ENVIRONMENTAL NICHE DIVERGENCE IN THE *KALMIA* LINEAGE; INTEGRATING PHYLOGENY, COMMUNITY COMPOSITION AND ECOLOGY TO UNDERSTAND PATTERNS OF REGIONAL PLANT DIVERSITY

A Thesis
by
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Abstract

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The ongoing synthesis of the formerly disparate fields of ecology and evolution is resulting in a proliferation of insights, highlighting the interdependence and feedback between ecological and evolutionary processes. There is increasing evidence that evolutionary processes can influence community dynamics through geographic patterns of speciation, mutualist interactions, and other processes governing community phylogenetic patterns (Weber et al., 2017; Weeks et al., 2016). Here we adopt a clade-focused perspective to understand patterns of niche evolution in a single lineage, and subsequently address the regional community context of habitats which have facilitated the persistence and diversification of members of the genus.

Hypothesized to have originated in eastern North America, the genus *Kalmia* consists of ten species exhibiting widely varying and disjunct distributions while occupying a large spectrum of habitats- from alpine bogs to xeric sandhill scrub (Gillespie & Kron, 2013; Weakley, 2015). Given this extent of ecological and geographic divergence, we asked the following questions: what potential processes or factors underlie the patterns of lineage bifurcation and habitat differentiation in *Kalmia*, and what has been the role of phylogenetic niche conservatism in these lineage divergences? We constructed ecological niche models for seven of ten species of *Kalmia* using available climatic and topographic variables, and identified the variables contributing most to the observed distributions. We calculated the extent of niche overlap among all species, and subsequently used these metrics to assess the potential geographic pattern of divergence using a recent molecular phylogeny for the genus. We then subjected these results to an age-range correlation (ARC) test. We assessed the extent of niche conservatism in both morphological as well as abiotic traits that we could further use to infer processes underlying niche evolution. We suggest that the long evolutionary history of the *Kalmia* lineage in eastern North America coinciding with climatic and/or topographic changes has resulted in considerable niche lability, subsequently allowing *Kalmia* species to track suitable oligotrophic habitats while diverging in larger-scale climatic and topographic niche characteristics as well as less ecologically important morphological traits.

To understand speciation and niche evolution in a community context, we investigated the habitat use among three of these closely related taxa that exhibit overlapping disjunct ranges. We assessed the taxonomic and phylogenetic patterns of local communities along an elevation gradient among three distinct floristic regions of the southeastern US that all contain at least one *Kalmia* species. We asked if there were differences in abiotic and biotic attributes among coastal plain, piedmont and mountain habitats, given that they all support the same focal taxa. Using community data from both field collection and an open-source vegetation database, we find that differences in edaphic and phylogenetic patterns among regions were minimal with only soil pH exhibiting differences. Our results of taxonomic and phylogenetic beta diversity support the prevalence of allopatric speciation patterns from closely related lineages establishing in similar habitats. This research highlights the importance of considering habitat-specific lineage pools when interpreting patterns of regional diversity and local community assembly, as well as consideration for lineage-specific history when evaluating regional diversity patterns.

Acknowledgments

My sincerest gratitude is extended to all of the assistance and mentorship I have received throughout my graduate studies. My committee members Zack Murrell, Emily Gillespie and Mike Madritch for their guidance and edits; the exceptional volunteers that helped me in the field, including Richie Hum, Adrian Hill, Ben Banick and Ryan Rebozo; and the enthusiastic assistance from professionals helping me learn new methods including Will Pearse and the many commenters on various forums. We live in an incredible time for information exchange, and it has been truly inspiring to see the extent that open-source data and programming culture has fostered global scientific collaboration and knowledge transfer.

Dedication

This thesis is dedicated to all of the passionate, curious field botanists dedicating their efforts to noticing and documenting otherwise unrecognized patterns in our natural world. These caring and perceptive individuals include my many mentors whom have nurtured my love of plants, and my ongoing pursuit of ecological questions.

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Foreword

Chapters 2 and 3 of this thesis will be submitted to *The Journal of Biogeography*, an international peer-reviewed journal, as separate publications; they have been formatted according to the style guide for that journal.

Chapter 1: General Introduction

As we progress further into the Anthropocene and bear witness to the reverberating consequences of industrial culture, biologists are increasingly tasked with understanding the biotic patterns that have been produced as well as the underlying evolutionary mechanisms structuring those patterns. Elucidating how regional diversity is organized into local species assemblages inherently involves considering the role of abiotic and biotic factors that influence lineage diversification (Swenson, 2011). By drawing upon the large pool of big data available to the public, we can better recognize patterns and more readily identify processes generating and maintaining biodiversity. By studying the geographical distribution of closely related taxa, putting them in a community, phylogenetic, and ecological context, we can gain insight as to the mechanisms governing their distribution, and potential factors that result in ecological divergence.

The following research began with a personal interest in the geographical and ecological disjunction of one plant species, *Kalmia buxifolia*, an ericaceous shrub which occupies disparate habitats over a regional geographic disjunction. Originally interested in the molecular relationships of these disparate populations and overall biogeographical history that has led to the disjunction, I subsequently added the component of community characterization as an attempt to understand habitat affinity and ecological associations across the regions in which this species occurs. In the summer of 2017, ten community plots were sampled across the range of *K. buxifolia*, as well as collection of leaf tissue material for genetic analyses. As my personal interest grew in community ecology, I sought to incorporate this ecological context to better understand patterns of divergence within the genus.

Realizing the extent of ecological diversity among members of the genus, my inquiry grew toward understanding how closely related species can occupy such diverse geographical and environmental conditions. Since the radiation of plant lineages is typically associated with biome conservatism, in which species tend to occupy the same broad ecological regions as their ancestors, lineages that have ecologically diverged to occupy contrasting biomes represent a rare phenomenon (Crisp et al., 2009). Given the extent of biome diversity, and accompanying divergence in climatic, topographic and habitat affinities exhibited within the *Kalmia* lineage, this thesis has evolved as an effort to understand niche evolution in a closely related group of plants, as well as the implications for regional community assembly. Connecting long-term evolutionary processes of speciation and diversification with local ecological patterns represents a new and insightful avenue of research, and my efforts here were to use *Kalmia* as a model lineage to investigate larger questions of macroecology; how has lineage diversification, both geography of speciation and niche divergence, influenced regional diversity patterns? And in turn, how have regional patterns of ecological diversity influenced the present distributions of these taxa in terms of habitat selection?

Within the floristically rich region of eastern North America, the *Kalmia* lineage has diversified to occupy a range of geographically disjunct habitats that are predominantly characterized by high insularity- due to either high-elevation isolation, or edaphic discontinuities such as oligotrophic bogs and xeric residual sandhills (Kruckerberg, 1991; Weakley, 2015). As climatic niche divergence has been suggested to be an important driver of speciation (Hua & Wiens, 2013; Kozak & Wiens, 2007) and given the wide variability in climatic and topographic affinities among *Kalmia* species, the genus represents a potential model clade to investigate patterns of niche evolution and range expansion within a context of high environmental heterogeneity. Furthermore, as suggested by Warren, Cardillo, Rosauer, & Bolnick (2014), the legacy of speciation mode can leave an imprint on community phylogenetic patterns, while vice versa- the ecological sorting process at local scales can exhibit effects on species' range distributions. Given this interplay of ecological and evolutionary feedback, by focusing on a single clade's distribution and diversification patterns, and subsequently investigating local community structure through the lens of an historical perspective, we can begin to understand the macroevolutionary dynamics contributing to biotic patterns over longer timescales (McPeek, 2008; Weber, Wagner, Best, Harmon, & Matthews 2017; Weeks, Claramunt, & Cracraft, 2016).

A central theme explored in the field of community ecology has long been that of elucidating the mechanisms involved in generating local community assemblages. Inquiry into whether non-random patterns exist dominated early attempts at understanding community assembly mechanisms, while interpreting observed patterns to understand how taxa are filtered from a common species pool has taken the research field into new directions (Weiher & Keddy, 1995). The recognition of non-randomness in species composition led to the widespread development of null models to test for associations between species pairs (Conner & Simberloff, 1979) as well as other patterns of occurrence such as nestedness (Patterson, 1987; Wright & Reeves, 1992). Though former investigations into community-wide patterns focused on species identity for understanding assembly, the incorporation of species' traits was advocated based on the principle of limiting similarity (Gause, 1934), which could produce community patterns of traits being overdispersed or underdispersed to avoid niche overlap (Moulton & Pimm, 1987; Weiher & Keddy, 1995; Weiher, Clarke, & Keddy, 1998). Initially noted by Darwin (1859), the tendency for closely related species to more intensely compete and limit each other's abundance has been subsequently developed as the competition-relatedness hypothesis (Cahill, Kembel, Lamb, & Keddy, 2008), which builds from the theory of limiting similarity in which niche differences promote coexistence by limiting competition (MacArthur & Levins, 1967). This focus on species' similarity in structuring community patterns has been a central theme in subsequent attempts to elucidate mechanisms underlying community assembly.

Understanding the factors that limit species distributions is important as we face impending rapid climatic changes that could have major consequences for organisms unable to easily migrate, such as plants. While we face drastic predictions regarding the magnitude of future change, the consequences of recent change are already having a large effect on biota. A recent meta-analysis showed that local extinctions are already a widespread phenomenon across taxa and climatic zones owing to recent climate change, indicating that the majority of local populations will likely be unable to adjust their physiological characteristics to adapt to new conditions (Wiens, 2016). By integrating available technologies to address the mechanisms behind historical range determinants, we can more accurately infer future shifts in plant distribution parameters. Furthermore, by understanding underlying mechanisms of biotic interactions and community assembly at various spatial scales, we can better predict ecological responses at individual, community, and regional scales.

Niche dynamics and range distributions

The concept of an organism's ecological occupation in the environment- what we refer to broadly as an organism's niche was first defined by Joseph Grinnell, observing that "The extent and the persistence of a given kind of environment bear intimately upon the fate of the species we find occupying that environment… the existence and persistence of species is vitally bound up with environments." (Grinnell, 1924). In a subsequent paper, Grinnell more specifically defined the niche as "the concept of the ultimate distributional unit, within which each species is held by its structural and instinctive limitations, these being subject only to exceedingly slow modification down through time" (Grinnell, 1924). These earliest concepts of the niche were formulated primarily on the basis of geographical limitations- that the limits of species distributions are determined solely by physical and climatic factors; a pre-interactive concept that failed to incorporate biotic interactions (Vandermeer, 1972). Concurrently, and independently, another concept of the niche was being developed by Charles Elton in his study of food webs. Elton concluded that "the niche of an animal can be defined to a large extent by its size and food habits" (Elton, 1927), thus introducing the notion of a biotic effect influencing a species' niche- and therefore incorporating a post-interactive framework (Vandermeer, 1972).

The Grinnelian and Eltonian niche concepts amalgamated into a single widely accepted niche definition. An important contribution to this early theoretical development came from *Gause's theorem* which states that no two species can occupy the same ecological niche- thus invoking the long- observed phenomenon that closely related species possess subtle ecological differences that allow them to coexist (Vandermeer, 1972). Niche theory was formalized by Hutchinson (1957) when he differentiated between the fundamental and realized niche; the fundamental representing the abiotic tolerance of a species, and the realized representing the limitations imposed by biotic interactions. As originally articulated by Hutchinson, and now a widely accepted broad definition, a species' niche encompasses the abiotic and biotic conditions in which viable populations can be maintained (Hutchinson, 1957).

Leibold (1995) recognized the importance of the niche concept in linking disparate fields of ecology, and drawing upon resource-based competition theory, offered a modern context of the niche definition by recognizing two critical components: 1) species have resource requirements that determine their limitations- the "requirement" niche, and 2) species also have an effect on their environment in terms of their resource use- their "impact niche." Laying the foundation of modern niche theory, Chase and Leibold (2003) offered the now widely implemented definition of the niche as "the environmental conditions that allow a species to satisfy its minimum requirements so that the birth rate of a local population is equal to or greater than its death rate along with the set of per capita effects of that species on these environmental conditions" (p. 15).

Understanding the requirements and impacts of an organism's occupation in time and space is key to understanding their geographic distributions. The important information contained in species' distributions was recognized by MacArthur, noting that "future [biogeographic] theory will concentrate on the boundaries of species ranges as they are encountered on ecologically uniform or continuously varying terrain" (MacArthur & Wilson, 1967, p. 182). The rate and magnitude of impending global climate change has renewed biologist's interests in the determinants of species' geographic ranges, as well as potential ecological effects of biotic redistributions. While a multitude of research has focused on range redistributions under expected warming scenarios, relatively few studies have taken into consideration the mosaic of complex interactions at local scales that will alter habitat-scale competition dynamics, potentially causing unexpected range alterations (Lenoir et al., 2010). Climatic-driven changes that induce shifts in individual species' ranges can result in novel interspecific interactions (Tylianakis, Didham, Bascompte, & Wardle, 2008) resulting in strong changes in fitness due to a lack of co-evolutionary history- that can either enhance range expansion or hinder it (Gilman, Urban, Tewksbury, Gilchrist., & Holt, 2010). Reich et al. (2015) found that species' geographic distributions were strong predictors of their differential responses to climate warming, with climate-mediated competitive success varying between their cold and warm adapted range margins. Furthermore, species evolutionary relatedness can also impact range expansion effects, as community ecological interactions change in the new habitats of expanding species dependent on the degree of phylogenetic proximity (Koorem et al., 2018).

As outlined by Soberon (2007), there are three properties that contribute to the geographical distributions of species: 1) Dispersal factors that govern the accessibility of habitats to an individual; 2) the spatial configuration of environmental conditions that are conducive to an individual's ability to survive and reproduce; and 3) biotic factors that govern an individual's success in an environment. Interacting species can have both inhibitory effects on a species' range, such as through competitive exclusion, or can have a facilitative effect and thereby increase rates of range expansion (Svenning et al., 2014). For example, plant species experiencing competitive release of antagonists can experience rapid range expansion rates, as demonstrated by exotic species (Keane & Crawley, 2002).

While more rarely considered, multi-trophic interactions can have strong effects on an organism's range dynamics. Because trophic interactions determine the fitness levels of all species, they govern key ecosystem processes and their disruption could result in unforeseen species losses, as well as the loss of various selection pressures within their respective habitats (Van der Putten et al., 2004). Plants interacting with herbivores, pathogens and mutualists may either co-migrate or become decoupled as ranges shift, which may enhance or counteract their ability to adapt to local conditions (Van der Putten, Macel, & Visser, 2010). Plant-soil feedbacks encompass both the effect of plants on their rhizosphere as well as the effect of the soil community on plants and are likely of high importance relative to other plant growth factors (Kulmatiski, 2008). Range expansion may result in increased performance in a new habitat due to enhanced soil community interactions in the expanded range compared to the native species experiencing more negative plant-soil feedback, as found by Van Grunsven et al. (2010). Furthermore, plants connected through common mycorrhizal networks, through extensive resource exchange can drastically mediate an organism's ability to expand or contract its range based on the availability of mutualists (Gorzelak, Asay, Pickles, & Simard, 2015). Rapid plant responses to the colonization of mycorrhizal fungi in mycorrhizal networks include changes in root and shoot growth, photosynthetic rates, and plant defense chemistry (Gorzelak et al., 2015); thus, mutualist interactions could drastically accelerate or decelerate a species' migratory ability.

Understanding historic patterns of biotic responses to changes in climate is of paramount importance in making viable predictions at mitigating future ecological consequences. Since the rate and magnitude of historic climatic change events (e.g., mid-Pliocene warm period, recent interglacial transition to the Holocene) are similar to those predicted for the next century, these past climatic fluctuations have much to offer in understanding biotic responses to future change (Willis & MacDonald, 2011). By reducing population sizes *in situ*, tracking small refugial locations and range migrations, the predominant response to rapid climate shifts and warmer intervals in the plant fossil record has been persistence, with local extinctions being relatively minimal (Willis & MacDonald, 2011). If ecological turnover and range adjustment have been the dominant response of vegetation to historic climate fluctuations, the importance of understanding the factors governing species' present range distributions is of crucial relevance.

Though the idea of species' exploitation of new environments resulting in diversification can be traced back to Darwin, the formal concept of ecological opportunity as a prerequisite to adaptive diversification was pioneered by George G. Simpson (Simpson, 1953), on the principle that species competitively superior to or released from competitors will exploit new habitats. As defined by Schluter (2000, p.69), ecological opportunity may be defined as a "wealth of evolutionarily accessible resources little used by competing taxa," and is central to understanding the mechanisms underlying adaptive radiations- and patterns of species diversity. Simpson's (1944) three sources of ecological opportunity-which include dispersal to novel environments, key innovations in traits for exploiting a new resource, and the elimination of antagonists, explain drivers of diversification (Yoder et al., 2010).

The longstanding and ongoing controversy among biologists as to the definition of a species has been problematic due to the complexity describing speciation. As suggested by Coyne and Orr (2004), reproductive barriers are the “currency” of speciation, and efforts put into species definitions should focus on identifying the mechanisms of reproductive isolation and elucidating how such barriers arise. Ecological speciation has been defined as natural selection contributing to divergence and subsequent speciation events, but most typically puts emphasis on ecologically-mediated disruption of gene flow (Schluter, 2001; Schluter, 2009). Ecological adaptation to new habitats, resulting in geographical isolation, is the major cause of reproductive isolation and plays a prominent role in the speciation process (Sobel, Chen, Watt, & Schemske, 2010).

The increasing support for ecologically-mediated diversification has led to a resurgent interest in the role of the environment in generating and maintaining biological diversity. Assessing the niche differences among closely related species of plants, Grossenbacher, Veloz, & Sexton (2014) found that sister species tended to be highly asymmetrical in their niche characteristics- both in their range size and niche width- compared to more similar niche characteristics in distantly related taxa. They attributed divergence in habitat and resource use to geographically nested budding speciation as the diversifying mechanism (Grossenbacher et al., 2014). Similarly, Anacker and Strauss (2014) examined 71 pairs of plant sister-species in the California Floristic Region and found 93% of sister pairs demonstrating at least partial ecological shifts in at least one dimension with 80% occurring in sympatry- to which they inferred the pattern of budding speciation. This pattern of fine-scale local adaptation leading to divergence is in accordance with a recent meta-analysis that found genetic isolation by ecology to be more pronounced than isolation by geographic distance (Sexton, Hangartner, & Hoffmann, 2014). This predominant role of local environmental conditions structuring genetic distance lends more widespread support for the concept of ecological speciation (Shafer & Wolf, 2013). Indeed, environmentally-driven selection and disruption of gene flow is now proposed to have generated a substantial portion of current biodiversity (Bird, Fernandez-Silva, Skillings, & Toonen, 2012).

Niche conservatism and evolution

As observed and repeatedly noted by Darwin over 150 years ago, the biotic web is comprised of lineage strands that have produced the diversity of forms that can be traced through time;

> *"All the foregoing rules and aids and difficulties in classification are explained... on the view that the natural system is founded on descent with modification; that the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, and, insofar all true classification is genealogical; that community of descent is the hidden bond which naturalists have been unconsciously seeking."*
> (Darwin 1859, p. 420)

One of the greatest advancements of our understanding of the natural world has been the recognition that biological entities are products of a genealogical history, and thus can be classified into a hierarchy of relatedness (Mayr, 1982). A widely recognized pattern in the distribution of biota is that of phylogenetic niche conservatism (PNC; Harvey & Pagel, 1991). As first expounded by Darwin (1859), "the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent" (p. 420). Phylogenetic niche conservatism broadly refers to this tendency of closely related species to retain their ancestral resemblance in traits, and thus ecological niche characteristics, and has been considered a critical underlying component to understanding patterns of species richness, historical biogeography, invasive species' spread, as well as predicting biotic responses to climate change (Roberts & Hamann, 2012; Wiens & Graham, 2005).

As proposed by Harvey and Pagel (1991), two mechanisms responsible for the existence of PNC include divergence into empty ecological space by close relatives, and stabilizing selection being reinforced by the increased fitness and better exploited resources in the ancestral niche. Additionally, Wiens and Graham (2005) recognized other non-adaptive explanations for niche conservatism in close relatives, including gene flow that prevents local adaptation of populations to new niches, genetic constraints from pleiotropic links to traits reducing fitness, and lack of appropriate genetic variation to adapt to novel conditions.

