

Unraveling patterns of ant diversity: Drivers through space and time

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Comprehensive Exam Proposal

Overview

Understanding the distribution of biodiversity and the factors that drive it is central to biology. For my dissertation, I plan to study the diversity of ants in the context of elevational gradients, detailing the patterns and underlying drivers across spatial scales. Patterns of species diversity have been of interest and relevance to humans for millennia, though our understanding of both the patterns and what shapes them is still relatively early in its development (Humbolt, 1805; Darwin, 1859; Wallace, 1876; Pianka, 1966; Rahbek, 1995; Rosenzweig, 1995; Lomolino, 2001; Hillebrand, 2004). On a global scale, nearly all taxa show highest diversity in the tropics with a decline toward the poles (Willig et al., 2003; Hillebrand, 2004; Mittelbach et al., 2007). Unfortunately, the factors that drive this remarkably consistent pattern are difficult to convincingly disentangle because many of the proposed hypotheses generate similar predictions (Pianka, 1966; Mittelbach et al., 2007). Elevational gradients provide compact systems replicated across mountain ranges on every continent, allowing for more rigorous studies of the key factors that shape biodiversity (Rahbek, 1995; Lomolino, 2001; McCain & Grytnes, 2010). Importantly, hypothesized drivers of diversity do not always covary across mountain ranges and, consequently, their effects on the distribution of diversity can be more effectively tested in comparison to the latitudinal gradient (Lomolino, 2001; McCain, 2007a).

Over decades, many hypotheses have been proposed to explain the distribution of diversity, including geographic-, climatic-, biotic-, and evolutionary-based drivers (Pianka, 1966; Rohde, 1992; Mittelbach et al., 2007). In the face of increasing pressures from habitat loss, invasive species, and climate change, understanding the patterns of diversity and what structures them is critical to effective conservation efforts (McCarty, 2001; Bertelsmeier et al., 2013). In addition to being valuable macroecological study systems, mountain ranges are highly diverse, comprising more than half of the global biodiversity hotspots (Spehn & Körner, 2009). Elevational gradients, with many biomes compressed into a small spatial extent, provide key habitats for many species and the opportunity to test ecological theory with natural experiments (Terborgh, 1977; Brown, 2001; McCain, 2007b; McCain & Sanders, 2010).

In my dissertation, I will improve our understanding of what structures biodiversity across spatial scales and test hypotheses that have not been sufficiently or rigorously tested, including productivity and competition. While elevational diversity studies typically only sample along a single transect (e.g., Olson, 1994; Fisher, 1996; Sabu et al., 2008; Longino & Colwell, 2011), I will use a uniquely detailed and extensive dataset with replicated elevational transects in two Colorado mountain ranges to investigate ant diversity and communities at the species, genus, and subfamily levels and at nested spatial scales that span from a pitfall trap to an elevational site to a mountain range. This dataset will form the basis for Chapters 2-5.

In Chapter 1, I performed a global reanalysis of ant elevational diversity using published data to detail broad patterns and to test four prominent diversity hypotheses. Ant diversity, like other taxa (McCain, 2005, 2009a, 2010; Sanders & Rahbek, 2012), most often peaks at middle elevations. Though the hypothesis tests were somewhat equivocal, the diversity patterns are most likely driven by a combination of temperature, precipitation, and available area. In Chapter 2, I will use data from four elevational transects in Colorado to develop a hierarchical Bayesian model of ant diversity informed by the results of Chapter 1. With this framework, I will test multiple possible diversity drivers that may be acting simultaneously or through several mechanisms. In Chapter 3, I will explore patterns of ant diversity along the Colorado transects across spatial scales, detailing and comparing the trap, habitat, elevational site, and transect levels.

Additionally, I will examine changes in diversity, abundance, and production of reproductive individuals over the course of a summer across elevations. In Chapter 4, I will test predictions generated by the hypothesis that cold temperatures limit diversity at high elevations while competition limits diversity at lower elevations (Pianka, 1966; Rohde, 1992; Willig et al., 2003). This hypothesis has not been well evaluated across elevational gradients (McCain & Grytnes, 2010; Machac et al., 2011). Finally, in Chapter 5, I will use historic data on ant elevational ranges in Colorado (Gregg, 1963) in comparison with current data to ask whether ant species are responding to climate change with shifts in elevational distribution.

Though insects are an astoundingly diverse taxon (Gullan & Cranston, 2010), a majority of the research on macroecological patterns of diversity has focused on chordate or plant groups (Rahbek, 2005; Beck et al., 2012), leaving large gaps in our knowledge of insect patterns and processes (Diniz-Filho et al., 2010; Herzog et al., 2013). Lomolino (2001) advocated that insight into the underpinnings of diversity patterns would be aided by investigating patterns across taxa. In comparison to the better-studied birds and mammals, ants present several contrasts relevant to diversity hypotheses and studies along elevational gradients. Ants are more diverse and typically more abundant (Lach et al., 2010), potentially reducing the effect of sampling error. As ectotherms, ants have been suggested to be more sensitive to temperature and would thus be expected to respond more directly to the elevational temperature gradient (Malsch et al., 2008; Dunn et al., 2010). Competition between ants is famously intense, suggesting that biotic interactions may be of particular importance (Hölldobler & Wilson, 1990; Cerdá et al., 2013). Finally, in contrast to most insects, the individuals used for ant identification are wingless and consequently distance-limited from their colony (Hölldobler & Wilson, 1990), eliminating the potential for accidentals that were carried by the wind to elevations where the species cannot long survive.

My primary goal is to detail patterns of species diversity, communities, and the underlying drivers that shape the distribution of species, using ants as a focal system. My work differs from previous elevational diversity research because the high resolution data replicated across four elevational transects allows me to test hypotheses, including productivity and competition, that have been not been appropriately or rigorously addressed with adequate data or at spatial scales relevant to elevational diversity patterns. Additionally, I will build a model incorporating the sampling scheme and data structure across different scales to test multiple hypotheses simultaneously, an approach more

consistent with natural systems that is lacking in the literature. Additionally, these will be the first systematically sampled elevational transects for ants in the Rocky Mountains.

Planned Dissertation Chapters

1. Global reanalysis of ant elevational diversity
2. Disentangling elevational diversity: A hierarchical Bayesian approach
3. Exploring Colorado ant diversity through space, time, and taxonomy
4. Competition, climate, and diversity: Testing an age-old hypothesis
5. Is climate change affecting elevational ranges of Colorado ants?

Chapter 1: Global reanalysis of ant elevational diversity

This meta-analysis is in review at the *Journal of Biogeography*. Here, I provide a brief overview of the context of the work, theoretical underpinnings, primary results, and conclusions. If you are interested in seeing more detail, I would be happy to provide the entire manuscript.

It is commonly held that, in contrast to patterns observed in other taxa (Rahbek, 1995; Brown, 2001; Bhattacharai et al., 2004; McCain, 2005, 2007b, 2009a), ant diversity most often decreases with increasing elevation, likely in response to temperature (e.g., Brühl et al., 1999; Malsch et al., 2008; Dunn et al., 2010). However, this reanalysis is the first to test this assumption rigorously using many elevational gradients. I used ant diversity data from elevational gradients across the globe to test the predictions of four hypotheses that had seen previous support or that had been suggested as particularly important for ant diversity. Specifically, I assessed temperature, the mid-domain effect, area, and the interaction of temperature and precipitation as drivers of ant elevational diversity patterns.

Temperature

The decline in temperature with increasing elevation is one of the most consistent and apparent trends on mountain gradients; it is often suggested to drive diversity and has been shown to be relevant for ant diversity in particular (Sanders et al., 2007; Malsch et al., 2008). Thermal energy is an established predictor of foraging activity and larval development in ants, and warmer temperatures may allow longer foraging periods or increased food resources through increased productivity (Hölldobler & Wilson, 1990; Kaspari et al., 2000, 2004). Alternatively, the metabolic theory of ecology (MTE) posits that metabolic rates drive ecological and evolutionary processes. Because metabolic rates increase with temperature, speciation rates may increase correspondingly (Allen et al., 2002; Brown et al., 2004). Specifically, MTE predicts a linear relationship with $\ln(S) = b*(kT)^{-1} + c$, where S is the diversity within an elevational band, k is Boltzmann's constant ($k = 8.62 \times 10^{-5}$ eV/K), and T is the mean annual temperature in Kelvin. The predicted slope is $-0.7 < b < -0.6$ (Brown et al., 2004; Hawkins et al., 2007; McCain & Sanders, 2010). Regardless of the mechanism, temperature-based hypotheses all rely on a close relationship between temperature and diversity across the elevational gradient, predicting a monotonic decline in diversity from the mountain base to the summit (Pianka, 1966; Kaspari et al., 2000; Allen et al., 2002; Dunn et al., 2010).

Mid-domain effect

The mid-domain effect (MDE) is a geometric null model based on the overlap of observed ranges constrained within a bounded domain (Colwell & Hurtt, 1994; Colwell & Lees, 2000). On elevational gradients, the simulated random placement of observed elevational ranges between the mountain base and summit results in highest diversity at the middle elevation with a symmetric decline in diversity toward the boundaries (Colwell & Lees, 2000; McCain, 2004; Dunn et al., 2007). Arita (2005) used theoretical range size distributions to show that the MDE also generates predictions of the mean range size across elevations. If the MDE is a primary driver of ant diversity across elevations, simulations based on the random placement of observed elevational ranges should predict both the empirical diversity and the mean range size in elevational bands across the gradient.

Geographic area

The geographic area hypothesis, based on the species-area relationship, predicts that as the area of an elevational band increases, diversity in that band should increase (Terborgh, 1973; Rosenzweig, 1992). Typically, this relationship is linear when both variables are log-transformed (Rosenzweig, 1995; Rahbek, 1997; McCain, 2007b). Theory suggests that multiple scales may contribute to the species area relationship. Over broad spatiotemporal scales, larger areas allow for larger ranges, decreasing extinction probability and increasing speciation probability through the introduction of a barrier (Rosenzweig, 1995 and references therein). Over narrow spatiotemporal scales, larger areas will likely include more habitats, increasing the probability of detecting additional species from adjacent habitats (Terborgh, 1973; Rosenzweig, 1995; Romdal & Grytnes, 2007). However, the effect of area may be greater over larger spatial scales since sampling area is often standardized in local studies (McCain, 2007b; Karger et al., 2011).

Productivity: precipitation & temperature

The elevational climate model (ECM) qualitatively approximates productivity and proposes that the combination of temperature and precipitation drives diversity, resulting in highest diversity at the warmest, wettest elevations (McCain, 2007a). The pattern of diversity predicted by the ECM depends on the local mountain climate (McCain, 2007a). On arid mountains, water availability is typically highest at middle elevations due to the dry climate at the base and increased run-off toward the summit (Mollhagen & Bogan, 1997; Brown, 2001). Thus, water limitation restricts diversity toward the base while temperature restricts diversity toward the summit, resulting in a mid-elevation diversity peak. On mountains with wet climates, water is not limiting, so temperature drives diversity across the entire gradient, resulting in high diversity at the base with a decline toward the summit (McCain, 2007a). The ECM offers currently testable predictions while fine-scale, reliable global productivity data is lacking. A more direct assessment of the productivity hypothesis is possible along select gradients if data are collected at an appropriately high resolution.

