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 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). 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 in northern New Hampshire, near the border of Maine. Finally, the northernmost site was located at the Station de biologie des Laurentide in Quebec. The Station de biologie des Laurentide is slightly larger than Harvard Forest, spanning 4000 acres, and is 75 kilometers northeast of Montreal. Due to the varying latitudes, the northern-most sites see a climate of colder winters and shorter growing seasons. All follow mild summers.

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

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.

Results

There was little to no correlation between increasing latitude (approaching northern edges) and the competitive index of the focal trees.

Figures

Figure 1

Run 0 stress 0.2055906 Run 1 stress 0.2164318 Run 2 stress 0.2075753 Run 3 stress 0.2113677 Run 4 stress 0.2132322 Run 5 stress 0.2059573 . . . Procrustes: rmse 0.03339321 max resid 0.1891671 Run 6 stress 0.2224483 Run 7 stress 0.2054885 . . . New best solution . . . Procrustes: rmse 0.006485895 max resid 0.05477055 Run 8 stress 0.2057772 . . . Procrustes: rmse 0.01655322 max resid 0.1196581 Run 9 stress 0.2152448 Run 10 stress 0.2146475 Run 11 stress 0.2084303 Run 12 stress 0.2170413 Run 13 stress 0.2083217 Run 14 stress 0.2112105 Run 15 stress 0.209692 Run 16 stress 0.2143791 Run 17 stress 0.2145516 Run 18 stress 0.2153057 Run 19 stress 0.2097501 Run 20 stress 0.209199 Run 21 stress 0.2181667 Run 22 stress 0.2069888 Run 23 stress 0.2209821 Run 24 stress 0.2241434 Run 25 stress 0.2081062 Run 26 stress 0.2125596 Run 27 stress 0.2158797 Run 28 stress 0.210615 Run 29 stress 0.212648 Run 30 stress 0.2076968 Run 31 stress 0.2146096 Run 32 stress 0.2163421 Run 33 stress 0.2163788 Run 34 stress 0.2238808 Run 35 stress 0.2070789 Run 36 stress 0.2079706 Run 37 stress 0.2093658 Run 38 stress 0.2077529 Run 39 stress 0.2089012 Run 40 stress 0.2130351 Run 41 stress 0.222163 Run 42 stress 0.2153456 Run 43 stress 0.2090693 Run 44 stress 0.2138381 Run 45 stress 0.2089025 Run 46 stress 0.2125581 Run 47 stress 0.2087962 Run 48 stress 0.2053559 . . . New best solution . . . Procrustes: rmse 0.01098307 max resid 0.1177172 Run 49 stress 0.2072147 Run 50 stress 0.2156374 Run 51 stress 0.2067378 Run 52 stress 0.2226972 Run 53 stress 0.2113283 Run 54 stress 0.2055339 . . . Procrustes: rmse 0.02536924 max resid 0.1767531 Run 55 stress 0.2056237 . . . Procrustes: rmse 0.02547889 max resid 0.1752453 Run 56 stress 0.2123767 Run 57 stress 0.2147967 Run 58 stress 0.2081291 Run 59 stress 0.2154802 Run 60 stress 0.2156015 Run 61 stress 0.2164653 Run 62 stress 0.2091401 Run 63 stress 0.2164115 Run 64 stress 0.2064633 Run 65 stress 0.2164078 Run 66 stress 0.2128813 Run 67 stress 0.2145379 Run 68 stress 0.2195638 Run 69 stress 0.2071092 Run 70 stress 0.2077059 Run 71 stress 0.2052179 . . . New best solution . . . Procrustes: rmse 0.02863619 max resid 0.1748217 Run 72 stress 0.2195433 Run 73 stress 0.2073473 Run 74 stress 0.207742 Run 75 stress 0.2237112 Run 76 stress 0.214637 Run 77 stress 0.214033 Run 78 stress 0.2156624 Run 79 stress 0.2161793 Run 80 stress 0.2095558 Run 81 stress 0.2095426 Run 82 stress 0.2082165 Run 83 stress 0.2063845 Run 84 stress 0.2168047 Run 85 stress 0.2110665 Run 86 stress 0.2152588 Run 87 stress 0.2143737 Run 88 stress 0.2123779 Run 89 stress 0.2106882 Run 90 stress 0.2073209 Run 91 stress 0.2112682 Run 92 stress 0.2093425 Run 93 stress 0.2083687 Run 94 stress 0.2151604 Run 95 stress 0.2100314 Run 96 stress 0.2166664 Run 97 stress 0.2068843 Run 98 stress 0.2160578 Run 99 stress 0.2136146 Run 100 stress 0.2145274 *** No convergence – monoMDS stopping criteria: 100: stress ratio > sratmax

