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Ecological processes regulating geographic distributions of *Plethodon* salamanders in the Southern Appalachian Mountains

By

James O’Connor Church

A dissertation submitted to the graduate faculty in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Ecology and Evolutionary Biology

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Iowa State University

Ames, Iowa

2011

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ABSTRACT

Understanding how dispersal, adaptation to environmental characteristics, and interactions among species set the limits to species geographic distributions is one of the primary goals of biogeography. Evolutionary history of a species allows for a species to be adapted to a particular environment and is thought to have the greatest influence on where, geographically, a species can exist. However, often the species distribution is much smaller than its potential range based solely on environmental characteristics alone, and both local and regional ecological processes are responsible for this range restriction. For instance, the ability to disperse to suitable habitat and interspecific associations also factor in to the capability of a species to access and successfully colonize regions outside of its distribution.

In this study, I assess patterns in trophic morphology, environmental characteristics, and spatially-explicit population models to assess the geographic distribution of *Plethodon teyahalee*. I find that the mechanisms regulating this species’ distribution varies geographically, and that it is a combination of both environmental characteristics and interspecific competition which regulate this species’ geographic range limits in this group. Further, this research also demonstrates that local processes, such as interspecific competition, can be important in understanding regional patterns such as species geographic distributions.
CHAPTER 1. GENERAL INTRODUCTION

Overview

Understanding why a species lives where it does is one of the central questions in biogeography. The extent of species distributions is a product of historical and contemporary factors. Environmental factors may restrict colonization if the species is not adapted to these conditions. Alternatively, dispersal limitation can also limit colonization of suitable habitats (Goldberg and Lande 2007; Shurin 2001). Invasion resistance, where the species is excluded by interspecific interactions is another mechanism that can restrict species range expansion (Price and Kirkpatrick 2009). Finally, a combination of the above factors can regulate species distributions (Case and Taper 2000; Goldberg and Lande 2007).

In this dissertation, I explore the biotic and abiotic factors that influence the distributions of *Plethodon* salamander species in the southern Appalachian Mountains. I use trophic morphology, regional environmental characteristics, ecological niche modeling and spatially-explicit population modeling to assess how contemporary environmental characteristics and interspecific competition regulate the distributions of these species. I focus on a single species, *Plethodon teyahalee*, assessing its relationship to the environment, and how it may interact with parapatric and sympatric congenic species to better understand which factors maintain its distribution, and how these factors vary geographically. In the remainder of this chapter, I provide a brief overview of the scholarly areas in ecology and evolution germane to my research project.
Ecology of Species Distributions

Mechanisms regulating the extent of species distributions have been of interest to ecologists, evolutionary biologists and biogeographers for hundreds of years. Often, changes in the environmental conditions to which a species is not adapted can set the boundary of its distribution. Other times, barriers to dispersal to, or colonization of, habitats can restrict the distribution of a species. Biotic, interspecific interactions can also restrict where a species can occur.

The lack of adaptation to a change in environmental characteristics has long been understood to prohibit colonization of novel habitats. In this case, the genetic variability necessary for successful colonization of these habitats is not available, as the species may be maladapted to such an environment (Kirkpatrick and Barton 1997). For example, Kellerman et al (2009) found that habitat specialist species have low genetic variation, thus potentially limiting the likelihood that they will have genotypes adapted to habitat conditions outside of their distributions.

In other cases, barriers to dispersal can limit expansion of a species distribution into an environment that is otherwise suitable (Cornell and Lawton 1992; Shurin 2000). Dispersal barriers may be classified as partial or complete (Goldberg and Lande 2007). Complete barriers are impassable, and thus absolutely limit range expansion. For terrestrial animals, oceans are generally an example of a complete barrier to dispersal between continents. Partial barriers often limit dispersal, but it is the interaction between the barrier and other factors, such as biotic mechanisms which inhibit range expansion.
Interspecific interactions may also limit species distributions. Often competitive interactions between ecologically similar species may lead to abutting, parapatric, distributions or narrow zones of sympatry (Bull 1991; Price and Kirkpatrick 2009). The influences of predator-prey, herbivore-primary producer, and facultative mutualism can also limit the ability of a species to expand its distribution. In another instance, hybridization between closely related species can also limit species distributions.

The theories of competitive exclusion and limiting similarity have long been used to explain coexistence of competing species. Darwin (1859) noted that often closely related species occupy similar habitats in different geographic localities (now treated as evidence of phylogenetic niche conservatism: Wiens and Graham 2005). In instances where ecologically similar species have abutting parapatric distributions, and there is not a dispersal barrier, competitive interactions may be an important factor limiting range expansion of one or both of the species (Bull 1991). Competition can occur directly for space or resources, or indirectly (apparent competition). In resource competition theory, the more similar two species are in their utilization of a limiting resource, the less likely they are to stably coexist (Chase and Leibold 2003). However, the outcome of competitive interactions can be largely influenced based on other environmental factors. These outcomes and local adaptation can result in evolutionary stable range limits (Price and Kirkpatrick 2009).

**Niche theory**

One of the most fundamental objectives in ecology is identifying the relationship between an organism and its interactions with the environment. Understanding the mechanisms
that regulate these relationships can help lead to a better understanding of several ecological phenomena. One of the central conceptual principles in ecology is the niche. Long before Grinnell (1917) brought this term into ecology, several other ecologists, evolutionary biologists and biogeographers were examining how organisms interact with their environments and how environmental characteristics regulated species distributions (e.g., Darwin 1859). While the niche of an organism has been used in several different ways (reviewed in Chase and Leibold 2002), here I define the niche of a species to be both the ecological function it has, and the environmental conditions in which it can exist. Hutchinson (1957) proposed a distinction between the fundamental and realized niche. The fundamental niche is the region where a species can exist, in the absence of biotic mechanisms. The realized niche is where the species does exist and is constrained by both the abiotic and biotic environment. On the other hand, Elton (1927) viewed the niche as the ecological role a species has. Synthesizing both aspects of the niche will help to make the concept more general, and thus make it more amenable to understanding how an organism responds to an environment, where local processes are at play, as well as how it is related to its environmental characteristics at the regional scale (Chase and Leibold 2002).

**Ecological niche modeling**

In recent years, ecological niche modeling (ENM) has become a common method for understanding how environmental characteristics influence species’ distributions. These methods model the relationship between a species presence or absence and the environmental characteristics at those locations. The resulting model is then projected
onto the landscape to predict where the species is likely to occur (Peterson 2001; Raxworthy et al. 2007), and can be used to understand which environmental characteristics constrain the distribution at particular geographic locations (Elith and Leathwick 2009; Wiens et al. 2006; Kozak et al. 2008). While most applications of these methods assess relationships with the abiotic environmental variables, there is opportunity to explore how both the abiotic and biotic mechanisms are associated with the limits of species distributions (Elith and Leathwick 2009: Chapter 3 of this dissertation).

**Plethodon salamanders**

Over the past few decades, salamanders of the genus *Plethodon* have become a model system for studying ecology and evolutionary biology. This group is diverse, occupying a diversity of habitats, and they are among the most abundant vertebrates in the forests in which they occur. Further, the evolutionary relationships of these species are relatively well known (Wiens et al. 2006; Adams et al. 2009).

**Overview of the genus**

*Plethodon* salamanders are woodland salamanders, in the family Plethodontidae. Altogether, there are 55 species of *Plethodon* salamanders in the United States (Highton 1995; Highton and Peabody 2000; Highton 2004; Mead et al. 2005). They are lungless salamanders, and are direct developers which do not have an aquatic juvenile or larval phase (Highton 1995; Petranka 1998). Species in this genus are found throughout the forests of eastern North America. They become sexually mature between two and four years of age and can live to be 13 to 16 years of age (Marvin and Price 2001).
Plethodon salamanders are generalist predators, feeding primarily on small arthropods and worms. Since Plethodon salamanders can be the most abundant vertebrates in a community (Burton and Likens 1975), their effect on invertebrates can have profound consequences on several characteristics of the forest community. For example, in an experiment which examined the influence of Plethodon cinereus on invertebrate communities, Wyman (1998) found that invertebrates decrease in the presence of these salamanders. As a consequence of this effect on invertebrate abundance, forest floor decomposition rates declined by 11-17 percent, suggesting that Plethodon salamanders not only have a direct effect on invertebrates, but also indirectly influence nutrient cycling within the forest ecosystem.

Ecology

Salamanders in this genus have been used extensively in ecological research due to their high abundances, their well-known distributions and location data, and the structure of their communities. A study conducted at Hubbard Brook on the populations of Plethodon cinereus indicated that densities of this species alone could reach at least 2,583 individuals per hectare, and comprised 93.5 percent of the salamander biomass in north-eastern forests (Burton and Likens 1975). Many studies have documented interspecific competition, and have found that competition for resources and territories may be common in this group.

Behavioral Ecology

Interspecific territorial competition has been documented in a variety of cases (Anthony et al. 1997; Deitloff et al. 2009; Jaeger 1970; Jaeger and Forester 1993; Marshall et al. 2004; Nishikawa 1985). In some instances, these competitive relationships
have led to alpha-selection, where interspecific competition results in the evolution of increased levels of territorial aggression in sympatry (see Gill 1974). Additionally, ecological character displacement is known to occur in geographic regions where competing species come into contact (e.g., Adams and Rohlf 2000, Adams 2004, 2010). Interspecific competition between congeners can also restrict the ranges of potential competitors. For instance, in the Great Smoky Mountains, interspecific competition between *P. teyahalee* and *P. jordani* regulates this narrow zone of sympatry between the distributions of these two species (Nishikawa 1985), excluding *P. teyahalee* from inhabiting the high-elevation habitat where *P. jordani* is found (Hairston 1980).

Similarly, interspecific competition appears to be the mechanism that excludes *P. cinereus* from invading *P. hubrichti*’s distribution (Arif et al. 2007); and competition with *P. cinereus* has restricted the distribution of the endangered *P. shenandoah* to a few isolated mountain peaks (Jaeger 1972).

**Community Ecology**

Salamanders in this genus provide additional opportunities for understanding interspecific interactions between species and more generally community dynamics. Local, alpha richness of these salamander communities ranges from one to five species per community. The distribution of five-species communities occurs in the southern Blue-Ridge Mountains, and with a few exceptions contains the same member species (*P. cinereus, P. cylindraceus, P. montanus, P. richmondi,* and *P. yonahlossee*) (Adams 2007). Interestingly, the region where these five species localities occur coincides with the periphery of each of these species’ distributions. Further, all of these communities are in a “favored-state” (sensu Fox 1987), in the number of large versus small *Plethodon* (i.e.}
body-size guilds) observed in these communities (3:2). Other analyses of *Plethodon* salamander communities have provided evidence consistent with the idea that salamander communities are structured in a non-random fashion (Adams 2007).

*Plethodon* geographic distributions can be typified by a number of characteristics that are repeated geographically across the landscape. For instance, *Plethodon* distributions often abut one another (parapatry), have narrow sympatric zones, and also can widely overlap with other species (Highton 1995; Highton 1972). In the case of wide geographic overlap, species may co-occur rather infrequently. Some species occupy a few isolated mountain tops, while other species have distributions that span several states. These patterns lend themselves particularly well to using *Plethodon* as naturally-replicated evolutionary models to address several questions regarding what mechanistic explanations regulate these geographic distributions and coexistence. For example, *P. hubrichti* has a small geographic distribution that is entirely surrounded by *P. cinereus*. Along the periphery of *P. hubrichti*'s distribution, these two species are found syntopically. Arif et al. (2007) examined the relationship these two species had with one another, as well as modeled the limits to each other’s distribution, thus allowing the simultaneous testing of hypotheses of competitive exclusion and environmental filtering. The data were consistent with both hypotheses in that *P. hubrichti* excludes *P. cinereus* from the interior of its distribution, while the environment outside of this distribution in not suitable, thus range expansion of *P. hubrichti* is limited by habitat characteristics. Two species of *Plethodon* salamanders, *P. cinereus* and *electromorphus* have a broad area of overlap in Ohio. While these salamanders have a broad distributional overlap,
coexistence occurs less often than expected by chance, which is a pattern consistent with competition regulating community structure (Deitloff 2008).

**Evolution**

*Plethodon* salamanders have been used as a model system for addressing several questions related to evolutionary biology. A recent study identified evolutionary relationships among the species in this group (Wiens et al. 2006). Previous work on this genus indicates that there was a rapid diversification of species in the Pliocene (Highton 1995; Wiens et al. 2006). Calibration of molecular phylogenies for the group reveals that speciation often occurs during periods of climate change. For instance, in the Pliocene, *Plethodon* salamanders are believed to have become isolated from one another, and as a result of this isolation, underwent rapid speciation (see e.g., Highton 1999).

One consequence of these rapid speciation events appears to be the evolution of phylogenetic niche conservatism, where sibling species continue to evolve in allopatry, and occupy ecological niches with similar characteristics (Kozak and Wiens 2006). As evidence of this hypothesis, sister species in the genus show a higher degree of similarity in their bioclimatic niches as compared non-sister species, suggesting that sister species cannot evolve in sympatry due to their similar climatic tolerances (Kozak and Wiens 2006). Further, many researchers have identified that morphological variability between closely related species is low (Carr 1996; Highton 1995). *Plethodon* salamanders generally occupy similar microhabitats, and their diets are mostly composed of small invertebrates (reviewed in Petranka 1998). Thus it is likely that closely related species in this group occupy not only similar habitat dimensions of the niche, but also display similar patterns of resource utilization. Consequently, the evolutionary history of the
species in this group, combined with contemporary ecological traits, may help explain the current species distributions.

