

FACTORS LIMITING THE DISTRIBUTIONS OF TRAILING-EDGE POPULATIONS IN  
THE SOUTHERN APPALACHIAN MOUNTAINS

by

SAMUEL ALFRED MERKER

(Under the Direction of RICHARD CHANDLER)

ABSTRACT

The ranges of many species are shifting toward higher latitudes because of climate change, affecting the viability of many trailing-edge populations. Forecasting the dynamics of these populations requires information about the factors limiting their distributions. To understand the roles of abiotic and biotic factors in limiting trailing-edge populations of bird species in the southern Appalachian Mountains, I collected three years of point count data and conducted two manipulative experiments. One manipulation used simulated territory intrusions to understand the role of interference competition between a cool-adapted species (*Cardellina canadensis*) and warm-adapted species (*Setophaga citrina*). The other used playback to assess the role of socially-mediated Allee effects in limiting the distribution of *C. canadensis*. My results indicate that trailing-edge populations of cool-adapted species are more strongly affected abiotic factors than by competition with warm-adapted species. In addition, I found no evidence that socially-mediated Allee effects limit the distributions of trailing-edge populations.

INDEX WORDS: Abiotic, aggression, Allee effects, biotic interactions, Canada warbler, climate change, hooded warbler, interference competition, range limits, social information

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SAMUEL ALFRED MERKER

AS, Johnson & Wales University, 2006

BS, University of New Hampshire, 2010

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SAMUEL ALFRED MERKER

Major Professor:	Richard Chandler
Committee:	Robert Cooper
	Jeffrey Hepinstall-Cymerman
	Leonard Reitsma

Electronic Version Approved:

Suzanne Barbour  
Dean of the Graduate School  
The University of Georgia  
May 2017

## DEDICATION

In classic dedication form I dedicate this document and all the work that went into it to David Merker and Sharry Baker. Without their endless support this would not exist and I would not be here today. Thanks!

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## CHAPTER 1

### Introduction

The distributions of many species are shifting towards higher latitudes and elevations in response to climate change (Parmesan and Yohe 2003). Most studies of range shifts have focused on the dynamics of populations at the leading edge of an advancing range (Parisod and Joost 2010). Trailing-edge populations, in contrast, are often understudied even though they may face a high risk of extinction if they are unable to track climate change via dispersal or adaptation (Hampe and Petit, 2004). Loss of trailing-edge populations could negatively affect regional biodiversity because they represent a large segment of the species in some regions and because they are often genetically distinct from populations in the core of the range (Parisod and Joost 2010).

To understand how trailing-edge populations respond to climate change it is important to understand what factors limit their distributions. In the Americas, longitudinal range limits are often shaped by physical features such as the Rocky Mountains, with distinct groups of species occurring on either side of them. Conversely, in the Eurasian landmass longitudinal limits are often less clear due to a general east-west orientation of geographical features (Baselga et al. 2012). In the Americas, latitudinal limits are more enigmatic than longitudinal limits, occurring in the absence of predominant physical landforms (Cahill et al. 2014), but it is generally believed that populations near high latitude range boundaries are limited by climatic extremes like cold temperatures (Brown et al. 1996). The factors limiting species' distributions at lower latitudes are not well understood and have been the subject of debate for many years. Much of the debate has centered on the relative importance of abiotic versus biotic factors (Darwin 1859, MacArthur 1972,

Cahill et al. 2014). Many ecologists have hypothesized that warm-edge range limits are primarily set by biotic factors due to the increased possibility for interspecific interactions resulting from latitudinal trends in biodiversity (Darwin 1859, MacArthur 1972, Gross and Price 2000, Cunningham et al. 2009, Jankowski et al. 2010, Freeman and Montgomery 2016a). However, evidence also exists that abiotic factors, such as temperature and precipitation, can limit species at the warm-edge (Root 1988, Hampe and Petit 2005). Abiotic factors are studied more often because broad scale climate and environmental data are widely available and because biotic interactions can be very hard to identify in the field (Wiens 1992).

Each of these hypotheses is based on theory about the processes limiting species' distributions and population dynamics at range margins. For individuals at the warm-edge, where a species may be at its physiological limit, climate change may negatively impact physiology, potentially affecting metabolism and reducing reproductive ability (Hoffmann and Blows 1994, Sekercioglu et al. 2008). A recent study of Shiras moose (*Alces alces shirasi*) showed that reproductive rates decreased over three decades in trailing-edge herds at the species' low-latitude range limit because of increased thermal stress from rising temperatures and lack of high quality food due to decreased precipitation (Monteith et al. 2015, Ruprecht et al. 2016). In some cases, climate change can affect species indirectly via direct influence on a food resource. For example, major climate cycles such as El Niño and La Niña are of great importance because they can stochastically affect food abundance (Sillett et al. 2000). Global environmental change may alter the timing and frequency of these climate cycles, with unknown consequences for trailing-edge populations. Furthermore, climate driven range shifts are difficult to predict for all taxa at once, and the likelihood of a species' suite of necessary resources shifting simultaneously and vice versa is low (Sekercioglu et al. 2008).

Environmental change may also have indirect effects on trailing-edge populations via impacts on biotic interactions such as competition and predation. Unfortunately, few examples exist demonstrating how biological interactions limit species distributions. Snowshoe hares (*Lepus americanus*) in Wisconsin experienced increased predation when transplanted just outside their low-latitude range limit (Sievert and Keith 1985). The increased predation pressure on hares was likely due to the transition zone from northern hardwood-evergreen forest to prairie forest, where the former was highly fragmented and thus hares could not find ample cover. There is also evidence that over the last few decades some warm-adapted species have forced closely related cool-adapted species to higher elevations through climate-mediated competitive interactions (Warren et al. 2016). A recent study with thrushes (*Catharus spp.*) in the Adirondack Mountains of New York found that, through aggressive interactions, a lower elevation species excluded a putative competitive congener from low elevations (Freeman and Montgomery 2016b). Finally, at a larger scale, the diversity of bird species in eastern North America has increased over the last few decades because of a changing climate, indicating that the potential for novel biotic interaction between bird species has increased (McDonald et al. 2012).

The purpose of this thesis is to understand the factors limiting the distributions of trailing-edge populations in the southern Appalachian Mountains. The goal of chapter two is to document the high diversity of trailing-edge populations of vertebrate species in the southern Appalachian Mountains. Furthermore, I propose a research agenda for understanding how these populations will respond to a changing climate. This research is needed to effectively conserve the large number of trailing-edge populations that occur in this region.

The primary objective of chapter three is to test different hypotheses regarding the importance of abiotic and biotic factors in setting the distributional range limits of trailing-edge

populations. Three years of point count data are used to evaluate the effects of climate, microclimate, understory evergreen vegetation, and the presence of putative competitors on the occupancy dynamics of five species of cool-adapted songbirds who meet their low-latitude range limit in the southern Appalachian Mountains of North Carolina. Chapter three combines this observational approach with two manipulations. The first is a manipulation testing for an effect of interference competition between two species of migratory songbird (Freeman and Montgomery 2016). The second is a test of the presence of socially-mediated Allee effects in a single species of migratory songbird (Schmidt et al. 2015).

The thesis concludes with major findings from chapters two and three. A brief review of the proposed research agenda from chapter two is provided for increased study of trailing-edge populations in the southern Appalachian Mountains of the United State. This final chapter also emphasizes the importance of this region as a biodiversity hotspot and a region of current and future conservation importance, followed by major findings from chapter three and concluding remarks regarding the future for research and conservation efforts.

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CHAPTER 2  
THE DIVERSITY OF TRAILING-EDGE POPULATIONS IN THE SOUTHERN  
APPALACHIAN MOUNTAINS<sup>1</sup>

<sup>1</sup>Merker S, Chandler, R. and Cooper, R. to be submitted to *Southeastern Naturalist*

## **Abstract**

Rapid environmental change is causing the ranges of many North American species to shift northward and to higher elevations. Although these range shifts are pervasive, their outcomes and consequences are difficult to predict without a thorough understanding of the ecological processes involved. Species with shifting ranges often have trailing-edge populations at their low-latitude range limit. These population segments are thought to be at high risk of extinction because of rapid environmental change. Despite this, there is a lack of research on trailing-edge populations. This information is much needed to conserve these species; however, little information exists as to where trailing-edge populations occur and how they will respond to future environmental change. We identify the southern Appalachian Mountains as a region with a high diversity of trailing-edge populations. Sixty-one vertebrates were found to have trailing-edge distributions in this region. The list is composed of 25 species of birds, 2 species of reptiles, 4 species of amphibian, 20 species of mammals, and 10 species of fish. Given the high diversity of trailing-edge populations in this region, and the lack of information regarding their demographic and ecological responses to climate change, we propose a research agenda for advancing knowledge about the dynamics of these populations. Specifically, we suggest research focused on combining observational and experimental data in order to better describe ecological processes rather than biogeographical patterns. Furthermore, we suggest that this is best accomplished through work based on identifying important demographic parameters.

## Introduction

Rapid environmental change is causing the ranges of many North American species to shift northward and to higher elevations (Parmesan and Yohe 2003, Campbell et al. 2010, McDonald et al. 2012, Auer and King 2014). Although these range shifts are pervasive, their outcomes and consequences are difficult to predict without a thorough understanding of the ecological processes involved. Several studies have investigated recent range shift dynamics by focusing on high-latitude, leading-edge populations, but little work has been done on low-latitude, trailing-edge populations (Angert et al. 2011, Cahill et al. 2014, Beauregard and de Blois 2016).

Information about trailing-edge populations is needed because they are thought to be highly sensitive to climate change. At low latitudes, range shifts can result from either the extinction of trailing-edge populations or from dispersal-based climate tracking. Little information exists to predict which process is more likely, but the consequences of losing trailing-edge populations could be harmful because many trailing-edge populations are evolutionarily older and more genetically diverse than populations in other portions of the range (Hampe and Petit 2005).

One region where many species meet their low-latitude range limit is in the southern Appalachian Mountains in the eastern United States, and the diversity of trailing-edge populations in this region has not been quantified. The southern Appalachian Mountains have been described as a biodiversity hotspot and one of the most diverse areas in the temperate region (SAMAB 1996). It is also the home to headwaters of several major rivers. It includes 7 of the United States and covers over 37 million acres, much of which is forest (SAMAB 1996). The forests in this region are extremely diverse ranging from bottomland forests at low elevations to spruce fir forests at the highest elevations. Before the onset of anthropogenic environmental change, low-latitude populations in this region appear to have been diverging from populations at higher latitudes,

suggesting that declines of trailing-edge populations could reduce genetic diversity, or perhaps even reverse the speciation process (Hampe and Petit 2005). This risk is highest for species with low dispersal capabilities, such as salamanders, many of which have already diverged from their high-latitude relatives, resulting in high levels of regional endemism (Kozak et al. 2006). For species with greater dispersal capability, gene flow between northern and southern populations may prevent speciation, but such flow can be sufficiently limited to result in genetic differentiation and phenotypic variation across the range. For example, the black-throated blue warbler (*Setophaga caerulescens*) has two distinct male breeding plumages, with bluer backed individuals occurring north of Pennsylvania and individuals with black backs occurring south to Georgia (Holmes et al. 2005, Grus et al. 2009). For this species, few genetic differences have been found across the range, but recent evidence indicates that the Canada warbler (*Cardellina canadensis*), another migratory bird species with a similar breeding distribution, does have genetically distinct southern and northern populations (Ferrari et al, In Prep).

Although few studies have focused on trailing-edge populations in the southern Appalachian Mountains, recent research has investigated the potential impact of different climate change scenarios on a variety of taxa. For example, most eastern tree species are expected to shift north or into higher elevations in response to current or accelerated climate change conditions (Iverson et al. 2008). These shifts indicate a change in species composition in the southern Appalachian Mountains, with extirpation of some cool-adapted species, and the colonization of some warm-adapted species (Matthews et al. 2007).

Several observational studies suggest that endemic species are likely to become extinct if climate warming continues. For example, many *Plethodontid* salamanders face high extinction risk due to climate driven habitat loss (Milanovich et al. 2010). A long-term study implementing

niche and demographic models to predict the response of the high elevation herb, *Geum radiatum*, to future climate scenarios showed that high elevation plants endemic to this region are at high risk of extinction (Ulrey et al. 2016). Results from observational studies and modeling efforts have been supported by manipulative experiments aimed at understanding the mechanisms by which environmental change affects populations. A study on southern Appalachian *Desmognathus* salamanders found, through controlled manipulations, body size and competition were mediated by different temperature regimes (Liles et al. 2017).

Unique genetic makeup, potential for speciation, and high risk of extinction, make conserving southern Appalachian trailing-edge populations of great importance, but conservation requires detailed information on the factors limiting distribution and population growth, information not available for most species. The impact of climate change and change in land use in the southern Appalachian Mountains is poorly understood but of great importance due to the high level of biodiversity at risk from local extirpation from shifting distributions. Understanding if and how patterns in species abundance and distribution will respond to future environmental change should be a focus of future research. It is impossible to fully understand these large-scale changes in patterns without detailed knowledge of the processes, like extinction and colonization, driving them. Understanding these processes facilitate strategic conservation and preservation, ideally mitigating or preventing potential negative outcomes. Currently, we do not have enough information about where species exist in this region, and to-date no studies have attempted to document the diversity of trailing-edge populations. The objectives of this study were to 1) provide a list of vertebrates that have trailing-edge populations in the southern Appalachian Mountains, and 2) outline a future research agenda for studying the dynamics and

conservation status of trailing-edge populations in the southern Appalachian Mountains and globally.