Results and discussion

The literature search returned sixty-six candidate ant elevational diversity datasets. Of those, forty-five were unique and provided data along a single gradient or region. Only twenty datasets (44%) met the *a priori* sampling criteria (high sampling effort with standardized methods; sampling of $\geq 70\%$ of the elevational gradient; sampling within the lowest 400m of the gradient; no sampling gaps $> 500\text{m}$ in elevation;

little anthropogenic disturbance). This proportion is comparable to similar analyses focusing on birds (41%: McCain, 2009a), bats (44%: McCain, 2007a), vertebrate ectotherms (51%: McCain & Sanders, 2010), reptiles (67%: McCain, 2010), and small non-volant mammals (73%: McCain, 2005). The qualifying datasets represented both temperate and tropical latitudes, with eleven local scale studies and nine regional scale studies. Additionally, eight studies were in arid climates and twelve were in wet climates.

Ant diversity showed three distinct patterns, with the distribution nearly identical between local and regional studies (Fig. 1.1); most transects showed mid-elevation peaks ($n = 14$), followed by monotonic declines ($n = 3$) and low plateaus ($n = 3$). Of the datasets

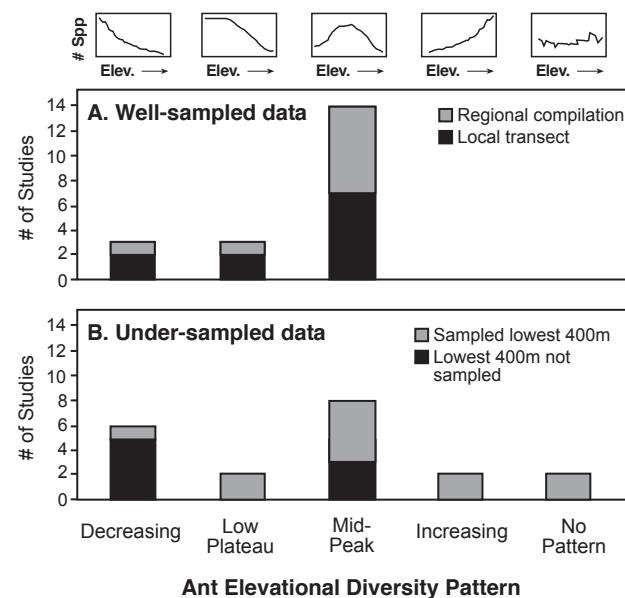
that were excluded due to sampling issues, 64% either did not sample $\geq 70\%$ of the gradient or did not sample within the lowest 400m. Because diversity nearly always decreases beyond a certain elevation, an absence of data at the mountain base will often lead to the observation of declining diversity regardless of the true pattern (Nogués-Bravo et al., 2008). Thus, the use of rigorous *a priori* standards is crucial to understanding and disentangling the drivers of diversity.

Temperature was not well supported as a primary driver of diversity in the datasets used in this analysis. Contrary to the monotonic decrease in diversity predicted by the temperature hypotheses, the majority of studies, including excluded studies, detected highest diversity at intermediate elevations rather than at the base. Moreover, temperature was not a strong predictor of diversity across all gradients when analyzed with individual linear regressions. Likewise, the metabolic theory of ecology was not supported as the

Figure 1.1. (a) The number of well-sampled ant studies showing each of the diversity patterns ($n = 20$). Mid-peaks were most common with equal numbers of decreasing and low plateau patterns observed. Regional (gray bars) and local (black bars) scales did not differ in the pattern distribution. (b) Unique datasets that did not meet the *a priori* criteria ($n = 25$; see text) showed five patterns: mid-peaks and decreasing patterns were most common with equal numbers of low plateaus, increasing patterns, and no pattern. Most studies that did not sample within the lowest 400m (black bars) reported monotonic decreases while studies that sampled within the lowest 400m (gray bars) reported other patterns.

confidence intervals of the slope did not fall within the predicted range. Though temperature was not supported as the primary driver across the entire elevation gradient, all studies did show a decrease in diversity above some elevation, consistent with the hypothesis that low temperatures limit diversity (Olson, 1994; Currie et al., 2004).

The mid-domain effect was not well supported by these data. Although the majority of studies exhibited highest diversity at intermediate elevations as predicted by the MDE, the details were inconsistent as assessed by the proportion of observations



within the 95% prediction bands and by linear models. These results are consistent with other taxa including mammals, geometrid moths, birds, and reptiles (Dunn et al., 2007; McCain, 2007b, 2009a, 2010; Beck & Chey, 2008).

Support for area as a driver was mixed. Many studies showed a strong fit with the Arrhenius model ($S = cA^z$), but 20% fit very poorly. Additionally, regional datasets did not show the predicted stronger fit compared with local datasets. It is possible that local studies along elevational gradients are at a scale intermediate to alpha and gamma diversity, resulting in similar dynamics in local and regional studies (Grytnes & McCain, 2007). Alternatively, the local species richness may be influenced by regional area indirectly via the regional species pool (Rosenzweig & Ziv, 1999; Romdal & Grytnes, 2007). Area has also seen mixed support for other taxa (Grytnes, 2003; McCain, 2007b, 2009a, 2010), suggesting that it may be a factor of secondary importance, influence diversity conditionally, or act in conjunction with other drivers.

Likewise, the interplay of temperature and precipitation as described by the ECM received mixed support. Though mid-peaks were not more likely on arid mountains than on wet mountains, wet mountains showed significantly higher diversity at the mountain base as well as a better fit to temperature when compared to arid mountains. Energy and water are well-established physiological constraints and have been implicated as important drivers of diversity and abundance in both plants and animals (Kaspari et al., 2000; Hawkins et al., 2003; Bhattacharai et al., 2004). For animals, this may occur directly through physiology or indirectly through effects on productivity and food resources (Gaston, 2000; Kaspari et al., 2000; Hawkins et al., 2003; McCain, 2007a). Because the ECM is an approximation of productivity (McCain, 2007a, 2009a), high resolution data on productivity, once available, could address this hypothesis more directly and allow tests of the combined effects of multiple hypotheses.

Conclusions

This reanalysis shows that patterns of ant diversity across elevations are consistent with patterns commonly seen in other taxa (Rahbek, 1995; Brown, 2001; Bhattacharai et al., 2004; McCain, 2005, 2007b, 2009a). A variety of patterns occurs and diversity is typically highest at middle elevations rather than declining monotonically from the mountain base. Additionally, a large proportion of published studies across many taxa do not sample rigorously or completely, leading to a heavy bias toward observations of monotonic declines in diversity, particularly when the lowest 400m are not sampled (Fig. 1.1; McCain, 2005, 2007a, 2009a, 2010; Nogués-Bravo et al., 2008; McCain & Sanders, 2010). Finally, the drivers of ant diversity across elevations are still equivocal, though both the mid-domain effect and temperature hypotheses were unsupported. Temperature moderated by precipitation, however, received some support, as did the area available at an elevation. To disentangle these hypotheses, and to test others such as habitat complexity or productivity, future studies will be required with extensive fine-scale data across multiple elevational gradients as will be conducted in my following chapters.

Chapter 2: Disentangling elevational diversity: A hierarchical Bayesian approach

Introduction

The changes in species diversity in space and time have interested humans for centuries (Humbolt, 1805; Darwin, 1859; Wallace, 1876; Pianka, 1966; Brown, 1971; Lomolino, 2001). Understanding the factors that drive diversity patterns is becoming increasingly important for conservation efforts as the climate changes and both the quantity and quality of habitat continues to diminish worldwide (McCarty, 2001; Gering et al., 2003; Diniz-Filho et al., 2010; Munyai & Foord, 2012; Bertelsmeier et al., 2013). A multitude of hypotheses have been proposed to explain the large scale patterns that have been observed (Pianka, 1966; Rohde, 1992; Mittelbach et al., 2007), though definitive and generalized progress has been limited. Experiments are often infeasible or impossible due to the timescale required by many hypotheses, many predictions are confounded particularly along the latitudinal gradient, and high resolution data is often lacking (Mittelbach et al., 2007; McCain, 2009a; McCain & Grytnes, 2010).

Elevational gradients in mountains provide a more amenable study system than the latitudinal gradient. Mountains, occurring on every continent, provide compact, globally replicated systems (Rahbek, 1995; Lomolino, 2001; McCain & Grytnes, 2010). Because mountain ranges can vary in characteristics including climate, productivity, and history, comparisons among mountain ranges decouple variables and constraints (Lomolino, 2001). The simultaneous study of multiple elevational gradients is crucial, though rare due to the time and effort involved. Global analyses of elevational gradients have suggested that a small subset of factors likely determine patterns of diversity (McCain, 2007a, 2009a, 2010).

Temperature

Temperature has often been proposed as a driver of diversity and, though consistent in some cases (Sanders et al., 2007; Malsch et al., 2008), it is not broadly supported as a sole mechanism (Szewczyk & McCain, *in review*). Temperature could affect ant diversity through several mechanisms. As ectotherms, both foraging activity and larval development are dependent on temperature and, consequently, warmer temperatures may allow for increased access to food resources and colonies that grow more quickly (Hölldobler & Wilson, 1990; Kaspari et al., 2000, 2004). Alternatively, warmer temperatures may cause increased metabolic rates and corresponding increases in ecological and evolutionary processes such as speciation, as advocated by the metabolic theory of ecology (Allen et al., 2002; Brown et al., 2004).

Productivity: precipitation & temperature

The effect of temperature may be contingent on precipitation, though data at an appropriately high resolution across a large spatial scale have been lacking (McCain, 2010). The elevational climate model generates qualitative predictions testable by current data and proposes that diversity will be highest at the warmest, wettest elevational band because that will coincide with highest productivity (McCain, 2007a). The ECM is broadly consistent with global ant diversity (Szewczyk & McCain, *in review*), though more direct tests of productivity are needed.

Area

The geographic area hypothesis, based on the species-area relationship, predicts that diversity will be highest at elevations with the largest area (Terborgh, 1973;

Rosenzweig, 1992). Typically, this relationship is linear when both variables are log-transformed (Rosenzweig, 1995; Rahbek, 1997; McCain, 2007b). Though the mechanisms are less well developed for elevational gradients than for the latitudinal gradient, theory suggests that both ecological and evolutionary scales may contribute to the relationship. As larger area allows for larger ranges, extinction probability decreases and speciation probability increases (Rosenzweig, 1995). Larger areas are also more likely to include more habitats, increasing the probability of detecting species from adjacent habitats (Terborgh, 1973; Rosenzweig, 1995; Romdal & Grytnes, 2007). Area was partly consistent as a driver of ant elevational diversity globally (Szewczyk & McCain, *in review*).

Habitat heterogeneity

The diversity of habitats will inevitably affect species diversity. However habitat diversity does not necessarily follow a consistent pattern across elevational gradients, and in fact, the relevant axes along which the habitats vary will depend heavily on the taxon of interest (Rosenzweig, 1995; Grytnes & McCain, 2007). For ants, it has been suggested that litter depth (Sarty et al., 2006; Bharti et al., 2013), undergrowth height and cover (Lassau & Hochuli, 2004; Pacheco & Vasconcelos, 2011), or canopy cover (Lassau & Hochuli, 2004; Pacheco & Vasconcelos, 2011) may be of particular importance. Thorough studies across an appropriately broad spatial extent are lacking due to the difficulties of appropriately measuring habitat heterogeneity (Grytnes & McCain, 2007).

Evolutionary and historic factors

The distribution of diversity within a taxon is influenced by the evolutionary history of that taxon (Ricklefs, 2004). The climate during a major diversification will likely have long lasting effects, with subsequent species' niches reflecting the niche of their ancestor (Wiens & Donoghue, 2004; Romdal, 2013). Alternatively, the climate or geography may influence rates of speciation and extinction which ultimately drive the patterns of diversity currently observed (Wiens et al., 2007). Unfortunately, robust tests of these hypotheses rely on species-level time-calibrated phylogenies that are not currently available for ants.

