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FORAGING ECOLOGY OF A WINTER BIRD COMMUNITY IN SOUTHEASTERN GEORGIA

by

RACHEL MOWBRAY

(Under the Direction of C. Ray Chandler)

ABSTRACT

Classical views on community structure emphasized deterministic processes and the importance of competition in shaping communities. However, the processes responsible for shaping avian communities remain controversial. Attempts to understand distributions and abundances of species are complicated by the fact that birds are highly mobile. Many species migrate biannually between summer breeding grounds and wintering grounds. The goal of this study was to test four hypotheses that attempt to explain how migratory species integrate into resident assemblages of birds (Empty-Niche Hypothesis, Competitive-Exclusion Hypothesis, Niche-Partitioning Hypothesis, and Generalist-Migrant Hypothesis). I collected data on birds foraging during the winter of 2017-2018 in Magnolia Springs State Park, Jenkins County, Georgia, U.S.A. Foraging behavior, substrate, perch height, horizontal location, plant used, and habitat type were recorded for each observation. Three focal species, Tufted Titmouse (resident), Ruby-crowned Kinglet (migratory), and Yellow-rumped Warbler (migratory), were chosen to test the above hypotheses by comparing their niche location, breadth, and overlap.

Tufted Titmice changed their niche location after migrant arrival, but neither of the focal migrant species moved into the exact niche space vacated by residents. This satisfies most of the predictions for the Competitive-Exclusion Hypothesis, but not the prediction that migrants would move into habitat vacated by residents. Because Tufted Titmice did not change their niche breadth after migrant arrival and did not decrease their niche overlap with migrants significantly after migrant arrival, I reject the Niche-Partitioning Hypothesis. I also reject the Generalist-Migrant Hypothesis because resident focal species did not differ significantly in their niche breadth from migratory species. While several predictions were met for the Empty-Niche Hypothesis, resident species did change their niche location, in contradiction of one

prediction for Empty-Niche Hypothesis. To determine if competition or other seasonal factors are responsible for this change in niche location for resident birds, future studies should account for all members of the bird community and quantify resource availability.

INDEX WORDS: Avian ecology, Competitive exclusion principle, Niche partitioning, Winter communities, Migratory birds, Foraging behaviors.

FORAGING ECOLOGY OF A WINTER BIRD COMMUNITY IN SOUTHEASTERN GEORGIA

by

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CHAPTER 1

INTRODUCTION

General Background

The structure of a community is determined by the overlapping niche requirements of its inhabitants as well as the abiotic environment. To understand distributions and abundances, we need to first understand the niches in which species occur. The term niche was first introduced by Grinnell (1917) to describe the California Thrasher's physical environment and their behavioral adaptations that allowed them to survive in their environment. The niche, in Grinnell's view, was essentially the constellation of habitat features required by a species (see also James et al. 1984). This contrasted with Elton's (1927, 1946) view of the niche as an animal's functional attributes and trophic position in a community. Hutchinson (1957) expanded the concept of niche to include all the factors, the n-dimensional hypervolume, that includes the environmental conditions and resources required for a population to survive and persist. Gause (1934) connected the concept of niche to competition when he asserted that two species cannot coexist and occupy the same niche. When two coexisting species occupy the same ecological niche, one will eventually out compete the other. This concept was termed the competitive exclusion principle or Gause's Principle (Hardin 1960).

The competitive exclusion principle states that the niche of one species might be altered by another species; species may need to shift their niche due to competition. Lack and Southern (1949) were among the first to link niche shifts to competition by documenting eight examples in which bird species occupied a wider range of habitats in locations with fewer competing species. The role of competition in shaping community dynamics was also stressed by Lack, who found that closely related species of passerines (Lack 1944) and non-passerines (Lack 1945) coexisting in the same location differed in their diet and habitat use. He also found that birds of prey partitioned resources by favoring different prey

species (Lack 1946). These studies emphasize the importance of interspecific competition in shaping community structure.

Hutchinson's (1958) expanded niche concept led scientists like MacArthur and Levins to look for ways to more rigorously quantify niche space (MacArthur 1968, 1970, 1972; Levins 1968). These works provided the means to quantify and compare parameters such as niche breadth or overlap. The ideas of MacArthur (1968) and Diamond (1975) are good examples of the classic view of ecology. Both of their works emphasized deterministic processes and the importance of competition in shaping communities.

Despite competitive exclusion being generally accepted by ecologists, some bird communities appeared to conflict with this principle. In New England forests, Cape May (*Setophaga tigrina*), Yellow-rumped (*S. coronata*), Black-throated Green (*S. virens*), Blackburnian (*S. fusca*), and Bay-breasted (*S. castanea*) Warblers are insectivorous birds found foraging in the same habitat and even the same trees during the breeding season (MacArthur 1958). This appears to conflict with the view that no two species can occupy the same niche (MacArthur 1958). However, MacArthur (1958) used various measures of niche space to show that the five species foraged using different methods, at different heights, and on branches with different diameters. This study introduced new standards for quantitative measurement of niches in natural settings (MacArthur 1958). MacArthur's work emphasized that community structure is the result of competition driving deterministic processes towards a dynamic equilibrium (MacArthur 1968, 1970, 1972).

Jared Diamond's studies of the assembly of avian communities are another good example of this deterministic view. His work on New Guinea and surrounding islands revealed that resident land bird species appeared nonrandomly distributed (Diamond 1973, 1975; Diamond and Mayr 1976; Diamond and Marshall 1977). Diamond (1975) proposed that this pattern is largely due to interspecific competition. Because of this competition, only some groups of species are able to coexist. Diamond (1975) emphasized that competition between species drives community assembly towards the most stable combinations, which are better able to resist intrusion by colonizing species. He formulated this view as a set of "rules" about permissible combinations of species (Diamond 1975).

MacArthur's and Diamond's studies emphasized deterministic processes as shaping community structure, which generated controversy in the 1970s and 1980s. For example, Connor and Simberloff (1979) criticized Diamond's rules as untestable, tautological, or descriptions that would also be true if species were randomly distributed. Conner and Simberloff (1979) claimed Diamond (1975) did not test a null hypothesis but assumed that competitive exclusion drives community structure and then sought to rationalize his observations. While Conner and Simberloff did not completely discredit the hypothesis that competitive exclusion drives community structure, they argued that this idea should be tested by observing one species replacing another directly. More generally, several authors have objected to interpreting niche shifts as definitive evidence for competition because there could be numerous other causal factors (Andrewartha and Birch 1955, Williamson 1972, Connell 1975).

Weins and Rotenberry (1981a), in their studies of North American grassland shrubsteppe bird communities, found no support for competition as a primary factor shaping bird communities. After studying morphology (Weins and Rotenberry 1980), diet (Weins and Rotenberry 1979, Rotenberry 1980), and habitat selection (Weins and Rotenberry 1981b, Weins and Rotenberry 1980), they concluded that these bird communities were not heavily impacted by competition for resources. Instead, the authors proposed that resources are not limiting bird communities and factors other than competition for resources must determine population sizes.

While some authors report a lack of support for the role of interspecific competition in shaping communities, it could be that competition played a more critical role historically than it does now. This concept, termed the "ghost of competition past," asserts that current communities display little evidence for competition because competition in the past provided selection pressures that influenced species to modify their behaviors to minimize the negative impacts of competition (Connell 1980). There continues to be debate over how communities are shaped, particularly the importance of deterministic processes such as competitive exclusion versus chance (Gilpin and Diamond 1982, 1984; Colwell and Winkler 1984; Gotelli 2000; Gotelli and McCabe 2002; Miklos and Podani 2004; Sfenthourakis et al. 2005).

Seasonal Changes in Community Structure

Migration complicates attempts to understand the structure of avian communities. In areas like the Arctic, for example, establishment of bird communities during summer would be expected to follow patterns similar to community establishment on islands, because there are relatively few permanent residents (Meltofte 2013). Migratory birds arrive to their breeding grounds to occupy previously unavailable and unoccupied niche space (Meltofte 2013). However, in temperate and tropical regions the presence of resident birds makes seasonal assembly of community structure more complicated. In these areas, seasonal migrants arrive into diverse, established communities of potentially competing permanent resident species.

Tropical and temperate migrants potentially face competition as they attempt to locate foraging sites in habitat already occupied by residents. In contrast, resident birds must respond to seasonal changes in community structure and presumably increased competitive pressure as migrants pass through or reside twice annually at the beginning and end of the breeding season (Lewke 1982, Johnson and Sherry 2001). While studies have historically focused on competition and its impacts on reproductive success during the breeding season, an individual's ability to survive and prepare for reproduction during the nonbreeding season impacts the reproductive success for both migrants and residents (Johnson and Sherry 2001). Despite the importance of the nonbreeding season for future fecundity, the interactions between permanent and winter residents during the nonbreeding season has received little attention and is poorly understood (Hiron et al. 2006).

Interactions Between Winter Migrants and Residents

Migratory birds could assimilate into communities of permanent residents in one of four general ways (Figure 1). First, migrants might occupy niches that are unoccupied by resident birds (Empty-Niche Hypothesis). This would mean migratory birds use habitat and resources that resident species are not using even when migrants are absent (Figure 1A). There has been some support for Empty-Niche Hypothesis. Rusterholtz (1981) found little evidence of competition between residents and migrants,

citing scarce overlap in foraging behavior and the rarity of aggressive interspecific interactions. When diet was examined, little dietary overlap was found between Nearctic migrants and permanent residents in central Panama (Paulin & Lefebvre 1996). One explanation for these results is the hypothesis that certain foraging strategies served as an evolutionary prerequisite for migration (Salewski et al. 2003). It is possible that migratory bird's foraging does not differ from residents as a response to current competition, but because these differences are what enabled their ancestors to become migratory in the first place. It is assumed that competition drives the need to occupy an empty niche. In this case, migratory birds could have shifted their niche to avoid competition they historically encountered with residents.

The Empty-Niche Hypothesis implies two key predictions (Table 1). If arriving migrants do not compete with resident species, residents should not change niche location or breadth as migrants arrive. Resident birds are, on average, expected to forage in the same type of habitat in the same manner before and after migrant birds arrive and display no significant difference in their niche breadth. Migrants should occupy niche space unused by residents resulting in little to no niche overlap between migrants and residents. For example, a bird that forages predominantly in pine trees in edge habitat during the fall before migrants arrive would also forage predominantly in pine trees in edge habitat after the arrival of migrants.

Interactions between migrant and resident species could also be explained by the Competitive-Exclusion Hypothesis (Figure 1B). This hypothesis is premised on the resource competition hypothesis and suggests that migrants consume preferred resources and force residents to shift their realized niche as they arrive (Jedlicka et al. 2006, Bensusan et al. 2011). In this scenario, niches are already filled when migrants arrive, and migrants outcompete resident species. If migrants are the better competitors, this would result in migrants foraging in habitat previously filled by residents and residents being forced to shift their niche. Under competitive exclusion, the opposite scenario can also exist. Migrants could prefer the habitat used by residents but be outcompeted by resident species (Figure 1B). This would result in migrants shifting their habitat use. This scenario would be indistinguishable in pattern from the Empty-Niche Hypothesis.

