high incidence of novel climates in near future with climate change the factors controlling distribution of species and overall diversity in tropical montane forests is not fully understood. Further, the extent to which these species will need to migrate upslope to reach suitable climates and the different factors driving this migration require more research.

Predictions of species distributions and range shifts are often based on correlative species distribution models (Thuiller et al. 2008, Bellard et al. 2012). These widely applied species distribution models have received criticism (Lots of Jim Clark REFS here) for assuming (Hannah 2011) predicted species ranges represent factors determining the fundamental niche of a given species. Such an assumption may make these models unrealistic and prone to inaccurate predictions of current and future distributions (Pearson 2003, Buckley et al. 2010).

Improving bioclimate envelop models as tools predicting for future tropical montane diversity

Correlative species distribution models (SDM) are widely used for predicting species distributions and range changes (Thuiller et al. 2008, Bellard et al. 2012). These widely applied species distribution models are based on the assumption that the species ranges represent factors determining the fundamental niche of a given species and not their realized niche, i.e., species cannot tolerate conditions different than they experience in their current distribution (Ibanez et al. 2006). Such an assumption makes these models unrealistic and prone to be inaccurate in predicting current and future species distributions, especially in cases where species have a wider range of tolerance than conditions found along their current distributions of (Pearson 2003, Ibanez et al. 2006, Ibanez et al. 2008, Buckley et al. 2010).

The correlative SDMs use a combination of climate variables to define current climate distributions of species. Abiotic variables, such as temperature and moisture, correlated with the species' elevational and/or geographic ranges are assumed to be the factors that control the distribution of a species (Hannah 2011). The ranges of climate variables are thought to constitute the climate niche distribution of the species. An appropriate time scale for searching and predicting the future distribution is selected (Buckley et al. 2010, Hannah 2011). Often, the future distribution is determined by the future locations where the current climate variables or associated groups of variables are found (Bush et al. 2011).

Insufficient information on species ranges as well as reliable climate data associated with the species ranges affect the accuracy of predictions from SDMs(Feeley and Silman 2011a, Feeley and Silman 2011b, Hannah 2011). Insufficient range information for a majority of tropical plants collected in herbaria make correlative SDMs unreliable for these species (Feeley 2012). Because of scarce empirical range data and associated geographic data to parameterize the models, with increase in temperatures, current SDMs predict a wide range of responses (Feeley and Silman 2011b). In addition, building SDMs for nearly nine out of 10 tropical plant species is not practical because of incomplete range information for these species (Feeley and Silman 2011a). Availability of tropical climatic data at fine spatial scales in conjunction with species range distributions is critical for building and improving SDMs(Cayuela et al. 2009). Lack of fine-scale meteorological and distribution data is especially critical for tropical montane species as tropical mountains are heterogeneous environments, with climate and associated species turning over across small spatial scales. Mountains are spatially heterogeneous environments with microhabitat and microclimate variability at local scales; and regional and continental scale projections are not suited to predict local scale migrations and extinctions in montane communities (Trivedi et al. 2008).

Data poverty is possibly one of the reasons why fine spatial scale tropical SDMs are uncommon. While there exists a number of predictions for tropical biodiversity on a regional/global scale (e.g., (Thomas et al. 2004)), there are only a handful of climate envelope models that yield region specific/biome specific predictions for tropical regions. Better understanding of range sizes in tropical species as well as the abiotic factors in those regions can be an important first step in generating higher resolution species distribution model predictions for tropical mountains and tropics as a whole. Data poverty in tropical regions also leads to tropical SDMs being unlikely to be validated and parameterized with empirical data (Cayuela et al. 2009).

