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Abstract

Plant species' ranges are determined through biotic and abiotic factors such as competition and the level of environmental stress (e.g., from drought or cold). Tree species in broadleaf temperate forests in the Northeast face changes to these ecological limits due to shifting temperatures across their range. The effect of this shift is predicted to be most apparent at 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 limit, 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, I examined the relationship between the competitiveness of a species at its limits and the variation in its functional traits, using previously-collected data on the functional traits of the same seven species. Using convex hull values for each species at each site, I examined 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

A fundamental aim 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). Studies into species distributions shed light on what factors specifically cause the limitations of particular species, with the larger goal of understanding the overarching rules dictating community assembly. Two general processes have been proposed: (1) habitat filtering that limits species' life strategies, and (2) resource partitioning that limits similarity in co-occurring species (Begon et. al 1986; Cornwell and Ackerly 2009). Fundamentally, the rules of community assembly can be described by examining the species that appear in a given community, and their interactions with their environment.

The concept of a species' niche is useful in describing both intra- and inter-specific interactions, as well as in illustrating the effect the environment may have on a species. 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 results from the interplay of many abiotic (i.e. environmental) and biotic (e.g. competition) factors (Ackerly 2003).

Species distribution and ranges serve as an actualization of the concept of a niche. Indeed, understanding the sorting processes that prevent a species from inhabiting space across continuous landscapes has long been the subject of research. Seminal works have theorized about the different causes underlying the filtering out of a species at its range limit (Darwin 1859). 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 (Louhan 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). 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; Hargreaves et. al 2014). Darwin long ago theorized that abiotic factors constrain species at high latitudes, high elevation, and likewise environmentally stressful areas. Meanwhile, community interactions limit species in less stressful environments (Louthan et. al 2015). In a meta-analysis of both elevational and latitudinal range studies, Hargreaves et. al (2004) found that studies conducted with latitudinal range limits showed a pattern that upper range limits were governed solely by abiotic factors. However, there were too few studies conducted at lower latitudes to ascertain a concrete alternative behavior at the lower limits. Thus, it is likely that biotic interactions will increase in importance in governing range limits as the climate warms (Hargreaves et. al 2014).

The relative importance of biotic factors and abiotic factors varies greatly among species, complicating our ability to predict how a species within a given community will respond to a warming environment. Additionally, there is a dearth of research looking at both biotic and abiotic factors for the same species, thus controlling for variation among species (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. By understanding the factors limiting a species, we can predict more accurately how well a species will be able to extend its realized niche in a changing environment.

Functional traits and niche differentiation

Certain traits in plants have long been theorized as a major determining factor in a plant species' success in different landscapes, as well as in the ability of species to co-exist (Schimper 1898). In Schimper's theory, the success of different plant species across landscapes is due to different quantitative traits, such as leaf nitrogen and carbon concentrations, wood densities, leaf sizes, and potential canopy heights. Such traits are dubbed plant functional traits. Although they are far from a recent concept, functional traits have seen a resurgence in focus among community ecologists (Pigot and Tobias 2013), so much so that McGill et. al (2006) suggests rebuilding the entire study of community ecology with an emphasis on functional traits as a core concept.

Phenotypic differences among species impact diversity in communities (MacArthur and Levins 1967). In the rules of community assembly, functional traits provide insight into co-occurring species' ecological strategies. McGill et. al (2006) posit that functional traits are one of four major themes governing the composition of a species' fundamental and realized niches (the others being environmental gradients, interaction milieu, and performance currency). 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. By examining functional traits, we can more fully understand the resource partitioning within niches.

Functional traits also serve as useful predictors of other traits that are more difficult to measure, but that may provide better projections of success. For example, certain seed sizes and shapes strongly correlate with persistence of the seed in soil (Thompson et. al 1993). These studies have seen subtle differences in traits in co-occurring species, theorizing that these differences contribute to species coexistence. Additionally, a large amount of intra-specific variation in functional traits may reduce the effect of phylogenetic relatedness in nearby species (i.e. limiting similarity) (Burns & Strauss 2012). Kraft et. al (2008) showed

that species with a broad distribution of trait values co-occur more often than expected by a null model, indicating that variable trait patterns enable more co-occurrence of species within a community. Similarly, certain suites of functional traits can enable individuals to be more successful than others of the same species under environmental conditions that favor those traits (Jung et. al 2010). It follows that in a changing environment, certain functional traits may prove to be better suited to the new conditions.

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. Intraspecific variation in physiological traits may give species the chance to survive in the face of rapid climatic changes within their range (Davis & Shaw, 2001; Nussey et al., 2005; Skelly et al., 2007). The functional traits of a species across its range can thus provide valuable information about the biotic and abiotic factors that limit it beyond its range, and how it is responding to those limiting factors. By using 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.

Range shifts and response to climate change

In particular, studies into range limits have come to the foreground in attempts to understand how these ranges might shift with changes in climate. Observing a species at its range edge can help test the conditions by which some populations adapt successfully (or not) to novel conditions. Based on the niche conservatism hypothesis, when environmental conditions stretch beyond a species' physiological tolerances, that species will either shift 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) small-scale changes in distributions of local populations; 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, Franco & Hill 2006).

Species ranges are very mobile, often contracting or expanding over time (Brown, Stevens & Kaufman 1996; Davis & Shaw 2001). 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 (Fig. 2, Sexton et. al 2009; Ackerly 2003; Parmesan 2006). Past studies have observed a noticeable expansion of woody plants north past their original northern range limits in response to rising mean annual temperatures (Matías & Jump 2015).

Yet on their southern range edges, species are faced with possible extinction. 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). The same effect has been seen earlier in history. As the temperature increased late in the last glacial interval, woody species populations established themselves at increasingly higher latitudes in so-called “migrations” (David & Shaw 2001).

To compensate for population loss at their southern edge due to the loss of their preferred environment, a species must shift northwards. Evidence shows that this shift may not occur quickly enough to account for the rate of changing temperatures and population loss. 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. Since species often track their optimal environment (Ackerly 2003), strong limiting factors due to intra-specific competition may signal that a species will not be able to migrate at a rate sufficient to account for population loss at their southern range edge.

In addition to shifts in distribution, there is evidence that plant species underwent

local (genetic) adaptation in response to changing climates over the last 10,000 years (Davis & Shaw 2001). Yet populations are unlikely to undergo local adaptation at the pace necessary to match many current changes. Such changes include the invasion of competitors from adjacent positions and climate change (Ackerly 2003). Furthermore, studies show that competition hinders the advancement of colonists into new environments during shifts due to changing environments (Suttle, Thomsen & Power 2001; Urban et. al 2012), which 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.

Work across species range extremes and range interiors such as the work that I have conducted allows us to see whether a species is primed to migrate. Additionally, such experiments have the potential to reveal how many limiting factors a species might face during migration, given its decreasing preferred climatic envelope. Because edge populations may see more variability in survival and reproduction due to the frequency at which they must respond to limiting factors (Reich & Oleksyn 2008; 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 field laboratories

The study of range expansions and retractions is best accomplished through studies across latitudinal gradients. 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). Generally, there is a reliable poleward decrease in temperature across latitudes. 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). Looking at species' traits and community composition across latitudes can provide insight into the effect of environmental variables on range limits and species' future success.

There is a dearth of research using latitudinal gradients, with many recent studies using altitudinal gradients as a predictor of species' responses to climate change (Walther 2003). This is likely due to the relative ease of collection relative to sampling across latitudes (Matías & Jump 2015). Altitudinal gradients have a much smaller rate of spatial change in temperature as compared to latitudinal gradients (Jump et. al 2009). This further increases the chances that local adaptation will successfully occur due to genetic drift (Davis & Shaw 2001).

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. Because the observed pattern of range shifts is up and poleward, studying a species across its latitudinal range provides important information about the effect of biotic and abiotic interactions that might decrease the possible rate of migration for a species. 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 its latitudinal and climatic range limits, since populations at 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 a mix of possible factors (e.g., the presence of fewer competitors, or increasing competitive ability of species at the abiotic environment of the edge etc.), 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 habitat or resource availability, 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 local community composition around each tree is most predictive of its competitive success, with little overall pattern across the latitudinal gradient.

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 differ from functional traits of individuals at their range interiors. Since species' functional traits that are linked to life strategies have been shown to vary based on the latitude of their origin (Cavender-Bares 2007), it seems likely that functional traits will exhibit variation across a species' range.

A1: Increases in intra-specific trait variation across a latitudinal gradient at the range limit could 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 resource partitioning in the presence 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 intra-specific 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.

Here I report on a study to test these hypotheses (H1 and H2) by examining six woody species with individuals across their latitudinal ranges. I will evaluate (a) the effect of latitude on six woody species' competitiveness indices and functional traits and (b) the effect of distance from the environment at the center of a species' distribution (taken as its preferred environment) on the species' competitiveness indices and functional traits.

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 during the summer of 2016. I collected data on the community composition of the understory species, as well as current competitive environment for each focal tree. Harry Stone and colleagues collected data on functional traits the summer of 2015.

Sites

To test my two hypotheses, I collected data on deciduous trees at four sites (Fig. 1). The sites were all spaced approximately one latitudinal degree apart from each other, and were already established as part of the Wolkovich lab's field sites. All sites were temperate deciduous forests with a small amount of human disturbance. The southernmost site was located at Harvard Forest (42.5°N ; 72.0°W), an LTER in Petersham, Massachusetts. The altitude of plots ranged from 220 m to 410 m above sea level. The Harvard Forest spans approximately 3000 acres, and lies 110 kilometers west of Boston in the New England Upland Region. The second site (44.0°N ; 71.4°W) was located in the southern White Mountains in New Hampshire, off the Kancamagus Highway (altitude 250 m to 505 m above sea level). 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, I assumed it to be well-protected from human intrusion. The third site was in the Dartmouth College Second Grant (44.9°N ; 71.1°W), a site maintained by Dartmouth College for logging, recreational use, and scientific research. The site is located in northern New Hampshire, near the border of Maine (altitude of plots ranged from 281 m to 505 m above sea level). Finally, the northernmost site was located at the Station de biologie des Laurentide in Quebec (46.0°N ; 74.0°W). The Station de biologie des Laurentide is slightly larger than Harvard Forest, spanning 4000 acres, and is 75 kilometers northeast of

Montreal. Altitude of plots ranged from 345 m to 437 m above sea level. 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 *C. alternifolia* and *S. americana* which frequently appear on forest edges.

Species Selection

I studied 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. I selected the study species based on two criteria: (a) whether the species had been a part of past studies as part of the Wolkovich lab's work, and (b) the location of its range limits with relation to the four sites. I estimated each species' latitudinal range limits through data from the websites bonap.org, plants.usda.gov, and gbif.org, as well as Little's atlases of tree species' distributions (Little 1971; Little 1977).