An increased interest in PNC has arisen with the availability of dated molecular phylogenies for most extant taxa that allow for the exploration of hypotheses regarding the prevalence and nature of PNC (e.g., Zanne et al., 2014) and has subsequently led to conflicting ideas about what is and what is not PNC, and whether it is a pattern or process (Münkemüller, Boucher, Thuiller, & Lavergne, 2015). Some have argued that PNC is an inevitable ecological and evolutionary process due to conditions that restrict population expansion, impeding the emergence of novel adaptations (Lavergne, Mouquet, Thuiller, & Ronce, 2010). Multiple studies and meta-analyses have found widespread support for PNC (Blomberg, Garland, & Ives, 2003; Pyron, Costa, Patten, & Burbrink, 2015; Wiens & Graham, 2005) and recently emerging patterns support the tropical niche conservatism hypothesis, in which niche conservatism has been a primary feature governing community assembly along latitudinal temperature gradients across the globe (Qian & Ricklefs, 2016).

In addition to promoting the retention of an ancestral niche, the failure of a species to adapt to novel ecological conditions is also a manifestation of phylogenetic niche conservatism and has been suggested to be an important and overlooked mechanism leading to the initial geographic splitting of lineages during early allopatric speciation (Wiens, 2004), as well as a major force producing current biogeographical patterns (Wiens & Graham, 2005). In a recent review, Pyron et al. (2015) investigated the relationship between niche conservatism and lineage divergence, noting that ecologically-mediated divergent selection, leading to ecological speciation, will result from a lack of niche conservatism. Conversely, while niche divergence may be promoted by the retention of ancestral niche preferences (PNC) in varying ecological conditions during times of rapid environmental change. Thus, the evolutionary process of niche conservatism can result in varying patterns of diversification, rendering the importance of incorporating evolutionary history in studying the distribution of biota.

Given the widespread support for phylogenetic niche conservatism, the incidences of lineages diverging in both local and large-scale niche attributes remain a largely unresolved phenomenon that deserves increased focus to understand how lineages have transcended such constraints. As environments undergo rapid change, lineages are faced with the option of either evolving in situ or tracking suitable climatic and other ancestral niche attributes in adjacent habitats. If neither of these options is feasible, they may contract in their range and face geographical disjunctions (Donoghue, 2008). The response of species to environmental change depends on both the spatial properties of the contrasting environments as well as the ability to adapt to novel conditions as determined by evolutionary constraint (Edwards & Donoghue, 2013). The concept of the niche as consisting of multi-dimensional niche axes, as originally suggested by Hutchinson (1957), is a particularly valuable framework in considering niche evolution and ecological specialization.

Among the niche axes of divergence and specialization in plants, climatic variables relating to temperature and precipitation have recently received considerable attention. At larger geographic scales, climatic tolerances are assumed to structure an organism's range (Smith & Donoghue, 2010), and climatic niche divergence can be an important driver of speciation (Hua & Wiens, 2013; Kozak & Wiens, 2007). Climatic niche lability and subsequent niche evolution may result from either increased intrinsic lability, or from greater variability in selection pressures (Weeks et al., 2014). Using a clade-based approach, Emery et al. (2012) found considerable lability among species of *Lasthenia* in climatic niche axes, while localized microhabitat niche axes were more conserved, reinforcing the notion that niche specialization and subsequent niche width can vary among different niche axes. Though most studies have assessed niche conservatism at local and regional scales, the ancestral retention of ecological occupation may be a dominant force governing the distribution of biota on a global scale over millions of years, and lineages diverging from their ancestral habitat represent insightful anomalies (Nash, 2017). Crisp et al. (2009) evaluated over 11,000 species of globally distributed vascular plants and found that, though they have occurred, biome shifts were rare and offered strong support for phylogenetic conservatism in both ecological niche characteristics as well as strong constraints on biome shifts. In addition to the prevalence of biome conservatism, they found that among lineages that have exhibited biome shifts, sclerophyll biomes tend to be a net source habitat with grassland, arid and alpine habitats being net sinks (Crisp et al., 2009). Additionally, the influence of growth form can govern an organism's capacity for climatic niche evolution, with woody angiosperms exhibiting slower divergence than herbaceous plants (Smith, & Beaulieu, 2009). Similarly, Hawkins, Rueda, Rangel, Field, & Diniz-Filho (2014) found phylogenetic niche conservatism to be a dominant factor structuring North American temperate tree communities through conserved cold tolerance. As we face rapid impending global climate change, it is vital that we not only describe the climatic niche of species, but also understand the underlying factors governing niche width and evolution to predict species' adaptive potential (Guisan et al., 2014).

Niche breadth can be defined as the "variety of resources, habitats, or environments used by a given species" and is relevant to understanding many eco-evolutionary processes (Sexton, Montiel, Shay, Stephens, & Slatyer, 2017). It is still largely unknown how the evolution of niche breadth proceeds and represents an important avenue of research for predicting climate change responses of organisms and communities. The multidimensional nature of Hutchinson's niche definition makes the prediction that multiple biotic and abiotic variables determine the performance of a species (Hutchinson, 1957), resulting in a geographic mosaic of fitness and performance across a species' range (Brown, 1995). Species that use a greater variety of resources and are able to persist in a wider variety of conditions should result in more widespread geographic distributions, thus suggesting a positive correlation between niche breadth and range size (Brown, 1998). Though factors such as increased dispersal ability and lineage age were formerly suggested to govern a species' range size, a recent study showed that there is indeed a positive relationship between niche breadth and range size that is consistent across taxonomic groups as well as spatial scales (Slatyer & Sexton, 2013).

Community assembly and coexistence

The mechanisms structuring local communities of plants are many and complex, involving longer-scale biogeographical factors as well as contemporary ecological factors. Past immigration, speciation, extinction, and associated interactions are the processes governing a community's composition (Emerson & Gillespie, 2008). The community assembly framework provides a conceptual foundation for understanding the processes that govern the local assemblages of co-occurring species in time and space, and seeks to elucidate the roles of biotic, abiotic, and historical factors in structuring community composition and abundance (Weiher et al., 1998). Early studies focusing on community assembly sought out "assembly rules" by focusing on the effects of competitive interactions that determine composition (Cody & Diamond, 1975). It is now widely recognized that competitive interactions are important determinants of community structure at a local scale (Chesson, 2000), while large-scale environmental factors and evolutionary diversification structure the regional species pool from which local communities are assembled (Emerson & Gillespie, 2008). Therefore, both biotic interactions as well as abiotic factors operating at various spatial scales are important to the community assembly process (HillRisLambers et al., 2012).

Modern coexistence theory states that species coexistence depends on the extent of niche differences as well as average fitness differences that determine competitive outcomes (Chesson, 2000). While the idea of niche differences stabilizing coexistence dates to Gause (1934), modern coexistence theory builds on earlier work by distinguishing two specific categories of niche differences: stabilizing niche differences, in which differences among species enable coexistence, and relative fitness differences, which drive competitive dominance and exclusion from communities (HillRisLambers et al., 2012). Stabilizing niche differences can influence community structure by eliminating species that are too similar, which could mean the exclusion of close relatives, while fitness differences can drive the exclusion of competitively inferior taxa (HillRisLambers et al., 2012).

The prominent role of the abiotic environment in structuring local assemblages of plants has been recognized since some of the earliest formal ecological observations. Since the development of community assembly theory, the abiotic environment has been recognized as a metaphorical filter, by only allowing organisms able to tolerate certain conditions to establish and persist, and therefore acting as a community-level analogue of natural selection (Keddy, 1992). By imposing specific abiotic conditions, a strong environmental filter can result in a community assemblage of phenotypically similar plants possessing traits that confer adaptation to such conditions (e.g., Cornwell & Ackerly, 2007).

The distribution of species, at both local and geographic scales, fluctuates according to both ecological factors as well as evolutionary factors, such as coevolutionary dynamics and adaptive potential; thus, allowing both of these dynamics to influence biodiversity patterns (Ricklefs, 2007). As more recently defined by Fukami (2010), community assembly is “the construction and maintenance of local communities through sequential, repeated immigration of species from the regional species pool.” This perspective raises the question of when history and timing should matter in the assembly of local communities. According to the deterministic view of community assembly, environmental conditions rather than species immigration determine community composition (Fukami, 2010). The contrasting view of community assembly is one in which environmental conditions are relatively unimportant, and that immigration history is the predominant force structuring the local community (Fukami, 2010). This recently emerging theory, termed historical contingency, suggests that the history of immigration- the timing and order of arrival- could play a large role in subsequent community development (Chase, 2003). In the latter scenario, alternate stable states result from differences in biotic interactions exerted by earliest arriving species, which can result in very dissimilar communities with similar abiotic conditions (Fukami 2010). Emerging theory recognizes that both deterministic as well as stochastic processes are important to community assembly outcomes, and that their relative importance varies along environmental gradients (Michalet, Bagousse-Pinguet, Maalouf, & Lortie, 2014; Qian, Zhang, Zhang, & Wang, 2013).

According to the historical contingency framework, the immigration history of species assembling in a community can affect local-regional diversity relationships (Fukami, 2004) and can have large effects on ecosystem properties such as productivity, decomposition, and nutrient flow (Dickie et al., 2012; Tan, Pu, Ryberg, & Jiang, 2012). The idea that earlier species arrival confers an advantage over later colonists was proposed by Silvertown (2004) to explain the prevalence of monophyletic plant lineages dominating oceanic archipelagos. Referring to this effect as niche preemption, species arriving earlier have opportunity to establish and grow, reducing available resources to other species- thus having 'priority' over the available resources- that ultimately leads to the exclusion of future colonists (Silvertown, Francisco-ortega, & Carine, 2005). In addition to inhibiting subsequent immigrants, early-arriving species to a habitat can also have positive effects by facilitating their coexistence, and these priority effects can occur within the generation of species interacting, or over multiple generations (Fukami, 2015). Indeed, research has produced support for these 'priority effects', with the order and timing of species immigration influencing both the structure and the function of communities through mediating biotic interactions (Chase, 2003). For example, soil legacy effects can cause enhanced rates of succession through positive interspecific plant-soil effects amongst early-successional species (Shannon, Bauer, Anderson, & Reynolds, 2014; van de Voorde, van der Putten, & Martijn Bezemer, 2011). While historical contingency can refer to both biotic as well as abiotic factors affecting the order and timing of assembly patterns- such as disturbances, resource pulses and arrival of species- priority effects refer specifically to the pattern of temporal colonization of species determining their biotic interactions (Fukami, 2015).

Evolutionary Perspective on Community Assembly

One of the most persistent questions regarding the causes of species macroevolutionary distributions is the role of biotic versus abiotic factors. Van Valen's Red Queen hypothesis (Van Valen, 1973) suggests that biotic interactions are primary drivers of evolutionary dynamics, and thus structure macroevolutionary patterns. Invoking microevolutionary processes to explain larger-scale patterns, the

Red Queen suggests that the evolutionary success of one species may affect the success of others, and that these biotic interactions govern speciation-extinction dynamics over long timescales. There is increasing evidence that evolutionary processes can influence community dynamics through geographic patterns of speciation, mutualist interactions, and other processes governing community phylogenetic patterns (Weber et al., 2017; Weeks et al., 2016). In turn, interactions among taxa in communities can influence both micro- and macroevolutionary processes and patterns, through both indirect and direct interactions (Johnson & Stinchcombe, 2007). Furthermore, ecology has a strong influence on patterns of speciation, extinction, and trait evolution at the macroecological scale via mediation of trait-based interactions and diversification (Weber et al., 2017).

Community Phylogenetics

Perhaps one of the earliest documented insights regarding the role of evolution in the generation of biodiversity patterns came from Darwin's famous 'entangled bank' commentary:

> *"It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us. These laws, taken in the largest sense, being Growth with Reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of the external conditions of life, and from use and disuse; a Ratio of Increase so high as to lead to a Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less-improved forms. Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved."*
>
> -Origin of Species, 1859

Though the consideration of evolutionary history in ecological observations has been noted as early as Darwin's 'tangled bank,' the study of how quantitative phylogenetic relationships may reflect community assembly remains a burgeoning avenue of research (Swenson, 2011). Though both evolutionary biologists and ecologists share a common goal of elucidating how biodiversity is produced and distributed, their respective approaches have been pursued in isolation until relatively recently (Mouquet et al., 2012). While early advocates for the integration of ecology with an evolutionary perspective highlighted the utility of incorporating cladistics into ecological questions to help explain patterns of trait evolution and distribution (e.g., Wanntorp et al., 1990), it wasn't until the rapid rise in computing power and availability of phylogenetic information that evolutionary relationships could be fully incorporated into various areas of ecological inquiry (Cavender-Bares et al., 2009).

The recognition that phylogenetic data could be used to explain scenarios of community assembly, under the premise that communities exhibit nonrandom patterns of relatedness, comprised the original foundation for the field of 'community phylogenetics' (Webb, Ackerly, McPeek, & Donoghue, 2002). This initial framework proposed the use of phylogeny as a proxy for species similarity (Webb, 2000; Webb et al., 2002), since closely related species tend to be ecologically similar (Darwin, 1859; Lord, Westoby, & Leishman, 1995; Wiens & Graham, 2005). Representing a major advance in integrating community ecology and phylogenetic biology, this new avenue of research offered the potential to answer long-standing and controversial questions regarding the role of niche-based versus neutral process governing community assembly, as well as further understanding the specific assembly mechanisms involved (Cavender-Bares, Keen, & Miles, 2009).

One of the core assumptions underlying community phylogenetic patterns is the prevalence of phylogenetic niche conservatism, and thus using phylogenetic diversity as a surrogate for species' traits rests on the assumption that species' traits are evolutionarily conserved (Wiens et al., 2010; Prinzing et al., 2001). Therefore, some have advocated for the measurement of niche traits directly before inferring processes from patterns in community phylogenetic structure (Araya et al., 2012). Testing for phylogenetic 'signal' is a common approach for assessing the extent to which traits are reflected by the phylogeny (Blomberg et al., 2003). Phylogenetic signal is the "tendency for related species to resemble each other more than they resemble species drawn at random from the [phylogenetic] tree" (Blomberg &

Garland, 2002, p. 905) and would be a result of a Brownian motion model of evolution, in which small random changes in traits are the result of genetic drift and natural selection randomly varying through time (Losos, 2008a). Though testing for conservatism in species' functional traits is ideally a prerequisite to interpreting community phylogenetic patterns, these data are not always accessible, and phylogenetic diversity measures have been shown to adequately capture species' functional trait diversity (Cadotte et al., 2009, 2010; Devictor et al., 2010).

According to the community phylogenetic framework, contrasting patterns of relatedness have been used to infer different assembly mechanisms in local communities. Phylogenetic clustering, when species are more closely related than is expected by chance, is attributed to the presence of an environmental filter limiting species persistence. This pattern would reflect the exclusion of less well-adapted lineages to colonize a site of particular abiotic conditions. Alternatively, phylogenetic overdispersion occurs when species are more distantly related than would be by chance. The later scenario has been attributed to competitive exclusion being the dominant assembly mechanism (Webb, 2000; Webb et al., 2002). Because these two processes- environmental filtering and competitive exclusion- are expected to have contrasting effects on patterns of relatedness, they can be helpful in revealing which is the dominant mechanism involved in structuring communities (Cavender-Bares et al., 2009).

While the clustering / overdispersion pattern interpretations have contributed to understanding the influence of evolutionary relatedness in community assembly, these binary patterns of relatedness may reflect many potential processes beyond the competition versus filtering explanations, and thus require more careful interpretation (Gerhold et al., 2015; Vamosi, Heard, Vamosi, & Webb, 2009). For example, patterns of phylogenetic relatedness are strongly scale-dependent (Cavender-Bares et al., 2006; Swenson et al., 2006; Vamosi et al., 2009) due to environmental heterogeneity and subsequent habitat sorting of species increasing with spatial scale (Cavender-Bares et al., 2009). Although competitive exclusion of closely related species can drive patterns of phylogenetic overdispersion, recent research challenges this interpretation, as trait conservatism would have to be highly conserved across the regional species pool in order to reflect trait overdispersion as influenced by competitive outcomes (Kraft, Cornwell, Webb & Ackerly, 2007). Likewise, because facilitation tends to occur among more distantly related species, this positive interaction should result in phylogenetically over dispersed communities (e.g., Valiente-Banuet & Verdú, 2007), which would mirror that of competitively-structured communities. Therefore, to better explain the community context of evolution, it is necessary to move beyond the filtering versus competition explanations to encompass multidimensional, multi-scale analyses that consider trait and niche evolution in more complexity, as well as addressing the strong underlying assumptions implicit in the interpretation of phylogenetic patterns (Mayfield & Levine, 2010; Mouquet et al., 2012).

Patterns of phylogenetic distribution across a region can exhibit strong non-random effects of past climate change, with communities experiencing rapid climatic changes exhibiting reduced phylogenetic diversity- or clustering- of surviving species (Eiserhardt et al., 2015). Similarly, a recent study investigating the causes of observed phylogenetic patterns in plant communities found that the colonization of distantly related species, rather than the extirpation of close relatives, caused phylogenetic overdispersion (Li et al., 2015). Therefore, historical factors, including patterns of regional climate change and diversification of lineages, must be taken into consideration when interpreting phylogenetic patterns of local communities.

The distribution of phylogenetic lineages within communities across a region can leave signatures of lineage-specific tolerances as well as dynamic interactions with other clades over time (Eiserhardt et al., 2015). It has recently been suggested that to fully understand community assembly at the local scale we must incorporate information regarding the formation of the regional species pool and the feedback between local and regional eco-evolutionary processes (Mittelbach & Schemske, 2015). Since habitat types within a region can persist throughout geologic time, the community composition and phylogenetic patterns of specific habitats represent the interplay between local abiotic conditions and regional diversification acting over millions of years. This historical perspective can be informative regarding patterns of macroevolutionary diversification within these habitat-specific lineage pools (Gerhold et al., 2015). As highlighted by recent research, adopting a clade-focused perspective to understand lineage-specific diversification patterns and subsequent community structure can provide insight into the drivers of macroevolutionary patterns and their effects on species distributions (Cardillo et al., 2017; Donoghue & Edwards, 2014; McPeek, 2008; Nash, 2017).

Study region and taxa

The eastern North American coastal plain is a region of high plant species endemism referred to as a ‘biodiversity hotspot’ (Noss et al., 2015). Although the region has experienced major oscillations in its coastal inundations, it’s climate has remained relatively stable, which has enabled the region to serve as a refugium for the persistence and speciation of older plant lineages (Noss et al., 2015) with the majority of endemics hypothesized to have originated in situ (Sorrie & Weakley, 2001). Additionally, the region represents an anomaly in what we know about biodiversity hotspots: centers of endemism are generally found in mountainous regions that have had reduced extinction during past climate change events (Sandel et al., 2011). These coarse sandy habitats, and xeric rocky habitats, that have functioned as regional habitat ‘islands’, have generated substantial diversity and are well-known for high rates of endemism in plant species (Sorrie & Weakley, 2001; Zollner, MacRoberts, MacRoberts, & Ladd, 2005). The southeastern United States is one of the north temperate centers of diversity for the Ericaceae family, where it contributes as a dominant component of the regional flora and represents many narrowly endemic species (Weakley, 2015).

The Ericaceae is a large, cosmopolitan plant family comprised of more than 125 genera and 4500 species occupying temperate and montane tropical habitats (Kron et al., 2002). Ericoid plants can exert a profound effect on ecosystem nutrient cycling, taking up organic sources of nitrogen and having roots with high amounts of phenolic compounds that result in large changes to soil chemistry and exert an allelopathic effect on co-occurring species (Adamczyk et al., 2016; Mallik, 2003). The uptake of organic nitrogen allows plants to utilize the nitrogen pool from their own litter and is particularly common in plants producing high levels of phenolic compounds (Jones & Hartley, 1999). This high nitrogen-conserving strategy characterizes ericaceous species, and these traits allow them to persist in the harshest of conditions, potentially harboring more nitrogen in their biomass than plants found in richer conditions (Chapman et al., 2006).

Insofar as the strong allelopathic effect interferes with forest successional dynamics and resultant vegetation and habitat shifts, species in the Ericaceae can be considered ecosystem engineers, as suggested by Mallik (2003). Ecosystem engineers are those which directly transform the environment, generating changes in biotic and abiotic conditions, and thus modulating resource availability to other organisms (Angelini, Altieri, Silliman, & Bertness, 2011; Jones, Lawton, & Shachak, 1997), and ultimately impacting community structure and diversity (Badano, Jones, Cavieres, & Wright, 2006). In a recent study, Malatesta, Tardella, Piermarteri, & Catorci (2016) found that facilitative effects through the creation of microhabitat patches by interacting engineering species provide a substantial contribution to the species pool- and are ultimately driving community assembly. Other studies have likewise found dominant shrub species to be ecosystem engineers, increasing beta diversity at the community level by their modification of abiotic factors in occupied patches, ultimately changing structural properties and biogeochemical cycling (Kleinhesselink, 2014; Paz-Kagan, Zaady, Shachak, & Karnieli, 2015).