A. Empty-Niche Hypothesis
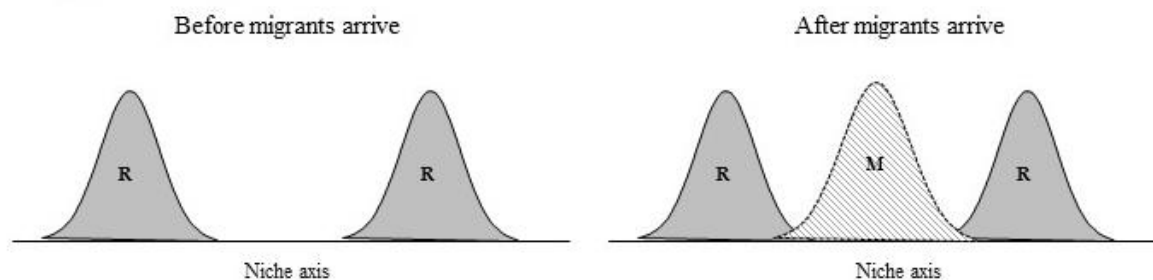
Before migrants arrive

After migrants arrive

R   R

Niche axis

R   M   R

Niche axis

B. Competitive-Exclusion Hypothesis

Before migrants arrive

After migrants arrive
(migrant exclusion of resident)

After migrants arrive
(resident exclusion of migrant)

R

Niche axis

R ← M

Niche axis

or

R → M

Niche axis

C. Niche-Partitioning Hypothesis

Before migrants arrive

After migrants arrive

R

Niche axis

R   M

Niche axis

D. Generalist-Migrant Hypothesis

Before migrants arrive

After migrants arrive

R   R   R

Niche axis

R   R   R
M
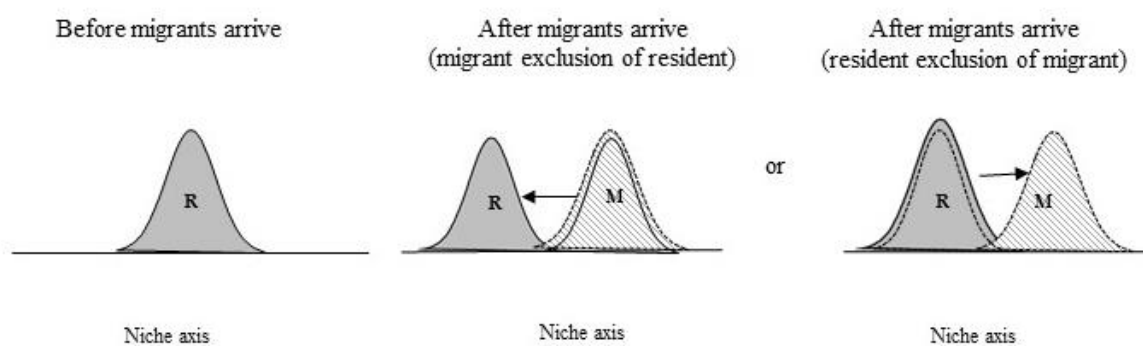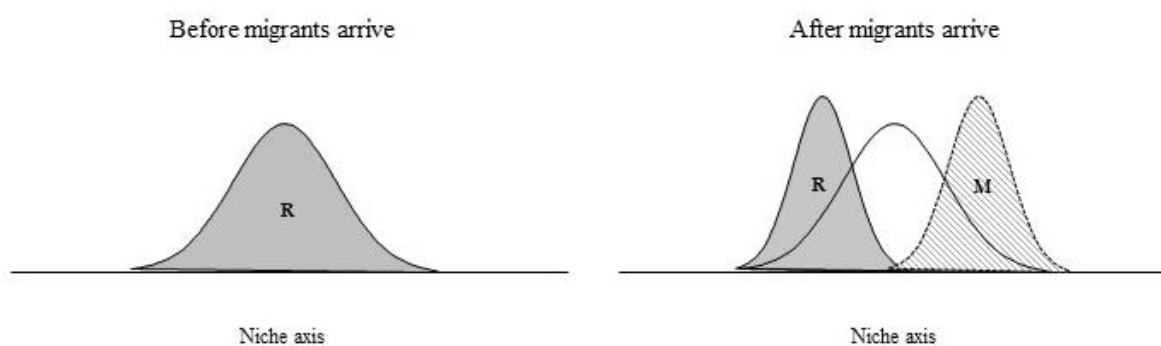
Niche axis
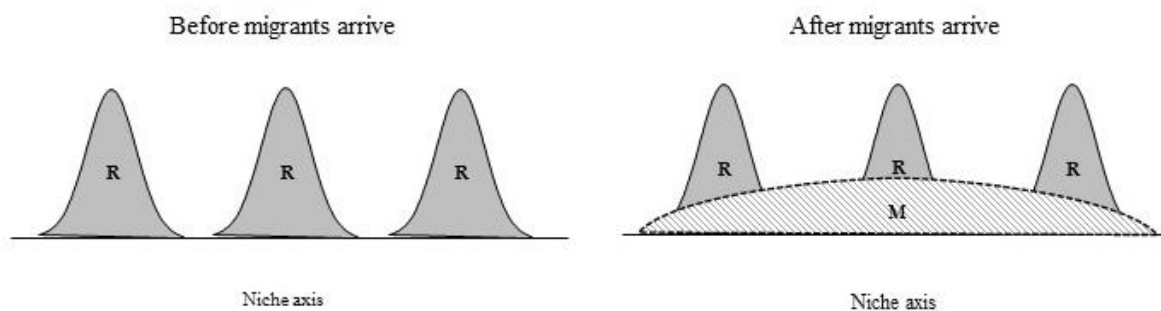
Figure 1. Alternative hypotheses for the impact of migratory birds on resident species.

Table 1. Key predictions for the four hypotheses described in Figure 1. Location refers to the mean of quantitative data or the mode of qualitative observations. Niche breadth refers to calculations of Leven's measure of niche breadth. Niche overlap refers to calculations of Simplified Morisita Index.

Hypotheses	Key Predictions	Metrics
A. Empty-Niche Hypothesis: There are open niches available to migrants and migrants take empty niche pace	There is no significant change in resident niche use (location) after the arrival of migrants. Migrants occupy niche space unoccupied by residents.	No significant change in resident location No significant change in resident niche breadth Little niche overlap before and after migrant arrival
B. Competitive-Exclusion Hypothesis: Niches are filled and migrants displace residents to occupy space previously occupied by residents	There is a significant change in resident habitat use (location) and no significant niche overlap and migrants use that space.	Significant change in resident location No significant change in resident niche breadth High degrees of niche overlap before migrant arrival followed by a reduced overlap after migrant arrival
C. Niche-Partitioning Hypothesis: Niches are filled and migrants partition resources with residents	Residents exhibit a significant reduction in niche breadth and a significant decrease in niche overlap with migrants.	Significant change in resident location Significant change in resident niche breadth Partial decrease in niche overlap after migrant arrival
D. Generalist-Migrant Hypothesis: Migrants have a broader niche and are able to forage over a wider range than residents	Migrants display a significantly wider niche breadth than residents.	No significant change in resident location No significant change in resident niche breadth Significant niche overlap Niche breadth of migrants much greater than niche breadth of resident

If the migrants competitively exclude resident species (Figure 1B), we predict that resident species will shift their niche space as a result of the migrant's presence (Table 1). Under this hypothesis, resident species will display a significant change in their average use of habitat type or foraging behavior. The Competitive-Exclusion Hypothesis predicts high competition between residents and migrants that leads to migrants displacing resident species. If this is true, I expect high degrees of niche overlap between the niche occupied by residents before migrant arrival and the niche used by migrant species after they arrive. After migrants arrive, niche overlap between resident and migrant species should decrease as the residents are excluded by the migrants from a preferred niche. As residents shift their niche space to avoid competition, there should be no significant change in niche breath for resident species.

If migrant and resident species compete for resources, but one species is unable to completely competitively exclude the other from the entire niche space, resident species could share (partition) that niche with migrants when they arrive (Niche-Partitioning Hypothesis; Figure 1C). Residents would occupy a narrower niche breadth with migrants occupying a fragment of the niche previously occupied by residents. Residents will become more specialized after arrival of migrants. A study of abundance and species richness of residents, short-distance migrants, and Neotropical migrants during different seasons demonstrated seasonal differences in habitat selection for migrants as well as residents (Griffis-Kyle & Beier 2005). If resident and migrant species are partitioning resources, seasonal shifts for residents would be expected.

The Niche-Partitioning Hypothesis predicts that migrant arrival will result in a reduced niche breadth for the resident species (Table 1). Residents will occupy a portion of the niche they formerly used. Migrant species are expected to occupy the niche vacated by the compression of resident species' niche breadth. Little to no niche overlap is expected between migrants and residents. This would appear similar to the predictions for Competitive-Exclusion Hypothesis with residents changing their niche use and reducing their niche overlap with migrants. The key difference is the prediction that residents will significantly reduce their niche breadth after migrant arrival.

The last hypothesis posits that migrant species could display a greater flexibility in their habitat use and foraging behavior (Generalist-Migrant Hypothesis; Figure 1D). Migrants have been observed foraging at relatively higher foraging speeds in more open habitat, leading some to speculate that migrants have a more flexible, generalist foraging strategy compared to resident species (Salewki et al. 2003, Salewski and Jones 2006, Jones et al. 2010, Cresswell 2014). This theory, outlined by Cresswell (2014), proposes that as more of a generalist, migrants avoid competition with residents by taking advantage of any underexploited resources. In this case, resident species do not exhibit significant changes to their foraging behavior after the arrival of migrants, and migrant individuals are seen both foraging in areas unused by residents and with resident species. Telleria and Perez-tris (2004) found that residents tend to saturate more "favorable" habitats, forcing migrants to forage in poorer quality areas. If migrants are generalists, they will be able to forage wherever competition is the least costly.

The Generalist-Migrant Hypothesis predicts that migrants display a significantly wider niche breadth than resident species (Table 1). Due to this wider niche breadth, migrants exert a smaller, but still present, competitive pressure on residents and residents might not display significant differences in their niche breadth with the arrival of migrants. As a generalist, the migrant would be seen in a greater variety of locations and using a greater variety of foraging behaviors compared to the resident species.

Study System

To test the above hypotheses, I investigated the niche relationships of a community of forest birds in southeastern Georgia, U.S.A. This community's common residents include the Tufted Titmouse (*Baeolophus bicolor*), Carolina Chickadee (*Poecile carolinensis*), Northern Cardinal (*Cardinalis cardinalis*), Eastern Bluebird (*Sialia sialis*), Pine Warbler (*Setophaga pinus*), and Carolina Wren (*Thryothorus ludovicianus*). Several migratory species of birds spend the entire winter season in this area, including Yellow-rumped Warblers (*Setophaga coronata*), Ruby-crowned Kinglets (*Regulus calendula*), Yellow-bellied Sapsuckers (*Sphyrapicus varius*), Eastern Phoebe (*Sayornis phoebe*), and Blue-headed Vireos (*Vireo solitarius*).