Based on these criteria, I selected the species: *Acer pensylvanicum* (striped maple), *Betula papyrifera* (paper birch), *Cornus alternifolia* (pagoda dogwood), *Fagus grandifolia* (American beech), *Hamamelis virginiana* (witch-hazel), and *Sorbus americana* (American mountain ash). Four of the six species reach their northern range extremes within or just outside of the latitudinal range covered by the four study sites (Fig. 3; Figs. 5-7). Two of the species, *B. papyrifera* and *S. americana*, near their southern range limits at the southern-most site at Harvard Forest (Figs. 3 & 7). *H. virginiana*'s northern limit is located near the site located in the White Mountains (Fig. 7).

To calculate a species' distance from its minimum latitude (Figs. 10 & 12), I used presence/absence data of my six focal species from the US Forest Service's Forest Inventory and Analysis (FIA) database (<http://www.fia.fs.fed.us>). I then compared the latitude of each of my focal individuals to the species' minimum recorded latitude in the FIA data.

Competition and community data

To test my hypothesis on the competitiveness of trees across their ranges, I compared total basal area of the focal individual with other species of tree in the competitive environment around each focal individual. I estimated the direct competitive environment as a 5-m radius around the focal tree. I sampled the competitive environment of six individuals per all six species across all sites where that species was present. Within the plots, I recorded the DBH of all trees falling within this circle. I also noted the presence and absence of species in the understory, including species of saplings appearing under 1.3m.

To determine competitiveness of the focal individuals, I used the percentage of total basal area attributable to the focal individuals as a proxy for competitive advantage in each plot. The sum of basal area included only individuals that were larger than my focal individual at that plot, a distance-independent competition index 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 to account for any general trend of decreasing basal area in trees across latitudes.

Climate data

To test my hypotheses on the effect of a species' location within its climatic range on its functional traits and its competitiveness, we calculated the location of each species' climatic centroid. We downloaded climate data from the 30 arc-second WorldClim database (available

at <http://www.worldclim.org/>, accessed December 2016) at each set of coordinates that my focal species appeared, based on the species presence/absence data taken from the FIA database. Once we had downloaded the climate data, we averaged it within an equal area grid of 50km^2 . I extracted three measures of temperature: mean annual temperature (BIO1), mean diurnal range (BIO2), temperature seasonality (BIO4). I also extracted annual precipitation (BIO12).

We combined the distribution data and the climate data to generate a matrix of all six focal species, their ranges, and the values of the four climatic variables at those sites. We conducted a principal component analysis of the climatic variables, the first two axes of which we averaged to find the value of the coordinates of the climatic centroid. Using my own species presence/absence data of the six species of interest, we then calculated the euclidean distance between the coordinates from the PCA of my focal species and the climatic centroid coordinates from the same PCA.

Functional Traits

To test my hypothesis on the effect of latitude and climate on functional traits, I used the data collected the previous summer by Harry Stone during the Harvard Forest REU Summer Program in 2015. He collected data on leaf area, dry mass, stem volume, stem mass, height, and diameter at breast height (DBH). While he collected data on many tree species, I included only the data from the six focal species I had chosen for my study species. I did not measure functional traits for newly-tagged individuals, but instead used the traits measured in 2015 as a representation of all species within that site.

Data on the functional traits of Specific Leaf Area (SLA), leaf N%, leaf C%, leaf dry matter content, and height were all collected for at least six individuals of the six species across the four sites (when applicable). They collected leaf samples near the center of the tree canopy, and measured leaf size using a 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 calculated by dividing the leaf size by the dry mass of the leaves (Cornelissen 2003).

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Harry Stone and colleagues measured leaf dry matter content by comparing the fresh mass and the dried weight of the leaves. They measured height of the individual 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. He then dried the stems for 24 hours in a drying oven at 60 degrees celcius.

I selected functional traits to use in my analysis that served as proxies for understanding plant resource allocation and structural strengths. Specific Leaf Area (SLA) provides a ratio

of the light-capturing area deployed (leaf area) per dry mass allotted by the plant. 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 relative investment in the structures of the plant that harvest light. Stem-specific density is an effective proxy for a plant's drought resistance and/or growth rate (Cornwell et. al 2006; Westoby et. al 2002).

We analyzed functional traits using the convex analysis framework proposed in Cornwell et. al (2006). The convex hull is defined as the smallest convex shape enclosing a set of points and in this case, represents the smallest volume that encloses all values of functional traits. A larger volume indicates more variation.

We calculated convex hull volumes at both the species level and the community level for each site as a way to estimate functional richness. Functional richness is defined as a way to describe the amount of niche space a species occupies (Mason et. al 2005). By examining a species' relative convex hull volume to the overall functional richness of a community, we can better represent a species' niche in its community across the different sites.

For the species level convex hulls, I used the *R* package *geometry* to find the convex hull volume for all the species. For the community level, I used the *R* package *FD*. The package requires a presence/absence matrix for species composition to calculate the Functional Richness value (equivalent to the convex hull volume). I then used the mean trait values for each species at each site and the distribution matrix to calculate the functional richness at each of the four sites. Using this data, I calculated the relative convex hull volume of my focal species to the community functional richness (or convex hull volume).

Results

Composition differences of sites

Species composition varied greatly between the site at Harvard Forest and the northern three sites in both the understory and the overstory (Fig. 9). The convex hulls in the non-linear multidimensional scalar plots overlap significantly at the White Mountains, Dartmouth College Second Grant, and the Saint Hippolyte sites. Many combinations of species appearing together at the sites appeared across all three sites, and were not recorded together at the Harvard Forest site. The understory NMDS plot (Fig. 9b) was composed of a smaller number unique species combinations, compared to the overstory community composition (Fig. 9a).

Focal species' competitiveness across latitudinal and climatic gradients

Position in latitudinal range did not reliably predict competitiveness across all six species (Fig. 10). There was little to no correlation between increasing latitude (approaching northern edges) and the competitive index of the focal trees. In a linear mixed effects model with all six species, there was a statistically insignificant positive correlation between latitude and relative basal area ($p = .368$, $R^2 = .404$). However, all species except *B. papyrifera* exhibited a negative relationship between the competition index and increasing latitude. *B. papyrifera*'s distribution lies predominantly north of Harvard Forest with the center of its range located near the northern-most testing site (Fig. 4). Although *S. americana*'s distribution puts it near its southern edge at Harvard Forest as it does for *B. papyrifera* (Fig. 8), *S. americana* exhibited the opposite trend as *B. papyrifera*. In the model, *S. americana* exhibited a negative correlation between its relative basal area and an increase in latitude (moving away from its southern edge).

Distance from the climatic centroid also did not consistently predict competitiveness across climatic space. In a linear mixed effects model with all six species, there was a statistically insignificant negative correlation between a species' distance from its climatic centroid and its relative basal area in a plot ($p = .376$, $R^2 = .473$). *B. papyrifera* was once again an outlier out of all species, exhibiting a strong negative relationship between its competitive index (relative basal area) and its position in its climatic range. Thus, individuals of *B. papyrifera* that lie farther from their climatic centroid generally tend to be smaller compared to other species around them. The other five species exhibited slightly positive correlations between their competitiveness and their distance from their climatic centroids, meaning that individuals were generally slightly more competitive the farther away from their climatic centroid they were located.

Functional traits of focal species and range differences

The suites of functional traits I examined did not vary predictably with latitude (Fig. 12). In a simple linear model, there was a small overall negative correlation between latitude and relative convex hull volume of species (adjusted $R^2 = -0.0258$; $\sigma^2 = 0.02683$; $p = .435$) Only four of the six focal species had enough trait data to calculate convex hull volume (which requires n to exceed the number of traits examined). In a simple linear model for each of the tree species, there was no discernible pattern in the relationship between latitude and the relative convex hull volume of the focal species at the four sites.

Of the four focal species, *A. pensylvanicum* (adjusted $R^2 = 0.6628$; $\sigma^2 = 0.07001$; $p = .1195$) and *F. grandifolia* (adjusted $R^2 = 0.7788$; $\sigma^2 = 0.09291$; $p = 0.1054$) exhibited a slight decrease in their relative convex hull volume across latitudes in simple linear models within each species. Thus for these two species, the data suggest that individuals take up less functional trait space relative to their community at higher latitudes than at lower latitudes, though the results were statistically insignificant. Conversely, *C. alternifolia* (adjusted $R^2 =$

0.7788 ; $\sigma^2 = 0.09291$; $p = 0.2158$) and *B. papyrifera* (adjusted $R^2 = .7004$; $\sigma^2 = 0.1414$; $p = .53$) exhibited statistically insignificant slight increases in the relative convex hull volumes of their traits across latitudes. For these two species specifically, the data suggest that the amount of space taken up in a community's functional richness by the focal species increases as it moves north (at increasing latitudes).

A species' distance from its climatic centroid was a better predictor than latitude of its relative convex hull volume (Fig. 13). The three species included in the analysis all showed a negative relationship between the distance from their climatic centroid and their relative convex hull volume. Without taking into account species type, the data exhibited a strong overall negative correlation between relative convex hull volume and distance from climatic centroid (adjusted $R^2 = 0.2657$; $\sigma^2 = 0.007459$; $p < 0.05$). Generally across all three species, as a species moved farther away from its climatic centroid, its convex hull volume decreased in relation to the overall functional richness of the community.

The degree of correlation varied across species. There was a stronger negative correlation across the climatic range for *A. pensylvanicum* (adjusted $R^2 = 0.3674$; $\sigma^2 = 0.008541$; $p < 0.05$) and *B. papyrifera* (adjusted $R^2 = 0.2683$; $\sigma^2 = 0.007309$; $p < 0.05$). *F. grandifolia* also exhibited a negative relationship between its relative convex hull volume and an individual's distance from its climatic centroid (adjusted $R^2 = 0.6234$; $\sigma^2 = 0.06553$; $p < 0.05$). Based on analysis through a simple linear model, I can reject the null hypothesis ($H_1: A_3$) that there is no effect of a species' distance from its climatic centroid on its relative convex hull volume (and its suite of functional traits).

Though the volume of a species' convex hull and its competitiveness both exhibited a negative relationship with distance from its climatic centroid, relative convex hull volume did not reliably predict competitiveness (Fig. 14). *A. pensylvanicum* exhibited an insignificant slight negative correlation between its relative convex hull volume and its competitiveness (adjusted $R^2 = -0.03713$; $\sigma^2 = 0.0004784$; $p = 0.6783$). *F. grandifolia* showed a more negative

relationship between relative convex hull volume and its relative basal area in a plot (adjusted $R^2 = 0.03305$; $\sigma^2 = 0.005842$; $p = 0.1998$). For both species, there was a slight (insignificant) decrease in their competitiveness as an individual's relative convex hull volume increased, or when that individual took up more of a community's functional richness with its own functional traits. And finally, *B. papyrifera* displayed the opposite relationship, with a positive correlation between relative convex hull volume and relative basal area (adjusted $R^2 = -0.007968$; $\sigma^2 = 0.008198$; $p = 0.3637$).

