**INTRODUCTION**

*Range extremes and community ecology*

Range edges have long been of interest in the discipline of community ecology. In particular, studies into range limits have come to the foreground in attempts to understand how these ranges might shift with changes in climate. Scientists have long observed the presence of species across an area, and a petering out of species at latitudinal range limits. Seminal works have theorized about the different causes underlying the filtering out of a species at its range limit (Darwin 1859). A fundamental tenet of community ecology is to determine the rules by which a community assembles.Community assembly is an ecological sorting process that filters out some species but allows others to survive (Ackerly 2003). Two general processes have been proposed for community assembly: (1) habitat filtering that limits species’ life strategies, and (2) resource partitioning that limits similarity in co-occurring species (Cornwell and Ackerly 2009). Studies into species distributions aim to shed light on what factors specifically might cause the limitations of a species as a way to more fully understand the rules dictating community assembly.

In Hutchinsonian niche space, there are two types of niche. The fundamental niche, acknowledges the environment a species may tolerate, while the realized niche describes the performance of a species in the presence of competitors. The final distribution of a species and its community composition is the result of interplays between a combination of abiotic (i.e. environmental) and biotic (e.g. competition) factors (Ackerly 2003). More specifically, the two limitations imposed on species in determining their ranges are theorized as (1) abiotically stressful environments that limit species at high latitudes and altitudes and (2) species interactions that further impose restrictions on the species through competition (Louthan et. al, 2015; Pigot & Tobias, 2013). On the edges of its range, a species sees either biotic and/or abiotic factors forcing it out in a process called habitat filtering (Weiher et. al 1998). A species’ range is thus the spatial representation of its realized niche. Range limits are then predetermined by a species’ environment and the strength of its surrounding biotic factors (Pigot and Tobias 2013; Sexton et. al 2009).

It is currently uncertain to what extent range limits are caused by biotic versus abiotic factors (Sexton et. al 2009). Darwin long ago theorized that abiotic factors constrain species at high latitudes, high elevation, and likewise environmentally stressful areas. Meanwhile, species interactions limit species in less stressful environments (Louthan et. al 2015). Yet there is much variation across species. It is likely that this variation is due to different dispersal capabilities, competition, and freezing tolerance (Louthan et. al 2015). Even so, there is a dearth of research looking at both biotic and abiotic factors. Many studies focus on one or the other, rarely examining both in conjunction with each other (Sexton et. al 2009). Examining a species at its range edge compared to its range interior, taking note of both the competitive niche it occupies and the environment the species lives in, thus provides important information on the interplay of factors limiting it. In all, examining a species at its range limit and range interior provides both information on the current preferred environment of that species and/or its realized niche, as well as its potential for adaptation given a changing environment.