As warmer range margins are thought to be limited by biotic interactions such as competition, tropical montane species may be able to persist in warmer conditions. This possibility contrasts with the SDM assumption that species occupy their fundamental niche and not their realized niche, i.e. species do not have tolerance for conditions they do not currently occupy. Current species distributions may not correlate with their current optimal climate conditions, as species may be relics from past populations or species may still be responding to past climates (Hannah 2011). Indeed, SDMs rarely accommodate for the assumption that species niches do not stay constant over time or that species current occupy their realized niche (Pearson 2003, Nogues-Bravo 2009). A couple of shadehouse studies in montane Costa Rica show that montane tropical species can grow better in elevated soil temperature conditions and that in the short term, growth of seedlings of montane tropical species *Quercus insignis* and *Viburnum costaricanum* remain undiminished in elevated soil temperature and novel moisture conditions (Khan et al., unpublished data). This suggests that montane tropical species may occupy their realized niche and are able to tolerate novel growth conditions to an extent. Plasticity of response in montane species to novel conditions such as these can make SDM predictions less accurate. Mechanistic insight gained from mensurative and manipulative studies focusing on plasticity in ecophysiological rates, such as photosynthesis and transpiration, and growth responses can make

SDM predictions for montane tropics and tropical regions in general more accurate. Accordingly, mensurative as well as experimental studies can be a vital first to understand how important abiotic variables and combinations of them affect range distributions of montane tropical plants. In conjunction with information gleaned from range distribution studies, careful selection of such variables to build mechanistic SDMs can improve the accuracy and utility of SDMs for tropical mountains and the tropics in general.

Additional anthropogenic factors that may interfere with species migrations

Beyond the abiotic and biotic variables constraining current and future species compositions of tropical montane forests, concurrently changing social and economic divers influence anthropogenic factors that have the potential to interact and affect biodiversity on tropical mountains. These anthropogenic factors can influence forests in critical ways, potentially synergistically with climate change. These factors make predictions of near future biodiversity difficult.

Nitrogen deposition

The tropics in general are projected to experience high nitrogen (N) deposition via industrialization and biomass burning in this century (Galloway et al. 2004). Nitrogen deposition has changed community composition via altering competitive interactions among species, especially in N poor systems (Rajaniemi 2002, Humbert et al. 2016), and has affected plant species abundance and floristic diversity in temperate plant communities (Stevens et al. 2004). Given that tropical montane regions are thought to be N limited or N and P co-limited (Vitousek and Matson 1988, Tanner et al. 1998, Fisher et al. 2012), increased N deposition in these regions will have important consequences for species abundance and diversity. Concomitant effects of climate change and N deposition on species diversity may be more complex than each of these drivers acting alone, making predictions of future biodiversity more challenging.

Landscape connectivity

Landscape scale factors will play a key role in whether species are able to migrate to a new area or are able to persist in their current location (Krupnick 2013). Connectivity between patches is a key conservation issue with climate change that determines whether species are able to disperse to new locations from their current distributions. Fragmented habitats may prevent a species from colonizing a more suitable patch upslope with favorable climate as the climate in the species' native elevation changes (Corlett and Westcott 2013). For example, Amazonian forests are projected to face heightened vulnerability and species extinctions when human made dispersal barriers, including deforested patches, prevent species migrating to their climate analog of 2050 (Feeley and Rehm 2012). With increased deforestation and fragmentation in much of the tropics (Bawa et al. 2004), landscape connectivity will be a key filter determining what species will be present in near future forests. Species with high dispersal (wind or insect dispersed) may gain over species with short dispersal distances (large animal or mechanically dispersed) (Bazzaz 1996). Similarly, species with smaller seed size may gain over species with larger seed size with reduced landscape connectivity because of ease of dispersal (Cramer et al. 2007).

Deforestation

Deforestation can alter abiotic conditions concurrently with climate change. Deforestation increases mean temperature and temperature variability, as well as increasing moisture variability (Laurance et al. 2011a). Regional deforestation can change height of cloud formation and cloud cover in general. Lowland deforestation/land-use change results in increased height of cloud formation (Nair et al. 2003), changing cloud and moisture conditions for highland forests in Costa Rica (Lawton et al. 2001). As tropical regions are likely to experience widespread land use change by the end of this century, land use change and deforestation is projected to be the largest driver of biodiversity, exceeding negative impacts of climate change, in tropical regions (Sala et al. 2000). Deforestation also reduces the pool of trait variations and genetic diversity (Santos et al. 2010) potentially needed for species adaptations to novel conditions. Undoubtedly, deforestation is a key factor for future tropical montane species composition, along with climate change.

