RADAR ANALYSIS OF BIRD MIGRATION STOPOVER SITES IN THE SOUTHEASTERN U.S.

Final Report

March 2013

DAVID A. LA PUMA[1,2*], JEFFREY J. BULER[1]

[1] Aeroecology Program, Department of Entomology and Wildlife Ecology, University of Delaware, 531 S. College Ave., Newark, DE 19716.

[2] SILVIS Lab, 1630 Linden Drive, Department of Forestry and Wildlife Ecology, University of Wisconsin, Madison, 53706.

*dlapuma@wisc.edu

The work on which this report is based was performed in accordance with a cooperative agreement between the U.S. Fish and Wildlife Service and the University of Delaware.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Executive Summary

During migration birds require stopover habitat that provides energy resources and safety from predators. Because stopover use of land birds during migration can vary dramatically from day to day and locally in space, comprehensive and long-term monitoring of stopover use is necessary to identify areas that are consistently used by migrant birds in high densities. We analyzed two years of archived data from eight weather surveillance radars to produce maps of seasonal bird stopover density the South Atlantic Coastal Plain and Peninsular Florida. Using radar reflectivity as a measure of relative bird density, we identified important stopover areas and ranked them based on the magnitude (mean across two years) and daily variability in bird density (coefficient of variation of the mean). We used Boosted Regression Trees (BRT) to model landscape features associated with bird density, and predict bird density across the entire study region, including areas not observed by the radars. BRT models performed better in fall than spring (percent deviance explained: 62% vs. 35%) and identified mean canopy height, distance to coast, and mean normalized difference vegetation index (NDVI) as the most important predictors of bird density in spring, and mean canopy height, NDVI and elevation in the fall. These general relationships were consistent within the two sub-regions although importance value thresholds and ranking of several variables varied, such as relative elevation becoming the most important variable in predicting stopover habitat in Peninsular Florida. Our findings highlight the disparity in bird stopover density between the two sub-regions along the migratory route, as well as the spatial nonstationarity of relationships therein. By determining migration flight direction, we also identified areas where birds are initiating over-water flight during fall to wintering destinations throughout the Neotropics. Our findings represent an improved understanding of the spatiotemporal variation in stopover habitat use by migratory birds and their general migration routes in the southeastern U.S. Our explanatory models provide guidance for conservation of important stopover sites.

Introduction

Billions of landbirds migrate across North America twice each year, to and from wintering and breeding grounds. During migration birds require stopover habitat that provides both food resources and refuge from predators between migratory flights. While most conservation efforts for migratory landbirds in North America have focused on protecting or enhancing breeding habitat, several lines of evidence imply a much higher risk to survival during migration than in either the breeding or wintering periods (Sillett & Holmes 2002), which may also lead to carryover effects of the migration period on demographic rates on the breeding grounds (Moore et al. 2005; Norris & Marra 2007) and have an important role in limiting migratory bird populations (Sherry & Holmes 1995; Hutto 2000; Newton 2006).

In part, survival during migration is related to conditions birds encounter during stopovers (i.e., habitat availability and quality). Additionally, daily fluxes in migratory activity in relation to local weather and migrant species composition leads to local variation in stopover habitat use. Regardless of their ecological function, stopover sites that are consistently used by migrants in relatively high densities are important from a conservation perspective because they will harbor the most birds per unit area through the course of a migration season (sensu Mehlman et al. 2005). Thus, an understanding of which stopover areas and habitats are consistently used during migration is essential for developing habitat management and conservation strategies for migratory birds (Moore & Simons 1992; Hutto 2000; Ruth et al. 2005; Mehlman et al. 2005; Moore et al. 2005; Faaborg et al. 2010a; 2010b).

The national network of weather surveillance radars (model WSR-88D or NEXRAD) has been used to observe the spatial and temporal distribution of migrating landbirds, by measuring the density of birds in the radar beam shortly after they leave daytime stopover sites at the onset of well-synchronized nocturnal migratory flight (e.g., Diehl & Larkin 2002; Gauthreaux & Belser 2003; Buler & Diehl 2009; Bonter et al. 2009; Buler & Moore 2011). These data can be geo-referenced to map relative bird density on the ground across broad regions, summarizing data over the course of a migration season to identify sites that receive high or consistent use by birds during migratory stopovers. NEXRAD data are stored within a continuous archive going back more than a decade; thus annual variation in stopover habitat use and identification of areas that are used consistently through time can be assessed.

The southeastern U.S. (i.e., U.S. Fish and Wildlife Service Region 4) contains stopover sites for many long-distance migratory landbirds of eastern North America during their southbound migration in the fall, including millions of juvenile birds on their first migratory flights. The region also includes points of departure for migrants embarking on overwater flights en route to tropical wintering areas, and the first stopover sites for many returning northbound migrants during spring.

Our objective was to use data collected by eight coastal NEXRAD radars to map important stopover sites used by landbirds during fall and spring migration within two sub-regions of

Region 4: the South Atlantic Coastal Plain and Peninsular Florida. Additionally, we used these data to develop statistical models to predict potentially important stopover sites in areas not sampled by the radars and assess general migratory flight direction of birds. Data collected by some of these radars have been used previously to identify stopover sites in portions of the region (Gauthreaux & Belser 2003). However, the radars were upgraded in 2008, greatly increasing the spatial resolution of the data collected; this enhancement, coupled with recent methodological advances that reduce biases in radar measures (Buler & Diehl 2009), provided more precise and accurate discrimination than was previously possible of the sites and habitats from which migrants emerge. Our work complements similar work recently completed for USFWS Region 5 (Buler & Dawson 2012). Together, the two projects have mapped important stopover sites for southbound migrating landbirds throughout the Atlantic Coast Joint Venture and across four Landscape Conservation Cooperatives (North Atlantic, Appalachian, South Atlantic, Peninsular Florida), greatly broadening our understanding of the habitat use and spatiotemporal distribution patterns of migrating landbirds in the Atlantic Flyway.

Methods

Study Region

Our study region included the Coastal Plain of North Carolina, South Carolina, and Georgia, and most of Florida. This area lies within two Bird Conservation Regions (BCRs; http://www.nabci-us.org/map.html): the Southeastern Coastal Plain (BCR 27) and Peninsular Florida (BCR 31) (Figure 1).

BCR 27

Five of the radar stations we used fall within the South Atlantic Coastal Plain portion of BCR 27, which is under the purview of the South Atlantic Migratory Bird Initiative (SAMBI; see http://www.acjv.org/sambi.htm). From north to south these are Morehead City, NC (KMHX), Wilmington, NC (KLTX), Charleston, SC (KCLX), Jacksonville, FL (KJAX) and Tallahassee, FL (KTLH). This region includes extensive marsh complexes along the Atlantic coast, and large tracts of bottomland hardwood forests and forests dominated by southern pines.

This region provides critical stopover habitat for Neotropical migrants *en route* to and from their wintering areas. Species of conservation concern that regularly pass through this region during migration include the federally endangered Kirtland's Warbler (*Setophaga kirtlandii*), as well as Bicknell's Thrush (*Catharus bicknelli*), Wood Thrush (*Hylocichla mustelina*), Golden-winged Warbler (*Vermivora chrysoptera*), Blue-winged (*Vermivora cyanoptera*), Prothonotary Warbler (*Protonotaria citrea*), Swainson's Warbler (*Limnothlypis swainsonii*), Kentucky Warbler (*Geothlypis formosa*), Cerulean Warbler (*Setophaga cerulea*), Bay-breasted Warbler (*Setophaga castanea*), Prairie Warbler (*Setophaga discolor*), Canada Warbler (*Cardellina canadensis*), Henslow's Sparrow (*Ammodramus henslowii*), and Painted Bunting (*Passerina ciris*) (Watson et al. 2005).

BCR 31

Three of the radar stations we used fall within BCR31, Peninsular Florida. These include, from north to south, Melbourne, FL (KMLB), Tampa Bay, FL (KTBW), and Miami, FL (KAMX). This ecoregion varies from temperate pine and bottomland hardwood forests to the north, to subtropical wetlands and mixed hardwood forests to the south. This region serves as the wintering grounds and points of departure for many Neotropical migrants heading south in the fall. Additionally, the Florida coastline is the first landmass many birds encounter after hours or even days of migrating from the Yucatan Peninsula of Mexico or the various islands in the Caribbean during the spring. Many of the species mentioned in the previous section are also found in BCR 31 (http://www.nabci-us.org/bcr31.html).

Radar operations and data

The National Weather Service's network of NEXRAD stations includes over 150 installations across the United States that together comprises the largest terrestrial sensor network in the world. Data are collected every five or ten minutes, depending on the radar's mode of operation, in "volume scans" (Crum & Albertny 1993). Each volume scan is composed of a series of "sweeps". Each sweep is a complete rotation of the radar at a fixed elevation angle. The sweep at the lowest elevation (0.5° above horizon) is best suited for detecting birds during migratory exodus as it samples the atmospheric strata lowest to the ground.

The NEXRAD data products we used are Mean Reflectivity (hereafter "reflectivity") and Mean Radial Velocity. Reflectivity is a measure of returned electromagnetic energy per unit volume of space that is directly related to the density of birds in the atmosphere (Gauthreaux & Belser 1998). We used reflectivity to represent the relative density of birds occupying underlying stopover areas (Buler & Diehl 2009). Mean radial velocity is the average speed and direction of targets relative to the radar's physical location. Together with reflectivity, these data products provide measures of the relative density, heading, and speed of birds in the atmosphere. We used Level II data for analysis, which has sampling volume dimensions of 250 m in range by 0.5° in diameter (i.e., "super" resolution). We obtained all data through the online archive hosted by NOAA's National Climatic Data Center (NCDC).

Data screening and processing

We screened radar data from the period of peak landbird migration for two fall seasons (mid August through early November 2008 & 2009) and two spring seasons (April through May 2009 & 2010) to identify nights in which radar targets were dominated by migrating birds with no discernible contamination by precipitation, insects, or anomalous beam propagation following the methods of Buler et al. (2012).

We produced base maps for each NEXRAD station to georeference the radar data and extract landscape characteristics for our analyses. Each base map is a polar grid of polygons matching the spatial resolution of radar measures (0.5° in azimuth by 250 m in range) radiating out to a distance of 100 km. Each polygon represents the two-dimensional boundary of a sample volume, the elemental sampling unit of the radar. For each radar site, we produced a masking map of individual sample volumes where reflectivity measures were regularly influenced by persistent ground clutter contamination or partial radar beam blockage from human infrastructure or topography. Data from masked sample volumes were excluded from all analyses (see Buler et al. 2012 for masking map methods).