Advantages of a Bayesian framework

Progress in understanding broad scale patterns of species diversity has been hindered by several challenges. Many hypotheses have been proposed and it is likely that multiple factors may be acting on species diversity simultaneously. In particular, several global analyses have suggested that climate is a key driver, though the effects may be modified by other factors such as area or may be indirect, acting through effects on productivity (McCain, 2009a; Kessler et al., 2011; Beck et al., 2012). Factors, including temperature, precipitation, and productivity, can be correlated or causally linked while potentially affecting diversity through multiple mechanisms (Rosenzweig, 1995; Beck et al., 2012). Finally, a lack of high resolution data has prohibited rigorous evaluations of productivity-based hypotheses (McCain, 2010).

A hierarchical Bayesian framework is able to incorporate the intricacies of the sampling design, the possibility of multiple factors acting in concert, and causal relationships among those factors (Clark, 2005; Beck et al., 2012; Gelman et al., 2013), solving several of the problems that have plagued macroecological studies of species diversity. However, hierarchical Bayesian models have seen limited use in macroecology (Gelfand et al., 2005; Latimer et al., 2006; Beck et al., 2012). Additionally, very few

studies of elevational diversity have sampled along multiple transects. The results of those that have reveal that diversity patterns can differ along replicated transects even in the same mountain range (Grytnes, 2003; Sanders et al., 2003).

In this study, I use data from four elevational transects in Colorado across two mountain ranges. With high resolution, replicated data for productivity, climate, and species diversity, I will investigate the drivers of ant diversity in Colorado. Specifically, I will test the hypotheses that temperature, productivity, area, and habitat complexity act singly or in conjunction to determine the patterns of ant species diversity across elevations.

Methods

Study Area

The mountains of Colorado comprise a majority of the Southern Rocky Mountains. The Front Range runs primarily north to south through the north central part of the state while the San Juan Range is a massif found in the southwestern corner of Colorado. In the Front Range, most area is at the lowest elevations while in the San Juans, the largest amount of area is found approximately a third of the way up the gradient (Fig. 2.1). Temperature declines on average 0.5°C for every 100m gained in elevation and with the exception of the lowest elevations, precipitation is generally higher in the San Juan Range than in the Front Range, particularly in the summer due to the monsoons (Fig. 2.1; Gregg 1963, Barry 1992). The Front Range extends from semi-arid grassland at 1600m through Ponderosa pine, Douglas fir, and Engelmann spruce forests to the alpine at 4352m. The base of the San Juan Range is desert shrubland and extends from 1400m through pinyon-juniper, Gambel's oak, Douglas fir, and Engelmann spruce forests to the alpine at 4365m (Fig. 2.1; Gregg 1963, McCain 2009a). Based on temperature and precipitation, productivity is expected to be highest at middle elevations in both mountain ranges.

Sampling

Four elevational transects in Colorado were sampled during the summers of 2010-2012 with each transect composed of eight elevational sites separated by ~200m and with two transects in the Front Range and two transects in the San Juan Range (Table 2.1). In

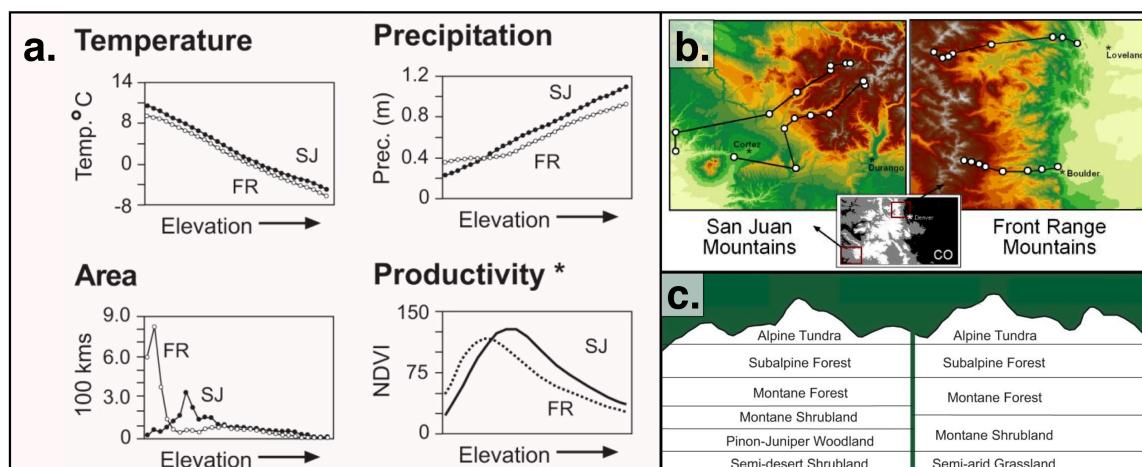


Figure 2.1. Comparison of the Front Range and San Juan Range (adapted from McCain, 2009b). Elevational temperature trends are similar across the mountain ranges, though the San Juans are slightly warmer; precipitation, area, and modeled (*) productivity across elevation all show different patterns (a). Two elevational transects surveyed from the mountain base to the alpine in each mountain range, totaling 36 sites (b). Biomes also differ between mountain ranges, particularly at the lower elevations (c).

Table 2.1. Sites sampled in the Front Range (FR) and the San Juans (SJ). Sites marked with an asterisk will be excluded because pitfall traps were heavily disturbed by bears or marmots. Worker abundances and trap counts are only included for sites that have been fully identified to genus; sites with genus-level identification still in progress are marked “IP”.

Mtn Range	Transect	Site Name	Elevation (m)	Lat	Long	Ant worker count	Number of trap pairs with ants	Year
FR	Big Thompson	Sylvandale	1728	40.43	-105.23	3,635	20	2010
FR	Big Thompson	Cow Camp	1938	40.46	-105.28	8,219	20	2011
FR	Big Thompson	Cedar Park	2153	40.45	-105.30	5,752	20	2010
FR	Big Thompson	McGraw	2410	40.42	-105.50	3,355	20	2011
FR	Big Thompson	Beaver Pond*	2811	40.40	-105.64	619	9	2011
FR	Big Thompson	Hidden Valley	3022	40.38	-105.66	6,588	20	2011
FR	Big Thompson	Tombstone	3364	40.39	-105.67	IP	IP	2012
FR	Big Thompson	Sundance*	3640	40.40	-105.70	192	8	2011
FR	Boulder	Sunshine Canyon	1811	40.02	-105.30	441	20	2010
FR	Boulder	Betasso	1904	40.01	-105.33	890	19	2010
FR	Boulder	A1	2215	40.01	-105.37	4,679	20	2010
FR	Boulder	B1	2712	40.02	-105.48	6,200	20	2010
FR	Boulder	MRS	2881	40.02	-105.53	2,035	20	2010
FR	Boulder	C1	3117	40.03	-105.55	718	19	2010
FR	Boulder	Saddle	3466	40.05	-105.58	4,382	20	2010
FR	Boulder	Green Lakes*	3659	40.05	-105.61	NA	NA	2010
SJ	Dolores	Airport	1796	37.30	-108.67	IP	IP	2012
SJ	Dolores	Weber Canyon	1970	37.24	-108.30	IP	IP	2012
SJ	Dolores	Grouse Point	2349	37.47	-108.39	IP	IP	2012
SJ	Dolores	Spruce Pond	2580	37.52	-108.31	IP	IP	2012
SJ	Dolores	556H	2887	37.54	-108.22	IP	IP	2012
SJ	Dolores	Little Bear*	3241	37.55	-108.10	IP	IP	2012
SJ	Dolores	578	3386	37.72	-107.93	IP	IP	2012
SJ	Dolores	Hermosa	3508	37.71	-107.91	1,324	20	2012
SJ	Lizardhead	Yellowjacket	1493	37.33	-109.03	10,051	20	2011
SJ	Lizardhead	Hovenweep	1717	37.43	-109.02	9,531	20	2011
SJ	Lizardhead	McPhee	2240	37.55	-108.46	15,039	20	2011
SJ	Lizardhead	Mavreeso	2528	37.69	-108.33	5,780	20	2011
SJ	Lizardhead	Willow Creek	3038	37.80	-108.12	4,004	20	2011
SJ	Lizardhead	616	3228	37.82	-108.13	4,151	20	2011
SJ	Lizardhead	Navajo	3390	37.84	-108.03	IP	IP	2012
SJ	Lizardhead	El Diente*	3517	37.84	-108.01	NA	NA	2012

the Front Range, one transect ('Boulder') sampled the St. Vrain watershed from 1811m to 3659m in 2010 and the other transect ('Big Thompson') sampled the Big Thompson watershed from 1728m to 3640m in 2010-2012. In the San Juan range, the two transects sampled the McElmo and Upper Dolores watersheds through different drainages, with one transect ('Dolores') spanning from 1796m to 3508m in 2012 and the other transect ('Lizardhead') from 1493m to 3517m in 2011-2012 (Fig. 2.1, Table 2.1).

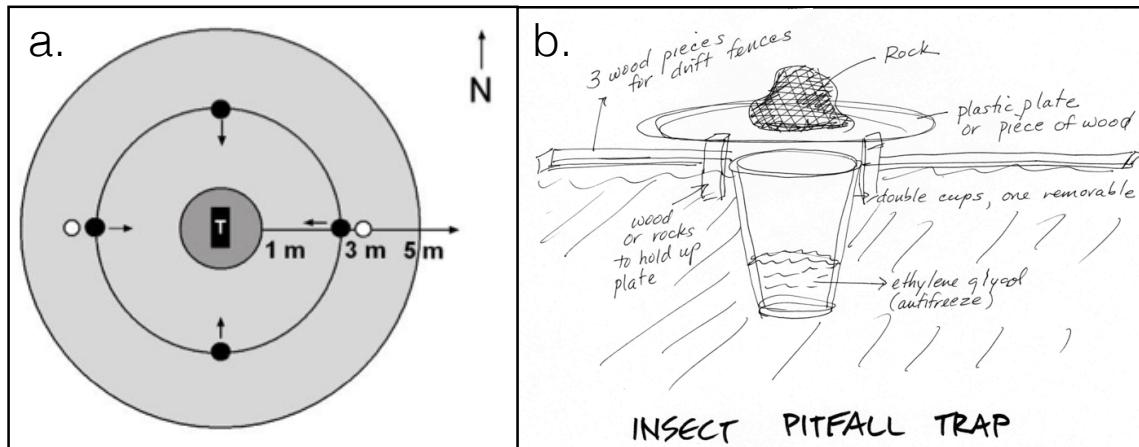
At each of the eight sites along each transect, 20 pairs of pitfall traps were placed in meadow, forest, rocky, and riparian habitats in proportion to the relative abundance of each habitat. The pairs of pitfall traps were placed 70m apart through each habitat. At each site, sensors measured air temperature, soil temperature, and precipitation for one year beginning when the pitfall traps were set. Pitfall traps remained set for three months

at each site. At five sites, pitfall traps were removed due to excessive disturbance by bears or marmots (Table 2.1). Those sites will be excluded from this analysis.

Each pitfall trap consisted of two nested plastic cups (diameter = 9cm, height = 12cm), the top cup filled with approximately 125 mL propylene glycol (preservative) and the bottom to hold the soil in place when periodically removing samples (Fig. 2.2). Three wooden shims radiated from the edge of each trap to intercept and direct insects toward the traps. A plastic plate covered each pitfall trap from rain and was held in place at least 4cm off the ground. The 40 pitfall traps at each site were placed in pairs in a sampling plot (Fig. 2.2). At each sampling plot, two pitfall traps were placed 3m east and 3m west of a center point. Data from each pitfall pair will be pooled to avoid independence issues. Vegetation coverage was estimated within a 1m radius of the center point for grass, forb, shrub, cactus, and bare ground using Braun-Blauquet coverage classes (+: < 1% coverage, sparse; 1: 1–5%, plentiful and scattered; 2: 5–25%; 3: 25–50%; 4: 50–75%; 5: >75%). At 3m north, south, east, and west of the center point, understory vegetation height (<1m) was measured and canopy coverage recorded with a densiometer taken facing the plot center. Within a 5m radius of the center point, the number and species of trees were counted along with the diameter at breast height (dbh) of each tree with a dbh \geq 3cm. Pitfall traps were collected every 2-3 weeks while vegetation surveys were performed at the start, middle, and end of the sampling season.