**Study system: *Plethodon teyahalee***

The Southern Appalachians Slimy Salamander (hereafter, *P. teyahalee*) is a member of the *P. glutinosus* species complex, and is distributed primarily in the very southern portion of the Blue-Ridge Ecoregion. This species occurs syntopically with several other species of *Plethodon* salamanders, and its distribution is parapatric to five other species of *Plethodon* salamanders. Prior ecological studies on this species indicate that there is strong interference competition with *P. jordani* in the Smoky Mountains and substantially less competition with *P. metcalfi* in the Balsam Mountains (Nishikawa 1985; Hairston 1980). Adams (2004, 2010) found data consistent with ecological character displacement where this species comes into contact with *P. jordani*. Further, this morphological divergence was strongly associated with patterns of aggressive territorial behavior in the contact zone between these two species, suggesting a functional link between evolutionary changes in head morphology and levels of behavioral aggression (Adams 2004). *Plethodon teyahalee* also occurs syntopically with several other species of *Plethodon* salamanders: *P. aureolus*, *cheoah*, *montanus*, *serratus* and *shermani*. It is unlikely that *P. teyahalee* has a strong relationship with *P. serratus* as these two salamanders have little overlap in activity time, and these salamanders are in separate functional groups (see Adams 2007; Hairston 1987). Thus, competitive interactions are likely to be minimal relative to species within the same guild. Further, the activity time of *P. serratus* and *P. teyahalee* is quite different. *Plethodon serratus* is active early in the spring and in the fall, while *P. teyahalee* can be found throughout the
summer months. The relative patterns of coexistence between *P. teyahalee* and other sympatric species can vary from very common (*P. cheoah*) to relatively infrequent (*P. shermani*) coexistence. This pattern in coexistence varies from common coexistence to hard parapatry, where the species distributions abut but do not overlap. Previous work indicating that competition is a predominant mechanism in regulating the structure of some communities makes this system ideal for studying the traits of these species and how these may relate to community composition.

**Dissertation Organization**

In the following chapters I investigate mechanisms constraining the geographic distribution of *Plethodon teyahalee*. In Chapter 2, I identify patterns in trophic morphology and environmental characteristics of *P. teyahalee*, and compare them to congeneric species displaying parapatric and sympatric distributions with *P. teyahalee*. Using trophic morphology as a surrogate for the resource-utilization dimension of the niche, I assess the theory of limiting similarity. Environmental characteristics of these distributions are used to assess how the environment may constrain species distributions.

In Chapter 3, I use ecological niche-modeling to assess the distributions of *P. teyahalee*, *P. jordani*, and *P. cylindraceus*. I use standard niche-modeling procedures, and develop a method which indirectly assesses competitive interactions between *P. jordani* and *P. cylindraceus* with *P. teyahalee*. In Chapter 4 I use a local population-level modeling approach to investigate how density dependent interspecific competition models can be used to demonstrate the interplay between biotic and abiotic constraints on species
distributions. Finally, in Chapter 5 I detail general conclusions, and provide insights into how these works can be applied to further research.

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CHAPTER 2. THE INTERPLAY OF ENVIRONMENT AND SPECIES INTERACTIONS IN REGULATING SPECIES DISTRIBUTIONS AND COMMUNITIES IN PLETHODON SALAMANDERS IN THE SOUTHERN APPALACHIAN MOUNTAINS

A paper submitted to the Journal of Animal Ecology

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Running Head.- Species distributions in Plethodon
Abstract

Both adaptation to the local environment and species interactions play important roles in determining the distributional extent of species’ ranges. Ecological theory predicts that environmental characteristics often delimit which species are present in the regional species pool, with subsequent species interactions affecting which species are capable of co-existing in a given community. Yet despite the pervasive influence that environmental effects and species interactions have on ecological communities, their relative influence for particular systems remains underexamined. In this study, we quantified niche overlap and morphological variation to predict which factors were governing local community structure of Plethodon salamander communities in the Southern Appalachian Mountains. For some species, we found that distinct environmental niches were occupied, suggesting that their parapatric distributions were the result of environmental filtering and adaptation to the local environment. In other instances, we found that sympatric species were distinct morphologically, suggesting that competitive divergence had occurred. Taken together, our study demonstrates that examining both environmental conditions and species interactions simultaneously can provide further insight into which mechanisms that regulate community structure.

Key words: Community assembly, Competition, Environmental filtering, Limiting similarity, Niche theory,
Introduction

One of the fundamental questions in ecology is determining what factors limit species distributions. Both environmental characteristics and interspecific mechanisms are recognized as important determinants of community structure, and numerous field studies have shown them to be important determinants that regulate species’ distributions, and a community’s composition (e.g., Peres-Neto and Jackson et al. 2001; Gotelli 2010; Arif et al. 2007). Yet, despite the pervasiveness of these forces across a wide variety of taxa and communities, their relative importance varies from system to system. In some instances, interspecific interactions such as predation (e.g., Paine 1969; McPeek 1998) and competition (e.g., Chesson 2000; Hairston 1980) appear to dominate, with competition frequently restricting the distributions of competitors (Hairston 1980). Such patterns where competing species appear to restrict one another’s distributions are consistent to the notion of limiting similarity, and that organisms that are too similar in their characteristics cannot coexist due to intense competition for resources (see e.g., MacArthur and Levins 1967; Abrams 1983; Chase and Leibold 2002).

In other ecological systems, environmental factors appear to dominate which species occur in a local community (Tuomisto et al. 2003; Brown and Lomolino 1998; see also Case and Taper 2000). In these instances, adaptive differentiation between species selecting different habitat attributes may determine why certain species co-exist and others do not. In this context, species with parapatric or abutting distributions often do not coexist due to differences in their environmental tolerances, rather than being determined by species interactions per se (Bull 1991). For example, along the slopes of mountains in the Sierra Nevada Mountains, Ponderosa and Digger Pines have adjacent
ranges with no observable barrier to dispersal, yet these species do not overlap in their distributions because Ponderosa Pine is adapted to the wetter habitats along the slope while Digger Pine is adapted to drier environmental conditions (Yeaton et al. 1981). However, while environmental factors and species interactions each play a large role in dictating species ranges, the interplay between the two can also determine the limits of species distributions and the degree of range overlap (Bull 1991; see also Chase and Leibold 2003). For instance, environmental suitability may act as the preliminary determinant of where a species may occur (habitat filtering: sensu Keddy 1992), but this range may be further restricted by interactions with additional species that can inhabit the same region (Jackson et al. 2001; Dunson and Travis 1991). As such, a full understanding of what factors limit species coexistence requires that both environmental and interspecific interactions be considered.

The salamanders of the genus *Plethodon* are a naturally-replicated evolutionary experiment for examining the effects of environmental pressures and species interactions on community composition and patterns of phenotypic variation within and among taxa. *Plethodon* are long-lived terrestrial salamanders found in North American forests (Highton 1995). Extensive field collecting at thousands of geographic localities has documented their geographic distributions (Highton 1995). Some species in the genus display broad geographic overlap with one another, while other species exhibit distributions that are geographically distinct, some with extensive parapatric boundaries. Where species overlap geographically, interspecific competition appears to be common (Jaeger 1970; Hairston 1980; Anthony et al. 1997; Marshall et al. 2004). In some instances, interspecific competition has restricted the geographic distributions of ranges
of potential competitors (e.g., Jaeger 1970; Hairston 1980; Griffis and Jaeger 1998), and likely influences community composition at both local and regional scales (Adams 2007). Interspecific competition has also resulted in the evolution of sympatric morphological divergence (character displacement) between some species (Adams 2000; Adams and Rohlf 2000; Adams 2004; Adams et al. 2007; Adams 2010), although in other cases, more unique phenotypic patterns have evolved (e.g., Arif et al. 2007; Myers and Adams 2008). Finally, several studies have shown that geographically isolated sister species display similar climatic niches, a pattern consistent with phylogenetic niche conservatism (Kozak and Wiens 2006). These results imply that climatic factors can also influence the distributions of particular Plethodon species. Taken together, this body of ecological work suggests that both environmental niche characteristics and species interactions are important in defining and regulating the distributions of Plethodon, although the relative importance of these effects on particular species’ distributions is less well understood.

In the Southern Appalachian Mountains, the distribution of Plethodon teyahalee provides a unique opportunity to examine the relative influences of environmental characteristics and species interactions on range limits and species boundaries.

Geographically, P. teyahalee is completely surrounded by the distributions of five other Plethodon species (Figure 2.1), each of which shares an extensive parapatric boundary with P. teyahalee. In addition, five other congeneric species are sympatric with P. teyahalee, displaying distributions that overlap with part of its distribution (Figure 2.1). When viewed in light of ecological theory and prior work on Plethodon (e.g., Hairston 1980; Adams 2004; Kozak and Wiens 2006), these distributional patterns generate several testable hypotheses which may be examined to reveal the mechanisms regulating
community assembly and species distributional limits. In this paper, we examined patterns of niche use and patterns of morphological variation to test predictions of environmental characteristics and limiting similarity at regulating species distributions and local community structure. Specifically, we examine the environmental niches of congeneric *Plethodon* species in the Southern Appalachian Mountains to determine whether species exhibiting parapatric, but non-overlapping distributions with *P. teyahalee* are distinct in their environmental niches, or whether their niche utilization was sufficiently similar that they could conceivably co-exist in sympatry. Subsequently, we examine patterns of morphological variation among species to test the prediction that coexisting species displayed less morphological overlap than did species with parapatric distributions. Importantly, by examining both patterns of niche use and patterns of morphological overlap, we determine whether species displayed parapatric distributions in a manner consistent with resource specialization, or whether their distributions were potentially limited as a result of interspecific competition.

**Methods**

**Data Collection**

We characterized the environmental niche of each species using a total of 2,707 georeferenced localities obtained from the collections of the United States National Museum of Natural History. For each locality, we extracted five climatic variables from the WORLDCLIM database (Hijmans et al. 2005) using DIVA GIS v. 7 (Hijmans et al. 2009). The five variables we used were: Bio2, mean diurnal temperature; Bio5, maximum temperature of the warmest month; Bio6, minimum temperature of the coldest
month; Bio 15, precipitation seasonality; and Bio17, precipitation of the driest quarter. These variables were selected because they represent means and extremes of annual temperature and moisture and are, thus, likely to be important in setting the range limits of *Plethodon*, whose life history makes them sensitive to fluctuations in moisture and temperature (Grover 1998; Jaeger 1970; see also Kozak and Wiens 2006). From these, a multivariate climatic envelope was obtained for each species, and their degree of niche overlap was determined.

To examine patterns of head shape variation, we used geometric morphometric methods (Bookstein 1991; Adams et al. 2004; Zelditch et al. 2004). These methods use a set of homologous landmarks to quantify the shape of biological structures, while holding constant the effects of position, orientation, and scale. For this analysis, 3,554 adult specimens from 11 *Plethodon* species were obtained from the United States National Museum of Natural History. These specimens were originally collected from 351 distinct geographic localities that encompassed the known geographic ranges of these species. From each specimen, we obtained a digital image of the left lateral side of the head using a Nikon DXM1200 camera mounted on a Nikon SMZ 1500 stereomicroscope. We then quantified the head shape of each specimen using the locations of 11 homologous landmarks on the head and jaw of each specimen (Figure 2.2). Variation in the gape of the jaw was taken into account by standardizing the articulation angle across all specimens (Adams 1999; see e.g., Adams 2010). Specimens were then optimally aligned using a generalized Procrustes superimposition (Rohlf and Slice, 1990), and Procrustes tangent space coordinates were obtained from each specimen and treated as a set of shape
variables (Rohlf 1999). In addition, centroid size was retained for each specimen as a measure of overall head size.

**Statistical Analyses**

To test the prediction that parapatric species occupied similar environmental niches, we quantified the degree of niche overlap for pairs of species in the climatic data space. First, we performed a principal components analysis of the bioclimatic data for all species at all geographic localities. We then quantified the pairwise environmental overlap for pairs of species in the PC space using the following procedure (see Butler et al. 2007; also Adams et al. 2009). We divided the first three PC axes of the environmental data space into distinct regions (10 divisions for PC1, and 9 for PC2), forming a multi-dimensional grid that spanned the data space. The number of grid cells jointly occupied by localities from pairs of species was then estimated, and treated as a quantitative measure of the degree of niche overlap. This measure was then calculated for all pairs of species, and was evaluated using a permutation procedure (for details see Butler et al. 2007). Finally, we repeated the overlap analysis using different grid cell sizes to evaluate the sensitivity of our results to arbitrary choices of grid-cell size.

To determine the degree of morphological similarity between *P. teyahalee* and its sympatric and parapatric congeners, we used permutational MANOVA (Anderson 2001). Analyses were performed separately for each species pair, and patterns of head size and head shape were examined. Bonferroni correction was used to assess the significance of each pairwise comparison. Overall patterns of morphological variation in shape space were examined using principal components, and thin-plate, spline-deformation grids (Bookstein 1991) were used to facilitate graphical descriptions of shape differences.
between specimens. All analyses were performed in R 2.11.1 (R Development Core
Team 2010), and thin-plate, spline- deformation grids were generated in TpsRelW 1.49
(Rohlf 2010).