For each suitable sampling night, we temporally interpolated radar reflectivity data collected near the time of evening civil twilight (dusk) to when the sun is 5.5^o below horizon (i.e., shortly after the typical onset of nocturnal migration). This approach capitalizes on the fact that birds initiate nocturnal migratory flights en masse in an abrupt exodus closely synchronized to position of the sun (Akesson et al. 1996), minimizes the displacement of birds aloft from their ground sources, and allows for comparison of data among radars. We processed radar data using preexisting algorithms and software developed by the University of Delaware to reduce known measurement bias caused by the systematic change in how the vertical distribution of birds in the airspace is sampled as the beam spreads with range from the radar (Buler & Diehl 2009).

As the radar beam travels up and away from the radar antenna it differentially samples the distribution of birds in the airspace, eventually reaching a point where it samples such a small portion of the distribution that reflectivity measures become unreliable. Accordingly, we censored measures from sample volumes that observed ≤ 10% of bird distribution aloft or had a bias-adjustment factor < 0.05 (i.e., adjusted reflectivity is > 20 times raw reflectivity). The detection of birds varies among days due primarily to variability in the sampling heights of the beam and the vertical distribution of birds in the airspace at the time they are sampled. Therefore, we used the semiparametric robust linear regression on order statistics (ROS) to estimate summary statistics of our multiply-censored radar data (Lee & Helsel 2005). ROS is applicable to any dataset that has 0 to 80% of its values censored. However, we conservatively restricted analysis to sample volumes that had < 25% of their values across nights censored. We used the software package NADA (Lee & Helsel 2005) for the R environment for statistical computing (R Development Core Team 2003) to perform the ROS analyses. For each sampling day, we used the minimum observed reflectivity value among sample volumes at a given range to determine the range-specific censoring limit values for the ROS algorithm. We summarized reflectivity measures using ROS for each sample volume by pooling radar data across days and years. For each sample volume we estimated the geometric mean reflectivity as a relative measure of the mean daily stopover density of birds and the coefficient of variation of reflectivity as a measure of the daily variability in bird stopover density. We excluded the top 1% of reflectivity values since these likely included intermittent ground clutter contamination that return high values. This resulted in a quality-controlled dataset of relative bird stopover densities comparable throughout the radar domain.

Classifying bird stopover distributions

We characterized bird stopover areas within each radar-sampled area by the mean radar reflectivity (MN) and the coefficient of variation of radar reflectivity (CV) across all nights. We used five classes to rank sites based on the magnitude (MN) and daily variation (CV) in site use. These five classes are as follows: “Consistently high density of emerging migrants” (MN>85%; CV <25%), “Moderately variable high density of emerging migrants” (MN>85%; CV 25-75%), “Highly variable high density of emerging migrants” (MN>85%; CV > 75%), “Moderate density of emerging migrants” (MN 50-85%; All CV), and “Low density of emerging migrants” (MN < 50%; All CV). Stopover classifications of observed data are relative to each radar site since percentile rankings were computed on a radar-by-radar basis. We then classified stopover habitat across all radars analyzed (so classifications are relative to the entire region rather than to each radar).

Modeling bird stopover distributions

Creating our analysis surface

We created a grid of 1-km^2 polygons within the Partners In Flight boundaries for the SAMBI and BCR 31 regions. We selected those grid cells within the terrestrial landmass of the continental U.S and outlying barrier islands within a 20-km buffer to this selection. The final modeling surface grid contained 362,000 polygons. During spring, 64,000 polygons contained observed bird density data from seven radar stations. During fall, 86,000 polygons contained observed bird density data from eight radar stations.

Aggregating radar data to the 1-km resolution grid

Aggregating the radar data to 1-km resolution had several advantages. First of all, it reduced the dataset resulting in faster computing time. Since we used these data to model across the entire southeast region, this benefit is non-trivial. Secondly, by resampling reflectivity values to 1 km, we reduced some of the variance in the data, which resulted in a smoother and more interpretable pattern of bird density. Thirdly, and possibly most importantly, by resampling we reduced some of the variance associated with spatial displacement of birds from their source ground location. While the raw radar data is recorded on a 250 m x 0.5^o polar grid, at this resolution reflectivity values at any given point are likely to represent bird density within a variable distance around that point. By aggregating the data we minimized error associated with this displacement and therefore smooth out the relationship between the landscape and bird density. In order to aggregate the radar data while minimizing the loss of information, we took a two-step approach. First, we rasterized the vector radar data to a 20-m^2 resolution grid. This resolution retains the spatial pattern visible in the vector data. We then aggregated the 20-m resolution data to 1-km resolution grid cells using the mean of all 20-m cell values falling within each 1-km cell.

Predictor variables

We used 13 variables (Table 2) to build statistical models to predict important stopover sites in portions of the study region not sampled by the radars. We used 2006 National Land Cover

Dataset (NLCD) data (http://www.mrlc.gov/nlcd2006.php) to calculate percent cover within each 1-km grid cell of five landcover classes: Open Space (class 21), Developed (classes 22, 23, 24), Hardwood Forest (classes 41, 43, and 90), Grassland (class 71), Pasture/Cultivated (classes 81, 82). We used the Morphological Spatial Pattern Analysis (MSPA) software GUIDOS (v. 1.4; Vogt et al. 2006) to segment each of the first three landcover types (Open Space, Developed, and Hardwood Forest) into "core" or "edge" classes according to the number of adjacent pixels (30 m^2) of similar type. We used the 8-neighbor rule for determining foreground connectivity and three pixels for edge width (90 m). Foreground connectivity controls the cluster tolerance of adjacent pixels by requiring a shared border and corner for two pixels to be considered connected. The edge width parameter defines the width, or thickness, of the non-core classes in pixels. The MSPA analysis resulted in a raster grid with several classes of 'edges' and one class for 'core'. We reclassified all edge classes into a single 'edge' class for analysis. Thus we had eight landcover predictor variables for model analysis.

We calculated two measures of vegetative canopy height: mean and standard deviation of canopy height within each 1-km grid cell. These predictors provide information on vertical structure of forested areas that are not available using land cover information alone. We measured canopy height using 30-m resolution basal-area-weighted canopy height data from the National Biomass and Carbon Dataset (Kellndorfer et al. 2000).

We used the Normalized Difference Vegetation Index (NDVI) from the MODIS (Huete et al. 2002) satellite sensor product MYD13Q1 as a measure of vegetative productivity. This measure may help explain differential habitat use within a land cover type. For instance, birds may use certain areas of deciduous forest over others based on productivity of that area during the migration period. MODIS NDVI has aspatial resolution of 250-m and a temporal resolution of 16 days. We aggregated the NDVI data to our 1-km grid. We then used the 16-day-mean NDVI dataset that corresponded with each sampling night of radar data to produce a weighted mean NDVI value across nights for fall and spring separately.

Localized studies demonstrate dramatic differences in the use of coastal habitats for stopover depending on location and time of year. Buler and Moore (2011) demonstrated the influence of proximity to the coast in modifying the relationship between bird density and the amount hardwood forest cover. Therefore we considered distance to coast to be a potentially important variable and possibly one that would interact with other variables of interest. Moreover, since we conducted this study across two seasons, we expected the importance of distance to coast to vary whether birds were arriving at or departing from coastal areas from over land or over water. We calculated distance to coast for each 1-km grid cell to the nearest 1 km using the Euclidean Distance tool in ArcGIS 10.1 (Spatial Analyst Toolbox).

Because elevation plays a significant role in shaping vegetative communities via local and regional climate (precipitation and temperature) and processing of radar data is sensitive to elevation, we expected it to influence stopover habitat selection and bias adjustments of radar measures. We used 30-m National Elevation Dataset (NED) data (www.ned.usgs.gov), and aggregated it to the 1-km grid. Because maximum elevation within the study region greatly exceeds the maximum value measured within radar-sampled areas, we created a new variable called 'relative elevation' instead of using absolute elevation. To do so we used a 3x3 pixel moving window to calculate the relative elevation of each pixel to the surrounding landscape by determining the minimum elevation within the 3x3 window, and subtracting that value from the target pixel elevation. Therefore, in places with high absolute elevation (such as the foothills of the Appalachian Mountains), final values would be scaled down to represent the relative difference in elevation to adjacent pixels.

Boosted Regression Tree Models

Boosted regression trees (BRT) combine statistical and machine learning methods into a single model framework. Regression trees have traditionally been part of a class of statistics called CART models (or classification and regression trees) reflecting the type of response variable being explored (categorical for classification trees, and continuous for regression trees) (Franklin 2010). Typically these regression trees, though, fit only a single global model to the data resulting in a dichotomous tree structure, which works well for identifying breakpoints where the relationship between the response variable and explanatory variable diverge. The results of a regression tree provide the analyst with a "recipe" for the response variable (if variable x is less than value x, then expect response y, otherwise expect response z, etc.). However, standard regression trees do not handle complex relationships well (or at least become very difficult to interpret), and because they settle on a single solution they tend to perform poorly in predicting the response variable to new data (low predictive power). Boosting, or the machine learning method within BRT models, is an iterative process of building new trees at each new step in the tree model. Each new tree is created to fit the unexplained variation at that point (the residual deviance). The final BRT model, then, is a linear combination of many trees. BRT models have an advantage over general linear models in that they can incorporate more complex response functions (i.e., threshold response) and do not rely on data conforming to specific distributions. Covariates in BRT models generally did not exhibit strong multicollinearity (Appendix A).

We parameterized our BRT models according to methods described in Elith and Leathwick (2008). Parameters that require selection include Tree Complexity (TC), Learning Rate (LR) and Bag Fraction (BF). For all of our models we used a TC of 5 and BF of 0.75 (withhold 25% of dataset for cross validation), and adjusted the LR to reach a minimum number of trees > 1000 in the final model. Because of presumed inherent ecological differences between the two BCRs within our study region (BCRs 27 and 31), we chose to produce six total models; these included for each season a model for the entire radar dataset (pooled across all seven or eight radar stations, depending on season) and then one model for radar data within each BCR. Models were run using the cross validation method provided by Elith and Leathwick (2008) using code that builds upon (and therefore includes) the R package GBM (Ridgeway 2013). Models were evaluated using percent deviance explained according to the following equation:

Equation 1

$$\% \text{ Deviance Explained} = \frac{NullDev - ResDev}{NullDev} * 100,$$

where NullDev is the deviance of the evaluation data and ResDev is the residual deviance of the evaluation data in relation to probabilities predicted by the model. Percent deviance explained is a measure of overall goodness-of-fit of the model to actual observations.

BRTs have been shown to be powerful tools for prediction, and therefore are becoming more widely used in species distribution modeling (Leathwick et al. 2006; Elith & Leathwick 2008; Martínez-Rincón et al. 2012). Since one of our goals was to predict areas of high bird density outside of the areas sampled by the radars, we used final BRT models for each region (pooled vs. BCR) and season (fall and spring) to create predictive maps of bird density across the entire South Atlantic Coastal Plain. We used the code provided by Elith and Leathwick (2008) to predict mean bird density (MN) and coefficient of variation (CV) to the 362,000 km^2 modeling grid. We then used the same five classes of stopover site use applied to the observed radar to classify our predicted maps. The result is a seamless model output of stopover habitat classified by magnitude (MN) and variation (CV) of use by migrants.