Tufted Titmice and Carolina Chickadees are known to form mixed species flocks during the summer and winter season with woodpeckers, nuthatches, kinglets, and wood warblers (Dolby and Grubb 1998, 2000). These flocks have a social hierarchy, with titmice and chickadees being the nuclear species (Morse 1970). Members of mixed-species flocks are potential interspecific competitors for prey items. To determine why potentially competing species would forage together, many studies have investigated the vocalizations and predator response of titmice and chickadees (Branch and Freeberg 2012, Courter and Ritchison 2010, Damsky et al. 2017, Dutour et al. 2016, Freeberg et al. 2016, Hetrick and Sieving 2012, Hill 1986). While the interactions within these flocks have been heavily studied, few studies have attempted to examine the entire community surrounding these flocks or the impact migratory species have on residents.

CHAPTER 2

METHODS

Study Site

This study was conducted in Magnolia Springs State Park (32°52'59.8"N 81°57'16.1"W), a 40.8-hectare state park located in Jenkins County, Georgia, U.S.A. The park surrounds Magnolia Lake and consists of mixed pine and hardwood forest. The plant community is a typical southeastern mixed pine-hardwood forest. The forest is dominated by pine (mostly *Pinus taeda* and *P. elliottii, with some P. palustris*) and numerous oaks (*Quercus spp.*) especially swamp laurel (*Q. laurifolia*), live oak (*Q. virginiana*), and water oak (*Q. nigra*). Also common are sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), and wax myrtle (*Morella cerifera*).

Foraging Observations

Observations of resident species before migrant arrival began on 18 September 2017 and were concluded on 15 October 2017. Residents and winter migrants were observed from the first observation on 16 October 2017 until 20 March 2018. The study area was searched systematically to observe as many individual residents and migrants as possible. The four different habitat types (open, forest, edge, and water-edge) were searched for equal amounts of time each day and the starting place for sampling varied to avoid searching the same locations and habitat types in the same order throughout the study. When flocks were encountered, one individual was chosen for observations and followed until no longer visible. After losing sight of the focal individual selected, no other observations were recorded for at least fifteen minutes to avoid sampling from the same flock. The three species with the highest sample size were chosen as focal species for analysis.

All observations took place from 0700 to 1100. For each individual sighted, I recorded: type of foraging behaviors observed, perch height, plant species used, foraging substrate, horizontal position in

tree (estimated distance from the center trunk), and habitat type. Height was estimated with the assistance of a tangent height gauge clinometer. The weather conditions, including temperature and estimated percent cloud cover, were recorded. Individuals were followed for as long as they remained visible and foraging maneuvers were constantly dictated into a Tsumbay 8GB Digital Voice Recorder Wristband. Immediately following the observation of a focal individual, all birds seen or heard within a 50-m radius were recorded. Any aggressive interactions between individuals were recorded. Observations were ended when the first spring migrant was observed on 20 March 2018.

Foraging maneuvers were defined as follows: glean was recorded when a prey item was picked from the surface by a standing or hopping bird; hover was when a prey item was picked from a surface by a flying bird; a hawk was when birds were seen in aerial pursuit of flying prey; a probe was when birds were seen penetrating or overturning a substrate to capture prey from below the surface. Heights of plants and perches were categorized into five strata: forest floor, shrub layer (0 - 1.5 m), sapling layer (1.5 - 4.5 m), mid-canopy layer (4.5 - 7.5 m), and the upper canopy (above 7.5 m; Sabo and Holmes 1983). These heights were estimated using a clinometer. The substrate that birds were observed foraging from was recorded as one of the following categories: leaf (including deciduous leaves and pine needles), twig (any woody part of a plant with an estimated diameter of less than 5 centimeters), branch (any woody part of a plant with an estimated diameter of between 5 and 30 cm), trunk (any woody part of a plant with an estimated diameter of greater than 30 cm), fruit (any reproductive part of a plant), ground, and artificial (including all man-made structures such as railings, boardwalks, and bridges). For birds observed in trees, distance from the central trunk was estimated as a percentage. For example, a bird observed foraging on leaves as far away from the center trunk as possible was said to be 100% from the center. A bird observed foraging directly on the trunk was said to be located 0% from the center. These estimated percentages were later put into one of three categories: inner (0-29%), mid (30-69%), and outer (70-100%). Habitat type was categorized as forest, open, water-edge, and forest-edge habitat.

Data Analysis

The differences in frequencies between focal species was quantified using contingency tables (G-test) in JMP® (SAS Institute Inc.) to determine if resident Titmice before and after migrant arrival differed significantly in their niche location from Yellow-rumped Warblers or Ruby-crowned Kinglets. Contingency tables were also used to determine significant differences in Tufted Titmouse behavior before and after the arrival of migrants.

Niche breadth was calculated for each category of data collected for resident Tufted Titmice and every species of migrants with more than twenty observations. Niche breadth for Tufted Titmice was calculated both before and during migrant occupancy. Levin's measure of niche breadth (1968) was used to quantify niche breadth:

$$B = \frac{1}{\Sigma \, p_j^2}$$

Where B is Levin's measure of niche breadth and p_j is proportion of individuals found in or using resource state *j*. Levin's measure of niche breadth calculates the width of a species' habitat or resource use, with larger values representing a wider niche breadth and lower values representing lower niche breadth.

The Simplified Morisita Index was used to calculate niche overlap between migrants and residents for all categories recorded:

$$C_H = \frac{2 \, \Sigma_i^n p_{ij} p_{ik}}{\Sigma_i^n \, p_{ij}^2 + \Sigma_i^n \, p_{ik}^2}$$

Where C_H is the Simplified Morisita index of overlap (Horn 1966) between species *j* and species *k*, p_{ik} is the proportion resource *i* is of the total resources used by species *j*, p_{ik} is the proportion resource *i* is of the

total resources used by species $k,$ and n is the total number of resource states ($i = 1,2,3, . . ., n$). The Simplified Morisita Index quantifies the degree of overlap between two species by reporting a value between 0 and 1, with 0 representing no overlap and 1 representing complete overlap. The proportion of observations in each resource state, niche breadth, and niche overlap between focal species was used to test the four hypotheses outlined in Table 1.

To analyze the overall foraging behavior for each species, a multivariate approach was used in PRIMER (PRIMER-e Ltd.). A Principle Coordinate Analysis (PCO) was used to analyze the overall location of individuals sampled by ordinating variations in habitat use and behavior. This analysis incorporated variation due to twenty-five variables relating to microhabitat selection and was overlaid with vectors showing how foraging behavior related to microhabitat selection. A permutational multivariate analysis of variance (PERMANOVA) was calculated using Euclidean distances to run pair-wise comparisons between migrants and residents at the community level and between all focal species.

CHAPTER 3

RESULTS

Community Overview

During the study, I observed 42 species at Magnolia Springs State Park, and I recorded a total of 382 individual foraging behaviors of thirteen species (Appendix 1, summarized in Table 2). Common permanent resident species observed included the Northern Mockingbird, Carolina Chickadee, Northern Cardinal, Blue Jay, and Red-bellied Woodpeckers (Table 2). The most common winter migrants were Ruby-crowned Kinglets, Yellow-rumped Warblers, and Black-and-white Warblers.

Overall Community Structure

Over the entire study period, the core resident bird community at Magnolia Springs was composed of Tufted Titmice, Northern Cardinals, Eastern Bluebirds, Pine Warblers, Blue Jays, Carolina Chickadees, Northern Mockingbirds, and Brown-headed Nuthatches (n > 10 for each, Table 3). After fall migration, several migratory species joined this community, most notably Yellow-rumped Warblers, Ruby-crowned Kinglets, and Dark-eyed Juncos (n > 10, Table 3). Species varied in their foraging behavior and habitat use (Table 2). Some species, like the Dark-eyed Junco, and White-breasted Nuthatch, were only observed in a few locations using a narrower range of behaviors (Table 2). Several species were observed using a more generalist foraging strategy and were found in a much wider variety of habitats (Table 2).

Table 2. The most frequently observed foraging behaviors and locations for each species during the winter of 2017-2018 at Magnolia Springs State Park and the proportion of observations seen exhibiting that variable.

Species	Alpha code	N	Status	Behavior	Substrate	Perch height	Horizontal location	Plant species	Habitat type
Yellow-rumped Warbler	YRWA	111	Migrant	Glean (0.73)	Twig (0.40)	Sapling (0.44)	Outer (0.51)	Wax myrtle (0.61)	Water-edge (0.55)
Ruby-crowned Kinglet	RCKI	67	Migrant	Glean (0.76)	Leaf (0.70)	Sapling (0.57)	Outer (0.55)	Wax myrtle (0.54)	Water-edge (0.52)
Black-and-white Warbler	BWWA	15	Migrant	Glean (0.53)	Trunk (0.87)	Mid (0.60)	Inner (1.00)	Water oak (0.87)	Forest (1.00)
Yellow-bellied Sapsucker	YBSA	11	Migrant	Probe (0.54)	Branch (1.00)	Mid (1.00)	Inner (1.00)	Pine (1.00)	Open (1.00)
Dark-eyed Junco	DEJU	10	Migrant	Glean (1.00)	Ground (0.80)	Floor (1.00)	-	-	Open (1.00)
Tufted Titmouse	TUTI	118	Resident	Glean (0.74)	Twig (0.39)	Upper (0.56)	Mid (0.50)	Pine (0.61)	Forest (0.39)
Northern Mockingbird	NOMO	12	Resident	Glean (0.83)	Fruit/nut (0.83)	Sapling (0.50)	Outer (0.83)	Dogwood (1.00)	Open (0.83)
Eastern Bluebird	EABL	9	Resident	Glean (0.89)	Leaf (1.00)	Floor (1.00)	-	-	Open (0.89)
Carolina Chickadee	CACH	8	Resident	Glean (1.00)	Leaf (1.00)	Upper (1.00)	Mid (0.75)	Water oak (1.00)	Open (1.00)
Northern Cardinal	NOCA	6	Resident	Glean (1.00)	Fruit/nut (1.00)	Sapling (0.67)	Outer (1.00)	Muscadine (1.00)	Forest (0.83)
White-breasted Nuthatch	WBNU	6	Resident	Glean (0.83	Trunk (1.00)	Mid (1.00)	Inner (1.00)	Pine (1.00)	Open (1.00)
Pine Warbler	PIWA	5	Resident	Glean (1.00)	Ground (1.00)	Floor (1.00)	-	-	Open (1.00)
Carolina Wren	CARW	4	Resident	Glean (1.00)	Twig (1.00)	Shrub (0.75)	Mid (1.00)	Water oak (1.00)	Forest (1.00)

Table 3. Species observed at Magnolia Springs State Park during winter 2017-2018 listed by total number of individuals observed.