Pitfall samples in a small amount of propylene glycol were returned to the lab for cleaning and sorting. All ants were separated from the samples and transferred to 70% ethanol. Ant specimens are first identified to and separated by genus by me or trained undergraduate assistants. All ants are then identified to species or morphospecies using appropriate keys. Abundances from each collection of each trap are recorded. Specimens

Figure 2.2. Sampling plot layout (a) and pitfall trap design (b). At each elevational site, 20 vegetation and insect sampling plots were distributed among habitat types. Each sampling plot was centered on a mammal trap. Within a 1m radius of the center, coverage was estimated for grass, herb, shrub, cactus, and bare ground using Braun-Blauquet coverage classes. At the black dots 3m from the center, understory vegetation height (\leq 1m) was measured and canopy coverage was estimated with a densiometer taken facing the plot center. Within a 5m radius from the center, all trees were counted and identified to species with diameter at breast height (dbh) measured for all trees \geq 3cm in diameter. Two pitfall traps, represented by white dots, were installed 3m east and west from the plot center. Each pitfall trap (b) consisted of two nested plastic cups with the inner cup filled with ~125mL propylene glycol. Three wooden shims intercepted insects and directed them toward the cups. A plastic plate placed above the cups shielded the trap from rain.



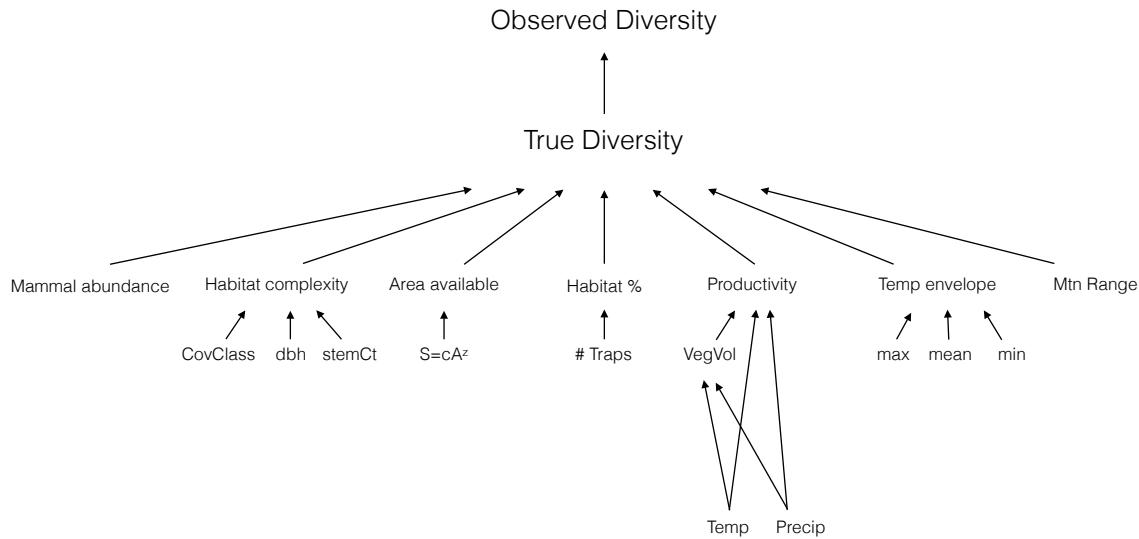


Figure 2.3. Preliminary model framework. Ant diversity will be modeled directly with possible covariates chosen to test theory. Using variable selection, I will estimate the probability that each covariate should be included in the model as well as a posterior distribution for the slope of the relationship of each covariate with diversity.

are currently stored in 70% ethanol and will eventually be incorporated into the University of Colorado Museum's entomology collections.

Though the high sampling effort was consistent across sites, reaching a convincing asymptote in a species accumulation curve is rare for studies of invertebrate diversity, so diversity estimators are commonly employed (Gotelli et al., 2011). Additionally, individual ant workers collected in pitfall traps do not provide the independent samples required by abundance-based estimators; often, hundreds of ants from a nearby colony fall into a single pitfall trap (Agosti et al., 2000; Gotelli et al., 2011). Therefore, I will use a sample-based approach to calculate asymptotic estimators of diversity at each site rather than using the raw number of species observed (Gotelli & Colwell, 2010).

Preliminary Model Framework

Species diversity is a property that emerges from the species composition. However, modeling it as such would require that parameters be estimated for each species, essentially as an occupancy model with more than 150 species of Colorado ants of varying abundance. Since such an approach is intractable, I plan to model species diversity directly as the response variable (Fig. 2.3). Using a hierarchical framework similar to the model described in Cressie et al. (2009), I will include effects of temperature, precipitation, productivity, area, and habitat complexity. The latter will be assessed with vegetation coverage classes, canopy cover, and tree density (Lassau & Hochuli, 2004). As mammals have been shown to be competitors with ants in some systems (Heaney, 2001), I will also include the abundance of small mammals at a site as a possible driver. Finally, the mountain range and transect will be random effects.

To test the importance of each possible driver, I will use variable selection (George & McCulloch, 1997; O'Hara & Sillanpää, 2009). A vector of indicators is used with an indicator for each parameter estimated by the model. The indicator takes values of either 0 or 1 and acts as a method to include or exclude each parameter. For instance, in the hypothetical model term $\gamma_i \beta_i X$, the parameter β_i is multiplied by the indicator γ_i and

the covariate X which represents a measured independent variable. When $\gamma_i = 0$, the term is set to 0 and is effectively excluded from the model. When $\gamma_i = 1$, the term is included in the model. Using Gibbs sampling, the MCMC algorithm determines the value of each parameter and indicator variable for each iteration and calculates the likelihood of that model given the data. Over thousands of iterations, the algorithm converges on the values with the highest likelihood while generating probability distributions for each parameter and indicator variable. The model output will include estimates and uncertainty for each parameter in addition to essentially an inclusion probability distribution for each parameter. Thus, I will use variable selection to estimate the probability that each

modeled driver is influencing ant diversity across elevations in Colorado. To my knowledge, this will be the first time this type of approach has been applied to elevational diversity analyses.

Preliminary Results

Ants were present with high abundance at nearly all sites (Fig. 2.4). Because of the trail-forming foraging habits of ants and the structure of colonies, pitfall traps do not sample workers independently and thus do not provide a reliable estimate of ant abundance (Agosti et al., 2000; Lanan, 2014). Instead, colony abundance, a variable in many ways more relevant to ant ecology, can be approximated with occupancy models or by calculating the proportion of traps where a taxon occurred (Fisher, 1998; Gotelli et al., 2011). By either method, ants were abundant in samples at all sites without heavy disturbance (Table 2.1).

This chapter relies on the completion of all ant identifications. Presently, 98,312 ants have been identified to genus and 42,423 have been identified to species. With the help of a trained undergraduate, I plan to finish all species-level identifications by the end of summer 2015 (see timeline). Currently, genus-level identifications are complete for the majority of both

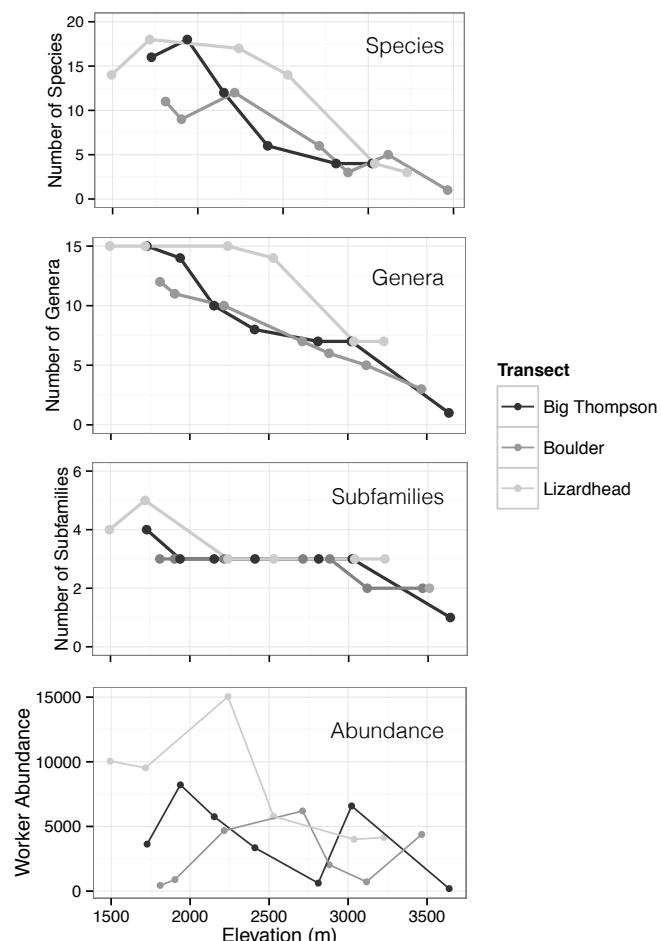


Figure 2.4. Preliminary diversity and abundance patterns at the site-level for the Big Thompson (FR), Boulder (FR), and Lizardhead (SJ) transects. Species diversity patterns on all transects will likely become more hump-shaped as identifications continue. The number of genera declines monotonically on both transects in the Front Range, but shows a low plateau on the Lizardhead transect. The number of subfamilies is largely constant across elevations, with additional subfamilies occurring at the lowest elevations or dropping out at the highest elevations. Overall worker abundance was highly variable.

Front Range transects and for one San Juan transect. Based on samples that have already been processed, I anticipate approximately 125,000 ant workers in total from all four transects.

The Front Range transects show a steady decline in the number of genera across elevations while one San Juan transect shows a low plateau followed by a decline (Fig. 2.4). Preliminary patterns of species diversity show shallow mid-elevation peaks; this hump-shaped pattern is expected to become more pronounced as identifications of several speciose genera continue. Additionally, the San Juan transect has higher diversity across most elevations, particularly in the middle third of the gradient.

I plan to develop the framework this semester and to code and debug the model during the spring semester. I will test and refine the model using simulated data generated with known parameter values to ensure that the parameters can be recovered consistently and reliably.

Preliminary discussion and conclusion

I will use a Bayesian approach to address several pitfalls common to elevational diversity studies. Species diversity is, in all likelihood, influenced by multiple factors simultaneously (Beck et al., 2012) and, consequently, many hypotheses have been proposed (Pianka, 1966; Hillebrand, 2004; Mittelbach et al., 2007). A hierarchical Bayesian model allows for the incorporation of multiple factors acting through different mechanisms in addition to including the details of the sampling design (Clark, 2005; Gelman et al., 2013). Additionally, this will be among a very limited number of studies using replicated elevational transects (Grytnes, 2003; Sanders et al., 2003; McCain, 2004), producing a more robust dataset. The replicated transects combined with the high resolution data on habitat structure and productivity will allow me to evaluate hypotheses that have been untested at this scale (McCain & Grytnes, 2010).

Finally, insects are relatively underrepresented in studies of elevational diversity compared to vertebrates (Sanders et al., 2007; Diniz-Filho et al., 2010; McCain & Grytnes, 2010; Herzog et al., 2013). In particular, ants provide a good study taxon. They are relatively well-described, highly diverse, and ecologically important in many systems in a variety of roles (Hölldobler & Wilson, 1990; Lach et al., 2010). In this study of ant diversity, I will help to fill in gaps in our understanding of the broad scale drivers of the diversity of insects, the most speciose animal clade.