Data Sampling

Because radar provides a continuous surface of data across the radar viewshed, neighboring pulse volumes are spatially autocorrelated. Buler et al.(2012) found spatial autocorrelation in radar observations of bird distributions extended out to about four kilometers. Therefore we derived our model dataset by subsampling the radar data in such a way to reduce bias from spatial autocorrelation. We used a subset of 1 km grid cells that were separated by at least five kilometers. The number of sampled cells for each subset varied depending on whether we were modeling the entire southeastern Coastal Plain or the individual BCRs (Table 1). We used the random point generator in ArcGIS 10.1 to generate our subsample set and repeated the procedure three times for each sample: the entire region, each of the two BCRs separately, and for each season (for a total of 18 sample draws). We report our results for only one of the three sample sets for each of the model outputs (3 spatial extents x 2 seasons = 6 final model outputs) (Figure 2).

Identifying flight direction

We used radar radial velocity data from the 3.5° tilt angle sweep collected approximately 3 hours after sunset (i.e., peak of nocturnal migration) to determine the mean direction of movement of targets relative to the ground each night at each radar using methods outlined by Browning and Wexler (1968). This higher tilt angle sweep provides greater precision in altitude-specific measures of target direction than lower tilt angle sweeps, and is less affected by beam refraction and blockage. We determined the mean direction of flight for each night by weighting flight directions calculated at multiple altitudes (~20 m height intervals) according to the concurrent altitudinal distribution of targets derived through the bias adjustment algorithm of Buler and

Diehl (2009). We used the program Oriana (Kovach Computing Service) to calculate mean flight direction across nights for each season at each radar station.

Results

Mapping bird stopover densities

Qualitatively, classified observed reflectivity data from individual radars revealed that important stopover areas were associated with coastal forests, forested riparian floodplains, and, especially within Peninsular South Florida, forests in a matrix of wet prairie and marsh (Fig. 3; see Appendix B for detailed classified stopover maps for each radar station).

The results of our BRT models identified the most important predictor variables for both mean and coefficient of variation of bird density. Model performance, evaluated by the percent deviance explained, was higher when all data were pooled than when data were separated by BCR (Table 3). Because we were interested in identifying important stopover areas within each subregion, we still considered the BCR analysis to be important and therefore report our results at both spatial scales.

Bird densities were consistently four times higher across the SAMBI region versus Peninsular Florida (SAMBI mean (fall) = 20.56±11.93SD) vs. BCR31 mean (fall) = 5.18±5.58SD); SAMBI mean (spring) = 7.85±9.63SD) vs. BCR31 mean (spring) =2.0±2.27SD). Thus, when we modeled bird density using the entire dataset (pooled across all radars) our predictions for both spring and fall resulted in few regionally classified areas of high bird density in the south (Figs 4a & 5a). However, the predictive map for Peninsular Florida indicates classified areas of high bird density at the BCR scale (Figs 4b & 5b). Classified stopover areas for SAMBI differed little between regional and BCR scale classifications.

Spring

Regional Scale

The most important predictors of bird density during the spring were Mean NDVI (22% of total deviance explained), Mean Canopy Height (21%) and Distance to Coast (19%), followed by Proportion of Hardwood Forest Core (8%) (Fig. 6). Partial dependency plots indicate that birds density was highest in areas of high vegetative productivity (Mean NDVI >0.6), increasing canopy height (Mean Canopy Height > 10m), between 5 and 15 km from the coast, and with relatively lower proportions of hardwood forest core (Appendix C). Also, low proportions of Developed Open Space Edge were associated with higher bird densities, which taken together with hardwood forest core suggests birds packing into forest fragments within urban landscapes. While considerably less important, increased Canopy Height Heterogeneity (5%) was associated with greater bird density.

BCR Scale

For BCR 27, the most important predictors of bird density in spring were Distance to Coast (23%), Mean NDVI (22%), and Mean Canopy Height (11%), followed by smaller contributions from Proportion of Hardwood Forest Edge (7%), Relative Elevation (7%), Proportion of Developed Open Space Edge (7%), Proportion of Hardwood Forest Core (6%) and proportion of Developed Low-Med-High Edge (5%). These BRT results indicate bird density was highest within 30 km of the coast, and decreased sharply thereafter with increased distance. Bird density was also positively related to mean NDVI > 0.5, and with mean canopy height above 15 m. High bird density was also associated with small amounts of Hardwood Forest Edge and core, as well as small amounts of Developed Open Space Edge and Developed Low-Med-High Edge.

For BCR 31, Distance to Coast (39%) was the paramount variable in explaining bird density, followed by Mean NDVI (13%), Relative Elevation (10%) Canopy Height Heterogeneity (7%), Proportion of Cultivated Lands (6%), Proportion of Developed Open Space Edge (6%), and Proportion of Hardwood Forest Core (5%). Across peninsular Florida bird density was highest within 10 km of the coast and decreased precipitously at farther distances. While Mean NDVI was the second highest contributor to the overall model, the relationship seen in the partial dependency plot indicated a threshold effect where densities sharply increased with values > 0.4 and remained constant at higher values. Bird density increased with increases in relative elevation up to about 8 m (which is much of the high ground in South Florida), and only increased slightly with increases in Canopy Height Heterogeneity. High bird densities are characterized by small amounts of Pasture/Cultivated lands, Developed Open Space Edge, and Hardwood Forest Core, again suggesting that birds are packing into small woodland patches within an agricultural and suburban/urban matrix.

Fall

Regional Scale

During fall, the most important predictors of bird density were Mean Canopy Height (35%), Relative Elevation (18%), Mean NDVI (14%) and Canopy Height Heterogeneity (10%), followed by Distance to Coast (8%) (Fig. 7). Partial dependency plots indicate that bird density increased linearly with mean canopy height > 5 m, areas higher in elevation relative to the surrounding landscape held more birds, and sites with moderate to high productivity were favored (one peak at NDVI = 0.3, and linear increase after 0.4). High levels of canopy heterogeneity were also associated with higher bird density. The relationship between bird density and distance to coast was rather flat, but did show a peak near the coast and a decline to about 25 km inland. Specific landcover classes were less important in fall than in spring, at least at this scale.

BCR Scale

For BCR 27, the Southeastern Coastal Plain, the most important predictors of bird density were Mean Canopy Height (20%), Canopy Height Heterogeneity (19%), Distance to Coast (11%), Mean NDVI (11%), and Relative Elevation (11%), followed by smaller contributions from Proportion Grassland (6%), and Proportion Pasture/Cultivated (5%). The main predictor of increased bird density was a tall and complex forest structure, with larger trees (> 15m) and increased heterogeneity (>50) associated with higher bird density in the region. While distance to coast was important, the partial dependency plots indicate a bimodal process whereby bird density was highest near shore and declined inland to 30 km, and then increased again around 50 km and remained elevated to around 80 km, roughly the limit of the dataset. Higher bird densities were also associated with higher primary productivity (>0.7) and greater relative elevation (>5m).

For BCR 31, peninsular Florida, bird density was best predicted by Relative Elevation (28%), Mean NDVI (23.2%) and Distance to Coast (19.3%), followed by Mean Canopy Height (8%). Other landscape metrics provided little predictive power (all < 5% each) with very flat fitted functions. Bird stopover density increased with increased elevation relative to the surrounding landscape, moderate to high primary productivity (>0.6), and closer proximity to the coast (highest within 5 km). Again, bird density showed a positive relationship with Mean Canopy Height although the strength of this relationship after considering the previous three predictors was relatively weak.

Migratory flight direction of birds along the southeastern coast

In general we expected birds to migrate north in the spring and south in the fall, while we also expected some offshore movement of birds throughout our survey area. Results from our directional analysis indicated North/Northwest movement in spring across Peninsular Florida as birds arrive from the Caribbean, Central and South America, while movement across the Southeastern Coastal Plain varied between Northeast (LTX) and Northwest (TLH, JAX, and MHX) (Figure 3). In the fall, movement through the Carolinas was strongly southwesterly with birds appearing to follow the coast toward Florida. Migration across Northern and Central Florida suggests most birds headed southwest toward the Gulf Coast, and therefore likely bypass the southern half of Peninsular Florida entirely. Of those birds that stopped in southern Florida, their flight direction suggests they departed from the end of the peninsula presumably heading to the Caribbean and South America in fall. Some evidence for Trans-Atlantic migration can be seen from both BCR 27 (LTX, CLX, JAX) and BCR 31 (MLB) where on several nights the mean flight direction was towards open water. Since part of the screening process for usable data involves dropping nights with no clear directional signal, it’s quite possible that there are nights when birds are simultaneously moving offshore and over land, which our screening algorithm would not select for the analysis. We address this further in the Discussion.

Discussion

While radar observations indicate broad front bird migration across the entire Southeastern US region, radar observations at the onset of nocturnal migration clearly indicate preferential use of certain areas by birds during stopover. Spatial distribution of resources may vary from season to season as annual weather phenomenon affect the timing and magnitude of biological processes such as insect emergence, bud burst, and senescence (Hutto 1985; Johnson & Sherry 2001; Ellwood et al. 2013). In addition, resource requirements shift between seasons according to life history traits such as the protein-heavy requirements of reproduction versus the carbohydrate-heavy migratory period. By using mean and variability of bird density throughout the migration season, we were able to map areas of the greatest importance for landbird stopover during spring and fall in the Southeastern Coastal Plain and Peninsular Florida. Those areas characterized by consistently-high bird density may represent the greatest return on conservation dollars spent regardless of the quality of resources or function of different areas for migrants (Mehlman et al. 2005). Even without understanding the underlying mechanisms driving stopover habitat use, the comprehensive observation of bird distributions by radar, provides for visual interpretation of the gross patterns of stopover habitat use by migrant landbirds. In general, we found that the most consistent and highest bird stopover densities occurred primarily in areas in close proximity to the shores of major water bodies and within coastal forests and forested riparian floodplains.

We identified several covariates of particular importance for predicting bird density across the Southeast Coastal Plain and Peninsular Florida. Comparisons to previous studies are made difficult by the lack of published research within our area of study. Our finding that bird density is highest near, but not on, the coast and increases with increasing canopy height and heterogeneity supports earlier findings along the Gulf of Mexico where bird density increased with proximity to the coast and within bottomland hardwood forests (Buler & Moore 2011). Across seasons the major contributing variables remained relatively consistent, although their relative importance shifted considerably at the BCR scale.