Plants in the Ericaceae host specialized mycorrhizal symbionts, known as ericoid mycorrhizae, and these specialized fungal partnerships allow Ericaceous plants to occupy harsh edaphic conditions, alleviating environmental stresses and allowing their establishment and persistence in a range of harsh environments such as heathlands and alpine tundra (Cairney & Meharg, 2003; Read, Leake, & Perez-Moreno, 2004). Across all terrestrial biomes, plants associate with symbiotic fungi that facilitate survival and growth (Peay 2016). Litter inputs from plants in the Ericaceae are often high in phenolic compounds and lipids that, upon microbial transformation, can accumulate as phenolic acids and polyphenolic compounds that can inhibit decomposition (Bending & Read, 1996a) and exclude non-Ericaceous plant taxa (Read, 1991). While ericoid fungal symbioses are often characterized by host specificity, it is now recognized that when co-occurring with ectomycorrhizal tree taxa, ericoid endophytes can also associate with these non-Ericaceous taxa (Bergero et al., 2000). Additionally, fungal communities of host Ericaceae species can vary according to region (Hamim et al., 2017). A recent study examining the Ericaceous plant-fungal associations across different habitats found that communities of ericoid mycorrhizal fungi varied geographically, with niche-specific fungal associations specialized to microhabitats within habitats, and this observed partner specificity may allow persistence in harsh abiotic environments (Toju et al., 2016). Additionally, this local-scale symbiotic partner specificity may also allow Ericaceous plants to more readily coexist within the same habitats.

The Phyllodoceae, first described by Drude (1889) are among the most morphologically diverse groups within the subfamily Ericoideae Juss (Gillespie & Kron, 2013). While characterized by their articulated pedicels and lack of abaxial calyx stomata, the monophyly of the Phyllodoceae is not well-supported by their morphology, as these characters are both present in other groups (articulated pedicels in Bryanthus), as well as absent in some members of the Phyllodoceae (abaxial calyx stomata occurring in Elliottia and some members of the *Kalmia* genus) reflecting great morphological variability (Kron et al., 2002). Hypothesized to have originated in eastern North America, the genus *Kalmia* consists of ten species mostly occurring in the eastern US, with one Caribbean and one circumboreal species (Gillespie & Kron, 2013). While the group has experienced various debated taxonomic treatments, ranging from the circumscription of seven to eleven species by different authors (Ebinger, 1974; Judd, 1983; Kron & King, 1996; Southall & Hardin, 1974; Stevens, 1971; Wood, 1961), the most recent molecular phylogeny for the group recognizes the following taxa: *K. ericoides, K. hirsuta, K. cuneata, K. angustifolia, K. latifolia, K. carolina, K. buxifolia, K. procumbens, K. microphylla,* and *K. polifolia* (Gillespie & Kron, 2013).

Ecological affinities among species in the genus are widely divergent, occupying habitats as disparate as coastal bogs, high-elevation rocky summits, and alpine tundra throughout eastern North America and the Caribbean. *Kalmia angustifolia* L., commonly known as Northern Sheepkill, is a wide-ranging species in the eastern United States and Canada- extending from Labrador west to Minnesota and reaching its southern limit in northern North Carolina and southeastern Virginia, occupying a diversity of habitats (Weakley, 2015). In the northeast, *K. angustifolia* is a common understory shrub of coniferous and hardwood forests, with common associated overstory species including red spruce (*Picea rubens*), jack pine (*Pinus banksiana*), and paper birch (*Betula papyrifera*) (Van Deelen, 1991). Additionally, *K. angustifolia* occurs in peatland and sphagnum bog communities, where it may become dominant, and generally thrives in sites characterized by dry summer and saturated spring conditions (Van Deelen, 1991). *K. angustifolia* also inhabits wetlands in the New Jersey Pine Barrens (Ehrenfeld, 1986).

Kalmia buxifolia (P.J. Bergius), or Sand Myrtle exhibits a widely disjunct distribution in the eastern United States. Populations occur in the New Jersey Pine Barrens, in the Southern Appalachian Mountains, as well as the Sandhills and Coastal Plain regions of the Carolinas, with distinct morphological differences among regions (Strand & Wyatt, 1991). In addition to the widely divergent geographic range, the physiographic regions where *K. buxifolia* occurs have distinct differences in habitat and subsequent niche differences; specializing on rock outcrops with a procumbent growth form in the southern Appalachians (Weakley, 2015), while exhibiting a taller shrub form in the understory of coastal pine forests, in addition to occupying bluff and streamside flatwoods in the Sandhills region (Sorrie, 2011).

Kalmia carolina Small, Carolina Bog Myrtle, is endemic to the southeastern US, and shares a disjunct distribution in the Carolinas similar to *K. buxifolia* (Weakley, 2015). *Kalmia carolina* inhabits moist habitats in predominantly the coastal plain, but also in wetlands at higher elevations in the mountains, it’s range from southeast Virginia to central South Carolina (Sorrie, 2011). In the coastal plain, *K. carolina* occurs in wet pine flatwoods, streamhead ecotones and Carolina bay pocosins (Sorrie, 2011). *Kalmia polifolia* Wangenh., or Bog Laurel, is restricted to bog and other wetland habitats, and is distributed throughout the northern US and Canada (Weakley, 2015). Inhabiting a variety of microform habitats within northern peatlands- including forest borders, hummocks, and sphagnum ‘lawns’- some common associated species include *Vaccinium oxycoccos, Ledum groenlandicum, Sphagnum cuspidatum* and *Trichophorum cespitosum* (Trudeau, Garneau, & Pelletier, 2013). Research on the effects of climate change on northern boreal peatlands found *K. polifolia* to decrease in response to soil temperature increase and decreased water-table elevation, in contrast to increases in other shrub species (Weltzin et al., 2003).

Kalmia latifolia L., or Mountain Laurel, is a widespread species in eastern North America, very common in the Appalachian Mountains and more restricted elsewhere; occupying a wide range of habitats- bogs, acidic forests, bluffs and sandhill streams (Weakley, 2015). *Kalmia hirsuta* Walter, known as Hairy Wicky, is geographically restricted to the southeastern United States, predominantly occurring in peninsular Florida, and occurs as a component of pine savannas and pine flatwoods (Weakley, 2015). *Kalmia procumbens* (L.) Desv, or Alpine Azalea, is distinct from the genus in possessing a circumboreal distribution and occupying arctic-alpine high mountain habitats. A recent molecular study of this species found genetic distinction between alpine and arctic regions, and that this differentiation likely occurred during the last glacial cycle (Ikeda et al., 2017).

Chapter 2

Environmental niche divergence in the *Kalmia* lineage of eastern North America

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ABSTRACT

The extent to which species retain or diverge from their evolutionary ecological heritage, as well as their potential for adaptation to new conditions, has important implications for predicting biotic responses to future climate change. Phylogenetic niche conservatism, in which species tend to resemble close relatives ecologically, is a widely observed pattern in the distribution of biota, and is a major mechanism producing current biogeographical patterns (Harvey & Pagel, 1991; Wiens & Graham, 2005). Hypothesized to have originated in eastern North America, the genus *Kalmia* consists of ten species exhibiting widely varying and disjunct distributions while occupying a large spectrum of habitats- from alpine bogs to xeric sandhill scrub (Gillespie & Kron, 2013; Weakley, 2015). Given this extent of ecological and geographic divergence, we asked the following questions: what potential processes or factors underlie the patterns of lineage bifurcation and habitat differentiation in *Kalmia*, and what has been the role of phylogenetic niche conservatism in these lineage divergences?

We constructed ecological niche models for seven of ten species of *Kalmia* using available climatic and topographic variables, and identified the variables contributing most to the observed distributions. We calculated the extent of niche overlap among all species, and subsequently used these metrics to assess the potential geographic pattern of divergence using a recent molecular phylogeny for the genus. We then subjected these results to an age-range correlation (ARC) test. We assessed the extent of niche conservatism in both morphological as well as abiotic traits that we could further use to infer processes underlying niche evolution. From our ARC analysis, we found a pattern consistent with a model of allopatric divergence followed by secondary sympatry, as overlap was greater for more distantly related species. We found phylogenetic signal only in one trait, while all other morphological and niche-related traits were unrelated to phylogeny. Given these data, we suggest that the long evolutionary history of the *Kalmia* lineage in eastern North America coinciding with climatic and/or topographic changes has resulted in considerable niche lability, subsequently allowing the seven Kalmia species to track suitable oligotrophic habitats while diverging in larger-scale climatic and topographic niche characteristics as well as less ecologically important morphological traits.

INTRODUCTION

Understanding the extrinsic factors and intrinsic traits that underlie a species' climatic tolerances could be of value when attempting to predict the evolutionary and adaptive potential of organisms under climate change (Condamine, Rolland, & Morlon, 2013). By integrating available technologies to address the mechanisms behind historical range determinants, we can more accurately infer potential future shifts in plant distributions. Furthermore, it has been suggested that elucidating the origin and persistence of biodiversity patterns necessitates understanding of factors contributing to divergence among species, and the role of geography in mediating speciation processes (Fitzpatrick, Fordyce, & Gavrilets, 2009).

A widely recognized pattern in the distribution of biota, resulting from shared ancestry, is that of phylogenetic niche conservatism (PNC; Harvey & Pagel, 1991) in which closely related species tend to retain their ancestral resemblance in traits, and thus ecological niche characteristics (Wiens & Graham, 2005). Phylogenetic niche conservatism has been considered a critical underlying component to understanding patterns of species richness, historical biogeography, invasive species spread, as well as providing a mechanism to predict biotic responses to climate change (Roberts & Hamann, 2012).

Mechanisms promoting the evolutionary retention of niche characteristics include divergence into empty ecological space by close relatives, as well as stabilizing selection being reinforced by the increased fitness and better exploitation of resources in the ancestral niche (Harvey & Pagel, 1991). In addition to promoting the retention of an ancestral niche, the failure of a populations to adapt to novel ecological conditions is also a manifestation of phylogenetic niche conservatism and can be an important and overlooked mechanism leading to the initial geographic splitting of lineages during early allopatric speciation (Wiens, 2004) as well as a major force producing current biogeographical patterns (Wiens & Graham, 2005). In a recent review, Pyron et al. (2015) investigated the relationship between niche conservatism and lineage divergence, noting that ecologically-mediated divergent selection, leading to ecological speciation, will result from a lack of niche conservatism, while niche divergence may be promoted by the retention of ancestral niche preferences (PNC) in varying ecological conditions during times of rapid environmental change. Thus, the evolutionary process of niche conservatism can result in varying patterns of distributional dynamics.

Methodological advances in the development of spatial modeling techniques has enhanced field-based habitat characterization and estimates of niche breadth (Elith & Leathwick, 2009). Niche modeling techniques, by providing the power to explore the environmental factors involved in limiting species' distributions, can help elucidate the mechanisms of niche evolution and divergence among closely related species. For example, integrating phylogenies with niche models can provide insight into the geographic mode of speciation within a lineage (e.g., Anacker & Strauss, 2014; Nakazato et al., 2010). As reviewed in Kozak et al. (2008), ecological niche modeling can help address some of the most fundamental questions in evolutionary biology regarding the mechanisms of speciation as well as the evolution of phenotypic character divergence.

One of the biggest challenges and sources of criticism to species distribution modeling is the issue of sampling bias and thus the accuracy of model interpretation. Species distribution models are predicated on the assumption that the samples of location points used reflect the full ecological range of the focal species (Raes, 2012). One of the most critical issues with constructing niche models in regard to model accuracy is that of sample size for occurrence records (Mateo et al., 2010). Recent studies that evaluated model performances for various taxa have concluded that the minimum number of records required to obtain quality models depends on range size of focal species, with optimal records from 14 for narrow-ranged species to 25 for widespread species (van Proosdij et al., 2015). The model accuracy was also dependent on regional niche variation and ecological heterogeneity, with higher occurrences required for ecologically diverse species (Mateo et al., 2010).

An important consideration in ecological niche model construction is that of collection bias, in which occurrence records are more numerous from easily accessible areas with greater collection effort and thus are spatially and ecologically bias by potentially not capturing the full ecological extent of a species' range (Hortal et al., 2007). Because MaxEnt software relies on presence-only records for its predictions, it is crucial to consider the sampling records as they accurately reflect the ecology and geography of the species' true range (Phillips et al., 2009). One method for avoiding such spatial bias is to thin occurrence records so that each grid cell is only represented by a single occurrence record, which minimizes omission errors (false negatives) and commission errors (false positives) (Boria et al., 2014; Kramer-Schadt, 2013). Additionally, because background samples in the generation of pseudo-absences are generated uniformly across the user-defined study region, model accuracy depends on how well the given background represents the full range available to the given species over relevant time periods (Barve et al., 2011).

Though criticized for various assumptions implicit in niche modelling, the use of such models when applied with careful consideration of their intended purpose, can be informative in generating hypotheses regarding the niche requirements and range determinants of species (Dormann et al., 2012;

e.g., Angert & Schemske, 2005). As reviewed in Kozak, Graham, & Wiens (2008), ecological niche modeling can help address some of the most fundamental questions in evolutionary biology regarding the mechanisms of speciation as well as helping to elucidate the mechanisms of niche evolution and divergence among closely related species. For instance, integrating phylogenies with niche models can provide insight into geographic speciation patterns within recently diverged species (Warren et al., 2014). For instance, Nakazato et al. (2010) used MaxEnt software with a molecular phylogeny to evaluate the likely geographical and ecological modes of speciation within a clade of plants, finding a more important role for environmentally-mediated divergence rather than geographical isolation alone. By modeling multiple species in a clade, evaluating the niche space occupied by each species, differences between taxa can generate hypotheses regarding biological reasons for observed divergence (Warren et al., 2008).

The southeastern United States is one of the north temperate centers of diversity for Ericaceae, where it is a dominant component of the regional flora and represents many narrowly endemic species (Weakley, 2015). Hypothesized to have originated in eastern North America, the genus *Kalmia* consists of ten species mostly occurring in the eastern US, with one Caribbean and one circumboreal species (Gillespie & Kron, 2013). Ecological affinities among species in the genus are widely divergent, occupying habitats as disparate as coastal bogs, high-elevation rocky summits, and alpine tundra throughout eastern North America. *Kalmia angustifolia* L., commonly known as Northern Sheepkill, is a wide-ranging species in the eastern United States and Canada- extending from Labrador west to Minnesota and reaching its southern limit in northern North Carolina and southeastern Virginia, occupying a diversity of habitats from sphagnum bog communities to coniferous forest (Weakley, 2015). *Kalmia buxifolia* (P.J. Bergius) Gift, Kron, & Stevens, or Sand Myrtle, exhibits a widely disjunct distribution in the eastern United States. Populations occur in the New Jersey Pine Barrens, in the Southern Appalachian Mountains, as well as the Sandhills and Coastal Plain regions of the Carolinas, with distinct differences in habitat; occupying rock outcrops, the understory of coastal pine forests, as well as xeric scrub communities (Sorrie, 2011; Weakley, 2015). *Kalmia carolina* Small, Carolina Bog

Myrtle, is endemic to the southeastern US, and shares a bimodal distribution in the Carolinas similar to *K. buxifolia* (Weakley, 2015), inhabits moist habitats in predominantly the coastal plain, but also in wetlands at higher elevations in the mountains (Sorrie, 2011). *Kalmia polifolia* Wangenh. or Bog Laurel, is restricted to bog and other wetland habitats, and is distributed throughout the northern US and Canada (Weakley, 2015) inhabiting a variety of microform habitats within northern peatlands- including forest borders, hummocks, and sphagnum 'lawns' (Trudeau et al., 2013). *Kalmia latifolia* L., or Mountain Laurel, is a widespread species in eastern North America, very common in the Appalachian Mountains and more restricted elsewhere; occupying a wide range of habitats- bogs, acidic forests, bluffs and sandhill streams (Weakley, 2015). *Kalmia hirsuta* Walter, known as Hairy Wicky, is geographically restricted to the southeastern United States, predominantly occurring in peninsular Florida, and occurs as a component of pine savannas and pine flatwoods (Weakley, 2015). *Kalmia procumbens* (L.) Desv., or Alpine Azalea, is distinct from the genus in possessing a circumboreal distribution, occupying arctic-alpine high mountain habitats.

Given this extent of ecological and geographic divergence within this lineage, we asked the following questions: what potential processes or factors underlie the patterns of lineage bifurcation and habitat differentiation in *Kalmia*, and what has been the role of phylogenetic niche conservatism in evolution of the clade? Using the most recent molecular phylogeny and fossil-calibrated divergence times, we inquired as to which geographic modes of speciation may have resulted in present distributional patterns. To characterize current niche positions, as well as infer potential climatic niche axes governing present-day distributions and divergence, we constructed ecological niche models using available climatic and topographic data. We sought to evaluate whether climatic niche divergence is phylogenetically constrained in the *Kalmia* lineage, and if specific traits correspond to climatic niche position or breadth.

MATERIALS AND METHODS

Ecological Niche Modelling

Since becoming available in 2004, MaxEnt (Phillips, Anderson, & Schapire, 2006) has become one of the most widely used and highest performing predictive methods for niche modeling (Elith et al., 2006). Using presence only data, MaxEnt is a machine-learning algorithm that estimates the probability of a species' occurrence in the gridded environment based on the predictor values (e.g., Climate data) at given occurrences, by extracting a sample of background locations that it contrasts against presence locations (Merow, Smith, & Silander, 2013). Maxent v.3.3 (Phillips et al., 2006) was used to construct niche models for seven focal species of Kalmia.

To estimate the current climatic and topographic niche characteristics of eastern North American *Kalmia* species, and to facilitate further analyses of interspecific niche comparison, we generated ecological niche models for seven species for which adequate data were available. Georeferenced occurrence records for seven *Kalmia* species were obtained from multiple publicly-available sources; the Global Biodiversity Information Facility (GBIF ehttp://www.gbif.org last accessed in February 2018), iNaturalist (http://www.inaturalist.org. Accessed February 2018), SERNEC (http//:sernecportal.org/portal/index.php), iDigbio (http://www.idigbio.org/portal. Accessed February 2018). Insufficient records were found in the focal region of eastern North America for remaining species of *Kalmia* and were thus excluded from subsequent niche analyses. To obtain only one occurrence record per grid cell, we thinned the occurrence records for each species using the thin function in package *spthin*. After thinning we use the following number of occurrences to produce the final models: *K. angustifolia*= 139, *K. buxifolia*= 41, *K. carolina*= 45, *K. hirsuta*= 80, *K. latifolia*= 484, *K. polifolia*= 462, *K. procumbens*= 49.

Since adding additional environmental predictors beyond climate for niche modeling resulted in minor effects on the accuracy of species distribution models (Bucklin et al., 2015), we focused on available climatic and topographic variables to infer niche dimensions for this study. We obtained 19 bioclimatic variables, in addition to altitude, which were downloaded from WorldClim (http://worldclim.org/version2) (Hijmans et al., 2005) at a 30-arcsec (~1-km) resolution. Because correlation in predictor variables can lead to overfitting models (Warren et al., 2013), and can be more difficult in ecological interpretation, correlated variables were excluded from the analysis using variance inflation factor analysis (‘vifcor’ function in *usdm* package in R) (Naimi, 2015), removing variables with high collinearity (>0.7). After excluding the correlated variables, we selected the following uncorrelated layers for the model: mean diurnal range (BIO2), mean temperature of wettest quarter (BIO8), precipitation seasonality (coefficient of variation) (BIO15), precipitation of warmest quarter (BIO18) and altitude.

Each model was generated using 10,000 random background points and were averaged over 15 replicates using the subsampling method, with 75% of the data used for model calibration and the remaining 25% was used for model evaluation. Models were evaluated using the area under the curve of the receiver operating characteristic (AUC), which represents the model’s ability to discriminate between suitable versus unsuitable areas for a given set of occurrences; generally, higher AUC values indicate better model performance, with models between 0.7 and 0.9 considered to be good, and values above 0.9 considered highly accurate (Araújo et al., 2005; Phillips et al., 2006;). We used the logistic output, which allows for easier biological interpretation of the estimated probability (Phillips and Dudik, 2008). Jack-knife tests, produced by MaxEnt, were used to evaluate the specific contributions of each climatic and topographic variable to the accurate estimation of each species’ abiotic niche.