Species	Scientific name	Alpha code	Number of individuals
Yellow-rumped Warbler	*Setophaga coronata*	YRWA	123
Tufted Titmouse	*Baeolophus bicolor*	TUTI	92
Ruby-crowned Kinglet	*Regulus calendula*	RCKI	76
Northern Cardinal	*Cardinalis cardinalis*	NOCA	42
Eastern Bluebird	*Sialis sialis*	EABL	42
American Robin	*Turdus migratorius*	AMRO	31
Dark-eyed Junco	*Junco hyemalis*	DEJU	29
Pine Warbler	*Setophaga pinus*	PIWA	20
Blue Jay	*Cyanocitta cristata*	BLJA	16
Carolina Chickadee	*Poecile carolinensis*	CACH	12
Northern Mockingbird	*Mimus polyglottos*	NOMO	12
Brown-headed Nuthatch	*Sitta pusilla*	BHNU	11
Eastern Phoebe	*Sayornis phoebe*	EAPH	9
Common Grackle	*Quiscalus quiscula*	COGR	9
Northern Flicker	*Colaptes auratus*	NOFL	8
Yellow-bellied Sapsucker	*Sphyrapicus varius*	YBSA	7
White-breasted Nuthatch	*Sitta carolinensis*	WBNU	7
Pileated Woodpecker	*Dryocopus pileatus*	PIWO	6
Red-bellied Woodpecker	*Melanerpes carolinus*	RBWO	5
Purple Martin	*Progne subis*	PUMA	5
Blue-gray Gnatcatcher	*Polioptila caerulea*	BGGN	4
Hermit Thrush	*Catharus guttatus*	HETH	4
Song Sparrow	*Melospiza melodia*	SOSP	4
Black-and-white Warbler	*Mniotilta varia*	BAWW	4
Northern Parula	*Setophaga Americana*	NOPA	4
Red-headed Woodpecker	*Melanerpes erythrocephalus*	RHWO	3
Red-shouldered Hawk	*Buteo lineatus*	RSHA	2
Belted Kingfisher	*Megaceryle alcyon*	BEKI	2
White-eyed Vireo	*Vireo griseus*	WEVI	2
Blue-headed Vireo	*Vireo solitarius*	BHVI	2
Golden-crowned Kinglet	*Regulus satrapa*	GCKI	2
Carolina Wren	*Thryothorus ludovicianus*	CARW	2
Brown-headed Cowbird	*Molothrus ater*	BHCO	2
Downy Woodpecker	*Picoides pubescens*	DOWO	1
Eastern Wood-Pewee	*Contopus virens*	EAWP	1
European Starling	*Sturnus vulgaris*	EUST	1
Cedar Waxwing	*Bombycilla cedrorum*	CEDW	1
House Finch	*Haemorhous mexicanus*	HOFI	1
Eastern Towhee	*Pipilo erythrophthalmus*	EATO	1
White-throated Sparrow	*Zonotrichia albicollis*	WTSP	1
Prothonotary Warbler	*Protonotaria citrea*	PROW	1
Summer Tanager	*Piranga rubra*	SUTA	1

When variations in behavior and habitat use were ordinated and species were compared using PERMANOVA, there were significant differences in the niche space of all the species in the bird community at Magnolia Springs State Park (Pseudo-f = 15.042, df = 12, P = 0.001, Figure 2). When a PERMANOVA pair-wise test was run to compare differences between migratory and resident species, they were found to differ significantly in their habitat use (t = 3.4654, P = 0.001).
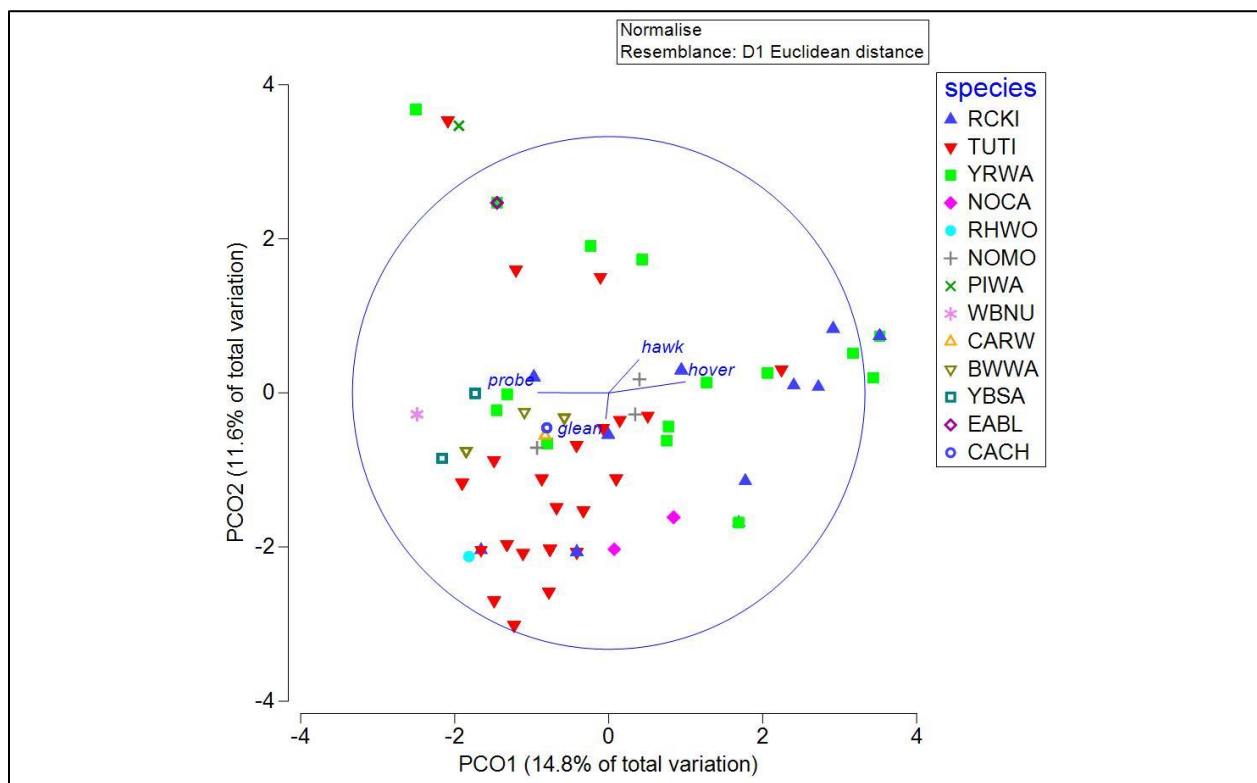
Figure 2. PCO plot of bird community of Magnolia Springs State Park showing variation due to twenty-five factors relating to microhabitat selection with vectors relating to variation due to differences in foraging behaviors. Bird species included are listed by alpha codes (see Table 2). For several species, multiple observations were recorded in identical locations with identical foraging behaviors. This results in several points in the plot that appear as one observation but are several very similar foraging events observed.

Table 4. Cumulative variation in the community PCO plot explained by individual variables sorted by category.

Category	Variable	Cumulative %
Foraging substrate	Leaf	14.82
	Twig	26.45
	Branch	34.88
	Trunk	42.74
	Fruit/nut	49.78
	Ground	56.61
	Artificial	62.67
Foraging height	Floor	68.48
	Shrub	73.33
	Sapling	77.63
	Mid canopy	81.83
	Upper canopy	85.63
Horizontal location	Horizontal location	88.85
Plant species	Laural oak	91.81
	Water oak	93.99
	Pine	95.70
	Sweet gum	97.16
	Wax myrtle	98.21
	Dogwood	98.98
	Muscadine	99.40
	Red maple	99.73
Habitat type	Forest	99.9
	Edge	99.96
	Open	99.99
	Water-edge	100

Multivariate Analysis of Focal Species

When focal species were oriented using PCO, Yellow-rumped Warblers are clustered towards the bottom of the plot and are more associated with hawking behaviors (Figure 3). Ruby-crowned Kinglets are clustered towards the top. Tufted Titmice before the arrival of migrants are found scattered throughout most of the plot, however they were unlikely to be found towards the right of the plot.

Tufted Titmice were found in different locations before and after the arrival of migrants (t = 3.4355, P = 0.001). The two focal migratory species, Ruby-crowned Kinglets and Yellow-rumped Warblers, were compared to the focal resident's niche location before and after migrant arrival. Ruby-crowned Kinglets differed from the behavior of Tufted Titmice both before (t = 4.0782, P = 0.001) and after (t = 4.8814, P = 0.001) the arrival of migrants. Yellow-rumped Warblers also differed in their overall foraging strategy from Tufted Titmice before (t = 3.6328, P = 0.001) and after (t = 5.2113, P = 0.001) migrant arrival.

Niche Shifts

A total of 41 Tufted Titmice observations were conducted without the presence of winter residents. Yellow-rumped Warblers and Ruby-crowned Kinglets were the only migrant species with more than 20 observations. A total of 111 Yellow-rumped Warbler and 67 Ruby-crowned Kinglet observations were recorded. Seventy-seven Tufted Titmice observations were recorded when winter migrants were present.

Two aggressive interactions were observed during the investigation. A migratory Yellow-rumped Warbler was observed chasing a migratory Eastern Phoebe away from an area where a group of Yellow-rumped Warblers were foraging near the water. A migratory Ruby-crowned Kinglet was later observed chasing another Ruby-crowned Kinglet. Resident species were never observed engaging in aggressive behaviors.
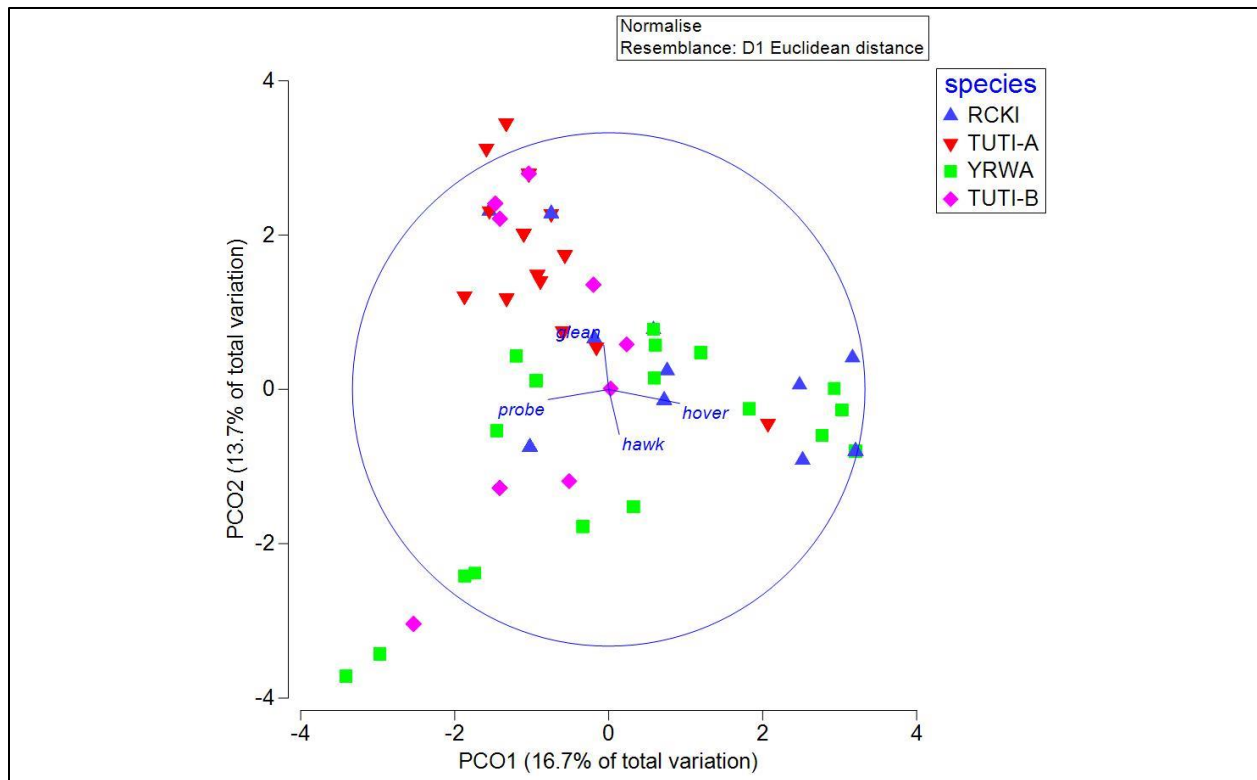
Figure 3. PCO plot for Tufted Titmice before and after migrant arrival, Ruby-crowned Kinglets, and Yellow-rumped Warblers showing variation due to twenty-five factors relating to microhabitat selection with vectors relating to variation due to differences in foraging behaviors. Species are listed by alpha codes (see Table 2).

