

ABSTRACT

PAGE, JESSICA HOPE. Improving Inferences about the Occupancy Dynamics of Forest-Dwelling Passerines in the US Gulf Coast Region Using Multiple Land Cover Data Sets (Under the direction of Jaime A. Collazo).

Forest loss and fragmentation has transformed landscapes across the globe, prompting concerns among conservationists because the scale and rate at which landscapes are being modified may undermine species persistence and result in homogenized biological communities. Of these drastically changing landscapes, the southeast region of the United States has undergone significant changes in recent decades with the Gulf region as one of the fastest growing areas in the country. The Gulf coast is not only important to shorebirds and other coastal migrants but is essential for forest dwelling avian species as well. However, the ability to exploit modified and novel habitats is not possible for all species. Migratory interior forest breeding birds have experienced steady decline for the past 40 years. Declines might be induced by the juxtaposition of modified and natural habitats that represent impenetrable barriers that, coupled with habitat fragmentation, create remnants of lower quality and higher isolation for many species. Low quality, reduced remnant patch size and isolation of habitat have direct implications on rates of colonization and extinction, and therefore, affect species abundance and distribution.

In this project, I addressed two objectives regarding the use of spatio-temporal models at landscape levels to advance conservation planning. For the first objective, I sought to understand how two commonly used land cover datasets, Global Forest Change (GFC) and National Land Cover Data (NLCD), could be used to better understand forest loss and change in the southeast around the Gulf of Mexico, and therefore, improve inferences from avian dynamic modeling. For the second objective, I determined local occupancy and colonization and extinction rates in

the coastal and inland habitats in the Gulf Coast region between 2000 and 2012 of three forest dwelling avian species of conservation interest.

To address the first objective, I compared the amount of forest cover at the initial and final time steps for the survey period (2000 to 2012) as well as the amount of change across the same period. Additionally, I created random transects to determine if BBS routes were good representatives of cover change across the landscape. The correspondence between GFC and NLCD datasets was high (85%). Discrepancies were localized and could be accounted by re-projection errors, differences (1-year) in starting year of the datasets, and thresholds between datasets regarding what is considered forested land. The utility of BBS routes as sentinels of land cover change was good, particularly at 1.2 and 5.5 km buffer distances, as in other studies.

To address the second objective, I estimated occupancy, colonization and extinction probabilities of three focal species using multi-season occupancy models. The species were the Wood Thrush, a migrant species exhibiting marked population declines, the Red-eyed Vireo, and the Brown-headed Nuthatch, a resident species in southeastern United States. I developed a candidate model set to test *a priori* hypotheses and predictions. These were that optimal habitat, not generic forest cover, were better predictors of occupancy, colonization and extinction rates. I also hypothesized that occupancy rates would be lower in the coastal zone due to higher rate of development and landscape changes. For the same reason, I predicted that occupancy dynamics in the coastal zone would be characterized by high rates of local extinction probability. Conversely, occupancy dynamics in the inland zone would be characterized by high rates of colonization probability. Parameter estimates correlated strongly with measures of optimal habitat, as hypothesized. However, the other predictions were poorly supported, largely because spatial variation in habitat cover at the route level occurred more evenly across the inland and

coastal zones than hypothesized. There were two common findings among all three species. First, there was no support in the candidate set of competing models for time-variant terms for colonization and extinction rates. Second, proportional change in optimal habitat, not generic forest cover as derived from the Global Change Forest dataset influenced occupancy, colonization and extinction probabilities. This work helps guide habitat management at landscape levels by setting up competing models that featured habitat covariates in terms of generic and known optimal forest cover for each focal avian species. In highlighting spatial variation in occupancy parameters and lambda values, my work identifies potential target areas for management.

Improving Inferences about the Occupancy Dynamics of Forest-Dwelling Passerines in the US
Gulf Coast Region Using Multiple Land Cover Data Sets

by
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BIOGRAPHY

Jessica Hope Page was born and raised in Appomattox County, Virginia where she completed high school at Appomattox County High School. In 2010 she moved on to attend Longwood University where she pursued her degree in Biology with a minor in Fine arts and Photography but found a true passion for wildlife ecology, education, and citizen science through the mentorship of her advisor, Dr. Alix Fink and her three years as an Americorps naturalist. It was these experiences that eventually led her to North Carolina where she found passion assisting in avian field research across the state where she found mentorship under Dr. Jaime Collazo at NC State. Under whom she found appeal in the visual aspect and complex problem solving process of using GIS analysis to map the landscape dynamics of the creatures she loved to study.

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CHAPTER 1

A COMPARATIVE ANALYSIS OF GLOBAL FOREST CHANGE AND NATIONAL LAND COVER DATA: IMPROVING INFERENCES ABOUT AVIAN DYNAMICS IN SOUTHEASTERN UNITED STATES

ABSTRACT:

Understanding the patterns of forest loss across the landscape is essential for understanding and predicting avian species occupancy patterns through time. Unfortunately, how we measure and classify forest cover can vary, and determining the scale and resolution relevant for estimating occupancy patterns can be difficult, particularly when we do not understand the potential sources of uncertainty affecting datasets employed for modeling. Herein, I sought to better understand how two commonly used land cover datasets, Global Forest Change (GFC) and National Land Cover Data (NLCD), could be used to better understand forest loss and change in the southeast around the Gulf of Mexico, and therefore, improve inferences from avian dynamic modeling. To meet this objective, I divided the region into two zones: coastal and inland based on their importance for avian conservation. I determined the degree with which both datasets matched, estimated the annual rate of forest cover loss between 2000 and 2012, and determined how representative were forest cover changes along BBS routes of changes on the landscape at three buffer distances. The first was 0.4 km or the distance surveyed along BBS routes, and 1.2 and 5.5 km represented natal dispersal distances with increasing likelihood (i.e., 50 and 90%, respectively) of harboring returning juveniles after their first overwintering season.

The match between GFC and NLCD datasets was high (85%). Discrepancies were localized and could be accounted by re-projection errors, differences (1-year) in starting year of the dataset time series, and thresholds between datasets regarding what is considered forested land. A closer scrutiny of the data revealed that the match was good at the 0.4 km and 1.2 km buffer distances, but not at the 5.5 km buffer distance, differing by ~6%. The annual rate of forest loss differed by year, but not by zone. The rates of loss ranged from 1% to 1.6% annually.

There was a difference of ~3.6% in forest cover between routes and randomly selected transects at 0.4 km distance, but the difference likely stems from the fact that random transects were not set along roads and that regenerating vegetation was not included in my assessment. Thus, I concluded that the utility of BBS routes as sentinels of land cover change was good, particularly at the 1.2 and 5.5 km. My work makes a case for the use of multiple land cover datasets to improve inferences about avian dynamics in two ways. First, the high match between NLCD and GFC allows partitioning the relative importance of forest cover quality and quantity in competing models. Second, the GFC data allows examination of forest cover on annual time steps, which is important if time-variant models are supported by the data.

INTRODUCTION:

Forest loss and fragmentation has transformed landscapes impacting wildlife across the globe (Betts et al. 2017). Much of these changes are due to increased urbanization and agriculture (Frost 2000, Hunter et al 2001). This has prompted concerns among conservationists because the scale and rate at which landscapes are being modified may undermine species persistence or result in homogenized biological communities (Gascon et al. 1999, Blair 2001, Fahrig 2003, Aronson et al. 2016). Reduced remnant patch size, habitat degradation and isolation affect rates of colonization and extinction, rates that determine species abundance and distribution (Hanski 1998, Yackulic et al. 2015).

The southeast region of the United States has undergone significant land cover changes in recent decades (Culliton et al. 1990, Barrow et al. 2000). For example, as much as 40% of natural vegetation communities in the South Atlantic Coastal Plain is fragmented or altered by human use (Hunter et al. 2001). Of particular note is the Gulf region, one of the fastest growing areas in the country with the population rising at more than double the national average. Changes across the landscape in this region are largely attributed to urbanization and agriculture (Partnership for Gulf Coast Land Conservation 2014), but other practices such wood-pellet facilities and wood sourcing areas also contribute to the changes in forest cover (Barrow et al. 2005, NRDC 2015). The dynamics of landscapes in the Gulf region are such that some portions of the coast exhibit forest loss and others have regenerated or are regenerating (Hansen et al. 2013).

The Gulf coast is important to resident and migratory species, and studies have shown that it is essential for forest dwelling species (Gauthreaux 1975, Simons et al 2000, Moore et al. 2005, Buler et al. 2007). A prominent type of forest cover in the region are bottomland hardwood

forests, which is essential for insectivores, and may explain why a majority of neotropical migrants occur within 65-85 km from the coast (Gauthreaux 1975, Simons et al 2000, Moore et al. 2005, Buler et al. 2007). Because northbound migrants engage in habitat selection within a 5 km radius after making landfall, the amount of habitat fragmentation and loss of forest cover in the Gulf region may contribute to population declines of some Neotropical migrants such as forest-interior species (Buler et al. 2007, North American Bird Conservation Initiative 2009). In contrast, for generalists like ovenbirds, forest fragments have proven to be beneficial. Indeed, there is increasing evidence that many avian species are adept at exploiting modified and novel habitats (Kennedy et al. 2011, Watling et al. 2011, Lugo et al. 2012, Irizarry et al. 2016) or that modified habitats may serve as functional equivalents of those replaced (Baum et al. 2004, Irizarry et al. 2018). However, the ability to exploit modified and novel habitats is not possible for all species (Crocini et al. 2008), which serves as the impetus for finding methodological improvements to assess the dynamics of avian species in the context of changing landscapes.

A tool that has proven useful in assessing landscape-level avian dynamics is the North American Breeding Bird Survey (BBS; Pardieck et al 2018; Clement et al. 2019). This monitoring program, which started in 1966, presently has approximately 3,700 active routes of which 2,000 are run annually. Many BBS routes have remained in the same location since 1966, but the majority, on average, have been surveyed for 14 years (Sauer et al. 2003). The average number of years routes in the southeast have been surveyed range from 16 (Mississippi) to 19 (Georgia; Sauer et al. 2003). New BBS routes are randomly placed on the landscape, but the density of routes surveyed per year varies among regions depending on the number of skilled birders (Pardieck et al. 2018). Importantly, land cover within 0.4 km on both sides of routes, the boundary within which birds are counted during surveys, was found to represent the land cover

of surrounding areas when compared to random samples within an expanded buffer of 10 km using 2011 NLCD data (Veech et al. 2017). These findings were consistent with Keller and Scallan (1999) that found that while the intensity of development was different on and off-route, the 200 m buffer on both sides of the route accurately represented the nature of changes in the landscape.

The aforementioned studies have strengthened the utility of BBS routes as indicators of land cover change on landscapes. Nonetheless, Clement et al. (2019) pointed at the need for additional assessments looking into patterns land cover temporal and spatial variation to help partition the effects of global environmental changes (e.g., land cover vs climate change). One such opportunity is possible with the Global Forest Change data (Hansen et al. 2013). Some of the unique attributes of these data are that is available in annual time-steps, thereby, allowing the combination of weather/climate and land cover covariates in ways not possible with NLCD. NLCD data are thematically more complex, but produced every 5 years. Another is that it allows for a comparison with NLCD data, thereby, opening the opportunity to use both data sets simultaneously in avian models to gain greater insights about avian dynamics as compared to using only a data set (*sensu* Pacifici 2017).

In this chapter, I compared forest cover change along BBS routes in the Gulf Coast region of southeastern United States using two sources of LANDSAT imagery data, the national land cover dataset and the global forest change dataset (Homer et al. 2004, Fry et al. 2011, Hansen et al. 2013, Homer et al. 2015). Specifically, I asked the following questions. First, when measuring forest cover, how interchangeable are the NLCD and GFC datasets, and does it vary with distance from the BBS route, as defined by natal dispersal distances for birds (Sutherland et al. 2000). Second, was the annual rate of forest cover loss different between 2000

and 2012, and between the coastal and inland zones? In this work, coastal zone refers to the extent within 127.5 km from the coast in the Gulf region, which includes 86 km deemed essential for land bird conservation (Simons et al 2000, Moore et al. 2005). The inland zone extends for another 127.5 km. Lastly, does forest loss along BBS routes accurately represent regional forest loss? We discuss findings in the context of the value of routes as sentinels of landscape cover change, expanded opportunities to model temporal dynamics of avian species, and extrapolate route-level findings to a regional scale.

METHODS:

Study area

The study area was the Gulf Coast region or southernmost portion of the South Atlantic Migratory Bird Initiative area (Figure 1, Watson et al. 2005). Initially, I had created three distance buffers from the shoreline, each measuring 85 km based on essential migratory habitat determined by Moore et al. 2005. However, I split the center band between the coastal and inland zones to create two zones of 127.5 km each, for a full extent of 255 km inland from the Gulf Coast. Each zone retained its biological relevance (e.g., coastal zone contained the 86 km deemed important for bird conservation), and each zone contained a higher number of BBS routes. The coastal zone had 78 routes, whereas the inland zone had 79. The full extent spans from east of the Mississippi River to the eastern coast of the United States, and includes Mississippi, Florida, Georgia, and a small portion of Louisiana.

Land cover datasets

I used two sources of land cover data to address questions in this work. The first was the LANDSAT Global Forest Change map (Hansen et al. 2013). This is a high-resolution map using Earth observation satellite data. This dataset uses GCS_WGS_1984 coordinate system and the D_WGS_1984 datum. Overall forest loss, with forest defined as tree cover of 5 m or higher, was quantified on a yearly basis from 2000 to 2012 at a resolution of 30m x 30m at the equator. A measurement of gain was taken exclusively in 2012. Forest cover was calculated during the growing season and only land classified with a canopy cover of 50% or more were included as forest for this analysis to match the threshold of the loss and gain mask data (Hansen et al. 2013). This dataset was validated using a combination of FAO data and LiDAR and estimated an

accuracy of 99.8% for measured loss in temperate forests (Hansen et al. 2013). However, a scaled down evaluation of maps when converted to a forest cover/non-cover binary estimated overall accuracy at $\geq 80\%$ (Song and Tang 2015).

The second was the National Land Cover Database (NLCD), produced by the Multi-Resolution Land Characteristics Consortium, contains 30 x 30m resolution Landsat-7 imagery derived maps that consists of 20 general land cover types (Homer et al. 2004, Fry et al. 2011, Homer et al. 2015). This dataset uses the NAD_1983_Albers coordinate system and the D_North_American_1983 datum. A new land cover dataset is generated every 5 years and this research utilizes the 2001, 2006, and 2011 datasets. The accuracy of single year data for each of the three years for Level II classification was 83%, 83%, and 82%, respectively. When the three datasets from these years are used in tandem, they provide accurate data to represent where urbanization has occurred, where forests have changed, and where land cover has not changed (Wickham et al. 2017).