Niche Overlap

We quantified the degree of niche overlap between each species pair using Schoener’s *D* (Schoener, 1968) and Warren’s *I* (Warren et al., 2008) statistics (a modification of Hellinger distance *I*), with both statistics ranging from 0 (no overlap) to 1 (identical distributions) (Warren et al., 2008). Overlap was calculated from the predictions of species distributions using the MaxEnt output probability surfaces in the R package ‘dismo’ (Hijmans et al., 2017). As a recent comparison of methods concluded that Schoener’s *D* metric is among the more robust for computing niche overlap in geographic space, we focus on the results of this metric for our study (Rödder & Engler, 2011). Additionally, to allow for easier interpretation as suggested by Rödder and Engler (2011), we classified the results as follows: 0–0.2= no or very limited overlap, 0.2–0.4=low overlap, 0.4–0.6= moderate overlap, 0.6–0.8=high overlap and 0.8–1.0=very high overlap.

Niche Breadth

To estimate the extent of niche shifts among species in the *Kalmia* clade, we calculated differences in niche breadth on MaxEnt output surfaces using ‘raster.breadth’ function in ENMTools v. 1.4 package (Warren et al., 2010). For each species’ niche model, the abiotic coverage is calculated by the average suitability score per cell using Levin’s inverse concentration metric (Levins, 1968; Warren et al., 2010).

Morphological Traits

As morphological traits can be tightly linked with a plant lineage’s potential to colonize new climatic niches (Onstein et al., 2016), we assessed the correlation of trait relationships with climatic niche evolution in *Kalmia* species. To estimate the extent of phylogenetic signal in morphological traits, we compiled trait data from the morphological study of the genus by Southall and Hardin (1974), which consisted of the following traits: petiole length, leaf length, leaf width, pedicel length, corolla tube length, style length and capsule width (Table 1). The remaining morphological data were calculated from the Flora of North America database (Flora of North America Editorial Committee, eds. 1993+): seeds winged/not winged, petal connation, number of locules and number of stamens (Table 1). Because the morphological study by Southall and Hardin (1974) did not include two additional species that are now included in the genus, we calculated the average trait values for *K. buxifolia* and *K. procumbens* from the

Flora of North America estimates. From the range of values for both data sources, we took the average value for each trait. Additionally, we extracted for each species values from all bioclimatic variables used in the niche models, averaged across all occurrence points, to include in subsequent trait analyses (Table 2). Values for each variable were extracted using the ‘extract’ function in the *Raster* package in R (Hijmans and van Etten, 2014).

Phylogenetic signal in traits

Phylogenetic signal is the “tendency for related species to resemble each other more than they resemble species drawn at random from the [phylogenetic] tree” (Blomberg & Garland, 2002) and would be a result of a Brownian motion model of evolution in which small random changes in traits are the result of genetic drift and natural selection randomly varying through time (Losos, 2008a). To assess the extent of phylogenetic pattern in traits, we estimated phylogenetic signal using Blomberg’s K statistic (Blomberg et al., 1993), in which a value of 1 represents the null Brownian motion model, while lower values (< 1) indicate a lack of statistical dependence on phylogenetic relationship; higher values (>1) representing an excess dependence on phylogeny (Revell et al., 2008). The Brownian motion model is a commonly used model representative of an evolutionary change in continuous characters as influenced by random genetic drift (O'Meara et al., 2006), so that variation in traits among taxa are directly proportional to their time since divergence (Felsenstein, 1985, 2004). Blomberg’s K was calculated using the ‘phylosignal’ function in the *Picante* package (Kembel et al., 2010), and significance values of K were compared using observed phylogenetic independent contrasts (PIC) and expected contrasts under 999 randomizations. The input phylogeny used was derived from Gillespie and Kron (2013) using combined chloroplast and nuclear data (Figure 1).

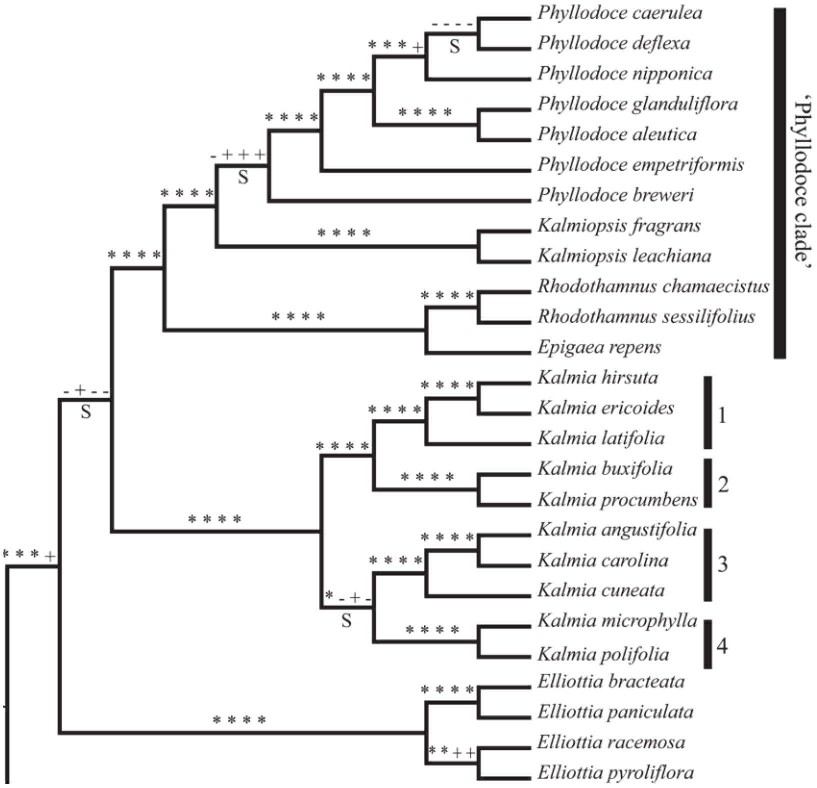

Figure 1. Molecular (nrITS, waxy,matK, ndhF, rbcL and trnS-G spacer) relationships of *Kalmia* with closely related Phyllodoceae (Gillespie & Kron 2013).

Traits associated with environmental tolerance

To assess the relationship between trait values and environmental variables and possibly to identify traits underlying the extent of abiotic tolerance, or of environmental variables influencing traits, we implemented phylogenetic generalized least squares regression (PGLS) (Garland & Ives, 2000), that uses a phylogenetic variance-covariance matrix within a standard linear model to account for the non-independent covariance between taxa, essentially estimating phylogenetic signal and regression parameters simultaneously (Freckleton et al., 2002; Orme et al., 2013). PGLS is commonly employed to assess the extent that traits are associated over evolutionary time, and because it takes into account and controls for phylogenetic signal, then in the absence of such signal results will be the same as for ordinary least squares regression (Symonds & Blomberg, 2014). Tests were performed using the 'pgls' function in the R package *caper* (Orme et al., 2013) using the maximum likelihood value of the scaling parameter λ

(Pagel, 1999) to adjust the strength of phylogenetic non-independence. A maximum likelihood value of λ equal to 1 indicates a strong phylogenetic signal, while a value of zero would indicate that trait data are independent of phylogenetic relationships. We used morphological traits as response variables to assess the influence of climatic and topographic variables, and also used niche breadth estimates as a response variable to test morphological as well as abiotic traits' influence on variations in niche width among species. We used each environmental trait as response variables for each morphological trait.

Age-range Correlation

We quantified the extent of overlap among Kalmia species in the context of their phylogenetic relationships using two analyses; age-range correlation, which performs a linear regression between the average overlap of range polygons and the topological distance of each node in the phylogeny (e.g., Fitzpatrick & Turelli, 2006), and a similar test that calculates the spatial overlap between species by using occurrence points directly in a point-proximity metric (Cardillo & Warren, 2016). Calculations were made using 50 replicates and implemented in the ENMTools v. 1.4 package (Warren et al., 2010) in R. Because age-overlap correlation tests violate assumptions of a normal linear regression, significance is tested using Monte Carlo permutations to compare with empirical slope and intercept.

Fossil calibration for divergence time estimates

Fossil calibration of the phylogeny was conducted using molecular dating with penalized likelihood as implemented in the 'chronospl' function in the *Ape* package (Paradis, Claude, & Strimmer, 2004). The function uses a semi-parametric method to estimate the node ages of the tree (Sanderson, 2002), with the branch lengths of the original tree interpreted as the average numbers of substitutions (Paradis et al., 2004). We used the only fossil available for the Kalmia genus (Mai, 2001), which is dated between 15.97 minimum to 125 maximum mya, for which we used as age constraints at the root of the phylogeny. We used lambda set to zero as the smoothing parameter, so that rates could vary as much as possible among branches.

Table 1. Morphological traits used in analyses of phylogenetic signal

Species	petiole length	leaf length	leaf width	pedicel length	corolla tube length	style length	capsule width	seeds winged	petals connate	locules	number stamens
K. latifolia	28.5	75	45	30	10.25	9	5.5	2	2	2	10
K. angustifolia	10.5	45	22.5	12.5	3.25	4.15	3.25	2	2	2	10
K. carolina	12	50	22.5	15	3.05	3.8	3	2	2	2	10
K. polifolia	2.5	55	20	25	4.05	5.75	4.75	2	2	2	10
K. hirsuta	0.75	8.5	3.5	7	3.5	6.65	3.25	1	2	2	10
K. buxifolia	1.05	9	4	8	3.5	3.5	2.75	1	1	2	10
K. procumbens	1.05	5	0.3	12.5	4	0.65	3.5	2	3	1	5

Table 2. Abiotic traits used in analyses of phylogenetic signal

Species	altitude	bio15	bio18	bio2	bio8	niche breadth B1	niche breadth B2
K. latifolia	425	12	328	119	158	0.91	0.165
K. angustifolia	208	12	300	113	137	0.909	0.157
K. Carolina	177	23	431	125	233	0.846	0.03
K. polifolia	248	20	279	104	104	0.967	0.527
K. hirsute	34	28	491	122	267	0.811	0.023
K. buxifolia	548	13	386	117	172	0.895	0.109
K. procumbens	573	26	316	95	74	0.95	0.377

RESULTS

Niche models

Using the evaluations of the area under the ROC curve (AUC), all seven of our models were estimated with high accuracy, with the lowest AUC at 0.831 and the remaining all above 0.872 (Table 3). Jackknife tests revealed that precipitation seasonality (BIO15) was the top variable contributor for *K. angustifolia* (77.9%), *K. buxifolia* (74.9%) and *K. latifolia* (88.7%). Mean temperature of wettest quarter (BIO8) was the highest contributing variable for *K. carolina* (57.4%) and *K. hirsuta* (85.1%), while mean diurnal range (BIO2) was the highest predictor for *K. polifolia* (54.3%) and *K. procumbens* (77.4%). Overall, the models visually represented the actual distributions, with some over-predicted probabilities (such as *K. buxifolia* in Canada) representing the absence of other important range determining factors that are unaccounted for in the models.

Niche overlap and niche breadth

Niche overlap was the highest between *K. latifolia* and *K. angustifolia* (*I*=0.94, *D*=0.75), followed by *K. procumbens* and *K. polifolia* (*I*=0.91, *D*=0.67; Table 5). Similarly, high overlap was found between *K. latifolia* and *K. buxifolia* (I=0.90, D=0.66; Table 5) and relatively high overlap between *K. angustifolia* and *K. buxifolia* (I=0.88, D=0.63; Table 5). Sister taxa, all generally exhibited lower values of niche overlap; *K. buxifolia* and *K. procumbens*: I=0.62, D=0.31; *K. angustifolia* and *K. carolina*: I=0.49, D=0.25; *K. latifolia* and *K. hirsuta*: I=0.20, D=0.06). In addition to *K. hirsuta* and *K. angustifolia* (I=0.18, D=0.06), *K. latifolia* and *K. hirsuta* had the lowest niche overlap (Table 5).

According to both metrics, *Kalmia polifolia* exhibits the widest niche breadth (B1=0.96, B2=0.52; Table 4), followed by *K. procumbens* (B1=0.95, B2=0.37; Table 4). *Kalmia latifolia* and *K. angustifolia* have the next widest breadth, followed by *K. buxifolia*. The species possessing the smallest niche breadth is *K. hirsuta*, with *K. carolina* slightly higher. This pattern suggests that increased niche breadth is related to increased topographic variability and elevation, with the highest breadth occurring in alpine species and the lowest breadth in Coastal Plain-restricted species.

Table 3. Maxent models AUC and variable contribution

Species	AUC	Variable	Percent contribution
K. angustifolia	0.947	bio15	77.9
K. buxifolia	0.960	bio15	74.9
K. carolina	0.977	bio8	57.4
K. hirsuta	0.979	bio8	85.1
K. latifolia	0.938	bio15	88.7
K. polifolia	0.831	bio2	54.3
K. procumbens	0.872	bio2	77.4

Table 4. Niche breadth calculated from Maxent models (Levins inverse concentration metric)

species	B1	B2
K. latifolia	0.910272	0.1653
K. angustifolia	0.9095884	0.157
K. carolina	0.8465332	0.0339
K. polifolia	0.9675219	0.5272
K. hirsuta	0.8115494	0.023
K. buxifolia	0.894728	0.1094
K. procumbens	0.950940	0.3776

Table 5. Niche Overlap as derived from ecological niche models

metric: I

	angustifolia	*buxifolia*	*carolina*	*latifolia*	*polifolia*	*procumbens*
buxifolia	0.888					
carolina	0.495	0.661				
latifolia	0.941	0.905	0.538			
polifolia	0.774	0.7	0.519	0.716		
procumbens	0.673	0.629	0.434	0.596	0.913	
hirsuta	0.189	0.284	0.362	0.204	0.367	0.287

metric: D

	angustifolia	*buxifolia*	*carolina*	*latifolia*	*polifolia*	*procumbens*
buxifolia	0.637					
carolina	0.254	0.365				
latifolia	0.751	0.662	0.28			
polifolia	0.486	0.381	0.26	0.426		
procumbens	0.378	0.317	0.191	0.314	0.67	
hirsuta	0.061	0.105	0.144	0.062	0.102	0.083