Overstory
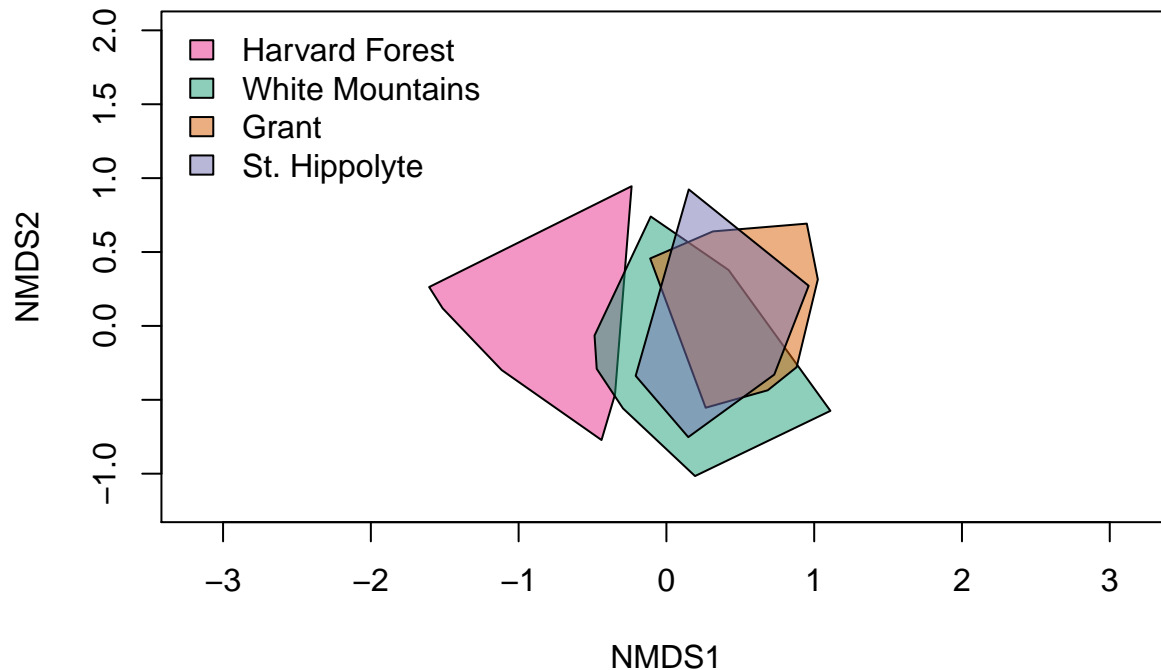
Run 0
stress 0.2442995 Run 1 stress 0.2565382 Run 2 stress 0.2518105 Run 3 stress 0.2513275 Run 4 stress 0.2492895 Run 5 stress 0.2438774 . . . New best solution . . . Procrustes: rmse 0.05897949 max resid 0.2262072 Run 6 stress 0.247862 Run 7 stress 0.2471762 Run 8 stress 0.2504769 Run 9 stress 0.2523666 Run 10 stress 0.244023 . . . Procrustes: rmse 0.05443267 max resid 0.2299599 Run 11 stress 0.250523 Run 12 stress 0.251922 Run 13 stress 0.2477475 Run 14 stress 0.2465931 Run 15 stress 0.2461495 Run 16 stress 0.2483538 Run 17 stress 0.238369 . . . New best solution . . . Procrustes: rmse 0.06160188 max resid 0.1791448 Run 18 stress 0.2460767 Run 19 stress 0.2620868 Run 20 stress 0.246486 Run 21 stress 0.250204 Run 22 stress 0.2528878 Run 23 stress 0.2468184 Run 24 stress 0.2551492 Run 25 stress 0.2437528 Run 26 stress 0.2447798 Run 27 stress 0.256205 Run 28 stress 0.2531712 Run 29 stress 0.2460265 Run 30 stress 0.2436208 Run 31 stress 0.2525557 Run 32 stress 0.2535758 Run 33 stress 0.2533479 Run 34 stress 0.2436337 Run 35 stress 0.2444799 Run 36 stress 0.2441653 Run 37 stress 0.2472763 Run 38 stress 0.2440656 Run 39 stress 0.2512125 Run 40 stress 0.2491057 Run 41 stress 0.2506888 Run 42 stress 0.2496734 Run 43 stress 0.2405716 Run 44 stress 0.2459212 Run 45 stress 