Table 5. Cumulative variation in the focal species PCO plot explained by individual variables sorted by category.

Category	Variable	Cumulative %
Foraging substrate	Leaf	16.67
	Twig	30.40
	Branch	40.29
	Trunk	49.98
	Fruit/nut	57.28
	Ground	63.79
	Artificial	69.56
Foraging height	Floor	74.78
	Shrub	79.63
	Sapling	84.39
	Mid canopy	88.43
	Upper canopy	91.98
Horizontal location	Horizontal location	95.16
Plant species	Laural oak	97.41
	Water oak	98.54
	Pine	99.6
	Sweet gum	100.29
	Wax myrtle	100.73
	Dogwood	101.05
	Muscadine	101.26
	Red maple	101.30
Habitat type	Forest	101.30
	Edge	101.26
	Open	100.16
	Water-edge	100.00

Behavior. Before the arrival of migrants, Tufted Titmice gleaned and probed to capture prey. Tufted Titmice were more likely to glean for food items after the arrival of migrants ($G = 6.134$, df = 2, $P = 0.046$). Tufted Titmice hovered only after the arrival of migrants (Figure 4). Migrant species were rarely observed probing for food items (only once for Yellow-rumped Warblers and never for Ruby-crowned Kinglets). Yellow-rumped Warblers were more likely to hawk for prey and less likely to probe compared to Tufted Titmice after the arrival of migrants ($G = 47.520$, df = 3, $P < 0.0001$). Ruby-crowned Kinglets were more likely to hover for prey than Tufted Titmice observed during migrant presence ($G = 30.941$, df = 3, $P < 0.0001$).

Substrate. Tufted Titmice foraged on a wider variety of substrates before the arrival of migrants than they were after migrant arrival ($G = 57.546$, df = 4, $P < 0.0001$). After the arrival of migrants, Tufted Titmice used leaves, twigs, and branches (Figure 5). Yellow-rumped Warblers were the only species found foraging off artificial structures such as wooden railings and boardwalks (Figure 3). Yellow-rumped Warblers used a wider variety of substrates than titmice after migrant arrival and were more likely to forage off the ground or artificial structure than titmice ($G = 81.737$, df = 5, $P < 0.0001$). Yellow-rumped Warblers were the only species found foraging off the ground after the arrival of migrants (Figure 5). Ruby-crowned Kinglets foraged on the same three substrates as the Tufted Titmice (Figure 5), however they were more likely to forage on leaves ($G = 31.279$, df = 2, $P < 0.0001$).

Perch Height. During the early fall, Tufted Titmice were found in all but one height category (Figure 6). They preferred the upper canopy but were also found frequently on the forest floor. After migrants arrived, Tufted Titmice used the mid- to upper canopy ($G = 54.645$, df = 3, $P < 0.0001$). Both migratory species were more likely to forage at lower heights than in the mid-canopy or higher (Figure 6). Yellow-rumped Warblers used the forest floor or sapling height more frequently than Tufted Titmice ($G = 138.362$, df = 3, $P < 0.0001$). Ruby-crowned Kinglets foraged more often at the sapling height than Tufted Titmice ($G = 84.929$, df = 3, $P < 0.0001$).

Plant Species. Tufted Titmice preferred to forage in swamp laurel oak and pine trees both before and after the arrival of winter migrants (G = 7.813, df = 3, P = 0.050). Yellow-rumped Warblers (G = 145.714, df = 4, P < 0.0001) and Ruby-crowned Kinglets (G = 125.306, df = 4 P < 0.0001) preferred to forage in wax myrtle and black oaks. Both migratory species were found more often in plants rarely used by resident Tufted Titmice (Figure 7).

Habitat Type. Tufted Titmice foraged predominantly in edge habitat before the arrival of migrants (Figure 8). After migrants arrived, Tufted Titmice were less likely to forage in edge habitat and showed a preference for forest and open areas (G = 23.752, df = 3, P < 0.0001). Both Yellow-rumped Warblers (G = 112.544, df = 3, P < 0.0001) and Ruby-crowned Kinglets (G = 51.593, df = 3, P < 0.0001) were more likely to forage in edge habitat bordering the water compared to Tufted Titmice. Yellow-rumped Warblers were rarely found in the forest and preferred open areas or the edge habitat near water. Ruby-crowned Kinglets were occasionally found in the forest but were more likely found near the water (Figure 8).

Horizontal location. Tufted Titmice were found foraging at all distances from the center trunk both before and after the arrival of winter migrants (G = 1.160, df = 3, P = 0.560). Yellow-rumped Warblers were also found at all locations relative to the center trunk (G = 4.215, df = 4, P = 0.121). Ruby-crowned Kinglets preferred to forage farther from the center trunk than Tufted Titmice (G = 7.307, df = 4, P = 0.025) and were never found in the inner portion of the horizontal tree space (Figure 9).