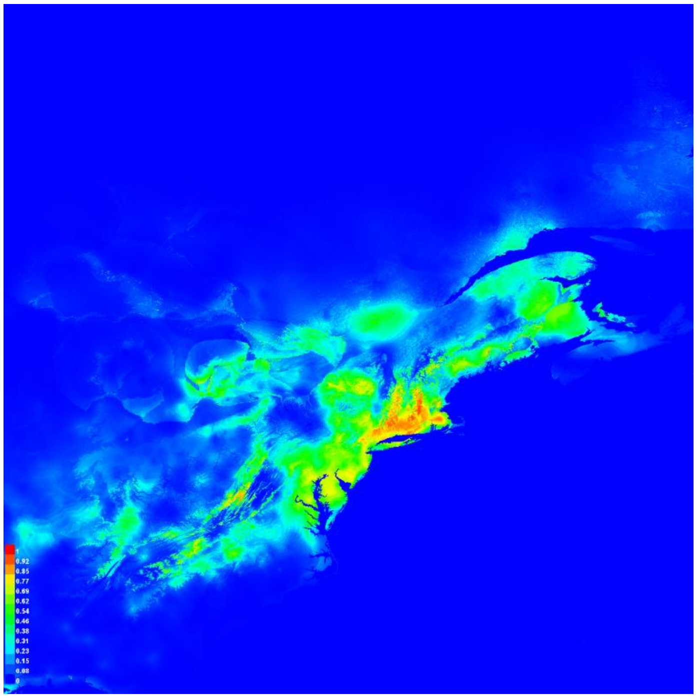

Figure 2. MaxEnt model for *Kalmia angustifolia*

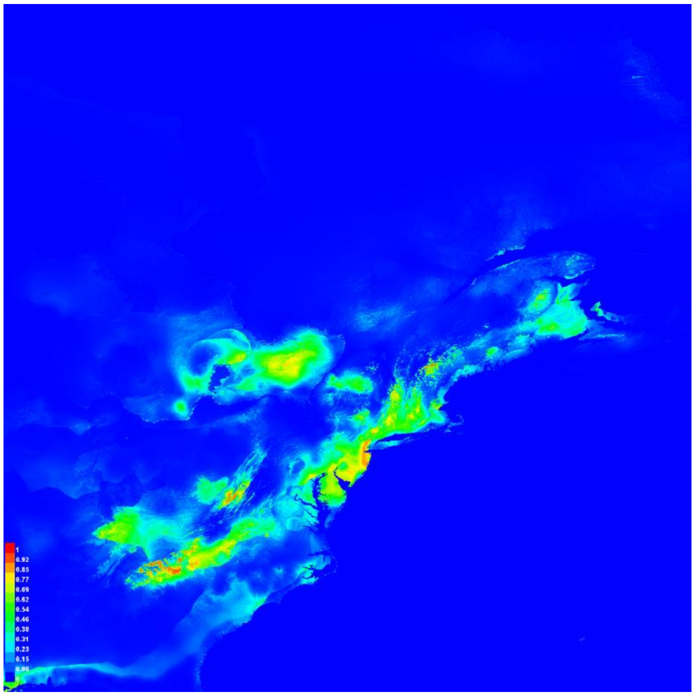

Figure 3. Maxent model for *Kalmia buxifolia*

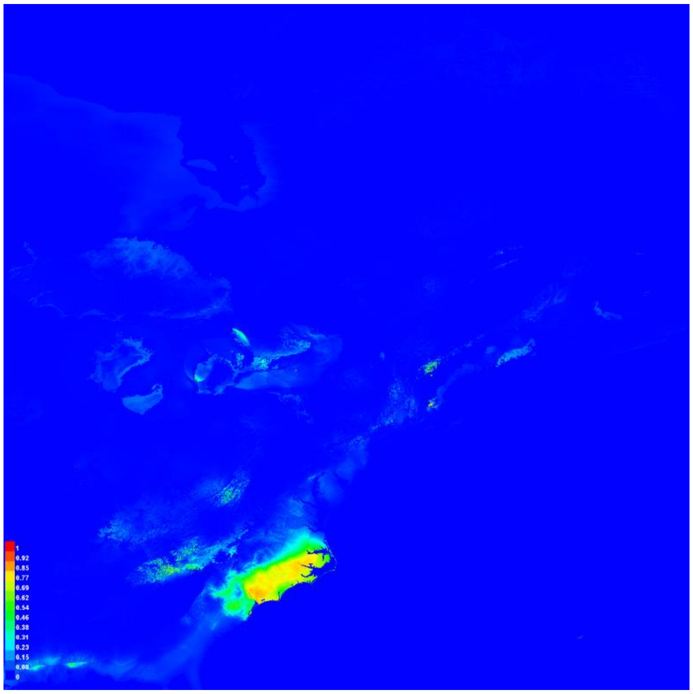

Figure 4. MaxEnt model for *Kalmia carolina*

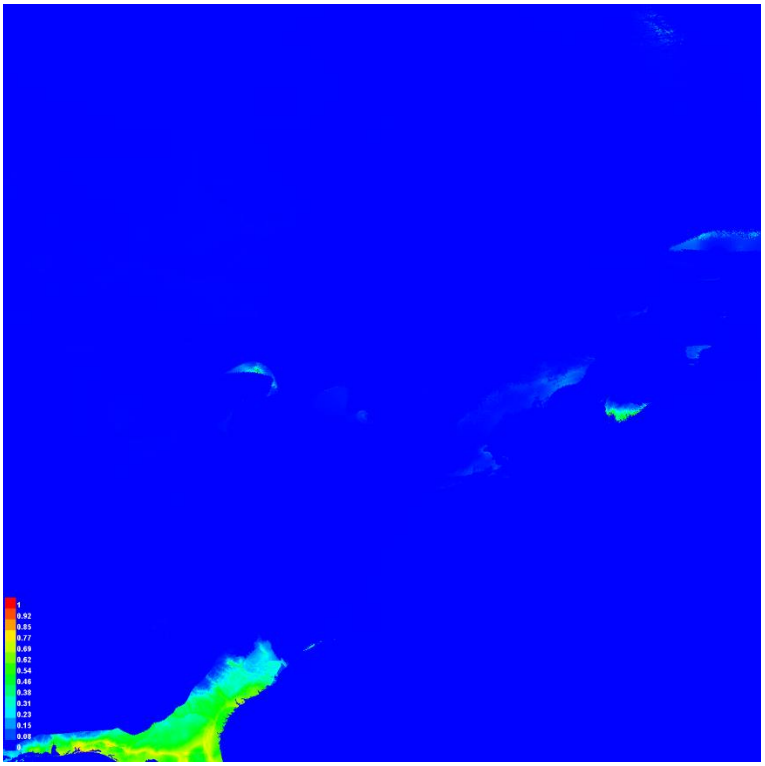

Figure 5. MaxEnt model for *Kalmia hirsuta*

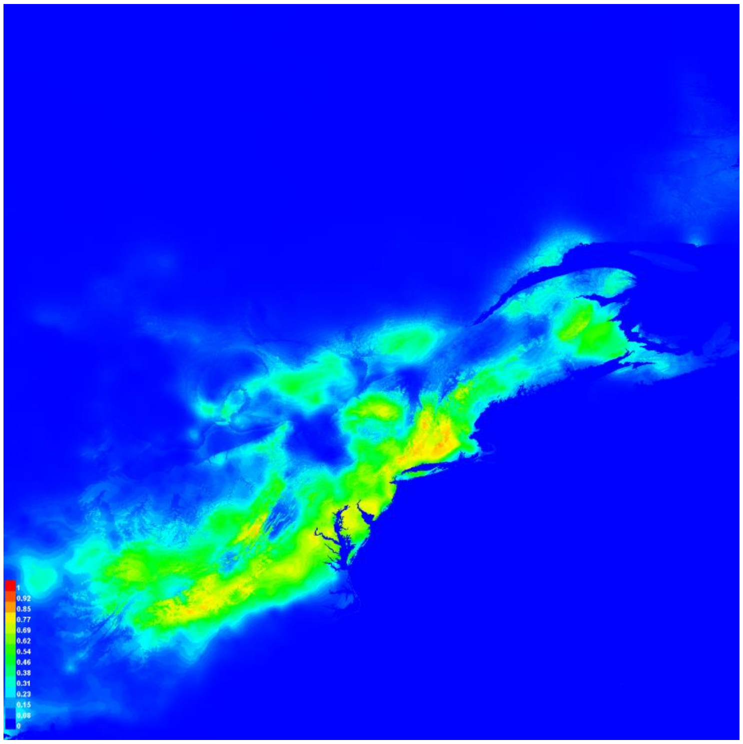

Figure 6. MaxEnt model for *Kalmia latifolia*

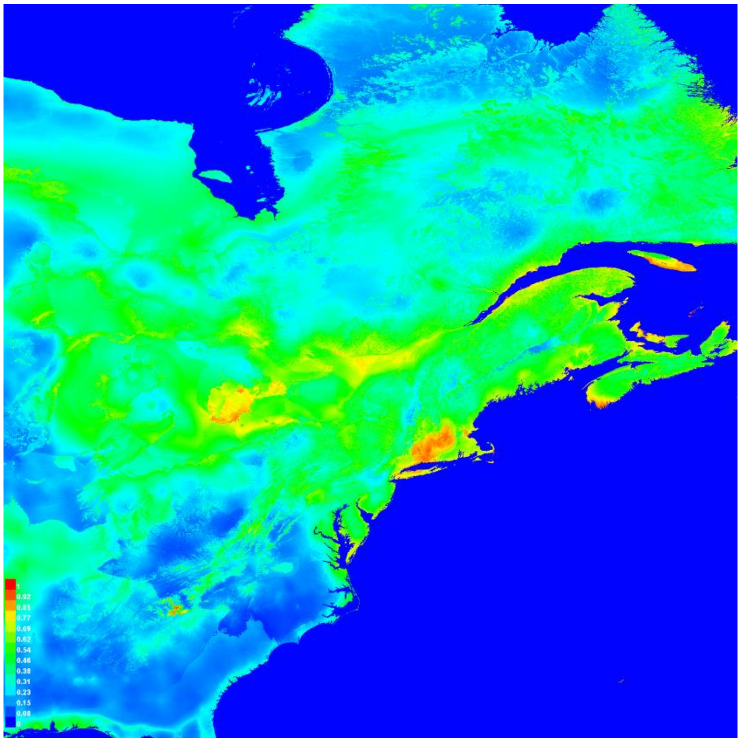

Figure 7. MaxEnt model for *Kalmia polifolia*

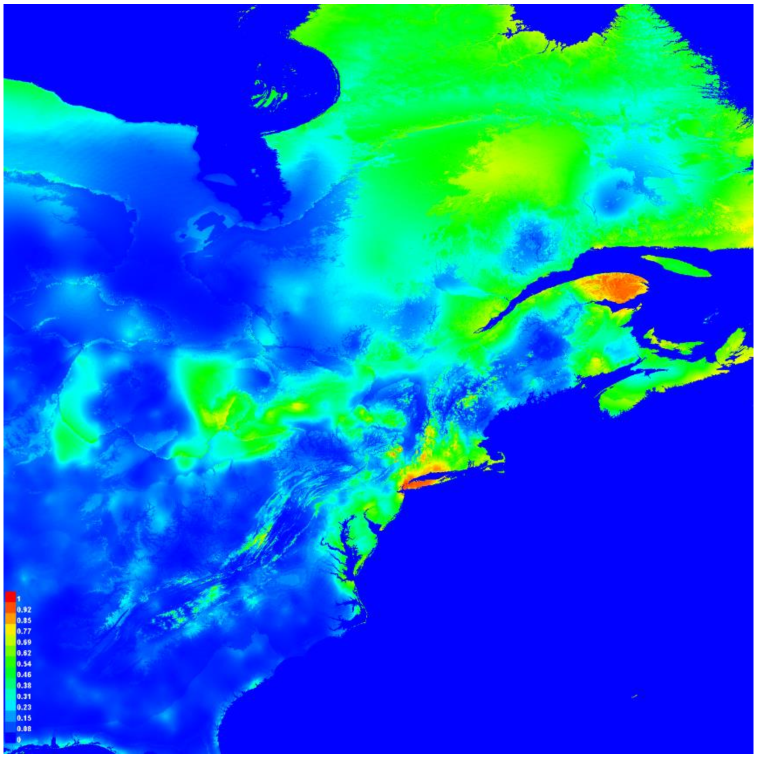

Figure 8. MaxEnt model for *Kalmia procumbens*.

Phylogeny

Based on the calibration using *K. saxonica* (Mai, 2001) fossil and the phylogenetic hypothesis of Gillespie and Kron (2013), the *Kalmia* lineage, as represented by extant species, are estimated to have diversified from 35 Myr to 17 Myr (Table 8). The oldest extant species in the lineage is *K. latifolia* (35.24 Myr), with *K. cuneata* close in age (35.17 Myr). The sister species pairs of *K. microphylla/K. polifolia* and *K. procumbens/K. buxifolia* were estimated to have similar divergence times: 26.44 Myr and 26.35 Myr, respectively. Similar divergence times were also found for the most recent sister species pairs: *K. angustifolia/K. carolina* at 17.63 Myr, and *K. hirsuta/K. ericoides* at 17.61 Myr (Table 8).

Age-overlap correlation

Our age-range correlation showed a low intercept and positive slope, with overlap increasing with relatedness (Figure 9). This pattern was shown using both the points ($p= 0.196$) method and range ($p= 0.431$) method. The positive slope shown is consistent with an allopatric mode of speciation, with more distantly related species exhibiting greater overlap through secondary sympatry.

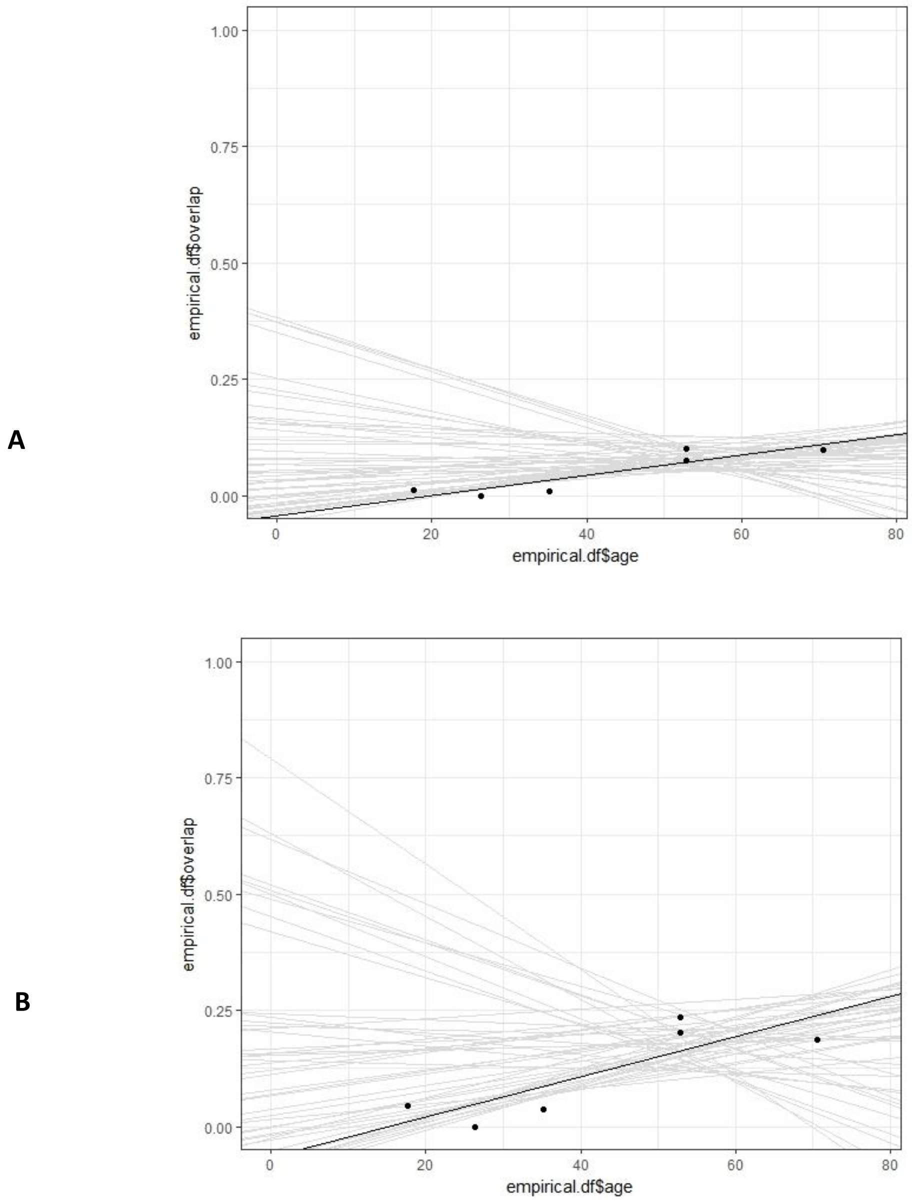

Figure 9. Age-overlap correlation using coordinate points (A) and range polygons (B).

Phylogenetic signal

We found only one trait to be significantly predicted by phylogeny, which was style length (*K*=1.18, p=0.04; Table 6), while one other trait-calyx lobe width- had a slight phylogenetic relationship (*K*=1.06, p=0.08). All vegetative morphological characters had lower *K* values than floral characters (Table 6), which suggests an ecological dependence.

Table 6. Phylogenetic signal calculations using Blomberg's *K* for morphological and niche-related traits.

Trait	*K*	*p*- value
petiole length	0.5252	0.6450
leaf length	0.6101	0.3965
leaf width	0.5462	0.5885
pedicel length	0.5180	0.5555
corolla tube length	0.5588	0.5440
style length	1.0803	0.0235
capsule width	0.6352	0.4055
seeds winged	0.6179	0.4380
petals connate	0.6494	0.4125
locules	0.8435	0.3040
num. stamens	0.8435	0.2810
altitude avg	0.7755	0.2730
bio15 avg	0.3421	0.8050
bio18 avg	0.3812	0.7725
bio2 avg	0.6686	0.3925
bio8 avg	0.4852	0.6715
niche breadth B1	0.5467	0.5395
niche breadth B2	0.8711	0.2160

Trait-environment relationships

Niche breadth, using the B2 metric, was predicted by style length (p=0.020, lambda=1) and capsule width (p=0.004, lambda=1), while vegetative traits showed no relationship with either metric of niche breadth (Table 7). Both capsule width and style length showed significant relationships with bio8 (p=0.039 style length, p=0.037 capsule width), bio2 (p=0.026 style length, p=0.040 capsule width), with marginal significance with bio18 (capsule width p=0.054) and altitude (style length p=0.068). These two morphological traits were consistently the only significant correlations with environmental variables or niche breadth metrics (Table 7). We found that niche breadth in the *Kalmia* lineage generally increases with species that occupy progressively higher elevations and more varied topography. Niche breadth was related to capsule width, with generally wider capsules in more widely ranging species. Style length, however, because of its closer relationship to phylogeny, correlated less with niche breadth.

Table 7. Results of phylogenetic generalized least squares regression using maximum likelihood transformation. B2 is niche breadth using Levin's inverse concentration metric.

Variables	Lambda	Delta	*p*-value
Altitude versus style length	0.00	1.00	0.068
BIO 18 versus capsule width	1.00	1.00	0.054
BIO 2 versus style length	1.00	1.00	0.026
BIO 2 versus capsule width	1.00	1.00	0.040
BIO 8 versus style length	1.00	1.00	0.039
BIO 8 versus capsule width	1.00	1.00	0.037
B2 versus style length	1.00	1.00	0.020
B2 versus capsule width	1.00	1.00	0.004
BIO 18 versus style length	1.00	0.02	0.017
BIO 18 versus capsule width	1.00	0.02	0.009
BIO 18 versus B2	1.00	0.02	0.020
Leaf length versus altitude	1.00	1.00	0.003
Leaf length versus BIO 15	1.00	1.00	0.014
Leaf length versus BIO 18	1.00	1.00	0.015
Leaf length versus BIO 2	1.00	1.00	0.005
B2 versus petiole length	1.00	1.00	0.042
Altitude versus pedicel length	1.00	1.00	0.009

Table 8. Fossil-calibrated age estimates using penalized likelihood

Species	Branch Length
Kalmia angustifolia	17.6341123
Kalmia carolina	17.6341123
Kalmia cuneata	35.17218614
Kalmia microphylla	26.44185536
Kalmia polifolia	26.44185536
Kalmia ericoides	17.61109844
Kalmia hirsuta	17.61109844
Kalmia latifolia	35.24081933
Kalmia procumbens	26.35109005
Kalmia buxifolia	26.35109005

DISCUSSION

Biologists studying speciation, as early as Mayr (1942), have noted the critical role of ecology in driving divergence among populations. However, elucidating the geographic mode of speciation remains a challenging task, as inherent difficulties exist in determining whether reproductive isolation was achieved in sympatry, allopatry, parapatry, or some combination- especially given the limited timeframe of observations of divergence relative to that required for speciation to occur (Bird et al., 2012). Particularly in taxa with older taxonomic splits, discerning mechanisms leading to ecological and geographic divergence can be difficult. However, comparing the nature of divergence and reproductive barriers among multiple close relatives can offer robust inferences (Hendry, 2017). The results of our age-overlap analyses, using two different methods, both exhibited the same relationship; overlap between taxa increases with age of divergence. According to recent interpretations, the low intercept and positive slope exhibited by our results correspond to a pattern of allopatric speciation followed by post-speciation range shifts that have resulted in secondary sympatry among distant relatives (Warren et al., 2014).

Our results show that all vegetative and most floral traits measured do not exhibit a phylogenetically-dependent relationship, which means that they have not evolved according to a random gradual pattern of change. As shown by Revell et al. (2008), when lineages exhibit an increase in the rate of niche shifts over time, the covariance among tips of the tree is reduced relative to null expectation, and phylogenetic signal is decreased. Alternatively, niche shifts early in the evolutionary history of a lineage, as in adaptive radiations (Schluter, 2000), will result in enhanced phylogenetic dependence and thus higher phylogenetic signal (Revell et al., 2008). It is important to note than any topological error in the phylogeny, in addition to error in the estimation of species' means, could result in reduced phylogenetic signal (Blomberg et al., 2003; Ives et al., 2007). Our results show little to no phylogenetic signal in nearly all traits, which, according to previous research interpretations, supports a pattern of more recent increase in niche shifts rather than an adaptive radiation (Revell et al., 2008).

By fragmenting formerly continuous ranges of single species, environmental changes resulting in divergent selective pressure that acted upon disjunct populations may have led to the evolution of new species (Mayr, 1942, 1963; Simpson, 1953; Stebbins, 1950). Large-scale environmental changes that result in the disruption of continuity and cohesiveness in a species' range can promote speciation in many global regions, including the effects of glacial cycles of the Pleistocene (Hewitt, 2000) as well as periods of rapid aridification (Linder, 2003; Richardson et al., 2001b). The vegetation of the southeast during the Eocene (55-37 Ma) consisted of warm-temperate upland forests with the development of pine forest on edaphically dry coastal sands (Graham, 2011). Also present during the middle Eocene was a near-modern version of bog community as well as a broad southeastern semideciduous dry tropical forest (Baskin & Baskin, 2016; Graham, 2011). According to our fossil-calibration estimates, *Kalmia latifolia* and *Kalmia cuneata* would have diverged from a common ancestor around 35 Ma, which would have coincided with the development of southeastern coastal pine forest and bog habitats. Following a sharp decline in global temperatures at the end of the Eocene, it is hypothesized that this global cooling event created barriers to gene flow and extinctions in eastern North America, resulting in divergence times of less than 30 Ma for most woody angiosperm taxa in the region (Manos & Meireles, 2015; Zachos et al., 2001). Additionally, this cooling and drying period corresponds to the mid-continental drying that could have fragmented the ranges of *Kalmia* occurring in the western US (*Kalmia polifolia*). This cooling period coincides with our estimated divergence times at about 26 Ma for all alpine and boreal distributed species in the *Kalmia* lineage. This alpine radiation likely included *K. buxifolia* shifting into alpine habitats, as the erosion of the Appalachians hadn't proceeded to modern elevations until the end of the Pliocene- about 3.6 Ma (Graham, 2011).

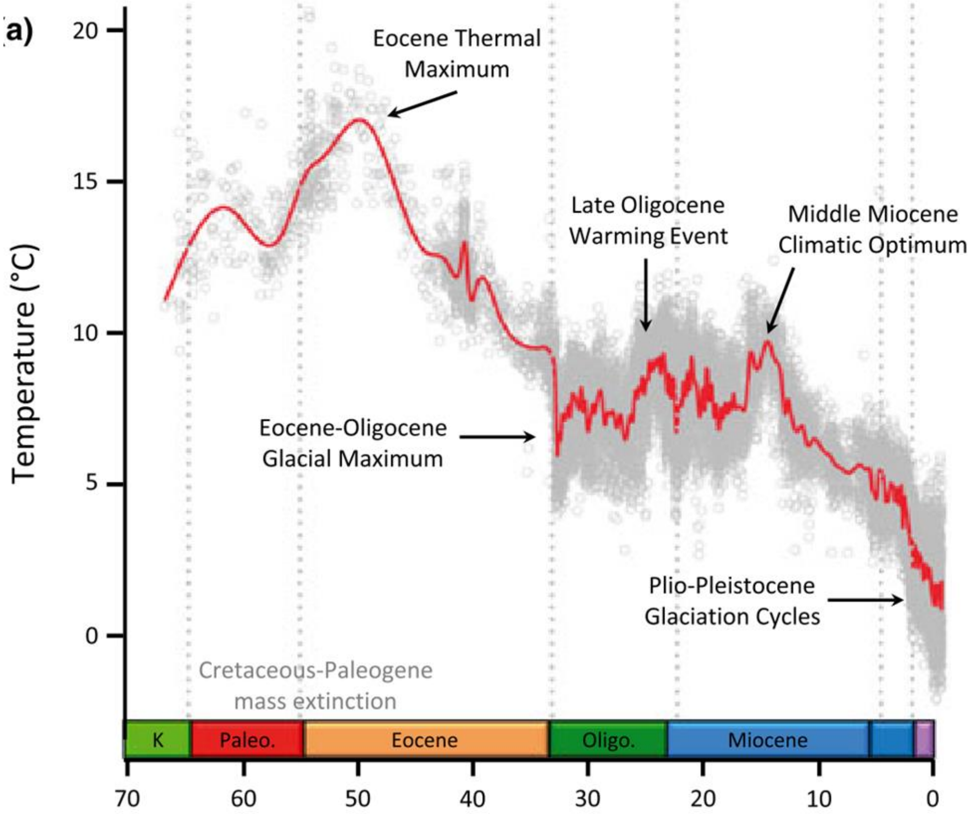

Figure 10. Major trends in global climate change during the Cenozoic (65 Ma to present) (Condamine et al., 2013).

During the middle Miocene the climate began a rapid shift; a temperature increase named the Middle Miocene Climatic Optimum (MMCO; Riishuus et al., 2006) occurred between 17 and 15 Ma, which coincided with the development and expansion of drier and more seasonally-adapted plant lineages (Graham, 2011). According to our divergence time estimates, this period would have supported the speciation events giving rise to sister taxa *K. carolina* and *K. angustifolia* (17.63 Ma) in the Coastal Plain of the Carolinas, and similarly a speciation event leading to the formation of sister species *K. hirsuta* and *K. ericoides* (17.61 Ma) further south into Florida and the Antilles.