Results

Niche Overlap

When patterns of climatic niche use were examined, congeneric species
geographically sympatric with *P. teyahalee* display considerable overlap in their climatic
niches (not shown). However, when the climatic niche of *P. teyahalee* was compared to
those of its parapatric congeners, patterns were considerably more varied (Figure 2.3).
For instance, one species (*P. chattahoochee*) displayed a climatic niche that was
completely surrounded by that of *P. teyahalee* (Table 2.1). This implies that the two
species exhibit a high degree of niche conservatism, as they share similar climatic
tolerances. This finding also implies that some mechanism other than adaptation to the
climatic environment is responsible for their parapatric distributions, as these parapatric
species would be expected to overlap in their geographic distributions had climate been
the dominant factor regulating their distributions. Similarly, *P. cylindraceus* exhibited a
high degree of overlap in its climatic niche with *P. teyahalee*. By contrast, *P.
chlorobryonis, P. yonahlossee*, and *P. glutinosus* all displayed significantly less climatic
overlap with *P. teyahalee* than was expected (Table 2.1, Figure 2.3), implying that these
geographically parapatric species occupied distinct environmental niches. Thus, when
compared to *P. teyahalee*, adaptation to distinct climatic niches was sufficient to explain
the parapatric distributions for these species.
Morphology

When morphology was examined, a number of distinct patterns were identified, with some species displaying significant differences in cranial morphology as compared to *P. teyahalee* and other species not differing in head shape (Figure 2.4). Specifically, some parapatric species, such as *Plethodon chattahoochee* and *P. cylindraceus*, are morphologically similar to *P. teyahalee*, and do not differ significantly in either head size or head shape (Table 2.2). Interestingly, these same species also displayed similar climatic niches when compared to *P. teyahalee*. However, those parapatric species that exhibited distinct environmental niches (*P. chlorobryonis*, *P. glutinosus*, and *P. yonahlossee*) also tended to be more distinct morphologically, differing from *P. teyahalee* in head size, head shape, or both (Table 2.2). Most of the anatomical differences observed were in these species were found in the relative depth of the head and relative length of the jaw (Figure 2.4); characteristics that have been associated with interspecific differences in food use and behavioral aggression in other species of *Plethodon* (e.g., Adams and Rohlf 2000; Adams 2004; 2010). In contrast to the parapatric species, all sympatric species displayed significant morphological differences when compared with *P. teyahalee* (Table 2.2), displaying anatomical differences largely in the shape of the jaw and skull (Figure 2.4). Finally, when morphological differences were compared to environmental differences, there was generally a positive relationship (Figure 2.5), where parapatric species with similar environmental niches were more similar in their morphology.
Discussion

Environmental characteristics and interspecific competition are two factors that determine species coexistence. In this study, we examined both broad-scale environmental characteristics and patterns of morphological variation to assess local community composition. Our results indicate that both environmental conditions and competitive interactions restrict local community composition. From our findings, several implications emerge. First, our analyses demonstrate that local community composition in these Plethodon salamanders is largely influenced by environmental conditions. Specifically, in several instances salamanders with abutting geographic distributions occupied distinct habitats, with their distributions separated by a dramatic environmental transition in habitat. These results reveal that some species of this genus display parapatric distributions because they occupy distinct environmental niches, and have likely evolved distinct adaptations to their local environment. As such, distributional overlap between them is not expected. These findings concur with patterns observed in other salamander systems, where environmental characteristics were found to be important for determining community composition (Arif et al. 2007; Cunningham et al. 2009). Further, several species of Plethodon salamanders display patterns consistent with phylogenetic niche conservatism in their environmental characteristics, where niche use appears to be the dominant force in dictating species ranges and distributional overlap (Kozak and Wiens 2006). Results from our system thus confirm these findings, and reveal that local adaptation to environmental conditions can be an important factor in restricting dispersal to and colonization of novel habitats.
Second, in some instances, we found support for the theory of limiting similarity, where species displaying similar habitat conditions did not occupy the same locations. In these instances, species displayed similarities in trophic morphology, but did not coexist sympatrically. Rather, they exhibited abutting geographic distributions with little geographic overlap. Additionally, we observed that species with dissimilar morphologies did co-occur sympatrically, implying that species of *Plethodon* can coexist, but only when they are sufficiently dissimilar in their morphological (and presumably ecological) characteristics. The latter conforms to the hypothesis of ecological character displacement (sensu Brown and Wilson 1956), where divergent selection from interspecific competition generates morphological and ecological differences among closely related sympatric species (see also Adams and Rohlf 2000; Pfennig and Murphy, 2003). Similar patterns have also been observed in other local *Plethodon* salamander communities (Adams and Rohlf 2000; Adams 2004; Adams et al. 2007; Adams 2010), where morphological divergence was associated with differences in resource use (e.g., Adams and Rohlf 2000) or levels of interspecific aggression (Adams 2004; 2010). More generally, patterns of species coexistence among *Plethodon* appear to conform to the hypothesis that interspecific competition is instrumental in generating community composition at a broader geographic scale (Adams 2007). Combining these observations with our findings, we therefore predict that *Plethodon teyahalee* and its sympatric congeners may similarly partition resources in a manner with ecological segregation as a result of interspecific competition.

Finally, our study demonstrates that examining both environmental conditions and species interactions simultaneously can provide further insight into which mechanisms
regulate community structure. Decades of ecological observations have demonstrated that species tend to ‘replace’ one another along environmental gradients. However, only by assessing environmental conditions along with biotic mechanisms can one determine which process is relatively more dominant in generating such patterns, as both can have varying influences in specific systems. Indeed, examining both biotic and abiotic influences in *Plethodon* salamanders in the Southern Appalachian Mountains provide instances where one or the other is relatively more dominant. For the case of some species (e.g., *P. chlorobronis* and *P. glutinosus*), environmental conditions and local adaptation appear to restrict their ranges, such that these species do not occur syntopically with *P. teyahalee*. On the other hand, other species such as *P. chattahoochee* and *P. cylindraceus* do occur in similar habitats to that of *P. teyahalee*, yet they do not co-occur in the same geographic regions. In these cases, competitive interactions with *P. teyahalee* appear to play a pervasive role in dictating species overlap. Thus, for these taxa, competitive exclusion remains a viable hypothesis for understanding community organization and explaining the limits of coexistence.

Recently, there has been interest in how local processes result in broad scale patterns of community composition (Gotelli et al. 2010). Environmental filtering and competitive interactions occur at local spatial scales for several species. Here, we demonstrated that understanding the interactions between local scale processes is critically important for revealing the causes of macro-ecological patterns of species distributions across the landscape. The ability to tease apart the relative influences of environmental conditions and interspecific relationships is critical for understanding community structure and how these factors can be scaled-up to biogeographic, patterns.
Further, in certain environments competition may favor one species, while in other environmental conditions the other species may have a competitive advantage (Dunson and Travis 1991). This may be the case where non-coexisting species appear to occupy similar habitat conditions. Analysis of both the abiotic and biotic mechanisms can more accurately predict which factors play predominant roles in determining community assembly, and further develop experiments to assess these predictions in future studies.

Acknowledgements

We thank Chelsea Berns, Nicole Seda, Audrey Weaver, and Meredith Zipse for assistance in data collection, and Addison Wynn and the USNM staff for continued support for our use of the museum’s repository of salamanders. Brent Danielson also made valuable comments on this manuscript. This work was sponsored in part by NSF grant DEB-0446758 to DCA.

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  between a patchily distributed salamander (*Plethodon petraeus*) and a sympatric


Table 2.1. Results of pairwise climatic overlap between *Plethodon teyahalee* and parapatric congeners. The number of geographic localities used to quantify the climatic envelope for each species is shown. Statistical assessment of climate overlap is based on a permutation procedure, following Butler et al. 2007.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Localities</th>
<th>Overlap Score</th>
<th>Proportion of Localities that Overlap with <em>P. teyahalee</em></th>
<th><em>P</em>&lt;sub&gt;rand&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. teyahalee</em></td>
<td>846</td>
<td></td>
<td>100%</td>
<td>0.050</td>
</tr>
<tr>
<td><em>P. chattahoochee</em></td>
<td>52</td>
<td>0.024</td>
<td>53.2%</td>
<td>1.000</td>
</tr>
<tr>
<td><em>P. chlorobryonis</em></td>
<td>109</td>
<td>0.011</td>
<td>57.5%</td>
<td>0.028</td>
</tr>
<tr>
<td><em>P. cylindraceus</em></td>
<td>543</td>
<td>0.022</td>
<td>21.5%</td>
<td>1.000</td>
</tr>
<tr>
<td><em>P. glutinosus</em></td>
<td>1,083</td>
<td>0.015</td>
<td>63.5%</td>
<td>1.000</td>
</tr>
<tr>
<td><em>P. yonahlossee</em></td>
<td>74</td>
<td>0.009</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.2. Morphological comparisons of *Plethodon teyahalee* versus sympatric (S) and parapatric (P) congeners. The number of specimens quantified for each species is shown. Comparisons for head size ($D_{\text{Head Size}}$) are based on centroid size, and are expressed as the mean difference between species. Comparisons of head shape are based on the Euclidean distance between species means ($D_{\text{Head Shape}}$). Significant values are in bold-face, and based on a Bonferonni-adjusted critical value of $\alpha = 0.005$.

<table>
<thead>
<tr>
<th>Species</th>
<th>P/S</th>
<th>Number of Specimens</th>
<th>$D_{\text{Head Size}}$</th>
<th>$D_{\text{Head Shape}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. teyahalee</em></td>
<td></td>
<td>1,026</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. aureolus</em></td>
<td>S</td>
<td>199</td>
<td>2.74</td>
<td>0.015</td>
</tr>
<tr>
<td><em>P. chattahoochee</em></td>
<td>P</td>
<td>46</td>
<td>0.33</td>
<td>0.014</td>
</tr>
<tr>
<td><em>P. cheoah</em></td>
<td>S</td>
<td>194</td>
<td>3.21</td>
<td>0.012</td>
</tr>
<tr>
<td><em>P. chlorobryonis</em></td>
<td>P</td>
<td>96</td>
<td>0.47</td>
<td>0.032</td>
</tr>
<tr>
<td><em>P. cylindraceus</em></td>
<td>P</td>
<td>598</td>
<td>0.34</td>
<td>0.008</td>
</tr>
<tr>
<td><em>P. glutinosus</em></td>
<td>P</td>
<td>130</td>
<td>3.05</td>
<td>0.021</td>
</tr>
<tr>
<td><em>P. jordani</em></td>
<td>S</td>
<td>289</td>
<td>2.82</td>
<td>0.020</td>
</tr>
<tr>
<td><em>P. metcalfi</em></td>
<td>S</td>
<td>459</td>
<td>1.43</td>
<td>0.011</td>
</tr>
<tr>
<td><em>P. montanus</em></td>
<td>S</td>
<td>396</td>
<td>2.84</td>
<td>0.013</td>
</tr>
<tr>
<td><em>P. yonahlossee</em></td>
<td>P</td>
<td>122</td>
<td>1.99</td>
<td>0.014</td>
</tr>
</tbody>
</table>
Figure 2.1. A) Distributions of *Plethodon teyahalee* and surrounding, parapatric species. Area in gray, green, blue, red, purple, and triangle fill are *P. teyahalee*, *chattahoochee*, *glutinosus*, *cylindraceus*, *chlorobryonis*, and *yonahlossee*, respectively. B) Distributions of species in this study with overlapping (sympatric) distributions to *P. teyahalee*. 
Figure 2.2. Positions of the 11 landmarks used in this study.
Figure 2.3. Principal component plot of climatic envelopes for *Plethodon teyahalee* (gray squares) and each of its parapatric congeners (black triangles). Parapatric species are: A) *P. chattahoochee*, B) *P. chlorobryonis*, C) *P. yonahlossee*, D) *P. cylindraceus*, and E) *P. glutinosus*. 
Figure 2.4. Principal components (Relative Warps) plot of the means for head-shape morphology. Triangles indicate species which co-occur with *P. teyahalee*, squares represent species with distributions parapatric to *P. teyahalee*, and the square represents the mean morphology for *P. teyahalee*. Thin-plate spline deformation grids of the average specimen for each species used in this study.
Figure 2.5. Relationship between climatic overlap and morphological similarity between *P. teyahalee* and its sympatric and allopatric congeners. Triangles represent species that are parapatric with *P. teyahalee*, while circles represent species that co-occur sympatrically with *P. teyahalee*. 
CHAPTER 3: USING ECOLOGICAL NICHE MODELING TO GENERATE AND EXAMINE SPATIAL HYPOTHESES OF COMPETITION: AN EXAMPLE IN PLETHODON SALAMANDERS

A paper submitted to PLoS-ONE

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Running Head.- Biotic niche models

Keywords: competition, ecological niche modeling, geographic information systems, Maxent, Plethodon, range restriction
Abstract

Ecological niche modeling techniques provide a rigorous tool in assessing limits to species distributions, and have been used in several applications in ecology, evolutionary biology and biogeography. Often, models built using solely abiotic environmental characteristics are insufficient at accurately describing a species distribution, in part because interactions with other species are usually not considered. Here we demonstrate how ecological niche modeling can be used to develop hypotheses regarding where biotic conditions limit habitat colonization. We exemplify this approach to ecological niche models for three *Plethodon* species salamanders using standard niche modeling techniques and complimentary methods that incorporate biotic information. Niche models incorporating a biotic layer for potential competitors provided a better estimate of known species distributions than using only environmental data layers alone. Comparing these models enabled us to generate testable and predictive hypotheses regarding where abiotic and biotic features appear to limit species’ distributions. These predictions were confirmed for one set of species where field data on ecological interactions had previously been shown competitive interactions and range limitation. Our approach complements existing procedures by developing explicit and testable hypotheses regarding which environmental characteristics limit the geographic distribution of a species. The methodology employed significantly contributes to the applicability of niche modeling and theory associated with the biogeographical and ecological hypotheses for which researchers utilize these tools.
Introduction

Understanding the effects of competitive interactions has long been a mainstay of ecological research. In many ecological systems, interspecific competition affects community composition ([1]), and influences community diversity and stability ([2]). Competitive interactions affect phenotypic variation (e.g., [3,4]), and can alter species boundaries, generating distinct parapatric distributions with limited geographic overlap among competitors ([5,6]). For some species, interspecific competition is the primary mechanism limiting species’ ranges in particular geographic directions (e.g., [7]).

In recent years, ecological niche modeling (ENM) has become a powerful tool for understanding the environmental influences on species’ distributions. These methods model environmental characteristics at locations where a species is known to occur, and project these onto the landscape to determine where the species is likely to occur ([8,9]). In many cases, ENM accurately represents a species’ distribution (e.g., [10]) and allows an assessment of which abiotic variables are most influential in a given model (e.g., ENFA: [11]; Maxent: [12]). The former provides an indication of which environmental parameters are critical in establishing and maintaining a species’ distribution (e.g, [13]).