### **Methods**

To create a list of species that meet their low-latitude range limit in the southern Appalachian Mountains, we systematically reviewed range maps of North American vertebrates using field guides (Hannibal 1981, Filisky et al. 1989, Conant and Collins 1991, Sibley 2000). For a few field guides, we cross checked older versions with newer versions to see if a species' documented range had shifted over time. The taxa were limited to vertebrates to maintain a manageable species list and to avoid complications with taxa, that commonly hybridize such as plants and insects. We classified species as having a trailing-edge population in the southern Appalachian Mountains if their low-latitude range boundary occurred in north Georgia, southwestern North Carolina, eastern Tennessee, western Virginia and in some cases southern West Virginia. We excluded species with distributions that did not extend south of the Alleghany Plateau or that extended west of the Mississippi River. In some cases, species were excluded because, even though they met their low-latitude range limit in this region, the range extended outside of the southern Appalachian Mountains into the surrounding Piedmont, sometimes as far as the Atlantic coast. In the case of migratory songbirds, our classification was based entirely on their summer breeding distributions. In some cases, species displayed a "horseshoe" shaped distribution with two low-latitude range limits, one in the southern Appalachian Mountains, and one in the central or southern Rocky Mountains. We included species with horseshoe shaped ranges if the lowest-latitudinal range limit occurred in the southern Appalachian Mountains, and we indicated whether we were referring to only the eastern population. We excluded endemic species whose ranges did not extend beyond southern Appalachia. Although the conservation of



these endemic species should be a high priority, we were primarily interested in drawing attention to species with trailing-edge populations in the southern Appalachian Mountains.

### **Results**

We found a total of 60 species of vertebrates with low-latitude range limits in the southern Appalachian Mountains (Table 2.1). The list is composed of 25 species of birds, 2 species of reptiles, 4 species of amphibians, 19 species of mammals, and 10 species of fish. Of these 61 species, 13 have a horseshoe shaped distribution, with a portion of their range occurring in the Rocky Mountains. An additional 25 species with low-latitude range margins in the southern Appalachian Mountains were excluded from our list because they are endemic to the region. Examples of endemic species include several species of cave fish and the many endemic salamanders of this region.

### **Discussion**

Our results suggest that the southern Appalachian Mountains have a high diversity of vertebrate species with trailing-edge populations. Numerous factors threaten the viability of these populations. For example, as warm-adapted plants and animals shift north and to higher elevations, biological interaction between them and trailing-edge populations of cool-adapted species will almost certainly increase. Increased competition and predation could accelerate declines of trailing-edge populations, especially for animals that are unable to shift with their host plant communities (Sekercioglu, 2008). Regardless of the ecological mechanism involved, the potential for large turnover in community structure is high in the southern Appalachian Mountains, and trailing-edge populations are likely to be strongly affected.

Although we excluded plants from our search, a few species are worth mentioning due to their distinct distributions, the presence of trailing-edge populations, and their importance to the

socioeconomic and ecological future of this region. Two species which are extremely common in the shrub layer, big rhododendron (*Rhododendron maximum*) and striped maple (*Acer pensylvanicum*), have low-latitude range limits in this region and are generally found at higher elevations. Rhododendron, in particular, is known to be an important species for migratory birds (Holmes et al 2005, Reitsma et al. 2009, Stodola et al 2013). Yellow birch (*Betula alleghaniensis*) is restricted to high elevations. Red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*) are species that only occur at the highest elevations in this region and thus form island populations at the tops of the tallest mountains, supporting animal species that would not exist without them. Finally, eastern white pine (*Pinus strobus*) shares a similar distribution to these other plants and may become the dominant conifer in future Appalachian forests due the recent loss of eastern hemlock (*Tsuga canadensis*) (Webster 2012).

The high diversity of trailing-edge populations in southern Appalachian Mountains is likely to be threatened by rapid environmental change. Unfortunately, the information needed to guide conservation efforts is lacking. Specifically, there is little information available that can be used to predict how trailing-edge populations will fare as ranges shift towards higher latitudes and elevations. A focused research agenda is needed to understand how rapid environmental change will influence population dynamics and viability. Below, we outline key research priorities that would reduce uncertainty about the future of trailing-edge populations in the southern Appalachian Mountains.

Given the increased interest in modelling these changes it is surprising how little information on population dynamics there is for this region. Population processes are likely to be the most important drivers of species range shifts. Understanding how these processes are affected by environmental and biological change is key to future research and conservation

efforts and should be a priority for research in this region. On top of this, a greater understanding of the physiology of species at their low-latitude range limit is needed because species at the range boundary are more likely to be at their physiological limit, and thus more sensitive to changes in abiotic and biotic factors. Habitat needs of trailing-edge populations is another area where information is lacking, even though habitat needs are often touted as the most needed piece of information for focused conservation efforts. It is important to note that populations of species at their low-latitude range limit often have different habitat requirements than populations at the center of the range. For example, the black-throated blue warbler nests primarily in hobblebush (*Viburnum lantanoides*) in the central part of its range in New England, whereas in the southern portion of its range nests are found primarily in rhododendron (*Rhododendron maxima*) (Holmes et al. 2005, Stodola et al 2013). Whether these preferences are due simply to structural similarity or to something else is completely unknown, but is important information because both black-throated blue warblers and rhododendron have trailing-edge populations in the southern Appalachian Mountains.

To inform conservation efforts it is important to understand the ecological processes affecting species distributions. However, given the complexity of potential abiotic effects and biotic interactions, it is difficult to identify the most important ecological processes. Furthermore, understanding these processes is extremely difficult without first understanding a species' natural history, which if ignored, can be detrimental when considering conservation initiatives and experimental design (Cotterill and Foissner 2010). To accomplish a holistic understanding of both process and natural history, we suggest that hypotheses should be evaluated by coupling observational studies with manipulative experiments. First, the regular and repeated collection of, ideally, long-term observational data allows for continued monitoring and

modeling of large scale trends like changes in abundance, extinction, colonization, and occupancy. With this approach, we can monitor the shifting distributions of trailing-edge populations and how they respond to environmental change. We suggest that the most effective observational techniques involve mark-recapture methods that allow for inferences on spatial and temporal variation in the demographic processes that contribute to range shifts (Royle et al 2014). However, implementing mark-recapture over large spatial extents is challenging, and we therefore recommend that such methods be coupled with count-based or occupancy-based surveys or intermediate approaches such as the rapid assessment measures developed by Burns and Reitsma (2016). Recently developed spatial models allow for the integration of mark-recapture data and survey data to understand the demographic processes affecting species distributions at broad spatial scales (Chandler and Clark 2014).

Although observational studies allow for the development of models that can be used to understand and forecast complex ecological processes, manipulative experiments are usually the only way to identify causal relationships. However, manipulative experiments in isolation do not always allow for general understanding of complex processes because it is often too difficult to control certain factors, and it can be challenging to study some processes at the appropriate spatial scales. The combination of observational studies and manipulative experiments is therefore critical to advancing knowledge about spatial population dynamics and range shifts. Finally, it is difficult to manipulate entire systems, for example changing the temperature or precipitation regime of a forest is likely impossible. However, it is not impossible to manipulate certain biotic processes like the presence of competitors, predators, population density, and the presence of social information, to name a few. Manipulating biotic factors allows for refinement of species distribution models by allowing a model to account for, or ignore, important or

unimportant processes. Although this approach to ecological research has been proposed before, it has rarely been implemented over large spatial scales and across multiple taxa because it requires substantial planning and resources.

The high diversity of species with trailing-edge populations in the southern Appalachian Mountains, and the rapid rate of environmental change occurring in this region, present a unique opportunity to implement the combined observation and experimental approach to studying the demographic processes governing range shifts. This information is needed to inform conservation efforts of these populations, and we therefore call for a collaboration of academics, agencies, and non-profit organizations to collaborate on a multi-state effort focused on the ecology and conservation of trailing-edge populations. Studying representative taxa over their respective range boundaries for multiple years would provide the information necessary to understand why many of these populations are declining, and what consequences of their loss.

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## Tables and Figures

Table 2.1. Vertebrates of eastern North America that share similar distributions (breeding for migratory birds), all meeting their low-latitude range limit in the southern Appalachian Mountains. A subset category indicates whether the eastern population is at the lowest latitude.

<b>Species</b>	<b>Eastern Only?</b>	<b>Scientific Name</b>
<b>Birds</b>		
American Bittern	No	<i>Botaurus lentiginosus</i>
Sharp-shinned hawk	No	<i>Accipiter striatus</i>
Ruffed grouse	No	<i>Bonasa umbellus</i>
Killdeer	No	<i>Charadrius vociferus</i>
Yellow-bellied sapsucker	No	<i>Sphyrapicus varius</i>
Alder flycatcher	No	<i>Empidonax alnorum</i>
Least flycatcher	No	<i>Empidonax minimus</i>
Blue-headed vireo	No	<i>Vireo solitarius</i>
Black-capped chickadee	No	<i>Poecile atricapillus</i>
Red-breasted nuthatch	No	<i>Sitta canadensis</i>
Winter wren	No	<i>Troglodytes hiemalis</i>
Veery	No	<i>Catharus fuscescens</i>
Cedar waxwing	No	<i>Bonbycilla cedrorum</i>
Golden-winged warbler	No	<i>Vermivora chrysoptera</i>
Chestnut-sided warbler	No	<i>Setophaga pensylvanica</i>
Magnolia warbler	No	<i>Setophaga magnolia</i>
Black-throated blue warbler	No	<i>Setophaga caerulescens</i>
Blackburnian warbler	No	<i>setophaga fusca</i>
Yellow-rumped warbler (myrtle)	No	<i>Dendroica coronata coronata</i>
Black-throated green warbler	No	<i>Setophaga virens</i>
Northern waterthrush	No	<i>Parkesia noveboracensis</i>
Mourning warbler	No	<i>Geothlypis philadelphia</i>
Canada warbler	No	<i>Cardellina canadensis</i>
Rose-breasted grosbeak	No	<i>Pheucticus ludocicianus</i>
Dark-eyed Junco	Yes	<i>Junco hyemalis</i>
<b>Reptiles</b>		
Northern ringneck snake	No	<i>Diadophis punctatus edwardsii</i>
Smooth green snake	Yes	<i>Opheodrys vernalis</i>
<b>Amphibians</b>		
Eastern Hellbender	No	<i>Cryptobranchus alleganiensis alleganiensis</i>
Mountain dusky salamander	No	<i>Desmognathus ochropaeus</i>
Green salamander	No	<i>Aneides aeneus</i>
Wood frog	No	<i>Rana sylvatica</i>

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**Mammals**

Masked shrew	Yes	<i>Sorex cinereus</i>
Long-tailed shrew	No	<i>Sorex dispar</i>
Smoky shrew	No	<i>Sorex fumeus</i>
Pygmy shrew	Yes	<i>Sorex hoyi</i>
Water shrew	Yes	<i>Sorex palustris</i>
Northern short-tailed shrew	No	<i>Blarina brevicauda</i>
Hairy-tailed mole	No	<i>Parascalops breweri</i>
Star-nosed mole	No	<i>Condylura cristata</i>
Eastern small-footed myotis	No	<i>Myotis leibii</i>
Appalachian cottontail	No	<i>Sylvilagus obscurus</i>
New England cottontail	No	<i>Sylvilagus transitionalis</i>
Snowshoe hare	No	<i>Lepus americanus</i>
Northern flying squirrel	Yes	<i>Glaucomys sabrinus</i>
Allegheny woodrat	No	<i>Neotoma magister</i>
Southern red-backed vole	Yes	<i>Clethrionomys gapperi</i>
Rock vole	No	<i>Microtus chrotorrhinus</i>
Southern bog lemming	Yes	<i>Synaptomys cooperi</i>
Woodland jumping mouse	No	<i>Napaeozapus insignis</i>
Least weasel	No	<i>Mustela nivalis</i>

**Fish**

Laurel dace	No	<i>Chrosomus saylori</i>
Tennessee dace	No	<i>Chrosomus tennesseensis</i>
River chub	No	<i>Nocomis micropogon</i>
Blacknose dace	No	<i>Rhinichthys atratulus</i>
Longnose dace	Yes	<i>Rhinichthys cataractae</i>
Rosyface shiner	No	<i>Notropis rubellus</i>
Silver redhorse	No	<i>Moxostoma anisurum</i>
Brook trout	Yes	<i>Salvelinus fontinalis</i>
Muskellunge	Yes	<i>Esox masquinongy</i>
Mottled sculpin	Yes	<i>Cottus bairdii</i>

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## CHAPTER 3

# FACTORS LIMITING THE DISTRIBUTIONS OF COOL-ADAPTED BIRD SPECIES IN THE SOUTHERN APPALACHIAN MOUNTAINS<sup>2</sup>

<sup>2</sup>Merker, S., Chandler, R., Cooper, R., Reitsma, L., Hepinstall-Cymerman, J. To be submitted to *Ecography*

## Abstract

Climate change is causing the ranges of many species to shift towards higher latitudes and elevations. These shifts have been observed worldwide across many taxa, and numerous hypotheses exist to explain how abiotic and biotic factors affect range shifts, yet little is known about the ecological processes involved. Information is particularly scarce for trailing-edge populations, which are predicted to be at high risk of extinction because of a changing climate. To understand how trailing-edge populations will respond to climate change, research is needed on the factors limiting their distributions. The southern Appalachian Mountains of the United States is a region with a high diversity of trailing-edge distributions, and we used observational studies and manipulative experiments to assess the relative roles of abiotic factors and biotic interactions on the trailing-edge distributions of bird populations in this region. Using three years of point count data and co-occurrence models, we tested hypotheses regarding the effects of abiotic factors and the presence of putative competitors on occupancy dynamics of 5 cool-adapted species. We developed two manipulations to test for interference competition and socially-mediated Allee effects in a single species of migratory songbird, the Canada warbler (*Cardellina Canadensis*). Although the point count data clearly indicated that cool- and warm-adapted species segregated over the climate gradient in our study area, neither our observational data or our manipulative experiments supported the hypothesis that competition was responsible. In addition, we found no evidence that socially-mediated Allee effects limited distributions because none of our experimental sites at the range boundaries were colonized following the addition of conspecific song. Rather, our results indicated that abiotic factors, especially temperature and precipitation gradients and microclimatic conditions had the strongest overall effect on the spatio-temporal dynamics of trailing-edge populations.