0.2456118 Run 46 stress 0.2527867 Run 47 stress 0.2476967 Run 48 stress 0.2518924 Run 49 stress 0.2511427 Run 50 stress 0.2554251 Run 51 stress 0.2512823 Run 52 stress 0.243989 Run 53 stress 0.2534774 Run 54 stress 0.2559595 Run 55 stress 0.254764 Run 56 stress 0.2473301 Run 57 stress 0.2468077 Run 58 stress 0.2447629 Run 59 stress 0.2495606 Run 60 stress 0.2482803 Run 61 stress 0.2466314 Run 62 stress 0.2524537 Run 63 stress 0.2437636 Run 64 stress 0.2469731 Run 65 stress 0.251004 Run 66 stress 0.2536161 Run 67 stress 0.249518 Run 68 stress 0.2476244 Run 69 stress 0.2548048 Run 70 stress 0.2520813 Run 71 stress 0.2491893 Run 72 stress 0.2529259 Run 73 stress 0.2498166 Run 74 stress 0.2498451 Run 75 stress 0.2529958 Run 76 stress 0.2520445 Run 77 stress 0.2464619 Run 78 stress 0.2475407 Run 79 stress 0.2460817 Run 80 stress 0.2484964 Run 81 stress 0.2431849 Run 82 stress 0.251021 Run 83 stress 0.2461161 Run 84 stress 0.2485912 Run 85 stress 0.2488688 Run 86 stress 0.2475941 Run 87 stress 0.2437415 Run 88 stress 0.2480168 Run 89 stress 0.2497776 Run 90 stress 0.246397 Run 91 stress 0.252549 Run 92 stress 0.2481194 Run 93 stress 0.2437571 Run 94 stress 0.2490347 Run 95 stress 0.2511086 Run 96 stress 0.2555869 Run 97 stress 0.2507338 Run 98 stress 0.2435851 Run 99 stress 0.2554657 Run 100 stress 0.2486651 *** No