Ecological niche modeling has proven effective in describing the environmental influences on species’ distributions in a wide range of organisms ([14]), but sometimes, the predicted distributions greatly exceed the known range of a species. Such findings may occur when the environmental variables included do not have a significant influence on a species’ distribution ([15]), or when there is a barrier to dispersal that limits migration and colonization ([9]). An additional possibility however is that other influences, such as biotic interactions with parapatric species, may be responsible for the
lack of fit between the predicted and realized distributions (e.g., [16,17]). Indeed, while niche modeling is increasingly utilized for examining environmental constraints on species distributions, it remains underutilized for assessing the effects on species’ ranges of biotic processes such as competition.

A number of recent studies have indirectly associated biotic factors, such as competition or mutualism, along with ecological niche models. For instance, projecting distributional overlap from ENM models from two species may allow one to hypothesize potential competitive limits of species’ distributions ([16]). Another approach is to identify regions of projected geographic overlap between niche models for competitors, and reveal specific environmental variables which discriminate between the species’ ecological niches ([18]). One can also incorporate absences into the model in locations where potential competitors may occur ([19]). Importantly, while it is generally acknowledged that direct biotic mechanisms such as competition or mutualism are important for understanding species distributions, incorporating these components into niche modeling will likely require methods not currently developed ([20]).

In this paper, we describe a new procedure that incorporates both environmental factors and biotic effects from potentially interacting species. Our method is useful for examining biotic effects in parapatric species, and extends existing approaches by proposing explicit and testable hypotheses regarding where a species’ distribution may be limited by abiotic factors, and where it may be restricted by biotic interactions. We exemplify the approach through two examples describing the potential competitive interactions between parapatric salamander species of the genus *Plethodon*. The first serves as a test case of our approach, as considerable prior ecological field data has
previously demonstrated intense interspecific competition between the two species. The second provides a scenario where less is known about the two species, and thus our approach example generates explicit hypotheses that may be empirically tested in future ecological studies on this system. We also discuss generalizations of our procedure to other types of biotic interactions, such as predation and mutualisms.

Ecological Niche Modeling

In ecological niche modeling, geo-referenced presence-absence data, often obtained from museum and herbaria collections ([21]), are statistically related to environmental data at those locations. The environmental data (typically climate data) are in the form of a continuous grid covering the study area ([9,11]). A model is generated characterizing each locality, such that under-prediction (classifying a location as unsuitable where the species does occur), and over-prediction (classifying a location as suitable where a species does not occur) are minimized. Several ENM algorithms exist, including: GARP ([22]), Maxent ([12]), MARS ([19]), and others (for a review see: [23]). Although these techniques differ in the formulation of the model, the approach generally follows what is outlined above ([9]). Many methods also determine the probability of species occurrence or the environmental suitability of each grid cell ([12,24]), based on some optimal ‘cut-off’ value (methods reviewed in [12,24]).

A: An Extended Niche Modeling Approach for Biotic Data and Hypothesis Generation

Previous researchers have compared several niche models that incorporated different abiotic environmental data layers to identify which environmental
characteristics are most influential in limiting species’ distributions, or range expansion. For instance, niche models incorporating different sets of variables can be compared, and using a backwards selection procedure, environmental variables that severely constrain species boundaries can be identified ([13]). We employ a similar logic here, but compare niche models based solely upon abiotic variables to niche models incorporating the relationship between abiotic niches for multiple species. By identifying geographic regions where both niche models align well, and regions of discord between the two, one can generate testable hypotheses regarding where, geographically, different ecological mechanisms may be more influential in setting a species distributional limits.

Typically, ENM approaches only incorporate environmental characteristics, though several studies have indirectly assessed patterns associated with biotic and abiotic mechanisms ([16,25]). One possible means of accomplishing this is to simply include the distribution of a potentially interacting species (a competitor, predator, or mutualist) as another variable with the environmental variables in the niche model; treating the presence or absence of this species across grid cells as a discrete variable. Unfortunately, this approach assumes that absence information for the interacting species is known without error, which is rarely the case (see: [26]). Additionally, combining continuous and discrete data in many mathematical and statistical procedures can lead to unpredictable outcomes ([27]). because species’ interactions vary in intensity across the landscape, treating these interactions as a simple binary variable may not accurately reflect how these varied interactions relate to distributional and abundance across the landscape (see: [28,29]). Another recent approach is to include the correlations of the relative abundance of a focal species with that of potentially competing species as an
additional layer along with abiotic predictor variables ([30]). However, while this approach incorporates aspects of competitors into ENM, it does not describe the relative competitive abilities of multiple species across the landscape, as would be defined by competitive interactions in a Lotka-Volterra modeling framework. Additionally, it may prove difficult to detect whether the species correlations in relative abundance are mainly driven by their relationships to environmental characteristic or to biotic interactions. Therefore, while straightforward, simply adding the competitor as an additional layer may not accurately capture the relative (and potentially differing) competitive abilities across the landscape.

Instead we propose the following alternative. The approach follows several simple steps, and is outlined here for the case of two potential competitor species: possible alterations of the approach for other types of biotic interactions are found in the Discussion. For the case of competition, species are selected based on prior, independent ecological information, whose data suggest that the species interact competitively. For these species, it is first of interest to determine whether or not the species’ distributional overlap is less than expected based on their environmental characteristics, as such a pattern is consistent with the hypothesis that the species interact competitively. This can be assessed by using the environmental niche models for each species, as the habitat suitability scores from ENM provide an estimate of species occurrence at particular geographic localities. First we generate ENM for each species separately based on their geo-referenced locations, and habitat suitability scores are obtained for all grid cells in the study region. From these the expected probability of co-occurrence is found as
\[
\sum_{i=1}^{k} P_A P_B
\]
where \( P_A \) and \( P_B \) represent the habitat suitability scores for species A and B in each grid cell. Similarly, the expected probability of observing only one species in a given geographic location is found as 

\[
\sum_{i=1}^{k} \left( P_A (1-P_B) + (1-P_A)P_B \right)
\]

and the expected probability of observing neither species is found as 

\[
\sum_{i=1}^{k} (1-P_A)(1-P_B)
\]

The expected frequency of co-occurrence, single-species occurrence, and no occurrence in each grid cell is obtained by multiplying the expected probabilities by the number of grid cells. Finally, a chi-square test is used to compare the expected values to those observed in the study region based on the actual species distributions and locality data.

This test provides an assessment of whether or not the observed distributions overlap more or less than expected based on their environmental characteristics alone. However, this does not allow an evaluation of where geographically the species limit each others’ distributions. To generate such predictions, one must incorporate biotic interactions directly into the niche modeling procedure. First, species are selected based on prior, independent ecological information, whose data suggest that the species interact competitively. Next, ENM are generated for both species based on their geo-referenced locations, and the index of habitat suitability for each species is obtained for all grid cells in the study region from these environmental models. These values are rescaled to a range of zero to one, and the ratio of habitat suitability scores between the two species (species 1/ species 2) is calculated for all grid cells in the study region (when grid cells have values of 0.00, a small constant [0.000001] is added to all cells to avoid division by zero). This ratio represents the relative environmental suitability of each species in each
locality, conditioned on the other species. Thus, it contains information on both the suitability of each species to the local abiotic environment, as well as relative biotic information for the two species (see below). Finally, environmental niche models are re-run for both species, using the habitat suitability ratio as the only environmental data layer. Thresholds for indicating habitat suitability from these models are the same as currently used in standard niche modeling procedures (reviewed in [24]).

The logic underlying the suitability ratio has firm biological grounding in the ecological theory of species interactions ([31,32]). For interspecific competition, if two species have similar ecological functions in resource use, then competitive interactions are likely similar, and one species has a negative impact on another. Thus, in terms of relative abundance, this negative relationship can be re-expressed as the effect of species x minus the effect of species y. Often, ecological data (e.g., body size) are examined on a log-scale (e.g., [33]), so \((\log(x)-\log(y))\) represents this relationship. The ratio between suitability scores for two species expresses this as: \(\log(x/y) = \log(x)-\log(y)\). One can also examine this ratio in terms of the relative difference in carrying capacities between two species. The ratio between the two niche models is analogous to the ratio of their carrying capacities, as suitability scores for each location should be positively correlated with carrying capacity. Thus, in areas where the suitability ratio approaches 1 between species with similar, symmetric competitive effects, stable or unstable co-occurrence is more likely to occur. However, in geographic regions where the ratio highly deviates from 1, then one of the species is predicted to have a greater competitive advantage as its carrying capacity is much greater, and would therefore likely exclude the other species through competition, leading to a sharp parapatric boundary between the two. However,
because of the potential for unequal (asymmetric) competitive coefficients, generating an
ENM using this ration as an ‘environmental layer’ allows a determination of where
potentially interacting species occur on this “competitive landscape”, as one would
through a standard ENM protocol of identifying the relationship between a single species
and abiotic environmental characteristics. This procedure is thus complimentary to
standard niche modeling procedures, and allows for the formulation of hypotheses
regarding where species are limited by biotic factors, and potentially develop better ideas
of the relative strengths of the interactions between these species, and how this may vary
across the landscape.

B: Generating Testable Ecological Predictions

An important step of our procedure is the comparison of multiple ENM models to
generate testable hypotheses regarding both how and where abiotic and/or biotic effects
are relatively more influential in regulating species’ distributions. First, for each model,
the suitability threshold, such as specificity-sensitivity equality, is identified to determine
where the habitat is suitable or unsuitable (reviewed in [24]). Next, the potential
distribution of one species determined from the ENM containing only environmental
variables is evaluated, and regions of over-prediction are identified. These are found as
regions of ‘discord’ between the niche model and the known species distribution, where
the niche model predicts presence of the focal species that is not corroborated by the
known species’ distribution. Next, the species’ distribution is compared to the ENM
containing both environmental and biotic information, using the same procedure. Finally,
the two niche models are compared to identify regions that are not jointly predicted by
the two models. This procedure is repeated for both species when it is believed that each impacts the other’s distributional limits.

Through this procedure, several explicit (and testable) predictions concerning the relative influence of biotic and abiotic effects can be generated (Figure 3.1). For instance, regions where the boundaries of both niche models align well to one another and to the known species distribution (Figure 3.1A) are predicted to represent geographic regions where environmental characteristics are relatively more important in regulating the species’ distribution. This prediction is based on the fact that inclusion of biotic information did not substantially alter the predicted distribution. Such regions may represent distributional ‘breakpoint’ of an environmental variable (e.g., temperature), or an ecological boundary between distinct ecological zones (e.g., ecotones: [34]). Second, regions where the ENM from environmental variables over-predicts the range of the species but the ENM from environmental and biotic data displays less over-prediction (Figure 3.1B) are predicted to be regions where biotic characteristics are relatively more important in regulating the species’ distribution. For the case of potential competitors, this represents the testable hypothesis that competitive exclusion has occurred. Finally, regions where both ENMs display over-prediction are those where the environmental variables included in both models are insufficient to characterize the ecological niche of the focal species. This over-prediction may be a consequence of the presence of a barrier to dispersal ([35]). Alternatively, over-prediction may also reveal that the species being modeled occurs in the region outside of its currently known distribution ([9]).

Examples
To demonstrate the approach, we examined the distribution of several species of *Plethodon* salamanders. *Plethodon* are small, terrestrial salamanders found in the forests of North America. In the eastern United States, decades of field and laboratory research have documented their distributions, evolutionary relationships, ecological requirements, and the effects of species interactions on community dynamics (see [36]). Where species overlap geographically, interspecific competition appears to be common (e.g., [37,38]). Competition for food ([39]) and space ([7]) can be locally intense, and in some cases has driven morphological evolution in sympathy ([40]; [3]; [41]; [42]; but see [43]). Further, territorial aggression has restricted the geographic ranges of potential competitors (e.g., [7,37]), and patterns of community composition suggest that interspecific competition has structured communities at both a local and regional scales ([44]).

In the Southern Appalachian Mountains, the distribution of *Plethodon teyahalee* is, in part, regulated by abiotic factors ([17]), but strong competitive interactions have also been documented ([3,7,44,45]). Five closely related species (*P. Chattahoochee*, *P. chlorobryonis*, *P. cylindraceus*, *P. glutinosus*, and *P. yonahlossee*) have distributions that abut the range of *P. teyahalee*, and another (*P. jordani*) has a narrow range overlap with *P. teyahalee* ([7]). Research has shown that competitive interactions likely regulate their distributions as well ([7]).

**Example 1**

*Plethodon jordani* and *P. teyahalee* exhibit altitudinal distributions, with *P. jordani* inhabiting higher and *P. teyahalee* lower elevations (Fig. 2A). Additionally, all known syntopic localities containing both species are found in a narrow sympatric zone
at mid-elevations ([7,46]). Considerable research has documented the interactions between these species, and determined that competition is a dominant force regulating distributions of *P. jordani* and *P. teyahalee* ([3,44,45,47,48,49,50,51]), and limits the altitudinal distributions of both species, such that the zone of overlap between the two is relatively narrow. Thus, this example serves as a useful test case to determine whether our approach is capable of predicting where regions of competitive exclusion have previously been identified.

We used 846 geo-referenced *Plethodon teyahalee* and 361 *P. jordani* localities in the southeastern United States obtained from the United States National Museum of Natural History database to develop ecological niche models for both species. For each geographic locality, climate variables from the WORLDCLIM database ([52]) were extracted, and niche models for each species were created using Maxent (Phillips [12]): ENM generated using the MARS method ([19]) provided similar outcomes (Supplemental Material). Based on prior bioclimatic modeling of *Plethodon* salamanders ([17,42,53]), we used the following environmental variables: mean diurnal temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation seasonality, and precipitation of the driest quarter. Suitability scores (rescaled from zero to one) were projected onto the landscape, and suitable and unsuitable habitat was defined using the value at which model sensitivity equals specificity (this value was previously shown to be an appropriate measure for making binary predictions: see [27]). We then calculated the habitat suitability ratio for all grid cell localities, and generated a second ENM for each species using these values. ENM models with and without biotic information were then compared to develop predictions
regarding where abiotic features and biotic relationships were regulating these species distributions.