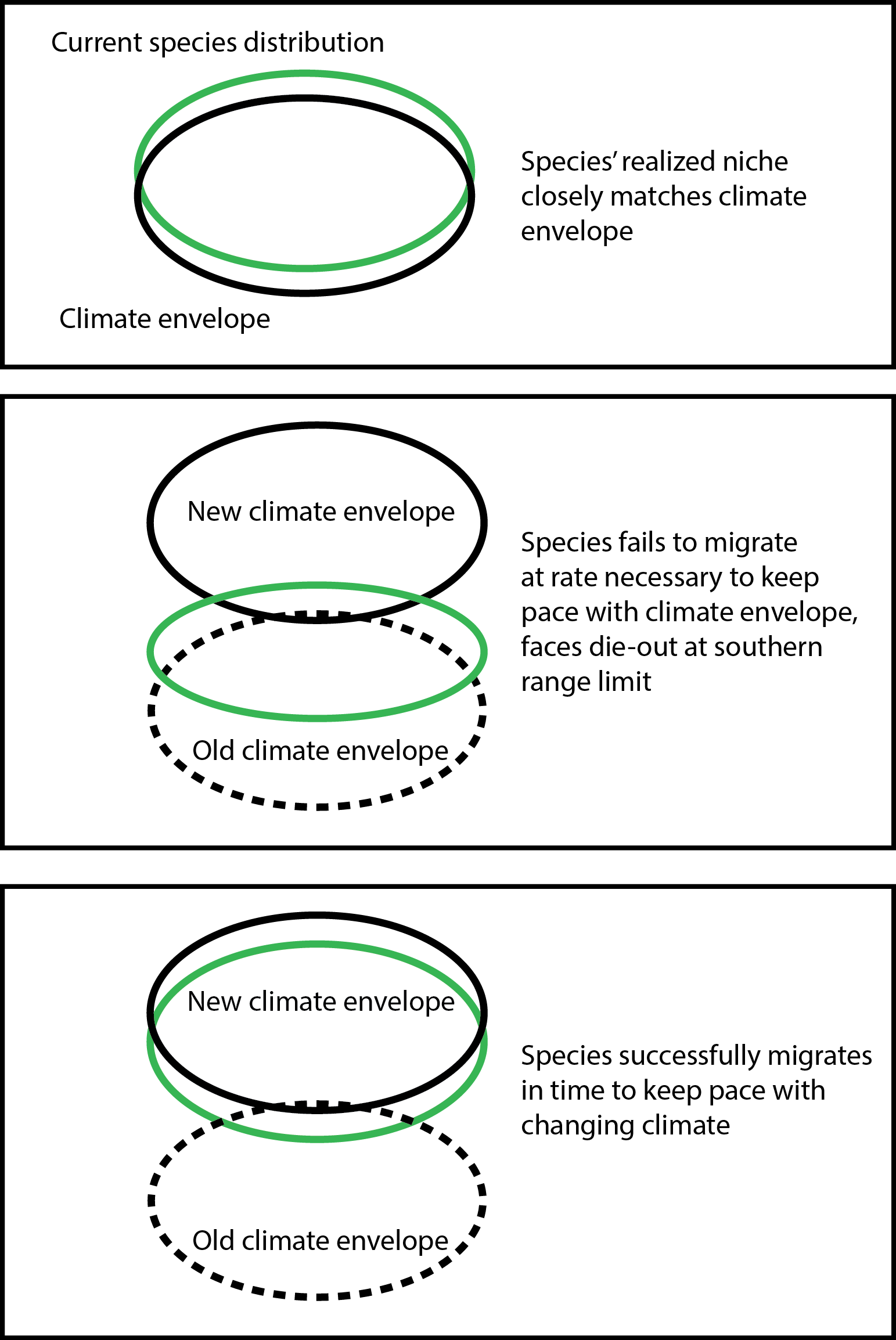
*Functional traits and niche differentiation*

To more fully understand the resource partitioning within niches in plants, it has become common practice to use functional traits as a proxy for understanding possible life strategies of different species. Functional traits have become a useful tool in understanding the nature of the relationship between plants within their communities, as well as understanding the relationship between environment and community assembly. Recent evidence has led to a shift away from the neutral model theory of general assembly (Hubbell 2001) towards the niche differentiation model (Kraft 2008). These studies have seen subtle differences in strategy differentiation contributing to species coexistence. Additionally, a large amount of intraspecific variation in functional traits may reduce the limiting effect of phylogenetic relatedness in nearby species (i.e. limiting similarity) (Burns & Strauss 2012). Functional traits have also been shown to be accurate predictors of species’ geographic ranges (Stahl et. al 2014), lending credence to the theory of niche differentiation and resource partitioning as a primary factor in determining a species’ geographic range.

Different functional traits correspond to varying plant life strategies. Taking note of specific leaf area (SLA) serves as a proxy for life history, while leaf shape exhibits strong latitudinal and climate gradients for some species. The nutrients of tissues in plants also serve to provide information on resource investment. The ratio of carbon to nitrogen in a leaf gives information on the life history strategy of the leaf, as well as relative investment in the structures of the plant that harvest light. The height of a plant is an indicator of its local performance, while stem specific density provides insight into drought resistance and/or growth rate. By using related functional traits to describe a plant’s resource partitioning across its geographic range, I can more accurately predict how a species could respond to shifts in climate. Incorporating trait-based models in our understanding of the roles that species interactions play in community assembly is crucial (Pigot and Tobias 2013).