In using NLCD data, I focused on the four major forest types, namely, deciduous (41), evergreen (42), mixed forest (43), and woody wetlands (91), which is also considered bottomland hardwood (NRDC 2015). These forest types represent optimal habitat for the Red-eyed Vireo, Wood Thrush, and Brown-headed Nuthatch (Hamel 1992), the avian focal species in this study.

Breeding Bird Survey Routes:

All routes run between the year 2000 and 2012 using the standard survey procedure (RPID: 101) were identified and considered for subsequent analyses. Routes were retained if: 1) they could be matched to corresponding polyline feature (Pardieck et al. 2018), 2) were within

the study region, and 3) were run for a minimum of two consecutive years. This yielded 157 routes. Most breeding bird survey routes are available as a shapefile (Pardieck et al. 2018) of linear features in the D_North_American_1983 datum. In some cases, routes contained minor breaks causing some variation in total length. These routes were merged as a single feature, creating routes that varied in length between 10.33 to 74.66 km (average = 41.49 km). Nearly all routes were contained within South Eastern Coastal Plain Bird Conservation Region (BCR 27).

Routes were surveyed between May 15th and June 15th. At each route, observers collect data for three minutes and records all birds seen or heard within a 0.4 km radius on either side of the route. This sampling distance defines the first buffer distance in our analyses. I also used two additional distance-from-route categories. These were 1.2 km and 5.5 km, and these represent average natal dispersal units for the 3 focal species. These units indicate that there was a 50% or 90% probability that juveniles, returning in year+1, returned to within 1.2 km or 5.5 km of their place of birth, respectively. Distance categories were derived from a body mass-dispersal distance relationship developed by Sutherland et al. (2000).

Comparative Analyses

The NLCD and GFC datasets originate from Landsat imagery data, but were processed and validated using different methodologies (Hansen et al. 2013; Wickham et al 2017). This may lead to some differences in what is identified as a forest patch by each dataset as well as potential differences caused by canopy cover thresholds. To test this possibility, I compared several metrics derived from NLCD and GFC datasets. All land cover analyses were completed using ArcGIS 10.5.1 and Python 2.7.13. Data for these tests met homogeneity of variance assumption (Levene's test, $P > 0.05$). All tests deemed significant at an alpha of 0.05.

Analyses started by creating a study extent for each dataset that extended 255 km inland from the shoreline as described in the study area. The time series for the GFC data ran from 2000 to 2012 (GFC) whereas the time series for the NLCD data consisted of three “snapshots” (2001, 2006, 2011). Due to the different projections of the two layers, the GFC data were transformed to match the NLCD dataset. We used these data to determine, by inspection, where forest and non-forest types by dataset agreed (matched) or not (mismatched), and by how much. As a second assessment of agreement between datasets, I estimated the proportional change of forest cover between the initial and final year of their respective time series. For these analyses, I used BBS routes to create a sample of geographic extents (buffer distances) across the landscape. The calculated area for each route varied between 795.34 ha to 5945.79 ha (0.4 km), 2510.1 ha to 17745.47 ha (1.2 km), and 17983.17 ha to 83521.7 ha (5.5 Km) due to variation in shape and length of the routes. Data for pairwise comparisons were obtained from the raster’s native data projection. I used region grouping 8 analysis tool with an iterator to avoid overlap when calculating the percentage of each land cover type within each route buffer distance. Percentage of a land cover type, or combination thereof, was calculated as the number of pixels of land cover type within a route/the number of pixels total for the route. I define proportional change as the percent change in forest cover (Net gain + loss) between the initial and final year relative to the amount of forest cover in the initial year of measure ($(\text{Initial Forest Cover} - \text{Final Forest Cover}) / \text{Initial Forest Cover} * 100$). I compared estimates from both data sets using paired t-tests (JMP Pro14 2018).

I assessed whether the annual rate of forest loss differed over time and by zone using a repeated measures ANOVA (Proc GLM, SAS 9.4). The response variable was forest loss estimated using GFC data on each of the 157 routes for 13 years (2000-2012). Forest loss is

defined as the percentage of pixels with greater than 50% forest cover ≥ 5 m in height in year t that was no longer present in year $t+1$. Forest loss does not include “cover gain,” which is defined as the percentage of pixels with greater than 50% forest cover reaching ≥ 5 m in height that were not present in year t . Model terms were zone (inland or coastal) and the interaction between time and zone. Model-generated estimates of annual cover were used to estimate the rate of forest loss over the entire time series at BBS routes (0.4 km) and two dispersal distance categories (i.e., 1.2 km, 5.5 km).

The utility of BBS routes as indicators of landscape land cover change (i.e., representativeness) was evaluated using a set of 300 randomly generated transects of ~ 39.43 km length (i.e., the standard BBS route) with a 300 m offset. I then randomly selected a subsample of 157 transects, and created buffer distances of 0.4 km, 1.2 km and 5.5 km before executing the region group 8 analysis loop in ArcPy using the GFC data set. I measured the amount of initial “older” forest cover (2000), defined as the percentage pixels with greater than 50% forest cover ≥ 5 m in height, that was no longer present in the final year (2012). I refer to this difference as total forest cover loss. This measure does not include gain, which is defined as the percentage of pixels with greater than 50% forest cover reaching ≥ 5 m that were not present in the initial year. I used a t-test to determine whether differences in forest loss between the GFC data and random routes were significant at each distance buffer category and by zone (JMP Pro13).

RESULTS:

There was a match of approximately 85.80% between the GFC and NLCD databases. The remaining extent had some areas of marked differences (Figure 2). For example, 8.92% of land classified as forest under the GFC data were not mapped as forest in the NLCD data.

Likewise, there was 5.28% of land classified as forest by NLCD not classified as such by the GFC data. A noteworthy mismatch occurred at the Santa Rosa Sound, along the Florida Panhandle (Figure 3). This region is part of Elgin Air Force Base, and with the exception of a few roads, not accessible to the public. Tree cover is visibly low along the BBS routes and likely do not meet the 50% threshold used for the GFC dataset.

Paired comparisons indicated that the proportional change in forest cover between datasets was not significantly different along routes (0.4 km) or out to 1.2 km (Table 1). However, there was a significant difference of nearly 6% at the 5.5 km buffer distance (Table 1). The negative average difference indicated that the proportional change was greater for NLCD.

The estimated annual loss of forest cover based on the GFC data was not significantly different between the coastal and inland routes at any buffer distance along BBS routes ($F = 0.78$, d.f. = 1, 155; $P = 0.38$). However, annual differences over time differed ($F = 358.70$; d.f. = 12, 1860, $P < 0.001$). The average percent loss of forest cover declined over time (Figure 3). Annual rate of forest cover loss was 1.06% at 0.4 km, 1.26% at 1.2 km, and 1.15% at 5.5 km. Lastly and based on GFC data, the average percent forest loss was significantly less (~3.6%) along BBS routes at 0.4 km as compared to random transects in the coastal and inland zones at that same buffer distance (Table 2). Differences, however, were not significant at the 1.2 km and 5.5 km dispersal distance buffers ($\leq 2.4\%$).

DISCUSSION:

The aim of this study was to determine how well two major land cover datasets, GFC and NLCD, matched over the Gulf Coast region of southeastern United States. We also evaluated the rates of forest loss between 2000 and 2012, and how well BBS routes represented forest

cover on the landscape. My findings showed that the matching between the two datasets was high (85%). Further scrutiny revealed that the match was not significantly different at the 0.4 km and 1.2 km buffer distances, but was at the 5.5 km buffer distance. These results are striking in that the match was high given that imagery for both datasets was processed independently. The high match between data sets is of interest to ecologists because questions regarding the interplay between quantity (GFC) and quality (NLCD) could be investigated more readily.

I can advance at least three explanations to account for the ~15% of the extent that did not match between datasets. One is that some error in matching stemmed from re-projecting datasets, seen along some fringes of forest by both datasets. Another is that the first year for the GFC data was in 2000 whereas the first year for the NLCD data was 2001. The 1-year difference is minimal, but may account for some mismatch. For example, there were small areas (900-1800 m²) classified as forest by the GFC database, that occurred in areas of high density neighborhoods and streets. It is likely that these areas were classified as developed areas by NLCD dataset. Finally, the threshold of required tree cover to be considered a forested land by the GFC database likely eliminated forested land with low density canopy cover such as in pine savannahs. This was likely the case with areas around Elgin Air Force Base which was confirmed as forested land in 2005 (Barrow et al. 2005)

The annual forest cover loss differed between years, but not between zones. Rate of loss ranged from 1.06% to 1.15% annually between 2000 and 2012. The low annual rate of forest loss, coupled with the high match between data sets, were strong justification to create a covariate that expresses change in the same terms for both datasets (i.e., terminal-initial yr/initial yr*100) to represent overall forest cover change between 2000 and 2012. The utility of this covariate was strengthened by the fact that although annual forest loss rates were statistically

significant, biologically, the rate of loss was not large enough to support time-specific models when assessing the occupancy dynamics of Wood Thrush, Red-Eyed Vireo, and Brown-headed Nuthatch (Chapter 2).

BBS routes exhibited significantly lower forest cover loss (~3.6%) than randomly selected routes. However, this discrepancy did not occur at larger extents (e.g., 1.2 and 5.5 km). This pattern is counter intuitive in that one would expect greater change along BBS routes. A possible explanation is that modifications to habitats within 0.4 km of the route were made when the road was constructed, followed only by maintenance. In contrast, modifications along randomly selected transects are “novel” modifications, and thus, have greater impact on rate of change. Certainly, BBS routes were established along routes that contained greater low-level non-forest cover types (e.g., low density urban, pasture/crop land), and the coverage of these thematic classes may vary by State (Keller and Scallan 1999). Admittedly, I did not include “gain” in my comparisons, which would reflect regenerating vegetation that could have helped offset differences at the 0.4 km buffer distance. Generally, however, the findings of more comprehensive assessments of the utility of BBS routes as representatives of land cover change were in agreement with mine when looking beyond the 0.4 km buffer (Veech et al. 2012). Veech et al. (2012) concluded that BBS routes were good representatives of most forest cover types (4 types) at the 0.4 km and 10 km buffer distances after evaluating 3,230 routes using NLCD 2001 data. More recently, they concluded that 92% of the 2,696 routes evaluated exhibited “good” representativeness of the surrounding landscape using NLCD 2011 data, with < 5% per cover type difference in proportional cover between the 0.4 km and 10 km distance buffer (Veech et al. 2017). Veech et al. (2017) concluded BBS routes were “good” to make inferences from avian surveys from the standpoint of being representative of surrounding landscapes. Of course, this

feature does not address the issues of estimation such as detection probability (Sauer et al. 1994, Kendall et al. 1996, Sauer et al 2003, Pacifici et al. 2016, Pacifici et al. 2017, Veech et al. 2017). Notwithstanding, my work expands the body of work that supports the use of BBS routes as sentinels of landscape change and of multiple land cover datasets to improve inferences about avian dynamics in two ways. First, the high match between NLCD and GFC allows partition the relative importance of forest cover quality and quantity in competing models. Second, the GFC data allows examination of forest cover on annual steps, important if time-variant models are supported by the data.

It is important to note that my evaluation of datasets did not adjust for accuracy or the possibility of thematic misclassification errors. The reported accuracy for the GFC data ranges from roughly 80% (binary) to 99.8% (temperate forest loss) and for the NLCD ranges between 82 and 83% for land cover classification though specific accuracy varies from region to region and was as low as 68-71% in 2001 (Wickham et al 2010, Hansen et al 2013, Wickham et al. 2013, Song and Tang 2015, Wickham et al 2017). One of the arguments used to ignore potential biases introduced by misclassification errors is that errors are not expected to differ between BBS routes and randomly selected transects on the landscape (Veech et al. 2012). If the researcher is concerned about these errors, then aggregating forest cover types might reduce uncertainty in classification (Wickham et al. 2010; Wickham et al 2017). I raise this point because the intent of jointly using BBS survey and habitat data is to increase our understanding of the parameter rates that influence distribution and abundance patterns. Veran et al. (2012) reported that classification errors can induce non-trivial biases in inferences about occupancy dynamics if not accounted for in models. Lastly, while differences in forest cover and loss over time and at various distance buffers seemed small, they are happening. Decision makers need to

be cautious that, while metrics indicating affinity for habitats (e.g., occupancy) might be strong, the long-term performance of species (e.g., reproductive output) might be inadvertently decreasing at different rates if not checked by other means (Furrer and Pasinelli 2016, Gilroy and Edwards 2017).

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Study Extent with Routes

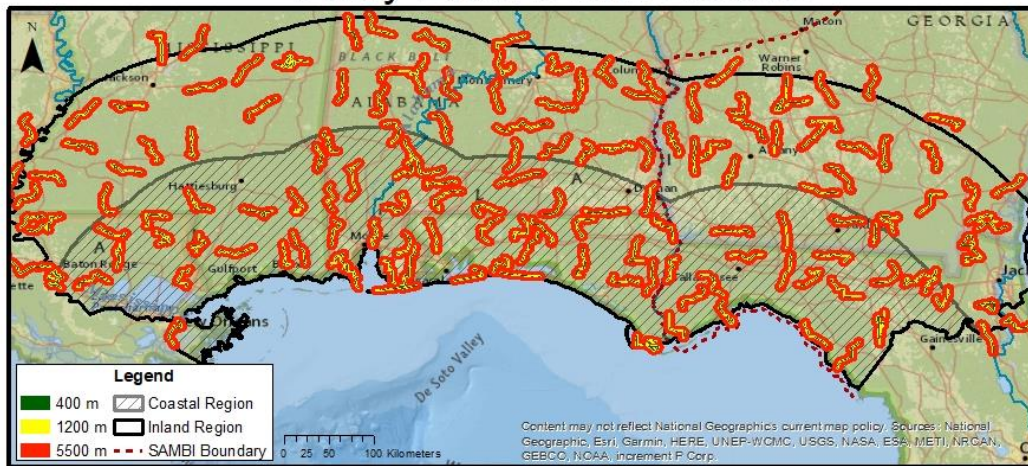


Figure 1. Map of study region with designated coastal and inland zone. Buffers around the routes show survey route and buffer distances. The dotted line represents the SAMBI boundary.