Chapter 3: Exploring Colorado ant diversity through space, time, and taxonomy

Introduction

In order to disentangle the factors that drive species diversity, it is essential to thoroughly detail and explore the patterns of diversity (Rahbek, 1995). The pattern of diversity observed can be contingent both on the spatial extent and on the resolution of the sampling (Rahbek, 2005; Dunn, 2006), the taxonomic resolution (Diniz-Filho et al., 2010), and the temporal scale (Bishop et al., 2014). Likewise, the factors that shape those patterns may also vary with scale (Rosenzweig, 1995; Rahbek & Graves, 2001; Karger et al., 2011). For example, biotic interactions may be more important in structuring species occurrences and abundances at a fine scale, while those effects may diminish in importance as the spatial scale increases and regional drivers increasingly influence the patterns (Ricklefs, 2004). Understanding the interplay of ecological and evolutionary processes, their relation to species diversity, and feedback between processes operating at different scales therefore relies on correspondingly describing patterns of diversity at multiple spatial, temporal, and taxonomic scales (Willis & Whittaker, 2002; Ricklefs, 2004; Svenning et al., 2011; Lessard et al., 2012a, 2012b; Bishop et al., 2014).

In elevational diversity studies, emphasis is often on the total number of species occurring within an elevational band (e.g., Olson, 1994; Longino & Colwell, 2011). Equivalent site-level diversity can emerge from vastly different communities, however, which may be evident at smaller spatial scales within each site. These differences may yield insight into the underlying processes driving diversity across the elevational gradient. For example, intense antagonistic interactions may lead to low diversity at a single pitfall trap, though high turnover among traps could lead to high site-level diversity. In contrast, high diversity within each pitfall trap that approximates the site-level diversity would suggest that abiotic factors may be more influential.

In this chapter, I will use a uniquely detailed and extensive dataset to investigate patterns of ant diversity and communities in two Colorado mountain ranges. In contrast with most elevational diversity studies that use a single transect (e.g., Olson 1994, Samson et al. 1997, Sabu et al. 2008, Longino and Colwell 2011, but see: Sanders et al. 2003, Grytnes 2003), I will use data from two transects in each mountain range. Additionally, sampling was standardized across sites with insect samples collected for three months in a nested spatial design, yielding a uniquely consistent, high-resolution dataset covering a broad spatial extent.

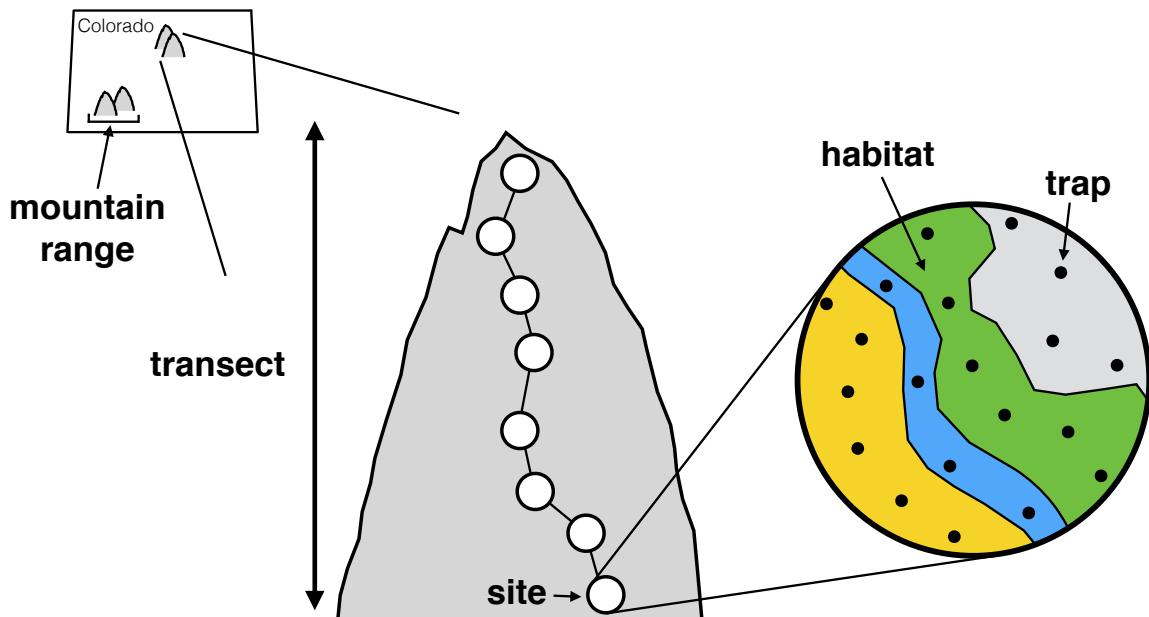
Specifically, I will explore and describe the diversity of Colorado ants at the spatial scales of the pitfall trap, habitat type, site, and elevational transect (Fig. 3.1). I will detail these patterns across taxonomic resolutions at the species, genus, and subfamily levels and compare the patterns across mountain ranges. Finally, I will investigate how ant diversity and communities change throughout the active season.

Methods

Site description and sampling procedure

The San Juan Range is a massif in the southwestern corner of Colorado, extending from desert shrubland at ~1400m to alpine tundra as high as 4365m. The Front Range extends from north to south through north central Colorado from dry grassland at ~1600m to alpine tundra with peaks as high as 4352m. Two elevational transects in each range were sampled during the summers of 2010-2012, with each transect composed of

Figure 3.1. Sampling design. Two mountain ranges were surveyed with two transects in each range. Transects consisted of eight sites separated by ~200m. Within each site, habitats (meadow, riparian, forest, rocky) were sampled in proportion to their abundance. Twenty pairs of pitfall traps (black dot = one pair) were set at each site, separated by 70m and remained set for three months.



eight elevational sites separated by ~200m in elevation. At each site, 20 pairs of pitfall traps were placed in habitat types (meadow, forest, rocky, riparian) in proportion to their abundance at that elevation with 70m between pairs (Fig. 3.1). Pitfall traps remained set at each site for three months and were collected every 2-3 weeks. During 2010, collections were sporadic, so temporal analyses will be restricted to the San Juan transects which were entirely sampled in 2011-2012. Ants were separated from the pitfall samples and transferred to 70% ethanol. Ant specimens are first identified to genus by me or by trained undergraduate assistants. All ants are then identified to species or morphospecies with appropriate keys. Specimens will be incorporated into the University of Colorado Museum's entomology collections. A complete description of the sites and sampling procedures can be found in Chapter 2.

Planned explorations and comparisons

Because this is a uniquely comprehensive, extensive, and standardized elevational diversity dataset, I intend to thoroughly explore the patterns of ant diversity, community composition, and abundance. I plan to describe how diversity changes across elevations when estimated at each spatial scale (Fig. 3.1). For each transect, I will detail the diversity at the level of site, habitats within sites, and pitfall traps within habitats and sites. Additionally, I plan to investigate whether ant communities in comparable climates are similar despite being geographically separated in different mountain ranges, using non-metric multidimensional scaling.

While a complete species-level phylogeny is currently unavailable, taxonomic levels allow for an approximation of evolutionary relatedness (Elton, 1946; Webb et al., 2002; Machac et al., 2011). Thus, I will explore how the patterns differ at the species, genus, and subfamily level across elevations and spatial scales.

Finally, I will investigate how the ant community changes throughout the course of a summer. All analysis involving phenological trends will be restricted to the San Juan transects which had samples collected every 2-3 weeks. Though the temporal resolution may be too coarse, I am also interested in elevational differences in the timing of the release of alates, the reproductive individuals produced by each colony. Release is often highly specific phenologically within a species (Hölldobler & Wilson, 1990), potentially creating an isolation mechanism across elevations since development is contingent on temperature (Hölldobler & Wilson, 1990; Nufio et al., 2010).

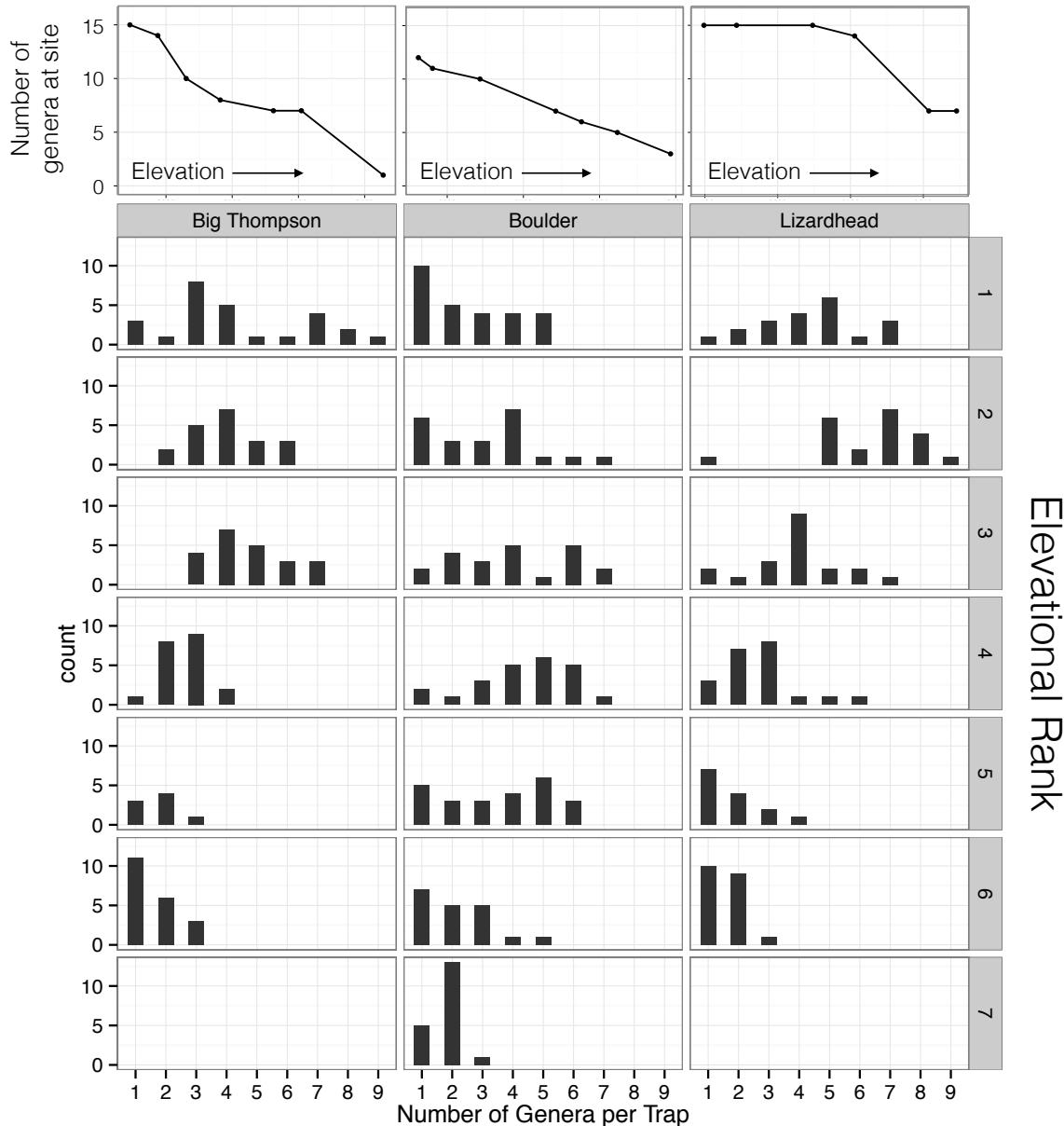


Figure 3.2. Diversity of genera within pitfall traps across three transects. Sites are ranked elevationally along each transect from lowest (1) to highest (7). Both Front Range transects show decreasing patterns of generic diversity across sites while the Lizardhead transect in the San Juans shows a low plateau (line graphs). However, none of the transects appear to have highest diversity at the lowest site when measured at the spatial scale of a pitfall trap (histograms). Rather, genus density at the trap level seems to be highest at middle elevations.