Figure 4. Frequencies of foraging behaviors for resident Tufted Titmice before and after migrant arrival, Yellow-rumped Warblers, and Ruby-crowned Warblers.
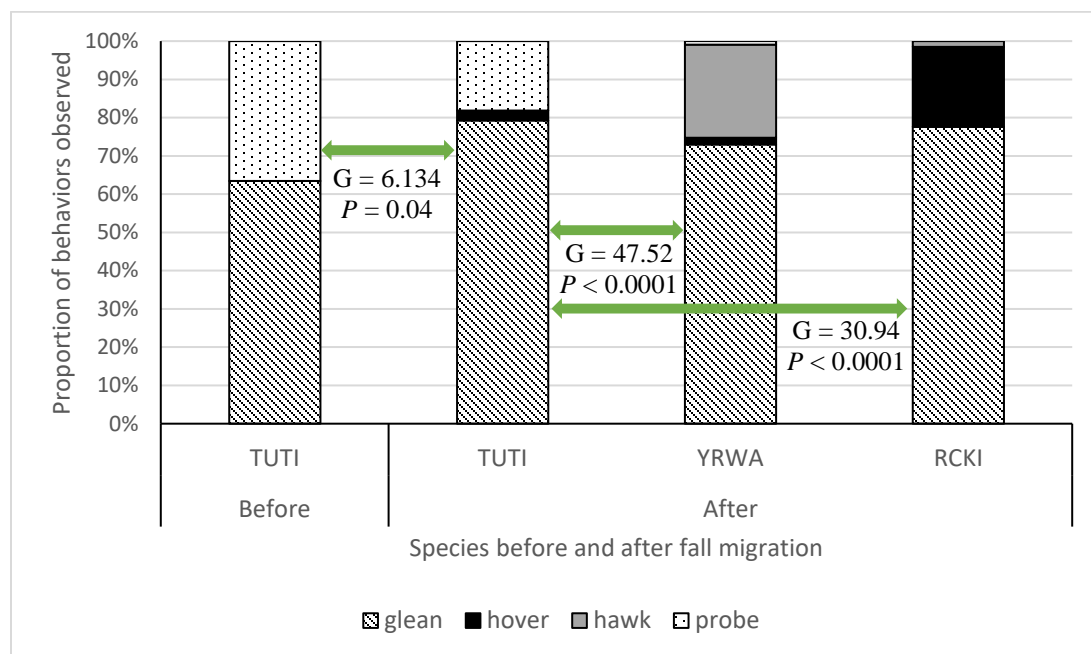
Figure 5. Frequencies of foraging observations on substrate for resident Tufted Titmice before and after the arrival of migrants, Yellow-rumped Warblers, and Ruby-crowned Kinglets.
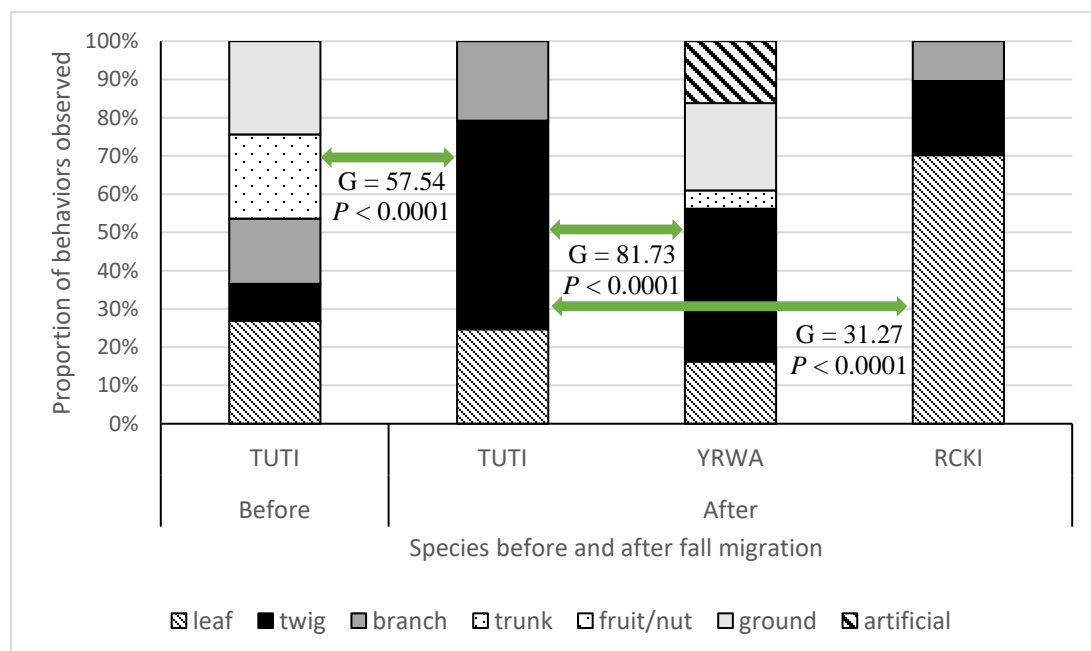
Figure 6. Frequencies of foraging heights for resident Tufted Titmice before and after the arrival of migrants, Yellow-rumped Warblers, and Ruby-crowned Kinglets.
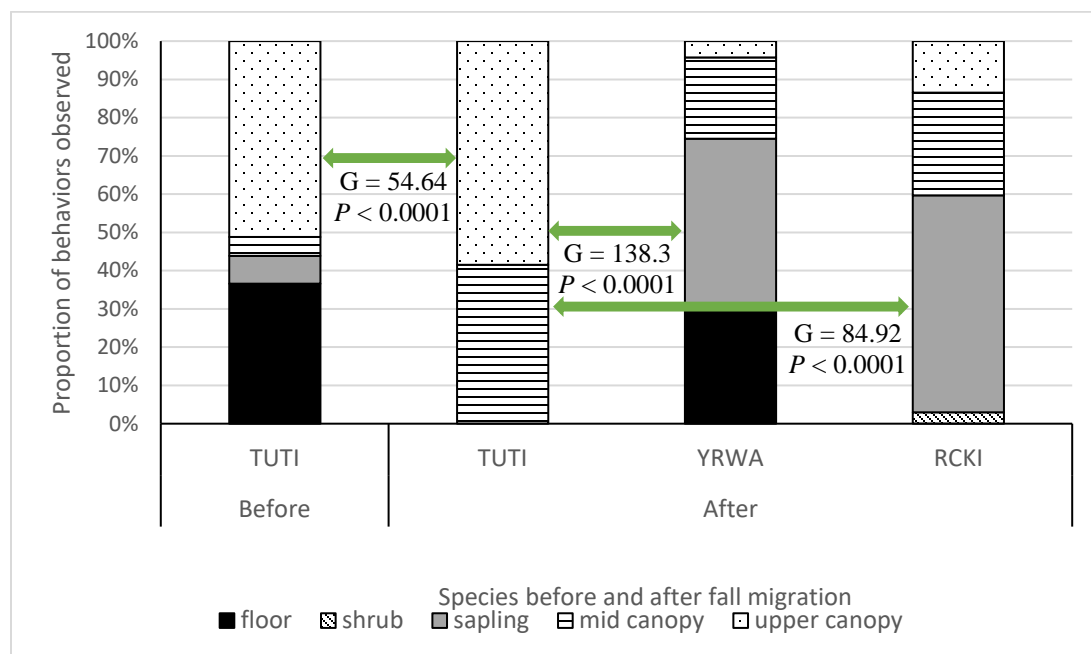
Figure 7. Frequencies of observations in each taxa of plants for resident Tufted Titmice before and after the arrival of migrants, Yellow-rumped Warblers, and Ruby-crowned Kinglets.
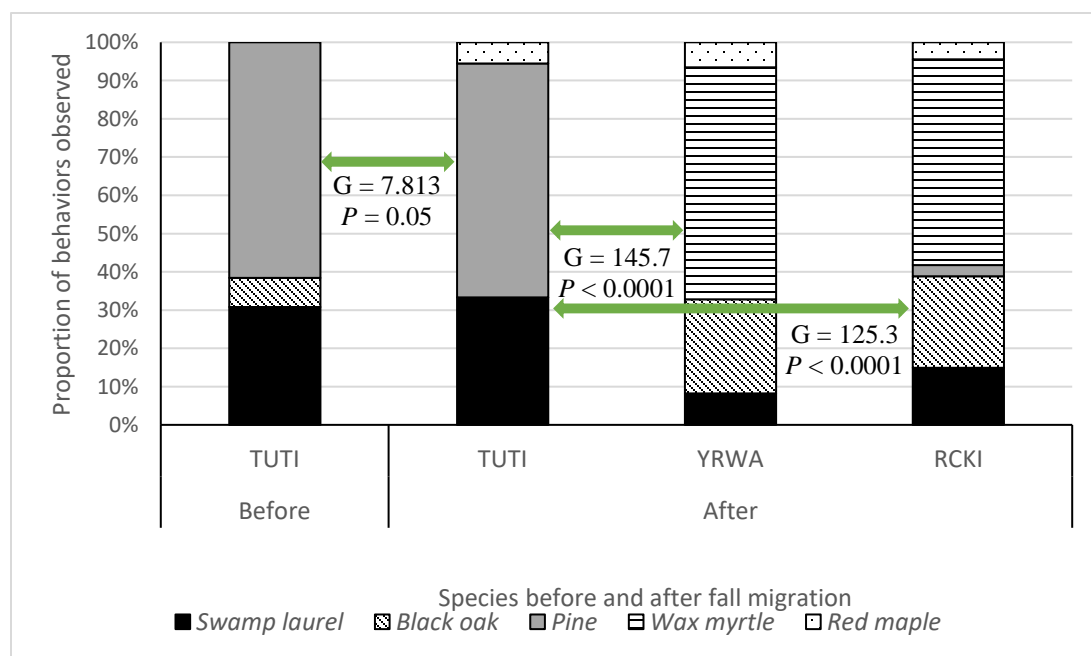
Figure 8. Frequencies of observations in each habitat type for resident Tufted Titmice before and after the arrival of migrants, Yellow-rumped Warblers, and Ruby-crowned Kinglets.
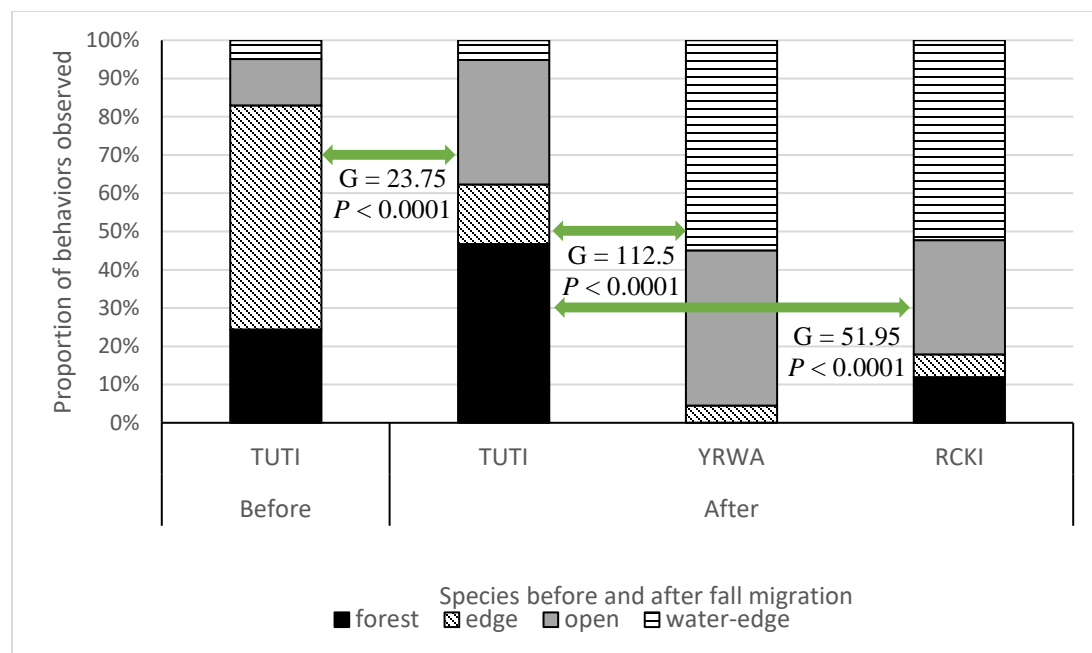
Figure 9. Frequencies of observations in categories of horizontal location for resident Tufted Titmice before and after the arrival of migrants, Yellow-rumped Warblers, and Ruby-crowned Kinglets
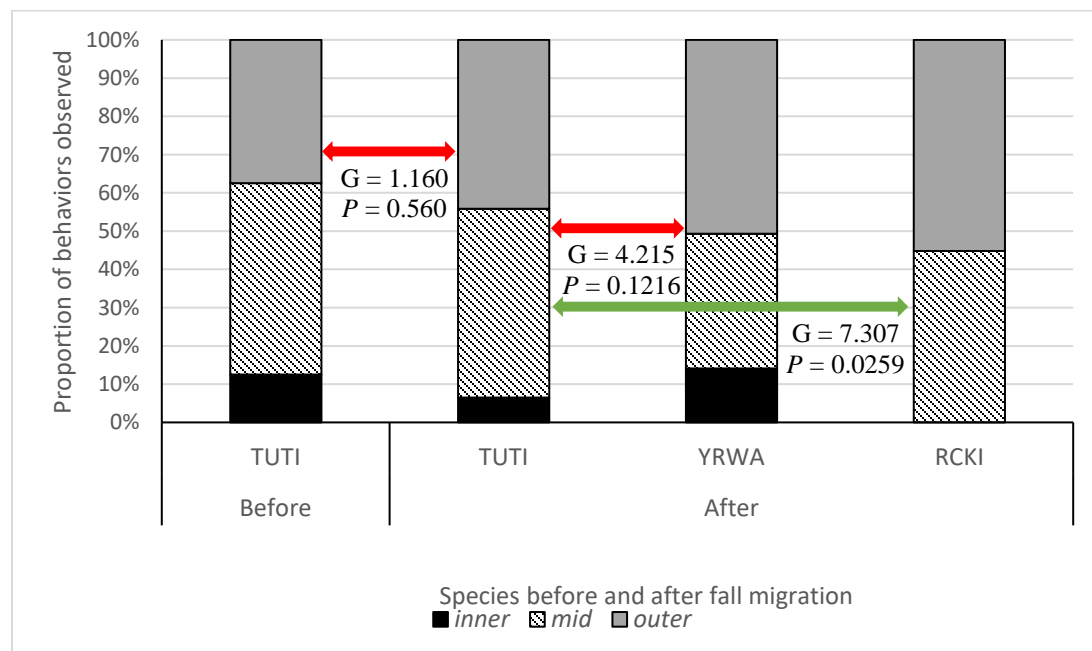
Measures of Niche Breadth and Overlap

Niche breadth for Tufted Titmice decreased after the arrival of migrants in four out of the six categories of data (Table 6); however, average niche breadth did not decrease significantly (t = 1.293, df = 5, P = 0.252). Migrant species did not display a wider niche breadth compared to Tufted Titmice (Table 6). Yellow-rumped Warblers did not differ in their average niche breadth compared to Tufted Titmice after migrant arrival (t = 1.407, df = 5, P = 0.218). Ruby-crowned Kinglets did not have a significantly different average niche breadth compared to Tufted Titmice either (t = .004, df = 5, P = 0.967).

Calculations of niche overlap were used to compare the overlap between migrants and Titmice both before migration and during the presence of migrants. After migration, Tufted Titmice had increased niche overlap with Yellow-rumped Warblers in four out of six categories (Table 7). However, the average change in niche overlap was not significant (t = 0.832, df = 5, P = 0.443). Measures of overlap between titmice and Ruby-crowned Kinglets decreased on average after migrants arrived (t = 2.701, df = 5, P = 0.042).

Table 6. Niche breadth for Tufted Titmice before and after migrant arrival, Yellow-rumped Warblers, and Ruby-crowned Kinglets calculated using Levin's measure of niche breadth. Statistics recorded in last row test the hypothesis that measures of niche breadth for Tufted Titmice after migration, Yellow-rumped Warblers, and Ruby-crowned Kinglets are the same as measures of niche breadth for Tufted Titmice before migration.

	TUTI before	TUTI after	YRWA	RCKI
Behavior	1.86	1.51	1.87	1.54
Substrate	4.58	2.49	3.74	1.84
Height	2.47	1.94	2.98	2.42
Plant	2.08	2.05	2.27	2.63
Habitat	2.38	2.84	2.13	2.63
Horizontal Location	2.46	2.25	2.49	1.97
Test Statistics	$t = 1.293$ $P = 0.252$		$t = 1.407$ $P = 0.218$	$t = 0.004$ $P = 0.967$

Table 7. Niche overlap between Tufted Titmice and migrant species calculated with Tufted Titmice data before and after fall migration using the Simplified Morisita Index. Statistics recorded in the last row test the hypothesis that the average niche overlap between migrant and resident is significantly different before and after migrant arrival.