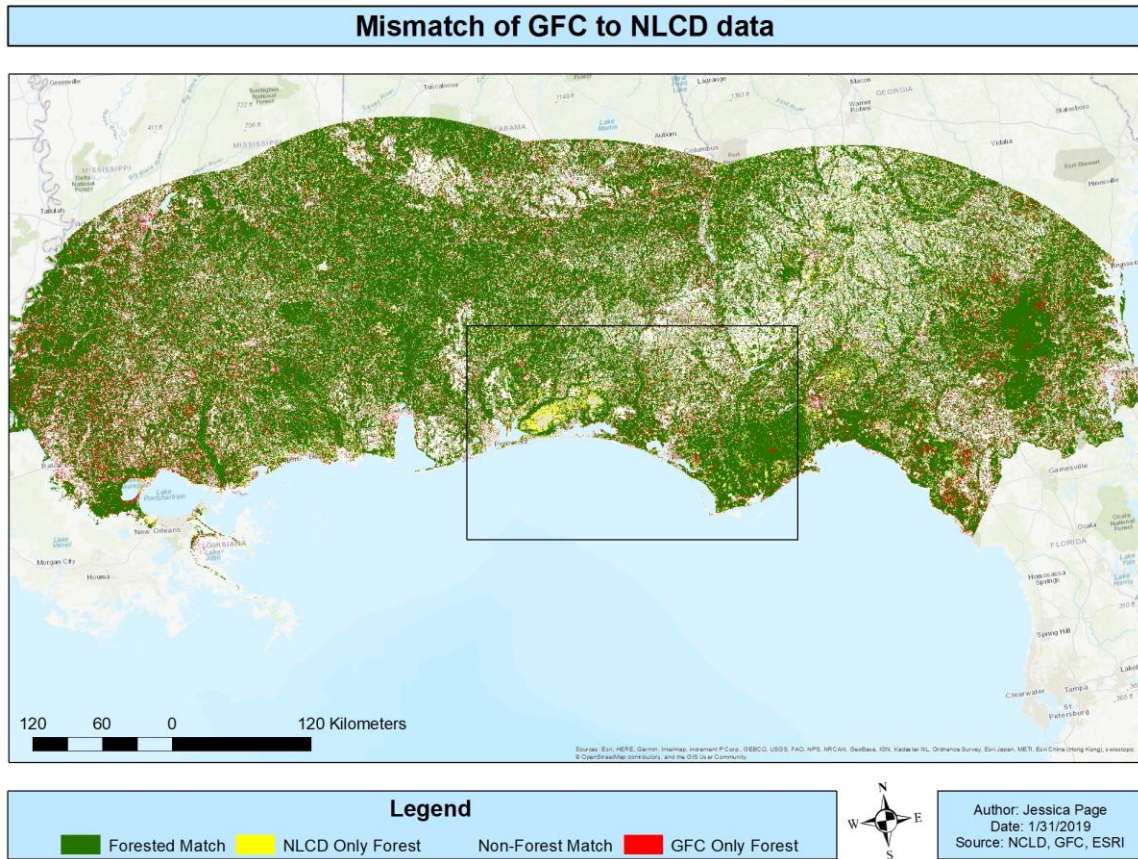


Figure 2. This map displays the disagreement of land cover classification between the two datasets and highlights the potential need for including tree cover in occupancy models. Though there is error introduced from the process of reprojecting and transforming one data set to match the coordinates of another, the larger red and yellow areas indicate where further ground truthing may need to be done to validate LANDSAT land cover classifications.

Mismatch of GFC to NLCD data

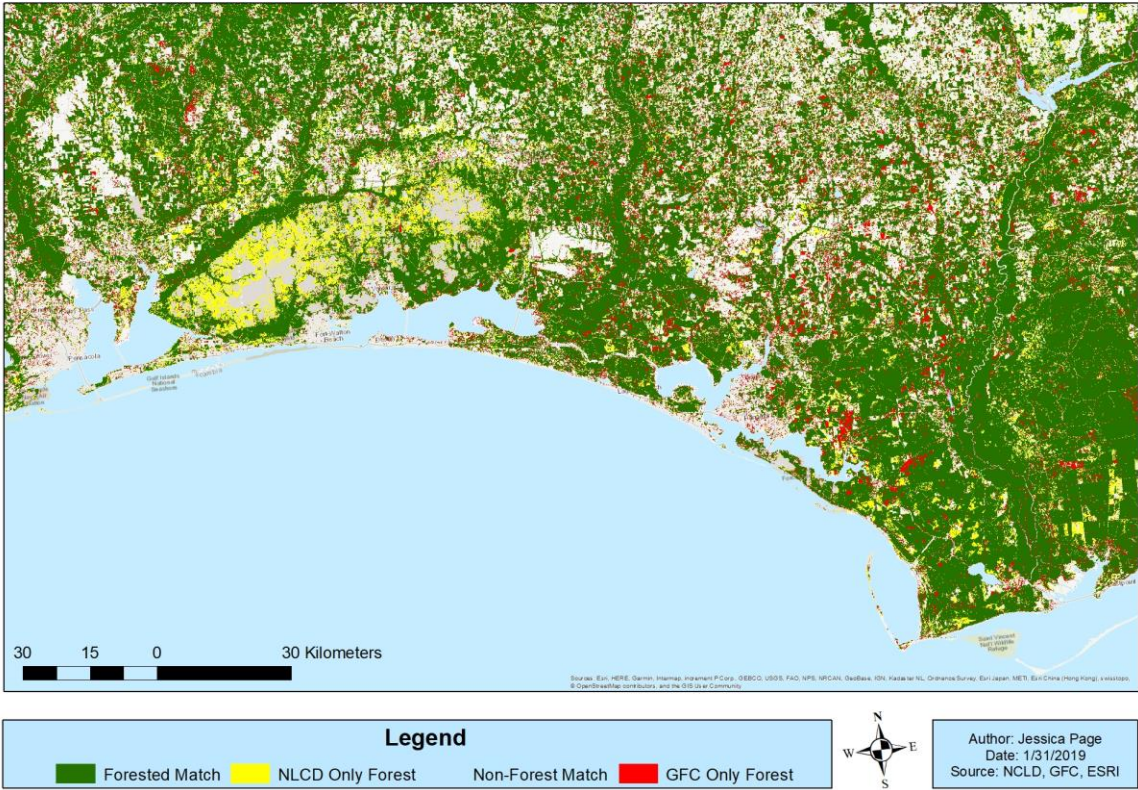


Figure 3. Highlights a region with a high amount of land cover designated as forest under National Land Cover Dataset but not under Global Forest Change data. The concentration of this mismatch on managed land give us insight as to why these two datasets do not match in certain regions.

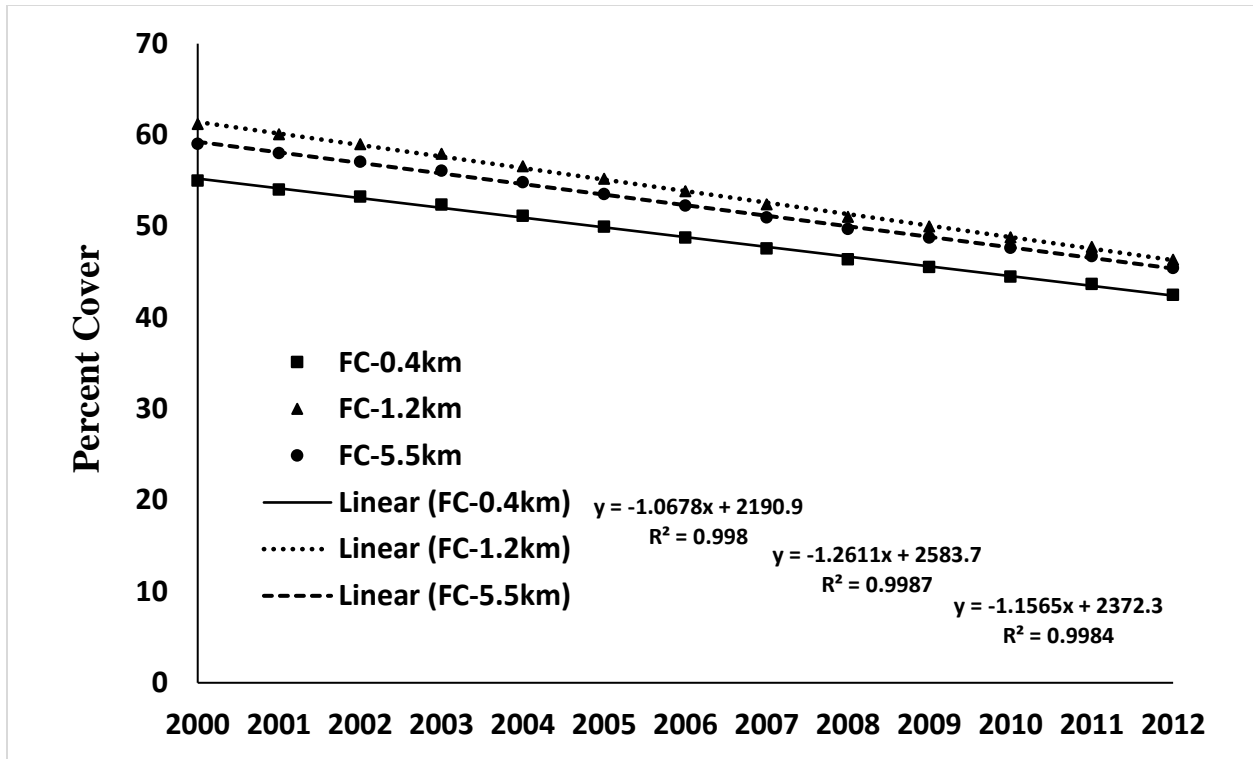


Figure 4. Rate of annual forest cover loss in three buffer distances from BBS routes in the Gulf Coast region, southeastern United States (2000-2012). Loss is defined as the percentage pixels with greater than 50% forest cover ≥ 5 m in height in year $t+1$, that was no longer present in year t . Linear equations for the relationship between forest cover loss and year, along with the R^2 , as included as insets. Since forest regeneration was only measured in 2012, it is not included here.

Table 1. Proportional change between GFC and NLCD datasets by buffer distances from BBS routes. Proportional change is the percent change in forest cover (Net gain + loss) between the initial and final year relative to the amount of forest cover in the initial year of measure ((Initial Forest Cover-Final Forest Cover)/ Initial Forest Cover). Significance tested using a paired t-test. A negative average difference indicates that proportional change was greater in NLCD data.

Dataset	GFC Avg Change	NLCD Avg Change	Avg Difference (SE)	Sig
400 m	-3.54%	-4.69%	-1.15% (0.61)	No
1200 m	-6.82%	-4.791%	2.03% (1.14)	No
5500 m	0.89%	-5.027%	-5.92% (1.25)	Yes

Table 2. BBS route representativeness of total forest cover loss at three buffer distances and two study zones (inland and coastal) in the Gulf Coast region of southeastern United States. Total forest loss was defined as the percentage pixels with greater than 50% forest cover ≥ 5 m in height present in 2000, that was no longer present in the final year (2012). Significance was tested using a t-test.

Two sample t-tests for representation of loss along BBS routes					
Dataset	Analysis	BBS Mean (SE)	Random Mean (SE)	Avg Difference (SE)	Sig
Coast	Loss in Cover 400	12.12% (0.89)	15.68% (0.91)	3.57% (1.27)	Yes
Coast	Loss in Cover 1200	14.12% (0.9)	15.33% (0.93)	1.21% (1.29)	No
Coast	Loss in Cover 5500	12.99% (0.85)	15.4% (0.87)	2.4% (1.22)	No
Inland	Loss in Cover 400	12.9% (0.93)	16.51% (0.91)	3.6% (1.3)	Yes
Inland	Loss in Cover 1200	15.64% (0.93)	16.52% (0.91)	0.88% (1.3)	No
Inland	Loss in Cover 5500	14.22% (0.9)	16.48% (0.88)	2.26% (1.26)	No

CHAPTER 2

OCCUPANCY DYNAMICS OF THREE FOREST-DWELLING PASSERINES IN THE GULF COAST REGION, UNITED STATES

ABSTRACT:

Decision makers and conservationists are seeking ways to understand and better predict the impact of major drivers of global change such as landscape level habitat modification and climate change. There is a vast literature documenting potential impacts of these two global forcings, but the number of papers assessing these impacts with dynamic models are scant, and these approaches provide a better foundation to make inferences and predictions about the impacts of global change and avian demographic parameters. I conducted an assessment of occupancy dynamics in the Gulf Coast region, a region known for its landscape changes, but also for its importance for North American land bird conservation. Herein, I determined local occupancy and colonization and extinction rates in the coastal and inland habitats in the Gulf Coast region between 2000 and 2012 of three forest dwelling avian species of conservation interest. These were the Wood Thrush (*Hylocichla mustelina*), Red-eyed Vireo (*Vireo olivaceus*), and the Brown-Headed Nuthatch (*Sitta pusilla*). I modeled Breeding Bird Survey data (presence/non-presence) with two land cover datasets (Global Change Forest and National Land Cover Data). I developed a candidate model set to test *a priori* hypotheses and predictions. These were that optimal habitat, not generic forest cover were better predictors of occupancy, colonization and extinction rates. I also hypothesized that occupancy rates would be lower in the coastal zone due to higher rate of development and landscape changes. For the same reason, I predicted that occupancy dynamics in the coastal zone would be characterized by high rates of local extinction probability. Conversely, occupancy dynamics in the inland zone would be characterized by high rates of colonization probability. Parameter estimates correlated strongly with measures of optimal habitat, as hypothesized. The other predictions were poorly supported, largely because spatial variation in habitat cover at the route level did not allocate itself

according to my inland and coastal categories of the study area. There were two common findings among all three species. First, there was no support in the candidate set of competing models for time-variant terms for colonization and extinction rates. Only detection probability varied by year. Second, proportional change in optimal habitat, not generic forest cover as derived from the Global Change Forest dataset influenced occupancy, colonization and extinction probabilities. This work helps guide habitat management at landscape levels by setting up competing models that featured habitat covariates in terms of generic and known optimal forest cover for each focal avian species. In highlighting spatial variation in occupancy parameters and lambda, my work identifies potential target areas for management.

INTRODUCTION:

Forest loss and fragmentation has transformed landscapes affecting wildlife across the globe (Betts et al. 2017), much of it due to increased urbanization and agriculture (Hunter et al. 2001; Frost 2000). The scale and rate at which landscapes are being modified has concerned conservationists because it may undermine species persistence and result in homogenized biological communities (Gascon et al. 1999, Blair 2001, Fahrig 2003, Aronson et al. 2016). However, many avian species are adept at exploiting modified and novel habitats (Kennedy et al. 2011, Watling et al. 2011, Lugo et al. 2012, Irizarry et al. 2016), partly because some of those habitats serve as functional equivalents of those replaced (Baum et al. 2004, Irizarry et al. 2018).