## Introduction

Climate change is causing the ranges of many species to shift towards higher latitudes and elevations (Parmesan and Yohe 2003, Hickling et al. 2006, Parisod and Joost 2010, Chen et al. 2011, McDonald et al. 2012, Auer and King 2014). Although these shifts have been observed among many taxa throughout the world, the ecological mechanisms involved in climate-induced range shifts are poorly understood, making it difficult to predict future dynamics and to understand the consequences for biodiversity. One of the greatest sources of uncertainty is the relative contribution of abiotic versus biotic factors to the decline of populations at the trailing-edge of a species range (Cahill et al. 2014).

The dynamics of trailing-edge populations have received increasing attention as accumulating evidence indicates that trailing-edge populations are often evolutionarily older, occupy high quality habitat, and are more genetically diverse than central and leading-edge populations (Hampe and Petit 2005, Lagerholm et al. 2016). This evidence stands in stark contrast to the center-periphery hypothesis, which predicts that peripheral populations should have lower genetic diversity and be more likely to go extinct than central populations (Brown 1984, Hampe and Petit 2005). The ecological and evolutionary uniqueness of trailing-edge populations makes it important to understand how environmental change influences their dynamics and viability, especially considering predictions that species in this portion of their range are at increased risk of extinction from increased interspecific interactions, increased climatic variability, and the interaction between the two (Aitken et al. 2008, Sekercioglu et al. 2008, Cunningham et al. 2009, Cahill et al. 2014). There is also evidence that peripheral populations near low-latitude range margins may be unable to track their climate optima as climate change accelerates (IPCC 2014, Kerr et al. 2015).

To understand the response of trailing-edge populations to climate change, it is important to understand the factors limiting their current distribution. Abiotic factors such as temperature and precipitation are often reported to limit species' distributions at low-latitude range margins (Root 1988a, Gross and Price 2000, Cahill et al. 2014). For example, cool-adapted species may experience stress and reduced reproductive performance near the warm edges of their ranges. A recent study on Shiras moose (*Alces alces shirasi*) in the Uinta and Wasatch Mountains of North America found that reproduction and recruitment were lower at the species' low-latitude range limit, likely a result of poor habitat quality and increased thermal stress (Monteith et al. 2015, Ruprecht et al. 2016). Conversely, some studies have supported the idea that biotic interactions are the dominant factor limiting species' distributions at low latitudes due to the higher diversity of warm-adapted competitors and predators (Darwin 1859, Dobzhansky 1950, MacArthur 1972, Cunningham et al. 2009, Cahill et al. 2014). For example, a transplant study of snowshoe hare (*Lepus americanus*) in Wisconsin indicated that the species' southern range limit was determined by increased predation pressure (Sievert and Keith 1985).

Interspecific competition is one of the most important types of biotic interactions that can limit species' distributions. Whether it be exploitative or interference, competition can result in the exclusion of species from regions with suitable habitat (Hardin 1960, Case and Gilpin 1974, Terborgh 1970, Diamond 1978). For example, when the invasive fish *Coregonus albula* invaded the habitat of the ecologically similar native *Coregonus lavaretus*, the invasive outcompeted the native for food, causing a massive decline in the native species' population (Bohn et al. 2008). Climate change may increase contact of formerly allopatric competitors as species' ranges shift. For trailing-edge populations, increased competitive pressure from low elevation, warm-adapted

species could accelerate range shifts toward higher elevations and latitudes, and could possibly result in widespread extirpations near low-latitude range limits.

Although several types of competition could be important in determining future range boundaries, it should be easier to detect direct interference competition. Interference competition is described as the process by which one species directly interferes with another species through a negative interaction such as territoriality or aggression (Case and Gilpin 1974). Interference competition has been demonstrated repeatedly, but its role in limiting distributions in forest populations has rarely been investigated (Case and Gilpin 1974, Amarasekare 2002, Svenning et al. 2014). One example of interference competition influencing range dynamics is with thrushes (*Catharus spp.*) in the Adirondack Mountains of New York, where it was found that, through aggression, one species excluded the other from low elevations (Freeman and Montgomery 2016).

Allee effects are another type of (intraspecific) biotic interaction that could limit species distributions (Allee 1949, Stephens et al. 1999). For species that utilize social cues in making habitat selection decisions, socially-mediated Allee effects could be particularly important (Schmidt et al 2015). Several studies have shown that when conspecific bird song is played in previously unoccupied yet suitable habitat, individuals of the same species will colonize these sites, often regardless of habitat quality (Betts et al. 2008). For example, by playing black-capped Vireo (*Vireo atricapilla*) song during the settlement period in suitable yet unoccupied habitat researchers were not only able to attract vireos to novel habitat, but they remained and attempted to breed for multiple seasons (Ward and Schlossberg 2004). For many species of birds, conspecific attraction can strongly influence the colonization processes, suggesting that individuals near range margins might be unlikely to colonize peripheral habitat that becomes unoccupied following local extinction events (Stamps 1988, Smith and Peacock 1990, Schlossberg and Ward 2004, Schmidt



et al. 2015). If species are strongly influenced by social cues to colonize suitable habitat, colonization rates may decrease due to lack of social information from a decrease in population density after a negative stochastic event.

Few studies have simultaneously evaluated multiple hypotheses about the factors limiting species distributions near low-latitude range margins (Cahill et al. 2014). The objective of this study was to determine the relative influence of abiotic and biotic factors in limiting the distributions of trailing-edge populations. To meet our objectives, we tested predictions from four competing hypotheses:

1. The distributions of cool-adapted species are limited by abiotic factors, not competition or Allee effects, at their warm-edge range limit because abiotic factors directly influence occupancy dynamics.
2. The distributions of cool-adapted species are limited by the presence of putative competitors, not abiotic factors or Allee effects, at their warm-edge range limit because competitors increase local extinction probability and reduce colonization rates.
3. The distributions of cool-adapted species are limited by Allee effects, not abiotic factors or interference competition from putative competitors, at their warm-edge range limit because the lack of social cues in peripheral suitable habitat will reduce colonization.
4. The distributions of cool-adapted species are limited by a combination of abiotic variables, interference competition from putative competitors, and the presence of Allee effects at their warm-edge range limit because interactions are possible between social information, competition, and unsuitable climate conditions and these factors are thus not mutually exclusive.

We evaluated these hypotheses using a combination of observational studies and manipulative experiments focused on bird species in the southern Appalachian Mountains.

## Methods

### Site Description

Research was conducted in the USFS Nantahala National Forest near the Coweeta Hydrologic Laboratory in southwestern North Carolina, United States. The area is characterized by steep topography ranging from 660–1590 m elevation over only a few kilometers. Precipitation increases with elevation; ranging from 1870 mm year<sup>-1</sup> at low elevations to 2500 mm year<sup>-1</sup> at high elevations (Hwang et al. 2014). Temperature tracks closely with elevation, becoming cooler at higher elevations. The study site is heavily forested and dominant tree species include oaks (*Quercus* spp.), hickory (*Carya* spp.), black gum (*Nyssa sylvatica*), yellow poplar (*Liriodendron tulipifera*), and formerly eastern hemlock (*Tsuga canadensis*). In recent decades, eastern hemlock has experienced massive die off in this region due to hemlock wooly adelgid, and mature trees are rare (Webster et al. 2012). At higher elevations (>1200 m) northern hardwood forests are present with species including yellow birch (*Betula alleghaniensis*), basswood (*Tilia heterophylla*), yellow buckeye (*Aesculus octandra*), northern red oak (*Quercus rubra*), and sugar maple (*Acer saccharum*) (Hwang et al. 2014). The understory is primarily mountain laurel (*Kalmia latifolia*), rhododendron (*Rhododendron maximum*), and occasionally large areas of *Vaccinium* spp. (Webster et al. 2012). Some areas have little or no shrub layer and are relatively open from the forest floor to the mid-canopy.

### Species of Interest

We selected five pairs of migratory songbird on which to test hypotheses. We selected five cool-adapted species with trailing-edge populations in the southern Appalachian Mountains, and

we paired each of these species with a warm-adapted species of approximately the same size with similar foraging and nesting habitat requirements. By pairing these species, we aimed to maximize our ability to detect competitive interactions if present. In one case, we paired one warm-adapted species with two of the cool-adapted species because the former is ecologically similar to both.

#### Cool-adapted birds

The Canada warbler (*Cardellina canadensis*, CAWA) is a small Nearctic-neotropical migrant passerine whose breeding range extends from north Georgia, USA into northwestern Canada. This is an ideal species on which to study trailing-edge range shifts because, like many species, Canada warblers meet their warm-edge breeding range limit in the southern Appalachian Mountains of eastern North America (Fig 3.1). Furthermore, the Breeding Bird Survey (BBS) indicates that they have been declining across their breeding range at approximately 2.3% year<sup>-1</sup> for the last several decades (Sauer et al. 2013). Although the BBS does not provide reliable estimates of trends for the southern Appalachian region (Reitsma et al. 2009, Sauer et al. 2013), forecasts indicate that southern breeding populations will decline precipitously in the coming decades (Matthews et al. 2004). The Canada warbler has also been listed as threatened by the Committee on the Status of Endangered Wildlife in Canada and has been called a species of conservation and research concern by several entities in the United States (Hallworth et al. 2008). Finally, Canada warblers are conspicuous during the breeding season and are easily detected by sight and sound. Canada warblers nest on the ground and primarily sing and forage in the shrub layer (Reitsma et al. 2009).

We selected four other cool-adapted species for which to develop models; black-throated blue warbler (*Setophaga caerulescens*, BTBW), blue-headed vireo (*Vireo solitaries*, BHVI), dark-eyed junco (*Junco hyemalis*, DEJU), and veery (*Catharus fuscescens*, VEER), (Table 1). These

species are small passerines, and all but the Dark-eyed junco are neotropical migrants (Nolan Jr. et al. 2002, Bevier et al. 2005, Holmes et al. 2005). These four species also have similar breeding distributions to that of Canada warblers, particularly in that they all meet their low-latitude breeding range limit in the southern Appalachian Mountains of North America (Fig 3.1). Moreover, each of these cool-adapted species has shown recent range wide breeding population declines (Sauer et al. 2013).

#### Warm-adapted birds

To investigate the potential effects of competition, we selected four warm-adapted species that are ecologically similar to the five cool-adapted focal species but have breeding ranges concentrated in the southeastern US (Table 3.1). The hooded warbler (*Setophaga citrina*, HOWA) was chosen as a putative competitor of both the Canada warbler and the black-throated blue warbler because of its morphological and behavioral similarities. The hooded warbler is a small neotropical migrant passerine whose breeding range is restricted to eastern North America and is concentrated in the southeastern United States (Fig 3.2). Hooded warblers primarily nest, sing, and forage in the shrub layer. Unlike many other warblers, hooded warblers do not appear to be experiencing range wide declines (Chiver et al. 2011, Sauer et al. 2013). We included wood thrush (*Hylocichla mustelina*, WOTH), as a putative competitor of veery because they are one of two other members of the family *Turdidae* that breed within our study area, and because wood thrush has more similar habitat requirements than does the other species, the American robin (*Turdus migratorius*) (Evans et al. 2011). We chose Red-eyed vireo (*Vireo olivaceus*, REVI) as a putative competitor of blue-headed vireo because of morphological and ecological similarities (Cimprich et al. 2000). Ovenbirds (*Seiurus aurocapilla*, OVEN), were included as a putative competitor of dark-eyed juncos because they share similar breeding ecology (Pomeluzi et al. 2011).

## Point count surveys

We conducted point count surveys for birds from May through July during three breeding seasons (2014-2016). Survey locations were fixed and formed a regular 500m grid, ranging from 800 m elevation to 1400 m elevation. The grid of 71 points was positioned to cross the range boundaries of all five cool-adapted species. Each survey was conducted by experienced observers once per season for 10 minutes in 2.5 minute intervals. During each interval, the species of each bird, its sex, how it was detected (sight or sound), and its distance to observer (up to 100 m) was recorded. Factors influencing detection, including noise, precipitation, and wind were recorded during each survey on a 0-5 scale. Generally, point surveys were conducted on days with little or no precipitation, low wind, and were limited to the hours between 6 AM and 11 AM, when birds are most active and more likely to sing.

## Co-occurrence models

Implementing the methods described by MacKenzie et al. (2003) we constructed two, two-species, multi-season co-occurrence models for each species pair (Table 1) using R statistical software version 3.3.2 (R Core Team, 2017) and version 4.0.0 of Just Another Gibbs Sampler (JAGS). Both models accounted for imperfect detection and included the same detection covariates.

We designed models to describe 2 different scenarios:

1. initial occupancy, extinction, and colonization of cool-adapted species are affected by abiotic factors and the presence of warm-adapted species, and warm-adapted species are modeled separately;
2. initial occupancy, extinction, and colonization of cool-adapted species are affected only by the presence of a putative competitor.