The phylogenetic hypothesis of Gillespie and Kron (2013) using combined nuclear and chloroplast data positions two main clades being derived from a common ancestor; one clade containing the *K. buxifolia* and *K. latifolia* sub-clades, while the other main clade containing the *K. angustifolia* and *K. polifolia* sub-clades. Within both of these two clades, there would have been a divergence of one sub-clade inhabiting alpine habitats with the other sub-clade inhabiting primarily the Coastal Plain. Since within both of these two main clades there is one sub-clade containing viscin threads and one lacking, this relationship would reflect a parallel derived feature in both younger sub-clades (*K. latifolia* clade and *K. angustifolia* clade). This relationship would also reflect the parallel divergence of generally smaller morphological features associated with alpine and mountainous species into generally larger features in more ancestral coastal plain species (*K. latifolia* and *K. cuneata*), followed by a secondary reduction in more derived species occupying the coastal plain. One of the most supportive trends of this combined molecular hypothesis is that of the two main clades occupying distinctly divergent hydrologic niches; the *K. latifolia* + *K. buxifolia* sub-clades occupying generally drier and more exposed sites, while the *K. polifolia* + *K. angustifolia* sub-clades occupy generally more wet habitats. As noted by Kron et al. (2002), certain vegetative features exhibit extensive homoplasy within the Ericaceae, such as leaf persistence and curvature, and are clearly under strong selective forces. Furthermore, *K. latifolia* and *K. polifolia* possess the largest character states for most floral features, which negates any size relationship to any of the phylogenetic hypotheses, as these taxa are consistently distantly related. The presence of viscin threads in more distantly related *Kalmia* that inhabit similar habitats underlies the importance of pollinator specificity in the Coastal Plain- supporting the ecological dependence of nearly all morphological traits in the genus.

Within the *Kalmia* lineage, we find considerable niche lability in both climatic niche axes as well as most morphological niche axes. Our finding that only one morphological trait is phylogenetically determined suggests the importance of ecologically-adaptive morphology to the successful radiation of the lineage. Because the one trait exhibiting a phylogenetic relationship is a floral character related to pollination, we suggest that the presence of specific mutualists is more important in enabling habitat divergence than are other ecological factors. Indeed, style length differences between closely related taxa can promote sympatric coexistence by facilitating pollinator divergence, and thus reducing interspecific pollen transfer and competition for pollinators (Miyake & Inoue, 2003). Furthermore, this phenomenon of disparate style lengths among co-occurring congeners has been exhibited in closely related species of *Rhododendron*, which are somewhat closely allied to the *Kalmia* lineage (Williams & Rouse, 1988).

In assessing the relationship between climatic niche and morphological characters, we found that style length and capsule width were both significantly predicted by most climatic variables. Since style length exhibits phylogenetic signal in the lineage, this relationship could indicate the important role of climate adaptation that has enabled biome divergence. Leaf length was also related to most climatic niche variables, which corresponds to the vegetative plasticity that has been previously noted in the genus (Southall & Hardin, 1974). Studying the montane radiations in Ericaceae, Schwery et al. (2014) found that increased speciation in mountainous habitats was facilitated by changes in specific leaf area, and suggested that increased disturbance from steeper slopes may generate locally ‘new’ fragmented habitats that enable allopatric speciation. These relationships of consistent morphological traits corresponding with climatic variables further suggests the adaptive nature of morphology in enabling climatic niche divergence, finding new ways to exploit novel habitats. However, it is difficult to determine whether preadaptation of traits enabled the range expansion and diversification in the group, or if traits evolved in response to new habitat occupation.

In our current research modelling the Grinnelian niches of Kalmia species, some of the predicted distributions either over-predicted species' ranges- such as for *K. buxifolia* in Canada- or under-predicted their actual distributions- such as for *K. angustifolia*. These discrepancies are attributable to the limitations of the data used- in this case climate and topography at a 1 km resolution- which fail to account for other abiotic and biotic factors at finer scales which further limit the realized distributions. Plants in the Ericaceae are known to host specialized mycorrhizal symbionts, known as ericoid mycorrhizae, and these specialized fungal partnerships allow Ericaceous plants to occupy harsh edaphic conditions, alleviating environmental stresses and allowing their establishment and persistence in a range of harsh environments such as heathlands and alpine tundra (Cairney and Meharg, 2003; Read et al., 2004). A recent study examining the Ericaceous plant-fungal associations across different habitats found that communities of ericoid mycorrhizal fungi varied geographically, with niche-specific fungal associations specialized to microhabitats within habitats (Toju, Tanabe, & Ishii, 2016). Due to the dependence of ericaceous species on this mutualism, it is likely that this partnership specificity is a prominent factor governing the range distribution of these taxa. However, it was not within the capabilities of this study to sample and sequence fungal associations, and availability of specific mycorrhizal distributions are limited. Ericoid mycorrhizae are also found to vary extensively among microhabitats (Toju et al., 2016), and therefore would not be well implemented into coarser geographic modelling without local-scale sampling.

Additionally, since this research incorporates divergence times for inferring biogeographical relationships, it is important to recognize that the estimation of divergence times can be distorted by the selection of calibrations (Smith & Peterson, 2002). We used the only fossil available representing the lineage without further calibrations due to data limitation, which could introduce error in our estimates. If our divergence time estimates are largely inaccurate, then the widespread climatic change that we found to correspond with speciation times could have not played a role in niche evolution at all.

Our measurements of morphological traits' extent of niche conservatism showed considerable non-phylogenetic variation leading us to assume extensive phenotypic variability more governed by habitat than evolutionary history. However, the measured traits used were derived from more than one source, Southall & Hardin 1974 as well as the Flora of North America. Furthermore, while our data incorporated many traits, there is the possibility of unmeasured traits exhibiting phylogenetic niche conservatism and therefore being more biologically important.

A major biological challenge presented to the inference of modes of speciation is that of post-speciational range shifts obscuring geographic patterns of speciation. If *Kalmia* species were once more continuously distributed, the fragmentation of ranges through millions of years of climate and landscape change could bear no signature at all of speciation mechanisms. Furthermore, a major biological ambiguity remains regarding the culprit of speciation- whether divergence into different niche dimensions occurred as a result of ecological adaptation with adjacent populations, resulting in reduced gene flow, or whether geographical separation led to ecological divergence. The extent and causes of reproductive isolation among *Kalmia* are well-documented and include temporal (*K. cuneata* and *K. carolina*; *K. polifolia* and *K. angustifolia*), spatial (*K. angustifolia* and *K. carolina*), and ecological (*K. latifolia* and *K. angustifolia* or *K. carolina*) separation (Southall & Hardin, 1974). However, we cannot know if species occupying adjacent or sympatric distributions diverged in traits/phenology as a result of intraspecific competition, or if the divergence occurred prior to their proximity.

Our results support other recent research in finding niche conservatism to be more prevalent in the alpha- or local-scale niche axes, while the beta- or coarser-scale niche axes show extensive lability (Ackerly et al., 2006; Emery et al., 2012). This pattern could be the case for lineages that rely on habitat-specific mutualists, such as pollinators and mycorrhizal symbionts, in which case fitness in a new habitat is more tightly dependent on mutualists. Likewise, the increased importance of local-scale niche conservatism may be pronounced generally for plants that occupy abiotically stressful patchily-distributed habitats, such as was shown with the *Lasthenia* lineage occupying vernal pools (Emery et al., 2012), and this conservatism in microhabitat niche may ultimately have led to allopatric divergence as once-widespread habitats became fragmented into ecological islands during periods of widespread climatic oscillations (Emery et al., 2012).

Chapter 3

Community composition and phylogenetic structure among habitats of co-occurring *Kalmia* species: a macroevolutionary perspective of lineage diversification

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ABSTRACT

The distribution of phylogenetic lineages within communities across a region can leave signatures of lineage-specific tolerances as well as dynamic interactions with other clades over time (Eiserhardt et al., 2015). To fully understand community assembly at the local scale we must incorporate information regarding the formation of the regional species pool and the feedback between local and regional eco-evolutionary processes (Mittelbach & Schemske, 2015). In this study we focused on a single clade that has diversified and inhabited the southeastern United States since the early Miocene (Gillespie & Kron, 2013; Mai, 2001). The study investigates the habitat use among three of these closely related taxa that exhibit overlapping ranges. We also assessed the phylogenetic patterns of local communities along an elevation gradient to identify the abiotic drivers of species and phylogenetic turnover, and to assess the degree of differences in habitat affinity. Dividing community plots into three regions, we asked if there were differences in abiotic and biotic attributes among coastal plain, piedmont and mountain habitats. By conducting this analysis, we intend to shed light on local scale community assembly and the interplay of local and regional ecological and evolutionary processes.

Community data were gathered from both field collection and an open-source vegetation database. Ten plots containing the focal species *Kalmia buxifolia* were sampled using the Carolina Vegetation Survey protocol, with the remaining fifty plots containing two other focal *Kalmia* species- *K. latifolia* and *K. carolina*- downloaded from the VegBank database. Along with community composition data, soil variables of pH, organic matter, CEC, and base saturation were included in analyses.

While differences in soil characteristics among regions were minimal with only soil pH exhibiting differences, species composition and turnover among plots were governed by edaphic factors and elevation. Likewise, soil pH was the most significant factor explaining phylogenetic dissimilarity among plots across the three regions. Our results of low phylogenetic beta diversity combined with higher taxonomic beta diversity supports the prevalence of allopatric speciation patterns from closely related lineages establishing in similar habitats. Our results highlight the potential importance of abiotic factors limiting Ericaceous species' co-distribution and the importance of considering habitat-specific lineage pools when interpreting patterns of regional diversity.

INTRODUCTION

The ongoing synthesis of the formerly disparate fields of ecology and evolution is resulting in a proliferation of insights, highlighting the interdependence and feedback between ecological and evolutionary processes. In a conceptual synthesis of community ecology, Vellend (2010) identified the four general processes underlying the patterns in composition and diversity of species: selection, drift, speciation and dispersal. The processes of speciation and dispersal add new species to communities, while drift and selection operate to structure the abundance of species (Vellend, 2010). While many studies have focused on the influence of selection and dispersal, relatively few studies have assessed the influence of speciation on producing patterns of community and regional diversity.

It is now well-established that local assemblages of species in a community are a cumulative product of habitat-scale ecological interactions, historical events, as well as neutral processes (Vellend, 2010). However, we still lack an understanding of the relative importance that each of these factors has on the community assembly process. It is recognized that competitive interactions are important determinants of community structure at a local scale (Chesson, 2000), while larger-scale environmental factors and evolutionary diversification structure the regional species pool from which local communities are assembled (Emerson & Gillespie, 2008). Though there remains much debate regarding the prevalence of certain patterns of community assembly, both biotic interactions as well as abiotic factors operating at various spatial scales are important (HillRisLambers et al., 2012).

Darwin (1859) noted the tendency for closely related species to more intensely compete and limit each other's abundance, and this concept has been subsequently developed as the "competition-relatedness hypothesis" (Cahill et al., 2008). This hypothesis builds from the theory of limiting similarity where niche differences promote coexistence by limiting competition (MacArthur & Levins, 1967). This focus on species similarity in determining community assembly patterns has been a central theme in attempts to elucidate mechanisms underlying community assembly. This theme has been the impetus for research examining community phylogenetic patterns, in which contrasting patterns of relatedness have been used to infer different assembly mechanisms in local communities (Webb et al., 2002). Phylogenetic clustering, when co-occurring species are more closely related than is expected by chance, is attributed to the presence of an environmental filter limiting species persistence. Alternatively, phylogenetic over-dispersion occurs when co-occurring species are more distantly related than would be by chance. The later scenario has been attributed to competitive exclusion being the dominant assembly mechanism (Webb, 2000; Webb et al., 2002). Because these two processes are expected to have contrasting effects on patterns of relatedness, they can be helpful in revealing the dominant mechanism involved in structuring communities (Cavender-Bares et al., 2009). Analyzing the phylogenetic structure of plant communities of insular habitats across California, Anacker (2011) found that communities' evolutionary relatedness reflected changes in an abiotic gradient in which arid communities were phylogenetically clustered, while cooler and wetter sites exhibited patterns of over-dispersion. In addition, contrasting soil types supported different patterns of relatedness among species filtered from the regional pool (Anacker, 2011). Therefore, abiotic factors as well as species' interactions both play a prominent role in determining community phylogenetic structure.

Recent studies suggest that historical and macro-ecological dynamics may play a larger role than previously considered in generating patterns found in local communities (Weeks et al., 2016; Wittmann &

Fukami, 2018). As suggested by Warren et al. (2014), the legacy of speciation mode can leave an imprint on community phylogenetic patterns, while ecological sorting at local scales can exhibit effects on species' distributions. There is increasing evidence that evolutionary processes can influence community dynamics through geographic patterns of speciation, mutualist interactions, and other processes governing community phylogenetic patterns (Weber et al., 2017; Weeks et al., 2016). In turn, interactions among taxa in communities can influence both micro- and macroevolutionary processes and patterns through both indirect and direct interactions (Johnson & Stinchcombe, 2007). Furthermore, ecology has a strong influence on patterns of speciation, extinction and trait evolution at the macro-ecological scale via mediation of trait-based interactions and diversification (Weber et al., 2017).

In regional assemblages of meta-communities, it is important to consider the effect of evolutionary dynamics such as local adaptive radiations when inferring the assembly mechanisms generating community structure. The assemblage patterns observed are likely explained by the temporal dynamics of local radiations (Pontarp, Ripa, & Lundberg, 2012). The theory of historical contingency suggests that the history of immigration, including the timing and order of arrival of new taxa, could play a large role in subsequent community development (Chase, 2003; Fukami, 2010). Earlier-arriving species may reduce available resources to subsequent colonists and thus exclude them (Silvertown, 2005) or they may facilitate colonization of new taxa resulting in greater community species diversity (Fukami, 2015). By focusing on a single clade's distribution and diversification patterns and investigating local community structure through the lens of an historical perspective, we can begin to understand the macroevolutionary dynamics contributing to biotic patterns over longer timescales (McPeek, 2008; Weber et al. 2017; Weeks et al., 2016).

The North American coastal plain is a region of high plant species endemism referred to as a 'biodiversity hotspot' (Noss et al., 2015). Although the region has experienced major oscillations in its coastal inundations, it's climate has remained relatively stable, enabling the region to serve as a refugium for the persistence and speciation of older plant lineages (Noss et al., 2015), with the majority of endemics hypothesized to have originated in situ (Sorrie & Weakley, 2001). Additionally, the region represents an anomaly in what we know about biodiversity hotspots: centers of endemism are generally found in mountainous regions that have had reduced extinction during past climate change events (Sandel et al., 2011). Coarse sandy habitats and xeric rocky habitats are scattered throughout the coastal plain, and these function as regional habitat 'islands'. There is evidence that this 'islands' have generated substantial diversity and are well-known for high rates of endemism in plant species (Sorrie & Weakley, 2001; Zollner et al., 2005). The adjacent southern Appalachian Mountains are a well-known center of biodiversity, owing to the substantial topographic heterogeneity and resultant climatic buffering that has allowed the region to act as refugium during periods of climatic oscillations, notably during cycles of glaciation (Wiser, 1994).

The southeastern United States is one of the north temperate centers of diversity for Ericaceae, where it contributes as a dominant component of the regional flora and represents many narrowly endemic species (Weakley, 2015). Hypothesized to have originated in the southeastern United States, the *Kalmia* lineage exhibits a wide range of geographic and ecological affinities throughout eastern North America. The members of the genus tend to inhabit nutrient-poor, insular habitats such as high elevation rock outcrops, coastal wetlands and mountain bogs (Gillespie & Kron, 2013; Weakley, 2015). To understand potential differences in habitat affinity among *Kalmia* species that co-occur in this region, we assessed the taxonomic and phylogenetic diversity patterns within and between communities spanning a 6500-meter elevation gradient from the southern Appalachian Mountains to the Coastal Plain. Given the insularity of habitats that support these three taxa, we asked whether soil factors or elevation play a larger role in structuring community diversity as well as regional turnover among communities.

METHODS

Focal Taxa

To understand the interplay between lineage diversification and community distribution, we focused on three species in the *Kalmia* lineage with overlapping ranges and incidences of community co-occurrence, *K. buxifolia, K. carolina* and *K. latifolia*. *Kalmia buxifolia* (P.J. Bergius), or Sand Myrtle, exhibits a widely disjunct distribution in the eastern United States, with populations occurring in the New Jersey Pine Barrens, in the Southern Appalachian Mountains, as well as the Sandhills and Coastal Plain regions of the Carolinas, with distinct morphological differences among regions (Strand & Wyatt, 1991). In addition to the disjunct geographic range, the physiographic regions where *K. buxifolia* occurs have distinct differences in habitat resulting in subsequent niche differences; specializing on rock outcrops with a procumbent growth form in the southern Appalachians (Weakley, 2015), while exhibiting a taller shrub form in the understory of pine forests in the Coastal Plain, in addition to occupying bluff and streamside flatwoods in the Sandhills region of the Piedmont (Sorrie, 2011). *Kalmia carolina* Small, Carolina Bog Myrtle, is endemic to the southeastern US, and shares a bimodal distribution in the Carolinas similar to *K. buxifolia* (Weakley, 2015). *Kalmia carolina* inhabits moist habitats in predominantly the Coastal Plain, but also infrequently occurs in wetlands at higher elevations in the mountains. The distribution of *K. carolina* extends from southeast Virginia to central South Carolina (Sorrie, 2011). In the coastal plain, *K. carolina* occurs in wet pine flatwoods, streamhead ecotones and Carolina bay pocosins (Sorrie, 2011). *Kalmia latifolia* L., or Mountain Laurel, is a widespread species in eastern North America, very common in the Appalachian Mountains and restricted elsewhere; occupying a wide range of habitats, from bogs and stream sides to acidic forests and bluffs (Weakley, 2015).

Community Data

Twenty plots containing each focal species were either collected for this study or gathered from pre-existing data. Community sampling to characterize the habitat of *K. buxifolia* were executed in the summer of 2017, following the Carolina Vegetation Survey protocol with plot size modifications made for steep and/or impenetrable terrain (Peet et al., 1998). Standard plot size is 50 m x 20 m containing four intensively-sampled 10 m x 10 m modules (Figure 2). All plots were surveyed using the CVS nested quadrat design, identification of all taxa to the species level using nomenclature of Weakley 2015, and sites were chosen based on representative community structure containing *K. buxifolia*. Soil samples were collected in each module, consisting of four 10cm by 2cm soil cores which were combined and sent for analysis at Clemson University. For characterizing the community of two other overlapping species, plot data were compiled from the vegetation plot database of the Carolina Vegetation Survey (VegBank; Peet et al., 2012). Plots to include in this study were chosen based on the following criteria: containing soil data, representative of the range of the focal taxa, at least 5km apart, resolution of taxonomic identity to the species level for >95% of taxa, and those containing abundance estimates for all taxa. The total community dataset included species from 60 plots across an elevation and habitat gradient, all including at least one *Kalmia* species (Table 1; Figure 1). Each plot was assigned to one of three regions, mountains, piedmont, and coastal plain, to investigate potential differences in assembly processes and to evaluate the community responses to environmental gradients.

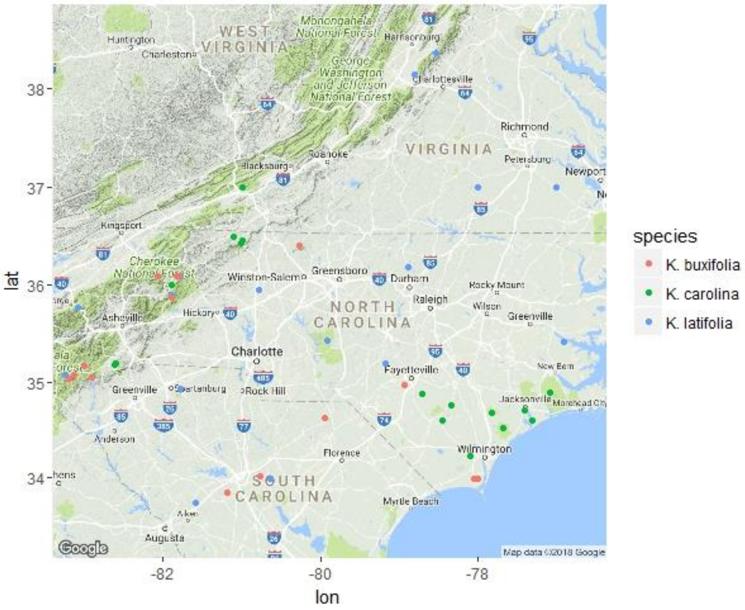

Figure 1. Map of community plots used in the study corresponding to each of three focal species.