The BRT models also identified primary productivity (NDVI) as a useful covariate in identifying areas of importance to migrant landbirds. Other research has found some positive relationships between bird species richness and bird density and NDVI (Mcfarland et al. 2012), while others have shown NDVI to be helpful in predictive modeling of bird habitat only when combined with other landscape variables (Osborne et al. 2001). NDVI shows up in the top predictors in all of our models yet never contributes more than 24% relative to the other variables in the model.

In general, then, birds appear to be choosing habitat that is structurally diverse with taller trees, higher primary productivity, within 30 km of the coast, and elevated relative to its surroundings. Areas that appear to fit this description are forested wetlands in riparian corridors and coastal forests and forest fragments.

Despite running our BRT models at two geographic extents we did not see an improvement in percent deviance explained, which suggests several possible things. First, our covariates may demonstrate spatial nonstationarity at a smaller spatial extent than either of our analyses. Second, we may be missing important explanatory variables in our models. Third, radar data is inherently noisy with regards to species composition and by extension habitat preference. This is because the radar collectively observes all individuals from a diverse array of bird species and other animals (bats and insects) that are in the airspace. By sampling within the defined temporal window we attempt to maximize the number of terrestrial songbirds contributing to the radar reflectivity but we know from studies of nocturnal flight calls and other nocturnal aerial counts that migrants from many functional guilds are represented in these seasonal flights (Bullis & Lincoln 1952; Bullis 1954; Gauthreaux 1991; Bruderer 1994; Farnsworth et al. 2004). Therefore a modest portion of this unexplained deviance may simply be due to the breadth of diversity subsumed in each radar pulse volume on a given night. However, even after considering these possible sources of error, our models produce levels of explained deviance consistent with other Boosted Regression Tree analyses (Martínez-Rincón et al. 2012), and the patterns that emerge when we use these models to predict onto areas of unknown bird density appear to be intuitive to our trained eyes. Strong general patters such as proximity to the coast and positive association with tall, structurally diverse and productive habitats are both intuitive and supported by a growing body of stopover habitat literature (Buler et al. 2007; Ktitorov et al. 2007; Bonter et al. 2009; Buler & Moore 2011)

Our predictive maps highlight the disparity of birds occurring in the southern extent of our study area. Regionally, the movement of birds is primarily through the Carolinas and into the Panhandle of Florida, with relatively fewer birds either moving into Peninsular Florida in the fall or entering the region via Peninsular Florida in the spring. Lack of forested habitat may be the cause for some of this movement, which also may explain the high explanatory power of both distance to coast and relative elevation in predicting bird densities in Peninsular Florida. Since most of Peninsular Florida lies near sea level, those areas with even moderate increases in elevation relative to their surroundings are therefore the locations of great vegetative change. This is apparent in the classified stopover habitat around KAMX where high bird densities are consistently recorded in the Long Pine Key area of Everglades National Park. This location, an overstory of Florida Slash Pine (*Pinus elliottii var. densa*) with an understory of Saw Palmetto and mixed emergent subtropical hardwoods and herbaceous plants, represents the only available forested habitat in a matrix of short-hydroperiod marsh. Clearly the latter is less desirable to typically forest-dwelling bird species.

By identifying the mean flight direction of birds initiating migration, we have identified those regions where over-water flight is most commonly occurring. While the mean flight direction at each radar station supports the notion that birds are moving parallel to the coastline en route to southerly wintering grounds, several observations of over-water flight were evident in coastal North and South Carolina. For instance, on 6 of 39 nights the mean direction of migration over Wilmington, NC was at a heading taking birds directly over water. For those radar stations along the south Atlantic coast, between 8 and 15% of the nights sampled showed mean trajectories where birds were heading out over water. Considering that our sample represents only those nights where a mean trajectory could be determined with a strong modeled fit (i.e., $r^2 \geq 0.5$), we consider our results to be a conservative estimate of over-water migration, with nights when equal proportions of birds were heading over land and over water removed from the analysis. For those radars along the Gulf Coast and for the Miami radar, flight direction in fall supports the notion of Trans-Gulf Migration towards the eastern Yucatan Peninsula of Mexico and over the Florida Straits to Cuba. The Tallahassee, FL station (KTLH) represents the only Gulf Coast station in our analysis where birds may continue to follow the coastline to wintering grounds, and while the mean vector is Trans-Gulf, 26% of the time birds were moving west over land, presumably circumnavigating the Gulf of Mexico or moving to more westward crossing points. Of some surprise is the lack of apparent migration into the western Caribbean from south Florida. We expected to see more of this since many of the birds seen in South Florida during the spring are of species that winter in the Caribbean Basin. While on 13% of the nights in fall birds appeared to be migrating over the Atlantic from Melbourne, FL, in only one case (8%) was the mean vector from birds over Miami heading southeast into the Caribbean. In the majority of cases birds over Miami were heading south or southwest toward Cuba.

In the spring we saw strong northwest movement across Florida with birds heading from the east coast to the Gulf coast en route to points north. This is interesting because it suggests birds are following the landmass rather than simply heading north to their presumed destination. Data from around the Tampa radar (KTBW) suggest that birds are actually making over-water crossing again toward the Florida Panhandle, rather than opting to stay inland after arriving from longer over-water crossings in the American Tropics and Caribbean. Along the Carolina coasts the flight patterns are more uncertain since we only have a few data points for Charleston, SC and Morehead City, NC. Data from around the Wilmington, NC radar provides the most robust estimate of mean direction and shows birds heading parallel to the coastline toward the Mid-Atlantic. While our directional analysis does provide some insight into the locations of staging areas for overwater migration, care must be exercised when interpreting these results for the following reason. Since we only used nights when a strong mean direction was apparent ($r^2 > 0.5$) we may have excluded nights where low r^2 values were driven by birds moving over both land and water simultaneously. Presumably, then, our analysis represents a conservative estimate of those nights where birds are initiating or ending overwater flights and further analysis should consider those nights when the relationship may be bi-modal.

Our data supports the notion that many birds move through the Southeastern U.S. to both wintering grounds in the region and en route to the American Tropics and Caribbean. That birds appear to be avoiding Peninsular Florida during both spring and fall migration is something that has been suggested anecdotally (Michelle Davis, pers. comm.) but empirical evidence is rare or nonexistent. One recent study using individually tracked Wood Thrush did show multiple instances of individuals bypassing Peninsular Florida via the Florida Panhandle and the Carolinas, as well as birds launching off for trans-Atlantic flights from the Carolina coasts

(Stanley et al. 2012). As more individual tracking studies of various species are carried out we may begin to see more examples to help explain the consistent differences in bird density we've observed in our radar data. We suggest several plausible mechanistic reasons why birds might choose to avoid Peninsular Florida. First we believe our sampling is biased towards forest-dwelling birds. This is supported by both the habitat affinities derived from our predictive models, as well as the fact that we are sampling nocturnal migrants during the period of migration when forest dwelling migrants are the predominant guild. Compared to the Southeast Coastal Plain, Peninsular Florida contains much less forested habitat and much more wetland. In South Florida, forests generally are restricted to small patches of emergent woody islands in a matrix of wetlands. The availability, then, of suitable forest habitat to support large numbers of migrants is probably much less than it is for birds making landfall on (or departing from) the Florida Panhandle or the coastal Carolinas.

While we are confident in the patterns elucidated by the radar data, we must acknowledge some possible caveats. All WSR-88D stations are considered to be calibrated and comparable across space. While this may hold true for the meteorological data for which these instruments are originally intended, there may exist some sampling bias or differential calibration of the radars which may cause one station to run "hot" or produce higher values than another radar sampling the same data. We have no way to account for this possibility in our analysis, but we assume that the general consistency observed across radars indicates that these effects are minimal and our signal is truly biological.

Acknowledgements

We thank Anna Pidgeon and Volker Radeloff and the SILVIS lab for housing David La Puma during this research and providing work resources and regular feedback towards completion of this project. We thank Jessica Gorzo for compiling NDVI data, Dan Greene and Jill Gautreaux for assistance with radar data screening, and Jaclyn Smolinsky for assistance with radar data processing and analysis. Deanna Dawson assisted with radar data screening and provided helpful discussions about study design and analysis. Partial funding was supported by a grant/cooperative agreement from the U.S. Department of the Interior, Fish and Wildlife Service and administered by Tim Jones of the Atlantic Coast Joint Venture. Use of trade, product, or firm names does not imply endorsement by the U.S. Government.

Literature Cited

Akesson, S., T. Alerstam, And A. Hedenström. 1996. Flight Initiation Of Nocturnal Passerine Migrants In Relation To Celestial Orientation Conditions At Twilight. Journal Of Avian Biology 27:95–102.

Bonter, D. N., S. A. Gauthreaux Jr, And T. M. Donovan. 2009. Characteristics Of Important Stopover Locations For Migrating Birds: Remote Sensing With Radar In The Great Lakes Basin. Conservation Biology 23:440–448.

Browning, K. A., And R. Wexler. 1968. The Determination Of Kinematic Properties Of A Wind Field Using Doppler Radar. J. Appl. Meteor 7:105–113.

Bruderer, B. 1994. Nocturnal Bird Migration In The Negev (Israel) - A Tracking Radar Study. Ostrich 65:204–212.

Buler, J. J., And D. K. Dawson. 2012. Radar Analysis Of Fall Bird Migration Stopover Sites In The Northeastern U.S. ftp://ftpext.usgs.gov/pub/er/md/laurel/Dawson/R5FallStopover_FinalReport/

Buler, J. J., And F. R. Moore. 2011. Migrant–Habitat Relationships During Stopover Along An Ecological Barrier: Extrinsic Constraints And Conservation Implications. Journal Of Ornithology 152:101–112.

Buler, J. J., And R. H. Diehl. 2009. Quantifying Bird Density During Migratory Stopover Using Weather Surveillance Radar. IEEE Transactions On Geoscience And Remote Sensing 47:2741-2751.

Buler, J. J., F. R. Moore, And S. Woltmann. 2007. A Multi-Scale Examination Of Stopover Habitat Use By Birds. Ecology 88:1789–1802.

Buler, J. J., L. A. Randall, J. P. Fleskes, W. C. Barrow, T. Bogart, And D. Kluver. 2012. Mapping Wintering Waterfowl Distributions Using Weather Surveillance Radar. Plos ONE 7:E41571.

Bullis, H. R., Jr. 1954. Trans-Gulf Migration, Spring 1952. The Auk 71:298–305.

Bullis, H. R., Jr., And F. C. Lincoln. 1952. A Trans-Gulf Migration. The Auk 69:34–39.

Crum, T. D., And R. L. Albertny. 1993. The WSR-88D And The WSR-88D Operational Support Facility. Pages 1669–1687. Bulletin Of The American Meteorological Society 74.

Diehl, R.H., And R.P. Larkin. 2005. Introduction To The WSR-88D (NEXRAD) For Ornithological Research. Pages 876–888. In: Ralph, C.J., Rich, T.D. Editors. Bird Conservation Implementation And Integration In The Americas: Proceedings Of The Third International Partners In Flight Conference. USDA Forest Service, Gen. Tech. Rep. PSW-GTR-191.