We used publicly available precipitation and temperature data in the form of 30 year normals, 1981-2010 (PRISM Climate Group 2016), however these two variables were highly correlated ( $r = -0.90$ ), and so we created a single principle component to reflect the dominant climate gradient in the region. This principle component explained 95% of the variation (Fig. 3.4). To account for factors at the landscape level we created a heat load index (a linearization of aspect) from a digital elevation model (10 m pixels) using the ‘raster’ package in R and the methods described by McCune and Keon (2002). Heat load index is often considered more biologically relevant than aspect alone because it accounts for thermal exposure, and can be considered a measure of micro-climate (McCune and Keon 2002). The understory of our field site is dominated by rhododendron and mountain laurel, both evergreen shrubs, which often form large thickets. These thickets appear to be heavily used by all the cool-adapted species selected and many of the warm-adapted species, and thus it is thought that these thickets will influence each species distribution (Stodola et al. 2013). To measure this, we used 2008 winter LANDSAT imagery to create a leaf-off Normalized Vegetation Difference Index (NDVI) raster layer (30 m pixels) for the study site. This gave us a measure of evergreen vegetation in the entire study site, which was primarily heath species now that most hemlock trees have died. Landscape-level variables were associated with survey points by creating a 100 m buffer around each point count location and extracting the average NDVI value from within each buffer.

We modeled initial occupancy of both cool-adapted and warm-adapted species using climate, heat load, and NDVI. For cool-adapted species, we also included the occupancy state of the paired warm-adapted species. This contrasts with most applications of co-occurrence models in that occupancy of species A in year t is typically modeled conditional on the occupancy state of species B at t-1. However, at our study site, warm-adapted species often arrive on the breeding

grounds before cool-adapted species, and we hypothesized that occupancy of cool-adapted species would be more affected by current occupancy of putative competitors than by their presence in previous years. The only exception to the earlier arrival by warm adapted species was for dark-eyed juncos whose short distance migratory behavior allows them to arrive on the breeding grounds before ovenbirds. However, we felt that if aggressive interference competition is strong enough then an effect should be detectable within the same season.

Like occupancy we included the occupancy state of warm-adapted species in the paired models of extinction and colonization probability for cool-adapted species. Again, we used the occupancy of warm-adapted species at time  $t$ , rather than  $t-1$ , because warm-adapted species tend to arrive earlier. We did not include the effect of cool-adapted species on warm-adapted species because we had no reason to hypothesize that cool-adapted species are expanding their range and out-competing their warm-adapted counterparts. We assumed that warm-adapted species would be pushing into higher elevations as they become warmer and drier. Because we expected the effect of competition to be exacerbated by climate change, warm-adapted species should be pushing cool-adapted species upslope. Cool-adapted species who would normally be able to colonize marginal edge habitat should be unable to do so because of the presence of aggressive competitors.

The model is described below and was fit using Markov chain Monte Carlo in a Bayesian framework.

Initial occupancy ( $t=1$ )

$$\text{Logit}(\psi^{A_{i,1}}) = \beta_0 + \beta_1 * \text{climate} + \beta_2 * \text{heat load} + \beta_3 * \text{NDVI} + \beta_4 * z^{B_{i,1}}$$

$$\text{logit}(\psi^{B_{i,1}}) = \beta_0 + \beta_1 * \text{climate} + \beta_2 * \text{heat load} + \beta_3 * \text{NDVI}$$

$$z^{A_{i,1}} \sim \text{Bernoulli}(\psi^{A_{i,1}})$$

$$z^{B_{i,1}} \sim \text{Bernoulli}(\psi^{B_{i,1}})$$

Subsequent occupancy (t=2,3)

$$\text{logit}(\gamma_{i,t}^A) = \gamma_0 + \gamma_1 * \text{climate} + \gamma_2 * \text{heat load} + \gamma_3 * \text{NDVI} + \gamma_4 * z_{i,1}^B$$

$$\text{logit}(\gamma_{i,t}^B) = \gamma_0 + \gamma_1 * \text{climate} + \gamma_2 * \text{heat load} + \gamma_3 * \text{NDVI}$$

$$\text{logit}(\varepsilon_{i,t}^A) = \varepsilon_0 + \varepsilon_1 * \text{climate} + \varepsilon_2 * \text{heat load} + \varepsilon_3 * \text{NDVI} + \varepsilon_4 * z_{i,1}^B$$

$$\text{logit}(\varepsilon_{i,t}^B) = \varepsilon_0 + \varepsilon_1 * \text{climate} + \varepsilon_2 * \text{heat load} + \varepsilon_3 * \text{NDVI}$$

$$z_{i,t}^A \sim \text{Bernoulli} (z_{i,t-1}^A (1 - \varepsilon) + (1 - z_{i,t-1}^A) * \gamma)$$

$$z_{i,t}^B \sim \text{Bernoulli} (z_{i,t-1}^B)$$

Detection (t=1,2,3)

$$y_{ijt}^A | z_{it} \sim \text{Bernoulli} (z_{it}^A p^A)$$

$$y_{ijt}^B | z_{it} \sim \text{Bernoulli} (z_{it}^B p^A)$$

$$p_{ijt}^A = \alpha_0 + \alpha_1 \text{wind}_{ijt} + \alpha_2 * \text{noise}_{ijt} + \alpha_3 * \text{date}_{ijt}$$

$$p_{ijt}^B = \alpha_0 + \alpha_1 \text{wind}_{ijt} + \alpha_2 * \text{noise}_{ijt} + \alpha_3 * \text{date}_{ijt}$$

where  $i=1, \dots, 87$  is the site index,  $j=1, \dots, 4$  is the 2.5-min time interval index, and  $t=1, 2, 3$  is the year index. Species A represents a cool-adapted species and Species B represents a warm adapted species. We used diffuse normal distributions with a mean of 0 and a variance of 100 as priors for all regression coefficients.

Interference Competition Experiments

We conducted paired aggression trials using hand-carved painted wooden decoys (Fig 3.3) and conspecific song recordings. Using Canada warbler, hooded warbler and a control species, Carolina chickadee, (*Poecile carolinensis*) decoys and playback of the appropriate song, we simulated territory intrusions into Canada warbler or hooded warbler territories. We selected Carolina chickadee as a control species because they are of similar size (9-12g), non-migratory, cavity nesters, and spend much of their time in the canopy or sub-canopy and thus are less likely



to interfere with either species. Aggression trials ranged over the climate gradient, and from 750 m to 1500 m elevation. Each trial lasted 10 minutes. During trials, we recorded the height and distance of the defending bird to the decoy at least every minute but as often as ever second if the defending species was particularly active. We also recorded behavior of the defending bird and possible aggressive behaviors. Specifically, we looked for evidence that the defending bird would attempt to make the intruding decoy leave by: modifying vocal behavior, attacking the decoy, making itself look bigger, or chipping at the decoy. We stratified trials across the strong climate gradient such that they were conducted both outside each species range, within each species range, and at mixing zones. We were confident in the ability of the decoys to incite an aggressive response because the same decoys were successfully used to capture conspecifics for a related study. Using decoys to capture conspecifics is a common practice which has been demonstrated with several species including prothonotary warblers, black-throated blue warblers, and American redstarts (Holmes et al. 1989, Slevin et al. 2016). In one case a decoy ‘experienced’ a prolonged physical attack, >10 minutes, by a conspecific. It has been found that when conspecifics attack wooden decoys they may become injured; no birds were injured during trials (Slevin et al. 2016).

We used binomial generalized linear models to determine if any of the measured aggressive behaviors were significantly more common in experimental trials or control trials. We tested the aggressive response variables: aggressive singing, counter singing, minimum distance to decoy, and physical attacks included “buzzing”, so called when birds come very near an individual without striking it. We used the type of trial (control or putative competitor invading) and the same climate variable created for the co-occurrence models as explanatory variables.

Conspecific Attraction and Allee Effects.

We used methods like those of Ward and Schlossberg (2004) to attempt to attract Canada warblers to previously unoccupied habitat both within and outside their range limit, which were delineated based on pilot data and our first year of point count data. We played Canada warbler song at 10 sites from April 19<sup>th</sup> – May 7<sup>th</sup> 2016, the period when Canada warblers arrive on the breeding grounds in North Carolina, establish territories and begin nesting. We selected sites from previously sampled point count survey locations where Canada warblers had not been detected in the previous two breeding seasons. Playback included a mix of hetero-familiar bird song, so as not to confound with potentially competitive relationships, and periods of silence to avoid habituation by Canada warblers. Each playback unit consisted of a Raspberry Pi<sup>®</sup> computer, a small amplifier, and a Yamaha<sup>®</sup> outdoor speaker. Each unit was powered by two, 12 v sealed lead batteries. Playback was set to between 80 and 90 dB, units were programmed to begin playback at 4 am and cease playback at 10 am every day. Playback units were constructed by the University of Georgia's Instrument Fabrication and Design shop. Experimental playback sites were visited every other day during the settlement period, primarily to change out batteries but also to survey the area for Canada warblers. We conducted three different point counts at each playback location, two during the playback period, and one after the arrival period to determine if birds remained on territory and attempted to breed at these sites.

## **Results**

We conducted 70 point count surveys in 2014 and 71 in 2015 and 2016. Point count surveys resulted in a total of 10534 detections of 58 species. Most birds (>80%) were detected by sound.

### Effects of climate on occupancy dynamics

The point count data clearly demonstrated that the cool- and warm-adapted species segregated over the climate gradient. Specifically, Canada warblers, black-throated blue warblers,

and veeries were encountered more frequently in the cooler and wetter conditions at higher elevations, whereas hooded warblers, ovenbirds, and wood thrush were detected more often at lower elevations where warmer and drier conditions prevailed (Fig 3.5).

Although our point count data suggested that abutting distributions of cool- and warm-adapted species could have resulted from competition, co-occurrence models and experimental data provided much more support for our first hypothesis that abiotic factors are much more important than biotic interactions in governing the occupancy dynamics of these species. Specifically, the principle component describing the climate gradient was the best predictor of occupancy dynamics of Canada warblers, black-throated blue warblers, veeries, hooded warblers and ovenbirds. For these species 95% CIs excluded zero for the effects of climate on initial occupancy (Fig 3.6 A&B). The model also showed little inter-seasonal variation in the effect of climate on occupancy for any species pairs (Fig 3.7). There is some evidence that some warm-adapted species, particularly hooded warblers and wood-thrush are shifting towards historically cooler and wetter areas as the climate gradient shifts (Fig 3.8). The model showed that the probability of extinction increased greatly in warmer drier conditions for Canada warblers and black-throated blue warblers, but had no significant effect on any warm-adapted species. (Fig 3.6, C&D). The model showed that black-throated blue warblers and dark-eyed juncos were more likely to colonize cooler, wetter, high elevation areas and that red-eyed vireos and wood thrushes were more likely to colonize warmer and drier areas at low elevations (Fig 3.6, E&F).

#### Effects of heat load on occupancy dynamics

We hypothesized that physical factors like heat load should have some impact on the occupancy dynamics of cool-adapted species. We found that only black-throated blue warblers appeared to be affected by heat load, indicating that they prefer cooler and wetter areas with low

thermal exposure. The only warm-adapted species whose occupancy was affected by heat load was wood thrush, preferring slopes with slightly more thermal exposure (Fig 3.9, A&B). Only black-throated blue warblers seemed to experience a significantly increased probability of extinction on warmer slopes, while no effect was found for other cool-adapted species. The only warm-adapted species whose probability of extinction decreased on warmer slopes was ovenbirds (Fig 3.9, C&D). Heat load appeared to have no significant effect on colonization for either cool-adapted or warm-adapted species (Fig 3.9, E&F). There was little inter-seasonal variation in occupancy dynamics and only for black-throated blue warblers, ovenbirds, and wood thrush did the 95% CI not include zero.

#### Effects of NDVI on occupancy dynamics

We hypothesized that leaf-off NDVI, as an indicator of rhododendron and mountain laurel thickets, would influence the occupancy dynamics of species in our study site but found that only a few species had a parameter estimate's 95% CI exclude 0. The model showed that only dark-eyed juncos and ovenbirds preferred areas with little vegetation in the understory (Fig 3.10, A&B). The model indicated that NDVI had no effect on the extinction probability for any cool-adapted species but that the probability of extinction for ovenbirds and wood thrushes increased in areas with higher levels of evergreen understory vegetation (Fig 3.10, C&D). The model showed variable effects of NDVI on colonization for warm-adapted species and no effect on cool-adapted species. Hooded warblers appeared more likely to colonize areas with an evergreen understory while red-eyed vireos, ovenbirds, and wood thrushes appeared unlikely to colonize similar areas, preferring forests with little understory vegetation (Fig 3.10, E&F). We found little inter-seasonal variation in the effect of NDVI on occupancy for cool or warm-adapted species (Fig 3.11).

#### Effect of putative competitors on occupancy, colonization, and extinction

We expected that the presence of putative competitors would have significant negative effects on the occupancy dynamics of cool-adapted species, but we found limited evidence of this. Only the presence of red-eyed vireos had a negative effect on occupancy of blue-headed vireos in both models; however, this result leads us to suspect that some observers may have improperly identified these species due to the similarity of their vocalizations (Fig 3.12). We compared the model including both abiotic and biotic factors with a model including only biotic factors and found mixed results (Fig 3.12). Surprisingly, we detected a positive effect of the presence of hooded warblers on the occupancy of Canada warblers and a positive effect of ovenbirds on dark-eyed junco occupancy in the first year, indicating that the two species pairs may select similar habitat where climate and structure are suitable. In contrast to the finding that hooded warblers had a positive effect on Canada warbler occupancy, both models indicated that hooded warblers also increased the probability of extinction in Canada warblers (Fig 3.12). No effect on probability of extinction was found for any other species pair. Both the model including abiotic and biotic factors and the model including only biotic factors showed a significant negative effect of ovenbirds on the colonization probability of dark-eyed juncos (Fig 3.12).