*Range shifts and response to climate change*

Observing a species at its range edge can serve to test the conditions by which some populations adapt successfully (or not) to novel conditions. Due to global climate change, many species’ optimum environments are shifting north or up. However, species ranges are very mobile, often contracting or expanding over time (Brown et. al 1996; Davis & Shaw 2001). As the temperature increased late in the last glacial interval, woody species populations established themselves at increasingly higher latitudes in “migrations” (David & Shaw 2001).

Based on the niche conservatism hypothesis, when environmental conditions stretch beyond a species’ physiological tolerances, that species will either shift their distribution or face extinction (Peterson et. al 1999). More specifically, in response to a changing environment, a population may respond one of a few ways: 1) local population changes in microhabitat or altitudinal distribution; 2) large-scale shifts in geographic distribution, consisting of range expansions and range contraction in the former range; 3) adaptive evolution of the niche in response to the new conditions; and 4) extinction (Ackerly 2003; Thomas et. al 2006). Historically, there is evidence that plant species underwent local adaptation (genetic) in response to changing climates, in addition to shifts in distribution (Davis & Shaw 2001). Yet populations are unlikely to undergo local adaptation at the pace necessary to match invasion of competitors from adjacent positions (Ackerly 2003). Additionally, competition has been shown to hinder the advancement of colonists into new environments during shifts due to changing environments (Urban et. al 2012). This limits a species’ options in terms of biotic factors. Simultaneously, the speed of climate change affects how prevalent adaptive responses are (Ackerly 2003). Species are left with only one option: to migrate.

Indeed, range shifts for many species have been observed in response to increasing temperature over time (Chen et. al 2011). The observed pattern is upward, to higher latitudes and elevations as populations track their preferred environments (Sexton et. al 2009; Ackerly 2003; Parmesan 2006). Past studies have examined the effect of range limits and changing mean annual temperatures on woody plants, seeing a noticeable expansion north past the original northern range limits (Matías & Jump 2015). Simultaneously, species are faced with extinction on their southern range edges. In a study observing the distributional shifts of *Silene acaulis* (moss campion) and the geophyte *Polygonum viviparum* (alpine bistort) across six years, both populations saw die-out at their southern range edge (Doak and Morris 2010). At their northern edges, species may still face problems as well. In a meta-analysis of plant distributions spanning 40 years, Bertrund et. al (2011) found a lag in the responses of herbaceous forest species to to climate change. Because edge populations may see more variability in survival and reproduction due to the frequency at which they must respond to limiting factors (Sexton et. al 2011), range extremes are a unique opportunity to understand current modes of community assembly, as well as to predict species’ future responses to climate change.

*Latitudinal gradients as nature’s laboratory*

Recording a species’ functional traits and community composition across a latitudinal gradient provides a proxy for understanding how that species will respond to warming temperatures in its range exterior. Using a latitudinal gradient as a study system allows for observations of a species across a larger spatial scale than in warming facilities, and provides a much more accurate representation of the habitat that either allows or prevents a species from establishing itself (De Frenne et. al 2013). Many recent studies use altitudinal gradients as a predictor of species’ responses to climate change in lieu of latitudinal gradients, likely due to the relative ease of collection relative to sampling across latitudes (Matías & Jump 2015). Yet altitudinal gradients have a much smaller rate of spatial change in temperature as compared to latitudinal gradients (Jump, Matias & Peñuelas 2009). This further increases the chances that local adaptation will successfully occur due to genetic drift (Davis & Shaw 2001).