Preliminary results & discussion

As detailed in Chapter 2, I have worked through the majority of ant samples and I plan to finish all species-level identifications by the end of summer of 2015 (see timeline). The species diversity patterns are preliminary; diversity will likely increase most dramatically at middle elevations as identifications continue (Fig. 2.4). Genus diversity shows a decline in the Front Range and a low plateau in the San Juans. The number of subfamilies is stable across much of each transect, with a slight increase at low elevations and a slight decrease at high elevations.

Genus diversity appears to be discordant across the site and pitfall spatial scales. That is, the number of genera at each elevational site declines monotonically with elevation in the Front Range and shows a low plateau along the Lizardhead transect (Fig. 3.2). However, individual pitfall traps seem to have captured more genera at intermediate elevations in all three transects. This suggests that ant communities are structured differently across elevations and that those processes may be different than the broader processes that determine the site-level richness.

A preliminary NMDS ordination plot using the genera at each site shows that the low elevation desert sites in the San Juans have a distinct ant fauna (Fig. 3.3). For the majority of sites, however, a smooth transition is seen in the ant communities corresponding to elevation regardless of transect. Intriguingly, the high elevation sites on each transect seem fairly individual. It is possible, however, that this is spurious and caused by the large impact of small differences when diversity is very low.

Though this chapter is intended to be primarily descriptive and exploratory, the potential benefit is large. Replicated elevational transects will allow for stronger, more robust conclusions than are typically warranted in elevational diversity studies where only one transect is sampled (Grytnes, 2003; Sanders et al., 2003; McCain, 2004). Additionally, the sampling design enables the analysis and comparisons across spatial scales ranging from local communities of individual ant colonies to elevational bands. To my knowledge, this will be the first time that a phenological comparison has been conducted across replicated elevational gradients, allowing for the comparison of abundance patterns and detection across elevations, dates, and growing degree-days. This data and analysis will be extremely useful for comparisons in future decades.

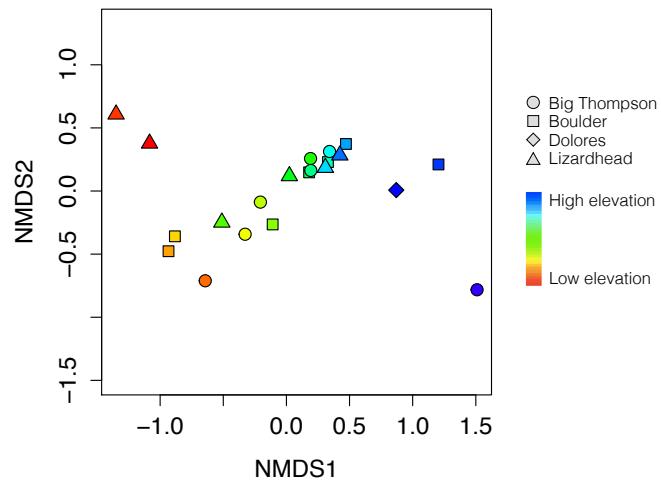


Figure 3.3. Preliminary NMDS with the genus composition at each site. The desert sites appear to have a distinctive ant fauna. Other sites show a transition from low to high elevation regardless of transect. The difference among high elevation sites may be artificial.

Chapter 4: Competition, climate, and diversity: Testing an age-old hypothesis

Introduction

Much of the focus in macroecological studies of diversity has been on abiotic hypotheses (Mittelbach et al., 2007; Beck et al., 2012) with biotic hypotheses often relegated to suggestion and speculation (e.g., Samson et al., 1997; Pfeiffer et al., 2003; Kessler et al., 2011; Longino & Colwell, 2011). The lack of rigorous tests is largely due to the methodological difficulties involved in testing biotic hypotheses with a sufficiently high resolution and broad spatial scale (McCain, 2009a; McCain & Grytnes, 2010).

Biotic hypotheses, particularly competition, nevertheless have a long history as an explanation for patterns of diversity (Darwin, 1859; Pianka, 1966; Terborgh & Weske, 1975; Lomolino, 2001; Mittelbach et al., 2007). An early intuitive hypothesis along the latitudinal gradient was that competition drives diversity in the tropics while cold temperatures limit diversity towards the poles (Pianka, 1966; Rohde, 1992; Willig et al., 2003). Along elevational gradients, the corresponding hypothesis, hereafter the ‘climate-competition hypothesis’, is that competition is most intense at low elevations, limiting species’ ranges and abundances and consequently diversity, while increasingly cold temperatures become the dominant factor as elevation increases (Heaney, 2001; Lomolino, 2001; Longino & Colwell, 2011; Machac et al., 2011; Sundqvist et al., 2013). Despite the long history, adequate tests of this hypothesis are lacking (Heaney, 2001; McCain & Grytnes, 2010; Longino & Colwell, 2011; Sundqvist et al., 2013).

Among ant species, competition can be particularly intense (Hölldobler & Wilson, 1990; Cerdá et al., 2013) and dominance hierarchies have been documented in ant communities across the globe (Andersen, 1997; Feener et al., 2008; Arnan et al., 2011; Blight et al., 2014). However, studies on dominance hierarchies, including those that introduce or exclude dominant species (e.g., Cole, 1983; Andersen & Patel, 1994; Sanders & Gordon, 2003), have been criticized as limited in applicability since, in addition to involving highly artificial situations over a short time scale, they reveal antagonistic interactions among individuals rather than competitive exclusion at a community scale (Cerdá et al., 2013). If competition results in exclusion, these well-documented individual scale interactions should result in firm range boundaries between competing species. In some cases, ant congeners have been shown to segregate spatially to avoid competition (Solidà et al., 2014). Recent simulations and meta-analyses also suggest that competition may be influential at a broader scale (Ritchie et al., 2009; Beck et al., 2012; Cabral & Kreft, 2012; Hargreaves et al., 2013). Nevertheless, the extent to which local competition between individuals scales up to affect large scale patterns of diversity remains unclear (Ricklefs, 2004; Cerdá et al., 2013).

If competition is an important driver of ant diversity across elevational gradients, its effects should be manifested in patterns of species turnover (Harrison et al., 1992). Recent studies have used beta diversity, partitioned into nestedness and replacement, to investigate the varying effects of history, environmental filtering, and neutral dynamics on diversity patterns of various taxa (Hortal et al., 2011; Leprieur et al., 2011; Svenning et al., 2011; Dobrovolski et al., 2012). The nestedness component refers to the loss of species between sites; the species composition of one site is a subset of the composition of the second site. Replacement refers to the substitution of species between sites; the composition of one is not a subset of the other, but rather includes unique species in place of an equivalent number of species that were lost. The appropriate methods of

partitioning beta diversity have been debated (Baselga, 2010, 2012; Almeida-Neto et al., 2012; Mouillot et al., 2013; Legendre, 2014). However, Dapporto et al. (2014) used multiple indices simultaneously to create a more complete understanding of the biogeography of Mediterranean butterflies, an approach I will use here. Processes such as competition cannot be inferred conclusively solely from spatial patterns (Cerdá et al., 2013; Connor et al., 2013), a common issue in macroecology where large-scale experiments are impossible or infeasible. A frequent solution is to test multiple predictions simultaneously in an observational study to evaluate the consistency of a hypothesis with the data (Gaston & Blackburn, 2000; McCain, 2009a, 2010). The climate-competition hypothesis generates specific predictions about nestedness and replacement contingent on both the spatial and taxonomic scales (Fig. 4.1).

At a small spatial scale, climate and habitat are consistent among pitfall traps at each site and closely related ant species should be competing intensely (Hölldobler & Wilson, 1990; Machac et al., 2011). If this competition results in spatial segregation,

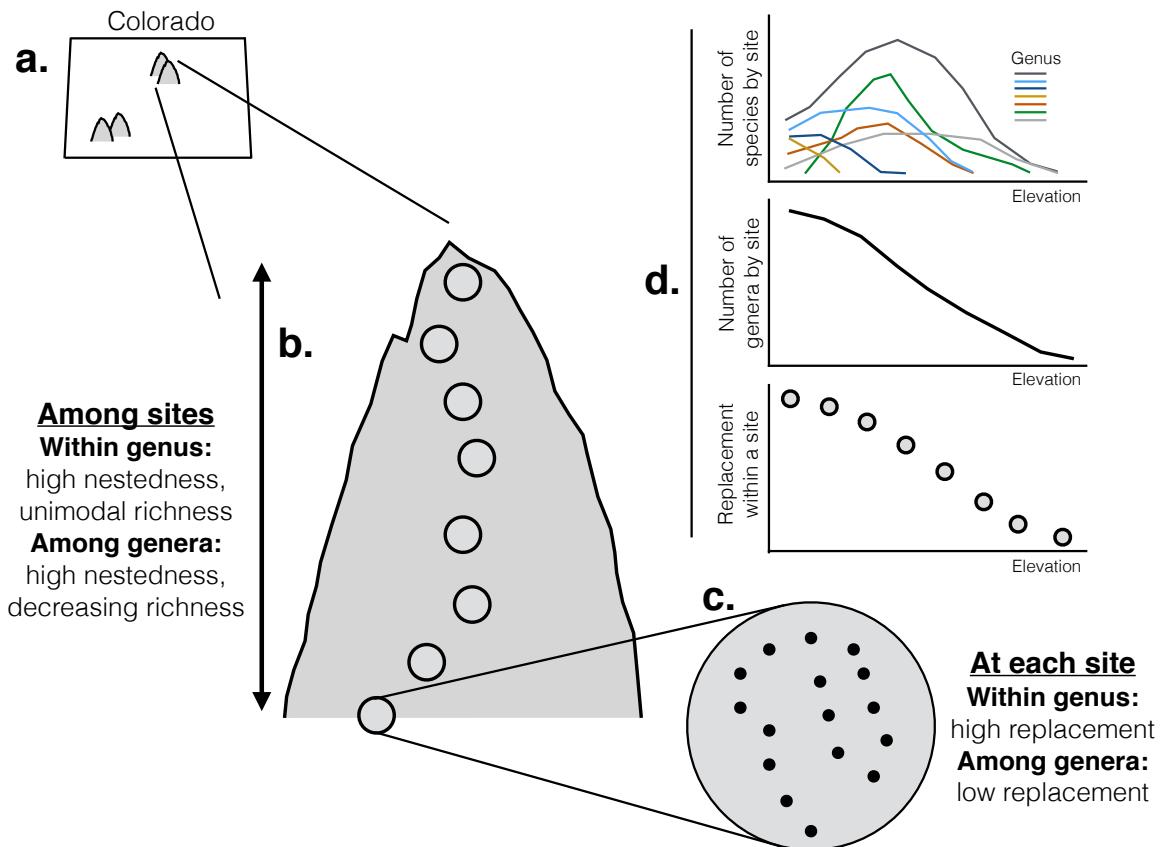


Figure 4.1. Diagram of the sampling design and predicted patterns. Two transects were sampled in the Front Range and two in the San Juan Range in Colorado (a) with eight sites along each elevational transect (b). At each site, 20 pairs of pitfall traps collected insects for the duration of one summer (c). Among sites along a transect (b), nestedness is expected to be high within each genus with predominately unimodal patterns of within-genus species richness (d, top). Nestedness is likewise expected to be high among genera, but with the number of genera declining monotonically with increasing elevation (d, middle). Among pitfall traps within each site (c), replacement is predicted to be high within each genus, reflecting intense competition. Replacement is expected to be low among genera within a site, however, since competition should be weaker. Replacement within a site is predicted to decline with elevation as competitive pressures give way to climatic influences (d, bottom).

species replacement within a genus should be high and nestedness low among pitfall traps at each elevational site. In contrast, more distantly related taxa are likely to be more ecologically and functionally distinct (Elton, 1946; Webb et al., 2002; Machac et al., 2011). Competition should consequently be weaker among genera, resulting in lower replacement among genera across pitfall traps at a given elevation. However, replacement among pitfall traps should decrease as elevation increases, reflecting the decrease in competition. Across elevational sites, nestedness should be high among genera as decreasing temperatures successively limit the genera that can survive. This pattern of environmental filtration and nestedness should produce a corresponding decline in the number of genera across elevations. Within each genus, nestedness should also be high across elevations since climatic tolerance of congeners should be related to the ancestral niche (Wiens & Donoghue, 2004; Wiens & Graham, 2005); this should result in a hump-shaped pattern of species diversity across elevation within each genus.

