

The Functional Rollercoaster: Community composition and functional traits of deciduous trees across their ranges

Abstract

Plant species' ranges are determined through biotic and abiotic factors such as competition and stressful environments. Tree species in broadleaf temperate forests in the Northeast face changes to these ecological limitations due to shifting temperatures across their range. The effect of this shift is predicted to be most apparent at the species' range limits, where such a change in conditions that previously halted population expansion can cause a range shift. By examining species at their range limits, we can predict their future responses to climate change and the implications for their distribution and success. The goal of this study was to determine how species richness and composition of competitive neighborhoods in broadleaf temperate forests in the Northeast change across a latitudinal and climatic gradient. I examined whether focal deciduous tree species face a competitive disadvantage at their range, represented by the competitive index of relative basal area of trees larger than the focal individual (a distance-independent strategy). To accomplish this, I recorded the size and community composition of seven deciduous tree species at their range limits, varying from the northeastern United States to southeastern Quebec. Additionally, using data a previous student collected on the functional traits of the same species across the four sites, I will examine the relationship between the competitiveness of a species at its limits and the variation in its functional traits. Using convex hull values for each species at each site, I will examine whether the variation in the suites of functional traits for each species points to evidence of habitat filtering or niche differentiation. This experiment can thus provide valuable insight into how the species will respond to changing temperatures in the future by determining the relative influence of biotic and abiotic factors on each species at their range extremes.

Introduction

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 & Keddy 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 & 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 history? strategies of different species (ADD citation). 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 & Wirth 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 (ADD citations). 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 & 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, Stevens & Kaufman 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 its distribution or face extinction (Peterson, Soberón, & Sánchez-Cordero 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 contractdion in the former range; 3) adaptive evolution of the niche in response to the new conditions; and 4) extinction (Ackerly 2003; Thomas, Franco & Hill 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 (Suttle, Thomsen & Power 2001; 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 & Morris 2010). At their northern edges, species may still face problems as well. In a meta-analysis of plant distributions spanning 40 years, Bertrand et. al (2011) found a lag in the responses of herbaceous forest species 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). On average, temperature decreases approaching the poles on the order of -0.73 C per degree latitude in the Northern hemisphere. Other climatic variables, such as precipitation, also change across latitudes (De Frenne et. al 2013). Latitudinal gradients are thus an apt study system with which to integrate species interactions and environmental stressors as predictors of a species’ future distributions with regards to climate change.

Predictions and hypotheses - To determine the nature of woody species’ future responses to climate change, I sampled six species of woody deciduous trees across four different sites on a latitudinal

gradient in the northeastern United States and into Quebec. I predicted that:

H1: a species would become less competitive as they approached their latitudinal and climatic range limits, since populations at their geographic range edges more frequently experience strong, limiting factors (Sexton et. al 2009).

A1: Alternatively, a species could grow more competitive as it approaches its range limit due to the presence of fewer competitors, thus leading to a greater realized niche.

A2: Finally, it is a possibility that competition is not predicted by position in its climatic or latitudinal range, indicating that local factors (such as ...) might matter more within each population. Similarly, other factors could determine competitiveness, such as community composition and local adaptation, rather than a species' position within its range limit. It is possible that a local community composition around each tree is most predictive of its competitive success, with little overall pattern across the latitudinal gradient.

Looking at a woody species' competitiveness across a latitudinal gradient provides information into the part that biotic factors play in its realized niche, and the possible effects of those biotic factors in a warming environment. Since species often track their optimal environment (Ackerly 2003), strong limiting factors due to competitiveness may indicate that a species will not be able to migrate at a rate sufficient to account for population loss at their southern range edge.

H2: I also predicted that trees at their range extremes would exhibit altered suites of functional traits from trees in the range interior (Weiher & Keddy 1998). Similar to the prediction (H1) above, because populations at their range limits often see more extreme environments, I predicted that their functional traits would altered plasticity compared to functional traits of individuals at their range interiors. Studies have shown that a species' functional traits that are linked to life strategies vary based on the latitude of their origin (Cavender-Bares 2007).