Understory
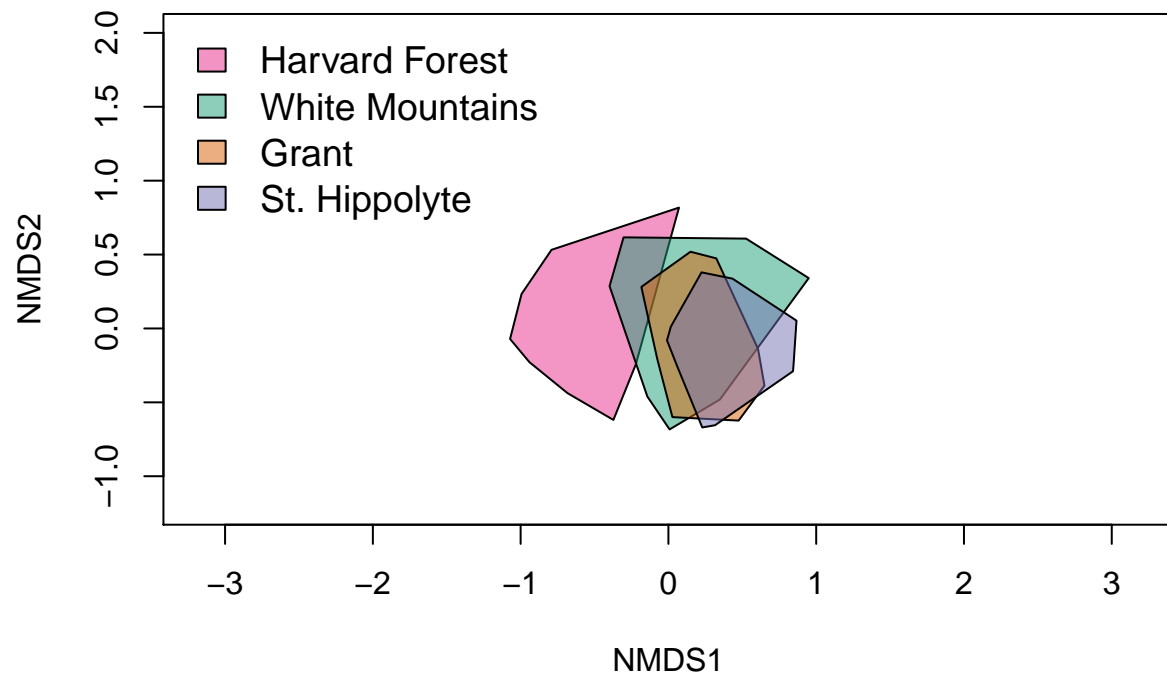
Figure 2
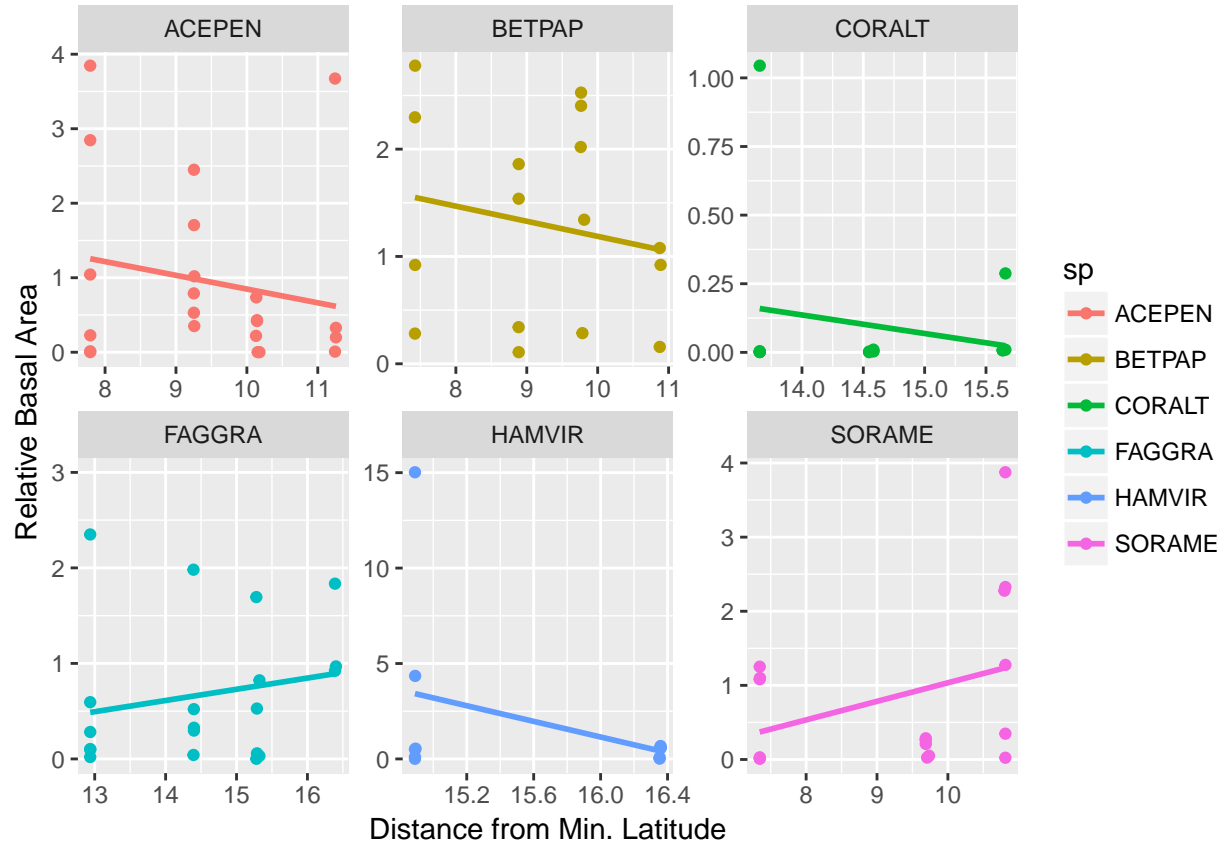
Table 1: Linear coefficients for Fig. 1