Elith, J., J. R. Leathwick, And T. Hastie. 2008. A Working Guide To Boosted Regression Trees. Journal Of Animal Ecology 77:802–813.

Ellwood, E. R., S. A. Temple, R. B. Primack, And N. L. Bradley. 2013. Record-Breaking Early Flowering In The Eastern United States. Plos One 8:1-9.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux Jr, P. Heglund, K. A. Hobson, A. E. Jahn, And D. H. Johnson. 2010a. Conserving Migratory Land Birds In The New World: Do We Know Enough? Ecological Applications 20:398–418.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux Jr, P.

Heglund, K. A. Hobson, A. E. Jahn, And D. H. Johnson. 2010b. Recent Advances In Understanding Migration Systems Of New World Land Birds. Ecological Monographs 80:3–48.

Farnsworth, A., S. A. Gauthreaux Jr, And D. V. Blaricom. 2004. A Comparison Of Nocturnal Call Counts Of Migrating Birds And Reflectivity Measurements On Doppler Radar. Journal Of Avian Biology 35:365–369.

Franklin, J. 2010. Mapping Species Distributions: Spatial Inference And Prediction. Cambridge University Press.

Gauthreaux, S. A., Jr. 1991. The Flight Behavior Of Migrating Birds In Changing Wind Fields: Radar And Visual Analyses. American Zoologist 31:187–204.

Gauthreaux, S. A., Jr, And C. G. Belser. 1998. Displays Of Bird Movements On The WSR-88D: Patterns And Quantification. Weather And Forecasting 13:453–464.

Gauthreaux, S. A., Jr, And C. G. Belser. 2003. Radar Ornithology And Biological Conservation. The Auk 120:266–277.

Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, And L. G. Ferreira. 2002. Overview Of The Radiometric And Biophysical Performance Of The MODIS Vegetation Indices. Remote Sensing Of Environment 83:195–213.

Hutto, R. L. 1985. Seasonal-Changes In The Habitat Distribution Of Transient Insectivorous Birds In Southeastern Arizona - Competition Mediated. The Auk 102:120–132.

Hutto, R. L. 2000. On The Importance Of En Route Periods To The Conservation Of Migratory Landbirds. Studies In Avian Biology 20:109-114.

Johnson, M. D., And T. W. Sherry. 2001. Effects Of Food Availability On The Distribution Of Migratory Warblers Among Habitats In Jamaica. Journal Of Animal Ecology 70:546–560.

Kellndorfer, J., W. Walker, K. Kirsch, G. Fiske, J. Bishop, L. Lapoint, M. Hoppus, And J. Westfall. 2000, March 7. NACP Aboveground Biomass And Carbon Baseline Data (NBCD 2000). ORNL DAAC, Oak Ridge, Tennessee, USA. Retrieved From Http://Daac.Ornl.Gov.

Ktitorov, P., F. Bairlein, And M. Dubinin. 2007. The Importance Of Landscape Context For Songbirds On Migration: Body Mass Gain Is Related To Habitat Cover. Landscape Ecology 23:169–179.

Leathwick, J. R., J. Elith, And T. Hastie. 2006. Comparative Performance Of Generalized Additive Models And Multivariate Adaptive Regression Splines For Statistical Modelling Of Species Distributions. Ecological Modelling 199:188-196.

Lee, L., And D. Helsel. 2005. Statistical Analysis Of Water-Quality Data Containing Multiple Detection Limits: S-Language Software For Regression On Order Statistics. Computers & Geosciences 31:1241–1248.

Martínez-Rincón, R. O., S. Ortega-García, And J. G. Vaca-Rodríguez. 2012. Comparative Performance Of Generalized Additive Models And Boosted Regression Trees For Statistical Modeling Of Incidental Catch Of Wahoo (*Acanthocybium Solandri*) In The Mexican Tuna Purse-Seine Fishery. Ecological Modelling 233:20–25.

Mcfarland, T. M., C. Van Riper, And G. E. Johnson. 2012. Evaluation Of NDVI To Assess Avian Abundance And Richness Along The Upper San Pedro River. Journal Of Arid Environments 77:45-53.

Mehlman, D. W., S. E. Mabey, D. N. Ewert, C. Duncan, B. Abel, D. Cimprich, R. D. Sutter, M. Woodrey, And K. G. Smith. 2005. Conserving Stopover Sites For Forest-Dwelling Migratory Landbirds. The Auk 122:1281–1290.

Moore, F. R., And T. R. Simons. 1992. Habitat Suitability And Stopover Ecology Of Neotropical Landbird Migrants. Pages 345–355 In Hagan, J.M. III., Johnston, D.W., Editors. Ecology And Conservation Of Neotropical Migrant Landbirds. Smithsonian Institution Press, Washington D.C.

Moore, F., R. Smith, And R. Sandberg. 2005. Stopover Ecology Of Intercontinental Migrants: En Route Problems And Consequences For Reproductive Performance. Pages 251–262 In R. Greenberg And P. Marra, Editors. Birds Of Two Worlds: The Ecology And Evolution Of Migration. The Johns Hopkins University Press.

Newton, I. 2006. Can Conditions Experienced During Migration Limit The Population Levels Of Birds? Journal Of Ornithology 147:146–166.

Norris, D. R., And P. P. Marra. 2007. Seasonal Interactions, Habitat Quality, And Population Dynamics In Migratory Birds. Condor 109:535–547.

Osborne, P. E., J. C. Alonso, And R. G. Bryant. 2001. Modelling Landscape-Scale Habitat Use Using GIS And Remote Sensing: A Case Study With Great Bustards. Journal Of Applied Ecology 38:458–471.

Ridgeway, G. 2013. Gbm: Generalized Boosted Regression Models. R Package Version 2.0-8. Retrieved From Http://CRAN.R-Project.Org/Package=Gbm.

Ruth, J.M., W.C. Barrow, R.S. Sojda, D.K. Dawson, R.H. Diehl, A. Manville, M.T. Green, D.J. Kreuper, And S. Johnston. 2005. Advancing Migratory Bird Conservation And Management By Using Radar: An Interagency Collaboration: U.S. Geological Survey Open-File Report 2005-1173. 12 p.

Sherry, T. W., And R. T. Holmes. 1995. Summer Versus Winter Limitation Of Populations: What Are The Issues And What Is The Evidence. In T. E. Martin And D. M. Finch, Editors. Ecology And Management Of Neotropical Migratory Birds: A Synthesis And Review Of Critical Issues. Oxford Unversity Press.

Sillett, T. S., And R. T. Holmes. 2002. Variation In Survivorship Of A Migratory Songbird Throughout Its Annual Cycle. Journal Of Animal Ecology 71:296–308.

Stanley, C. Q., M. Macpherson, K. C. Fraser, E. A. Mckinnon, And B. J. M. Stutchbury. 2012. Repeat Tracking Of Individual Songbirds Reveals Consistent Migration Timing But Flexibility In Route. Plos ONE 7:E40688.

Vogt, P., K. H. Riitters, C. Estreguil, J. Kozak, T. G. Wade, And J. D. Wickham. 2006. Mapping Spatial Patterns With Morphological Image Processing. Landscape Ecology 22:171–177.

Watson, C., C. Hayes, J. Mccauley, And A. Milliken. 2005. The South Atlantic Migratory Bird Initiative–An Integrated Approach To Conservation Of “All Birds Across All Habitats.” In C. J. Ralph And T. D. Rich, Editors. Bird Conservation Implementation And Integration In The Americas: Proceedings Of The Third International Partners In Flight Conference 2002. Alisomar, CA.

Table 1. Sample size for Boosted Regression Tree analysis. Values represent the number of $1km^2$ cells separated by 5 km used to test models.

Area of Analysis	Fall	Spring
Regional	1271	1178
BCR 27	815	617
BCR31	456	561

Table 2. List of predictor variables used in Boosted Regression Tree models. Mean and range shown for entire regional grid (n=362,000).

Variable name	Description	Mean value (range)
Hardwood Forest Edge	Proportion of Hardwood Forest Edge	0.2 (0.0 – 0.77)
Hardwood Forest Core	Proportion of Hardwood Forest Core	0.06 (0.0 – 1)
Pasture/Cultivated	Proportion of Pasture/Cultivated landcover class	0.19 (0.0 – 1)
Grassland	Proportion of Grassland landcover class	0.04 (0.0 – 1)
Open Space Edge	Proportion of Developed Open Space Edge	0.05 (0.0 – 0.78)
Open-space Core	Proportion of Developed Open Space Core	0.001 (0.0 – 0.9)
Developed Edge	Proportion of Developed (Low, Med, High) Edge	0.03 (0.0 – 0.76)
Developed Core	Proportion of Developed (Low, Med, High) Core	0.006 (0.0 – 1.0)
Canopy Height	Mean basal-weighted canopy height (dm)	85.32 (0.0 – 255.08)
Canopy Height Heterogeneity	Standard deviation of mean canopy height (dm)	60.38 (0.0 – 122.06)
NDVI	Mean Normalized Difference Vegetative Index	0.67 (0.0 – 0.91) (fall) 0.64 (0.0 – 0.9) (spring)
Distance to Coast	Distance to coast (km)	67.7 (0 – 287.5)
Relative Elevation	Elevation relative to surrounding landscape (3x3km window) (m)	4.39 (0.0 – 65.6)

Table 3. Percent deviance explained for each Boosted Regression Tree model.