A1: Increases in intraspecific trait variation across a latitudinal gradient at the range limit would indicate increased genetic adaptation and/or increased plasticity. Since populations at their range extremes (and at more northern latitudes) face harsher environments than populations in their range interior, this could be due to a plant's attempts to limit its phylogenetic similarity in the face of competitors in a sub-optimal environment, or simply because it is exhibiting greater plasticity in response to the more extreme environment.

A2: Alternatively, decreased intraspecific trait variation approaching a range limit would indicate that only one combination of traits is successful in that particular limiting environment (Burns & Straus 2012).

A3: Finally, no clear pattern in intra-specific variation in functional traits approaching the range limit of a species would indicate that other rules of community assembly are playing a larger part in the determining of range limits, such as competition or other biotic factors.

By examining community composition of certain woody species in conjunction with their corresponding functional traits across this latitudinal gradient, we can better predict how species composition will change at the forest level. In looking at both the community composition of species at these sites and their functional traits specifically at the range limits, we can understand which species are most at risk with the changing environment, and why they might not survive. *You should add here something along the lines of 'Here I report on a study to test the hypotheses by doing X, Y, Z.'*

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.

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 logging, recreational use, and scientific research. The Grant is in northern New Hampshire, near the border of Maine. Finally, the northernmost site was located at the Station de biologie des Laurentides in Quebec. The Station de biologie des Laurentides 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.

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 the four study sites. Two species, *Betula papyrifera* and *Sorbus americana*, reach their southern limits just below the 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.

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.

Competition index was calculated according to methods outlined in Biging and Dobertin 1995. I calculated the sum of the trees larger than the focal tree, and took the ratio of the basal area of the focal tree to this sum. By using relative basal area, the trend of decreasing DBH as species increase in latitude would not show in the model.

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 Diameter at Breast Height (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.

Harry Stone and colleagues 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.

Statistical analyses – *Competition-Latitude Relationships* – I used both linear mixed effects models and simple linear models to evaluate the relationship between competition and latitude for each species at each sampling location. Using the simple linear models allowed me to quantify the basic relationship between distance from minimum latitude and the competition index.

– where to include MDS plots?

Results

The species composition across the four sites, as evidenced by the multi-dimensional scalar plots (Fig. 1), show a marked difference between the species compositions of Harvard Forest and the other three sites. This is mirrored in both the overstory and understory species composition, suggesting that the type of competition seen by the deciduous trees present in Harvard Forest may differ from that of the other three sites.

The strength of competition index - latitude relationships differed by species, with no clear pattern across all six species. There was little to no correlation between increasing latitude (approaching northern edges) and the competitive index of the focal trees. *Acer pensylvanicum* showed a slight negative correlation ($R^2 = -0.011$) between the relative basal area of the focal individuals to the distance from the minimum latitude. This indicates a general trend of *Acer pensylvanicum* individuals growing less competitive as they grow more northward (closer to the species' northern range limit). *Betula papyrifera*, whose distribution lies predominantly north of Harvard Forest (with the center near the northern-most testing site), shows a slight negative correlation ($R^2 = -0.033$) between its relative basal area and its distance from its minimum latitude.