Certainly, the ability to exploit changing habitats is not possible for all species (Crocini et al. 2008). It follows that many migratory forest breeders have experienced a steady decline for the past 40 years (North American Bird Conservation Initiative 2009). Contributors to the decline are believed to be the juxtaposition of modified and natural habitats that often represents impenetrable barriers that, coupled with habitat fragmentation, create remnants of lower quality and higher isolation for many species. Reduced remnant patch size, lower habitat quality, and isolation have direct implications on rates of colonization and extinction, and therefore, affect species abundance and distribution (Hanski 1998, Yackulic et al. 2016).

The southeast region of the United States has undergone significant changes in recent decades, and in particular the Gulf of Mexico Coast (Culliton et al. 1990, Barrow et al. 2000). The Gulf region is one of the fastest growing areas in the country with the population rising at more than double the national average. This has led to significant changes across the landscape with factors such as urbanization and agriculture have a significant role in forest loss and fragmentation (Partnership for Gulf Coast Land Conservation 2014). Land cover around the

coast, particularly around southern Mississippi, southern Alabama and the panhandle of Florida have had significant forest loss in some areas but others have regenerated or are regenerating (Hansen et al. 2013). These highly susceptible areas are not only very important to shorebirds and other coastal migrants, but they are essential for forest dwelling species as well. For example, the majority of neotropical migrants were found in hardwood forest 65-85 km from the coast (Gauthreaux 1975, Moore et al. 2005). Because migrants engage on habitat selection within a 5 km radius after landing, as they move northbound, the amount for habitat fragmentation and loss of forest cover in the Gulf region may be a contributing factor to population declines (Simons et al 2000, Buler et al. 2007).

Decision makers and conservationists are seeking ways to understand and make better predictions about the impact of major drivers of global change such as landscape level habitat modification and climate change (Radeloff et al 2015). There is a vast literature documenting potential impacts of these two global forcings on avian species, but the number of papers assessing these questions using dynamic models are scant (Clement et al. 2016, Clement et al. 2019). Dynamic modeling yields stronger inferences because they do not merely establish relationships between occurrence (or abundance) and the current state of the habitat (static modeling), but between the parameter rates that influence distribution and abundance, local colonization and extinction rates, and changes in habitat over time.

The primary motivation driving my work was, therefore, to conduct an assessment of occupancy dynamics on a region known for its landscape changes and importance for North American land bird conservation. I combined three datasets collected over multiple years to gain insights on large scale processes that influence the abundance and distribution of North American land birds. These were the US Geological Survey North American Breeding Bird

Survey (BBS), and two land cover datasets, namely, the Global Forest Change (GFC; Hansen et al. 2013) and National Land Cover Database (NLCD; Homer et al. 2004, Fry et al. 2011, Homer et al. 2015). The North American Breeding Bird Survey (BBS) database is comprised of road-based avian surveys conducted along over 3,000 routes since 1966. The GFC land cover database was of value to this work because it can yield annual estimates of forest cover and forest cover loss between 2000 and 2012. The NLCD database, available only for 2001, 2006, and 2011, was of value because it can yield estimates of cover of various plant communities important to avian species (Hamel 1992). The combined use of these land cover datasets is suitable to expand our understanding of avian dynamics because I showed in Chapter 1 that: 1) the match (correspondence) between datasets is high (85%), 2) there was significant annual loss of forest cover between 2000 and 2012, amounting to 12-16% depending on location (coastal or inland), and 3) BBS routes were good representatives of land cover change at 1.2 km and 5.5 km buffer distances, distances representing the average natal dispersal distance of the focal species used in this study (Sutherland 2000) and also the scale used by northbound migrants to select habitat after making landfall in the United States (Buler et al. 2007).

Herein, I determined local occupancy and colonization and extinction rates in the coastal and inland habitats between 2000 and 2012 of three avian species in the Gulf Coast region (MacKenzie et al. 2009; Hines et al. 2014). These were the Wood Thrush (*Hylocichla mustelina*), Red-eyed Vireo (*Vireo olivaceus*), and the Brown-Headed Nuthatch (*Sitta pusilla*). These species are of conservation interest (e.g., declining trends), and vulnerable to habitat modification or loss. The first two are migratory species, whereas the nuthatch is a southeastern resident species. Coastal habitat or zone was defined as the extent in the Gulf Coast region from the shoreline to 127.5 km inland (Chapter 1). The inland habitat or zone was defined as the

extent from the outer boundary of the coastal zone out to 255 km. I modeled colonization and extinction probabilities as a function of macroecological covariates according to theoretical constructs governing these parameter rates (Hanski 1998, Yackulic et al. 2015). Colonization rates were modeled as a function of isolation (i.e., distance from BBS routes) and habitat quality, whereas extinction rates were modeled as a function of size of forested patches and habitat quality. The GFC data set provided annual estimates of forest cover loss (quantity and rate) as well as a measure of net change, whereas NCLD provided estimates of optimal habitat quality and change according to Hamel (1992) suitability classification. I hypothesized that optimal habitat, not generic forest cover, was a better predictor of occupancy, colonization and extinction rates (Hamel 1992). I also hypothesized that occupancy rates would be lower in the coastal zone due to higher rate of development and landscape changes. For the same reason, I predicted that occupancy dynamics in the coastal zone would be characterized by high rates of local extinction probability. Conversely, occupancy dynamics in the inland zone would be characterized by high rates of colonization probability. I discuss the conservation implications of results and ways to improve inferences about avian dynamics in future studies.

METHODS:

Study area

The study area was the Gulf Coast region and contained the southernmost portion of the South Atlantic Migratory Bird Initiative area (Figure 1; Watson et al. 2005). Initially, I had created three distance buffers from the shoreline, each measuring 85 km based on essential migratory habitat determined by Moore et al. 2005. However, I split the center band between the coastal and inland zones to create two zones of 127.5 km each, for a full extent of 255 km inland from the Gulf Coast. Each zone retained its biological relevance (e.g., coastal zone contained the 86 km deemed important for bird conservation), but importantly, each zone contained a higher number of BBS routes. The coastal zone had 61 routes, whereas the inland zone had 48 after further elimination of routes. The full extent spans from east of the Mississippi River to the eastern coast of the United States, and includes Mississippi, Florida, Georgia, and a small portion of Louisiana.

Focal Species

Each of the focal species are late-succession dependent forest species with varying preferences for minimum patch size (Hamel 1992; Buchanan et al. 2016). Aside from the Brown-headed Nuthatch, the focal species are trans-gulf neotropical migrants who are also predominantly insectivores (Hamel 1992; Evans et al. 2008, Slater et al. 2013, Crimprich et al 2018). It should be noted that the Wood Thrush is listed as a species in decline (59%) by Partners-in-Flight with a half-life of approximately 31 years (Rosenberg et al. 2016). Below I summarize criteria and attributes used to select minimum patch size to conduct occupancy dynamic analyses in this work.

Wood Thrush: This species displays little sensitivity in occupancy to small forest fragments and have been found to nest in patches as small as 0.3 ha (Weinberg and Roth 1998), and in riparian strips as narrow as <150 m (Sargent et al 2003). The area at which probability of occupancy was reduced by 50% was 1 ha (Robbins et al 1989). Additionally, some studies have indicated that the Wood Thrush has a maximum patch size of 500 ha (Robbins et al. 1989). Previous studies have shown that higher landscape forest cover is the best predictor of nest success as compared to microhabitat variable (Hoover and Brittingham 1998, Driscoll et al 2005). Optimal habitat for this species is made up of late succession Deciduous Forest and Woody Wetlands.

Red-eyed Vireo: The Red-eyed Vireo does not have a maximum patch size but the area in which occupancy probability is reduced by 50% is at 2.5 ha (Robbins et al 1989). Optimal habitat for this species is made up of late succession Deciduous Forest and Woody Wetlands.

Brown-headed Nuthatch: This species is most closely associated with open old-growth pine forest, but also regularly found in other pine and mixed pine-hardwood stands (Dickson et al 1980). Optimal habitat for this species is made up of Evergreen Forest and Mixed Forest. The minimum breeding patch size is 2.8 ha (Norris 1959).

Presence – Non-presence Data

All routes run between the year 2000 and 2012 in the study area were identified using the standard survey procedure (RPID: 101). Routes were retained for further scrutiny if: 1) they could be matched to corresponding polyline feature (Pardieck et al. 2018), 2) were partially within the study region, and 3) were run for a minimum of two consecutive years. This yielded 157 routes. Most breeding bird survey routes are available as a shapefile (Pardieck et al. 2018) of

linear features in the D_North_American_1983 datum. In some cases, routes contained minor breaks causing some variation in total length. Non-contiguous route segments were merged as a single feature, creating routes that varied in length between 10.33 to 74.66 km (average = 41.49 km). Nearly all routes were contained within South Eastern Coastal Plain Bird Conservation Region (BCR 27).

Of the 157 routes, I used only 109 routes for occupancy analyses. I eliminated BBS routes from the original 157 that did not have at minimum 8 years of count data between 2000 and 2012. The 109 routes were split between zones somewhat evenly; the coastal zone had 61 routes, whereas the inland zone had 48. All routes were surveyed between May 15th and June 15th. At each route, observers collect data on all birds seen or heard within a 0.4 km radius on either side of the route for three minutes. This sampling distance defines the first buffer distance in our analyses. I also used two additional distance-from-route categories in the analyses. These were 1.2 km and 5.5 km, and these represent average natal dispersal units for the 3 focal species. These units indicate that there was a 50% or 90% probability that juveniles, returning in year+1, returned to within 1.2 km or 5.5 km of their place of birth, respectively. Distance categories were derived from a body mass-dispersal distance relationship developed by Sutherland et al. (2000). Survey data for every surveyed station per route were converted into an encounter history of presence (1), non-presence (0), or missed (-).

Habitat Covariates

The first step in creating habitat covariates for analyses was to conduct a crosswalk between the plant communities identified by Hamel (1992) as optimal habitat and the NLCD land cover class classification. Hamel (1992) divides habitat types in the southeast into 23

distinct classes. Each class is sub-divided into four stages of succession. In this study, I only used the late successional forest stage for the crosswalk because the reported composition of optimal habitat for focal species was made up of late succession vegetation communities. Accordingly, I only used the following four NLCD forest types: evergreen, deciduous, mixed, and woody wetlands (Table 1).

To determine size and number of habitat patches, a system of reclassification was used for both the GFC as well as the NLCD data to create a binary of habitat (forest) and non-habitat (non-forest). Patches whose size the minimum size (ha) for each focal species were identified using the region group 8 tool in ArcGIS 10.5.1 (ESRI 2011). Area was calculated based on pixel size for each respective dataset. Average patch size was defined as the average size of all patches meeting the minimum patch requirement per species. For accurate area and distance calculations, the GFC dataset was reprojected to NAD_Albers_1983 with a cell size of 29.1X 29.1. Minimum patch sizes were rounded to the nearest pixel count. The reprojection and rounding differences yielded slight differences in minimum patch size threshold for each species, but differences were minimal between 0.16% and 2.58%. The average distance to patch was calculated as the average of the minimum Euclidean distance to each patch meeting the species requirement. This whole process was repeated for each of the three natal dispersal buffer distances per species.

Occupancy Modeling

We constructed multi-year occupancy models to estimate initial occupancy (ψ_1), local annual colonization (γ), and local annual extinction (ϵ) (MacKenzie et al. 2006). Initial local occupancy was defined as the probability that a surveyed route was occupied by a focal species in the initial season of the study (ψ_{2000}). Local extinction probability (ϵ_s) is the probability that a

survey route occupied by a focal species at year Y is no longer occupied by the species in year $Y + 1$. Local colonization probability (γ_s) is the probability that a survey route unoccupied by a focal species at year Y becomes occupied at year $Y + 1$. In this modeling framework, parameters were adjusted by detection probability, or the probability that at least 1 individual of a focal species was detected in year Y , provided the individuals were available to be detected. The framework also adjusted for correlated detections among the 50 survey stations within each BBS route (Hines et al. 2014).

We developed a candidate model set to test three *a priori* hypotheses and predictions. These were that occupancy rates would be lower in the coastal zone due to higher rate of development and landscape changes. For the same reason, I predicted that occupancy dynamics in the coastal zone would be characterized by high rates of local extinction probability. Conversely, occupancy dynamics in the inland zone would be characterized by high rates of colonization probability. The candidate set of competing models was created in two steps. First, I modeled the detection process to determine if detections were constant (.) or year-specific (Y) and whether detection was affected by the amount of forest cover measured by GFC and NLCD data at the 0.4 km buffer distance. Because land cover datasets matched well and annual rates of forest loss $\leq 1.6\%$, we used the proportional change in forest cover between 2000 and 2012 as the habitat covariate to model detection (Chapter 1). Proportional change is defined as $\text{forest cover in Final-Year/Initial Year} * 100$. During this process, I also modeled the theta parameters, those that adjust for correlated detection, as constant (.) or by zone (inland or coastal). I adopted the model with lowest AIC obtained in this process to model the rate parameters of interest—occupancy, colonization and extinction (Anthony *et al.* 2004). I determined whether colonization and extinction probabilities were constant or year-specific. I also determined if support in the data

avored a model whose initial occupancy probability was influenced by zone (inland/coastal). Occupancy was also modeled as a function of habitat covariates from GFC (quantity) and NLCD (quality). Colonization was modeled by distance buffer or natal dispersal distance (0.4 km, 1.2 km, and 5.5 km), the measure of isolation used in this study. We also modeled colonization by number of patches, our proxy of amount of habitat, generic forest cover (GFC) or optimal habitat (NLCD). I modeled extinction rates by measures of habitat quality (size and number of patches based on NLCD data), and quantity (number of patches) and average patch size of generic forest cover (GFC data). I modeled all covariates as additive factors because year-specific models were not supported by the data (low AIC values). To gain greater insights on the dynamics of the study area, I reported occupancy lambda (λ) and equilibrium occupancy estimates (colonization rates/colonization + extinction rates; Martin et al. 1981). Lambda occupancy refers to the probability that a BBS route was occupied from year to year. Equilibrium occupancy provides an estimate of the proportion of BBS routes exposed to either colonization or extinction rates. Before running models, all continuous covariates were normalized. Data were analyzed using program PRESENCE, correlated detection module (Hines *et al.*, 2006).