#### Allee effects

We found no evidence of socially-mediated Allee effects. Peripheral sites, those below 1000 m elevation, were not colonized by Canada warblers following the addition of social cues. In fact, no Canada warblers were detected at treatment sites where playback was added, regardless of elevation, whereas Canada warblers were detected at 2 of the 10 control sites, even though these sites had been unoccupied in the previous two breeding seasons.

## Interference competition

We conducted 62 aggression trials: Hooded warbler defending against Canada warbler (n=15); Canada warbler defending against hooded warbler (n=16); hooded warbler defending against Carolina chickadee (n=15); and Canada warbler defending against Carolina chickadee (n=16). We detected only a single instance of birds attacking heterospecific decoys. In this case, a hooded warbler attacked a Canada warbler decoy, however it was very brief and occurred in an area where hooded warbler and Canada warbler ranges overlap in elevation (1060 m). Individuals appeared to sing ‘aggressively’ towards decoys and playback in 9 trials. In 3 trials, individuals counter-sang with playback. In a single trial a hooded warbler made a perched ‘display’, twittering and vibrating its wings towards a Canada warbler. The average minimum distance a species approached a decoy was 6.3 m (Table 3.3). In most cases neither Canada nor hooded warblers responded aggressively towards intruding species. The exception was a significant interaction between treatment and climate in determining the minimum distance approached to a decoy ( $F_{2,47}=3.1679$ ,  $P=.034$ ).

## Discussion

Understanding how climate change will affect trailing-edge populations requires information about the factors limiting their distributions. Results from our observational and experimental studies support the hypothesis that the distributions of trailing-edge populations are influenced more by abiotic factors than by the biotic interactions investigated here. Consequently, efforts to forecast range shifts of trailing-edge populations in the southern Appalachian Mountains may not need to account for complex processes like competition or socially-mediated Allee effects, which are notoriously difficult to include in species distribution models (Guisan and Thuiller 2005, Araujo and Luoto 2007, Wisz et al 2013). More generally, our results contrast with the hypothesis

that biotic interactions should exert strong influence on species' distributions near low-latitude range margins (Dobzhansky 1950, MacArthur, 1970). Instead, our results add to a growing body of literature supporting the hypothesis that climate is a primary limiting factor at low-latitude range margins (Parmesan and Yohe 2003, Hampe and Petit 2005, Cahill et al. 2014).

We have provided evidence that the occupancy dynamics of trailing-edge populations are strongly influenced by the climate gradient in our study area as depicted by the relatively coarse resolution PRISM data (800m pixels). Specifically, as conditions become colder and wetter at high elevations, cool-adapted species are more likely to be present, less likely to go extinct, and more likely to colonize unoccupied sites. If warmer and drier climates reduce colonization rates and increase extinction rates of cool-adapted species in the southern Appalachian Mountains, then we may continue to observe the rapid declines of populations in this region. Given the current observed declines and the strong effect of climate on colonization processes the ecological mechanisms involved in setting species distributions deserve further attention. Temperature and precipitation are perhaps two of the most biologically important factors limiting species distributions because of their direct influence on physiology, landscape level patterns, and because of their distinct variation over time and space (Root 1988a, b, Jankowski et al. 2013). However, we were unable to distinguish between the effects of temperature and precipitation in our models because of high correlation between the two variables, which limits our ability to make precise predictions about the future of occupancy dynamics in this region. Regardless, one major value of this combined climate variable is that we can now make informed hypotheses aimed at improving future research, by targeting precisely these two major climate factors. It is important to separate these two factors because of the different ways they each affect different ecological processes.

The effect of temperature on range shifts may manifest itself clearly on a geographical scale, yet may be affecting species habitat at smaller scales. Many species have specific habitat requirements, often a specific community of plants. Plants experience direct and indirect effects of temperature on reproductive capabilities and therefore as temperatures increase the area of suitable climate conditions change causing a shift in plant community distribution (Bykova et al. 2012). Furthermore, plant communities host communities of invertebrates that in turn support vertebrate communities (Singer and Parmesan 1993). If the distribution of plant communities, which are arguably the backbone of most terrestrial ecosystems, shift with changing temperatures, then a major shift of invertebrate and vertebrate communities may follow. Even though plant communities have been reacting to changes in temperature they are also sensitive to changes in the hydrologic cycle, which is also influenced by climate change.

The precipitation regime of a region often dictates which communities are present because of how precipitation directly affects plants. At the Hubbard Brook Experimental Forest in New Hampshire, high elevations are generally wetter with denser vegetation hosting a greater abundance of insects than at lower elevations (Rodenhouse et al. 2008, Holmes 2011). This vegetation pattern is less defined in southern Appalachian Mountains, having distinct patchiness at high elevations. However, a similar pattern holds with precipitation, being much wetter at high elevations. If climate change continues to alter the hydrologic cycle, causing higher elevations in this region to get drier a shift in plant distributions may follow. It is unclear if animal communities will be able to shift at the same rate as the plant communities they rely on (Sekercioglu et al. 2008).

We predicted a negative effect of heat load on the occupancy dynamics of cool-adapted species in our study site. Our results suggest that cool north facing slopes, generally being colder and wetter, support cool-adapted species more often than warm, south facing slopes. Initially this



could be interpreted as reinforcing species persistence in this region, showing that cool-adapted species may find refuge on these cooler and wetter, north-facing slopes. But, if species are selectively occupying these areas of low heat loading, then increased population fragmentation is possible, especially if stochastic events cause localized extirpation. This may lead to Allee effects in trailing-edge populations with potential recruits failing to find populations into which they can integrate and thus further reducing the population growth rates of species in this region.

We predicted that winter NDVI would reflect the distribution of understory Ericaceous shrubs that are used for nesting and cover by many species in our study area, and that NDVI would therefore influence avian occupancy dynamics. However, the only effects we found were for dark-eyed juncos and ovenbirds that appear to avoid these vegetation conditions. It is surprising that we found no positive effects of NDVI on occupancy of species such as Canada Warbler and black-throated blue warbler, which often nest or forage in rhododendron. This may suggest that we need a finer measurement of heath vegetation. Another issue is that we are generally unable to distinguish rhododendron from mountain laurel in this layer, which may be an important distinction. Future work should attempt to evaluate the extent to which NDVI adequately describes Ericaceous vegetation structure by comparing it to field measurements. Finally, using LiDAR may be a potential alternative method to mapping understory vegetation at finer detail. Quantifying this aspect of the vegetation community is particularly important because species such as rhododendron and mountain laurel are distinct components of Appalachian forest communities, and their distributions may be shifting in response to climate change.

Results from the aggression trials between Canada warblers and hooded warblers indicated that the two species exhibit little aggressive behavior toward one another. Moreover, we found no negative effects of hooded warblers on the occupancy dynamics of Canada warblers. Although

these findings do not indicate that competition is nonexistent, they do provide evidence that interference competition is unlikely. The lack of interference competition is somewhat surprising given the abutting distributions of the two species, but we suggest that spatial segregation is the result of niche partitioning over the climate gradient. These results contrast with several studies that have presented strong evidence for competition acting as a direct or indirect factor limiting species distributions in the Andes and islands of New Guinea, where it was found that competitive exclusion accounted for significantly more elevational range boundaries than did ecotones (Terborgh 1970, Terborgh and Weske 1975, Diamond 1978). More recently, a study on *Catharus* thrushes in New York using interspecific playback showed that Swainson's thrushes (*Catharus ustulatus*) were aggressively dominant over their higher elevation relative the Bicknell's thrush (*Catharus bicknelli*) and that this aggressive interaction occurred primarily where the two species' elevational ranges overlapped (Freeman and Montgomery 2016). Similarly, in Costa Rica, it was found that thrush species experience aggressive interference competition at elevational range boundaries, where aggression is primarily from lower elevation species, again using interspecific playback (Jankowski et al. 2010). In a study of New Guinean birds, it was found that interspecific aggression was a dominant factor setting elevation range boundaries in some songbird species. However, this same study found that for species showing no aggression towards closely related species, there was a substantial spatial gap between their elevational distributions (Freeman et al. 2016). This is contrary to our findings, where we detected no aggression between Canada and hooded warblers even though they have some overlap in their distributions. Another recent study determined that abiotic factors were more important than competition in determining the distributions of 73% of Himalayan bird species (Elsen et al. 2017).

We found no evidence of socially-mediated Allee effects as none of our experimental playback sites was colonized following the addition of social cues. Although strong inference on Allee effects requires estimation of population growth rates, colonization rates should serve as a useful proxy, and the fact that colonization was not associated with social cues suggests that habitat immediately outside range boundaries is unoccupied for reasons other than the lack of social information. Although extensive theory exists to describe how Allee effects, socially-mediated or otherwise, can shape range boundaries, we know of no previous empirical investigation, and our results indicate that Allee effects may not be as important as theory has indicated. Nonetheless, additional work is needed given the well-documented role that social information can have on occupancy in other contexts (Schlossberg and Ward 2004, Hahn and Silverman 2006, Betts et al. 2008). In addition, it is possible that social cues are more important during the post-breeding season than during the territory establishment season that we studied. For example, young birds are often thought to prospect for future territories toward the end of the breeding season soon after fledging. This was demonstrated when, by playing black-throated blue warbler song in unoccupied habitat during the post-breeding season, previously unoccupied habitat was occupied by younger male black-throated blue warblers the following season (Betts et al. 2008). It is possible, given that Canada warblers and black-throated blue warblers have similar life histories, compared to that of black-capped vireos, that they share similar dispersal strategies and that had we provided playback during the post-breeding of 2015 we would have seen colonization of these sites in 2016.

Results from this study support the hypothesis that climate and other abiotic variables exert stronger influence on the distributions of trailing-edge populations than do biotic interactions. However, although we found no evidence of competition and socially-mediated Allee effects, others biotic interactions warrant additional study. Predation in particular can have a strong

influence on species range limits, and thus should be investigated (Sievert and Keith 1985). In our system, it is possible that warm-adapted nest predators, such as snakes, could shift their distributions upward in elevation and negatively affect the viability of cool-adapted species (Lumpkin et al 2012). Future work should also investigate the mechanisms underlying the influence of temperature and precipitation. In particular, information is needed on physiological tolerances of species near low-latitude range margins. Future work should also attempt to understand how abiotic factors and biotic interactions influence demographic processes, which would provide deeper insight than afforded by occupancy studies. Recently developed integrated population models provide an opportunity for doing this, while accounting for spatial processes and individual heterogeneity (Chandler and Clark 2014). Combined with manipulative experiments, such an approach would help advance empirical studies of species distributions and range shifts by focusing on specific ecological processes. This approach would also provide a framework for predicting how conservation efforts could most effectively reduce the impacts of anthropogenic climate change on vulnerable populations.

If we wish to conserve communities at the warm-edge, we must be able to make informed predictions and therefore we need a better understanding of which factors have the greatest influence on species range shifts (Hill et al. 2001, Hickling et al. 2006, McInnes et al. 2009). Our results provide a step towards this goal by identifying two potentially strong limiting abiotic factors, temperature and precipitation, and eliminating some biotic factors, competition and socially-mediated Allee effects.

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## Tables and Figures

Table 3.1. Five cool adapted migrant songbirds and corresponding putative warm-adapted competitors.

Cool adapted species	Mass(g)	Warm adapted competitor	Mass(g)
Canada warbler	9-12	Hooded Warbler	9-12
Black-throated Blue Warbler	9-12	Hooded Warbler	9-12
Dark-eyed Junco	18-30	Ovenbird	16-28
Blue-headed Vireo	13-19	Red-eyed Vireo	13-19
Veery	28-54	Wood Thrush	40-50

Table 3.2. Measured aggressive response variables and predictor variables used in analysis of aggression trials between Canada warblers, hooded warblers, and Carolina chickadees.

Aggressive Response	Predictor Variables
Attack	Treatment+Climate
Counter Song	Treatment+Climate
Minimum Distance	Treatment+Climate
Singing Aggressively	Treatment+Climate

Table 3.3. Observed aggressive behaviors from ‘aggression trials’ with Canada warblers and Hooded warblers in the southern Appalachian Mountains of North Carolina.