Season	Geographic Extent	Deviance Explained
Spring	Entire Region	35%
	BCR 27	20%
	BCR 31	24%
Fall	Entire Region	62%
	BCR 27	23%
	BCR 31	38%

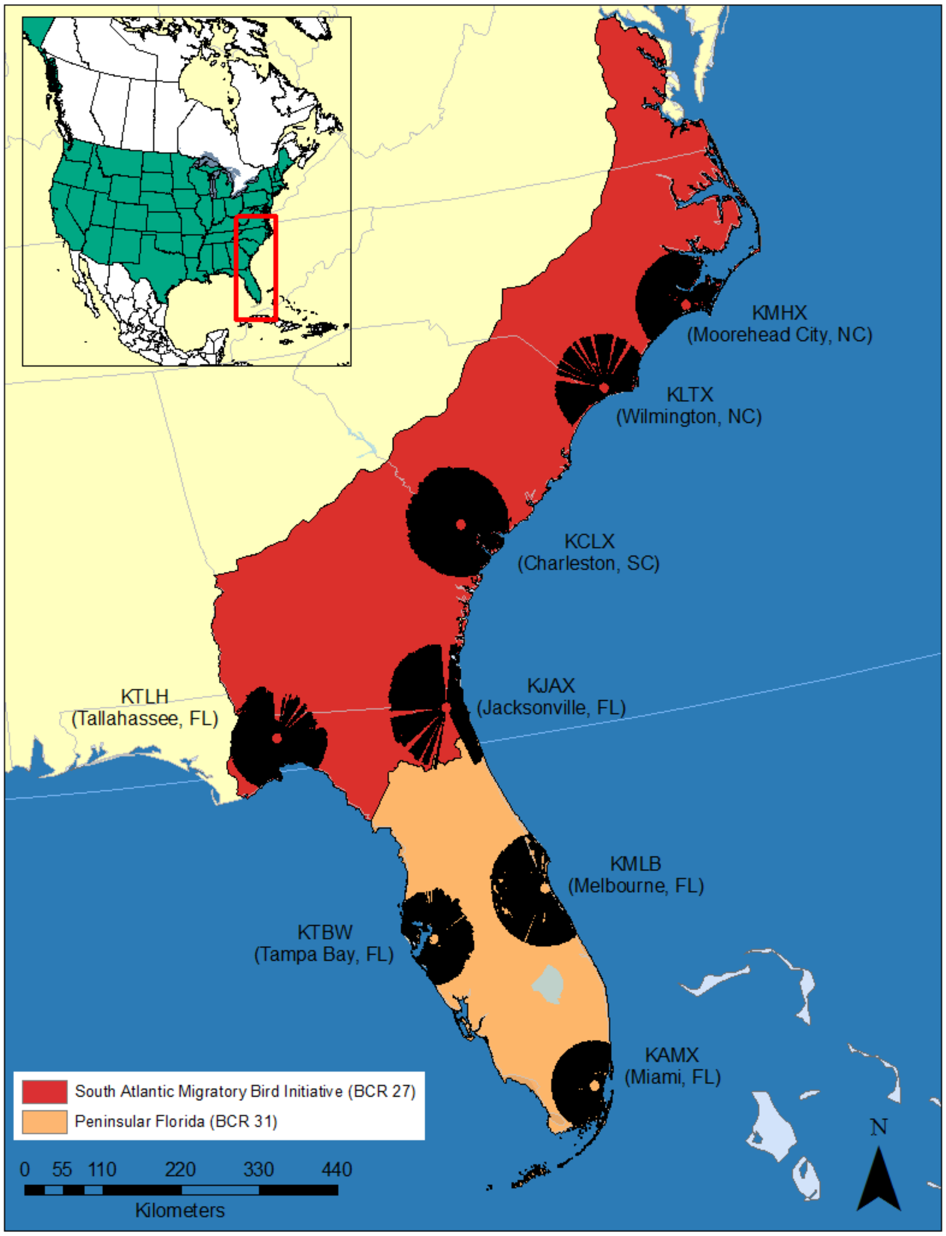


Figure 1. Map of Southeast US showing the study area including most of BCR 27 and all of BCR 31. Radar viewsheds are shown in black.

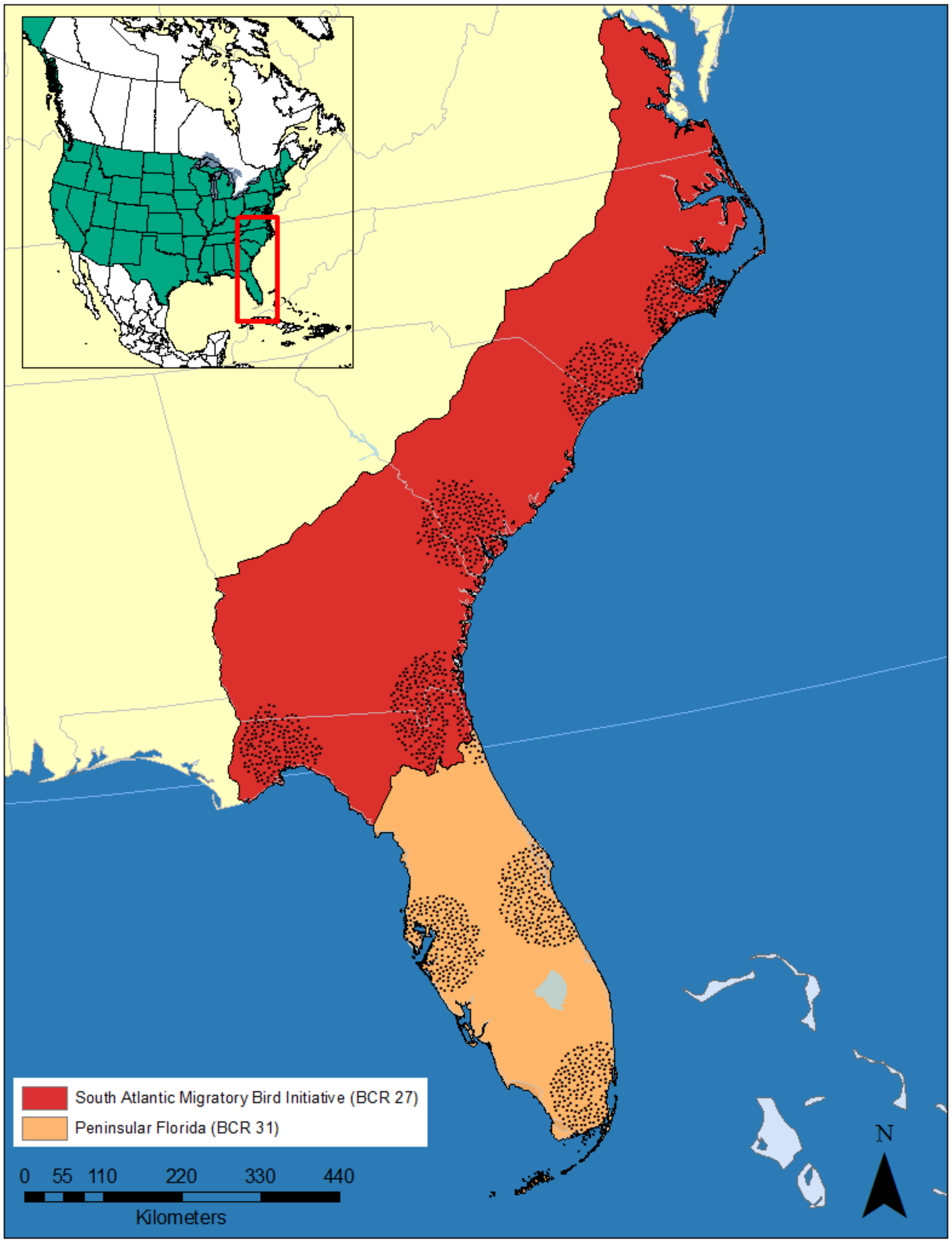


Figure 2. Map of 1-km resolution grid cells of observed radar data used for modeling relative bird stopover density.

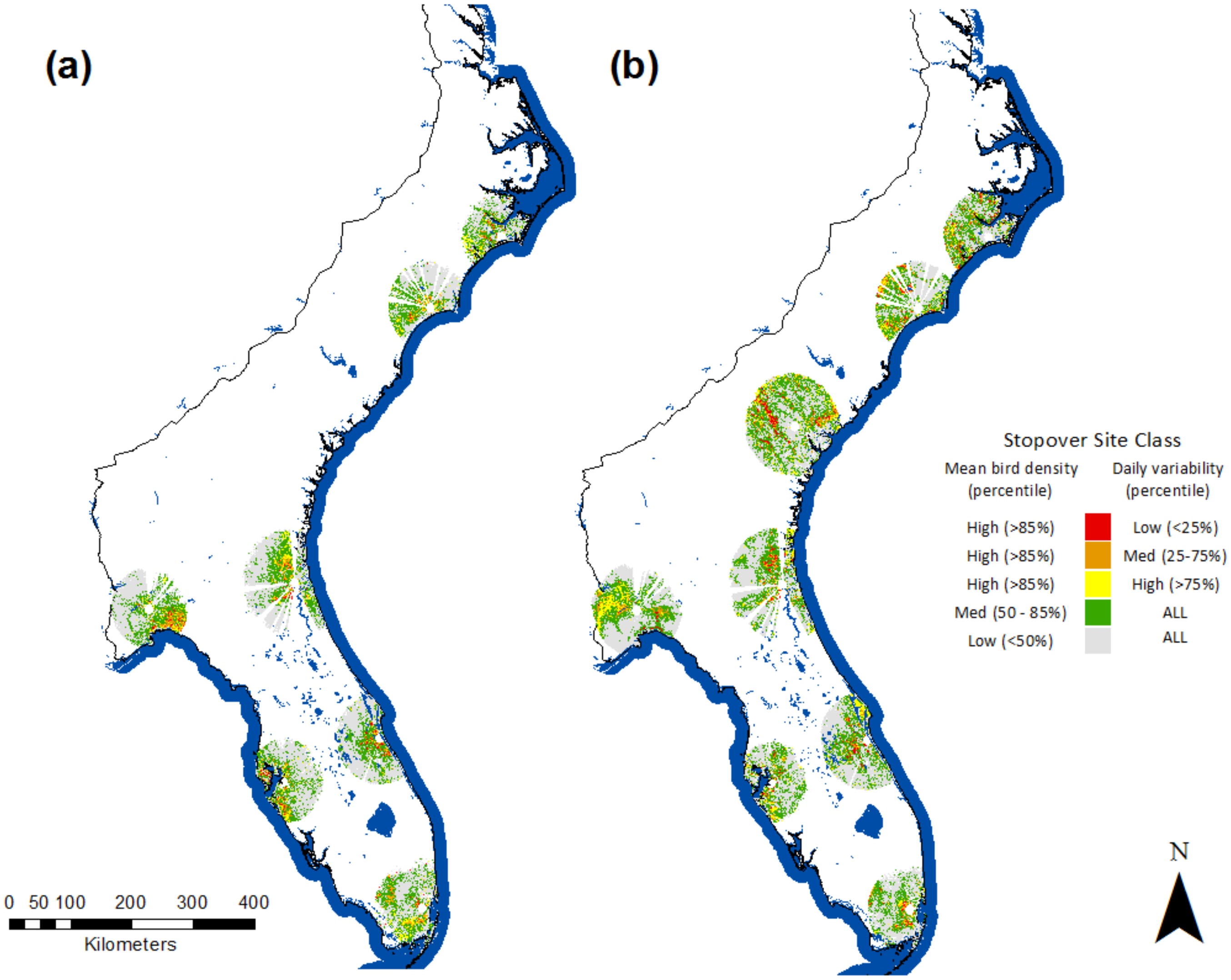


Figure 3. Map of locally-classified radar-observed bird stopover density during (a) spring 2008 & 2009 and (b) fall 2009 & 2010 for individual WSR-88D stations. Note KCLX (Charleston, SC) was not included during spring due to sparse data.