Careful consideration of model assumptions is important for interpreting results. Multi-year occupancy models assume that: (1) occupancy state at each survey site does not change over surveys within a year; (2) the focal species was not falsely detected; and (3) species detections and detection histories at each survey route were independent. The first two assumptions were likely met given that surveys were conducted in a short period of time (<2 months) by qualified observers. The third assumption was met because routes were at least 10 km apart.

I used Akaike's Information Criterion (AIC) to select the most parsimonious model (Burnham & Anderson, 2002). Models were ranked by AIC, and the model with the lowest AIC

value had the most support in the data. The difference in AIC values (ΔAIC) between the best-supported model and other models was used to calculate model weights (AIC wgt), which indicate the relative likelihood of the model given the data and the model set (Burnham & Anderson, 2002). Models with $\Delta\text{AIC} \leq 2$ were considered models with highest support (Burnham & Anderson, 2002). I considered an effect (i.e., covariate beta coefficient) to be strongly supported if the 95% confidence intervals did not overlap zero (otherwise the support was weak).

RESULTS:

Wood Thrush

Variation in occupancy was best explained by a model that featured zone (Z), colonization rates influenced by the proportional change of number of patches of optimal habitat between initial and final year at the 5.5 km buffer distance, and extinction rates influenced by the same covariates as colonization ($\text{AICc } w_i = 0.59$; Table 2). A competing model ($\Delta\text{AIC} \leq 2$) featured the same covariates except for colonization rates, which were influenced only by zone. Detection probability of the top model was influenced by year (Y), zone, and percent proportional change of optimal habitat cover between initial and final year (ΔC400^*) at the 0.4 km buffer distance. Detection probabilities ranged from 0.17 ± 0.02 to 0.31 ± 0.02 . Occupancy probability differed between zones (Beta = -1.77 ± 0.72), with rates at 0.65 ± 0.07 in the coastal zone and 0.92 ± 0.05 in the inland zone (Figure 1). The influence of the proportional change of number of patches of optimal habitat on extinction rates was negative and strong (Beta = -0.13 ± 0.04), with values ranging from 0.02 ± 0.01 to 0.54 ± 0.17 (Figure 2). Lambda values increased over time, approximating 1 (~ 0.95) by the end of the 13 year time series (Figure 3).

Average equilibrium occupancy was 0.48 ± 0.01 in the coastal zone, and 0.74 ± 0.01 in the inland zone.

Red-eyed Vireo

Variation in occupancy was best explained by a model that featured constant occupancy probability, colonization rates influenced by zone, and extinction rates influenced by the proportional change in the number of patches of optimal habitat at the 5.5 km buffer distance (AICc $w_i = 0.59$; Table 2). A competing model ($\Delta\text{AIC} \leq 2$) featured the same covariates except for colonization rates, which were also influenced by the proportional change in the number of patches of optimal habitat at the 5.5 km buffer distance. Detection probability of the top model was influenced by zone (Z) and percent proportional change of optimal habitat cover at the 0.4 km buffer distance. Detection probabilities ranged from 0.12 ± 0.02 to 0.30 ± 0.01 . Occupancy probability did not differ between zones, with rates at 0.79 ± 0.05 . The influence of the proportional change of number of patches of optimal habitat on extinction rates was negative and strong (Beta = -0.11 ± 0.04), with values ranging from 0.01 ± 0.01 to and 0.25 ± 0.10 (Figure 4). Lambda values improved over the period of study, converging around 1.0 (Figure 5). Average equilibrium occupancy was 0.77 ± 0.01 in the coastal zone, and 0.86 ± 0.01 in the inland zone.

Brown-Headed Nuthatch

Variation in occupancy was best explained by a model that featured zone (Z) and proportional change in optimal habitat at the 0.4 km buffer distance, colonization rates influenced by the proportional change of number of patches of optimal habitat between initial and final year at the 0.4 km buffer distance, and extinction rates influenced by the proportional

change of the average patch size between initial and final years at the 0.4 km buffer distance (AICc $w_i = 0.96$; Table 2). Detection probability was influenced by year (Y), zone, and percent proportional change between initial and final year ($\Delta C400^*$) at the 0.4 km buffer distance, and ranged from 0.05 ± 0.01 to 0.19 ± 0.02 . Occupancy probability ranged from 0.06 ± 0.12 to 0.84 ± 0.09 , with higher average occupancy rates in the coastal zone (0.72) than in the inland zone (0.53), although differences were not strongly supported ($\text{Beta}_{\text{zone}}$ overlapped zero; Figure 6). The influence of the proportional change of number of patches of optimal habitat on colonization rates was negative and strong ($\text{Beta} = -1.17 \pm 0.35$), with values ranging from 0.002 ± 0.002 to 0.63 ± 0.14 (Figure 7). By and large, lambda values converged toward 1, but there were some routes that had consistently low values (Figure 8). Average equilibrium occupancy was 0.73 ± 0.02 in the coastal zone, and 0.67 ± 0.02 in the inland zone.

DISCUSSION:

In this work, I quantified the occupancy dynamics of three avian species of conservation interest and contrasting migratory strategies in the Gulf coast, a region of where landscapes have been modified by in varying degrees by human activities (Culliton et al. 1990, Barrow et al. 2000, Barrow et al. 2005). The region is also known for its vital role in harboring North American migratory birds when they make landfall in the United States on its northbound migration (Simons et al 2000, Barrow et al. 2005, Moore et al. 2005, Buler et al. 2007), but also of importance for breeding of resident and migratory species (Hopp et al. 1995, Evans et al. 2011, Slater 2013, Sibley 2014, Allen et al. 2017, Burger 2018, Cimprich 2018).

Parameter estimates across all species correlated strongly with measures of optimal habitat, as hypothesized. However, predictions about colonization and extinction probabilities

by zones were poorly supported, largely because spatial variation in habitat cover at the route level did not necessarily allocate itself by zones. Notwithstanding, there were two emergent findings applicable to the three focal species. First, there was no support in the candidate set of competing models for time-variant terms for colonization and extinction rates. Only detection probability varied by year. This finding is of note because I showed that loss of generic forest cover occurred at a rate of 1-1.6% annually in the study area (Chapter 1). Yet, while statistically significant, the magnitude was not large enough to trigger annual changes in the aforementioned parameter rates. To capture change in a covariate for time-invariant models, I created a habitat covariate that allowed me to assess proportional change between initial and final year in the time series for both datasets. The covariate was justified because the match between NLCD and GFC datasets was high (85%) and because the rate of change between 2000 and 2012 was relatively low. This leads me to the second emerging pattern in results. Proportional change in optimal habitat (Hamel 1992), not generic forest cover as derived from the Global Change Forest dataset influenced occupancy, colonization and extinction probabilities. Note that while I documented spatio-temporal variation in forest cover changes between 2000 and 2012, time-invariant models suggested that variation in occupancy, colonization and extinction rates were driven primarily by spatial variation (route specific) in forest loss of optimal habitats for the focal species.

Initial occupancy for time-invariant models correlated well with expected habitat covariates (e.g., BHNU), and variation in colonization and extinction probability were influenced by isolation, number or size of patches within natal dispersal distances surrounding the BBS routes. For example, occupancy probability for the Wood Thrush was lower in the coastal zone, but not strongly. The lack of significance is consistent with our findings that showed that forest cover loss was not different between zones. Extinction probabilities were strongly and

negatively influenced by the number of patches of optimal habitat at the 5.5 km buffer distance, biologically interpreted as the area that would likely (90%) harbor returning juveniles for their first breeding season (Sutherland et al. 2000). Interestingly, change in the number of patches provides insights on fragmentation. I found a strong negative correlation between the number of patches and their size, suggesting that increasing number of patches are likely of smaller size and this trend was applicable for all species at all distances for optimal habitat (Figure 9). Wood Thrushes local extinction probability decreased as the number of patches increased between 2000 and 2012, suggesting that a higher number of smaller patches was conducive to lower local extinction along BBS routes. The literature suggests that this interpretation is plausible. Robbins et al. (1989) reported that the probability of occupancy asymptotes as patches increase up to approximately 500 ha, but may decrease as patch size increases beyond that point. The Red-eyed Vireo shares many of the habitat preferences of Wood Thrushes, but best supported models did not feature any of my explanatory habitat covariates for initial occupancy, and colonization rates was influenced only by zone. Where it resembles the Wood Thrush is that local extinction rates were influenced negatively by the number of patches of optimal habitat at the 5.5 km buffer distance. As such, it suggested that some breaking up of habitat patches was more conducive to higher occupancy.

Population trends of Brown-headed Nuthatches have exhibited declines in recent years (Sauer et al 2017). Their distribution is strongly associated with the optimal habitat, evergreen and mixed wood forests (Iglecia et al. 2012). As expected, initial occupancy varied by zone and the proportional change (forest cover) of optimal habitat along BBS routes. Moreover, colonization was strongly and negatively influenced by the proportional change in number of patches of optimal habitat along BBS routes (0.4 km buffer distance). I surmised from my

analyses of GFC and NLCD datasets that an increase in number of patches is more likely caused by habitat fragmentation than by new additions of regenerating forest. Certainly, the response of the nuthatch is opposite of the previous two species.

To gain greater insights on the dynamics of the three focal species, I calculated occupancy lambda and equilibrium occupancy over time. Lambda estimates indicated that the probability of a BBS being occupied from one year to the next for Red-eyed Vireos and Brown-headed Nuthatches were high (≥ 1). Exceptions illustrated spatial variation, likely reflecting modified conditions of some BBS routes as proportional change in optimal habitat. In the case of the Wood Thrush, lambda values were generally lower (≤ 1), a pattern that probably reflects declining population trends (references). I highlight, however, that over time the trend in lambda moved closer to a lambda of 1 (0.95), suggesting that routes were occupied more consistently over time.

Equilibrium occupancy provided insights on the exposure of BBS routes to either colonization or extinction processes (Martin et al. 2009), and as such valuable to help guide management efforts to influence either parameter rate. For example, average equilibrium for the Red-eyed Vireo and Brown-headed Nuthatch ranged from 0.67 ± 0.02 to 0.86 ± 0.01 . Values that > 0.5 suggest that BBS routes were more exposed to changes in extinction, and thus, decision makers could consider actions that prevent this process. Conversely, the Wood Thrush had an average equilibrium occupancy of 0.48 ± 0.01 in the coastal zone and 0.74 ± 0.01 in the inland zone. In this case, BBS routes in the coastal zone were characterized by higher local extinction rates, suggesting that management actions could be directed towards increasing colonization rates. Conversely, BBS routes in the inland zone were characterized by high

colonization rates, suggesting that management actions could be directed toward preventing local extinction.

Identifying habitat features to enhance colonization or prevent local extinction is the result of multiple biological processes at different scales, and should reflect various metrics of population performance (Furrer and Pasinelli 2016, Gilroy and Edwards 2017). This work makes a contribution towards guiding habitat management at landscape levels by tapping and setting up competing models that featured habitat covariates in terms of generic and known optimal forest cover for each focal avian species. In highlighting spatial variation in occupancy parameters and lambda, my work identifies potential target areas for management. It is important to stress that the occupancy parameters reported in this work were adjusted by detection probability.

Adjusting for detection probability is important to discriminate between where species occur and where species are detected (Guillera-Arroita et al. 2010). Moreover, Lahoz-Monfort et al. (2013) demonstrated that disregarding imperfect detection could compromise the identification of optimal habitat for a species and misguide spatial prioritization of habitat as in this work.

While the strengths of dynamic occupancy models are clear, it should not be the only means to assess and guide landscape level habitat management. Yirka et al. (2018) made a few suggestions worth underscoring here. First, Johnston et al. (2015) cautioned conservationists against relying solely on occupancy estimates to guide habitat conservation. If abundance estimation methods are not feasible (e.g., financial constraints), Nichols et al. (2007) developed multi-season, multi-state occupancy models as a means to include proxies of abundance. Lastly, I evaluated two land cover datasets, and while both have a high rate of accuracy in classification (Chapter 1), it is important for readers to be fully aware of the uses and limitations of thematic data. High rates of misclassification errors could lead to non-trivial errors when estimating

occupancy, colonization and extinction rates in landscapes characterized by transient dynamics
(Veran et al. 2012).

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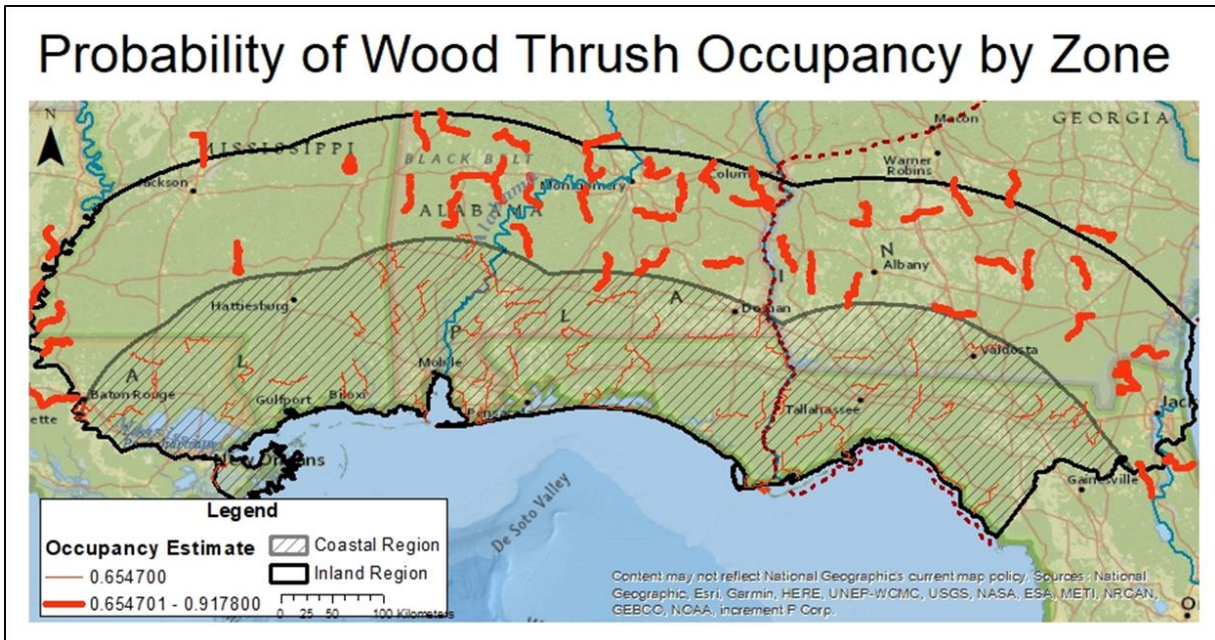