Number of trials with the following observed aggressive interactions							Mean Minimum Distance (m)
Species invading	Species defending	Attack	Aggressive Singing	Counter Singing	Display		
CAWA	HOWA	1	2	1	0	6.8	
HOWA	CAWA	0	3	2	1	3.9	
CACH	HOWA	0	1	0	0	6.8	
CACH	CAWA	0	3	0	0	6.8	

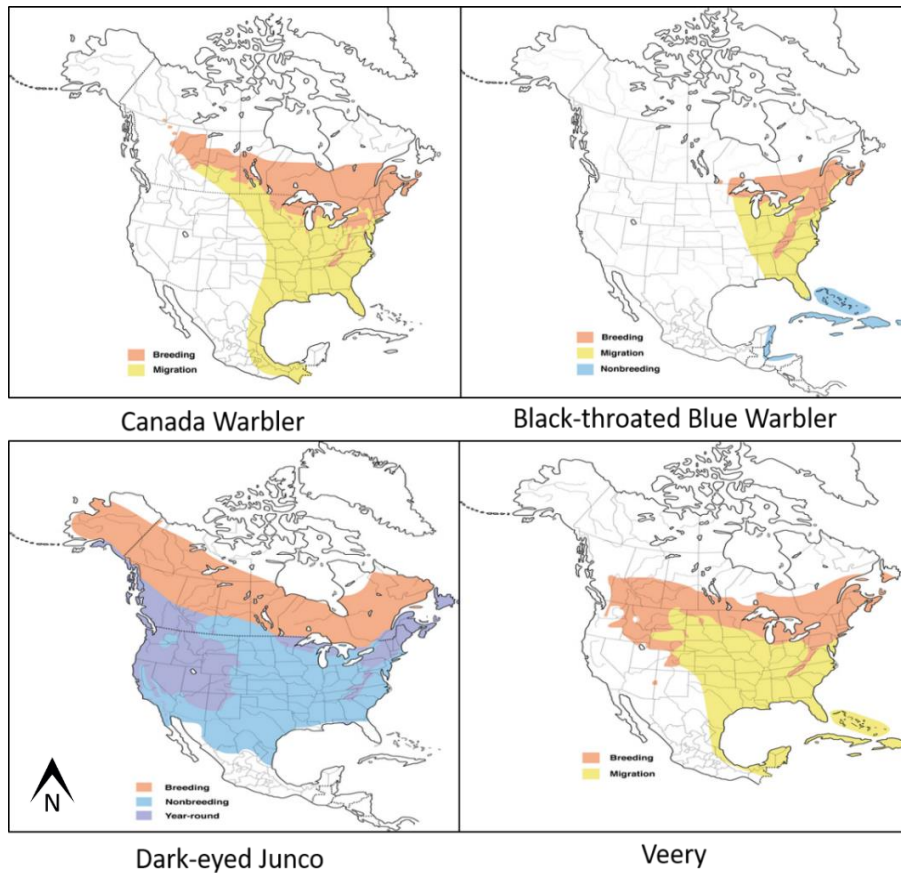


Figure 3.1. Breeding ranges for 4 species of cool-adapted migratory songbirds. More than 20 species of birds exhibit similar distributions whose warm-edge breeding range limit occurs in the southern Appalachian Mountains (Nolan Jr. et al. 2002, Bevier et al. 2005, Holmes et al. 2005, Reitsma et al. 2009).

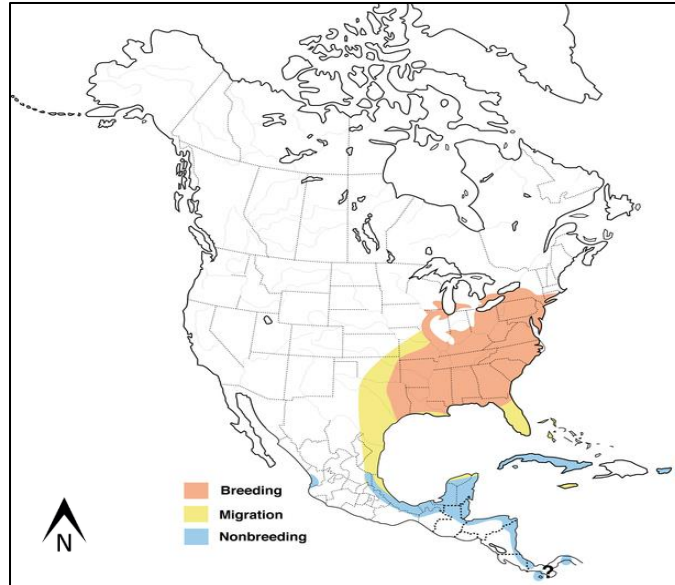


Figure 3.2. Breeding, migration and winter range of the Hooded Warbler, a warm-adapted migratory songbird. Many other species including ovenbirds and wood thrush exhibit similar breeding distributions concentrated in the eastern United States (Chiver et al. 2011) .



Figure 3.3. A hand carved wooden decoy of a Canada warbler (*Cardellina canadensis*) used in aggressive playback experiments with hooded warblers (*Setophaga citrina*) in the southern Appalachian Mountains of North Carolina.



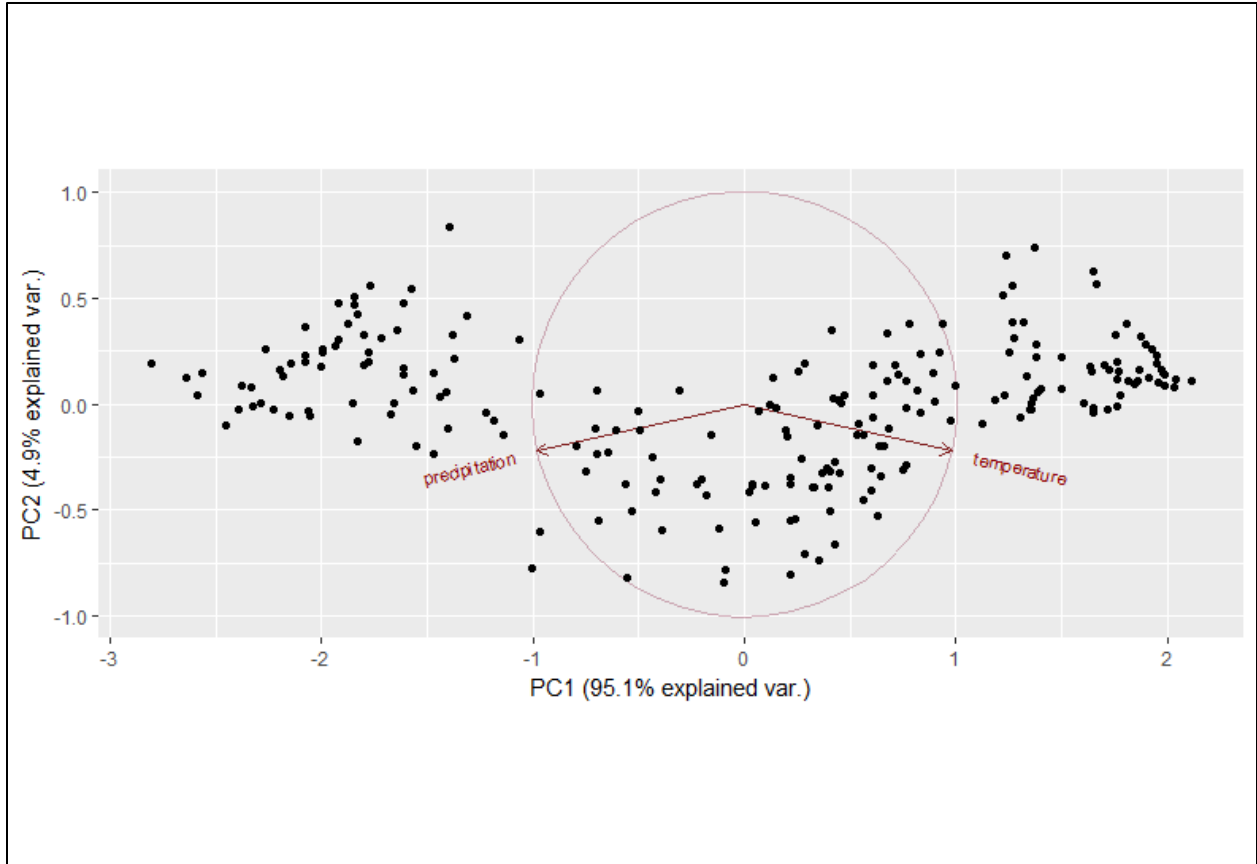


Figure 3.4. Principle component analysis output showing a high correlation between temperature and precipitation. Principle component 1 explained 95.1% of the variance.

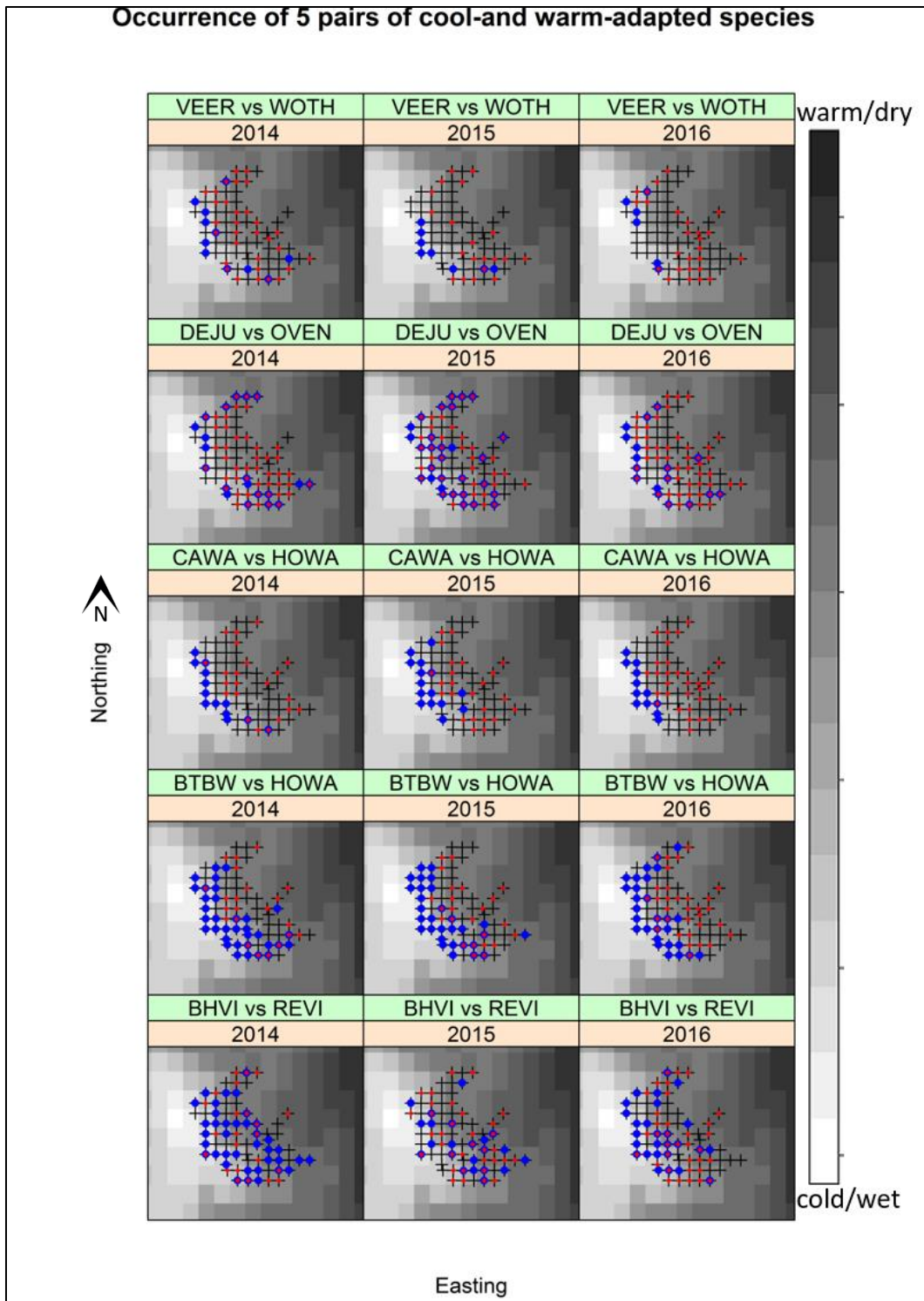


Figure 3.5. Point count detection maps of 5 pairs of cool(blue)- and warm(red)-adapted species in the southern Appalachian Mountains of North Carolina over the climate principle component. Lighter colors are cooler with more precipitation darkest colors are warmer and drier.

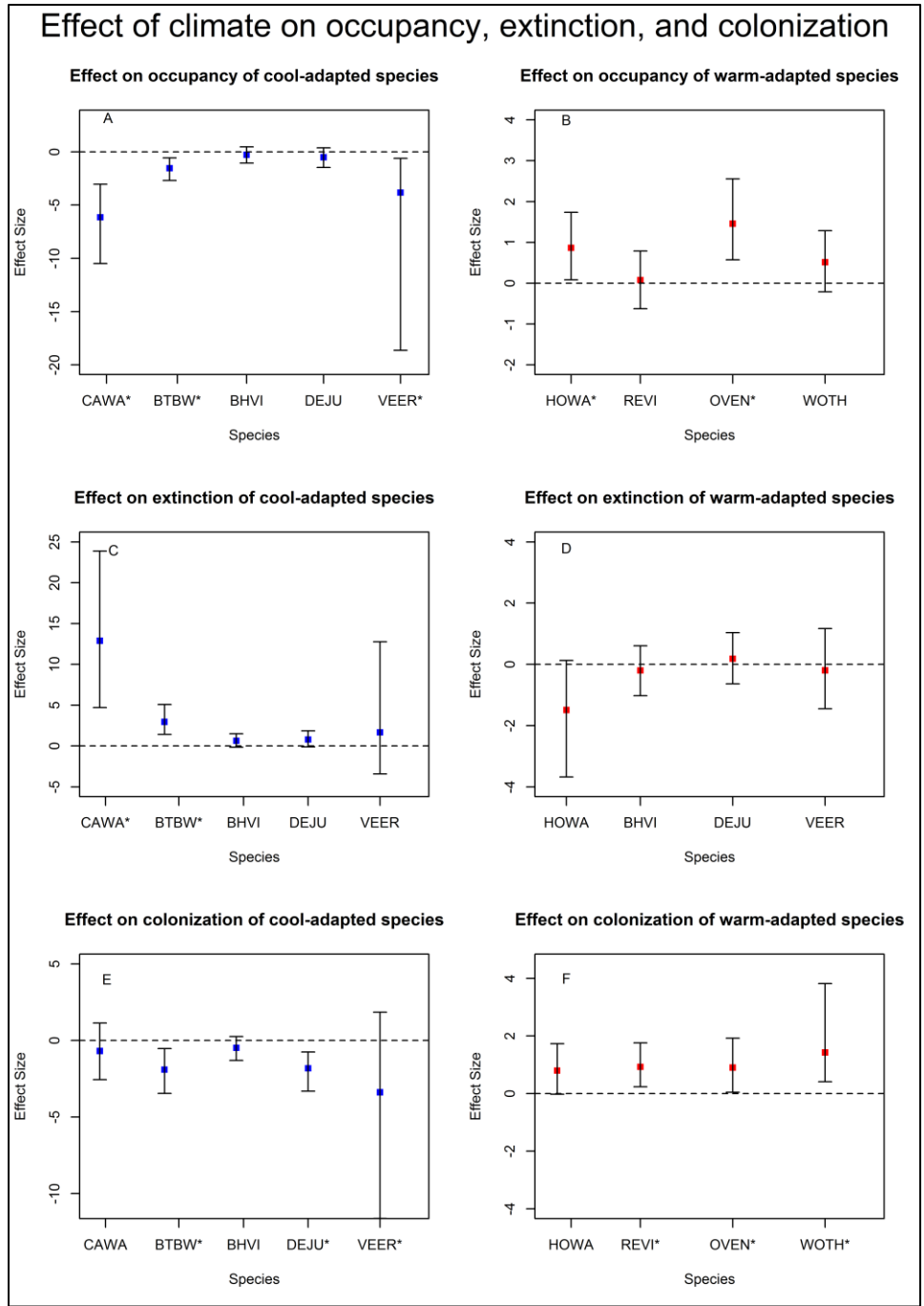


Figure 3.6. The effect of climate, including 95% CI, on occupancy, extinction, and colonization for 5 cool-adapted and 4 warm-adapted species in the southern Appalachian Mountains of North Carolina. Models including abiotic and biotic factors in blue and models including only abiotic factors in red. A “\*” denotes when a confidence interval does not cross 0.