Principal Component Analysis of Functional Traits

As a way to visualize traits in non-metric space, I plotted the convex hulls of the four traits I used in my analysis using the first two principal components of a principal component analysis of the traits (Fig. 15). The first principal component explained 34% of variance while the second explained 25.9% (cumulatively explaining 61.6% of variance). The first principal component was strongly negatively correlated with SLA (-0.7337) and strongly positively correlated with DBH (0.54773700). The second principal component placed a heavy bearing on %C:%N (0.667) and stem density (0.687). Thus, using the principal component analysis to take into account all traits, SLA and DBH are inversely related while %C:%N and stem density are directly related.

Statistical analyses and figures

To generate the NMDS plots (Fig. 9) and visualize species composition across sites, I used the species presence/absence data using the *vegan* package in *R*.

In order to test my hypothesis about competitiveness across latitudes and climatic ranges, I fit linear mixed effects models to my competitive index for each species (Fig. . Because I was interested in the effect of a species' position in its latitudinal and climatic range,

I used latitude and a species' distance from its climatic centroid as categorical explanatory variables. A significant effect of a species' position in its latitudinal or climatic range on its competitiveness would support my hypothesis that a species will see decreased competitiveness at its range extremes.

I used simple linear models to quantify the correlation between the relative convex hull trait volume for each focal species and it's position in its latitudinal and climatic range (Figs. 12 & 13). I also used simple linear models to test a species' relative convex hull trait volume in relation to their relative basal area (Fig. 14). Because three of my focal species (*S. americana*, *C. alternifolia*, and *H. virginiana*) did not have enough trait data to calculate relative convex hull volumes across all sites, I included only three species. Due to the low number of data-points, I was unable to use a generalized linear mixed-effects model as I had done in testing competitiveness across ranges.

Finally, to visualize intraspecific functional trait variation across sites (Fig. 15), I conducted a principal component analysis using the four functional traits of interest (SLA, DBH, %C:%N, and stem density). I then plotted the first two principal component values as coordinates for each individual, drawing a convex hull around each set of functional traits at each site and within each species.

Figures

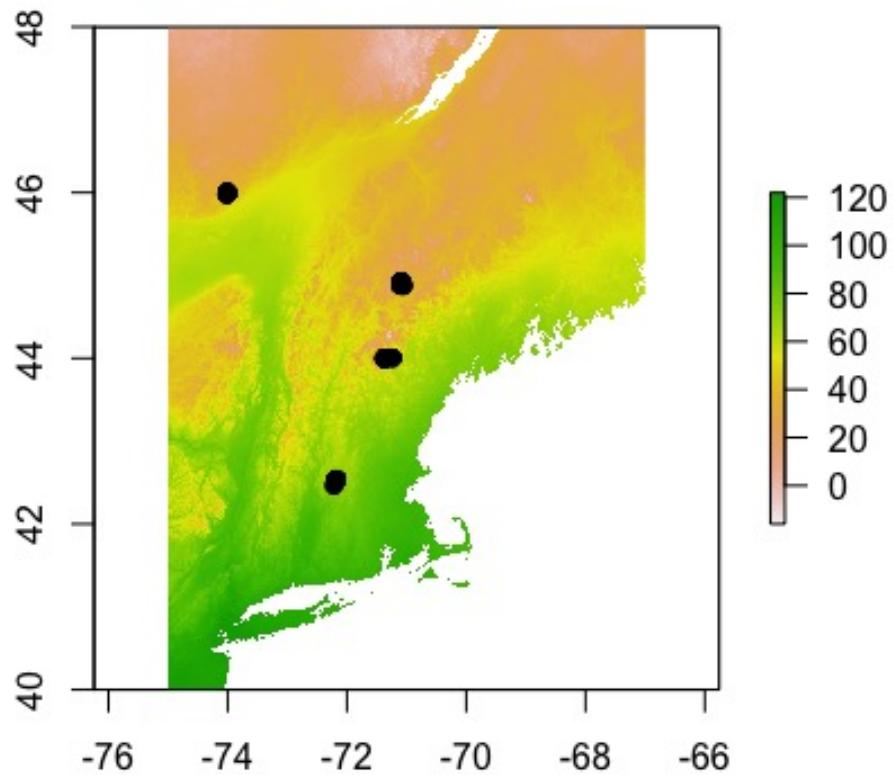


Figure 1: Map of all four sites mapped onto a raster image of their mean annual temperatures, compiled from the 30 arcsecond layer from <http://worldclim.org>.

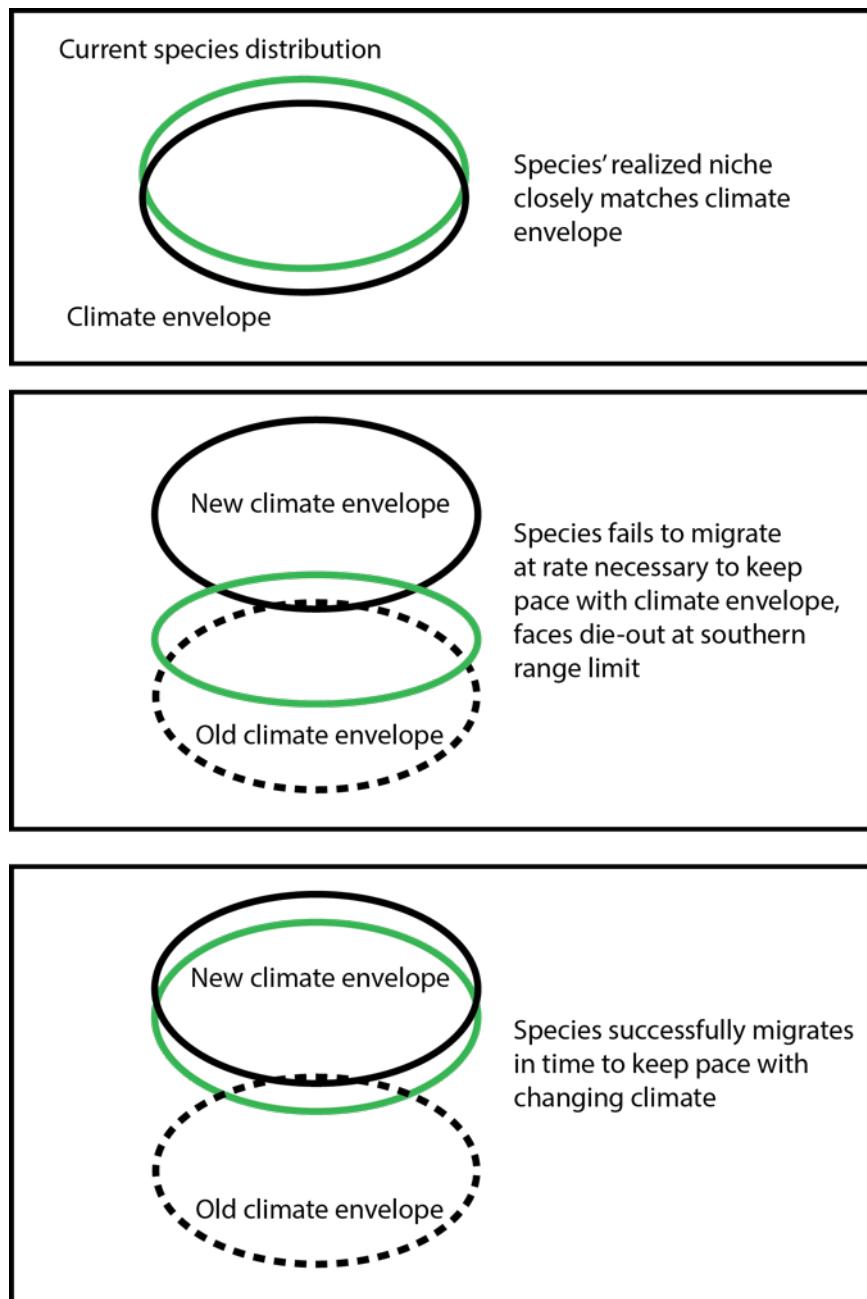


Figure 2: Anthropogenic warming can drastically alter the environment to which a species has adapted. This shift in climate also means that a species' ideal "climate envelope" shifts. If a species is limited by its preferred environmental variables, it may have to shift its range in order to compensate for the change in climate. It must match its realized niche with the shift climate envelope or face extinction at its southern (warming) edge.