Figure 1. Wood Thrush probability of Occupancy differed between zones (Beta = -1.77 ± 0.72), with rates at 0.65 ± 0.07 in the coastal zone and 0.92 ± 0.05 in the inland zone

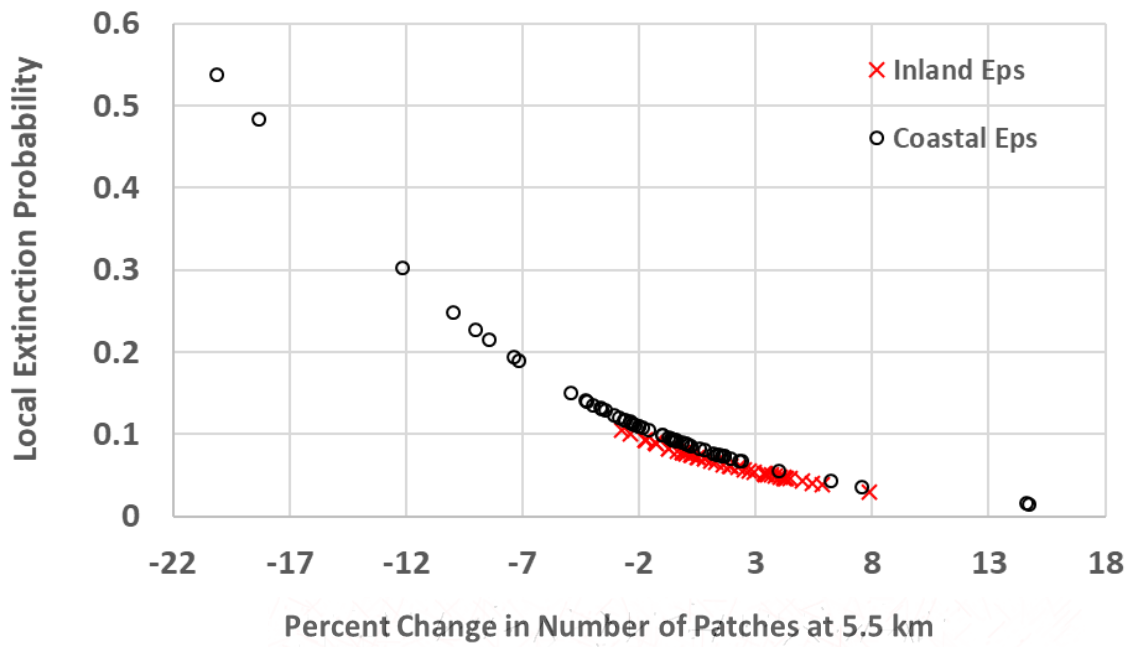


Figure 2. The influence of the proportional change of number of patches of optimal habitat on Wood Thrush extinction rates was negative and strong (Beta = -0.13 ± 0.04), with values ranging from 0.02 ± 0.01 to and 0.54 ± 0.17

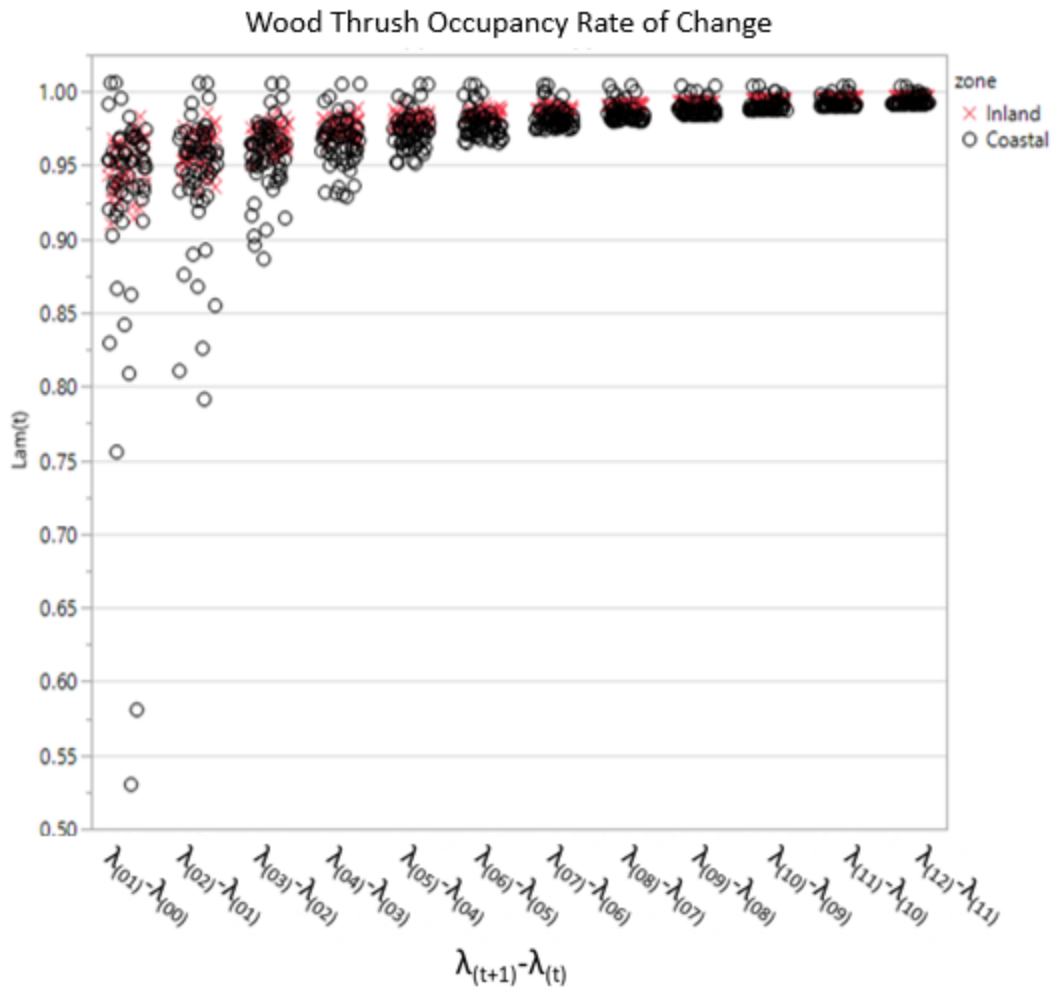


Figure 3. Wood Thrush lambda values increased over time, approximating 1 (~0.95) by the end of the 13 year time series.

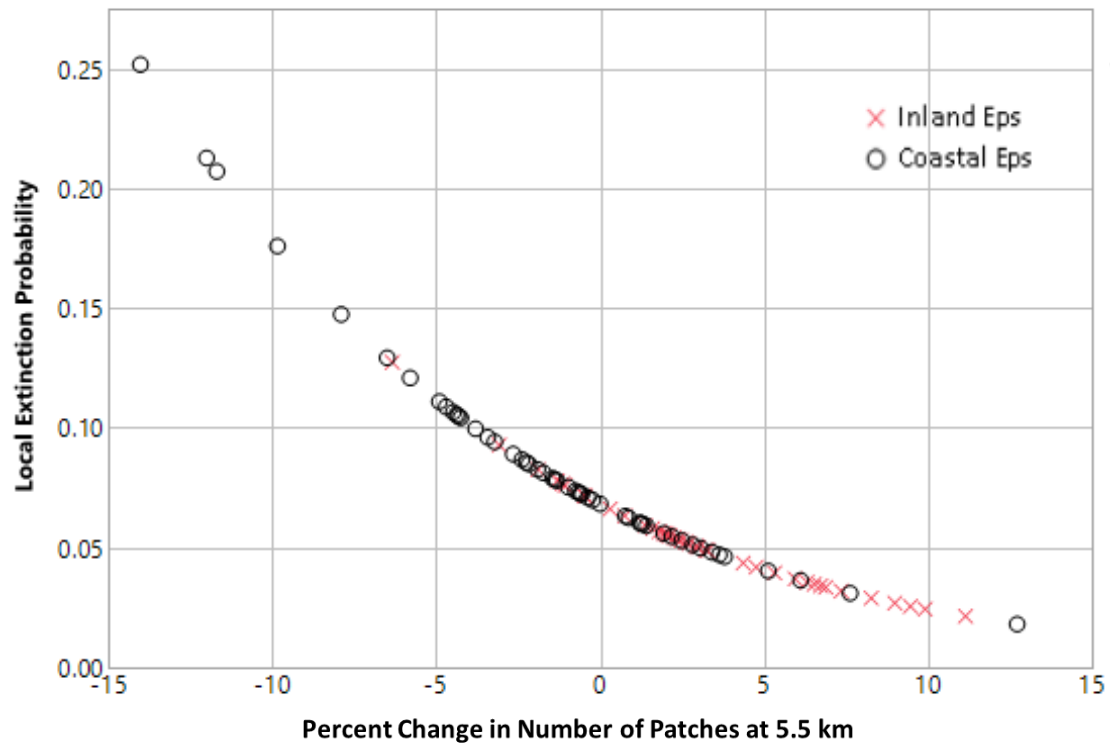


Figure 4. The influence of the proportional change of number of patches of optimal habitat at 5.5km on Red-eyed Vireo extinction rates was negative and strong ($\text{Beta} = -0.11 \pm 0.04$), with values ranging from 0.01 ± 0.01 to and 0.25 ± 0.10

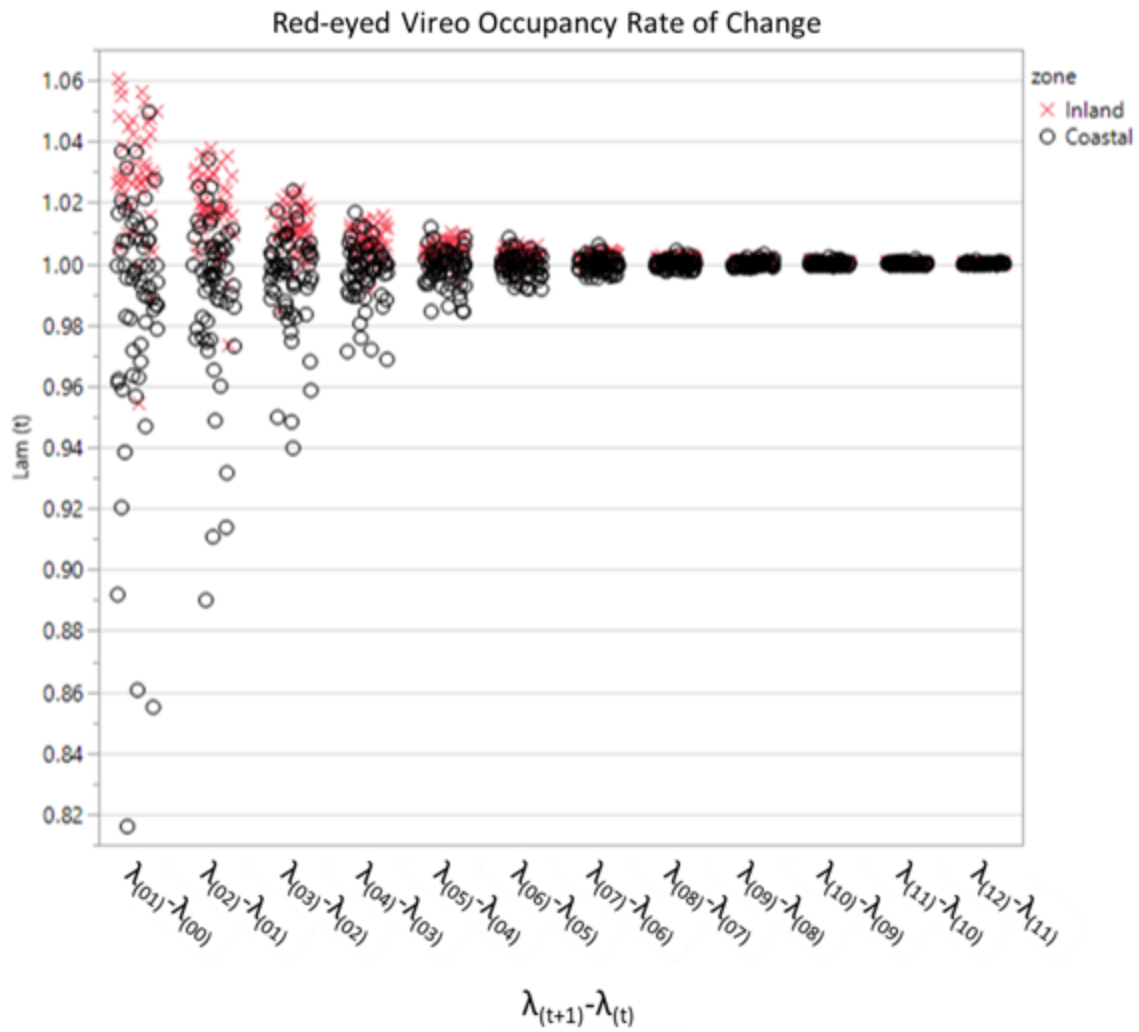


Figure 5. Red-eyed Vireo lambda values improved over the period of study, converging around 1.0

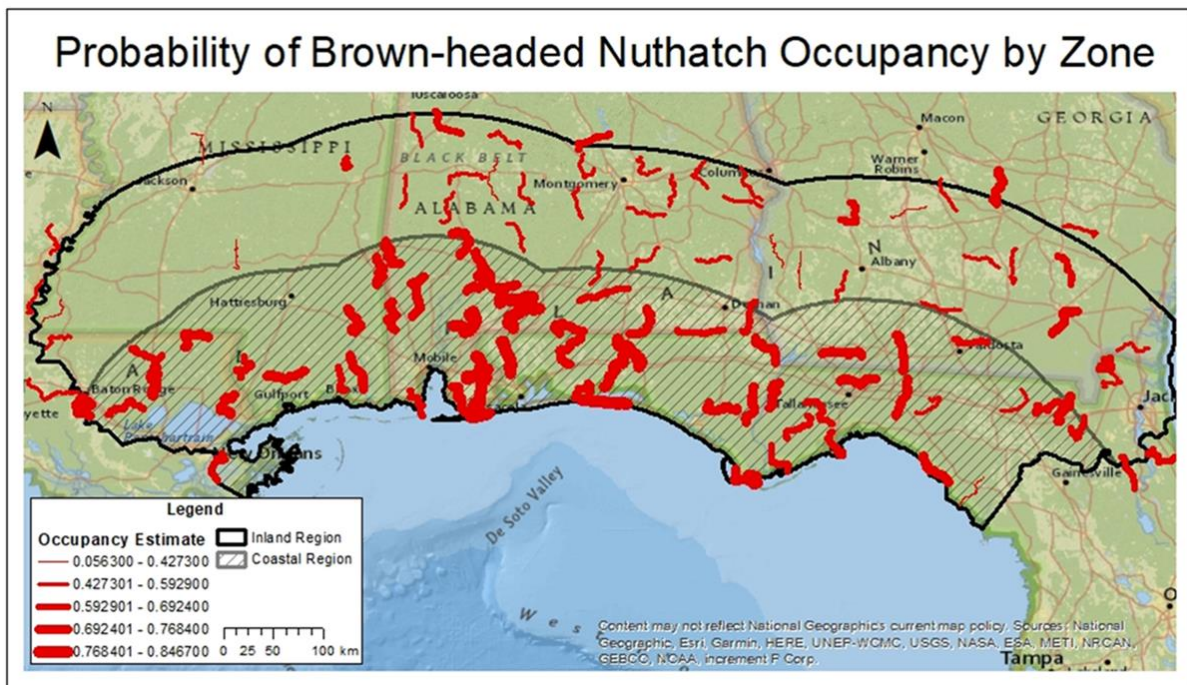


Figure 6. Occupancy probability for the Brown-Headed Nuthatch ranged from 0.06 ± 0.12 to 0.84 ± 0.09 , with higher average occupancy rates in the coastal zone (0.72) than in the inland zone (0.53), although differences were not strongly supported ($\text{Beta}_{\text{zone}}$ overlapped zero).