Research needs

Focusing on tropical montane forests, we propose the following research agenda to: 1) gain an improved understanding of how species are currently distributed in climate in order to effectively predict future species distributions across climates and 2) to inform conservation efforts in coming decades.

Better geographical representation both at local level and at biome scale: This review has focused mostly on evidence from Neotropical montane forests. Compared with Neotropical mountains, palaeotropical mountains may have species with wider elevation bands and fewer high elevation specialists (Laurance et al. 2011b). As a result, paleotropical montane communities may be more resilient with current climate change. However, focused examination of species geographic ranges in the palaeotropical mountains and cross-biome comparisons with neotropical mountains can help us understand whether these forests will be resilient with climate change. At a more local level, improving both distribution data for species and the microclimatic variations found in the montane tropics can yield important insight into the tolerance of these species.

Improving the quality of climatic data: Tropical montane areas are environmentally heterogeneous regions with abiotic/climatic factors changing at relatively small spatial scales (Trivedi et al. 2008). Fine scale, local climate data can help understand the local and regional variation in climate, especially as it is relevant to the distribution of species in space. Improving the quality and availability of long-term meteorological data at local and landscape scales will inform the understanding of the range of climate conditions a species can tolerate.

Identify key functional traits: While it is ideal to have detailed experimental knowledge of how climate variable affects the reproduction, growth and survivorship of each species, it is not practical and feasible given the high species diversity in many biomes, including the montane tropics. Functional traits are important in community interactions and what species persist in a community (Sterck et al. 2011). To make widely generalizable predictions, identifying common key functional traits of species that occupy these systems should be a research priority. These key functional traits can be traits related to drought tolerance, photosynthetic capacity, temperature tolerance, etc. Identifying key functional traits that enable montane tropical species to occupy their current ranges is a key step towards predicting future forest composition in these systems. Also, research into how these key functional traits are correlated with life history strategies of growth rates and dispersal can offer an insight into the future species composition in tropical mountains.

Plasticity in key functional traits: Plasticity in functional traits within a species in response to a range of climatic factors gives the species an ability to cope with changing climate. Even in biomes such as the tropical montane forests where species occupy narrow elevation-climate ranges, it is likely that species exhibit plasticity in their functional traits in order to cope with unfavorable conditions and maximize growth over time. A clear understanding of the plastic response of these species with respect to their key functional traits can enable accurate predictions of intolerance to new climates in these species. This understanding of plasticity needs to be pursued at both small spatial scales via micro/mesocosm experiments) and at larger spatial scales via mensurative studies in order to understand the variation that exists in natural populations and the extent to which such variation can enable plastic response to a range of climate conditions.

Manipulative experiments to assess growth in different climates: Well-thought-out laboratory and field experiments with treatments that compare current ambient conditions to future conditions will be essential to understand how the functional traits and their plasticity result in growth in current and future climate. There is a dearth of experimental studies pursuing the effects of climate change in tropical forests. There needs to be a full frontal attack on how the physiological processes relate to key functional traits and overall recruitment, growth, and survivorship in these species with climate change.

Mechanistic species distribution models: Detailed empirical data from mensurative and experimental studies is especially useful when such data are fed into models to calibrate the key parameters of the model. Inputting of empirical data into mechanistic species distribution models can improve understanding of future species distributions considerably. Mechanistic models that can accommodate generalizations and plasticity of trait responses can be especially informative (Moritz and Agudo 2013) and applicable for diverse biomes such as tropical mountains.