From summer proposal:

Plant species exist in certain ranges, the extent of which is determined through various biotic and abiotic factors. More specifically, the two limitations imposed on species in determining their ranges are theorized as (1) abiotically stressful environments that limit species at high latitudes and altitudes and (2) species interactions that further impose restrictions on the species through competition (Louthan et. al, 2015; Pigot and Tobias, 2013; Lamanna et. al, 2014). Climate change can alter species interactions and plant phenology, thus affecting the very factors that determine range limits (Parmesan & Yohe, 2003). Community assembly processes are also vital in determining functional trait values, necessitating the examination of both community composition and functional traits (Cornwell and Ackerly, 2009).

Furthermore, examining community composition of certain woody species in conjunction with their corresponding functional traits across this latitudinal gradient will allow us to predict how species composition will change at the forest level. Past studies have examined the effect of range limits and changing mean annual temperatures on woody plants, seeing a noticeable expansion north past the original northern range limits (Matías & Jump 2015). By looking at both the community composition of species at these sites and their functional traits specifically at the range limits, the results will yield which species are most at risk with the changing environment.

Introduction

* 1. Range extremes and community ecology
     1. Community assembly as an ecological sorting process (Ackerly 2003)
        1. plants in saturated communities occupy optimal or near-optimal environments
        2. distribution is due to abiotic and biotic factors
        3. plasticity within a species alters functional traits
     2. Range limits as predetermined by environment/strength of biotic factors (Pigot and Tobias 2013; Sexton et. al 2009)
        1. Environment biogeographical history as more important than species interactions—all references cited in Pigot and Tobias 2013 (Shmida & Wilson 1985; Pearson & Dawson 2003; Cavender-Bares et al. 2009; Peterson et al. 2011; Wiens 2011), and that contiguous distributions mainly reflect autoecological differences rather than competition (Case et al. 2005; Sexton et al. 2009).
     3. Unclear how much of range limits are due to biotic or abiotic factors
        1. Likely that it varies among species due to different dispersal capabilities, competition (varies on local scale), and freezing tolerance (Louthan et. al 2015)
        2. Mixture of abiotic external factors that constrain traits appearing within limits and biotic internal forces that keep coexisting species from being too similar (Weihar et. al 1998)
     4. Climate change’s influence on range extremes
        1. Poleward range shifts observed in many well-studied species (Parmesan 2006)
           1. Linked to global climate change through historical data and observation
        2. Population’s responses to changing environments (Ackerly 2003)
           1. Shifts in the optimal environment: microhabitat and/or altitude
           2. Large-scale shifts in geographic distribution (range expansion and extirpation at “trailing edge”)
        3. Parmesan 2006: species expected to migrate towards poles
        4. Chen et. al 2011
  2. Plants at their edge at a disadvantage -> how does this become apparent in their functional traits and competitiveness?
     1. Trailing edge hypothesis – climate change’s rate affects how prevalent adaptive responses are (Ackerly 2003)
        1. Historically, species replacement (migration) outpace local adaptation
        2. Leading edge will become either site of extinction or site of migration
        3. Plants at range extremes outside optimal environment
           1. can’t track preferred environment simultaneously in multiple dimensions, thus effective dispersal will cause species to track preferred conditions
     2. Importance of trait-based and phylogenetic-based models in isolating species interaction signals (Pigot and Tobias 2013)
  3. Altered opportunities for trees at their range extremes
     1. Look at range extremes to predict future responses to climate change
     2. Competition slows advance of colonists into new environments when combatting the changes in environment due to global climate change (Urban et. al 2012)
  4. Hypotheses
     1. H1: Less competitive as you approach (climatic and/or latitudinal) range limit (plant at disadvantage) – niche grows smaller as plant approaches range limit (Sexton et. al 2009)
        1. A1: More competitive as you approach (climatic and/or latitudinal) range limit due to fewer competitors, greater realized niche
        2. A2: Competition not predicted by position in (climatic and/or latitudinal) range

They differ across and within the range – local factors matter more, community composition and local adaptation determine competitiveness (not position in range limit)

* + - * 1. Local community composition around each tree is most predictive
    1. H2: Trees at their range extremes exhibit altered suites of functional traits from trees in the range interior (Weiher et. al 1998)
       1. A1: Trait variation increases as plants approach their range extremes (indicates plants trying many different combinations of traits)

Edge populations more frequently experience strong, limiting factors (Sexton et. al 2009)

Varying environment that is outside of individual tolerance might contribute to increased phenotypic plasticity (Sexton et. al 2009)

* + - 1. A2: Trait variation decreases as plants approach range extremes

One combination of traits functions well in specific (limiting) environment

* + - 1. A3: Trait means vary across range
  1. Prediction given data!