	YRWA-TUTI before migration	YRWA-TUTI after migration	RCKI-TUTI before migration	RCKI-TUTI after migration
Behavior	0.87	0.97	0.94	0.83
Substrate	0.56	0.77	0.63	0.59
Height	0.47	0.26	0.41	0.30
Plant	0.09	0.06	0.16	0.19
Habitat	0.23	0.51	0.40	0.31
Horizontal Location	0.95	0.96	0.98	0.94
Test Statistics	$t = 0.832$ $P = 0.443$		$t = 2.0701$ $P = 0.042$	

CHAPTER 4

DISCUSSION

The results of this study have shown the bird community of Magnolia Springs State Park to be diverse and dynamic. While the niche space of species in the community differed significantly, there appeared to be overlap between species in ordination (Figure 2). Resident and migrant species were generally found to differ in their use of niche space (Figure 3). Tufted Titmice changed their niche location after migrant arrival (Figures 4–9). However, focal migrants did not move into the niche space vacated by resident titmice. This is evidenced by low overlap between migrants and residents before migration in key locations like plants and habitat (Table 7). While Tufted Titmice did decrease their average niche overlap with one focal migrant species, their overlap was low with both species before and after migration in key categories (Table 7). Tufted Titmice did not change their niche breadth significantly after migrant arrival and did not differ in their average niche breadth compared to migrant species (Table 6).

Tufted Titmice preferred foraging in pine and oak trees throughout the field season (Figure 7). Resident titmice after migration were more likely to be found foraging in the forest and higher in the canopy than they were before migration (Figures 6 and 8). Both migrant species were usually found in the edge habitat by water and preferred to forage in wax myrtles at sapling height (Figures 6–8). Migrant species were found foraging farther from the center trunk than resident species, with Ruby-crowned Kinglets foraging the farthest on average (Figure 9). Despite the seasonal change in habitat use by Tufted Titmice, neither of the focal migrant species were found to occupy the exact niche space vacated by the focal resident species (Table 7). These results were used to evaluate the hypotheses outlined in the Introduction (Table 1).

Table 8. Key predictions for the four hypotheses described in Figure 1 and Table 1 with results indicating if predictions were met in the current study. Location refers to the mean of quantitative data or the mode of qualitative observations. Niche breadth refers to calculations of Leven's measure of niche breadth. Niche overlap refers to calculations of Simplified Morisita Index.

Hypotheses	Predictions	Supported by results
A. Empty-Niche Hypothesis: There are open niches available to migrants and migrants take empty niche pace	No significant change in resident location	No
	No significant change in resident niche breadth	Yes
	Little niche overlap before and after migrant arrival	Yes
B. Competitive-Exclusion Hypothesis: Niches are filled and migrants displace residents to occupy space previously occupied by residents	Significant change in resident location	Yes
	No significant change in resident niche breadth	Yes
	High degrees of niche overlap before migrant arrival	No
	Reduced niche overlap after migrant arrival	No
C. Niche-Partitioning Hypothesis: Niches are filled and migrants partition resources with residents	Significant change in resident location	Yes
	Significant change in resident niche breadth	No
	Partial decrease in niche overlap after migrant arrival	Yes
D. Generalist-Migrant Hypothesis: Migrants have a broader niche and are able to forage over a wider range than residents	No significant change in resident location	No
	No significant change in resident niche breadth	Yes
	Significant niche overlap	No
	Niche breadth of migrants greater than niche breadth of residents	No

Empty-Niche Hypothesis

The Empty-Niche Hypothesis predicts that residents do not change their habitat use or niche breadth with migrant arrival because migrants are filling empty niches (Figure 1). Resident Tufted Titmice displayed a change in their foraging behaviors, substrate use, perch height, and habitat type (Figures 4–8). I reject the Empty-Niche Hypothesis, because this change in niche location by residents contradicts my predictions (Table 8).

When niche breadth was analyzed, resident Tufted Titmice decreased their niche breadth in every category except habitat use but their average niche breadth did not significantly change (Table 6). Niche overlap between Tufted Titmice and Ruby-crowned Kinglets decreased on average after migrant arrival and both migratory species did overlap to some degree with residents (Table 7) This indicates that migrant species are not simply filling empty niches left by resident species but may be partitioning resources and sharing some niche space, at least for these focal species.

Competitive-Exclusion Hypothesis

If resident species were completely excluded by migrants, I predicted a complete shift in their foraging location, but not necessarily a change in niche breadth (Table 1). At the most extreme, this would involve migrants moving into the exact niche space occupied by residents before migrant arrival and residents changing habitat use completely to avoid competition. This hypothesis is best addressed when the seasonal changes of resident species like the Tufted Titmouse are taken into consideration. Calculations of niche breadth for Tufted Titmice decreased with the arrival of migrants in many of the categories but the overall change in niche breadth was not significant (Table 6).

While the results indicated that one migrant species, the Ruby-crowned Kinglet, decreased its niche overlap significantly with resident Tufted Titmice, both migrant species had low degrees of overlap with titmice in key categories of plant and habitat use (Table 7; summarized in Table 8). Competition

would be reduced when migrants and residents prefer different plant species for foraging. Therefore, I reject the Competitive-Exclusion Hypothesis (Table 8).

Yellow-rumped Warblers were found to be foraging predominantly in wax myrtle bushes (Figure 7). Yellow-rumped Warblers during the breeding season primarily glean insects from leaves and branches but are also known to hawk for small flying insects (Hunt and Flaspohler 1998). Known to display the most flexible foraging strategy in *Setophaga*, Yellow-rumped Warblers might be particularly suited to avoiding interspecific competition by foraging where competition is least likely (Morse 1989, Sabo 1980). During the nonbreeding season, Yellow-rumped Warblers are known to forage on the berries of wax myrtle and other plants, especially in the eastern portion of their range (Wilz and Giampa 1978). To facilitate this consumption of waxy berries, Yellow-rumped Warblers have specialized features for digesting waxes and lipids (Place and Stiles 1992). The known preference and specialization towards foraging on wax myrtle berries indicates that Yellow-rumped Warblers are likely to choose this microhabitat even if resident species were not present.

Ruby-crowned Kinglets are considered generalist foragers that capture food mostly by gleaning from the surface of leaves and branches and occasionally by hovering, pecking, and hawking (Morse 1967, Sabo and Holmes 1983). During the winter, Ruby-crowned Kinglets are often found foraging among leaves on the outer tips of branches (Wagner 1981). Ruby-crowned Kinglets are known to forage in mixed-species flocks with Yellow-rumped Warblers on the berries of wax myrtle in Florida (Swanson et al. 2008). My results were consistent with what is known about the winter foraging behavior of Ruby-crowned Kinglets. Ruby-crowned Kinglets often foraged with Yellow-rumped Warblers but were also found foraging from the outer branches and leaves of trees (Figures 5 and 9). Ruby-crowned Kinglets forage in similar microhabitat in their breeding range (Morse 1967). This indicates that Ruby-crowned Kinglets are most likely using their preferred microhabitat in their winter range and are also able to take advantage of seasonally abundant wax myrtle berries, implying a lack of competition between Ruby-crowned Kinglets and resident Tufted Titmice.

Niche-Partitioning Hypothesis

The Niche-Partitioning Hypothesis, like competitive exclusion, assumes competition is shaping communities; however, niche partitioning predicts a lesser response to this competition, resulting in a sharing of niche space to reduce the negative impacts of competition (Figure 1). As a result, resident birds are expected to respond to migrant presence by reducing their niche breadth to minimize niche overlap with migrants (Table 1). While some predictions for the Niche-Partitioning Hypothesis were met, I reject this hypothesis because my results did not meet the key prediction that residents reduce their niche breadth to avoid competition with migrants (Table 8).

The overall community showed that migrants differed from residents in their habitat use, indicating that migrant and resident species are partitioning niche space to avoid competition (Figure 2). When seasonal changes were considered, Tufted Titmice displayed a change in their foraging behavior after migrants arrived (Figures 4–9). Tufted Titmice decreased their niche breadth with migrant arrival, but the overall change was not significant (Table 6). When a multivariate approach was conducted, the PCO plot indicated that the overall habitat use of Tufted Titmice was more tightly clustered when plotted after the arrival of migrants than before (Figure 3). This confirms the slight reduction in niche breadth calculations when individual data categories were examined and could indicate that Titmice are compressing their niche slightly when migrants arrive.

Migrants and residents had low levels of niche overlap in key categories such as habitat, plant species, and height (Table 7). These measures of overlap were low before migrant arrival, which could indicate that competition would have been unlikely even if resident species did not change their behaviors with migrant arrival. It could be that competition was more important historically than it is now. Residents could be changing their foraging strategies to avoid competition that is no longer present or severe.

Generalist-Migrant Hypothesis

One hypothesis to explain the evolution of migration speculates that certain foraging strategies are prerequisites for a migratory lifestyle in birds (Salewski et al. 2003). One of these indicators of potential migratory success is a more generalist foraging strategy (Table 1). This was not case for Yellow-rumped Warblers and Ruby-crowned Kinglets at Magnolia Springs State Park. Both species displayed niche breadths statistically similar to the Tufted Titmouse (Table 6). Tufted Titmice did not demonstrate fewer types of foraging behaviors than migratory species, leading to the conclusion that these birds are in similar regions of the specialist-generalist spectrum (Figures 4–9). Therefore, I reject the Generalist-Migrant Hypothesis (Table 8).

This is not the first study finding a lack of support for the Generalist-Migrant Hypothesis. When Ivande and Cresswell (2016) studied generalism in Afro-tropical savannahs, they discovered little support for the idea that migrants are more generalist than residents as a group. Instead it was found that, while migrants might be generalists, they are not more generalist than similar resident species. A more generalist foraging strategy may have helped species evolve migratory lifestyles, but it does not appear to be an indicator of whether or not a species developed migration. The same traits that help some species migrate would also help others acclimate to a seasonal and interannual changes occurring in one region.

Conclusions

The role of interspecific competition in shaping communities has proven difficult to tease out due to the difficulty of measuring competition in the field (Salewski et al. 2003), the need to consider a plethora of biotic and abiotic factors (Abrams 1980), and the fact that current communities were probably shaped over time by factors that occurred a long time ago and may no longer be present (the ghost of competition past; Connell 1980). This study sought to explore the patterns of community structure to better inform future experimental studies that seek to understand the processes involved in shaping communities.

I failed to find sufficient support for any of the four hypotheses proposed. While resident Tufted Titmice did change their habitat location, their low degrees of overlap with migrant species before migration indicated a lack of competitive pressure. This lack of support for competition conflicts with some of the classic papers in ecology (Hutchinson 1959, MacArthur 1969, Schoener 1965, Cody 1968, and Diamond 1978), however there has been some evidence indicating a lack of interspecific competition in birds (Rotenberry and Wiens 1981, Greenberg 1986).

Another possibility is that the communities we observe today reflect "ghosts" of previous interactions. It would be unwise to assume that the community observed during the winter of 2017-2018 existed as a discrete moment in time, unconnected from previous events. The current distributions of species, structures of communities, and interactions between individuals do not exist in isolation, but are the culmination of many years of struggle and evolution. Species today may not compete for resources, but that does not necessarily imply that competition is not a key process shaping bird communities. On the contrary, it may indicate that competition has played a tremendous role historically shaping the current system we observe by pressuring individuals many years ago to change their foraging strategy and avoid competition with other ecologically similar birds.