### Effect of climate on occupancy

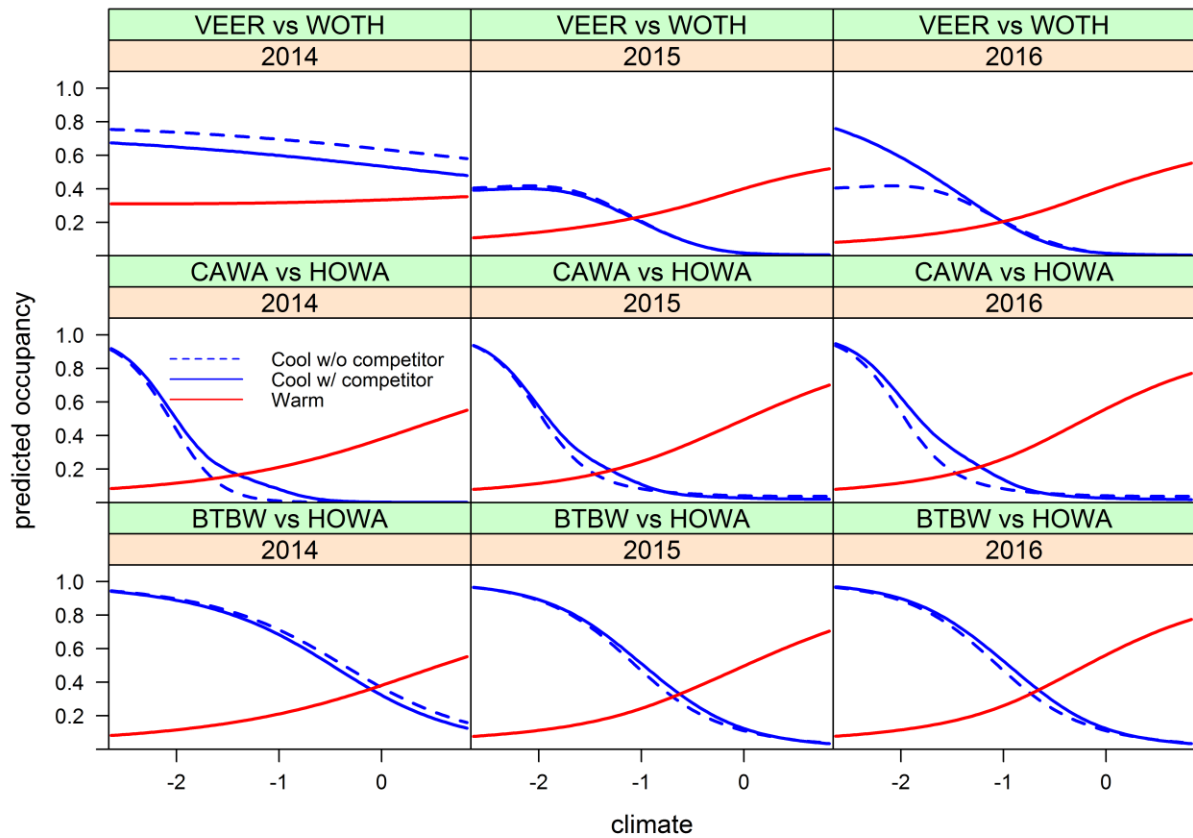


Figure 3.7. The effect of climate on occupancy of 3 cool-adapted and 2 warm-adapted species in North Carolina for 2014, 2015, and 2016. Climate values represent a principle component and are warmer and drier at smaller values.

### predicted occupancy for 3 cool-and warm-adapted species pairs

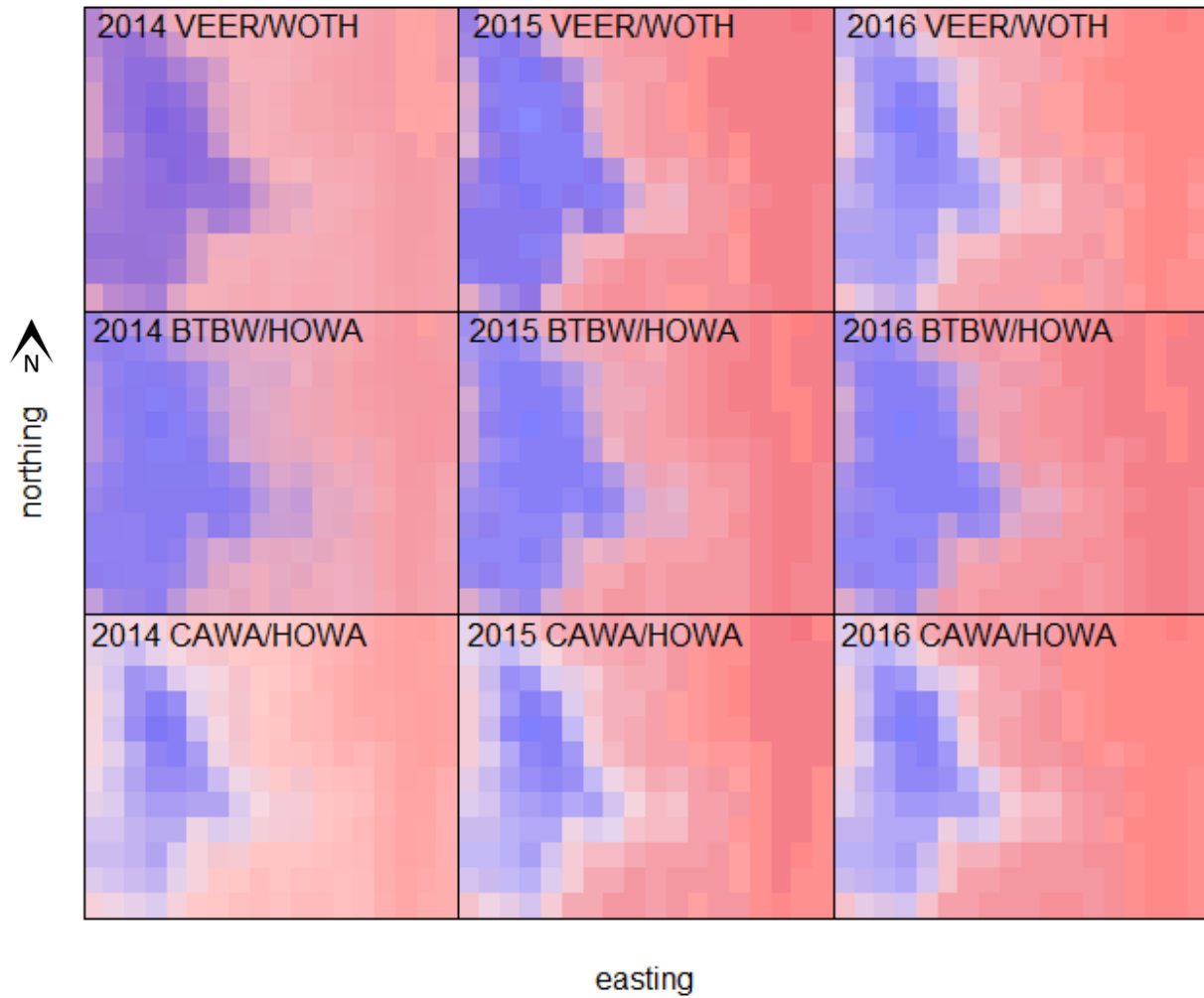


Figure 3.8. Predicted occupancy of 3 pairs of cool- and warm-adapted species in the southern Appalachian Mountains for 2014-2016. Bluer pixels represent higher occupancy of cool-adapted species and redder pixels represent higher occupancy of warm-adapted species. Purple or lavender colors are where species tend to overlap and white represents where neither species have high occupancy.

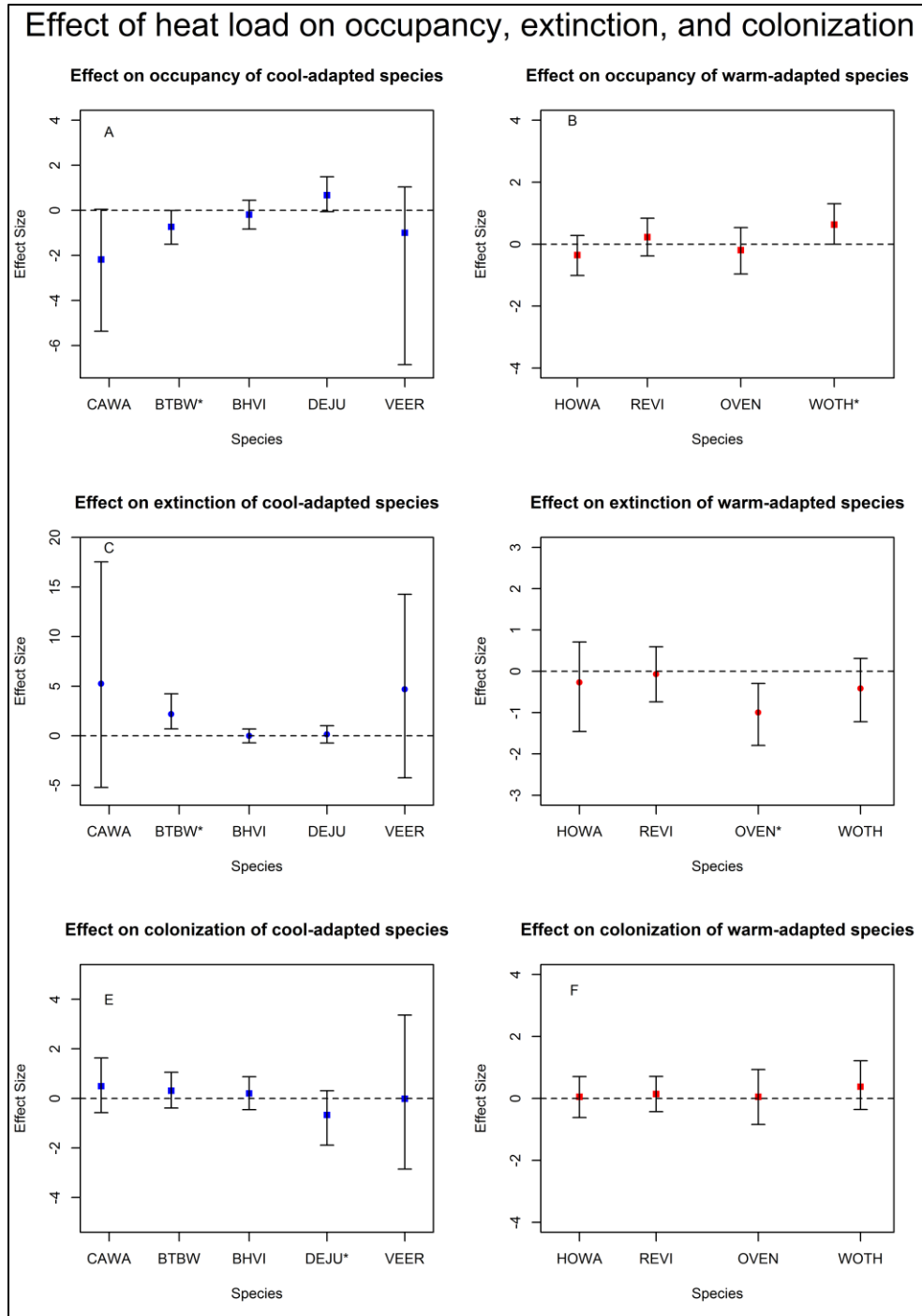


Figure 3.9. The effect of heat load, including 95% CI, on occupancy, extinction, and colonization for 5 cool-adapted and 4 warm-adapted species in the southern Appalachian Mountains of North Carolina. Models including abiotic and biotic factors in blue and models including only abiotic factors in red. A “\*” denotes when a confidence interval does not cross 0.