When only climate variables were used to generate the ENM, there was substantial over-prediction of the distributions of both species. Specifically, the entire range of *P. jordani* was predicted to contain suitable habitat for *P. teyahalee*, yet throughout much of this range *P. teyahalee* is not present (Figs. 2a and 2b). Similarly, the abiotic niche model for *P. jordani* demonstrated noticeable over-prediction, suggesting that the distribution of this species should extend far into the range of *P. teyahalee*. Thus, when these two niche models were overlaid (Fig. 2B), they suggested that much of this region should be jointly occupied by both species (Fig. 2B), with *P. teyahalee* inhabiting high elevations, sympatrically with *P. jordani* throughout its entire range, and *P. jordani* extending its range to lower elevations into much of *P. teyahalee*’s range. These predictions are not consistent with known locality data based on over 1,200 museum records for the two species. Finally, no obvious barriers to dispersal were identified for either species.

Using the chi-square approach above and all USNM salamander localities in the Great Smoky Mountain National Park, we found significantly less overlap between species distributions than was expected (*X^2 = 315; P <0.001*), implying that the two species have competitively limited each other’s’ distributions. We therefore generated niche models that incorporated biotic information. In contrast to the ENM generated only from environmental variables, niche models incorporating biotic characteristics exhibited considerably less over-prediction for both species, and the predicted distributions of both species corresponded much more closely to their actual distributions as compared to what
was predicted with environmental data alone. Further, when the biotic niche models for the two species were overlaid, the resulting predicted zone of sympatry was nearly identical to the known altitudinal zone where these two species are observed to be syntopic (Fig. 2C). Thus, this model provided a considerably better prediction of the distributions of both species, as well as their regions of geographic overlap.

Finally, comparing ENM based on environmental data alone to those that incorporated biotic information, we hypothesize that the regions of over-prediction in niche models based solely on environmental characteristics largely represented geographic regions where biotic interactions (here competition) were relatively more influential. In other words, in this example, our approach has identified distinct geographic regions where competitive exclusion is hypothesized. As considerable ecological research has already been performed on this system, we can confirm that our predictions are upheld by additional biological data (e.g., [7] [3,45]). Thus, in this case, our approach appears to correctly generate predictions of ecological interactions responsible for species distributions, as well as accurately predict the distributions themselves.

Example 2

Our second example depicts a scenario where corroborating ecological data have not yet been collected, thereby allowing us to generate hypotheses that can be empirically tested in future field studies on this system. Here we examine the distributions of *P. teyahalee* and *P. cylindraceus* (Fig. 3A). Extensive field collecting in this region has indicated that these two species do not co-occur at any locations; thus these two species are completely
parapatric. We generated environmental niche models for each of these two species, using the 846 geo-referenced localities for *P. teyahalee*, and 543 geo-referenced localities for *P. cylindraceus*, using the same bioclimatic variables as in the previous example. We then calculated the suitability ratio between models, and generated niche models containing biotic and environmental information. All models were then compared following the procedures described above.

As with the previous example, when using only climatic variables, the niche models display a broad region of potential co-occurrence between the two species (Figure 3.3B). The model for *P. teyahalee* indicated that much of the distribution of *P. cylindraceus* contains suitable habitat. The converse was also true; the range of *P. cylindraceus* could extend well into the distribution of *P. teyahalee* (Figure 3.3B). These predictions are not supported by the extensive known locality data for the species. We note that while the French Broad River does appear to separate the species’ distributions, it is not a complete barrier to dispersal, as one of the species (*P. teyahalee*) has been found on both sides of this potential dispersal barrier.

When the ratio between the two species initial abiotic niche models was used as an environmental layer, the projected niche model showed a highly reduced area of potential coexistence (Figure 3.3C). Further, the boundary between suitable habitats for both of these species aligned well with their actual distributional limits. Thus, both over- and under-prediction were minimized by using the ratio of the two species abiotic niches as an environmental layer in this geographic region. From this we hypothesize that biotic interactions are primarily responsible for the parapatric contact zone between the two
species, as the model incorporating biotic effects very closely matches the known distributions of the two species.

**Discussion**

Understanding the forces responsible for regulating species distributions is a fundamental question in ecology. Computer-intensive methods such as ENM provide a powerful tool for examining the environmental influences on species ranges, but these models typically do not consider biotic influences on species’ distributions. In this paper, we described an extension of current approaches that allows the incorporation of biotic data into ecological niche models. When combined with existing approaches, this method provides a means of developing testable hypotheses regarding how and where environmental and biotic processes limit a species’ distribution.

In the examples presented here, we used the ratio between two species niches to exemplify the use of niche models to develop hypotheses regarding where competition may regulate a species distribution. We note however, that other types of biotic interactions will require different formulations of the method. For example, while competitive interactions generally have a negative effect on species’ distributions, mutualistic interactions are generally additive. Thus, rather than a ratio of suitability scores, we propose that mutualistic interactions be represented through an addition or multiplication of their niche models. Alternatively, one mutualist may be represented as an additional data layer for the second species, as a presence-absence data layer or an index of relative abundance, though in this case the strength of the mutualism across the
landscape is not considered. Similarly, the effects of predation could be incorporated by obtaining a data layer representing predator population density or habitat suitability, and including it in the niche model. Alternatively, incorporating prey densities (or other resources) could be included as an additional environmental layer in a model. The efficacy of these proposed methods should be investigated through future research, using known study systems, such as those exemplified here for the case of competition.

The approach we present here may be used to generate testable hypotheses regarding how and where abiotic and biotic factors influence the distribution of a focal species. When compared to the known distribution of the species, this allows complementary prediction of where a species boundary is regulated by the abiotic environment and where it is limited by biotic interactions. In our examples, we identified regions where both niche models aligned well with one another, and to the known distribution of the species. By contrast, several geographic regions were found where the model based on biotic and environmental data more closely aligned with the known species distribution, while the niche model from environmental factors alone exhibited considerable over-prediction. In these cases, we hypothesize that biotic effects from potential competitors are a likely determinant of boundaries in these regions (i.e. competitive exclusion). We note that these hypotheses are based only from the niche models and the known distribution of the species. However, it should be emphasized that they are empirically testable hypotheses and we believe that this simple, logical procedure offers considerable utility for hypothesizing where biotic and environmental pressures are relatively more influential in range limitation.
It should also be noted that the results presented here do not appear to be an artifact of the Maxent algorithm. Some ENM algorithms may have a problem in transferability into areas where the species has not been sampled [54]. Thus, we compared the results shown here with the MARS ([19]) algorithm (Supplemental Material). The results were quite similar (Supplemental Material). Further, in a comparison of niche modeling algorithms, both Maxent and MARS performed well compared with other niche modeling procedures ([23]).

One potential weakness of our approach is that the results of the biotic model may reflect an artifact of using a ratio of the abiotic models as the environmental layer in this model, generating potential discontinuities in the environmental data space. However, our approach is based directly on the observable locations of the species in geographic space, and these observations result in predictions of environmental tolerances for each species. Thus, it is the original locations of the species, not their location in the ‘multidimensional niche’ that drives the predictions from our model. Finally, ecological niche modeling approaches have been demonstrated to reflect carrying capacities ([55]). If these two species have similar ecological function and competitive abilities (competition coefficients are approximately equal to 1), then the difference in carrying capacities should indicate whether or not the two species are able to co-exist at a given location. Similarly, our approach captures the relative carrying capacities of each species in each geographic location, and thus provides a hypothesis of the relative interaction strength between them.

It is well recognized in ecology that both biotic and abiotic pressures influence community dynamics and the distribution of species ([5]), but relatively few studies
examine both simultaneously. In this paper, we described an approach that incorporates biotic data along with abiotic in ecological niche modeling, and provided a procedure for developing hypotheses regarding what pressures may limit a species occurrence in particular locations. This approach complements current ENM procedures, and we believe it will benefit our understanding species distributions by examining its relationship between both abiotic and biotic environmental characteristics, and placing these in a geographical framework to determine where each is relatively more influential.

Acknowledgements

We thank Addison Wynn and the USNM staff for providing the locality data. We also thank Chelsea Berns, Jennifer Deitloff, Erin Myers, Leslie Rissler, Nicole Valenzuela and Brian Wilsey for comments on earlier versions of this manuscript, Kumudan Grubh for assistance with GIS, and A.T. Peterson for important discussions. This work was sponsored in part by NSF grant DEB-0446758 to DCA.

Literature Cited


Figure 3.1. Conceptual model depicting our approach. The example represents one possible outcome (see text for discussion). A) Area in dark gray represents the predicted distribution of the focal species based on abiotic variables. This ENM contains both the actual species distribution (solid outline) and a region of overprediction (dashed outline). B) Area in dark gray represents the predicted distribution of the focal species based on abiotic and biotic information. The difference between the two niche models is shown in light gray. Comparing the two niche models allows testable predictions to be formulated. In this case, one would predict that the original region of overprediction was due to the biotic interactions of a second species, which was taken into consideration in the second ENM.
A. Area of overprediction

B. True species distribution

[Diagram showing the overlap and area of overprediction between two geographic distributions]
Figure 3.2. A) Distributions of *P. jordani* (green circles) and *P. teyahalee* (yellow circles), and sympatric localities (gray diamonds) in the southern Appalachian mountains. Contour lines designate 800M and 1,400M elevations. All known sympatric localities for these two species are found within this elevational band. B) Predicted geographic distributions for both species based on ecological niche modeling, generated separately for each species using only environmental data. Yellow represents geographic regions predicted to be suitable for *P. teyahalee*, and gray represents geographic regions predicted to be suitable for both species (i.e. sympatry). There is no region predicted to be suitable for only *P. jordani* based solely on environmental parameters. C) Predicted geographic distributions for both species based on ecological niche modeling, generated separately for each species using both environmental and biotic information, generated from the ratio of suitability scores from ENM for the two species. Here, the predicted region of sympatry aligns nearly perfectly to the known sympatric region for the two species, and allopatric regions align well for each species.
Figure 3.3. A) Distributions of *P. cylindraceus* (circles) and *P. teyahalee* (triangles) in the southern Appalachian mountains. Dashed line represents the approximate boundary between the two distributions. B) Predicted geographic distributions for both species based on ecological niche modeling, generated separately for each species using only environmental data. Yellow represents geographic regions predicted to be suitable for *P. teyahalee*, gray represents geographic regions predicted to be suitable for both species (i.e. sympatry), and the green area represents geographic areas suitable to *P. cylindraceus*. C) Predicted geographic distributions for both species based on ecological niche modeling, generated separately for each species using biotic information, generated from the ratio of suitability scores from ENM for the two species. Here, the predicted region of sympatry aligns nearly perfectly to the known boundary separating the two species region for the two species.
Supplement

Methods

To determine if the results from the Maxent models were an artifact of the Maxent algorithm, we took the same approach to distribution modeling, but using the multivariate adaptive regression spline (MARS) method developed by Elith and Leathwick (2007). All models were run using R 2.8.1 (R Development Core Team 2008), using the script in the supporting information for Elith and Leathwick (2007). Model results were then projected using ArcView 3.3 (ESRI 2002). The rest of the methodology here is the same as for the Maxent models:

1. Project model onto continuous landscape from abiotic variables
2. Standardize the projection to range from 0 to 1
3. Take the ratio of the model results
4. Log-transform this ratio
5. Use the log-transformed ratio layer for subsequent niche models for each species.

Results

For the first example where we looked at the potential competitive effects between *Plethodon teyahalee* and *P. jordani*, we found the results for be very similar. Again, the abiotic niche models for both species indicated a high degree of overprediction (Figure 1A). The subsequent, biotic niche model, again accurately predicted the geographic
region where the species are known to co-occur, as well as where they occur allopatrically.

Also, the results for the relationship between *P. teyahalee* and *cylindraceus* were similar. The abiotic niche models indicate a broad area of potential sympatry. The second model which used the ratio method indicated sparse areas of potential sympatry which more accurately reflects the true distributions of these two species.
Figure 1. A) Distributions of P. jordani (green circles) and P. teyahalee (yellow circles), and sympatric localities (gray diamonds) in the southern Appalachian mountains. Contour lines designate 800M and 1,400M elevations. All known sympatric localities for these two species are found within this elevational band. B) Predicted geographic distributions for both species based on ecological niche modeling, generated separately for each species using only environmental data. Yellow represents geographic regions predicted to be suitable for P. teyahalee, and gray represents geographic regions predicted to be suitable for both species (i.e. sympathy). There is no region predicted to be suitable for only P. teyahalee based solely on environmental parameters. C) Predicted geographic distributions for both species based on ecological niche modeling, generated separately for each species using both environmental and biotic information, generated from the ratio of suitability scores from ENM for the two species. Here, the predicted region of sympathy aligns nearly perfectly to the known sympatric region for the two species, and allopatric regions align well for each species.
Figure 2. A) Distributions of P. cylindraceus (circles) and P. teyahalee (triangles) in the southern Appalachian mountains. Dashed line represents the approximate boundary between the two distributions. B) Predicted geographic distributions for both species based on ecological niche modeling, generated separately for each species using only environmental data. Yellow represents geographic regions predicted to be suitable for P. teyahalee, gray represents geographic regions predicted to be suitable for both species (i.e. sympatry), and the green area represents geographic areas suitable to P. cylindraceus. C) Predicted geographic distributions for both species based on ecological niche modeling, generated separately for each species using biotic information, generated from the ratio of suitability scores from ENM for the two species. Here, the predicted region of sympatry aligns nearly perfectly to the known boundary separating the two species region for the two species.
CHAPTER 4. WHY A SPECIES LIVES WHERE IT DOES: INSIGHTS FROM POPULATION DYNAMIC MODELING OF SALAMANDER DISTRIBUTIONS IN THE SOUTHERN APPALACHIAN MOUNTAINS

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Running Head.- Population modeling of salamander distributions

Keywords: biogeography, competition, ecological niche modeling, \textit{Plethodon}, range restriction, population dynamic modeling
Abstract