Summary remarks

We have outlined the potential uncertainties that can arise from a number of climatic and biotic factors that can make predicting future species composition in tropical montane forests and elsewhere challenging. We have also outlined the research needs in order to meet these challenges for accurate prediction of future species distribution with climate change. Future research and model development for predicting species diversity in tropical mountains will need to account for functional diversity, plasticity in species response, and anthropogenic factors that influence tropical mountains. Predicting future species composition in speciose biomes such as tropical montane forests will have important implications not just for conservation of biodiversity, but for the people that depend on these forests and their diversity.

CHAPTER 6

CONCLUSION

In this dissertation, I explored how tree species in tropical mountains may respond to novel climatic and biotic factors with climate change. This works attempts to contribute to the broader body of knowledge exploring a classic ecological pursuit of understanding the factors controlling species distributions as well as to an emergent understanding of how species and biodiversity will respond to anthropogenic climate change.

In the second chapter, we presented the results of an experimental study done in the mountains of Southern Costa Rica. In a transplant experiment along an 800 m elevation gradient, we examine the potential for tolerance to novel climate and future changes in biodiversity by exposing tropical montane tree species to novel climates. We exposed two species of high elevation trees as well as local populations of three species of trees with broad elevation ranges to novel, warmer climate downslope. We observed increased mortality of high elevation species when exposed to a much warmer climate, but some persistence in a slightly warmer climate. The elevation generalists in this study were able to grow equally well across elevations and source populations. . These results suggest that species limited higher elevations in montane tropics will respond negatively to a warming climate via increased mortality and local populations of species occupying a broad elevation gradient may not respond negatively to a warming climate. Our study also illustrates the need for investigations to understand what abiotic and biotic variables contribute to intolerance of species to novel conditions leading to range margins in tropical mountains.

In the third chapter, we investigated how soil communities downslope from a species' current distribution interacted with elevated soil temperature to affect the growth of tropical montane species. We conducted a three month long shadehouse study with seedlings of three tropical montane tree species *Quercus costaricensis* (Fagaceae), *Viburnum costaricanum* (Caprifloiaceae), *Cinnamomum costaricanum*(Lauraceae), and a tropical vine *Passiflora edulis* (Passifloraceae) exposed to soil communities from within and downslope of their elevation range in combination with elevated soil temperature. None of the species showed reduced growth when grown with soil communities from downslope of their range. However, all the species grew more with elevated soil temperature. The results from this study suggest that tropical montane trees in our study region are able to tolerate, to an extent, abiotic and biotic variables different than what they experience in their current range.

In the fourth chapter, we reported on a three-month shade house study on seedlings of two tropical montane tree species, *Quercus insignis* (Fagaceae) and *Viburnum costaricanum* (Caprifloiaceae), exposed to elevated soil temperatures and novel soil moistures from altered watering regimes. Neither species showed changes in biomass from altered soil moistures generated by reduced amounts and/or frequencies of watering. However, *Quercus* obtained a greater final biomass when grown in elevated soil temperature. Maximum photosynthetic capacity of *Quercus* also increased with higher temperature, while the photosynthetic capacity of *Viburnum* did not differ between the treatments. Under the warmest and driest conditions *Viburnum* reached the same size as under current temperature and moisture regimes. Taken together, the two species in this study, to an extent, may be able to tolerate novel temperatures and soil moisture.

In a literature review, focusing on tropical montane ecosystems, we explored the challenges and current uncertainties in gaining a predictive understanding of species' distributions. The review explored salient literature to understand how species distributions in tropical mountains may respond to changing abiotic and biotic variables as well as important anthropogenic factors that are driven by social and economic dynamics such as nitrogen (N) deposition and deforestation. We highlighted ways in which species distribution models (SDM) can incorporate understandings and uncertainties to provide predictions of changing biodiversity patterns in tropical mountains with current and future climate change.