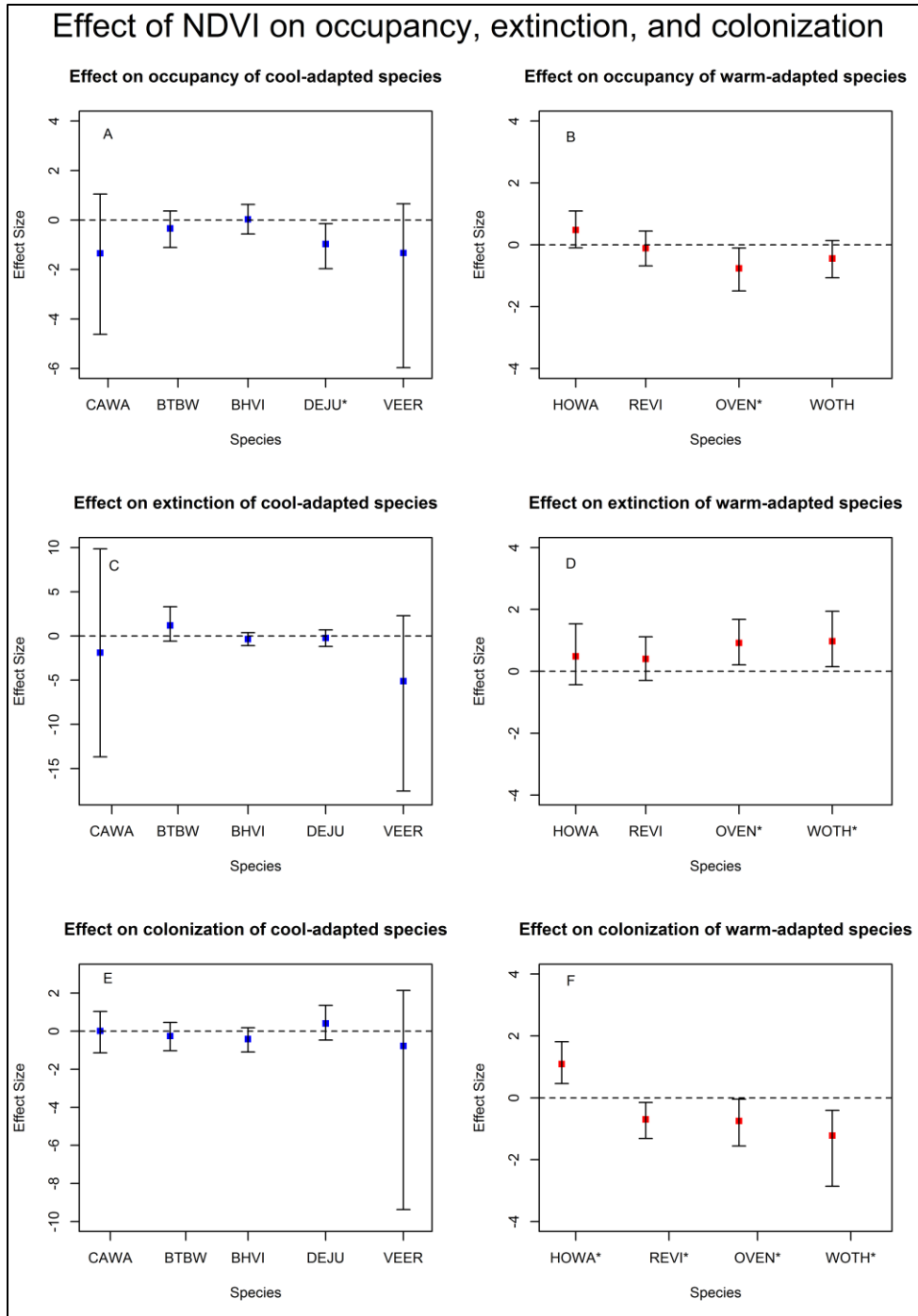


Figure 3.10. The effect of NDVI, including 95% CI, on occupancy, extinction, and colonization for 5 cool-adapted and 4 warm-adapted species in the southern Appalachian Mountains of North Carolina. Models including abiotic and biotic factors in blue and models including only abiotic factors in red. A “\*” denotes when a confidence interval does not cross 0.

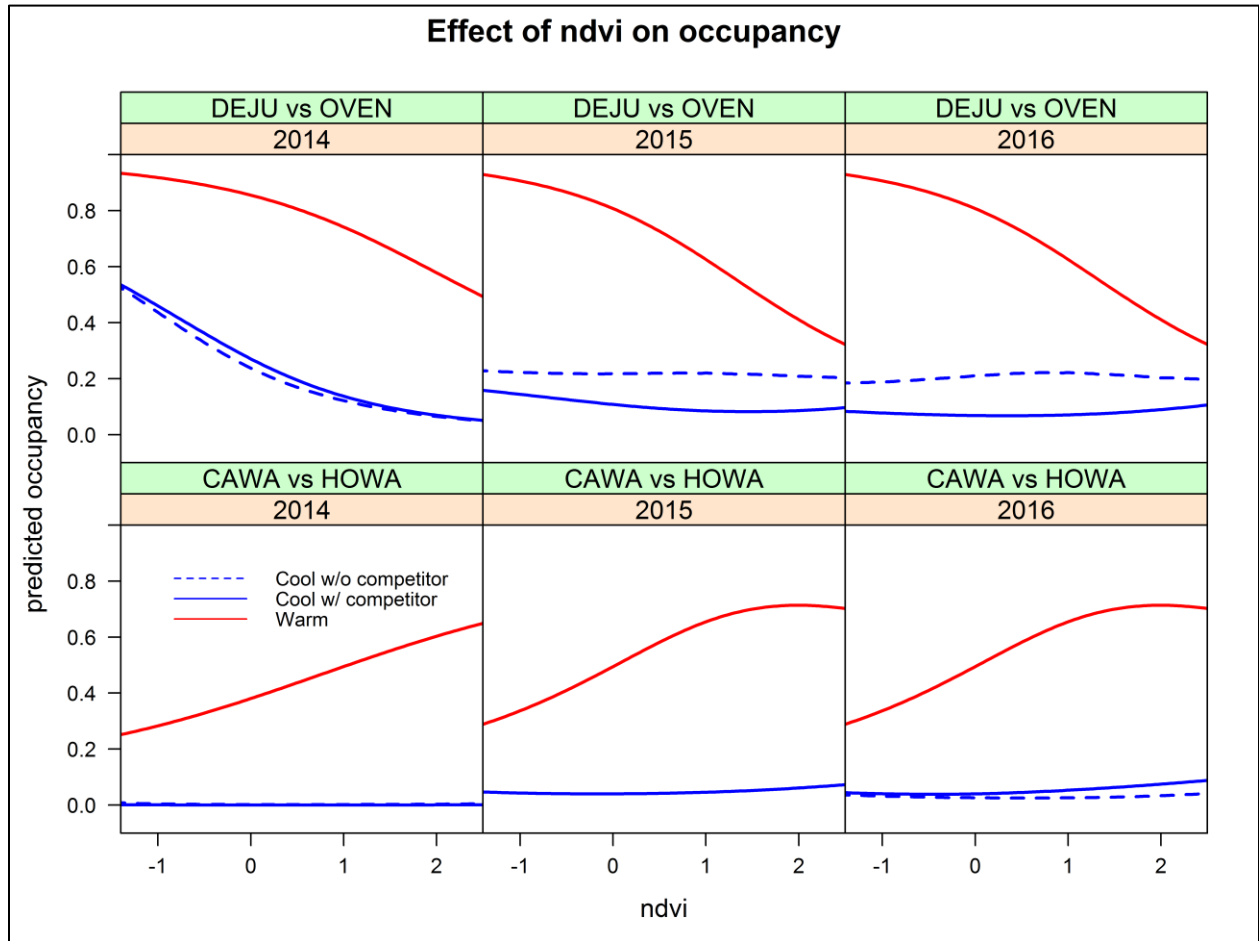


Figure 3.11. The effect of NDVI on occupancy of dark-eyed juncos, ovenbirds, Canada warblers, and hooded warblers in North Carolina for 2014, 2015, and 2016. Low NDVI values represent areas with little evergreen vegetation.



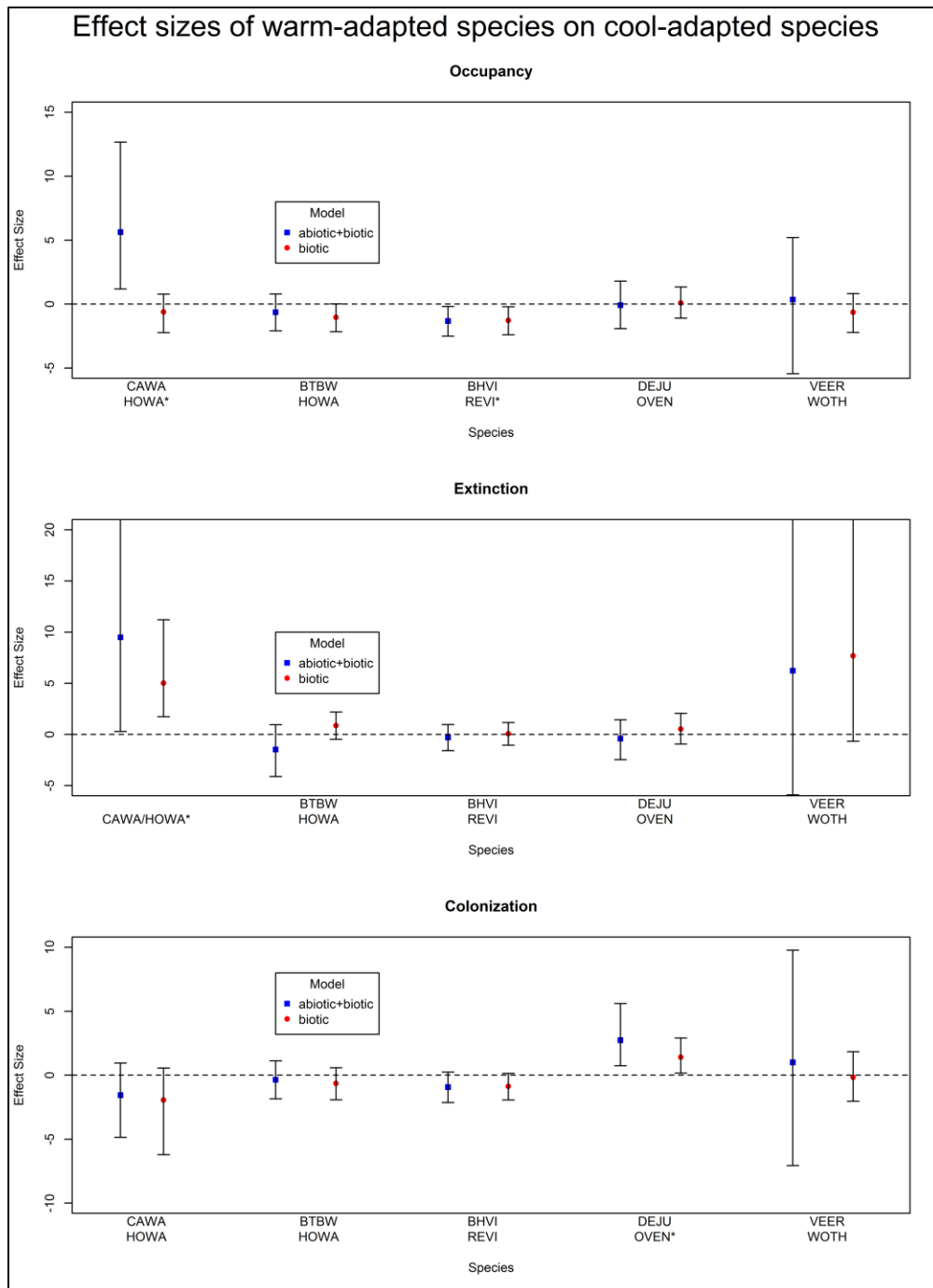


Figure 3.12. Effect size estimates including 95% CI for the effect of warm-adapted species on cool-adapted species in the southern Appalachian Mountains of North Carolina. A) Occupancy, B) Extinction, C) Colonization. Models including abiotic and biotic factors in blue and models including only biotic factors in red.

## CHAPTER 4

### Conclusions

Major findings of this thesis include support for the hypothesis that abiotic factors, not biotic interactions, primarily limit the distributions of trailing-edge populations. Specifically, we found that climate had the strongest effect on occupancy dynamics in the southern Appalachian Mountains of North Carolina. Other factors like heat load and evergreen vegetation had important, but lesser, impacts of occupancy dynamics. We found no evidence that biotic interactions like interference competition and socially-mediated Allee effects affected species' distributions.

The focus of this work is to identify factors limiting species distributions at their low-latitude range limit. We focused on the southern Appalachian Mountains of the United States because of its importance as a region of high biodiversity and because it is the trailing-edge for species in this study. By systematically reviewing range maps of North American vertebrates we found that many species have trailing-edge distributions in this region. Using this list and field observations, we selected five pairs of species with trailing-edge distributions to test different hypotheses concerning the importance of abiotic and biotic effects on limiting species distributions. We hypothesized that abiotic factors like temperature, precipitation, heat load (microclimate), and NDVI (habitat), would have a stronger effect on species distributions than biotic factors like competition or Allee effects.

To test for the effect of biotic factors on limiting species distributions we developed two manipulations; one to test for the effect of interference competition between two migratory songbirds, and one to test for socially-mediated Allee effects in a single migratory songbird. We

included observational methods in our analysis. Using point count observations and occupancy dynamics of 5 pairs of species under a Bayesian framework. We included climate, heat load, NDVI, and the presence of a putative competitor as covariates in determining species initial occupancy and probability of extinction and colonization.