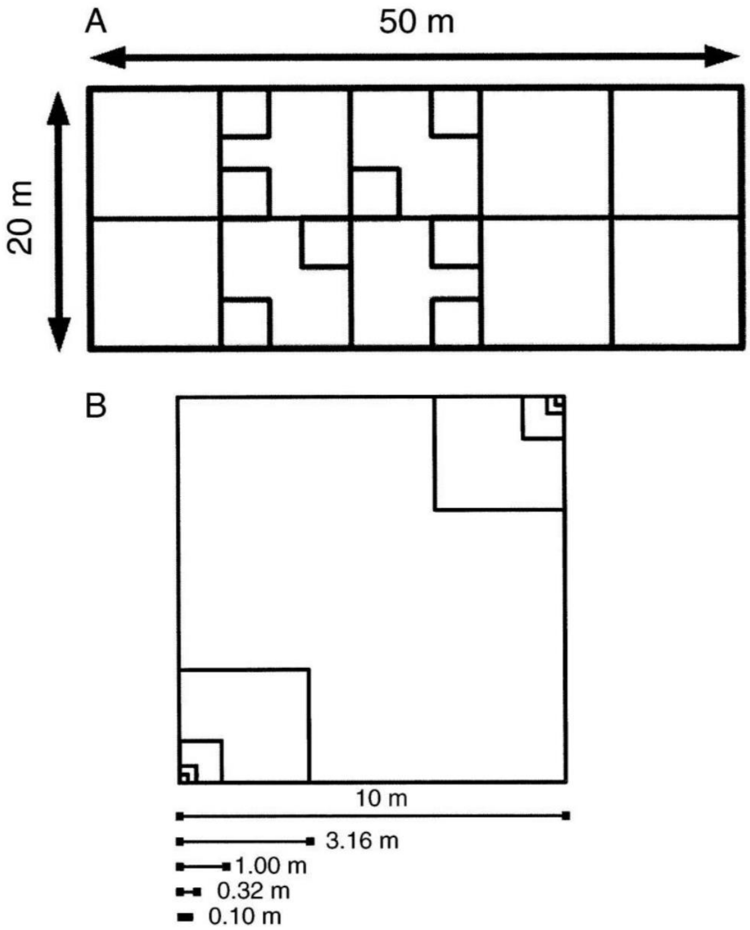

Figure 2. Vegetation plot design of the Carolina Vegetation Survey protocol (Peet et al. 1998). Each 20 x 50 m plot contains 10 x 10 m modules which contain nested quadrats from 0.10 m to 10 m.

Phylogenetic community structure

To estimate the relative contribution of community assembly mechanisms among different habitats of co-occurring *Kalmia* species, we first constructed a phylogeny using a backbone phylogenetic tree of over 10,000 species of angiosperms, constructed using seven gene regions and maximum likelihood analysis (Zanne et al., 2014). We then pruned the tree to contain only the species occurring in our 60 study plots, representing the habitat species pool of “potential colonists”. The final tree used

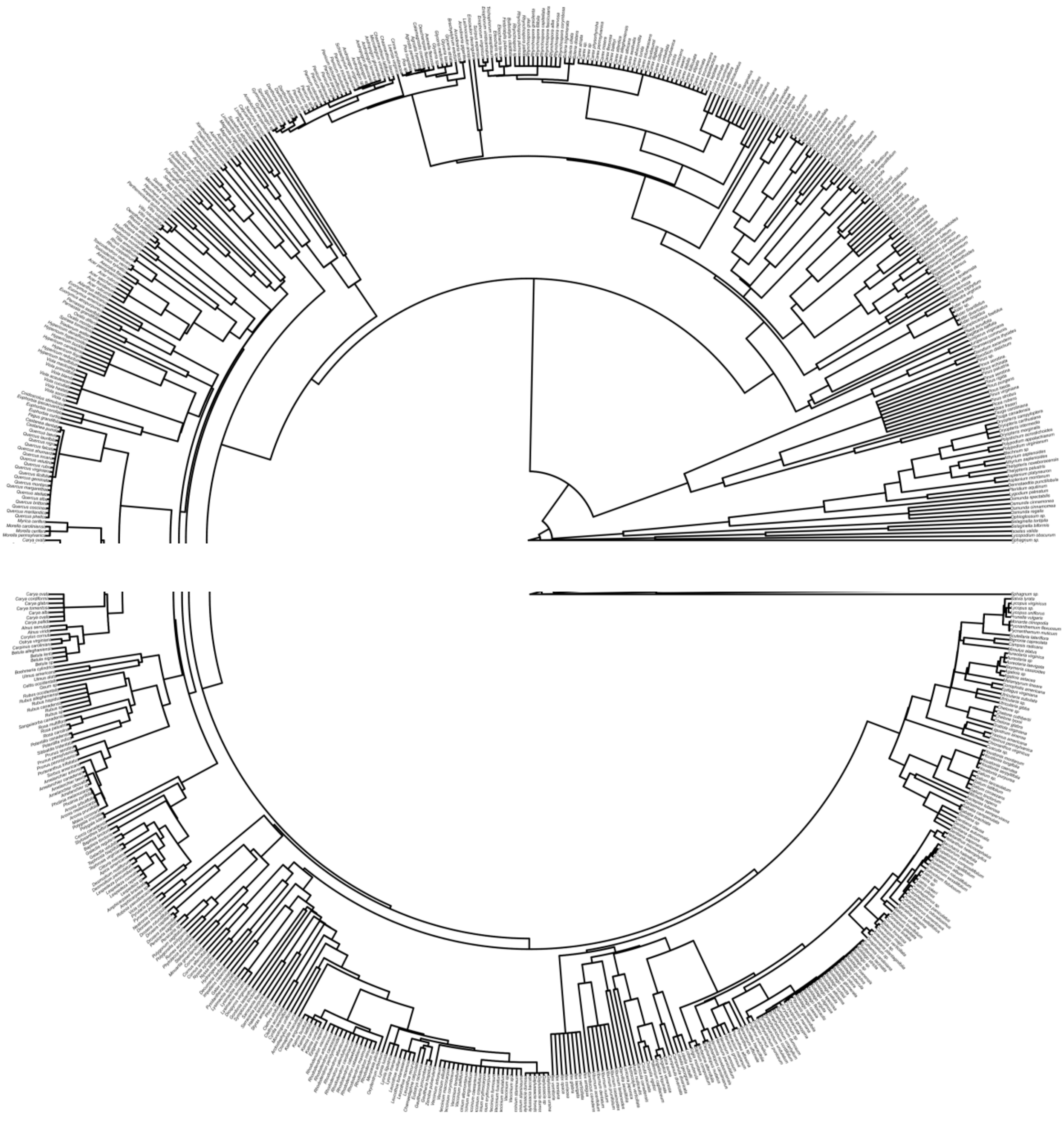

Figure 3. Mega-phylogeny of 664 taxa occurring in sixty plots within the study region. Phylogenetic relationships derived from Zanne et al. (2014).

contained a total of 664 taxa (Figure 3). The phylogeny was pruned using the *congeneric.merge* function in the ‘pez’ R package (R Development Core Team 2006; Pearse et al., 2015).

We measured the within-community phylogenetic structure by calculating the mean phylogenetic distance (MPD) and mean nearest-taxon distance (MNTD) for all 60 plots (Webb et al., 2002) (Table 1). MPD represents the average branch length between pairwise comparisons amongst every combination of species in a plot and is more sensitive to changes at deeper nodes within the phylogeny, while MNTD represents the average distance between each species in a community and its nearest relative and is more sensitive to changes at the species level. In order to compare how these values differ from random chance, we calculated the standardized effect size (SES) for each metric as:

SES = (observed value - mean of randomized values)/standard deviation

These metrics were calculated for 1000 null communities for comparison using the independent swap algorithm, which randomizes the tips of the community phylogenies so that species identities are re-shuffled across communities (Gotelli and Entsminger, 2003). Phylogenetic dispersion metrics were calculated incorporating abundance values using the function *pez.dispersion* in the package ‘pez’ (R Development Core Team 2006; Pearse et al., 2015).

The spatial patterns of composition among communities in a region (beta-diversity) is informative as to how the environment structures patterns of biodiversity (Anderson et al., 2011). To evaluate how taxonomic and phylogenetic community structure changes along soil and elevation gradients among communities, and to determine if regions are distinct in these patterns, we calculated phylogenetic beta diversity using the among-community equivalents to MPD and MNTD, by creating phylogenetic distance matrices using the *comdist* and *comdistnt* functions in the ‘picante’ package (R Development Core Team 2006; Kembel et al., 2010). To examine the differences in both taxonomic and phylogenetic beta diversity explained by region, we used permutational multivariate analysis of variance (PERMANOVA) as implemented in the *adonis* function of the ‘vegan’ R package (R Development Core Team 2006; Oksanen et al., 2013).

Environmental correlates of community composition and phylogenetic diversity

To investigate abiotic drivers of taxonomic and phylogenetic turnover among communities across the study area we used the *bioenv* function in the R package vegan (R Development Core Team 2006; Oksanen et al., 2013). The function uses the Euclidean distances of scaled environmental variables to find those that best correlate to the community dissimilarities. Distance matrices were made using Bray-Curtis for taxonomic distance, and phylogenetic distance matrices were calculated from phylogenetic beta diversity using the above.

We used Mantel tests to assess the correlation between community composition and environmental variables, calculating distance matrices using scores from principle components analysis with the *vegdist* and *mantel* functions in the ‘vegan’ R package (R Development Core Team 2006; Oksanen et al., 2013).

Non-metric multidimensional scaling (NMDS) analysis was used to visualize both taxonomic and phylogenetic distance among regions (Figure 4). Distance matrices were measured with the Bray-Curtis dissimilarity metric, as implemented with the *metaMDS* function in the ‘vegan’ R package (R Development Core Team 2006; Oksanen et al., 2013).

Regional differences among communities

To test for differences in abiotic variables between regions, we used one-way ANOVAs with region as the predictor for soil pH, organic matter, cation exchange capacity and base saturation. Similarly, to test for differences in community taxonomic and phylogenetic structure, we used one-way ANOVAs with these measurements as response variables and region as predictor. To assess the extent of co-occurrence among *Kalmia* species for regional differences, we likewise used region as a predictor and assigned each community plot with a binary value of 1 for multiple *Kalmia* species present, and zero for only one present. To assess whether plots containing each focal species differed in phylogenetic structure, we used Welch's two-sample t-tests between each species' plots assessing differences in both SES.MPD and SES.MNTD.

RESULTS

Phylogenetic community structure

To evaluate the extent of clustering or over-dispersion within communities, we used calculated z values from the null model comparison, in which z >1 indicates phylogenetic over-dispersion, while values of z < 1 indicate phylogenetic clustering. Overall, we found that communities in the mountains tended to be more phylogenetically over-dispersed than were communities in the piedmont or coastal plain (Table 1). However, our ANOVA results showed no significant difference in phylogenetic structure among these three regions (MPD: p=0.230), MNTD: (p=0.439).

Table 1. Community plots used in the study with calculated phylogenetic diversity metrics and taxonomic richness. Region codes are: mountains=3, piedmont=2, coastal plain=1.

plot	elevation	region	ntaxa	ses.mpd	z	p	ses.mntd	z	p
002-02-0034	44	2	30	300.08	-1.10	0.15	75.21	-2.50	0.00
002-04-0042	799	3	24	327.49	-0.45	0.34	116.89	-0.84	0.22
002-05-0038	61	2	85	350.76	0.33	0.65	120.44	2.23	0.98
003-01-0057	15	1	37	346.58	0.06	0.54	95.70	-1.25	0.11
003-01-0081	13	1	36	325.86	-0.53	0.32	94.01	-1.76	0.03
003-01-0111	20	1	42	369.78	0.89	0.80	107.40	-0.48	0.34
003-01-0116	35	1	35	325.47	-0.58	0.30	84.73	-2.05	0.01
003-04-0120	5	1	28	333.07	-0.33	0.38	88.02	-2.01	0.02
003-06-0054	15	1	44	367.49	0.84	0.80	98.56	-0.90	0.18
005-03-0306	1286	3	58	388.54	1.50	0.93	132.35	1.44	0.92
005-03-0318	1771	3	21	441.49	2.01	0.97	151.35	-0.26	0.41
010-0C-0063	1050	3	27	421.14	1.70	0.95	161.24	0.51	0.70
010-0C-0166	1050	3	17	290.01	-1.11	0.14	129.92	-1.10	0.14
012-0C-0675	1086	3	77	311.27	-1.43	0.08	96.01	-0.29	0.39
015-0R-0023	128	2	43	308.93	-1.03	0.15	102.73	-1.17	0.12
022-02-0375	1166	3	64	324.68	-0.78	0.22	107.03	0.01	0.50
022-02-0376	1381	3	26	349.23	0.14	0.56	151.65	0.08	0.53
022-09-0377	1457	3	33	325.29	-0.54	0.33	89.34	-2.02	0.02
025-03-0014	1231	3	34	316.48	-0.74	0.26	122.33	-0.61	0.29
028-01-0072	34	1	23	356.57	0.30	0.63	165.33	0.26	0.60

035-01-0507	524	3	63	354.89	0.42	0.67	116.21	0.65	0.74
035-09-0504	814	3	36	385.53	1.27	0.90	136.84	1.15	0.87
041-07-0586	829	3	44	328.22	-0.52	0.31	106.86	-0.92	0.18
041-07-0588	905	3	49	361.76	0.62	0.75	96.66	-0.70	0.24
041-07-0592	817	3	32	361.60	0.40	0.66	133.67	-0.24	0.40
042-01-0623	500	3	41	358.79	0.45	0.68	125.63	-0.01	0.49
057-01-0836	5	1	19	381.33	0.74	0.76	213.24	1.20	0.89
061-02-0902	8	1	11	420.22	1.18	0.87	273.92	1.53	0.93
061-09-0907	10	1	14	353.95	0.16	0.57	214.03	0.69	0.77
073-09-0001	765	3	38	370.05	0.69	0.77	142.67	0.46	0.68
073-09-0095	1065	3	52	401.15	1.84	0.96	111.93	-0.27	0.40
075-02-1002	19	1	16	341.74	-0.07	0.47	129.76	-1.08	0.15
083-01-1131	12	1	19	381.41	0.71	0.74	201.29	0.78	0.78
085-BIGS-0001P	799	3	40	365.88	0.73	0.77	117.77	-0.34	0.37
085-HICK-0004P	11	1	50	291.00	-1.81	0.03	105.14	-0.74	0.23
085-JWNF-0030	981	3	38	287.57	-1.62	0.04	99.41	-1.44	0.07
085-LUNE-0008	95	1	33	331.94	-0.28	0.40	154.20	0.76	0.78
085-YRSP-0011	24	1	23	323.46	-0.44	0.32	173.29	0.57	0.71
092-ATLAN-0001	6	1	19	345.61	0.05	0.57	114.64	-1.45	0.07
110-02-1308	0.25	1	20	348.84	0.08	0.58	216.81	1.43	0.93
114-01-0008	288	2	50	327.13	-0.61	0.29	97.70	-1.19	0.11
128-04-1481	126	2	29	366.83	0.55	0.73	171.72	0.99	0.84
129-04-1504	127	2	57	324.86	-0.60	0.28	122.78	0.46	0.69
133-01-1522	20	1	70	377.82	1.33	0.90	121.07	1.10	0.86
134-02-1544	178	1	31	315.81	-0.66	0.27	123.36	-0.74	0.23
135-10-1600	204	2	42	370.53	0.78	0.78	129.47	0.17	0.56
146-04-1681	74	2	36	348.01	0.06	0.53	112.04	-0.88	0.18
159-01-0001	6542	3	7	529.81	2.12	0.97	266.03	0.64	0.74
159-01-0002	6045	3	25	361.71	0.36	0.65	159.83	0.33	0.63
159-01-0003	4061	3	10	440.10	1.33	0.87	290.99	1.64	0.93
159-01-0004	4685	3	24	298.82	-1.06	0.16	131.83	-0.67	0.25
159-01-0005	1053	2	21	384.29	0.84	0.82	103.49	-1.69	0.04
159-01-0006	33	1	29	351.38	0.16	0.59	122.45	-0.77	0.22
159-01-0007	132	2	25	425.13	1.84	0.96	158.11	0.27	0.61
159-01-0008	461	2	37	325.42	-0.55	0.31	109.55	-1.01	0.17
159-01-0009	103	1	18	296.36	-0.96	0.22	111.21	-1.49	0.07
159-01-0011	68	1	15	296.86	-0.83	0.26	105.03	-1.68	0.03
159-01-0012	98	1	16	287.42	-1.04	0.18	128.86	-1.08	0.15
SHNP594	695	3	44	289.07	-1.72	0.04	128.27	0.33	0.63
SHNP597	506	3	20	413.78	1.38	0.90	157.35	-0.14	0.45

In our measurements of beta diversity, we found when using the taxonomic distances for NMDS, we see some segregation of regions, though there is considerable overlap as exhibited by ellipses (Figure 4). However, when using phylogenetic beta diversity as NMDS input, we see nearly indistinguishable regional differences (Figure 4). Thus, while taxonomic differences distinguish communities among the three regions, the communities all tend to be dominated by the same lineages.

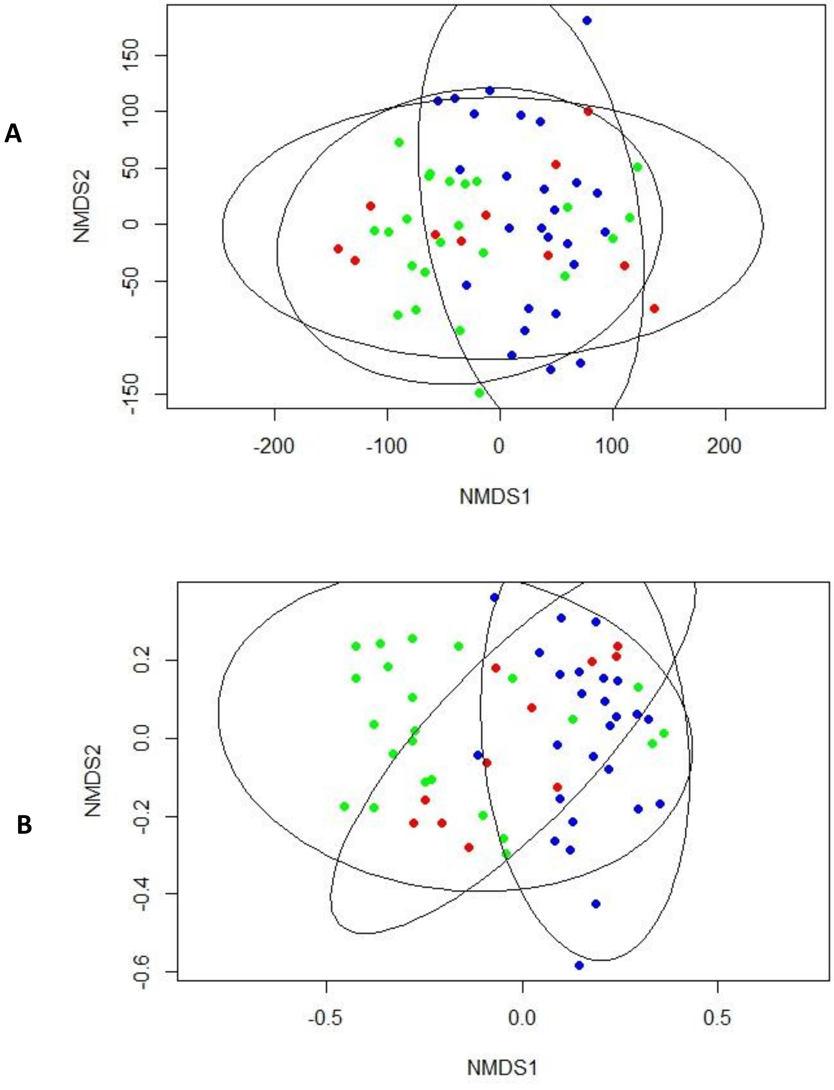

Figure 4. Non-metric multidimensional scaling ordination for 60 plots spanning the study region: (A) NMDS based on taxonomic distance matrix (B) NMDS based on phylogenetic beta distance matrix using

MNTD. Ellipses represent 95% confidence intervals in establishing regional groups. Colors represent region; green= coastal plain, red= piedmont, blue= mountains.