In general, the mortality of high elevation species in the field experiment contrasted with the subsequent shadehouse studies where novel soil temperature, novel soil microbial community, and novel soil temperature did not reduce growth or survivorship. This work suggests that while a warmer climate is likely to change species distributions by mortality of high elevation species, what climatic and biotic variables contribute to this pattern remains open to investigation. In order to better predict future forest composition in tropical mountains, in addition to temperature and moisture change, effects of clouds, UV insolation, and competitive interactions need to be considered. Next generation bioclimate envelop models could also use more mechanistic inputs from longer term empirical studies examining combined effects of these environmental factors on plant growth and survivorship.

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APPENDIX A

SUPPLEMENTARY INFORMATION FOR CHAPTER 3

Summary ANOVA table for main (soil temperature and inocula) effects. Asterisks indicate significant factors at $\propto< 0.05$

Species: *Viburnum costaricanum*

```
            Df  Sum Sq Mean Sq F value    Pr(>F)
Temp         1 0.38896 0.38896 15.3547 0.0002615 ***
Inoc         2 0.33839 0.16919  6.6792 0.0026197 **
Temp:Inoc    2 0.12049 0.06025  2.3783 0.1027239
Residuals   52 1.31724 0.02533
```

Species: *Cinnamomum costaricanum*

```
            Df  Sum Sq  Mean Sq F value   Pr(>F)
Temp         1 0.08287 0.082869  9.4530 0.003329 **
Inoc         2 0.09199 0.045995  5.2466 0.008337 **
Temp:Inoc    2 0.00318 0.001589  0.1812 0.834769
Residuals   53 0.46462 0.008766
```

Species: *Quercus costaricencis*

```
            Df  Sum Sq Mean Sq F value Pr(>F)
Temp         1   6.727  6.7268  2.7200 0.1049
Inoc         2   1.467  0.7335  0.2966 0.7446
Temp:Inoc    2   0.041  0.0205  0.0083 0.9918
Residuals   54 133.545  2.4731
```

Aboveground mass only for *Quercus costaricensis*

```
            Df Sum Sq Mean Sq F value  Pr(>F)
Temp         1  4.275  4.2750  3.1046 0.08384 .
Inoc         2  0.836  0.4178  0.3034 0.73955
Temp:Inoc    2  0.198  0.0992  0.0721 0.93056
```

Species: *Passiflora edulis*

```
            Df  Sum Sq Mean Sq F value    Pr(>F)
Temp         1 0.97233 0.97233 21.2430 2.585e-05 ***
Inoc         2 0.60851 0.30426  6.6472  0.002656 **
Temp:Inoc    2 0.09416 0.04708  1.0286  0.364540
Residuals   53 2.42591 0.04577
```

APPENDIX B

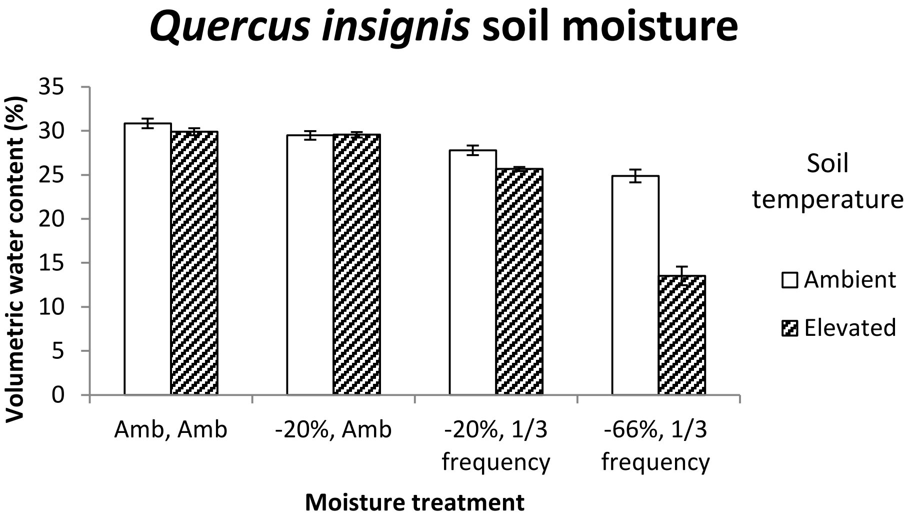
SUPPLEMENTARY INFORMATION FOR CHAPTER 4

Effect of watering on soil moisture:

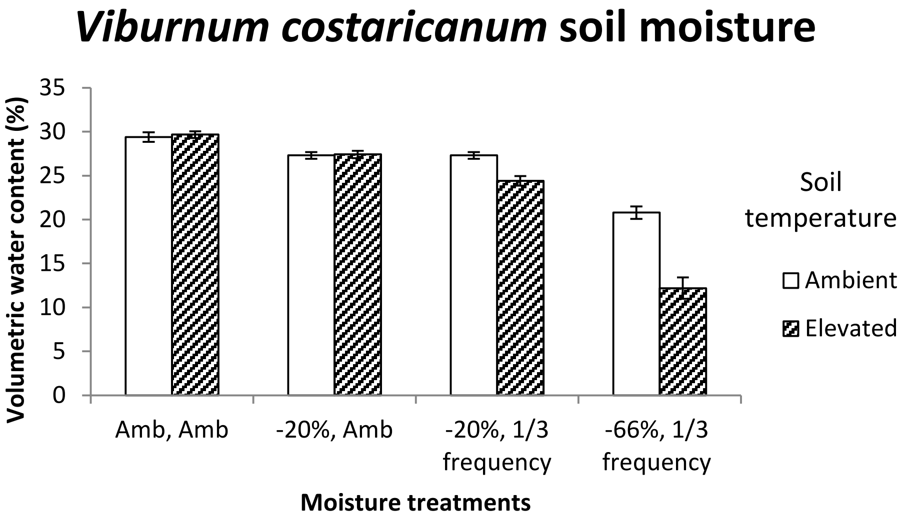
Effects of watering on soil moisture were modeled using a general linear model with daily average moisture as the dependent variable and the temp and moisture variable as the independent variables using R (R Development Core Team 2013). Watering regimes influenced soil moisture content for *Quercus* and *Viburnum* (*Figure B1* and *B2*). 20% reduced water applied daily resulted in 1.7% reduction in soil moisture compared to the ambient watering treatment ($p=0.075$). Twenty percent reduced amount applied at 1/3 frequency resulted in 3.7% reduction in daily moisture ($p=0.037$). 66% reduction in water applied at 1/3 frequency resulted in 7.2% reduction of soil moisture compared to ambient water applied every day ($p<0.001$). However, soil moisture was even more reduced with elevated soil temperature in -66% reduction treatments 10% reduction compared to ambient soil temperatures. However, when the soil temperature was elevated, 66% reduced water applied at 1/3 frequency resulted in even drier soil moisture when compared to ambient soil temperature ($p<0.001$).

Supplementary **Table B1**: Biomass regressed against Coefficient of Variation (CV(SM)) in soil moisture