Range Maps

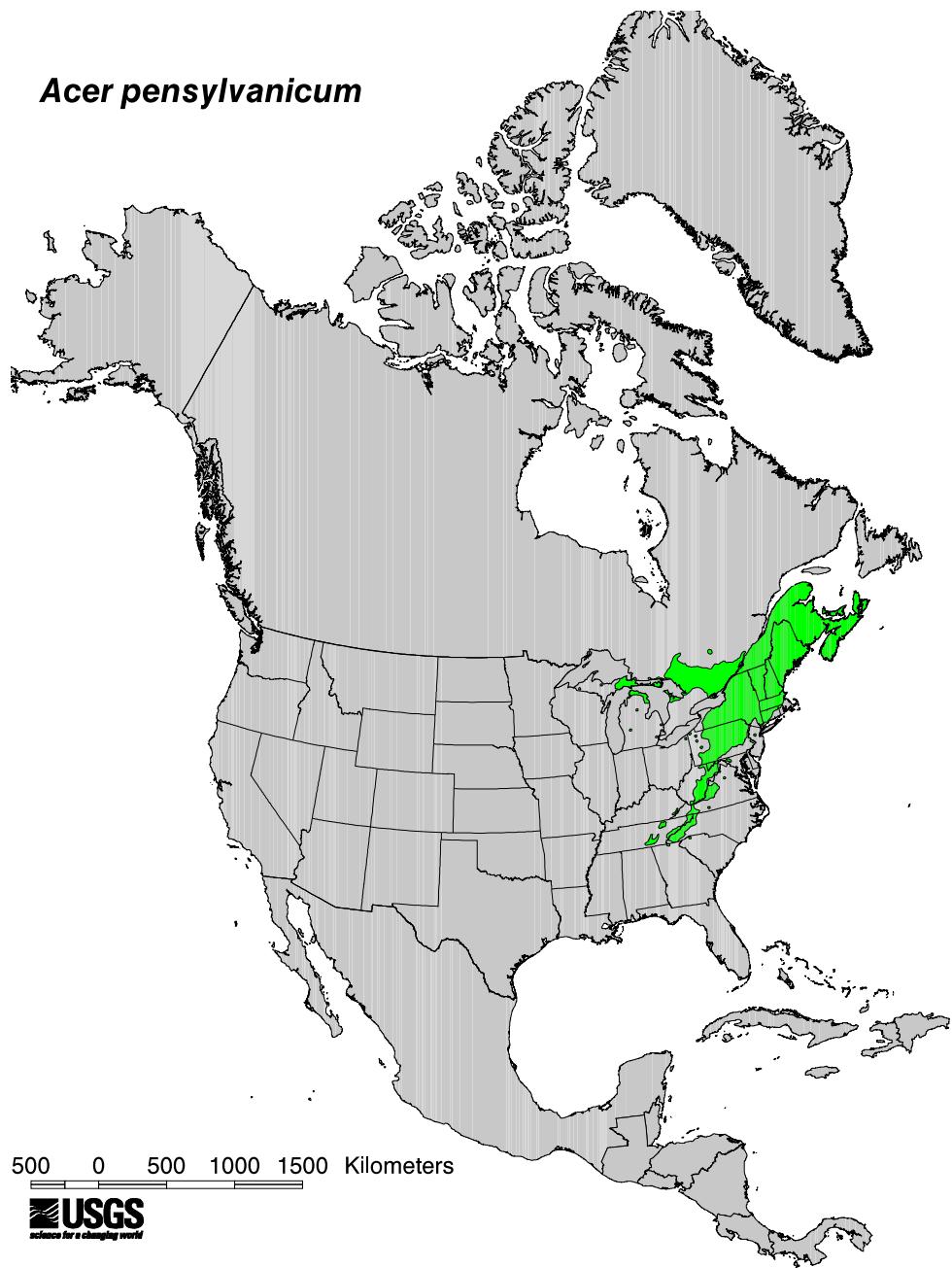


Figure 3: Representation of the range of *A. pensylvanicum*. Individuals were found at all sites, with functional trait data taken across all four. Used as one of four species approaching its northern range at the northernmost site at Saint Hippolyte. Image taken from <https://gec.cr.usgs.gov>.

Betula papyrifera

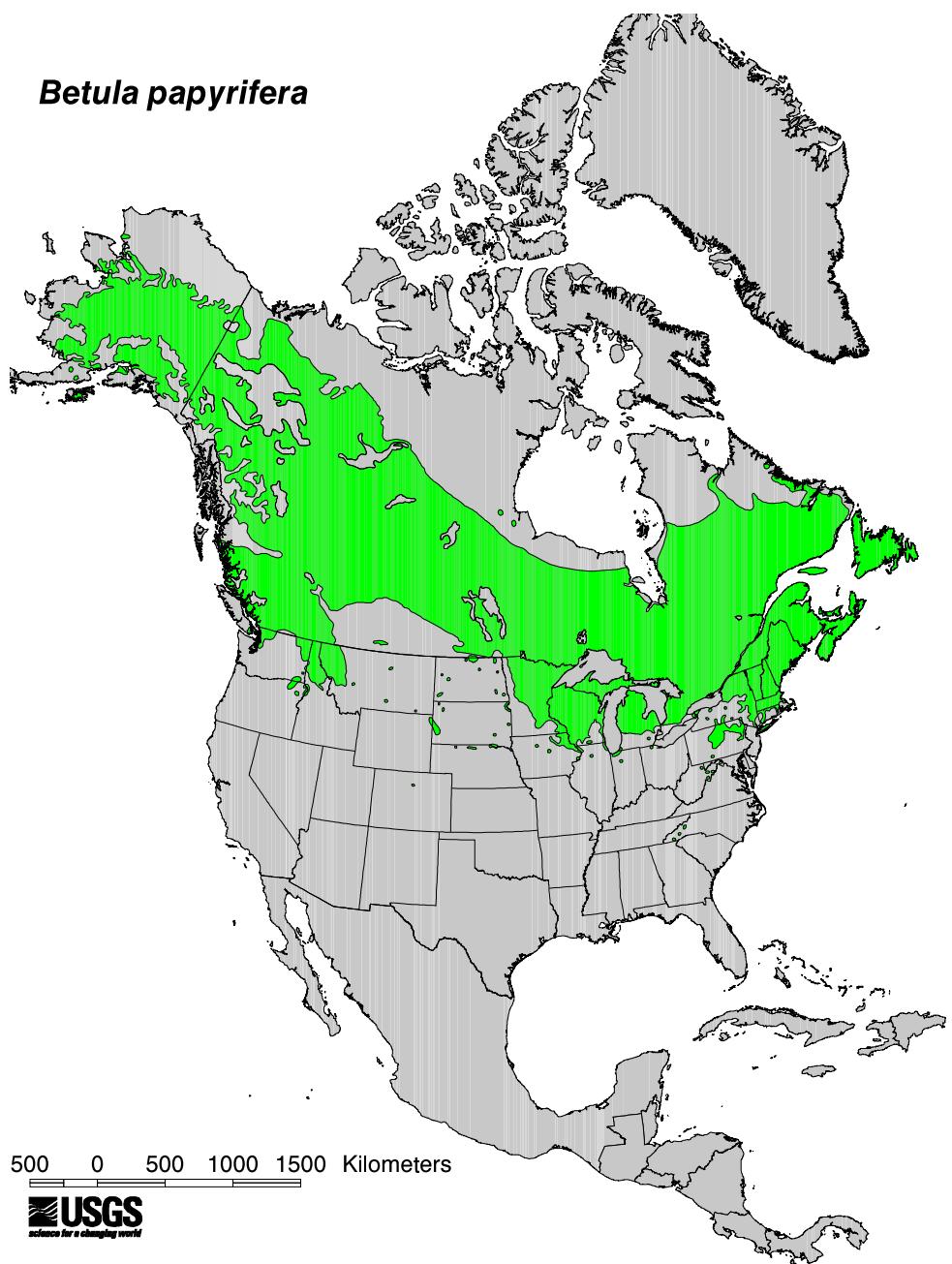


Figure 4: Representation of the range of *B. papyrifera*. Individuals were found at all sites, with functional trait data taken across all four. Used as one of two species entering its range interior away from Harvard Forest (taken as near its southern range extreme). Image taken from <https://gec.cr.usgs.gov>.

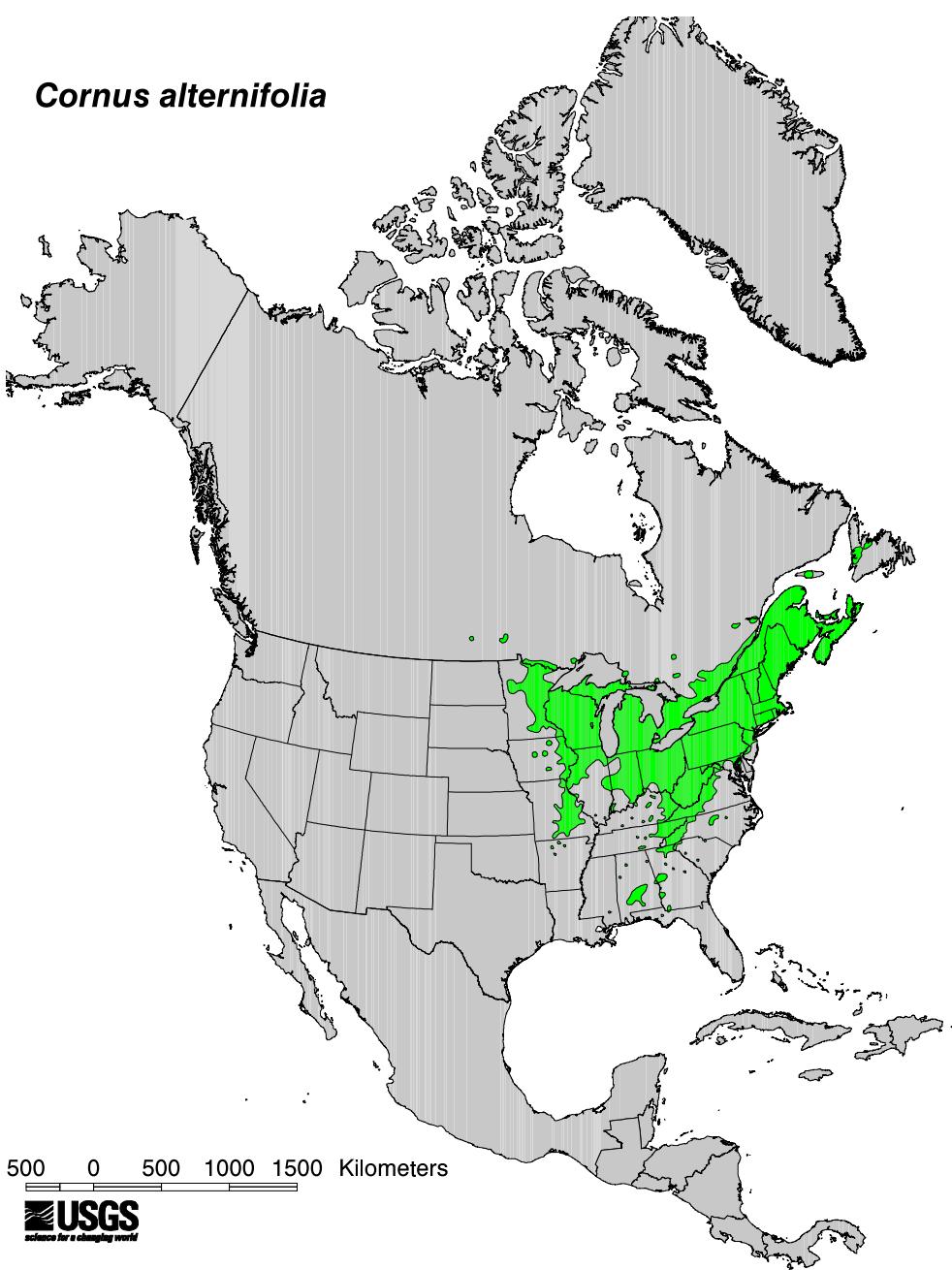


Figure 5: Representation of the range of *C. alternifolia*. Community composition and competition index data was collected at the White Mountains, Dartmouth Grant, and Saint Hippolyte sites. Functional trait data was taken at the Harvard Forest, Dartmouth Grant, and Saint Hippolyte sites (over the year between the trait data and community composition data collections, the individuals found at Harvard Forest became very unhealthy). Used as one of four species approaching its northern range at the northernmost site at Saint Hippolyte. Image taken from <https://gec.cr.usgs.gov>.

Fagus grandifolia



Figure 6: Representation of the range of *F. grandifolia*. Individuals were found at all four sites, with functional trait data taken across all four. Used as one of four species approaching its northern range at the northernmost site at Saint Hippolyte. Image taken from <https://gec.cr.usgs.gov>.