Methods

Survey design

Ants were sampled along four elevational transects in Colorado, with 20 pairs of pitfall traps at each of eight sites on each transect. A complete description of the study sites and methods can be found in Chapter 2. Using appropriate keys, all ants will be identified to species or morphospecies.

Beta diversity, nestedness, and replacement

Beta diversity can represent either a directional change across communities along a gradient or non-directional variation in structure within a community (Anderson et al., 2011). I will employ both concepts with the choice of index reflecting the ecology

Beta diversity	$\hat{\sigma}^2 = \frac{1}{N(N - 1)} \sum_{i,j < i} d_{ij}^2$	relevant to each of the two spatial scales. At each site, ant species captured by different pitfall traps represent variation within a community while differences among sites represent a directional change. I will calculate beta diversity, nestedness, and replacement as detailed in Table 4.1 using R scripts provided by Legendre (2014) and Baselga (2012).
Nestedness	$\beta_{NES} = \frac{[\sum_{i < j} \max(b_{ij}, b_{ji})] - [\sum_{i < j} \min(b_{ij}, b_{ji})]}{2[\sum_i S_i - S_N] + [\sum_{i < j} \min(b_{ij}, b_{ji})] + [\sum_{i < j} \max(b_{ij}, b_{ji})]} \times \frac{\sum_i S_i - S_N}{[\sum_i S_i - S_N] + [\sum_{i < j} \min(b_{ij}, b_{ji})]}$	
Replacement	$\beta_{SIM} = \frac{[\sum_{i < j} \min(b_{ij}, b_{ji})]}{[\sum_i S_i - S_N] + [\sum_{i < j} \min(b_{ij}, b_{ji})]}$	

Table 4.1. Methods to calculate beta diversity, nestedness, and replacement. The estimate of beta diversity will be calculated as in Anderson (2011) while the decomposition into nestedness and replacement will follow the multisite metrics in Baselga (2010, 2012). N is the number of pitfall traps, d_{ij}^2 is the difference in species composition between pitfall traps i and j , b_{ij} is the number of species in trap i but not j , b_{ji} is the number of species in trap j but not i , S_i is the number of species in trap i , S_N is the total number of species in all traps.

4.1 using R scripts provided by Legendre (2014) and Baselga (2012). I will explore whether communities and patterns differ among habitats within each site. If they are similar, I will lump all habitats. Otherwise, I will treat them as a random effect. Across elevations, I will use linear and curvilinear models to test whether replacement among

pitfall traps decreases with elevation as biotic interactions are predicted to be less influential (Harrison et al., 1992; Anderson et al., 2011). Correspondingly, I will use a linear model to test for the predicted increase in the proportion of beta diversity among sites due to nestedness with increasing elevation (Baselga, 2010, 2012; Anderson et al., 2011; Dobrovolski et al., 2012). Thus, I will calculate beta diversity, nestedness, and replacement among sites and among traps at both the genus and the species level. Only presence-absence data will be used as pitfall traps do not provide a reliable estimate of ant abundances (Agosti et al., 2000). Additionally, within-genus analyses will be restricted to genera with at least five species occurring along the transects for statistical robustness (Whitlock & Schluter, 2008).

Richness patterns

I will use generalized linear models with Poisson distributed errors to test the predicted richness patterns across the elevational gradients for species richness and genus richness. Using AIC, I will compare curvilinear and linear fits with a taxonomic mixed model approach (Hadfield & Nakagawa, 2010), incorporating higher taxonomic levels as random effects. Thus, design variables will include combinations of elevation, elevation², genus, subfamily, and transect.

Specific interactions

Though competition may be diffuse, studies of ants have revealed competitive interactions among specific species (Savolainen & Vepsäläinen, 1988; Hölldobler & Wilson, 1990; Blight et al., 2014). To examine whether this competition leads to spatial segregation, I will test pairs of species determined *a priori* based on competitive interactions reported in the literature (Fellers, 1987; Savolainen & Vepsäläinen, 1988; Davidson, 1998; Sanders & Gordon, 2003).

Preliminary results & discussion

This analysis relies on the species-level identification of ant specimens from all sites, a task scheduled to be completed by the end of summer 2015 (see timeline). Genus diversity is qualitatively consistent with the pattern expected; the number of genera declines with elevation along both Front Range transects, though it shows a low plateau on the San Juan transect (Fig. 2.4). These three transects have been completely identified to the genus level with the exception of three sites at high elevations that were sampled during 2012. Analysis of species-level patterns is more premature (Fig. 4.2). Though some genera with relatively high diversity such as *Camponotus* and *Temnothorax* have been identified at all 2010-2011 sites, other speciose genera including *Formica* and *Myrmica* are still in progress.

This chapter will exploit the replicated, extensive sampling design to address a diversity hypothesis that has yet to be thoroughly tested, namely that competition drives diversity at low elevations and gives way to temperature at high elevations. By investigating patterns of richness, beta diversity, and its components with a highly diverse taxon at two spatial scales, I hope to elucidate the role that the interaction between biotic and abiotic factors may play in structuring ant communities and diversity in Colorado. Competition is famously intense among ants and here I intend to test whether those interactions affect diversity at a broader scale across elevational gradients.

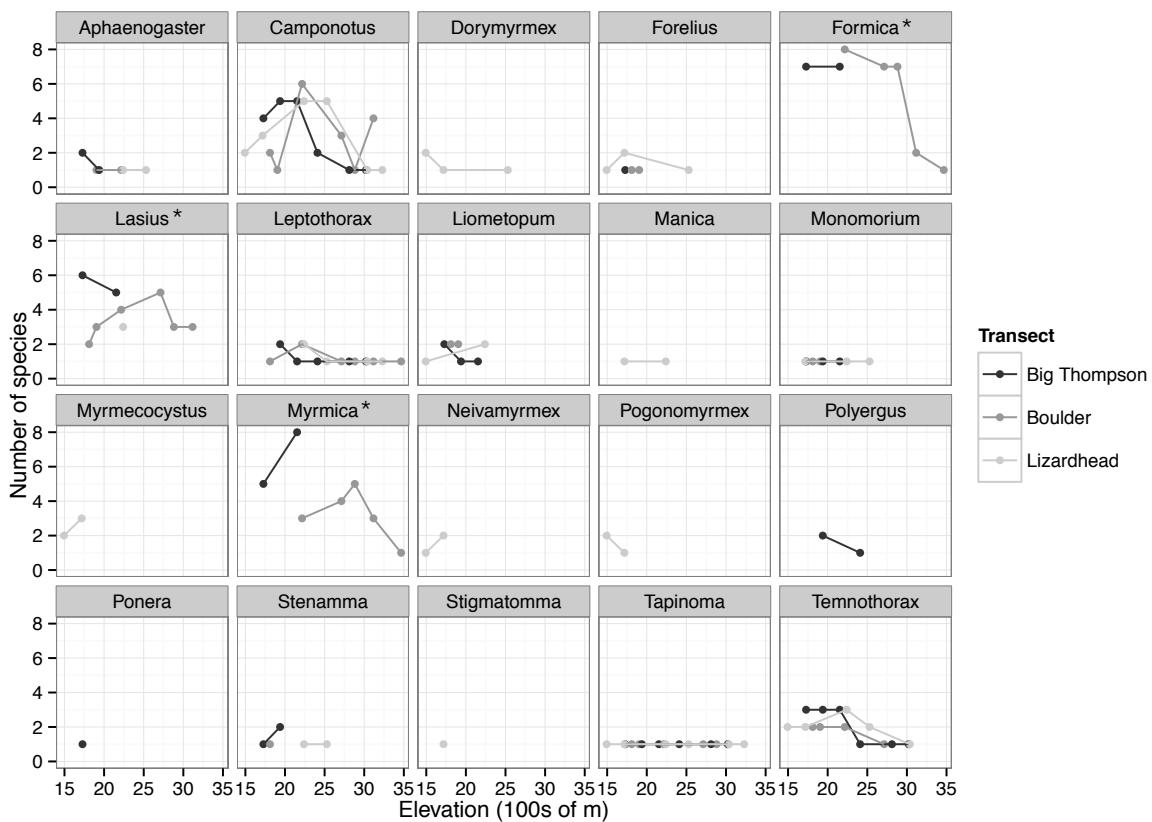


Figure 4.2. Preliminary pattern of species richness within each genus. Species-level identifications are still in progress on all transects for several speciose genera including *Formica*, *Myrmica*, and *Lasius*, so general conclusions should not yet be drawn.

Chapter 5: Is climate change affecting elevational ranges of Colorado ants?

Introduction

Over the past decades, locations around the globe have been experiencing warmer temperatures, a trend that will likely continue and accelerate (IPCC, 2014). There have already been measurable impacts on many species as they respond to the changing climate (McCarty, 2001; Parmesan & Yohe, 2003; Parmesan, 2006; Brusca et al., 2013). If temperature is a key factor influencing the range limits of species, then they may need to shift their geographic distribution to remain within their temperature envelope or risk extinction (Thomas et al., 2004). Montane regions are of particularly high diversity globally (Spehn & Körner, 2009). Because temperature declines rapidly with increasing elevation (Barry, 1992), species have shorter distances to disperse to experience cooler climates. Montane species are therefore expected to shift upward in elevation to track changes in temperature (Colwell et al., 2008; Chen et al., 2009).

Research efforts have focused on identifying changes in abundance or range limits along elevational gradients across many taxa, including mammals, birds, plants, butterflies, and moths (McCarty, 2001; Chen et al., 2009; Tingley et al., 2009; Brusca et

al., 2013). These studies typically resurvey a taxon or species assemblage at or near sites that were surveyed decades prior. Species' responses are often mixed, with combinations of range contractions, range expansions, and no change. There are many reasons why a given species may not track temperature changes. Some species may be limited by factors other than temperature and their range of tolerable temperatures may be broad.

Precipitation patterns are variable on mountains (Barry, 1992) and may not simply shift concordantly with temperature change, effectively eliminating a species' climate envelope (McCain & Colwell, 2011). Species may also be limited by dispersal, competitors, predators, or a specific resource that has not shifted. Range contractions and failure to colonize higher elevations may be exacerbated by other forms of anthropogenic influence, including habitat destruction and fragmentation. Alternatively, population abundances vary across years irrespective of climate change and this variability can obscure any underlying responses to climate change (McCain et al., *in prep*).