Understanding the roles of local and regional processes on local community structure and broad biogeographic patterns is one of the unifying questions in ecology and evolutionary biology. The outcomes of local processes, such as interspecific competition, can vary depending upon broad-scale environmental gradients. Thus, to develop a complete understanding of the effects of local or regional processes on species distributions, both must be taken into consideration. In the southern Appalachian Mountains, *Plethodon teyahalee* has a distribution that abuts several other closely related species, and occurs syntopically with several other *Plethodon* species. Previous research has indicated that competition likely restricts local community membership with one of these other species, while competition is minimal in other parts of its distribution. In this study, we used spatially-explicit population dynamic simulations to assess the relative role of competition across environmental characteristics with one of the sympatric species, and three species which have abutting parapatric distributions. Our simulations included density dependence, competition, and dispersal, as well as consideration of environmental factors across the actual landscape. Parameterization of the models was based on biologically-informed values derived from previous research in this genus. We assess several different competitive scenarios, from low to intense competition, and compare these results to known distributions of these species. Our results suggest where competitive interactions appear to limit species distributions, and how these outcomes are mediated by environmental conditions.
**Introduction**

One of the central objectives of ecology is determining the mechanisms regulating species geographic distributions, and how these factors vary geographically. Distributions may often be set by a change in environmental characteristics across which the species in question is not adapted to sustain itself. Other times, environmental changes are more subtle, and a species’ range limits are set by other factors, such as interspecific competition. Often, the boundaries of a species’ distribution abut those of ecologically similar species, resulting in parapatric distributions (Bull 1991; Darwin 1859). Outcomes of local interspecific competition between these ecologically similar species can depend upon the intensity of the competition and the carrying capacities of the competing species. In instances where there is intense and symmetric competition between two species, the species with the higher carrying capacity will often competitively exclude the other species (Gotelli 1998). Recently, there has been considerable interest in how local, biological processes ‘scale-up’ to regional patterns of co-occurrence (Gotelli et al. 2010). Ecologists have long been interested in assessing patterns of competition. Community assembly rules have been used, in various forms, to assess the role competition for regulating local community structure (Diamond 1975; Weiher and Keddy 1999; Ulrich and Gotelli 2010). Here, patterns of presence and absence of species are evaluated across several communities, and evaluated to determine whether or not species co-occurrence is less than expected by chance. Further developments of these methods have included analysis of guild structure (Fox 1987), and local community assembly constrained by environmental characteristics (Pere-Neto et al. 2001). However, there has been less research on how species geographic distributions are constrained by local processes, such
as competition, and how these interact with regional processes, such as changes in population characteristics across broader biogeographic regions (see e.g. Goldberg and Lande 2007).

In recent years, ecological niche modeling (ENM) techniques have proven useful in evaluating how species distributions relate to abiotic characteristics of the environment (e.g., climate, soil characteristics, landcover, etc.). These methods model environmental characteristics at locations where a species is known to occur, and project these onto the landscape to determine where the species is likely to occur (Peterson 2001; Raxworthy et al. 2007). Ecological niche models are increasingly used to evaluate ecological and evolutionary hypotheses that attempt to understand what factors are responsible for the geographic distributions of species (reviewed in Elith and Leathwick 2009; Kozak et al. 2008). For instance, Wiens et al. (2006) constructed ecological niche models for tropical Hylid frogs using different sets of environmental variables, and found that temperature seasonality was the most influential environmental variable in constraining the northern boundaries of these species. Recently, it was also shown that niche models can be used to predict the upper limit of populations at local scales (VanDerWal et al. 2009). As such, ENM can be used to estimate the overall carrying capacity of a species in a local community as based on its environmental niche. Oftentimes however, a species does not occur in all geographic locations where it is predicted by these models. There are a number of possible explanations for such model overprediction. For instance, Anderson (et al. 2002) identified competition as a potential mechanism associated with overprediction. Other reasons for overprediction may include barriers to dispersal (Elith and Leathwick 2009). When competitive effects are suspected, one logical step in
assessing this hypothesis is to build population models across the geographical area (with and without competition), and determine when and where the populations reach their estimated carrying capacities as set by the ecological niche model. Following this, several competitive scenarios may be directly applied to the local communities, and their results may be compared to the actual, observed, distributions to assess the potential effects of different competitive scenarios (see e.g., Goldberg and Lande 2007).

The salamanders of the genus *Plethodon* are an ideal system for understanding the effects of environmental pressures and species interactions on community composition and species distributions. *Plethodon* are long-lived terrestrial salamanders found in North American forests and extensive field collecting at thousands of geographic localities has documented their geographic distributions (Highton 1995). Some species in the genus display broad geographic overlap with one another, while other species exhibit distributions that are geographically distinct, some with extensive parapatric boundaries. Previous ecological research has documented how population demographics (Hairston 1980), and interspecific competition determine local community structure (Jaeger 1970; Hairston 1980; Anthony et al. 1997; Marshall et al. 2004). In some instances, interspecific competition has restricted the geographic distributions of ranges of potential competitors (e.g., Jaeger 1970; Hairston 1980; Griffis and Jaeger 1998), and likely influences community composition at both local and regional scales as well (Adams 2007). Finally, geographically–isolated, sister species display similar climatic niches, a pattern consistent with phylogenetic niche conservatism (Kozak and Wiens 2006). These results imply that climatic factors can also influence the distributions of particular *Plethodon* species. Taken together, this body of ecological work suggests that both
environmental niche characteristics and species interactions are important in defining and regulating the geographic distributions of salamanders in the genus *Plethodon*.

*Plethodon teyahalee* provides a unique opportunity to examine the relative influences of environmental characteristics and species interactions on range limits and species boundaries. The geographic distribution of this species is completely surrounded by the distributions of five other *Plethodon* species, each of which shares an extensive parapatric boundary with *P. teyahalee*. In addition, five other congeneric species are sympatric with *P. teyahalee*, displaying distributions that overlap with part of its distribution. When viewed in light of ecological theory and prior work on *Plethodon* (e.g., Hairston 1980; Adams 2004; Kozak and Wiens 2006), these distributional patterns generate several testable hypotheses which may be examined to reveal the mechanisms regulating community assembly and species distributional limits. For example, *Plethodon jordani* and *P. teyahalee* have been shown to have intense competitive interactions, which have resulted in a narrow region of sympatry between them (Hairston 1980; Nishikawa 1985; see also Adams 2004; 2010). Further, two species with parapatric distributions occupy geographic distributions in similar environments to *P. teyahalee* (Church and Adams Submitted). In these cases, we predict that competitive interactions may play a significant role in determining these geographic distributions. On the other hand, *Plethodon glutinosus* is a neighboring species whose distribution displays a distinct environmental niche (Church and Adams Submitted). Therefore, with respect to *P. teyahalee* and *P. glutinosus* we predict that competition has a relatively small influence on their parapatric boundary, which is instead driven more by differences in habitat (i.e. an ecotone boundary). Using a combination of environmentally-based ecological niche
models and simple Lotka-Volterra competition models, with and without dispersal, we elucidate 1: whether competition has an effect on pairwise species interactions, and if so, 2: how strong interspecific competition needs to be to result in observed local community assembly, and species geographic distributions.

In this paper, we examine how both environmental characteristics and interspecific competition can together determine the geographical distribution of *Plethodon teyahalee* using an approach which incorporates a population modeling across geographic space. We do this by estimating carrying capacities from standard ecological niche modeling methods for distinct geographically-defined populations across the landscape. We then evaluate the results of several competitive scenarios modeled using standard Lotka-Volterra competition in a spatially-explicit framework (both with and without dispersal), and compare these results to the realized distributional limits to assess how the relative effects of interspecific competition between congeners and adaptation to local environmental conditions may explain the distributional limits of *Plethodon teyahalee*.

**Methods**

**Modeling approaches**

We used several spatially-explicit modeling approaches to determine which competitive and dispersal scenarios might result in the currently observed geographic distributions of species. Here, we simulated population dynamics for a series of discrete populations (i.e., grid cells) across the landscape under different ecological conditions, where levels of interspecific competition and dispersal were varied. The estimated
species distributions obtained from these simulations were then compared to the currently observed species distributions to determine which ecological scenario best predicted the known ranges of these species.

First, a spatial grid was established that corresponded to the geographic region in which our study species of *Plethodon* are distributed (i.e. the Southern Appalachian Mountains). The study region for each species pair was divided into 2x2 km regions, and species distributions were examined in pairwise fashion. For the scenario between *P. jordani* and *P. teyahalee* a total of 1,450 cells were used as distinct populations. We used 9,919 cells for the scenario for *P. glutinosus* and *P. teyahalee*, 21,901 cells for *P. cylindraceus* and *P. teyahalee*, and 2,500 for *P. chattahoochee* and *P. teyahalee*. For all simulation scenarios described below, each grid cell was treated as a potential local population. All simulation models were run in R 2.12 (R Development Core Team, 2011).

The first simulation approach included density-dependent population growth as a base model, to which various competitive scenarios and dispersal between populations were subsequently incorporated. Here the discrete model of density-dependence was utilized:

\[
N_{t+1} = N_t + r_d N_t \left( 1 - \frac{N_t}{K} \right)
\]

where \( N_t \) is the population at time ‘t’, \( r_d \) is the instantaneous population growth rate, and \( K \) is the carrying capacity for that population. For each population (grid cell), the initial population density was set to \( (N_0 = 5) \). The carrying capacity for each local population
was estimated using ecological niche models of each species across the landscape (described below). The justification for this approach is based on the fact that ecological niche models can be used to determine the relative suitability of a particular location for the modeled species, which has been shown to be correlated with carrying capacity (VanDerWal et al. 2009). A variety of values for the instantaneous population growth rate \( r_0 \) were utilized (see Parameter estimation section below).

To estimate local carrying capacities for each species, ecological niche models were based on geo-referenced locality data from the National Museum of Natural History (Smithsonian Institution: see also Church and Adams, submitted). A total of 2,886 geo-referenced localities were used in this study, including: 846 geo-referenced localities for *Plethodon teyahalee*, 361 localities for *P. jordani*, 1,084 localities for *P. glutinosus*, 52 localities for *P. chattahoochee*, and 543 localities for *P. cylindraceus*. For each geographic locality, climate variables from the WORLDCLIM database (Hijmans et al. 2005) were extracted, and niche models for each species were created using Maxent (Phillips et al. 2006). Based on prior bioclimatic modeling of *Plethodon* salamanders (Kozak and Wiens 2006; Church and Adams Submitted), we used the following environmental variables: mean diurnal temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation seasonality, and precipitation of the driest quarter. The output of the models displays the probability of occurrence for each 1-km\(^2\) cell across the landscape. These cells were aggregated together to create 2x2km cells. To develop a realistic value of carrying capacity, the probability of occurrence for each cell (range: 0—1) was multiplied by a constant for all species (10,000). Thus, 10,000 represented the maximum density (carrying capacity) in a
given population. *Plethodon* are the most abundant vertebrates in North American forests. So this value, while relatively large, is biologically reasonable (see Burton and Likens, 1975; Hairston 1980). Note that increasing or decreasing this value would simply increase or decrease the number of simulated generations until equilibrium was reached.

We simulated density-dependent population growth separately for each grid cell population for each species, allowing the populations in each grid cell to reach carrying capacities as estimated from the local environmental conditions. A total of 200 generations were run for each simulation to allow populations to reach their equilibrium. Following this, all grid cells were evaluated for species occupancy, and a species was considered present in a grid cell if its final population density was at least 10% of carrying capacity (though results were robust to alternative choices of this cut-off value). From these, spatial maps of species distributions were generated and compared to the observed distributions for the two species.

In the second set of simulations, we incorporated potential competitive interactions between species. Here we used spatially-explicit Lotka-Volterra population models, and various levels of interspecific competition. The discrete competition models were parameterized using the following equation:

\[
N_{1t+1} = N_{1t} + r_d N_{1t} (1 - \alpha_{11} N_{1t} - \alpha_{12} N_{2t})
\]

Where \(N_{1t+1}\) is the population of species 1 at time \(t+1\), \(\alpha_{11}\) is a measure of intraspecific competition (i.e. density dependence), and \(\alpha_{12}\) is the competition coefficient measuring the effect of an individual of species 2 on species 1. Since there are now two species involved for each discrete generation, we implemented the above equation for both species at each time interval.
We evaluated several levels of interspecific competition by altering the competition coefficients (alphas) to range from low competition ($\alpha=0.5$) to high competition ($\alpha=1.0$). Additionally, we evaluated several scenarios where interspecific competition was asymmetric between the two competitors (e.g., $\alpha_{12}=0.5$ and $\alpha_{21}=1.0$). As with the density-dependent models, the Lotka-Volterra population models were run for 200 generations, and final population densities were used to estimate simulated species distributions for comparison to the observed species distributions (see above).

Subsequent to incorporating interspecific competition, the Lotka-Volterra population models were extended to also allow for dispersal between adjacent populations. Because we used a discrete-time Lotka-Volterra model, dispersal was easily incorporated at the end of each generation. We used rook-connections to identify adjacent populations and multiple levels of dispersal per generation were utilized (see below). Each of the spatially explicit models was run for 200 generations.

Parameter Estimation

The models described above contained a series of parameters for which initial parameterization was based on prior biological knowledge of these species from the literature, as described here.

*Instantaneous population growth rate ($r_d$):* Initial simulations were run for several values of the instantaneous population growth rate. However, because results did not vary greatly between these simulations (population densities simply reached carrying capacity in fewer or more generations), for all subsequent models, we set the $r_d = 1$, and ran the models for 200 generations.
Dispersal: Both field-based studies (e.g., mark-recapture) and population genetic studies have shown that dispersal rates in *Plethodon* are very low. The evidence for this is briefly summarized here. *Plethodon* are highly site-philopatric and territorial (Jaeger and Forester 1993), and mark-recapture studies reveal they display extremely small home ranges (10 - 25 m²: Kleeberger and Werner 1982). Defended territories are similarly small (less than a few square meters: Petranka 1998), and the same individual can be found under the same cover object (a rock or log) for months or even years (Gillette 2003). When displaced from their territory, *Plethodon* will return to the same cover object from distances as far as 90 meters (Kleeberger and Werner 1982); equivalent to 9,000 body lengths. As a consequence, dispersal rates per generation are thought to be quite low for this group (Highton 1995). Recent population genetics work has confirmed this notion, showing genetic differentiation in populations as close as 200m, with few migrants between populations at that distance (Cabe et al. 2007). Based on these observations, we selected dispersal levels between adjacent populations of 1, 5, and 10 percent.