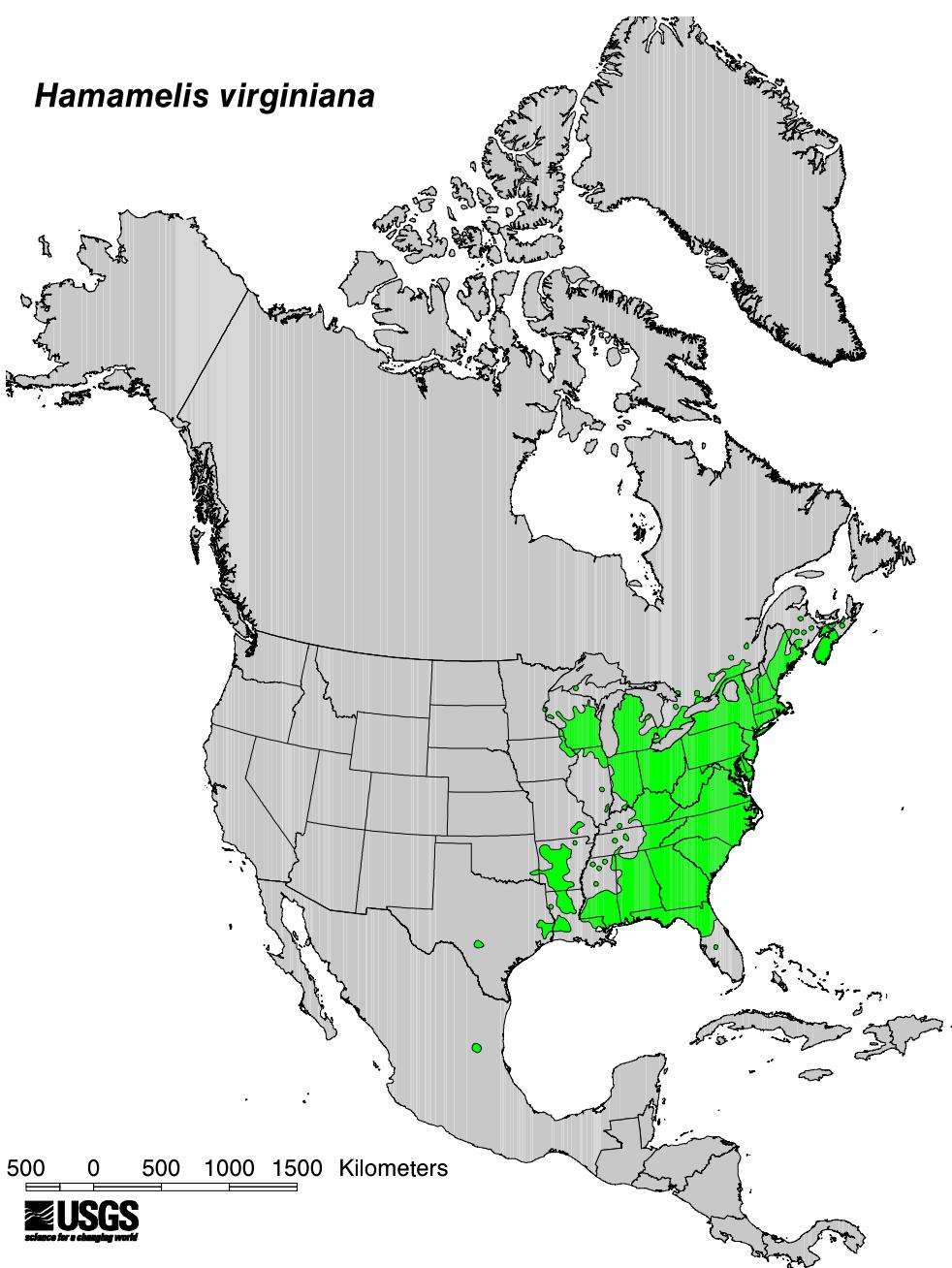


Figure 7: Representation of the range of *H. virginiana*. Individuals were found at only two sites, with functional trait data taken at both (though not enough to compute convex hull volumes). Used as one of four species approaching its northern range at the one of the middle sites in the White Mountains. Image taken from <https://gec.cr.usgs.gov>.

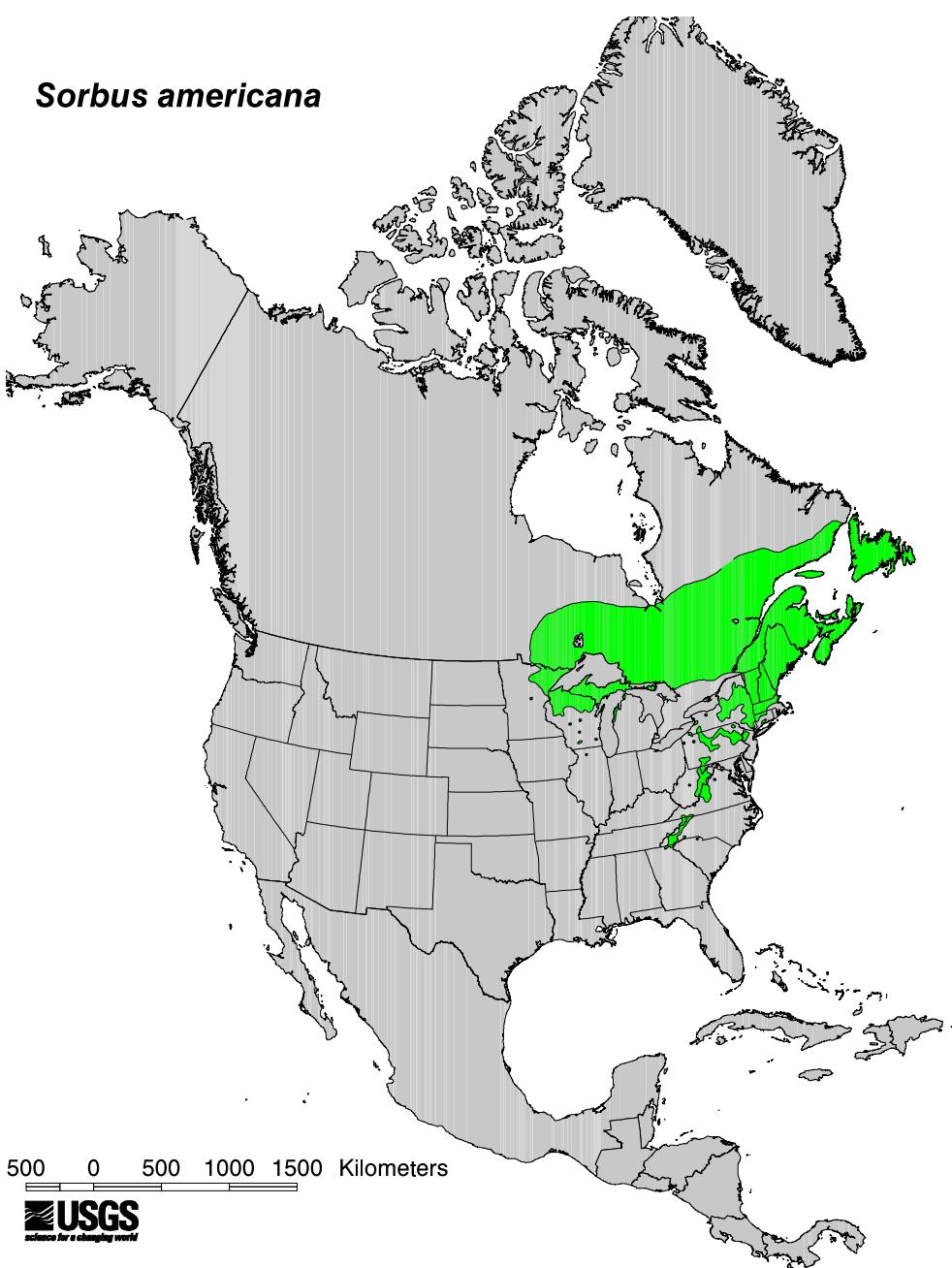


Figure 8: Representation of the range of *S. americana*. Individuals were found at all four sites, though not enough functional trait data was collected to determine convex hull volumes across all four sites (even though data was collected across all four). Used as one of two species that nears its southern range edge at the site near Harvard Forest. Image taken from <https://gec.cr.usgs.gov>.