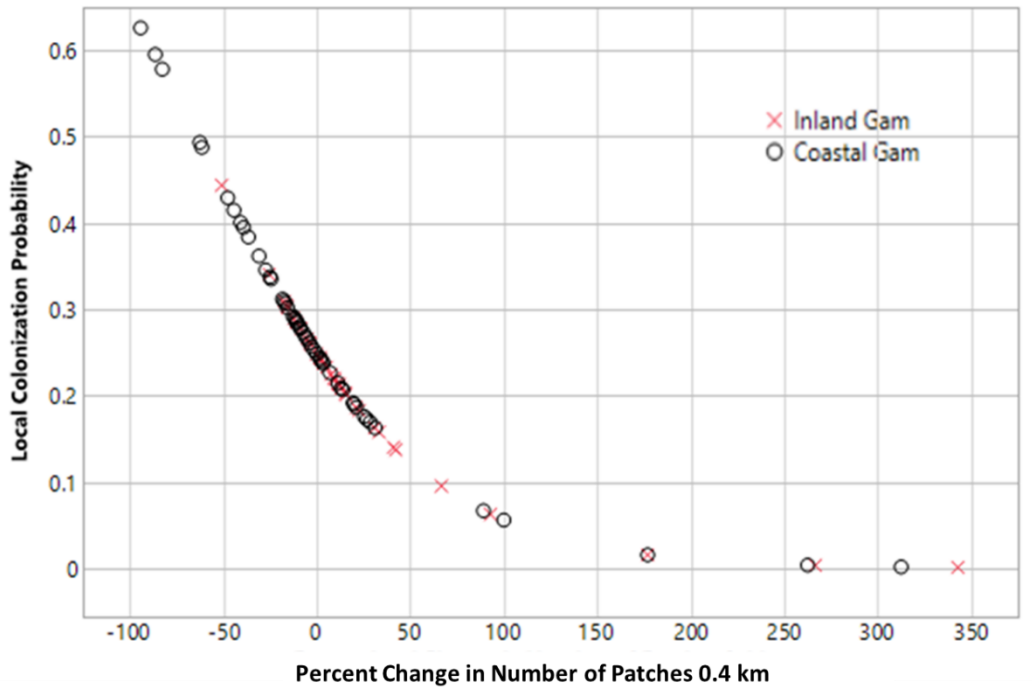


Figure 7. The influence of the percent proportional change of number of patches of optimal habitat at 0.4 km on Brown-headed Nuthatch colonization rates was negative and strong (Beta = -1.17 ± 0.35), with values ranging from 0.002 ± 0.002 to and 0.63 ± 0.14 .

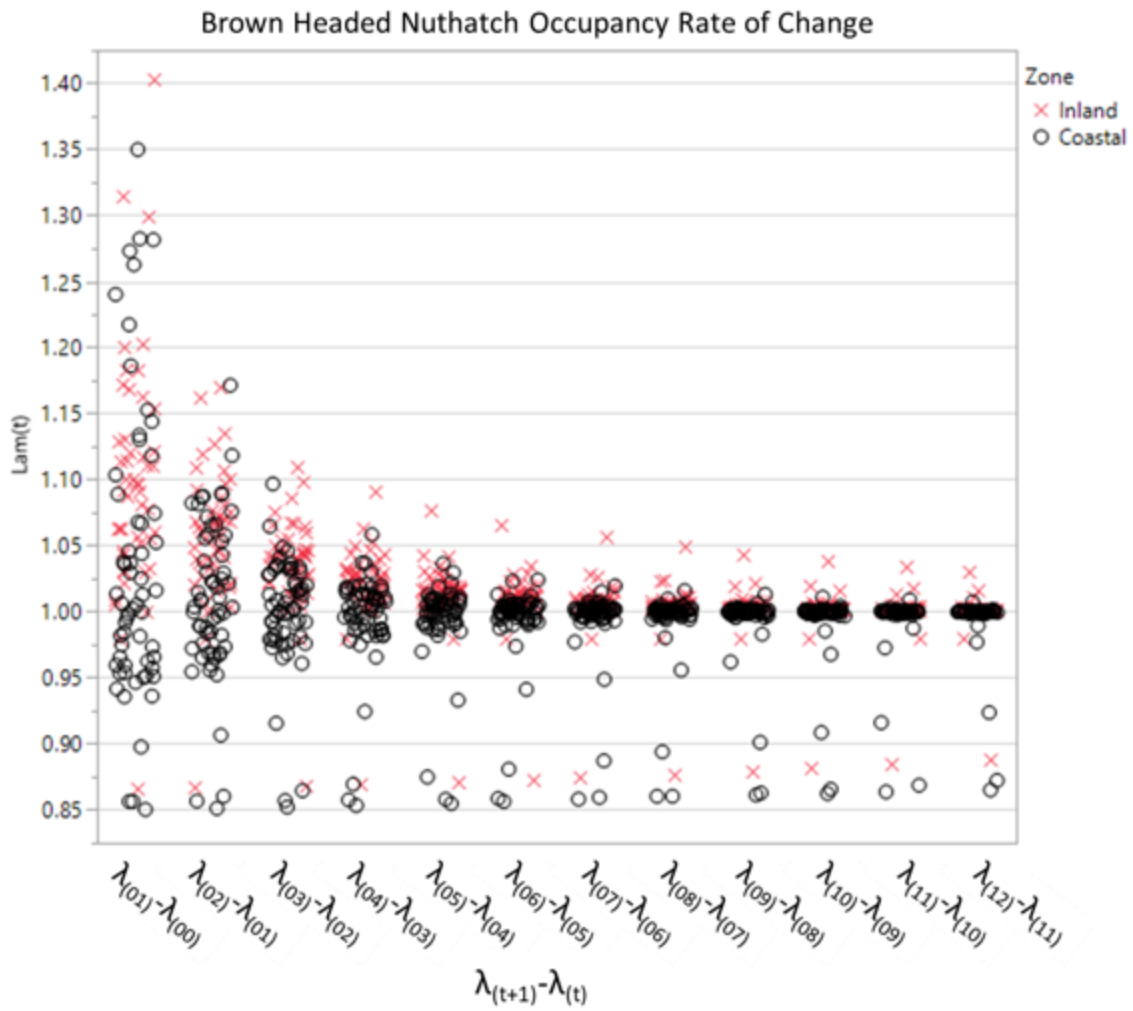


Figure 8. Brown headed Nuthatch lambda values converged toward 1, but there were some routes that had consistently low values.

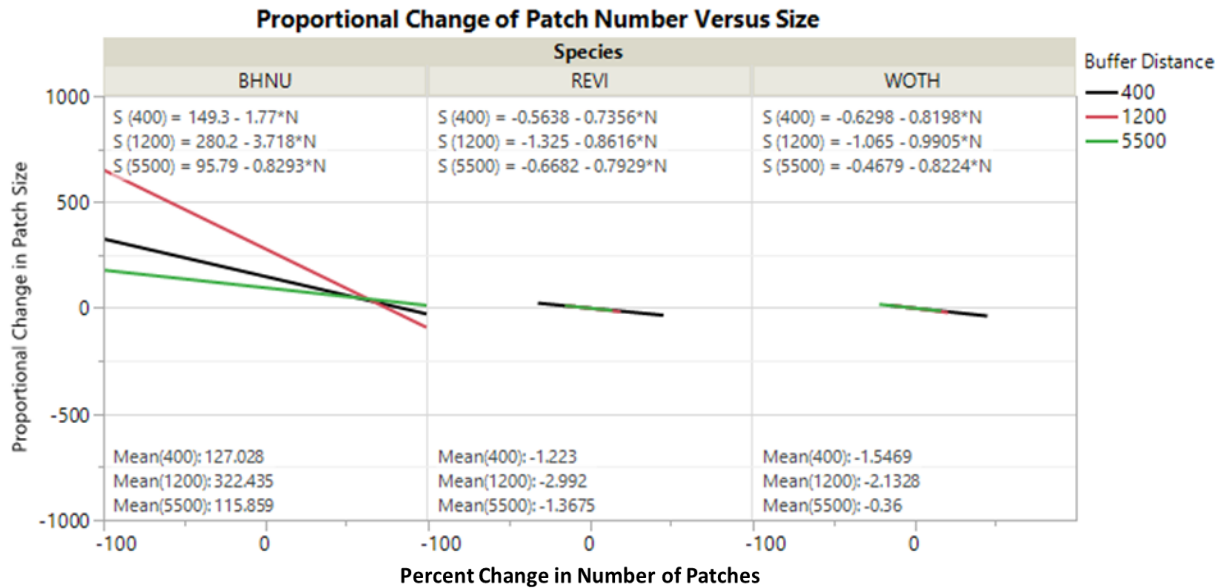


Figure 9. When the proportional percent change in patch number was plotted against the proportional percent change in size. I found a strong negative correlation between the number of patches and their size, suggesting that increasing number of patches are likely of smaller size and this trend was applicable for all species at all distances for optimal habitat. In this figure BHNU data had a much greater range and therefore some values extend beyond the axis values on this graph.

Table 1. Table 1 is the crosswalk between the plant communities identified by Hamel (1992) as optimal habitat and the NLCD land cover class classification. Hamel (1992) divides habitat types in the southeast into 23 distinct classes. Each class is sub-divided into four stages of succession. In this study, I only used the late successional forest stage for the crosswalk because the reported composition of optimal habitat for focal species was made up of late succession vegetation communities.

Land Cover Cross-walk		Optimal for Species		
Hamel Land cover type	Corresponding NLCD Type	BHNU	WOTH	REVI
Everglades	Emergent Herbaceous Wetland	No	No	No
Tropical Hardwoods	Woody Wetlands	No	No	No
Mangroves	Woody Wetlands	No	No	No
Pine Savanna	Evergreen Forest	Yes	No	No
Southern Scrub Oak	Deciduous Forest	No	No	No
Sand Pine-Southern Scrub Oak	Mixed Forest	No	No	No
Longleaf Pine-Scrub Oak	Mixed Forest	Yes	No	No
Sandhills Longleaf Pine	Evergreen Forest	Yes	No	No
Southern Mixed Mesic Hardwood	Deciduous Forest	No	Yes	Yes
Bay-Swamp Pocosin	Woody Wetlands	No	No	No
Pond Pine Pocosin	Woody Wetlands	No	No	No
Longleaf Slash Pine	Evergreen Forest	Yes	No	No
Oak-Gum-Cypress	Woody Wetlands	No	Yes	Yes
Live Oak-Maritime	Mixed Forest	No	No	No
Elm-Ash-Cotton Wood	Deciduous Forest	No	Yes	No
Loblolly Pine-Shortleaf Pine	Evergreen Forest	Yes	No	No
Virginia Pine-Pitch Pine	Evergreen Forest	No	No	No
Mixed Pine-Hardwood	Mixed Forest	No	No	No
Oak-Hickory	Deciduous Forest	No	Yes	Yes
White Pine-Hemlock	Evergreen Forest	No	No	No
Cove Hardwoods	Deciduous Forest	No	No	Yes
Maple-Beech-Birch	Deciduous Forest	No	No	No
Spruce Fir	Evergreen Forest	No	No	No

Table 2. Top AIC model selection results for multi-season correlated detection species-habitat occupancy models. All results shown in this table are those with a $\Delta AIC > 10$. Covariates are labeled as follows: (*) Indicates GFC data (C) % Proportional Change between initial/final year (D) % Proportional Change Average distance from route to viable patches (N) % Proportional Change of Number of viable patches between initial/final years (S) % Proportional Change of average patch size between initial/final years (Z) Zone (Y) Yearly effects