**INTRODUCTION**

Deadlines:

* Figures (all I need to do, write them, clump them, 2-4 clumps, deadline for each of the figures)
* very last clump is on the 10th of January
* one deadline on trait figure at or before Jan. 10
* update methods and intro with feedback
* update citations and bibliography
* discussion
* results (jot stuff down while I’m doing the figures)
* watch out for the rabbit hole: write down NOW what the figures show and are showing and then just stop
* use iMac — Go command, finder connect to server, officially keep WeldShare drive stuff on there, Tree Traits Summer 2015

Outline:

1. Range extremes and community ecology (2 pages)
   1. community assembly processes and history
   2. species distribution
   3. evolution of niches
   4. all serve to limit a species
   5. functional traits and range limits (1 page)
2. Climate change and range extremes (2 pages)
3. Latitudinal gradient (1 page)
4. Sites chosen (1 page)
   1. Climate change
   2. Range shifts

**MATERIALS AND METHODS**

To understand community composition and functional traits in response to range limits, I examined the immediate vicinity of six deciduous tree species. I collected data on the community composition of the understory species, as well as current competitive environment for each focal tree. Data on functional traits for some of the same individuals were collected the year prior across all four sites through the summer.

***Species selection*** *–* I sampled six different species of deciduous woody plants that are abundant across the latitudinal range of our sites in the Eastern US. The species’ ranges vary, though all reach a range extreme near one of our four sites. The species in question are: *Acer pensylvanicum, Betula papyrifera, Cornus alternifolia, Fagus grandifolia, Hamamelis virginiana,* and *Sorbus americana*. Four of the six species reach their northern range extremes within or just outside of the latitudinal range covered by our four sites. Two species, *Betula papyrifera* and *Sorbus americana,* reach their southern limits just below our southern-most site at Harvard Forest. *Hamamelis virginiana*, on the other hand, reaches its northern limit near our second southern-most site in the White Mountains.

Each species was selected based on (a) which species had been included in past studies at the four sites as part of the Wolkovich lab’s work, and (b) the location of its range limits with relation to the four sites. I found each species’ latitudinal range limits through the websites bonap.org, plants.usda.gov, and gbif.org. This was to account for records of tree species that were recorded outside their latitudinal limits (as evidenced by highly decreased abundance), but had still been recorded as appearing in different counties.

***Sites*** – I collected data at four sites, all spaced approximately one latitudinal degree apart from each other. Individuals of the six species had previously been tagged for past lab work. All sites were temperate deciduous forests with a small amount of human disturbance. The southernmost site was Harvard Forest, an LTER in Petersham, Massachusetts. The Harvard Forest spans approximately 3000 acres, and lies 110 kilometers west of Boston. The second site was located in the southern White Mountains in New Hampshire, off the Kancamagus Highway. As the southernmost part of the White Mountains, the site does not lie within a protected research area. However, as part of a national forest, it is fairly protected from human intrusion. The third site was in the Dartmouth College Second Grant, a site maintained by Dartmouth College for some recreational use and scientific research. The Grant in northern New Hampshire, near the border of Maine. Finally, the northernmost site was located at the Station de biologie des Laurentide in Quebec. The Station de biologie des Laurentide is slightly larger than Harvard Forest, spanning 4000 acres, and is 75 kilometers northeast of Montreal. Due to the varying latitudes, the northern-most sites see a climate of colder winters and shorter growing seasons. All follow mild summers.