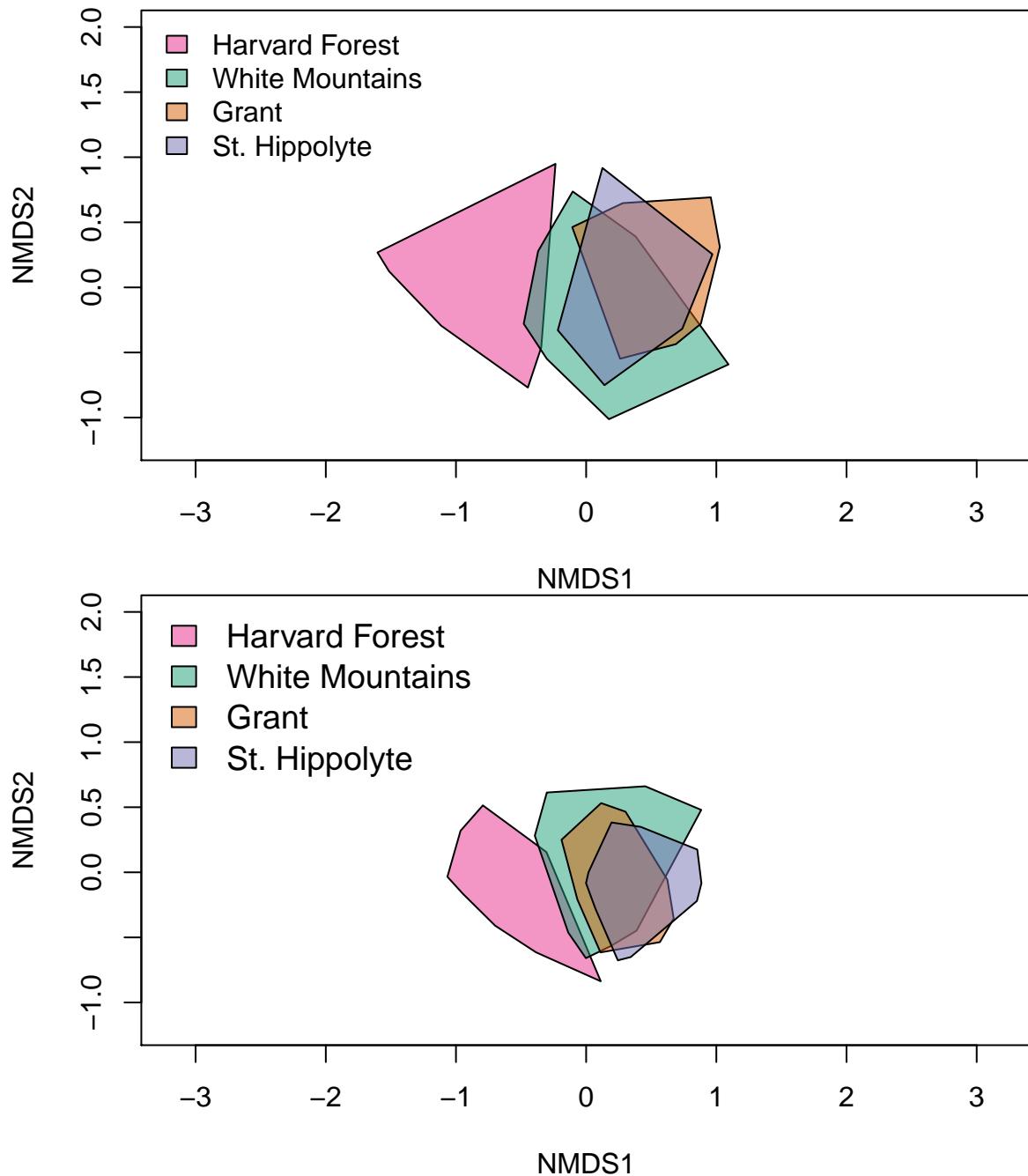


Figure 9: A non-metric multidimensional scalar plot representing the species composition and variation of the overstory across all four sites. The location of the polygon represents the different combinations of species that appear within each site, and the size represents the number of unique combinations of species. The overlap across the northern three sites signifies a great deal of similarity in combinations of species (species that appeared together in plots at those sites). Between the overstory and understory species composition, however, there are fewer unique combinations of species that occur in the understory. This is denoted by the slightly smaller polygons.

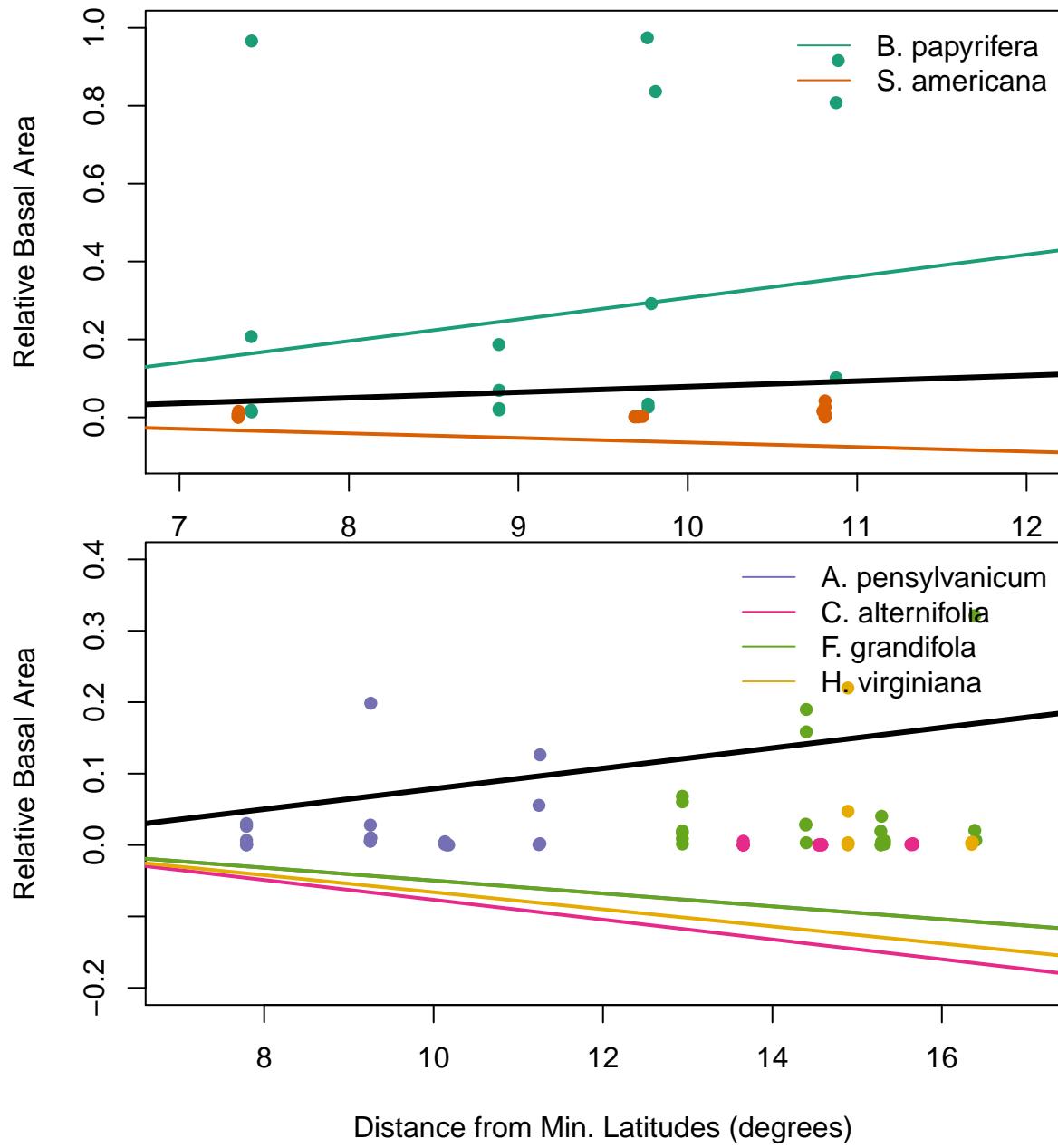


Figure 10: $p = .376$, $R^2 = .473$, CI = -0.02- 0.05. Competitiveness index across latitudes varies by species. Overall, there is a positive trend in competition index as individuals appear farther at sites located farther north. *B. papyrifera* and *S. americana* are separated from the other four species to emphasize that they are the two species that are moving away from their (southern) range extremes, rather than approaching their northern range extremes.

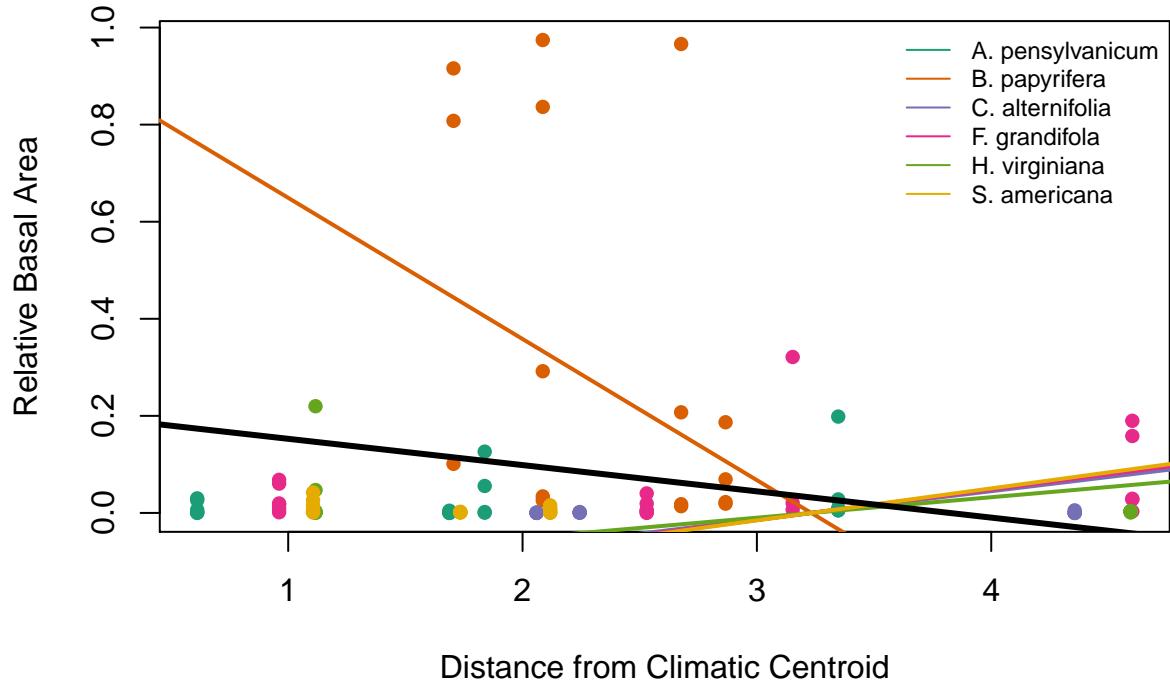


Figure 11: Across the six species, the intraspecific competition index of relative basal area did not vary predictably as species moved away from their climatic centroids ($p = .376$, $R^2 = .473$, CI = (-0.17 - 0.07)). *B. papyrifera* exhibited a strong negative correlation with its competition index, possibly due to its larger maximum size compared to the other species. Overall, there was a negative trend in a species' competition index as it moves away from its climatic centroid.

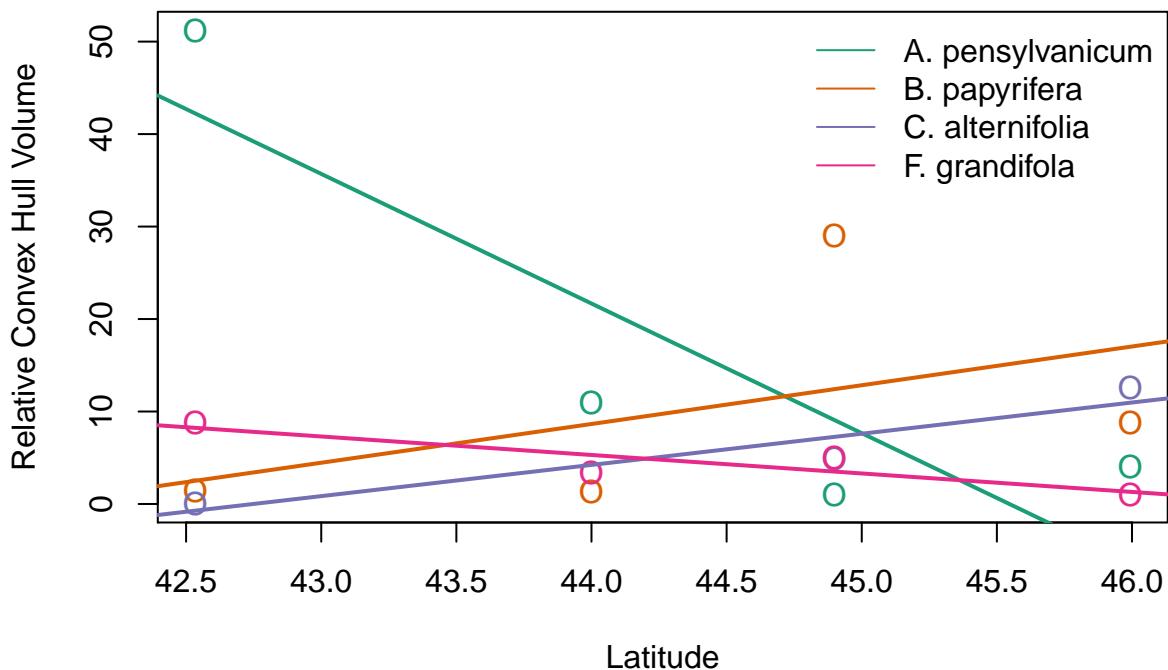


Figure 12: The suites of traits examined (SLA, %C:%N, DBH, Stem density) did not vary predictably with latitude. Across the four species that had enough trait data to calculate convex hull volume, two species (*B. papyrifera* and *A. pensylvanicum*) exhibited a decrease in their relative convex hull volume across latitudes. The other two increased across latitudes. All species appeared at all four sites, except for *C. alternifolia*, which appeared at three.