Figures

Figure 1

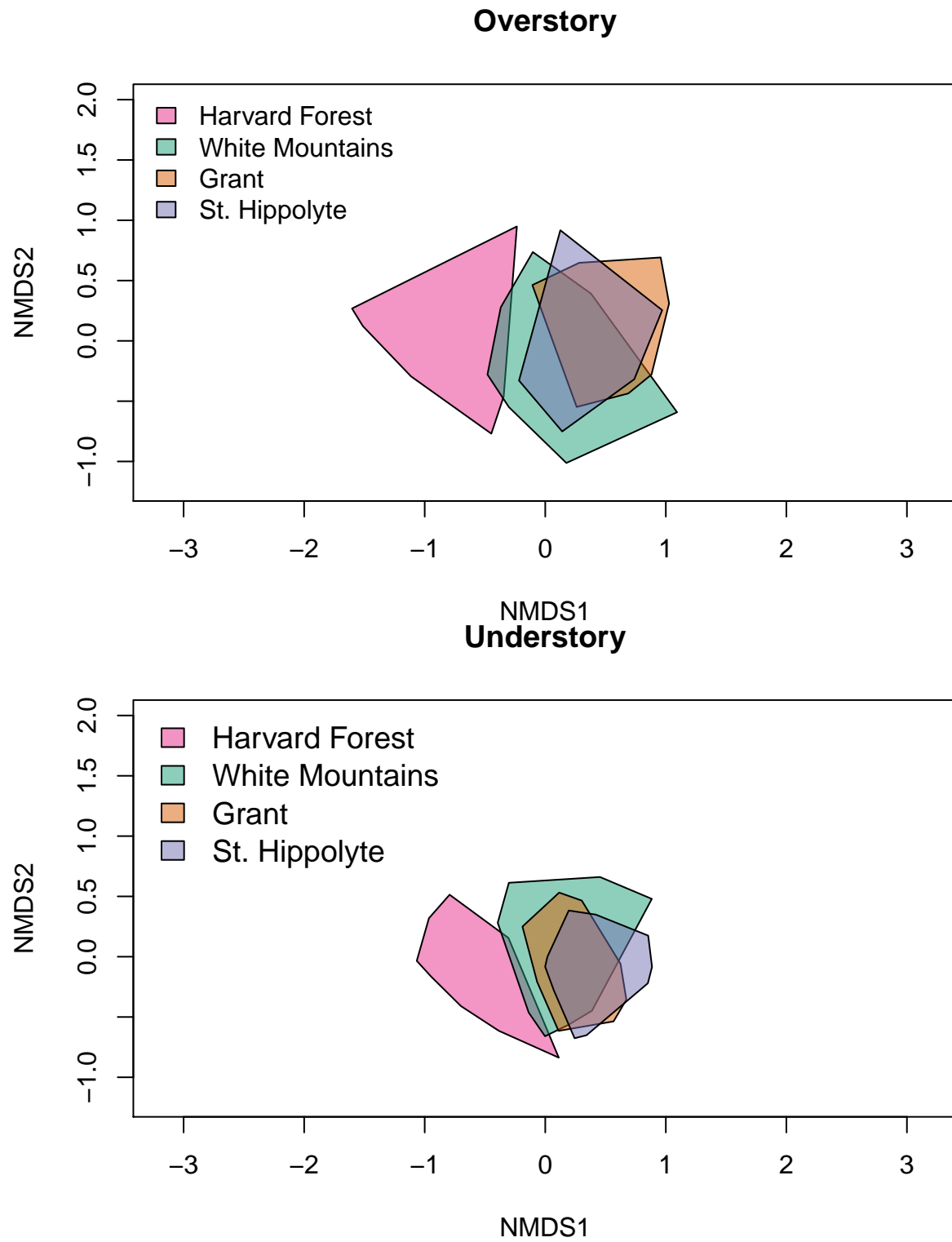


Figure 2

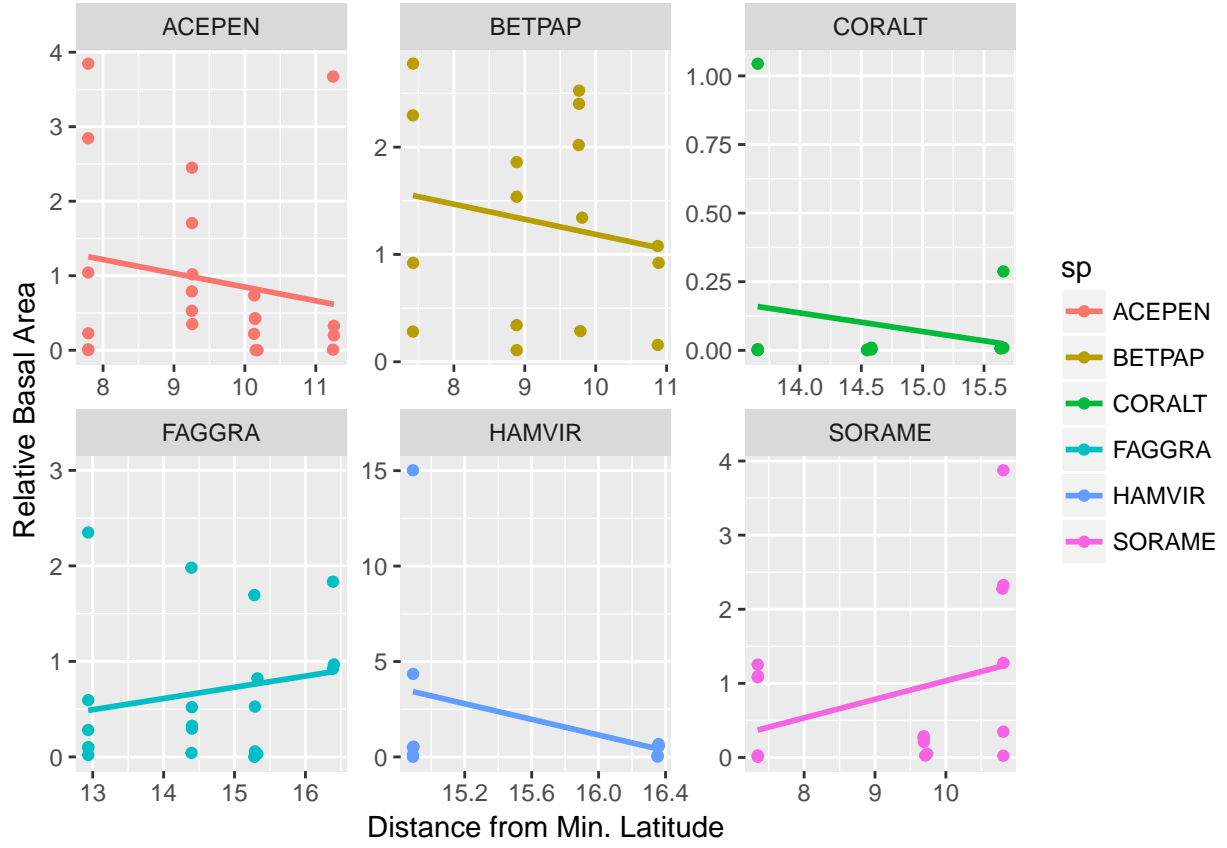


Table 1: Linear coefficients for Fig. 1

Species	Coefficient	R^2	p value
<i>Acer pensylvanicum</i>	-0.184	-0.011	0.390
<i>Betula papyrifera</i>	-0.1407	-0.033	0.484
<i>Corylus alternifolia</i>	-0.068	-0.041	0.499
<i>Fagus grandifolia</i>	0.117	-0.014	0.402
<i>Hamamelis virginiana</i>	-2.049	0.047	0.243
<i>Sorbus americana</i>	0.250	0.063	0.170

Table 2: Linear mixed effects model results

Coeff. of fixed general effects	p value	CI	SD of random effects
-0.0317	-0.18-.12	.677	2.911