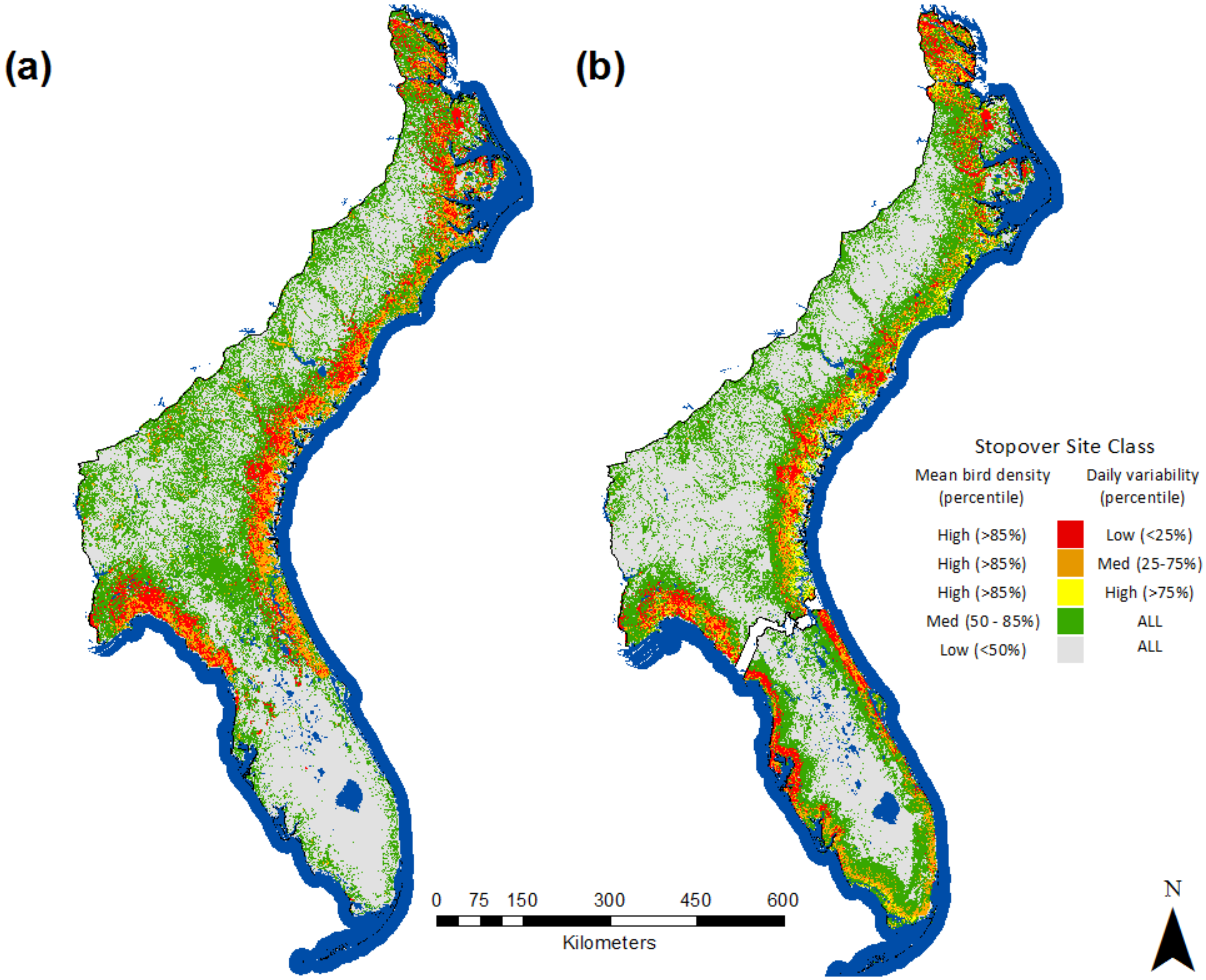


Figure 4. Map of classified bird stopover density during spring 2008 & 2009 as predicted by Boosted Regression Tree models-at the (a) regional scale and (b) each Bird Conservation Region separately.

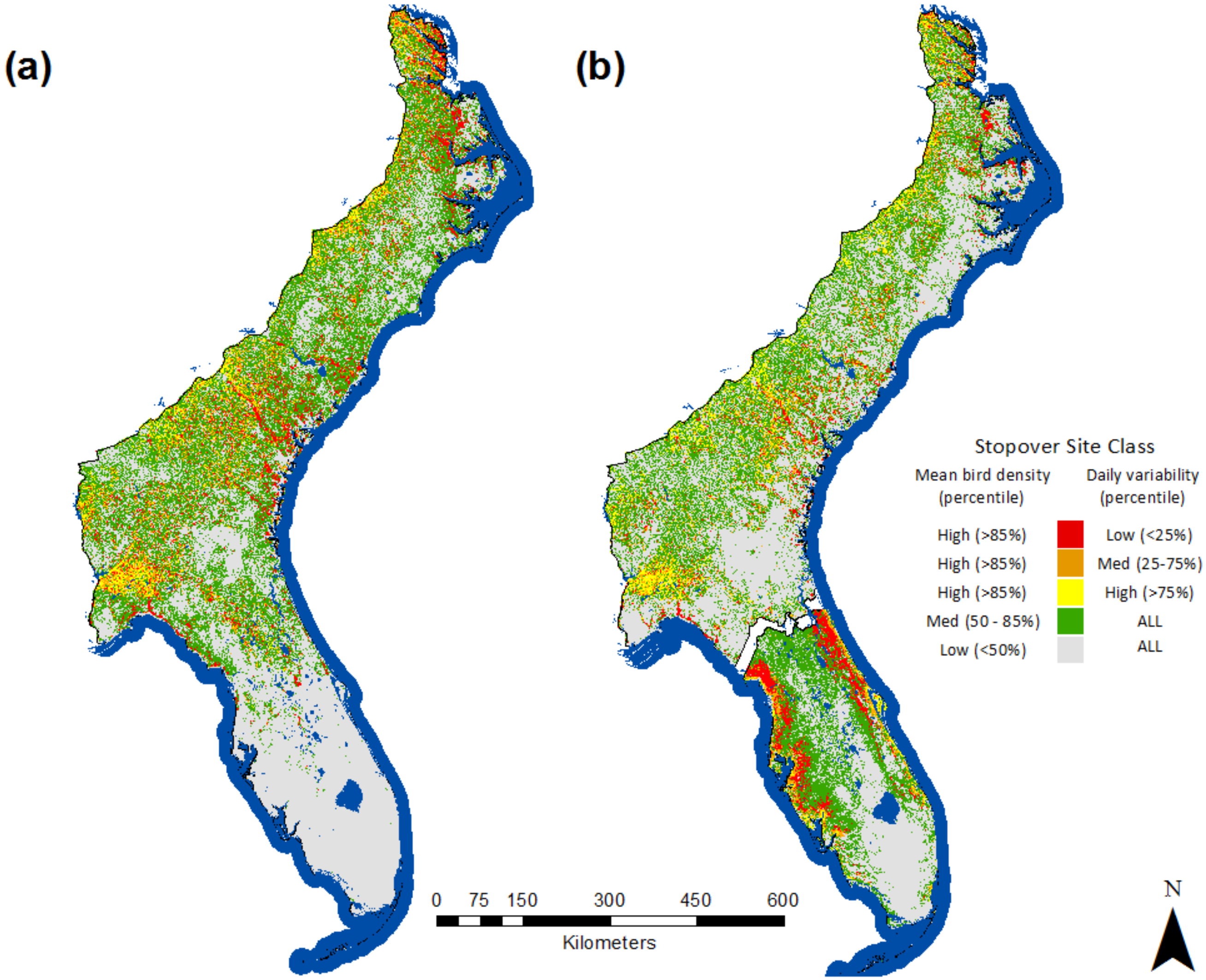


Figure 5. Map of classified bird stopover density during fall 2009 & 2010 as predicted by Boosted Regression Tree models at the (a) regional scale and (b) each Bird Conservation Region separately.

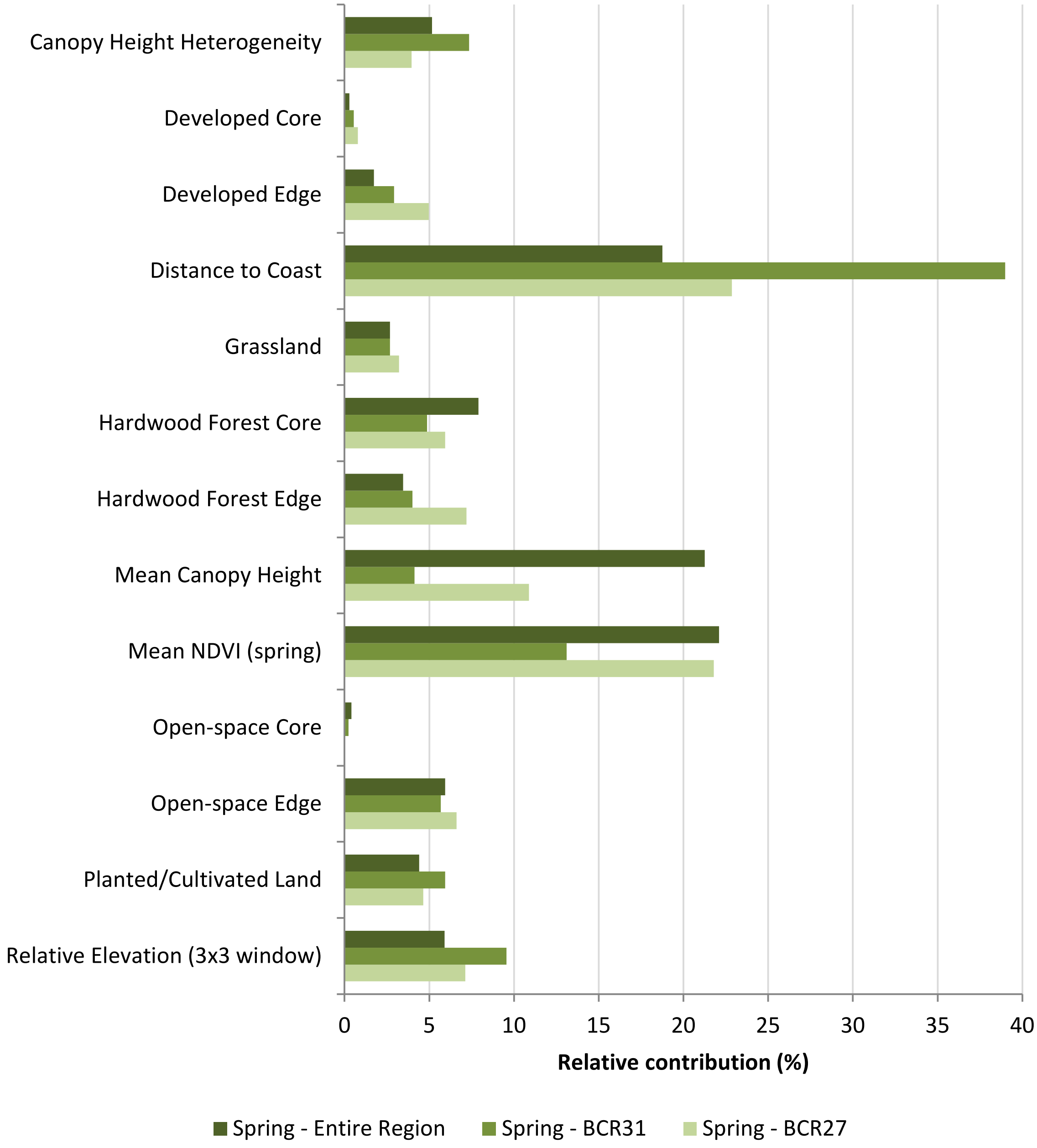


Figure 6. Relative contribution of predictors for each of the three spring BRT models in explaining mean bird density. Values represent the percent contribution of an individual variable (after accounting for the average effects of all other variables) to the total deviance explained by the model.