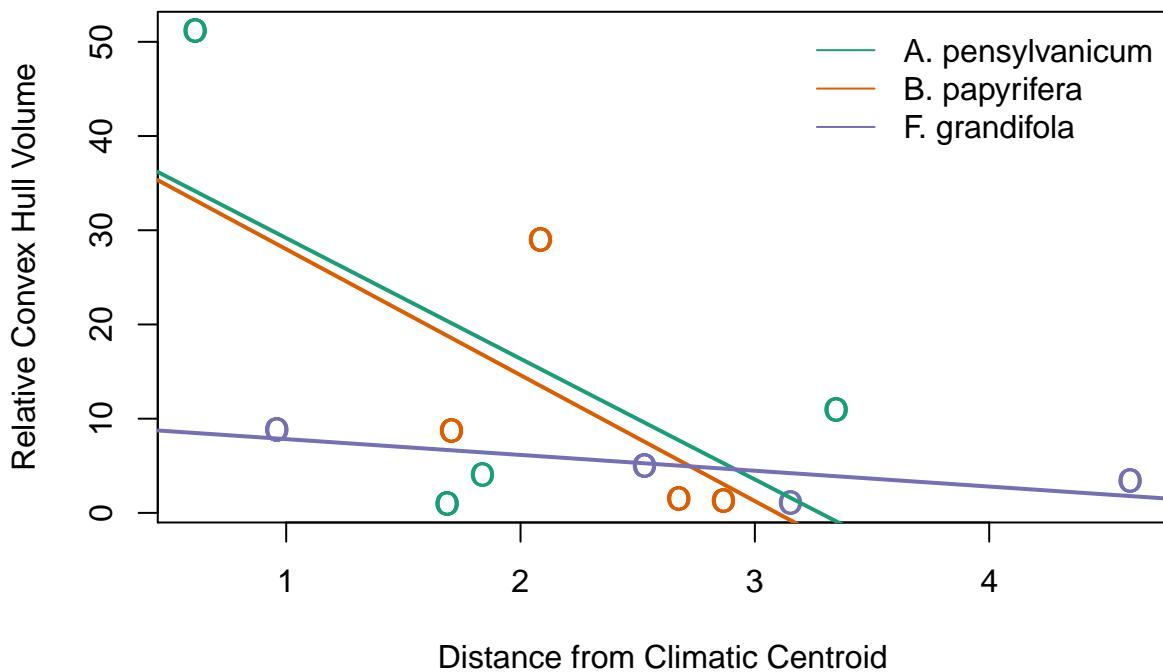


Figure 13: Relative convex hull volume decreased consistently across all four species examined as they moved away from their climatic centroids. Three of the species appeared at the four sites, and one appeared at three sites.

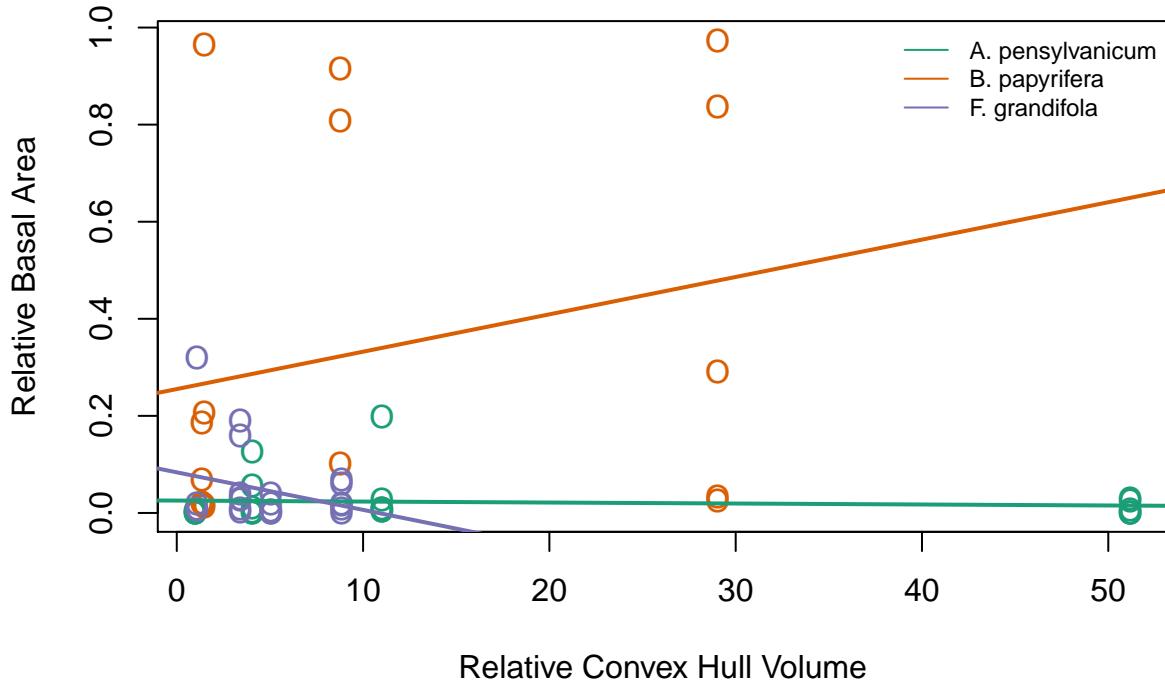


Figure 14: Across the four species with sufficient trait data, relative convex hull volume of species across all sites did not reliably predict the relative basal area. This suggests more complex factors at play in determining a species' suite of functional traits than an individual's competitiveness.

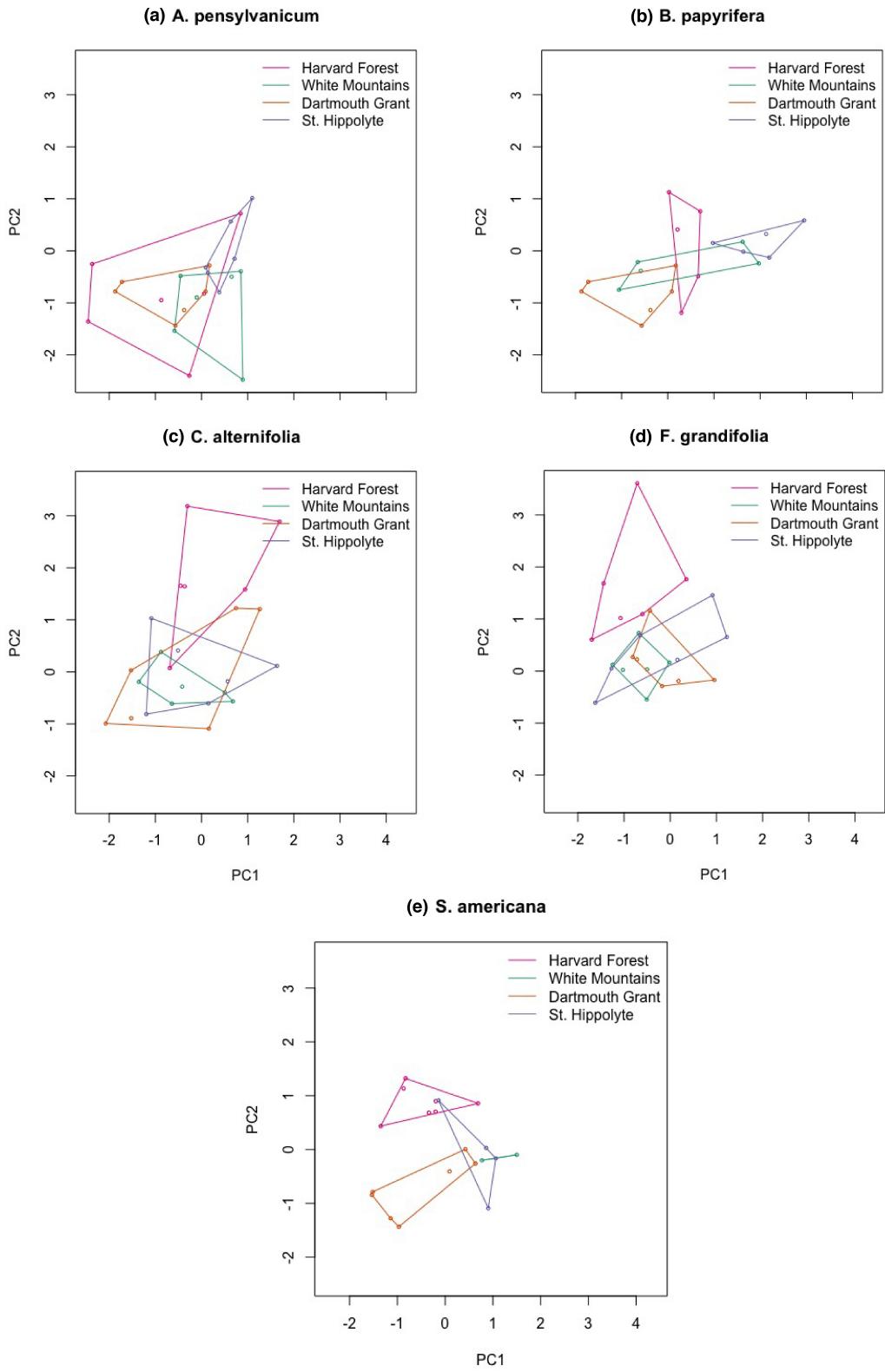


Figure 15: Convex hull volumes using a PCA across all species show marked variations in functional traits across sites.