Figure 3

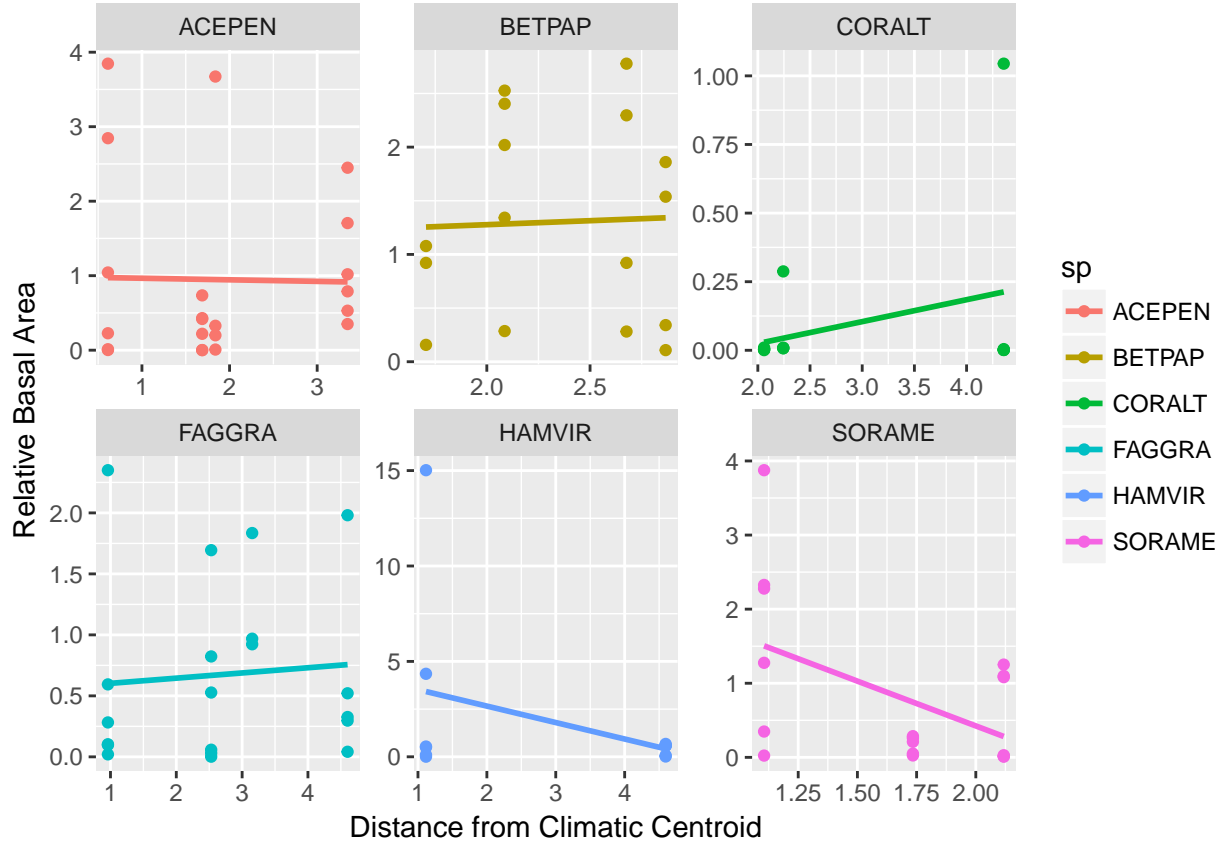


Table 3: Linear coefficients for Fig. 2

Species	Coefficient	R^2	p value
<i>Acer pensylvanicum</i>	-0.021	-0.050	0.934
<i>Betula papyrifera</i>	-0.074	-0.033	0.894
<i>Corylus alternifolia</i>	0.080	0.022	0.277
<i>Fagus grandifolia</i>	0.042	-0.049	0.734
<i>Hamamelis virginiana</i>	-0.863	0.047	0.243
<i>Sorbus americana</i>	-1.21	0.187	0.047

Table 4: Linear mixed effects model results

Coeff. of fixed general effects	CI	p value	SD of random effects
-0.23	-0.59-.14	2.666	0.221