Top Species Models					
	Model	AIC	Δ AIC	AIC wgt	no. P
BHNU	$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(\Delta N400), \varepsilon(\Delta S400), p(Y+Z+\Delta C400^*), \theta\pi()$	15853.1	0	0.96	27
	$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(\Delta N400), \varepsilon(), p(Y+Z+\Delta C400^*), \theta\pi()$	15860.5	7.34	0.02	26
WOTH	$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z+\Delta N5500), \varepsilon(Z+\Delta N5500), p(Y+Z+\Delta C400^*), \theta\pi()$	22929.3	0	0.59	28
	$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z+\Delta N5500), p(Y+Z+\Delta C400^*), \theta\pi()$	22930.5	1.23	0.32	27
	$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z+\Delta D1200), \varepsilon(Z+\Delta S1200), p(Y+Z+\Delta C400^*), \theta\pi()$	22936.6	7.32	0.02	28
	$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z+\Delta D1200), \varepsilon(Z), p(Y+Z+\Delta C400^*), \theta\pi()$	22936.8	7.54	0.01	27
	$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z+\Delta N5500^*), \varepsilon(Z+\Delta N5500^*), p(Y+Z+\Delta C400^*), \theta\pi()$	22937.6	8.35	0.01	28
	$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y+Z+\Delta C^*400), \theta\pi()$	22938	8.7	0.01	26
	$\Psi(Z+\Delta N400), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y+Z+\Delta C400^*), \theta\pi()$	22938	8.76	0.01	27
	$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z+\Delta S1200), p(Y+Z+\Delta C400^*), \theta\pi()$	22938.1	8.84	0.01	27
	$\Psi(Z+\Delta C400^*), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y+Z+\Delta C400^*), \theta\pi()$	22938.5	9.17	0.01	27
	$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z+\Delta S5500), p(Y+Z+\Delta C400^*), \theta\pi()$	22939.1	9.84	0.00	27
	$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z+\Delta N1200), \varepsilon(Z+\Delta N1200), p(Y+Z+\Delta C400^*), \theta\pi()$	22939.3	9.98	0.00	28
	$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z+\Delta D5500), \varepsilon(Z), p(Y+Z+\Delta C^*400), \theta\pi()$	22939.3	9.98	0.00	27
REVI	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(\Delta N5500), p(Z+\Delta C400), \theta\pi()$	29558.8	0	0.43	13
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta N5500), \varepsilon(\Delta N5500), p(Z+\Delta C400), \theta\pi()$	29559.2	0.46	0.34	14
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta N5500), \varepsilon(\Delta S5500), p(Z+\Delta C400), \theta\pi()$	29562.4	3.6	0.07	14
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(), p(Z+\Delta C400), \theta\pi()$	29565.1	6.28	0.02	12
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta D5500), \varepsilon(\Delta S5500), p(Z+\Delta C400), \theta\pi()$	29565.3	6.52	0.02	14
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(\Delta S5500), p(Z+\Delta C400), \theta\pi()$	29565.3	6.57	0.02	13
	$\Psi(\Delta C^*400), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(), p(Z+\Delta C400), \theta\pi()$	29565.6	6.79	0.01	13
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta D5500), \varepsilon(), p(Z+\Delta C400), \theta\pi()$	29565.6	6.83	0.01	13
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(\Delta S400), p(Z+\Delta C400), \theta\pi()$	29566	7.21	0.01	13
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(\Delta S1200), p(Z+\Delta C400), \theta\pi()$	29566.3	7.52	0.01	13
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta D1200), \varepsilon(), p(Z+\Delta C400), \theta\pi()$	29566.8	7.98	0.01	13
	$\Psi(\Delta C400), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(), p(Z+\Delta C400), \theta\pi()$	29566.8	8.03	0.01	13
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Z+\Delta C400), \theta\pi()$	29566.9	8.14	0.01	13
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta D400), \varepsilon(), p(Z+\Delta C400), \theta\pi()$	29567	8.27	0.01	13
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(\Delta N5500^*), p(Z+\Delta C400), \theta\pi()$	29567.1	8.28	0.01	13
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta N1200), \varepsilon(\Delta N1200), p(Z+\Delta C400), \theta\pi()$	29567.4	8.62	0.01	14
	$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta N400), \varepsilon(\Delta N400), p(Z+\Delta C400), \theta\pi()$	29568	9.24	0.00	14

APPENDICES

Appendix 1. All Wood Thrush AIC model selection results for multi-season correlated detection species-habitat occupancy models. All results shown in this table are those with a $\Delta AIC > 10$. Covariates are labeled as follows: (*) Indicates GFC data (C) % Proportional Change between initial/final year (D) % Proportional Change Average distance from route to viable patches (N) % Proportional Change of Number of viable patches between initial/final years (S) % Proportional Change of average patch size between initial/final years (Z) Zone (Y) Yearly effects

WOTH Models				
Model	AIC	ΔAIC	AIC wgt	no. Par
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z + \Delta N 5500), \varepsilon(Z + \Delta N 5500), p(Y + Z + \Delta C * 400), \theta\pi()$	22929.3	0	0.59	28
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z + \Delta N 5500), p(Y + Z + \Delta C * 400), \theta\pi()$	22930.5	1.23	0.32	27
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z + \Delta D 1200), \varepsilon(Z + \Delta S 1200), p(Y + Z + \Delta C * 400), \theta\pi()$	22936.6	7.32	0.02	28
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z + \Delta D 1200), \varepsilon(Z), p(Y + Z + \Delta C * 400), \theta\pi()$	22936.8	7.54	0.01	27
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z + \Delta N * 5500), \varepsilon(Z + \Delta N * 5500), p(Y + Z + \Delta C * 400), \theta\pi()$	22937.6	8.35	0.01	28
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y + Z + \Delta C * 400), \theta\pi()$	22938	8.7	0.01	26
$\Psi(Z + \Delta N 400), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y + Z + \Delta C * 400), \theta\pi()$	22938	8.76	0.01	27
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z + \Delta S 1200), p(Y + Z + \Delta C * 400), \theta\pi()$	22938.1	8.84	0.01	27
$\Psi(Z + \Delta C * 400), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y + Z + \Delta C * 400), \theta\pi()$	22938.5	9.17	0.01	27
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z + \Delta S 5500), p(Y + Z + \Delta C * 400), \theta\pi()$	22939.1	9.84	0	27
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z + \Delta N 1200), \varepsilon(Z + \Delta N 1200), p(Y + Z + \Delta C * 400), \theta\pi()$	22939.3	9.98	0	28
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z + \Delta D 5500), \varepsilon(Z), p(Y + Z + \Delta C * 400), \theta\pi()$	22939.3	9.98	0	27
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z + \Delta D 400), \varepsilon(Z), p(Y + Z + \Delta C * 400), \theta\pi()$	22939.3	10	0	27
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z + \Delta N 5500), \varepsilon(Z + \Delta S 5500), p(Y + Z + \Delta C * 400), \theta\pi()$	22939.4	10.08	0	28
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z + \Delta S 400), p(Y + Z + \Delta C * 400), \theta\pi()$	22939.6	10.36	0	27
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z + \Delta N 400), \varepsilon(Z + \Delta N 400), p(Y + Z + \Delta C * 400), \theta\pi()$	22939.8	10.55	0	28
$\Psi(Z + \Delta C 5500), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y + Z + \Delta C * 400), \theta\pi()$	22942.5	13.26	0	27
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y + Z), \theta\pi()$	22971.9	42.58	0	25
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y + Z + \Delta C 400), \theta\pi()$	22972.1	42.83	0	26
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y + Z), \theta\pi(Z)$	22973.3	44.04	0	26
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(t + Z), p(Y + Z), \theta\pi()$	22983.6	54.34	0	36
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(t + Z), \varepsilon(Z), p(Y + Z), \theta\pi(Z)$	22986.7	57.45	0	37
$\Psi, \theta(), \theta'(), \gamma(), \varepsilon(), p(Y), \theta\pi()$	23101.3	171.98	0	19
$\Psi, \theta(), \theta'(), \gamma(), \varepsilon(), p(), \theta\pi()$	23158.8	229.47	0	7

Appendix 2. All BHNU AIC model selection results. Covariates are labeled as follows: (*) GFC data (C) % proportional change between initial/final year (D) % proportional change avg. distance to patches (N) % proportional change of # patches between initial/final year (S) % proportional change of avg. patch size between initial/final year (Z) Zone (Y) Yearly effects

BNHU Models				
Model	AIC	Δ AIC	AIC wgt	no. Par
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(\Delta N400), \varepsilon(\Delta S400), p(Y+Z+\Delta C400^*), \theta\pi()$	15853.11	0	0.96	27
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(\Delta N400), \varepsilon(), p(Y+Z+\Delta C400^*), \theta\pi()$	15860.45	7.34	0.02	26
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(\Delta N1200+\Delta D1200), \varepsilon(\Delta S1200), p(Y+Z+\Delta C400^*), \theta\pi()$	15863.23	10.12	0.01	28
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(\Delta N1200), \varepsilon(), p(Y+Z+\Delta C400^*), \theta\pi()$	15863.37	10.26	0.01	26
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(\Delta N1200+Z), \varepsilon(\Delta S1200+Z), p(Y+Z+\Delta C400^*), \theta\pi()$	15865.57	12.46	0	29
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(\Delta N5500), \varepsilon(), p(Y+Z+\Delta C400^*), \theta\pi()$	15869.6	16.49	0	26
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(\Delta N5500), \varepsilon(\Delta S5500), p(Y+Z+\Delta C400^*), \theta\pi()$	15871.53	18.42	0	27
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(), \varepsilon(\Delta N400), p(Y+Z+\Delta C400^*), \theta\pi()$	15875.3	22.19	0	26
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(), \varepsilon(\Delta S400), p(Y+Z+\Delta C400^*), \theta\pi()$	15880.31	27.2	0	26
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(), \varepsilon(\Delta N1200), p(Y+Z+\Delta C400^*), \theta\pi()$	15881.81	28.7	0	26
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(), \varepsilon(\Delta S1200), p(Y+Z+\Delta C400^*), \theta\pi()$	15882.74	29.63	0	26
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(), \varepsilon(\Delta N5500), p(Y+Z+\Delta C400^*), \theta\pi()$	15884	30.89	0	26
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(\Delta D1200), \varepsilon(), p(Y+Z+\Delta C400^*), \theta\pi()$	15884.6	31.49	0	26
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(\Delta D5500), \varepsilon(), p(Y+Z+\Delta C400^*), \theta\pi()$	15884.85	31.74	0	26
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(), \varepsilon(), p(Y+Z+\Delta C400^*), \theta\pi()$	15885.01	31.9	0	25
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z+\Delta N5500), \varepsilon(Z+\Delta N5500), p(Y+Z+\Delta C400^*), \theta\pi()$	15885.42	32.31	0	24
$\Psi(Z+\Delta C400^*), \theta(Z), \theta'(Z), \gamma(), \varepsilon(), p(Y+Z+\Delta C400^*), \theta\pi()$	15885.52	32.41	0	25
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(\Delta D400), \varepsilon(), p(Y+Z+\Delta C400^*), \theta\pi()$	15887	33.89	0	26
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(), \varepsilon(\Delta S5500), p(Y+Z+\Delta C400^*), \theta\pi()$	15887	33.89	0	26
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(\Delta N1200^*+\Delta D1200^*), \varepsilon(\Delta S1200^*), p(Y+Z+\Delta C400^*), \theta\pi()$	15888.86	35.75	0	28
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(), \varepsilon(t), p(Y+Z+\Delta C400^*), \theta\pi()$	15890.89	37.78	0	35
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(t), \varepsilon(), p(Y+Z+\Delta C400^*), \theta\pi()$	15897.71	44.6	0	35
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(t), \varepsilon(t), p(Y+Z+\Delta C400^*), \theta\pi()$	15903.63	50.52	0	46
$\Psi(Z+\Delta C400), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y+Z), \theta\pi()$	15918.85	65.74	0	26
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(), \varepsilon(), p(Y+Z), \theta\pi()$	15921.17	68.06	0	23
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(), \varepsilon(), p(Y+Z+\Delta C400), \theta\pi()$	15923.16	70.05	0	24
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y+Z), \theta\pi()$	15923.71	70.6	0	25
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y+Z), \theta\pi()$	15923.71	70.6	0	25
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y+Z+\Delta C400^*), \theta\pi()$	15923.71	70.6	0	25
$\Psi(Z+\Delta C400^*), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Y+Z), \theta\pi()$	15923.71	70.6	0	25
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(t), p(Y+Z), \theta\pi()$	15929.07	75.96	0	35
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(t), \varepsilon(), p(Y+Z), \theta\pi()$	15933.52	80.41	0	34
$\Psi, \theta(), \theta'(), \gamma(), \varepsilon(), p(Y), \theta\pi()$	15936.57	83.46	0	19
$\Psi, \theta(), \theta'(), \gamma(), \varepsilon(), p(), \theta\pi()$	15940.47	87.36	0	7

Appendix 2. All Red-Eyed Vireo AIC model selection results. Covariates are labeled as follows: (*) GFC data (C) % proportional change between initial/final year (D) % proportional change avg. distance to patches (N) % proportional change of # patches between initial/final year (S) % proportional change of avg. patch size between initial/final year (Z) Zone (Y) Yearly effects

REVI Models				
Model	AIC	Δ AIC	AIC wgt	no. Par
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(\Delta N5500), p(Z+\Delta C400), \theta\pi()$	29558.77	0	0.43	13
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta N5500), \varepsilon(\Delta N5500), p(Z+\Delta C400), \theta\pi()$	29559.23	0.46	0.34	14
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta N5500), \varepsilon(\Delta S5500), p(Z+\Delta C400), \theta\pi()$	29562.37	3.6	0.07	14
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(), p(Z+\Delta C400), \theta\pi()$	29565.05	6.28	0.02	12
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta D5500), \varepsilon(\Delta S5500), p(Z+\Delta C400), \theta\pi()$	29565.29	6.52	0.02	14
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(\Delta S5500), p(Z+\Delta C400), \theta\pi()$	29565.34	6.57	0.02	13
$\Psi(\Delta C*400), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(), p(Z+\Delta C400), \theta\pi()$	29565.56	6.79	0.01	13
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta D5500), \varepsilon(), p(Z+\Delta C400), \theta\pi()$	29565.6	6.83	0.01	13
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(\Delta S400), p(Z+\Delta C400), \theta\pi()$	29565.98	7.21	0.01	13
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(\Delta S1200), p(Z+\Delta C400), \theta\pi()$	29566.29	7.52	0.01	13
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta D1200), \varepsilon(), p(Z+\Delta C400), \theta\pi()$	29566.75	7.98	0.01	13
$\Psi(\Delta C400), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(), p(Z+\Delta C400), \theta\pi()$	29566.8	8.03	0.01	13
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Z+\Delta C400), \theta\pi()$	29566.91	8.14	0.01	13
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta D400), \varepsilon(), p(Z+\Delta C400), \theta\pi()$	29567.04	8.27	0.01	13
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(\Delta N*5500), p(Z+\Delta C400), \theta\pi()$	29567.05	8.28	0.01	13
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta N1200), \varepsilon(\Delta N1200), p(Z+\Delta C400), \theta\pi()$	29567.39	8.62	0.01	14
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z+\Delta N400), \varepsilon(\Delta N400), p(Z+\Delta C400), \theta\pi()$	29568.01	9.24	0	14
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(), p(Z), \theta\pi()$	29581.5	22.73	0	11
$\Psi(), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(), p(Z+\Delta C*400), \theta\pi()$	29583.48	24.71	0	12
$\Psi(Z), \theta(Z), \theta'(Z), \gamma(Z), \varepsilon(Z), p(Z), \theta\pi(Z)$	29586.61	27.84	0	14
$\Psi, \theta(), \theta'(), \gamma(), \varepsilon(), p(), \theta\pi()$	29702.83	144.06	0	7
$\Psi, \theta(), \theta'(), \gamma(), \varepsilon(), p(YR), \theta\pi()$	29708.58	149.81	0	19
$\Psi, \theta(), \theta'(), \gamma(t), \varepsilon(t), p(), \theta\pi()$	29720.69	161.92	0	29