In the Colorado Front Range, temperatures have increased since 1953, though the warming has been most extreme at middle elevations (McGuire et al., 2012). Ants, as ectotherms, may be more affected by temperature changes than endothermic taxa (Diamond et al., 2012; Pelini et al., 2012). Grasshoppers in the Front Range have shown phenological responses corresponding to the degree of warming across the elevational gradient (Nufio et al., 2010), and ant foraging activities and larval development speed are known to increase with temperature (Hölldobler & Wilson, 1990; Kaspari et al., 2000, 2004). This suggests that temperature may drive upper range limits. Additionally, warming experiments on *Temnothorax curvispinosus* showed that both worker survival and colony growth decreased with warming (Diamond et al., 2013), suggesting that warming at the lower range boundary may lead to decreased fitness and extirpation. However, comparisons of historical and present ant richness and abundance in the southeastern US have shown mixed responses to warming within ant communities (Resasco et al., 2014). This may be due to differing thermal tolerances and responses to changes in the mean, maximum, and minimum temperatures among ant species (Stuble et al., 2013; Warren & Chick, 2013). Though elevational range shifts have been investigated for a small number of ant species (Warren & Chick, 2013), no studies exist on elevational range shifts of many ant species.

In this chapter, I will compare historic and current elevational ranges of Front Range ant species to address the following questions: (1) Have ant species contracted or shifted elevationally in the Front Range over the past 50 years, consistent with a response to climate change? (2) Does anthropogenic disturbance increase contraction of lower range boundaries and inhibit expansion of upper range boundaries?

Methods

Framework

Here, I propose to estimate the current elevational ranges of ant species in the Front Range and compare those with historical elevational ranges. Though some authors have compared changes in abundance (e.g., Rowe et al., 2011), I will use presence-absence data only. Because population parameters such as growth rate and its interannual variance are unknown for the vast majority of ant species, any conclusions about the underlying causes of observed abundance changes would be highly suspect. On the contrary, presence-absence data is much more robust against population variability that is unrelated to long-term trends (McCain et al., *in prep*).

Historical data

Pre-climate change ranges of ant species will be extracted from Gregg (1963). This work compiled data from museum specimens and many years of collecting ants with various methods across the state of Colorado. The geographic distribution, elevational abundance of records, and ecology are given for each of the 164 species and subspecies listed (for example Fig. 5.1). For each individual specimen, the location, date, and elevation are provided. Collections were most extensive in the Front Range, although every county in the state is represented. Consequently, I will restrict this analysis to Boulder and Larimer counties in the Front Range because sampling was less comprehensive in the San Juans. All current range data from the Front Range were collected along elevational transects within these two counties, allowing for reliable comparisons of elevational ranges. Because taxonomic revisions have occurred since publication, I will update all names prior to analysis (Bolton, 1995). If any species have been split into two, resulting in equivocal historical ranges, they will not be considered in the analyses. Finally, elevations stated in museum records have associated uncertainty. Potential methods of addressing this error include a variety of georeferencing tools (Murphy et al., 2004), use of a GIS and stated localities to estimate elevational error ranges (Rowe, 2005), and multiple analyses with varying degrees of uncertainty added to each elevational range. I will conduct a comparison of available error estimation methods and choose the method most robust for the Gregg ant data.

Current data

I will estimate current elevational ranges using ant specimens collected in the Front Range from 2010-2012 along two elevational transects, each composed of eight

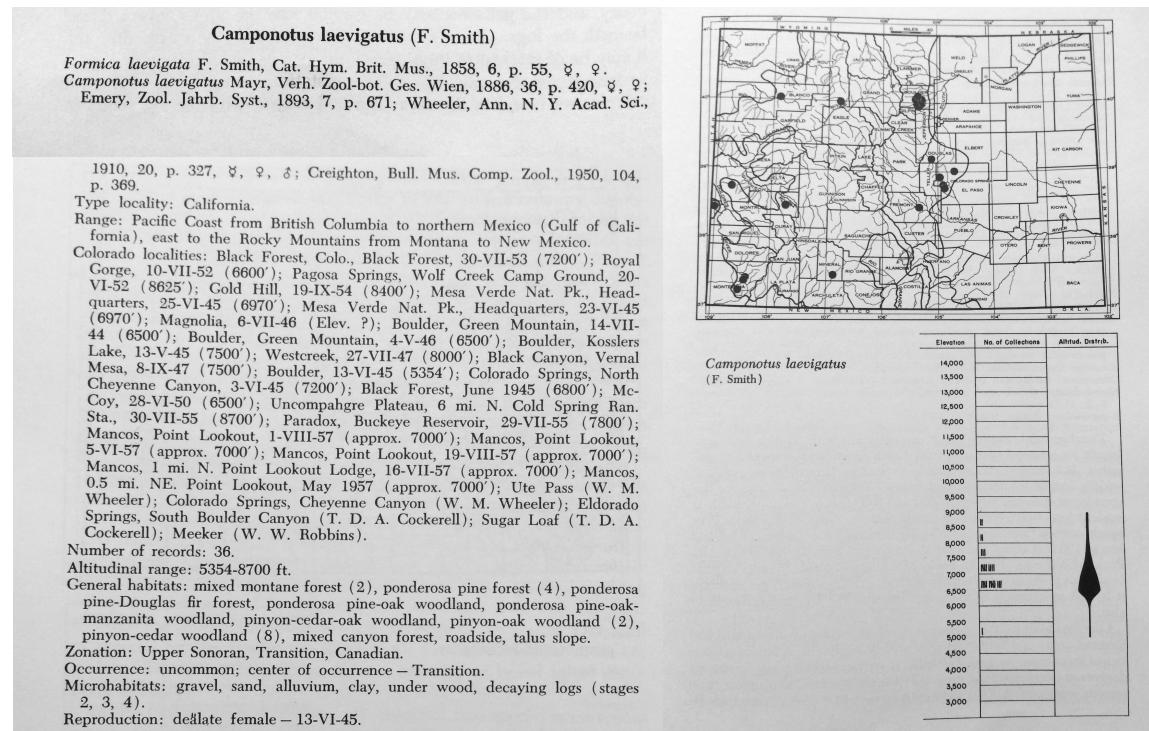


Figure 5.1. Example species account for *Camponotus laevigatus* from Gregg (1963). For all species represented in both datasets, localities in Boulder and Larimer counties will be extracted to estimate each species' historical elevational range.

elevational sites separated by ~200m in elevation. The ‘Boulder’ transect (1811m-3649m) sampled the St. Vrain watershed while the ‘Big Thompson’ transect (1728m-3640m) sampled the Big Thompson watershed. A complete description of sampling sites and methods can be found in Chapter 2.

Species may have been present but undetected at some elevations despite comprehensive sampling, leading to an underestimate of their current range size. One potential solution is to build occupancy models to separately estimate the probability of occupancy and the probability of detection for each species (Tingley & Beissinger, 2009). However, these models require repeated sampling along the gradient with the assumption that a species is always present at any site where it was detected at least once. Because both transects contain sites sampled in 2010 which were only collected once or twice and, consequently, sites that were not repeatedly sampled throughout the summer, a more complex approach may be required.

Though each of the eight sites along each transect were thoroughly sampled, the sites were separated by approximately 200m elevationally. This elevational resolution may be too coarse to confidently detect range expansions or contractions across elevations. However, previous studies of small mammals have shown that when there was evidence of range shifts, it was on the order of 300-500m, with changes of <100m considered nonsignificant or biologically trivial (Moritz et al., 2008). One solution to the possible problem of elevational resolution is additional sampling.

If recommended by my committee, I will apply for the Rocky Mountain National Park Research Fellowship to sample more extensively during the summer of 2015. New sampling sites would be interspersed with the sites already sampled along each transect to provide an elevational resolution of ~100m for current range sizes. This would require 8-10 new sites along each transect, each of which would be sampled a minimum of three times throughout the summer to allow for thorough sampling and estimation of the probability of occupancy for each species. Though pitfall traps would provide data most comparable to sites already sampled, the installation and processing time required is infeasible. Therefore, ants would be sampled with time-standardized hand collections along transects within each site (Agosti et al., 2000). If additional sites along both transects were sampled, this would result in between 48 and 60 site-visits. Ants would be collected by colony, reducing the processing and identification time. Identification to species or morphospecies would likely take 6-12 months depending on the number of ants collected per visit.

Climate data

McGuire et al. (2012) recently described temperature changes that have occurred in the Front Range, detailing changes across the elevational gradient and including multiple sites along the ‘Boulder’ transect described above. Additionally, climate stations were placed at each site along the ‘Boulder’ and ‘Big Thompson’ transects, recording air temperature, soil temperature, and precipitation for one year beginning at the start of the sampling season at each site. Thus, I have two high quality data sources to assess temperature changes along the transects.

Range boundary analysis

I propose a tiered approach to compare the pre-climate change range boundaries with the current range boundaries. First, I will compare all species that were detected in both datasets. I will analyze shifts in the lower range boundary and the upper range

boundary across all species with transect as a random effect, using available methods to account for uncertainty in range boundary estimation (Bates et al., 2014). Next, I will analyze the subset of species with the most robust data. These species will have at least moderately high abundances in both datasets and high detectability to maximize the probability of accurate detection of any underlying response to climate change (McCain et al., *in prep*). Finally, warming has been most intense at middle elevations in the Front Range (McGuire et al., 2012). Range boundary shifts should be most extreme at elevations that have seen the most warming. To test this, I will categorize boundaries as low, middle, and high elevation, anticipating the most extreme range boundary shifts at middle elevations.

Effects of anthropogenic disturbance

Additional anthropogenic impacts, such as habitat destruction and fragmentation, will likely lead to increased contraction of the lower range boundary and hindered expansion of the upper range boundary. The Boulder and Big Thompson transects present a system for comparing the effects of anthropogenic disturbance. The Big Thompson transect is largely contained within Rocky Mountain National Park (5 sites) and within private conservation easements (3 sites: Sylvan Dale Ranch properties), and thus sampled ants that enjoy broad habitat protection. The Boulder transect is much more heavily impacted by human activities as all sites are on multiuse land of the Forest Service and County and City open space near various degrees of settlements. The two transects are roughly 40km apart and, in the absence of human impacts, would be expected to share much or all of their ant fauna. Likewise, ant species would be expected to have similar elevational ranges and show comparable elevational shifts in response to climate change. By comparing the species compositions and the range boundary shifts of species common to the two transects, I will ask whether the patterns are consistent with the increased anthropogenic impact along the Boulder transect.

Preliminary discussion

Given the results of warming experiments (Pelini et al., 2012; Stuble et al., 2013; Resasco et al., 2014), I anticipate a mixed result for the Front Range community as a whole, with some range boundaries shifting upward, some showing no change, and potentially some shifting downward. Similarly complex patterns have been found in other taxa when entire assemblages were considered (Moritz et al., 2008; Rowe et al., 2009). Using the subset of species with the most robust data, I expect to see the most robust signal. By comparing two transects with different levels of protection, I anticipate that the Boulder transect will have anthropogenic impediments to expansion into higher elevations and accelerated contraction of lower range boundaries.

Timeline of proposed research

Semester	Ch. 1	Ch. 2*	Ch. 3*	Ch. 4*	Ch. 5*	Ant IDs
2014 Fall	Submitted	Develop framework				2010 spp. 2011 spp. 2012 gen.
2015 Spring		Build & debug model			Develop methods, plan fieldwork?	2010 spp. 2011 spp. 2012 spp.
2015 Summer		Analysis	Write analysis code		Fieldwork? Compile range data	2012 spp.
2015 Fall		Analysis; Writing	Analysis	Write analysis code	Analysis	New Ch5 IDs?
2016 Spring		Writing	Writing	Analysis	Analysis	New Ch5 IDs?
2016 Summer			Writing	Writing	Analysis	
2016 Fall				Writing	Writing	
2017 Spring					Writing	

* These chapters depend on the completion of species-level identifications of ants collected in the Front Range and the San Juan Range from 2010-2012.

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