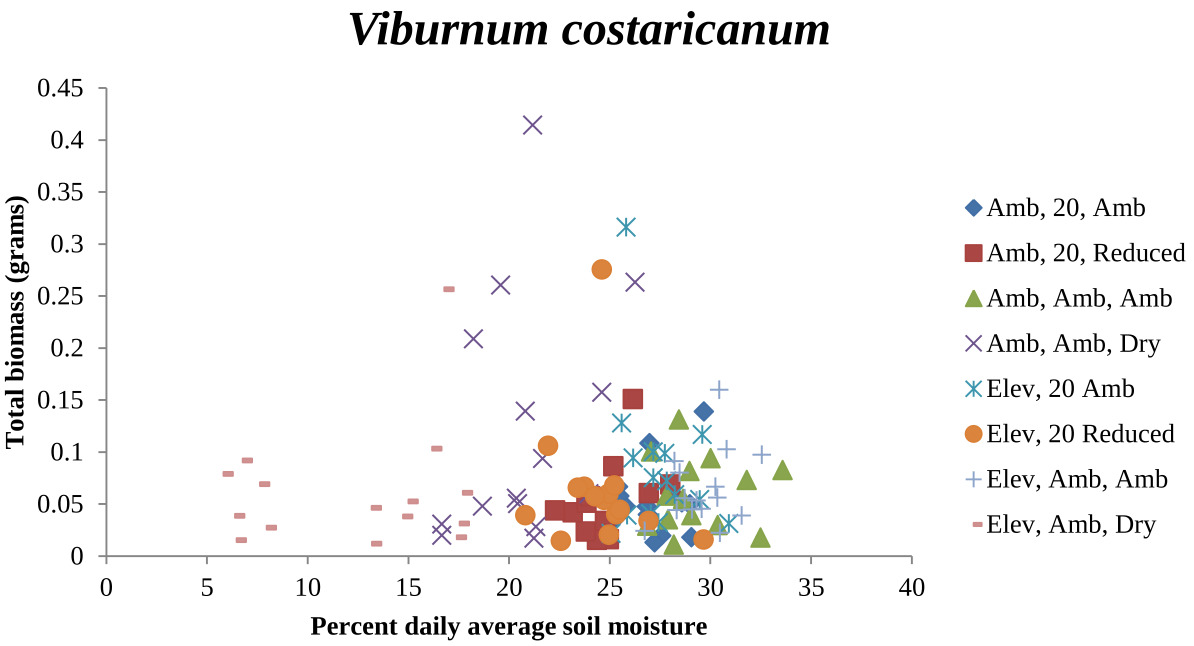
Species	DF	F-statistic	p value	Multiple R^2	Adjusted R^2
Viburnum	114	0.12	0.72	0.001	-.007
Quercus	113	5.01	0.02	0.04	0.03