Interspecific competition: We also ran the population models at several levels of interspecific competition between species. We used the following levels of competition coefficients: $\alpha = 0.5, 0.6, 0.7, 0.8, 0.9, \text{ and } 1.0$. The first set of competitive models were symmetric, where $\alpha_{1,2} = \alpha_{2,1}$. However, because competitive effects between *Plethodon* species have been found to be asymmetric in at least one instance (Hairston 1980: also Nishikawa 1985), we additionally ran a series of models which incorporated varying degrees of competitive asymmetry. Here, the two competition coefficient for one species
was set at 1.0, and competition coefficient for the second species ranged from 0.5-0.9. We than ran these models again, using the converse scenarios.

Species Simulations

We ran pairwise species simulations (described above) for *Plethodon teyahalee* versus three other species whose distributions abut with it, and versus one species with a narrow sympatric zone at the border of its distribution with *P. teyahalee*. Based on prior ecological work on this genus, the distributions of these four species pairs were expected to be the result of distinct ecological interactions between species and the environment. For example, previous work suggests that intense interspecific competition plays a key role in maintaining the narrow sympatric distribution between *Plethodon teyahalee* and *P. jordani* (Hairston 1980; Nishikawa 1985; Adams 2004). By contrast, the boundary separating the geographic distributions of *Plethodon glutinosus* and *P. teyahalee* aligns well with an environmental ecotone: most of the known populations of *P. glutinosus* occur in the Ridge and Valley ecoregion, while the vast majority of *P. teyahalee*’s distribution occupies the Southern Blue-Ridge ecoregion (Highton 1989; 1995). Due to the sharp transition in habitat at this boundary, we hypothesize that habitat factors regulate this boundary (see also Church and Adams, submitted). The final two remaining species included in this study have parapatric distributions with *P. teyahalee*. *Plethodon cylindraceus* occurs to the north and east of *P. teyahalee*’s distribution, while *P. chattahoochee*’s distribution is south of *P. teyahalee*. Both of these species occur in the same ecoregion as *P. teyahalee*, and previous work suggests that these two species are ecologically similar to *Plethodon teyahalee* (Church and Adams Submitted). However,
fewer data are available for these species to make *a priori* predictions concerning their ecological relationships with *P. teyahalee*.

**Results**

For each species pair, we ran 48 models, incorporating three different levels of dispersal, and 16 models in which there was no dispersal. Simulation models reached their equilibrium state in fewer than 200 generations (e.g., Fig. 4.1). Our results indicated that the relative degree of interspecific competition may be important in maintaining the geographic distributions of many of these species. As a general summary of these models, for three of the four species which potentially interact with *Plethodon teyahalee*, we found that models with high competition coefficients were most concordant with actual geographic distributions (Table 4.1). For the last species, models with no interspecific competition aligned well with current geographic distributions, and incorporating low levels competition did not alter these patterns, suggesting that competitive interactions are less important in maintaining this distributional boundary. In this case, the ecotonal boundary between distinct environments appears to be limiting range expansion of *Plethodon teyahalee*. Results for each pairwise scenario are described in more detail below.

*Plethodon jordani* x *P. teyahalee*

Throughout most of their ranges, the observed distributions of *Plethodon teyahalee* and *P. jordani* are separated altitudinally. Each species is found allopatric with respect to the other, with the exception of a narrow sympatric region at mid-elevations (Hairston 1980; 1983; Highton 1989). Considerable prior work on these species has
demonstrated that intense competition regulates this narrow zone of sympatry, and likely restricts the range of one or both species (Nishikawa 1985; Hairston 1980; also Adams 2004; 2010).

When our simulation models lacked competitive interactions, the predicted distribution of *P. teyahalee* did not match its current distribution, and extended far beyond the observed borders of the species’ range. Under these scenarios *P. teyahalee* was predicted to occupy the entire distribution of *P. jordani* (Figure 4.1): a condition not currently observed in nature. Further, when low to moderate levels interspecific competition were included in the models (α =0.5-0.7), this pattern persisted.

By stark contrast, when intense levels of competition were used (α =0.9-1.0), the predicted distributions from the model resembled the actual species’ distributions (Figure 1). Further, intense competition and low levels of dispersal displayed a similar pattern concordant with the observed distributions (Figure 4.1; Table 4.1). Finally, when asymmetric competition was examined, we found that the predicted distributions aligned well with the observed geographic distributions for the species only when *Plethodon jordani* had a greater competitive effect on *P. teyahalee*. When the converse scenario was examined, the predicted distribution of *P. teyahalee* far exceeded its observed limit, and in fact this species outcompetes *P. jordani* in a substantial portion of the distribution. These findings are notable, in that they match predictions based on interspecific behavior, where it was found that *P. jordani* is far more aggressive in territorial encounters as compared to *P. teyahalee*, suggesting that *P. jordani* could have a greater negative effect on *P. teyahalee* than the converse (Nishikawa 1985). However, these findings (and those of Nishikawa 1985) do not match competition coefficients estimated by Hairston (1980),
where the reverse relationship was found. Finally, increasing levels of dispersal did not significantly alter the observed patterns (Figure 4.1).

In conclusion, the simulation models for *P. jordani* and *P. teyahalee* that best predicted their observed distributions were those where competition was intense, and where *P. jordani* had a greater competitive effect on *P. teyahalee.*

*Plethodon glutinosus* x *P. teyahalee*

*Plethodon teyahalee* and *P. glutinosus* have abutting distributions that align with an ecotonal boundary (Highton 1989). Prior ecological work suggests that the distributions of these species are more intensely affected by environmental characteristics than they are by interspecific competition (Church and Adams submitted).

When the density dependent models lacked competitive interactions, the distribution of *P. teyahalee* closely matched its observed range, and populations found beyond its known distribution persisted only at low population densities and did not reach carrying capacity. These patterns indicated a sharp change in habitat suitability for this species, which corresponded closely to the known ecotone. When interspecific competition was incorporated in the models, both low to high levels of competition resulted in similar patterns, suggesting that the inclusion of interspecific competition did not alter predicted species ranges. Thus, from these models, interspecific competition does not appear to be a major factor regulating the distributional limits of these two species with respect to one another (Figure 4.3; Table 1). Simulations evaluating the effects of asymmetric competition revealed that when *Plethodon teyahalee* had a greater negative effect on *P. glutinosus*, the distributional limits aligned well with observed geographic distributions. However, when we tested the reverse, the distribution of *P.*
*glutinosus* can extend into the distribution of *P. teyahalee* (Figure 4.3). Still at slightly greater (but still low) levels of competition against *P. glutinosus*, the distributions of both species align well with the boundary between these two ecoregions. Overall, these patterns match with predictions from previous work (Church and Adams submitted), suggesting that environmental characteristics, rather than competition, limits local co-occurrence.

**Plethodon cylindraceus x P. teyahalee**

*Plethodon teyahalee* and *P. cylindraceus* have abutting distributions. These two species are closely related (Kozak and Wiens 2006), occupy habitats with similar environmental characteristics (Church and Adams submitted), and display a high degree of similarity in trophic morphology (Church and Adams submitted). Thus, prior work suggests that interspecific competition may play a role in dictating their distributions and restricting range overlap (Church and Adams submitted).

In the simulation models lacking competitive interactions, *P. teyahalee*’s distribution was predicted to extend far beyond of its actual distribution, and under these scenarios *P. teyahalee* and *P. cylindraceus* distributions are predicted to have a wide distribution of co-occurrence (Figure 4.3). Further, when interspecific competition was included in the models, this pattern persisted for relatively moderate levels of competition ($\alpha = 0.5 – 0.7$). Thus, the predicted distributions under these scenarios did not match the observed species ranges. However, at low levels of competition, *Plethodon cylindraceus*, is predicted to be able to outcompete *P. teyahalee* at the point of contact separating these species distributions (Figure 4.3). Nevertheless, even in these scenarios *P. cylindraceus* is
still predicted to be excluded from much of the distribution of *P. teyahalee*. Interestingly, when the contact zone between species is examined, this is not the case, and both species are predicted to have a sharp parapatric boundary that corresponds with their actual distributions. Thus, for *P. teyahalee* to occupy portions of the range of *P. cylindraceus*, this species must migrate in a southerly direction to circumvent the contact region where it is not found. However, extensive sampling in this region has never found *P. teyahalee* in this region (Highton 1995; Highton and Peabody 2000). Further, several other species of *Plethodon* exist in this region, and these species may interact competitively with *P. teyahalee*, thereby limiting its dispersal through this region. Therefore, for the simulations described here, we conclude that this prediction from the Lotka-Volterra models is not biologically realizable, and that competitive effects from another species limit dispersal into this region.

By contrast, when levels of interspecific competition were intense (\(\alpha = 0.9-1.0\)), the predicted distributions from the model resembled the actual species’ distributions (Figure 4.3). Further, intense competition and low levels of dispersal displayed a similar pattern concordant with the observed distributions (Figure 4.3; Table 4.1). Models incorporating asymmetric competition indicated that if at least one of these two species has a strong negative effect on the other, the predicted distributions generally concur with actual distributions. These patterns suggest that strong interspecific competition plays a role in dictating the distributions of these two species, which is consistent with previous ecological observations (Church and Adams submitted).

*Plethodon chattahoochee* x *P. teyahalee*
Similar to the previous example, *Plethodon chattahoochee* and *P. teyahalee* also have abutting, parapatric distributions, and occupy similar environmental conditions, and have similar trophic morphology (Church and Adams submitted). In simulations incorporating only density-dependent population growth, the distribution of *Plethodon teyahalee* is predicted to overlap entirely with the distribution of *P. chattahoochee*; a pattern not seen in their current distributions (Figure 4.4). Results indicate that none of the symmetric competition models aligned with the current distributional limits of either species. However, models where asymmetric competition coefficients were used, results reflected current distributional limits (Figure 4.4). In this case *Plethodon chattahoochee* is predicted to have a greater negative impact on *P. teyahalee*, indicating that *P. chattahoochee* has a greater influence on inhibiting successful colonization of *P. teyahalee* within its distribution. This result of intense competition corroborates previous observations (Church and Adams submitted).

**Discussion**

The interplay between abiotic and biotic characteristics of the environment set the limits on contemporary species’ geographic distributions. First, abiotic environmental characteristics set the limit as to whether a species can persist and maintain a population in a particular geographic location. In this case, and organism’s ‘fit’ to a particular environment is determined by its degree of adaptation to environmental conditions; which results from natural selection across multiple generations inhabiting that environmental context. Additionally, it has long been known that interactions between species (e.g., interspecific competition) can have a pervasive influence on the structure of
local community assemblages, and therefore, on where a particular species may be found (Sexton et al. 2009). Further, the outcomes of interspecific competition can vary or be mitigated as a result of local environmental conditions (Chase and Leibold 2003). Thus, the effect of competition is the direct result of the interaction between the differential population characteristics of the interacting species to the abiotic environment, and the differing environmental conditions in which they are found.

In this study, we demonstrate how population ecological models can be used to assess the potential roles of competition and dispersal on setting the limits to species distributions. Here, we use niche models to assess species relationships to the abiotic environment to estimate local carrying capacity, and how this varied across species distributions. From this, we built spatially explicit Lotka-Volterra models to determine the influence of interspecific competition on the species distributions. We ran our models under several different competitive scenarios with both asymmetric and symmetric competition ranging from low to high levels of competition. This allowed us to determine which scenarios best matched currently observed species limits, allowing us to predict the influences of competition and environmental characteristics on these species distributions.

Our results corroborate previous research that found intense competitive interactions between *Plethodon teyahalee* and *P. jordani* regulate their narrow zone of sympatry and their geographic distributions. Nishikawa (1985) found that the relationship between these two species was asymmetric; with *P. jordani* having a stronger negative influence on *P. teyahalee*. Our results also support previous work that demonstrates that competitive interactions between *P. teyahalee* and *P. cylindraceus*; and
P. teyahalee and P. chattahoochee, regulate the boundary between these parapatric
distributions. Both Plethodon cylindraceus and P. chattahoochee occupy similar
environmental conditions as P. teyahalee, and have similar trophic morphology,
indicating similarity in resource utilization (Church and Adams Submitted). Finally, our
results also confirm that habitat characteristics are the primary determinant regulating the
boundary between P. teyahalee and P. glutinosus. The boundary between these two
species aligns closely with the boundary between the southern blue-ridge and the ridge
and valley ecoregions.

The findings further demonstrate how the interplay between environmental
characteristics and interspecific associations can set the limits to geographic distributions.
Understanding how these mechanisms interact is vital for understanding the
biogeography of species distributions. Evolutionary history and the influence of
adaptation to an environment directly determine where a species can live in the absence
of biotic interactions. Further, understanding how population characteristics vary across
environmental characteristics can influence the outcomes of competitive interactions.
Thus, local competitive relationships between species can have different outcomes which
are determined largely by local environmental conditions. This then allows for these local
interactions and population characteristics to ‘scale-up’ to large-scale, biogeographic
patterns.

Recently, there has been a great deal of interest in how processes operating at
different spatial scales generate patterns at broader distributions (Gotelli et al. 2010;
Ricklefs 2008). Further, Gotelli et al. (2010) points out that to understand species
distributions at large spatial scales, it is necessary to incorporate interspecific interactions
at fine spatial scales. In this paper, we were able to model species distributions with different levels of interspecific interactions, and by comparing results of the models at these different levels we are better able to predict the nature of these relationships.

Acknowledgements

We thank Addison Wynne for providing us with geographic locality data and Dr. Karen Abbot for valuable discussions concerning modeling approaches.