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

Figure 3
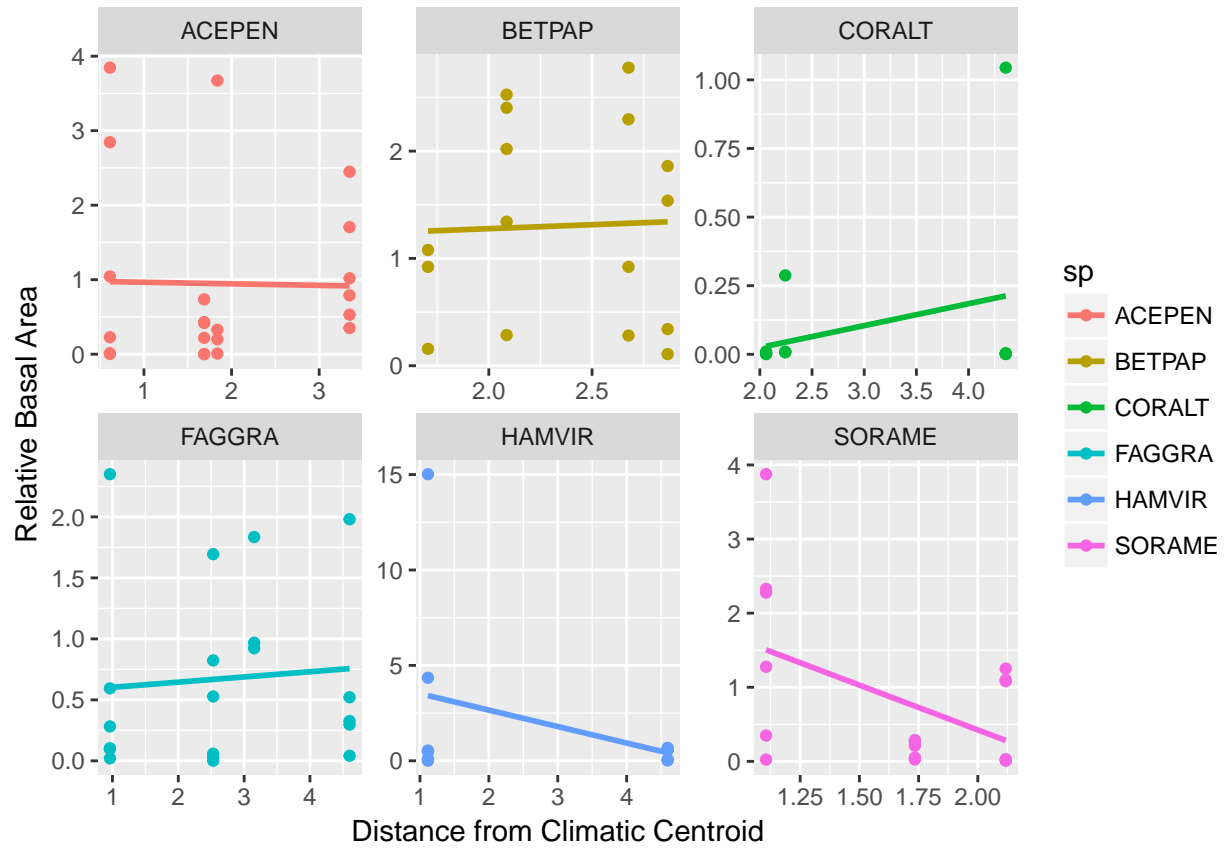
Table 2: Linear coefficients for Fig. 2

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

Figure 4

Figure 5

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