All four sites had previously been used by the Wolkovich lab for research in temporal ecology into the species used for this experiment, thus ensuring the presence of suitable individuals at each site. Nearly all sampling sites occurred in closed canopy forests, except for some sampling plots of *Cornus alternifolia* and *Sorbus americana* which frequently appear on forest edges.

***Competition and community data*** *-* For each of the six species, I tagged six (or found some previously tagged) individuals at each site that the individuals were present in. I compared total basal area of the focal individual with trees in the competitive environment around each focal individual. The direct competitive environment was estimated as being within a 5-m radius around the focal tree. I recorded the DBH of all trees falling within this circle. I took note of the presence and absence of species in the understory, including species of saplings appearing under 1.3m. To determine competitiveness of our focal individuals, I used the percentage of total basal area attributable to the focal individuals as a proxy for competitive advantage in each plot.

***Functional traits***- For functional trait data, I used the data collected the previous summer by Harry Stone during the Harvard Forest REU Summer Program in 2015. The height of individuals not measured summer 2015 was measured through a clinometer. Additionally, I measured the DBH of any newly-tagged individuals (in cases where an individual is too close to another focal plant). Functional traits for newly-tagged individuals were not measured, but instead the traits measured in 2015 served as a representation of the traits of all species within that site.

Data on the functional traits Specific Leaf Area (SLA), Leaf N%, leaf dry matter content, and height were all collected for at least six individuals of the six species across the four sites (when applicable). Samples were processed in the John Torrey laboratory at the Harvard Forest. When possible, leaf samples were collected near the center of the tree canopy. Leaf size was measured using the LI-COR 3100 leaf area meter. To account for variation within an individual, a wide range of leaf sizes were measured to achieve a representative average size. Specific leaf area (SLA) was determined by the leaf size divided by dry mass of the leaves (Cornelissen 2003). The leaves were weighed after drying for than 24 hours at 60 OC.

We measured leaf dry matter content by comparing the fresh mass of the leaves, determined immediately after removal from the individual and the dried weight. Height of the individual was measured using a clinometer from 15 meters away from the tree. Stem specific density was measured by comparing the volume of the stem sample to the dried mass. The volume of the stem was calculated by submersion in a container of water and the volume of the water displaced is equivalent to the volume of the stem. Then the stems were dried in excess of 24 hours in the drying oven at 60 OC. *Working Bibliography*:

Ackerly, David D. "Community Assembly, Niche Conservatism, and Adaptive Evolution in Changing Environments." International journal of plant sciences 164 (2003): S165-84. Print.

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Cornelissen, J. H. C., et al. "A handbook of protocols for standardised and easy measurement of plant functional traits worldwide." Australian journal of Botany 51.4 (2003): 335-380.

Louthan, Am, Df Doak, and A. L. Angert. Where and when do Species Interactions Set Range Limits? 30 Vol., 2015. Print.

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Pearson, Richard G., and Terence P. Dawson. "Predicting the Impacts of Climate Change on the Distribution of Species: Are Bioclimatic Envelope Models Useful?" Global Ecology and Biogeography 12.5 (2003): 361-71. Print.

Pigot, Alex L., and Joseph A. Tobias. "Species Interactions Constrain Geographic Range Expansion Over Evolutionary Time." Ecology Letters 16.3 (2013): 330-8. Print.

Sexton, Jason, et al. "Evolution and Ecology of Species Range Limits." Annual Review of Ecology, Evolution, and Systematics 40 (2009): 415. Print.

Urban, Mark C., Josh J. Tewksbury, and Kimberly S. Sheldon. "On a Collision Course: Competition and Dispersal Differences Create no- Analogue Communities and Cause Extinctions during Climate Change." Proceedings of the Royal Society B 279.1735 (2012): 2072-80. Print.

To add:

Weiher 1998

Brown 1996

Peterson et al 1999

Doak and Morris 2010

Burns and Straus 2012

Hubbell 2001

Kraft 2008

Matias and Jump 2015

Thomas et. al 2006

Davis 2001

De Frenne et. al 2013

Suttle et. al 2007

Jump, Matyas & Penuelas 2009

Bertrund et. al