Literature Cited


Table 4.1. Competition coefficients which result in distributional limits consistent with observed species distributions. *Plethodon jordani, P cylindraceus,* and *P. chattahoochee* appear to have intense competitive interactions regulating the distributional boundaries. The distributional limit between *P. teyahalee* and *P. glutinosus* was reflected in models with moderate to high levels of competition.

<table>
<thead>
<tr>
<th>Species</th>
<th>$\alpha_{i,t}$</th>
<th>$\alpha_{t,i}$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Plethodon jordani</em></td>
<td>0.8-1</td>
<td>0.9-1</td>
</tr>
<tr>
<td><em>Plethodon glutinosus</em></td>
<td>0.7-1</td>
<td>0.5-1</td>
</tr>
<tr>
<td><em>Plethodon cylindraceus</em></td>
<td>0.5-1</td>
<td>0.8-1</td>
</tr>
<tr>
<td><em>Plethodon chattahoochee</em></td>
<td>0.8-1</td>
<td>0.9-1</td>
</tr>
</tbody>
</table>
Figure 4.1. Representative simulation results for *Plethodon jordani* (Blue), and *P. teyahalee* (Black) at one population over the 200 generations. A) Population simulations at low levels of interspecific competition ($\alpha=0.5$), allowing for stable coexistence. B) Simulation at the same population at high levels of interspecific competition ($\alpha=1.0$), where *P. teyahalee* eventually becomes locally extinct.
Figure 4.2. Results of the simulations for the competitive interactions between *Plethodon jordani* and *P. teyahalee*. For all models yellow and green designate allopatric regions and gray designates sympatry. The ‘*‘ indicates the model results which best aligns with the known distributions.

A) Distributions of *P. jordani* (red), and *P. teyahalee* (blue) in the southeastern United States. B) Distributions of *P. jordani* and *P. teyahalee* based solely upon density-dependent population growth (Carrying capacity). C) Distributions of *P. jordani* and *P. teyahalee* with interspecific competition (alpha=0.5). D) Distributions of *P. jordani* and *P. teyahalee* with interspecific competition (alpha=1.0). E) Distributions of *P. jordani* and *P. teyahalee* with asymmetric interspecific competition, with *P. jordani* being competitively superior to *P. teyahalee* (α_{tj}=1.0, α_{jt}=0.5). F) Distributions of *P. jordani* and *P. teyahalee* with asymmetric interspecific competition, with *P. jordani* being competitively inferior to *P. teyahalee* (α_{tj}=0.5, α_{jt}=1.0). G) Distributions of *P. jordani* and *P. teyahalee* with asymmetric interspecific competition, with *P. jordani* being competitively superior to *P. teyahalee* (α_{tj}=1.0, α_{jt}=0.5), and dispersal set to 5 percent.
Figure 4.3. Results of the simulations for the competitive interactions between *Plethodon glutinosus* and *P. teyahalee*. For all models yellow and green designate allopatric regions and gray designates sympatry. The ‘*’ indicates the model results which best aligns with the known distributions.

A) Distributions of *P. glutinosus* (red), and *P. teyahalee* (blue) in the southeastern United States. B) Distributions of *P. glutinosus* and *P. teyahalee* based solely upon density-dependent population growth (Carrying capacity). C) Distributions of *P. glutinosus* and *P. teyahalee* with interspecific competition (alpha=0.5). D) Distributions of *P. glutinosus* and *P. teyahalee* with interspecific competition (alpha=1.0). E) Distributions of *P. glutinosus* and *P. teyahalee* with asymmetric interspecific competition, with *P. glutinosus* being competitively superior to *P. teyahalee* (α_tg=1.0, α_gt=0.5). F) Distributions of *P. glutinosus* and *P. teyahalee* with asymmetric interspecific competition, with *P. glutinosus* being competitively inferior to *P. teyahalee* (α_tg=0.5, α_gt=1.0). G) Distributions of *P. glutinosus* and *P. teyahalee* with asymmetric interspecific competition, with *P. glutinosus* being competitively inferior to *P. teyahalee* (α_tg=0.7, α_gt=1.0) and dispersal at 5 percent,
Figure 4.4. Results of the simulations for the competitive interactions between *Plethodon cylindraceus* and *P. teyahalee*. For all models yellow and green designate allopatric regions and gray designates sympatry. The ‘*’ indicates the model results which best aligns with the known distributions.

A) Distributions of *P. cylindraceus* (red), and *P. teyahalee* (blue) in the southeastern United States. B) Distributions of *P. cylindraceus* and *P. teyahalee* based solely upon density-dependent population growth (Carrying capacity). C) Distributions of *P. cylindraceus* and *P. teyahalee* with interspecific competition (alpha=0.5). D) Distributions of *P. cylindraceus* and *P. teyahalee* with interspecific competition (alpha=1.0). E) Distributions of *P. cylindraceus* and *P. teyahalee* with asymmetric interspecific competition, with *P. cylindraceus* being competitively superior to *P. teyahalee* (α_{tc}=1.0, α_{ct}=0.5). F) Distributions of *P. cylindraceus* and *P. teyahalee* with asymmetric interspecific competition, with *P. cylindraceus* being competitively inferior to *P. teyahalee* (α_{tc}=0.5, α_{ct}=1.0). G) Distributions of *P. cylindraceus* and *P. teyahalee* with asymmetric interspecific competition, with *P. cylindraceus* being competitively inferior to *P. teyahalee* (α_{ij}=1.0, α_{cj}=0.8), and dispersal set to 5 percent.
Figure 4.5. Results of the simulations for the competitive interactions between *Plethodon chattahoochee* and *P. teyahalee*. For all models yellow and green designate allopatric regions and gray designates sympatry. The ‘*’ indicates the model results which best aligns with the known distributions.

A) Distributions of *P.chattahoochee* (red), and *P. teyahalee* (blue) in the southeastern United States. B) Distributions of *P. chattahoochee* and *P. teyahalee* based solely upon density-dependent population growth (Carrying capacity). C) Distributions of *P. chattahoochee* and *P. teyahalee* with interspecific competition (alpha=0.5). D) Distributions of *P. chattahoochee* and *P. teyahalee* with interspecific competition (alpha=1.0). E) Distributions of *P. cylindraceus* and *P. teyahalee* with asymmetric interspecific competition, with *P. cylindraceus* being competitively inferior to *P. teyahalee* (α_{tc}=0.5, α_{ct}=1.0). F) Distributions of *P. chattahoochee* and *P. teyahalee* with asymmetric interspecific competition, with *P. cylindraceus* being competitively superior to *P. teyahalee* (α_{tc}=1.0, α_{ct}=0.5). G) Distributions of *P. chattahoochee* and *P. teyahalee* with asymmetric interspecific competition, with *P. chattahoochee* being competitively superior to *P. teyahalee* (α_{tc}=1.0, α_{ct}=0.9) with 5 percent dispersal.
CHAPTER 5. GENERAL CONCLUSIONS

The mechanisms restricting the boundaries of species distributions have received a great deal of attention. Dispersal and successful colonization of habitats depends not only on an organism’s adaptation to environmental characteristics, but also on the ability to maintain a sustainable population in light of interactions with other species. Thus, to accurately depict the limitations of a species geographic distribution, one must assess both environmental restrictions, and interactions with other species, such as the ability to coexist with, or competitively exclude a competitor. In this dissertation, I examined the relative importance of different ecological factors in maintaining species ranges in several species of *Plethodon* salamander in the southern Appalachian Mountains.

In Chapter 2, I assessed the potential competitive interactions between salamanders of the genus *Plethodon* and environmental characteristics within and between distributions of several species which come into contact. To evaluate the potential for competition, I used trophic morphological characteristics. Using morphology as a surrogate for competitive interactions has a long history in ecological research (Hutchinson 1959; Ricklefs and Travis 1981). I also evaluated niche overlap in the environmental characteristics of the species distributions. In cases where species occupied distinct environmental niches, I predicted that environmental characteristics regulated the parapatric boundaries between species. Where species with parapatric distributions occupied similar environmental niches, I predicted that competition was relatively more important in regulating the distributions of these species. As further evidence of this, morphological characteristics were more similar between species with these parapatric distributions than among sympatric species. My results were consistent
with these predictions, demonstrating that both processes were operating to regulate
*Plethodon* distributions. As a consequence, both the theory of limiting similarity (sensu
Macarthur and Levins 1967) and environmental sorting are important in regulating local
community structure and the geographic distributions of these species.

In chapter 3, I developed a new method of ecological niche modeling to further
assess how environmental characteristics are related to species distributions of *Plethodon*
salamanders. Ecological niche modeling techniques provide a rigorous tool in assessing
limits to species distributions, and have been used in several applications in ecology,
evolutionary biology and biogeography. These models are often created using only
abiotic environmental variables. Here I demonstrated how ecological niche modeling can
be used to develop hypotheses regarding where biotic conditions may limit range
expansion. I exemplified this novel niche modeling approach for three species of
*Plethodon* salamanders, by comparing predicted distributions from standard niche
modeling techniques to those obtained from the new method that incorporates biotic
information. Niche models incorporating a biotic layer for potential competitors provided
a better estimate of known species distributions than using only environmental data layers
alone. Additionally, comparing these models enabled the generation of testable and
predictive hypotheses regarding where geographically abiotic and biotic features
appeared to limit species’ distributions. These predictions were confirmed for one set of
species where previous ecological research (Hairston 1980; Nishikawa 1985) has shown
that competitive interactions between these two species inhibit range expansion to
otherwise suitable environmental conditions. This niche modeling approach complements
existing procedures by developing explicit and testable hypotheses regarding whether
environmental characteristics or biotic interactions limit the geographic distribution of a species.

In chapter 4, I assessed how local interspecific competition, while taking environmental gradients into account, can explain species geographic distributions. Here I used spatially-explicit population dynamic simulations to assess the relative role of competition across environmental characteristics with one of the sympatric species, and three species which have abutting parapatric distributions. First I expanded on chapter three and used ecological niche models based on environmental characteristics to predict carrying capacities for interacting species across the landscape. This was then incorporated into spatially-explicit population dynamic simulations that included density dependence, competition, and dispersal, as well as consideration of environmental factors across the actual landscape. Parameterization of the models was based on biologically-informed values derived from previous research in this genus. Using this modeling approach I assessed several different competitive scenarios, from low to intense competitive dynamics, and low to high dispersal, and compared these results to known the known distributions of these species. The models that most closely matched the known distributions allow us to make inferences on the intensity and symmetry of competition between pairwise species. Our results show that in some instances competition was important in maintaining the geographic distributions while in other cases competition was not as important. Results from the simulations were consistent with previous ecological work, further corroborating these conclusions. Further, our results demonstrate how the outcomes of these interactions are mediated by the separate species’ relationships to the environment. Thus, in conclusion, the geographic
distributions of these species appear to be dictated by the interplay of interspecific competition and environmental characteristics at specific geographic locations.

Future Research

The results of these studies indicate that it is the interplay between environment and interspecific competition that regulates these species distributions. All of these results generate testable hypotheses which can be confirmed through carefully designed field-based studies to assess the validity of these conclusions (similar to those of Chapter 2), and to develop a better understanding of the mechanisms regarding species relationships to the abiotic environment, and the mechanism of interspecific competition. This work also shows how simulation modeling techniques (particularly ecological niche modeling) can inform on the ecological factors that regulate species’ distributions. However, while these methods are being used with increasing frequency in recent years, it is important to remember that ecological niche models (as typically implemented) are generally phenomenological. Developing new and enhanced approaches that incorporate additional biological realism (such as the method proposed in Chapter 3) would provide a closer link between simulation studies and field-based ecological observations. A thorough understanding of life-history characteristics, population demographics, and other responses to environmental conditions would provide some much needed rigor to standard ENM and other modeling approaches, and incorporating this information would better explain a species’ characteristics, thus allowing for a more mechanistic understanding of how the environment restricts species distributions.

Finally, the work in this dissertation further demonstrates that interspecific competition is common in the salamanders of the genus *Plethodon*. However the means
of competition, interference or consumptive, cannot be known based solely on these results. In chapter 2 I assessed patterns of variation in trophic morphology, which is often associated with resource utilization. My findings suggested that competition for food resources may likely be the form of interspecific competition. However, morphological traits have also been found to be associated with territorial defense and aggression (Adams 2004; 2010). Thus, empirical models incorporating resource utilization and availability across the environmental characteristics are needed to more completely assess the resource-competition hypothesis. Further, studies assessing interference competition, and how the outcomes of this may be influenced across the ranges of these species would also be necessary to test my conclusions.

**Literature Cited**


ACKNOWLEDGEMENTS

This dissertation would not have been possible without the aid of several people and organizations. First, I thank my professor Dr. Dean Adams. Throughout my time at Iowa State University, Dr. Adams has aided in my development as a student and a philosopher of science. I thank him for his continued criticism and encouragement, and for consistently making himself available to me when I required guidance. I also thank my committee members: Drs. Anne Bronikowski, Brent Danielson, Lisa Schulte-Moore, and Brian Wilsey. I thank them all for their encouragement, criticism, and support.

Next I thank the Department of Ecology, Evolution and Organismal Biology for accommodating me, and supporting me financially through assistantships. I thank the faculty of this department, notably Drs. Stan Harpole and Karen Abbot for conversations related to my research, and for their encouragement. I thank Addison Wynne for accommodating my use of the salamander collections at the Smithsonian’s Natural History museum. Addison shared his experiences with *Plethodon* salamander which were invaluable to me, and I also thank him for accommodating my visits to the museum’s collections.

Finally, I thank my fellow graduate students in the Departments of Ecology, Evolution and Organismal Biology, and Natural Resources Ecology and Management. My fellow students assisted me in a variety of ways, from dealing with technical details of GIS, sharing their varied perspectives, and their continued moral support. Over the past six year, I have had the tremendous opportunity to work with some of the greatest people that I have ever known. I appreciate all of the time that I have shared with these people, and I could not have completed this without them.