Discussion

Ecologists have long understood that range limits are caused by complex dynamics between biotic and abiotic factors. These dynamics are especially important to understand in light of climate change. As a species' climatic envelope migrates north, looking at the limiting power of biotic and abiotic factors at range limits can provide insight into the future survival of that species.

My results suggest that the effect of biotic and abiotic factors on limiting trees at their range limits varies across tree species. They showed no clear pattern with regards to a species' competitiveness across latitudes or climatic envelopes, even within species positioned closer to their southern range limits.

Functional traits have recently seen a resurgence among community ecologists. They provide useful continuous variables that can be measured across species. In this way, they provide crucial information on how communities assemble, and can serve as proxies for other traits that are more difficult to measure. By examining functional traits across species' ranges, we can examine factors that have been shown to strongly influence organismal performances and thus make more accurate predictions about future success of those species.

There was a similar dearth of a clear pattern in examining the functional traits of four of the six focal species across the sites at which they were found. The functional trait space each species occupied relative to the average functional diversity of communities at each site reflected very little effect derived from latitudinal or climatic gradients.

Competition across latitudinal and climatic range limits

I found no strong support for my hypothesis that species would decrease in competitiveness as they approached their latitudinal and/or climatic range limits. The overall trend in competitiveness across latitudes was positive, indicating a slight increase in dominance as a

species goes north. This lack of clear pattern probably indicates that latitudinal range limits are caused by a complex interplay of biotic and abiotic factors that is not fully accounted for in simply examining a species' competitiveness.

The overall lack of a significant relationship competitiveness and position in range, combined with different relationships for certain species, indicate that there are other factors playing a part in determining a species' range limits. These other factors likely prevent a clear pattern from emerging in my data. For example, the average size of the focal species I chose varies greatly. With varying size, one would expect unequal rates of establishment or survival of saplings depending on the resource needs of the species. Species of trees that are mid-sized (such as *H. virginiana*, *A. pensylvanicum*, and *S. americana*) will never reach the same level of competitiveness in basal area as the larger species, such as *B. papyrifera*. These species could be more susceptible to biotic factors as they near their latitudinal range limits, whereas *B. papyrifera*'s size gives it a large advantage once it is successfully established, regardless of environment. This consideration of size class also highlights that some species of different sizes may compete strongly, but only at different life stages when they are similarly sized. Studies show that climate has been shown to be a strong limiting factor on tree species at their range extremes, depending on their growth stage (Ettinger and HillesRisLambers 2013).

Variation in size and rates of sapling survival make competition difficult to measure more generally. Studies in intra-specific competition often examine percentage cover in the canopy, which is widely recognized as constraining plant development over time due to possible loss of energy from sunlight (Biging & Dobbertin 1995, Contreras et. al 2011). To account for this, one could utilize a different competition index in a similar study on latitudinal and climatic ranges. More accurate competition indices are distance-dependent (whereas summing up the surrounding basal area of larger competitors than the focal individual is a distance-independent index). The best distance-dependent competition index is the sum of the horizontal angles multiplied by the ratios of the DBHs of the neighbor and the cored

individuals (outlined in Rouvinen & Kuuluvainen 1997 and as tested in Contreras et. al 2011). The downside of this method (and of distance-dependent competition indices in general) is that they require much more time to collect data. This is a major limiting factor in latitudinal studies, since so many resources are required to collect data in the field across such a large area.

It is also possible that community composition and local adaptation matter more for a species' size than its position within its latitudinal or climatic range. In this case, local community composition could be more predictive of a tree's success. The more important question to examine in studies of this nature would then be what other organisms are co-occurring with the species of interest, and the nature of their interactions. Invasive species that are more quick to colonize new environments than native species may prevent that native species from migrating north at a rate that allows it to account for population loss at its southern range limit. Ecological models predict that biotic interactions will create lags in climate tracking (Svenning et. al 2014). This has also been supported by experiments on the ground (Fisichelli et. al 2012). (*AHL Citation on invasive species?*)

It is also possible that a species is more limited by competition at its southern edge, and thus my results would not reflect this as they are heavily reliant on species that lie closer to their northern range limits across our sites. Additionally, studies have observed that the stronger limiting factors at a species' southern range limit are interspecific competition, while environmental factors limit species at their northern limits (Brown et. al 1996, Nakawatase & Peterson 2006). Due to the limited data I recorded of species with southern range limits close to the four sites, my study was lacking in this respect. The two species I did examine, *B. papyrifera* and *S. americana*, that near their southern range extreme at my southern-most site exhibited opposite trends in competitiveness across latitudes. *B. papyrifera* behaved as hypothesized decreasing in competitiveness as it neared its southern latitudinal range edge. For best results, a study would examine a species' entire latitudinal and climatic range,

though this is hindered by logistical difficulties in field sampling.

I saw a similarly unclear pattern in competitiveness across species' climatic envelopes. The only species to exhibit a decrease in competitiveness was *B. papyrifera*, suggesting that environment may be more of a limiting factor in its establishment than the other species examined. While overall in the mixed effects model there was a negative trend in a species' relative basal area in relation to the distance of the individual from its climatic centroid, individual species did not mirror this behavior. This confirms my hypothesis that a species will become less competitive as it approaches its climatic range limit (or moves away from the center of its climatic range, where environmental factors are most favorable for it). This suggests the species examined have climatic ranges that are not necessarily representative of their fundamental niche, and also that the latitudinal range limit as a proxy for harsh environmental conditions may not tell the whole story.

My results could mean that climate is not a limiting factor for the species that do not show a negative correlation. Instead, it is possible that they do not need to track their habitat and thus will not see a range shift in the face of a warming climate. A positive correlation between habitat preference and performance in the preferred habitat promotes specialization to the preferred habitat (Holt 1987). Seeing habitat preference have little effect when examined in relation to performance suggests that these species have not specialized to their preferred habitats, and so may not see the population loss that some species forced to shift in their range due to climate changes have faced in the past (Davis et. al 2001).

Beyond my findings that a species' position within its climatic centroid is not a reliable predictor of its competitiveness, there is evidence that plant distribution data does not match climatic tolerance estimates (Curtis and Bradley 2016). Additionally, climatic niche shifts are not reflected in species distribution, and many species in naturalized distribution were found outside native climatic conditions (Early and Sax 2014). If a species is not at climatic equilibrium, its competitiveness to individuals around it could reflect the effect of climate

from earlier in the individual's life. This could explain the absence of a strong effect of climate on a species' size (and competitiveness), and indicates climate could be much less of a limiting factor than initially thought.

Suites of functional traits across ranges

I hypothesized that trees at their range extremes would show altered suites of functional traits from trees in their range interior because species at their range limits often see more extreme environments (Sexton et. al 2009), and functional traits have been shown vary based on the individual's latitude of origin (Cavender-Bares 2007).

To examine this, I examined how much of a community's functional richness was occupied by each focal species. Across sites, latitude appeared to have no discernible effect overall on the species' relative functional richness (Fig. 12). This could indicate that biotic factors or environmental factors not consistent across latitudes are more predictive in a species' suite of functional traits. Past studies have found that latitude does predict trends of functional traits (De Frenne et. al 2011), but the traits examined differ from those examined in this study.

Conversely, across a climatic range there is an overall decrease in species' relative functional richness (Fig. 13). This suggests that environment, more than latitude, is a determining factor in the functional traits exhibited by a species. As a species moves farther away from its climatic centroid, its functional traits become more similar and show less variability relative to the functional richness of its community. Other studies examining SLA (Guittar et. al, 2016) have found consistent patterns across climatic ranges, similar to my results.

This result supports my hypothesis that trees moving away from their climatic range interior exhibit altered suites of functional traits from trees in their range interior, and

specifically *A1* (increases in intra-specific trait variation across a latitudinal gradient could signal increased genetic adaptation and/or increased plasticity). This suggests that certain suites of traits are successful depending on the environment and the species' location in the climatic range (Burns and Straus 2012).

However, functional trait similarity was not linked to a tree's relative size (i.e. competitiveness index) within a plot. This could suggest that environment (and abiotic factors) matter more in terms of what values of traits are observed in a species, though this is not supported by the literature (Burns and Straus 2012; Kunstler et. al 2015). In a study by Funk and Wolf (2016), certain suites of functional traits in grasses were a better predictor of competitive outcome than phylogenetic relatedness.

As an alternative method to measure variability in the suites of functional traits across sites, I plotted the convex hulls of the first two principal components values of the traits examined (Fig. 15). There was no discernible pattern across species in the changes of their suites of functional traits, based solely on the overlap of their convex hulls (indicating similarity in the values of their suites of traits). Two species, *C. alternifolia* and *F. grandifolia*, exhibited a marked difference in the convex hulls of their traits between the Harvard Forest and the other three of the sites. This mirrors the difference in species composition between Harvard Forest and the other three sites observed in both the understory and overstory (Fig. 9). Such results suggest that the type of species that co-occur with the focal species could affect the suites of traits exhibited in an individual.

Areas of future research

In predicting the future distributions of species in light of climate change, much is still unclear about the effect of biotic and abiotic variables. Above I discuss how size classes, life stage, and types of competitive indices can impact results. In modeling future species distributions and making long-term predictions in a warming world, it will be important to take into

account these factors. Another critical factor is whether the communities I measured were at environmental equilibria. By examining these factors together, models will provide a much clearer and more accurate idea of species' responses to climate change.

Based on my results, the relative strength of the two factors in limiting ranges seems to vary across species. The species *B. papyrifera* tends to grow much larger than any of the other species examined (and was one of two trees selected for the focal species that neared its southern edge rather than its northern edge). It seems likely that a major factor in *B. papyrifera*'s consistently larger relative basal area is the size and age of its mature trees, which will likely not be indicative of a species at climatic equilibrium, and thus will not provide an accurate forecast of species distributions due to climate change.

Yackulic et. al (2015) outlines this problem, and suggests that models and field work take into account colonization and extinction rates of species, thus looking at time-variant relationships between environmental conditions and changes in species distribution. With trees especially, it will be important to look at dispersal and seedling establishment within this, as plants in general are more likely to be limited by the extent of their dispersal when looking ahead at possible migrations due to climate change (Ackerly 2003). Future research into competitiveness across ranges should take this into account, as looking at current competitiveness cannot provide the full picture of the complex dynamics at a species' range edge.

Additionally, my results emphasize the importance of examining species at their southern ranges in future work. Unfortunately, I was only able to examine two species that neared their southern range edges (*S. americana* and *B. papyrifera*). Studies have shown that interspecific competition sets lower limits (Brown et. al 1996), necessitating the inclusion of southern range limits as a way to understand the complex dynamics of biotic factors and future success of species.

Conclusion here — do I make a whole new section for this?

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