Figure 4

Figure 5

References

- Ackerly, David D. "Community Assembly, Niche Conservatism, and Adaptive Evolution in Changing Environments." *International journal of plant sciences* 164 (2003): S165-84. Print.
- Bertrand, Romain, et al. "Changes in Plant Community Composition Lag Behind Climate Warming in Lowland Forests." *Nature* 479.7374 (2011): 517. Print.
- Brown, James H., George C. Stevens, and Dawn M. Kaufman. "The Geographic Range: Size, Shape, Boundaries, and Internal Structure." *Annual Review of Ecology and Systematics* 27 (1996): 597-623. Print.
- Burns, Jean H., and Sharon Y. Strauss. "Effects of Competition on Phylogenetic Signal and Phenotypic Plasticity in Plant Functional Traits." *Ecology* 93 (2012): S126-37. Print.
- Cavender-Bares, J. 2007. Chilling and freezing stress in live oaks (*Quercus* section *Virentes*): intra- and inter-specific variation in PSII sensitivity corresponds to latitude of origin. *Photosynthesis Research* 94. (2007): 437-53. Print.
- Chen, I. C., et al. "Rapid Range Shifts of Species Associated with High Levels of Climate Warming." *Science* 333.6045 (2011): 1024. Print.
- 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.
- Darwin, Charles. *On the Origin of Species*. Ed. Jim Endersby. Cambridge ; New York:, 2009. Print.
- Davis, M. B., and R. G. Shaw. *Range Shifts and Adaptive Responses to Quaternary Climate Change*. 292 Vol., 2001. Print.
- De Frenne, Pieter, et al. "Latitudinal Gradients as Natural Laboratories to Infer Species' Responses to Temperature." *The Journal of Ecology* 101.3 (2013): 784. Print.
- Doak, Daniel F., and William F. Morris. "Demographic Compensation and Tipping Points in Climate- Induced Range Shifts." *Nature* 467.7318 (2010): 959. Print.
- Hubbell, S. P. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA. (2001).
- Jump, Alistair S., Csaba Mátyás, and Josep Peñuelas. "The Altitude-for- Latitude Disparity in the Range Retractions of Woody Species." *Trends in Ecology & Evolution* 24.12 (2009): 694-701. Print.
- Kraft, Nathan J. B., Renato Valencia, and David D. Ackerly. "Functional Traits and Niche- Based Tree Community Assembly in an Amazonian Forest." *Science (New York, N.Y.)* 322.5901 (2008): 580. Print.
- Louthan, Am, Df Doak, and A. L. Angert. *Where and when do Species Interactions Set Range Limits?* 30 Vol., 2015. Print.
- Matías, Luis, and Alistair S. Jump. "Asymmetric Changes of Growth and Reproductive Investment Herald Altitudinal and Latitudinal Range Shifts of Two Woody Species." *Global Change Biology* 21.2 (2015): 882-96. Print.

- Parmesan, Camille. "Ecological and Evolutionary Responses to Recent Climate Change." *Annual Review of Ecology, Evolution, and Systematics* 37 (2006): 637. Print.
- Peterson, A. T., J. Soberón, and V. Sánchez-Cordero. "Conservatism of Ecological Niches in Evolutionary Time." *Science* 285.5431 (1999): 1265-7. 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.
- Stahl, Ulrike, Björn Reu, and Christian Wirth. "Predicting Species' Range Limits from Functional Traits for the Tree Flora of North America." *Proceedings of the National Academy of Sciences of the United States of America* 111.38 (2014): 13739. Print.
- Suttle, K. B., Meredith A. Thomsen, and Mary E. Power. "Species Interactions Reverse Grassland Responses to Changing Climate." *Science (New York, N.Y.)* 315.5812 (2007): 640. Print.
- Thomas, Chris D., Aldina M. A. Franco, and Jane K. Hill. "Range Retractions and Extinction in the Face of Climate Warming." *Trends in Ecology & Evolution* 21.8 (2006): 415-6. 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.
- Weiher, Evan, and Paul A. Keddy. "Community Assembly Rules, Morphological Dispersion, and the Coexistence of Plant Species." *Oikos* 81.2 (1998): 309-22. Print.