While the ghost of competition past does neatly reconcile traditional views on avian ecology with the current lack of support for competition, there are issues with an explanation that is impossible to test. If these processes were at work historically, we should be able to find evidence of them occurring today. It is possible that we aren't seeing evidence of interspecific competition because competition does not play as great a role as was historically thought.

Migratory species might be filling empty niche space and resident birds are moving their habitat use in response to a factor other than competition. While this would conflict with the Empty-Niche Hypothesis as outlined here, it would provide support for the idea that migratory birds are filling empty niche space and competition between residents and migrants is not a principle factor in shaping communities. To determine if this is the case, future studies should take into account prey abundance to determine why resident birds are shifting their location.

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APPENDIX

Appendix 1. Summary statistics and migratory status for all species with more than 5 foraging observations.

Yellow-rumped Warbler – migrant (N = 111)

Behavior	Glean	Hover	Hawk	Probe			
Frequency	0.73	0.02	0.24	0.01			
Substrate	Leaf	Twig	Branch	Trunk	Fruit	Ground	Artificial
Frequency	0.16	0.40	0	0.05	0	0.23	0.16
Perch Height	Floor	Shrub	Sapling	Mid canopy	Upper canopy		
Frequency	0.30	0	0.44	0.21	0.04		
Horizontal Location	Inner	Mid	Outer				
Frequency	0.14	0.35	0.51				
Plant Species	Laural oak	Water oak	Pine	Wax myrtle	Red maple	Muscadine	Dogwood
Frequency	0.08	0.25	0	0.61	0.07	0	
Habitat type	Forest	Edge	Open	Water-edge			
Frequency	0	0.05	0.41	0.55			

Ruby-crowned Kinglet – migrant (N = 67)

Behavior	Glean	Hover	Hawk	Probe			
Frequency	0.76	0.21	0.01	0			

Substrate	Leaf	Twig	Branch	Trunk	Fruit	Ground	Artificial
Frequency	0.70	0.19	0.10	0	0	0	0

Perch Height	Floor	Shrub	Sapling	Mid canopy	Upper canopy		
Frequency	0	0.03	0.57	0.27	0.13		

Horizontal Location	Inner	Mid	Outer				
Frequency	0	0.45	0.55				

Plant Species	Laural oak	Water oak	Pine	Wax myrtle	Red maple	Muscadine	Dogwood
Frequency	0.15	0.24	0.03	0.54	0.04	0	0

Habitat type	Forest	Edge	Open	Water-edge			
Frequency	0.12	0.06	0.30	0.52			

Black-and-White Warbler – migrant (N = 15)

Behavior	Glean	Hover	Hawk	Probe			
Frequency	0.53	0	0	0.47			

Substrate	Leaf	Twig	Branch	Trunk	Fruit	Ground	Artificial
Frequency	0	0	0.13	0.87	0	0	0

Perch Height	Floor	Shrub	Sapling	Mid canopy	Upper canopy		
Frequency	0	0	0.40	0.60	0		

Horizontal Location	Inner	Mid	Outer				
Frequency	1.00	0	0				

Plant Species	Laural oak	Water oak	Pine	Wax myrtle	Red maple	Muscadine	Dogwood
Frequency	0.13	0.87	0	0	0	0	0

Habitat type	Forest	Edge	Open	Water-edge			
Frequency	1.00	0	0	0			

Yellow-bellied Sapsucker – migrant (N = 11)

Behavior	Glean	Hover	Hawk	Probe			
Frequency	0.45	0	0	0.54			

Substrate	Leaf	Twig	Branch	Trunk	Fruit	Ground	Artificial
Frequency	0	0	1.00	0	0	0	0

Perch Height	Floor	Shrub	Sapling	Mid canopy	Upper canopy		
Frequency	0	0	0	1.00	0		

Horizontal Location	Inner	Mid	Outer				
Frequency	1.00	0	0				

Plant Species	Laural oak	Water oak	Pine	Wax myrtle	Red maple	Muscadine	Dogwood
Frequency	0	0	1.00	0	0	0	0

Habitat type	Forest	Edge	Open	Water-edge			
Frequency	0	0	1.00	0			

Dark-eyed Junco – migrant (N = 10)

Behavior	Glean	Hover	Hawk	Probe			
Frequency	1.00	0	0	0			

Substrate	Leaf	Twig	Branch	Trunk	Fruit	Ground	Artificial
Frequency	0.20	0	0	0	0	0.80	0

Perch Height	Floor	Shrub	Sapling	Mid canopy	Upper canopy		
Frequency	1.0	0	0	0	0		

Horizontal Location	Inner	Mid	Outer				
Frequency	0	0	0				

Plant Species	Laural oak	Water oak	Pine	Wax myrtle	Red maple	Muscadine	Dogwood
Frequency	0	0	0	0	0	0	0

Habitat type	Forest	Edge	Open	Water-edge			
Frequency	0	0	1.00	0			

Tufted Titmouse – resident (N = 118)

Behavior	Glean	Hover	Hawk	Probe			
Frequency	0.74	0.02	0	0.25			

Substrate	Leaf	Twig	Branch	Trunk	Fruit	Ground	Artificial
Frequency	0.25	0.39	0.19	0	0.07	0.08	0

Perch Height	Floor	Shrub	Sapling	Mid canopy	Upper canopy		
Frequency	0.13	0	0.03	0.29	0.56		

Horizontal Location	Inner	Mid	Outer				
Frequency	0.08	0.50	0.42				

Plant Species	Laural oak	Water oak	Pine	Wax myrtle	Red maple	Muscadine	Dogwood
Frequency	0.33	0.02	0.61	0	0.04	0	0

Habitat type	Forest	Edge	Open	Water-edge			
Frequency	0.39	0.31	0.25	0.05			

Northern Mockingbird – resident (N = 12)

Behavior	Glean	Hover	Hawk	Probe			
Frequency	0.83	0	0.17	0			

Substrate	Leaf	Twig	Branch	Trunk	Fruit	Ground	Artificial
Frequency	0	0.17	0	0	0.83	0	0

Perch Height	Floor	Shrub	Sapling	Mid canopy	Upper canopy		
Frequency	0	0.08	0.50	0.42	0		

Horizontal Location	Inner	Mid	Outer				
Frequency	0	0.17	0.83				

Plant Species	Laural oak	Water oak	Pine	Wax myrtle	Red maple	Muscadine	Dogwood
Frequency	0	0	0	0	0	0	1.00

Habitat type	Forest	Edge	Open	Water-edge			
Frequency	0	0.17	0.83	0			

Eastern Bluebird – resident (N = 9)

Behavior	Glean	Hover	Hawk	Probe			
Frequency	0.89	0	0.11	0			

Substrate	Leaf	Twig	Branch	Trunk	Fruit	Ground	Artificial
Frequency	1.00	0	0	0	0	0	0

Perch Height	Floor	Shrub	Sapling	Mid canopy	Upper canopy		
Frequency	1.00	0	0	0	0		

Horizontal Location	Inner	Mid	Outer				
Frequency	0	0	0				

Plant Species	Laural oak	Water oak	Pine	Wax myrtle	Red maple	Muscadine	Dogwood
Frequency	0	0	0	0	0	0	0

Habitat type	Forest	Edge	Open	Water-edge			
Frequency	0	0	0.89	0.11			

Carolina Chickadee – resident (N = 8)

Behavior	Glean	Hover	Hawk	Probe			
Frequency	1.00	0	0	0			

Substrate	Leaf	Twig	Branch	Trunk	Fruit	Ground	Artificial
Frequency	1.00	0	0	0	0	0	0

Perch Height	Floor	Shrub	Sapling	Mid canopy	Upper canopy		
Frequency	0	0	0	0	1.00		

Horizontal Location	Inner	Mid	Outer				
Frequency	0	0.75	0.25				

Plant Species	Laural oak	Water oak	Pine	Wax myrtle	Red maple	Muscadine	Dogwood
Frequency	0	1.00	0	0	0	0	0

Habitat type	Forest	Edge	Open	Water-edge			
Frequency	0	0	1.00	0			

Northern Cardinal – resident (N = 6)

Behavior	Glean	Hover	Hawk	Probe			
Frequency	1.00	0	0	0			

Substrate	Leaf	Twig	Branch	Trunk	Fruit	Ground	Artificial
Frequency	0	0	0	0	1.00	0	0

Perch Height	Floor	Shrub	Sapling	Mid canopy	Upper canopy		
Frequency	0	0.33	0.67	0	0		

Horizontal Location	Inner	Mid	Outer				
Frequency	0	0	1.00				

Plant Species	Laural oak	Water oak	Pine	Wax myrtle	Red maple	Muscadine	Dogwood
Frequency	0	0	0	0	0	1.00	0

Habitat type	Forest	Edge	Open	Water-edge			
Frequency	0.83	0.17	0	0			

White-breasted Nuthatch – resident (N = 6)

Behavior	Glean	Hover	Hawk	Probe			
Frequency	0.83	0	0	0.17			

Substrate	Leaf	Twig	Branch	Trunk	Fruit	Ground	Artificial
Frequency	0	0	0	1.00	0	0	0

Perch Height	Floor	Shrub	Sapling	Mid canopy	Upper canopy		
Frequency	0	0	0	1.00	0		

Horizontal Location	Inner	Mid	Outer				
Frequency	1.00	0	0				

Plant Species	Laural oak	Water oak	Pine	Wax myrtle	Red maple	Muscadine	Dogwood
Frequency	0	0	1.00	0	0	0	0

Habitat type	Forest	Edge	Open	Water-edge			
Frequency	0	0	1.00	0			

Pine Warbler – resident (N = 5)

Behavior	Glean	Hover	Hawk	Probe			
Frequency	1.00	0	0	0			

Substrate	Leaf	Twig	Branch	Trunk	Fruit	Ground	Artificial
Frequency	0	0	0	0	0	1.00	0

Perch Height	Floor	Shrub	Sapling	Mid canopy	Upper canopy		
Frequency	1.00	0	0	0	0		

Horizontal Location	Inner	Mid	Outer				
Frequency	0	0	0				

Plant Species	Laural oak	Water oak	Pine	Wax myrtle	Red maple	Muscadine	Dogwood
Frequency	0	0	0	0	0	0	0

Habitat type	Forest	Edge	Open	Water-edge			
Frequency	0	0	1.00	0			

Carolina Wren – resident (N = 4)

Behavior	Glean	Hover	Hawk	Probe			
Frequency	1.00	0	0	0			

Substrate	Leaf	Twig	Branch	Trunk	Fruit	Ground	Artificial
Frequency	0	1.00	0	0	0	0	0

Perch Height	Floor	Shrub	Sapling	Mid canopy	Upper canopy		
Frequency	0.25	0.75	0	0	0		

Horizontal Location	Inner	Mid	Outer				
Frequency	0	1.00	0				

Plant Species	Laural oak	Water oak	Pitusne	Wax myrtle	Red maple	Muscadine	Dogwood
Frequency	0	1.00	0	0	0	0	0

Habitat type	Forest	Edge	Open	Water-edge			
Frequency	1.00	0	0	0			