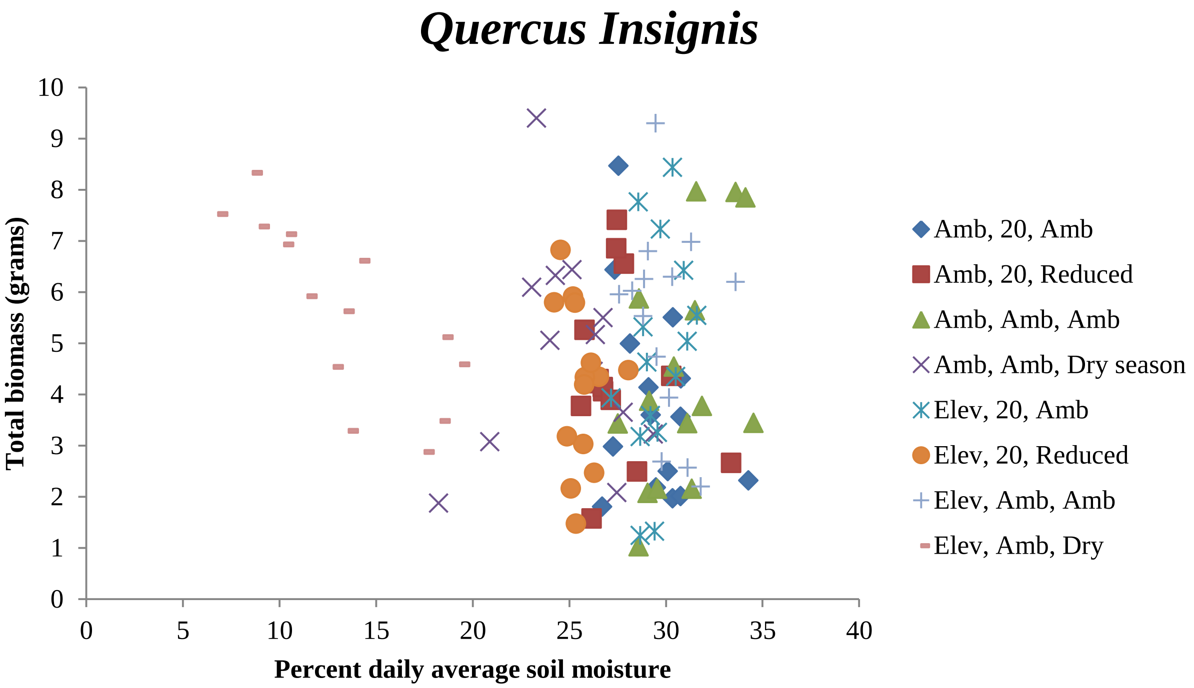


Supplementary *Figure B1*: Average daily soil moisture ± SE for *Quercus insignis* seedlings in 5 L pots. Moisture treatments with two levels of soil temperature are on the X axis and percent soil moisture is on the Y axis.

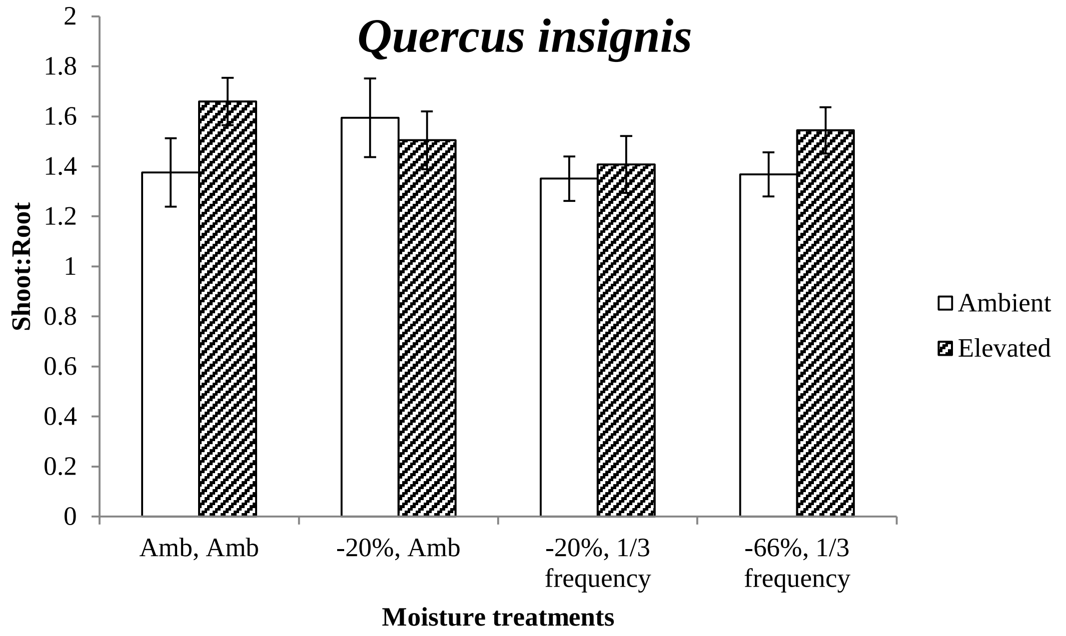


Supplementary *Figure B2*: Average daily soil moisture ± SE for *Viburnum costaricanum* seedlings in 3.5 L pots. Moisture treatments with two levels of soil temperature are on the X axis and percent soil moisture is on the Y axis.





Supplementary *figures B3* (top) and *B4* (bottom):*Quercus* (top) and *Viburnum* (bottom) biomass against average daily soil moisture. Average daily soil moisture in planting pots plotted on X axis and dry total biomass is plotted on the Y axis. The legend denotes the different temperature and soil moisture treatment combinations



Supplementary *Figure B5*: Root to shoot ratio of *Quercus insignis.* Moisture treatments with two levels of soil temperature are on the X axis and shoot to ratio is on the Y axis. Root to shoot ratio did not respond to any of the treatments, although shoot mass increased in response to elevated soil temperature. N=116