The PERMANOVA results showed that, while one metric of phylogenetic beta diversity was not significantly explained by region (p= 0.079), both taxonomic (p=0.001) and phylogenetic beta diversity as measured by MNTD (p=0.004) were significant in regional differences (Table 2). Given that MPD is more sensitive to changes deeper in the phylogeny, while MNTD is more sensitive to changes at the tips of the phylogeny, this pattern lends further support to the same lineages occupying all communities across the study area, with turnover occurring at the species level only. The turnover at the species level, and not at a deeper phylogentic level, would support the tendency of habitats within the focal regions potentially acting as ‘cradles’ generating new species, as has been recognized for these isolated communities within the broader region (Sorrie & Weakley, 2001; Weakley & Schafale, 1994).

Table 2. Variation in community taxonomic and phylogenetic structure as explained by region, determined by permutational multivariate analysis of variance (PERMANOVA)

Metric	F Model	r^2	*p*-value
Taxonomic	3.677	0.059	0.001
Phylogenetic- MPD	1.320	0.022	0.079
Phylogenetic- MNTD	5.773	0.090	0.004

A similar pattern is reflected in the results of our Mantel correlations; we find that both MNTD (Mantel r= 0.213, p=0.002) and taxonomic (Mantel r= 0.276, p= 0.001) beta diversity are significantly correlated with environmental gradients, while MPD is non-significant (Mantel r= -0.014, p=0.504) (Table 3); further supporting the deeper phylogenetic similarity among the three regions.

Table 3. Mantel correlations of community taxonomic and phylogenetic composition with environmental distance

Metric	Mantel r	Significance
Taxonomic	0.276	0.001
Phylogenetic- MPD	-0.014	0.504
Phylogenetic- MNTD	0.213	0.002

Regional differences

Dividing our study region into three distinct provinces, we found only one soil variable- pH- to be significantly different (F= 4.9, p=0.03). Soil organic matter (p=0.80), cation exchange capacity (p=0.91), and base saturation (p=0.11) were not different, indicating surprising similarity despite geographic, climatic and altitudinal differences (Figure 5).

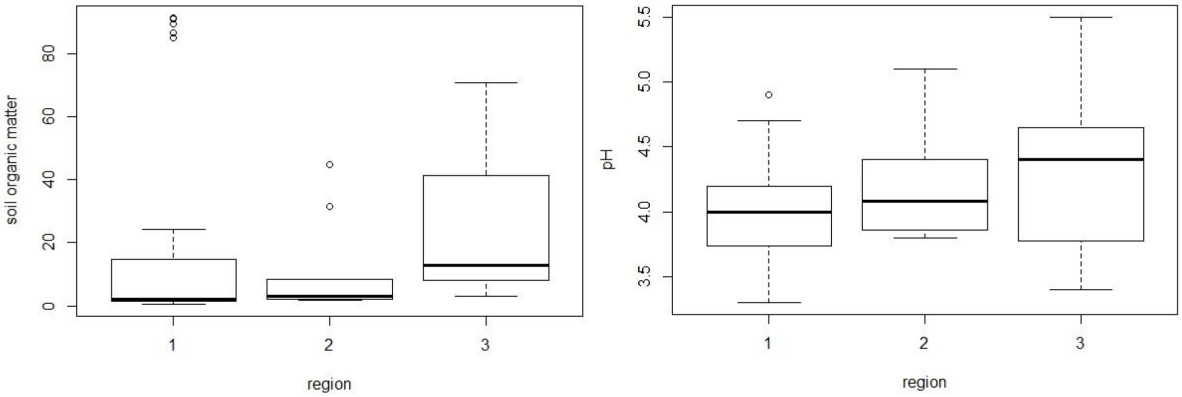

Figure 5. Regional differences in soil organic matter and soil pH. Organic matter content was not statistically different (p=0.80) but was generally higher in the mountains, while soil pH did exhibit significant regional differences (p=0.03) also being higher in the mountains. Region numbers correspond to 1) Coastal Plain 2) Piedmont and 3) Mountains.

Taxonomic richness was not significantly different (p=0.11) among regions, and surprisingly, measures of phylogenetic community structure were similar among communities (SES MPD: r^2=0.007, p=0.229; SES MNTD: p=0.434) (Figure 6). The frequency of co-occurring *Kalmia* species, however, was significantly different among regions (p=0.012).

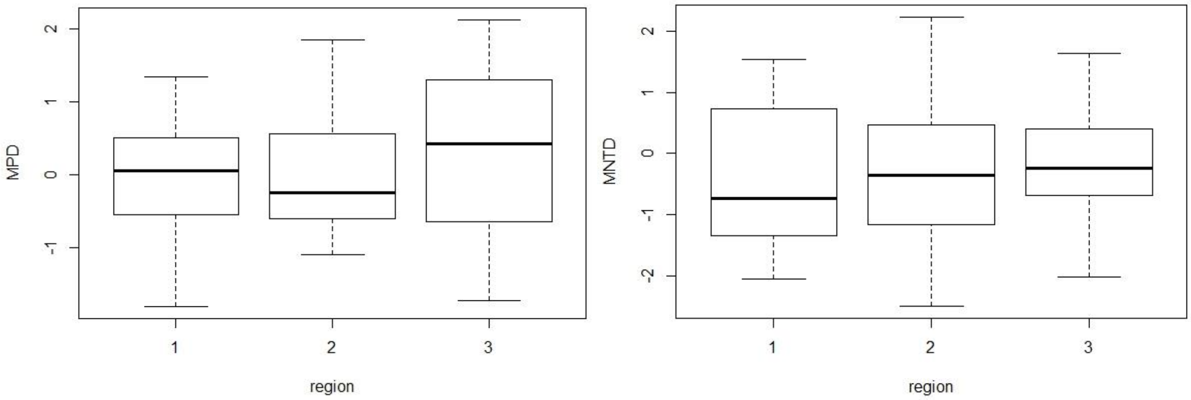

Figure 6. Phylogenetic structure among regions using mean pairwise distance (MPD) and mean nearest taxon distance (MNTD). Region numbers correspond to 1) Coastal Plain 2) Piedmont and 3) Mountains. Differences between regions were not significant (MPD: p= 0.229, MNTD: p=0.438).

DISCUSSION

The geological and ecological complexity of unglaciated eastern North America, particularly in the Southern Appalachians, could have produced current biotic distributions through a number of multi-faceted mechanisms, including geographic barriers to gene flow, dispersal constraints, bottlenecks in glacial refugia, and a diverse array of population genetic phenomena (Soltis et al., 2006). Species occupying harsh insular habitats that are surrounded by a matrix of contrasting benign conditions tend to be comprised of a nested subset of the regional species pool, with environmental tolerances of harsh conditions acting as a sorting mechanism (Sasaki et al., 2012). In this study, we found that edaphic variables were similar across the study area regardless of elevation, except for pH being higher at higher elevations. We found community compositional and phylogenetic turnover to be correlated with abiotic variables. Similarly, the abiotic variables of pH and elevation have been shown to best predict the community structure of moorland plant communities, which is an ecologically similar system characterized by insular, oligotrophic conditions (Sasaki, 2013).

Recent research investigating large-scale patterns of phylogenetic structure across latitude and climatic gradients in North America found that both arid and cold environments exhibited phylogenetic clustering, which lends support for the tropical niche conservatism hypothesis, in which fewer lineages have evolved tolerance to colder and more arid conditions (Qian & Sandel, 2017). Our results showed greater phylogenetic clustering in lower-elevation communities than in the mountains. Though seemingly contradictory to previous findings, our results likely reflect the lineage-specific patterns of diversification, since the majority of angiosperm clades show marked variation related to their ecophysiological tolerances as well as region-specific biogeographical history (Qian & Sandel, 2017). The mountain communities included in this study encompassed both high-elevation rock outcrops as well as wetland habitats. High-elevation rock outcrops in the Southern Appalachians are characterized by lower temperatures and high moisture from fog immersion (Wiser, 1994). Paleoecological data support the presence of a Pleistocene-era treeline at 1,500 m which has been hypothesized to have facilitated a widespread alpine flora, from which the current community composition is derived (Delcourt & Delcourt, 1988; Harshberger, 1903; White et al., 1984). While also inhabited by more widespread species, these communities are indeed comprised of a substantial floristic component representing relicts of a Pleistocene alpine flora, including many endemics as well as northern alpine disjuncts (Wiser, 1994). Southern Appalachian non-alluvial wetlands, though situated over nutrient-poor igneous or metamorphic rock, tend to have shallow, organic-rich, mineral soils and are seepage-fed, which distinguishes them from typical bog classification though the terminology is still used (Weakley & Schafale, 1994). These wetland communities contain a substantial floristic component of species with northern affinities, with some bog complexes comprised of up to 56% northern species, while species with a predominantly Coastal Plain distribution varying from 0-30% (Weakley & Schafale, 1994). Some of the plots used in this study contain deeper peat layers supporting more Coastal Plain species, which is thought to reflect a longer and more stable history that has been conducive to supporting species with relictual distributions (Weakley & Schafale, 1994). As discussed by Wiser (1994), these two habitat types- high-elevation rock outcrops and high-elevation bogs- support more endemic species than any other mountain habitats.

The species pool that ultimately gives rise to local communities is likely to be unique among different habitats within a region and may be represented by very different phylogenetic lineages occupying specific habitat types, perhaps reflecting past diversifications occurring in similar abiotic conditions (Bartish et al., 2016). For instance, cold habitats dating to the last 5 Myr contain high lineage diversities that relate to periods of global cooling, while open and dry habitats contain high lineage diversity dating to the last 34 Myr during periods of aridification in temperate regions (Bartish et al., 2016). Our results suggest that, though species composition in communities tend to reflect regional differences, the same phylogenetic lineages are occupying similar habitats across all three regions. It is likely that this pattern is a result of harsh, insular habitats selecting for pre-adapted lineages that track and/or diversify within these insular communities, potentially reflecting ecological opportunity available to a subset of the broader regional species pool.

Taken together, our results are comparable to other recent research on habitat-specific phylogenetic diversity that found wetter habitats tended to function as ‘museums’ of older lineages, while drier habitats function more as ‘cradles’ of younger lineages (Bartish et al., 2016). Our results of increased phylogenetic clustering might reflect the drier habitats in the piedmont and coastal plain, particularly in the sandhills region, as functioning ‘cradles’ of closely related lineage pools, while high-elevation communities are functioning more as ‘museums’ of distantly related lineages that have colonized and speciated during periods of cooler temperatures. Further research incorporating the estimated ages of divergence for species in each habitat type would be particularly helpful to test this relationship.

Mountainous topography on a global scale can facilitate increased speciation and trait diversification rates in plants triggered by island-like ecological opportunities (Hughes & Atchison, 2015). Investigating diversification patterns in global distributions of Ericaceae species, Bouchenak-Khelladi et al. (2015) found that steeper selective gradients and fragmented mountain habitats could have been the driver of montane radiations in Ericaceae species, and this mechanism might apply to other lineages that occupy mountainous insular habitats. The increased diversification coupled with mountain habitats acting as glacial refugia (Wiser, 1994) are both likely reflected in our finding of increased phylogenetic distance in mountain communities. Additionally, we found that pH and organic matter content was higher in mountain habitats, which would act as less-restrictive environmental filters than more harsh communities at lower elevations, thereby allowing species to colonize that are less well-adapted to edaphically harsh conditions. The more benign edaphic conditions in regard to soil pH and organic matter might also be contributing to support multiple co-occurring *Kalmia* species more frequently than Coastal Plain habitats.

As suggested by Graham and Fine (2008), if allopatric speciation is prevalent, resulting in lineages diverging into similar habitats, we could expect low phylo-betadiversity and high taxonomic beta diversity across regions such as mountains that have isolated patches of suitable habitat. This pattern would reflect the tendency for closely related species to establish in similar habitats. Our results showed that local communities occupied by *Kalmia* species across an elevation gradient exhibited higher compositional or taxonomic turnover than phylogenetic turnover, thus supporting this pattern and indicating the tendency of the same lineages to colonize and persist in the same habitats regardless of climatic or elevational differences. These insights also lend support to the overriding importance of mutualist interactions and/or local abiotic factors in determining the distributions of plant lineages occupying these harsh habitats. While this study incorporated communities occupying a wide range of elevation, temperature, canopy cover, and hydrologic conditions, we find that soil characteristics are quite similar among the three regions. This similarity also supports the higher importance of edaphic and soil-inhabiting mutualists in governing range distributions through filtering of these specialists from the regional species pool, allowing them to dominate communities that are inhospitable to other distantly related taxa- particularly in more edaphically harsh communities.

An area of concern in interpretation of phylogenetic metrics is that of geographic scale; particularly, the size of the local community relative to the regional species pool. This issue of scale-dependency, both temporal and geographic, has been recognized by ecologists for some time (Levin, 1992). However, consideration for scale in phylogenetic analyses has been scarce until recently. The concept of phylogenetic scale, defined by relative positions within an evolutionary hierarchy, is particularly important to define when assessing non-nested clades, such as within community phylogenetic patterns (Graham et al., 2018). One approach to account for phylogenetic scale, and to better discern processes governing community structure, is to examine the phylogenetic beta diversity (PBD) among communities along environmental gradients (Graham & Fine, 2008). Because a goal of this study was to understand the abiotic influences governing taxonomic and phylogenetic composition, as well as to compare patterns of phylogenetic structure within local communities, we chose to evaluate both alpha and beta diversity. Furthermore, comparing regional patterns of both taxonomic and phylogenetic beta diversity- instead of only alpha phylogenetic diversity- we can differentiate the relative roles of processes operating at a regional scale, such as trait evolution and species diversification. Additionally, our use of only specific communities inhabited by *Kalmia* species to investigate regional diversity is supported by recent literature advocating habitat-specific species pools within a region for separating local versus regional processes (Pärtel et al., 2016).

The proliferation of metrics and lack of unifying ways to measure and compare phylo-diversity has represented a challenge to the development of the field of community phylogenetics, as well as a challenge for researchers to choose metrics to employ (Pausas & Verdu, 2010). Among the 70 or more metrics available, we chose to use MNTD and MPD simply because these are the ‘anchor’ metrics assessing phylogenetic divergence that are commonly employed and therefore straightforward in interpretation (Tucker et al., 2017). Additionally, a recent study found that incorporating abundance data can substantially increase the power to detect phylogenetic patterns such as clustering and over dispersion, and these two metrics easily incorporate abundance data (Freilich & Connolly, 2015). Thus, by employing commonly used metrics- such as mean nearest taxon distance (MNTD) and mean pairwise distance (MPD), as well as incorporating abundance data, interpretations of patterns of community phylogenetic structure can be more accurately inferred. Because of the underlying assumption of phylogenetic niche conservatism among traits when inferring community assembly processes from phylogeny, it is important to first test if traits are conserved. One source of criticism to this study could be the lack of trait measurements and testing if traits are phylogenetically conserved before inferring patterns of community assembly. We did not include trait data due to both a lack of availability, and also because our interpretations of phylogenetic pattern focused on evolutionary relatedness in the context of regional speciation and immigration patterns.

To our knowledge, our results are among the first attempts to describe the community phylogenetic structure and turnover amongst insular habitats across an elevation gradient in the southeastern US. Because habitats included in this study tend to support rare and endangered taxa, and represent regionally-rare plant communities, these insights help understand the community assembly dynamics that have shaped these rare habitats, and potentially offer insight into future range redistributions under climate change.

Chapter 4: Conclusion

While understanding and describing the processes that govern the distribution of biota remains an ongoing pursuit, with many questions still unresolved and patterns undetected, the synthesis of the formerly disparate fields of ecology and evolution is resulting in a proliferation of insights, highlighting the interdependence and feedback between ecological and evolutionary processes. In a conceptual synthesis of community ecology, Vellend (2010) identified the four general processes underlying the patterns in composition and diversity of species- selection, drift, speciation and dispersal; speciation and dispersal adding new species to communities, while drift and selection operate to structure the abundance of species. While many studies have focused on the influence of selection and dispersal, relatively few studies have assessed the influence of speciation on producing patterns of community and regional diversity.

Phylogenetic and spatial data have enabled insights over the past decade as to the factors contributing to niche evolution and patterns of speciation, recognizing that at coarser geographic scales, climatic niche conservatism or divergence can both ultimately result in speciation events (Kozak & Wiens, 2006; Wiens, 2004), while at a local scale, competitive interactions contribute to ecological divergence amongst close relatives, promoting niche diversification and speciation (Silvertown, 2004). The relative roles of these climatic and biotic factors in promoting and enabling diversification has fueled extensive investigation and remains poorly understood. Within the *Kalmia* lineage, we find considerable niche lability in both climatic niche axes as well as most morphological niche axes. Our finding that only one morphological trait is phylogenetically determined suggests the importance of ecologically-adaptive morphology to the successful radiation of the lineage. Because the one trait exhibiting a phylogenetic relationship is a floral character related to pollination, we suggest that the presence of specific mutualists is more important in enabling habitat divergence than are other ecological factors. Additionally, plants in the Ericaceae family are known to depend on specific mycorrhizal mutualists for persisting in their characteristically harsh habitats (Read et al., 2004). A recent study examining the Ericaceous plant-fungal associations across different habitats found that communities of ericoid mycorrhizal fungi varied geographically and at fine scales, with niche-specific fungal associations specialized to microhabitats within habitats (Toju et al., 2016). This micro-habitat symbiotic partner specificity, in addition to pollinator divergence through disparate style length, may have facilitated *Kalmia* species to more readily coexist within the same habitats.

An important consideration is that current species' distributions likely do not reflect accurately the historical range dynamics, given that species' ranges can shift dramatically in a short timespan, and therefore must be approached with caution (Losos & Glor, 2003). However, by comparing multiple pairs of sister taxa in a lineage which represent a range of time since speciation, geographic inferences of speciation patterns can be made (Anacker & Strauss, 2014; Fitzpatrick & Turelli, 2006). Additionally, recent research has shown that, with the exception of very young lineages that are still in early and rapid phases of diversification, the majority of species' ranges are phylogenetically conserved, lending support for making inferences regarding speciation patterns using present distributions (Cardillo, 2015). Additionally, by correlating the coarse-scale climatic and topographic features across a landscape that characterize a species' observed range, ecological niche models capture and describe the Grinnelian niche of an organism (Grinnell, 1917). It is essential to interpret such models as representing potential distributions that inherently do not account for local scale factors, such as microtopography and biotic interactions, that further govern a species' Eltonian niche (Elton, 1927; Soberon, 2007).

Incomplete taxon sampling can result in inaccurate phylogenetic reconstructions and can give misleading branch length estimations as well as inaccurate dating estimates (Cusimano & Renner, 2010). Additionally, since this research incorporates divergence times for inferring biogeographical relationships, it is important to recognize that the estimation of divergence times can be distorted by the selection of calibrations (Smith & Peterson, 2002). We used the only fossil available representing the lineage without further calibrations due to data limitation, which could introduce extensive error in our estimates. However, for the purpose of this study, which is to broadly consider the role of ecology in lineage diversification, these estimates can still prove useful for giving a broad estimation.

By modeling the geographic range and niche differences in members of *Kalmia*, combined with a well-resolved molecular phylogeny, we have shown that allopatric diversification and coarser-scale niche evolution has produced the diverse ecological occupations within the genus- with range expansion and divergence a likely product of species tracking suitable insular habitats. While we cannot know if niche divergence occurred before or after species achieving sympatry, sufficient trait differentiation has allowed coexistence in local habitats of more benign abiotic conditions. By incorporating the speciation mode and niche characteristics of a single widespread lineage into a community-level framework, we have revealed the potential importance of evolutionary dynamics in structuring regional assemblages of plants. Given the ability for *Kalmia* species to persist in edaphically harsh habitats, which are similar in abiotic conditions and overall phylogenetic composition across climatic and elevational differences, other lineages adapted to these habitats have likely undergone diversification by similarly tracking insular communities across the region. If indeed allopatric speciation has resulted from tracking similar edaphic islands among co-occurring species, there is likely co-evolutionary influence from such interspecific clade interactions, which could prove insightful for future research involving the evolutionary influences structuring present-day communities.

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Vita

Tesa Madsen-McQueen was born and raised in the Missouri Ozarks, which is forever her ecological motherland. As a first-generation college student, she completed her Bachelor of Science degree at Missouri State University in 2015, majoring in Environmental Plant Science. She will complete her Master of Science in Biology in the summer of 2018 and will concurrently begin her PhD at the University of California- Riverside studying plant community ecology.

As a curious ecologist and passionate lover of the natural world, Tesa spends her extra time venturing outdoors and making visual art, and hopes to contribute equally to both science and art. She plans to pursue a life committed to deepening our understanding as well as appreciation for the complex and beautiful world around us.