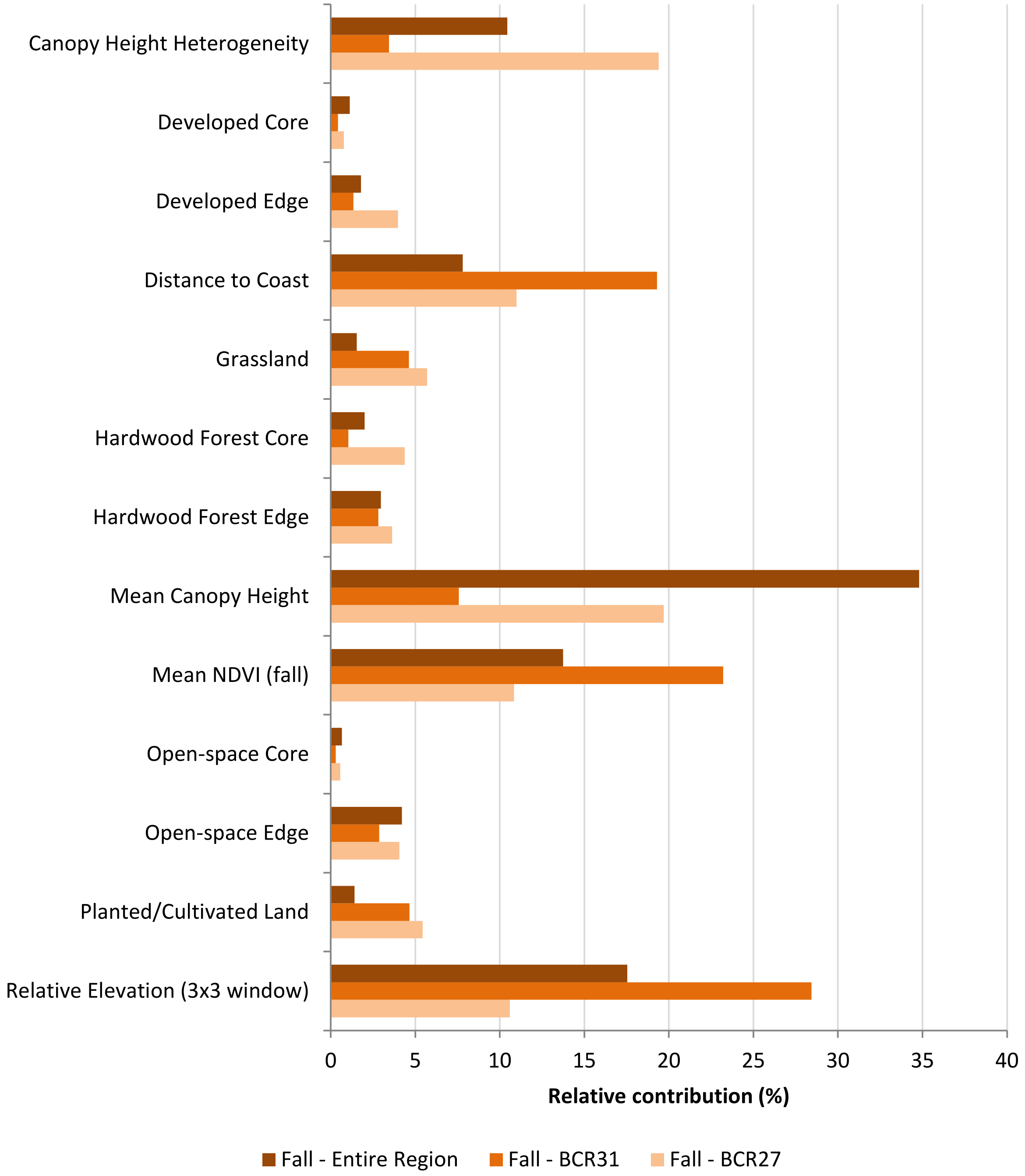


Figure 7. Relative contribution of predictors for each of the three fall BRT models in explaining mean bird density. Values represent the percent contribution of an individual variable (after accounting for the average effects of all other variables) to the total deviance explained by the model.

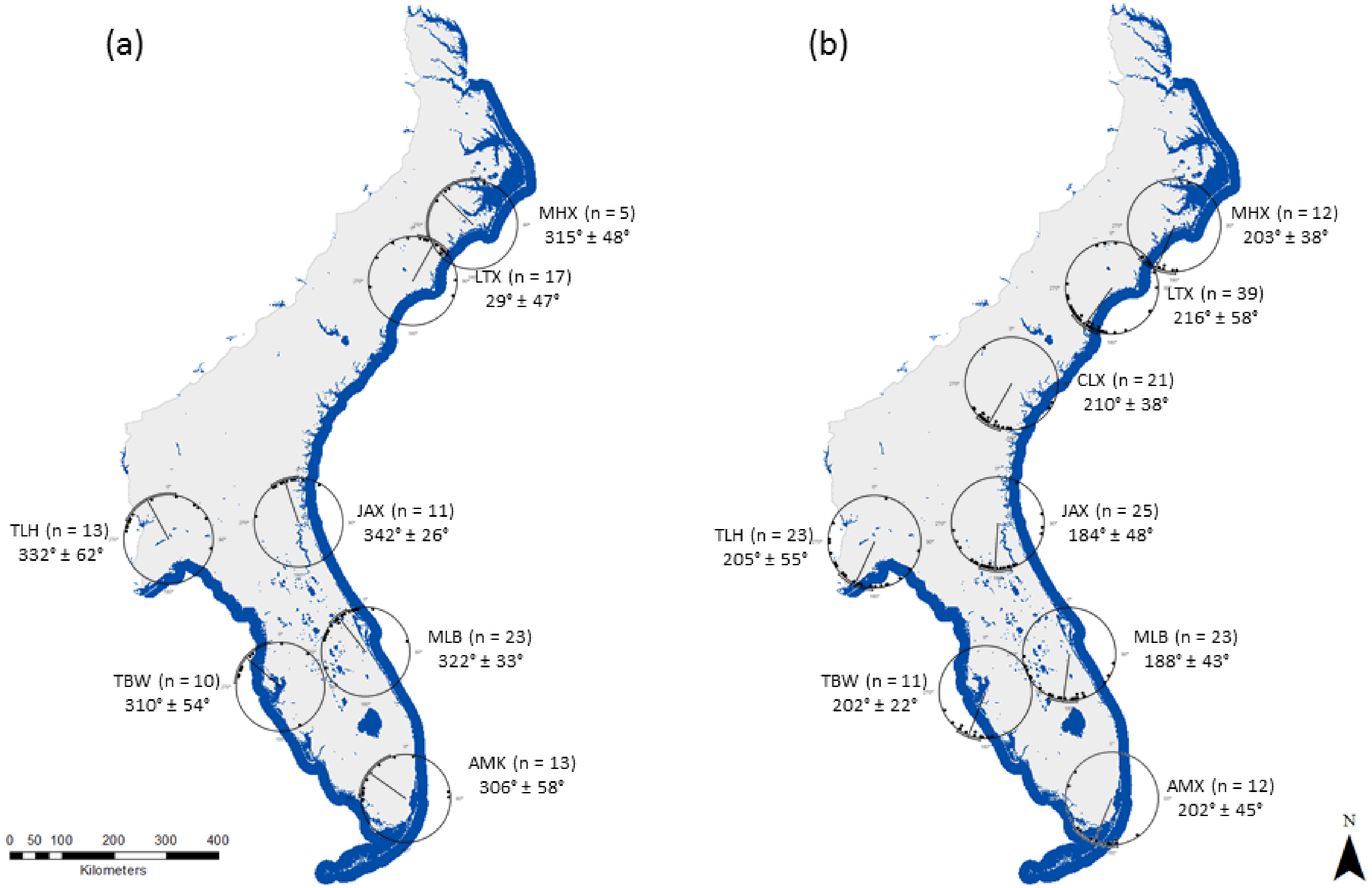


Figure 8. Overall mean ± SE flight direction of birds during (a) spring 2008 & 2009 and (b) fall 2009 & 2010 migration at 8 WSR-88D sites within USFWS Region 4. Names of WSR-88D sites and numbers of sampling nights are shown. Circular plots denote the location of WSR-88D site (center), mean flight direction of individual nights (dots), and overall mean (line) and SE (error bar) of flight direction among nights.

APPENDIX A. Pearson’s Rank Correlation Coefficients for final covariate set. This table is for the entire regional analysis of the fall season (n=1271).

Covariate	Pasture/Cultivated	Grassland	HardwoodForestEdge	HardwoodForestCore	OpenspaceEdge	OpenspaceCore	DevelopedEdge	DevelopedCore	MeanCanopyHeight	StDevCanopyHeight	MeanFallNDVI	DistanceToCoast	RelativeElevation
Pasture/Cultivated	1.00												
Grassland	0.20	1.00											
HardwoodForestEdge	0.02	0.06	1.00										
HardwoodForestCore	-0.14	-0.12	0.59	1.00									
OpenspaceEdge	0.06	0.27	-0.09	-0.26	1.00								
OpenspaceCore	-0.04	-0.02	-0.06	-0.09	0.35	1.00							
DevelopedEdge	0.01	0.11	-0.13	-0.21	0.68	0.32	1.00						
DevelopedCore	-0.17	-0.12	-0.23	-0.19	0.38	0.20	0.56	1.00					
MeanCanopyHeight	-0.26	0.13	0.43	0.47	-0.06	-0.12	-0.24	-0.24	1.00				
StDevCanopyHeight	0.34	0.47	0.20	-0.05	0.38	0.07	0.24	-0.01	0.11	1.00			
MeanFallNDVI	-0.09	0.15	0.35	0.34	-0.14	-0.16	-0.35	-0.37	0.75	0.14	1.00		
DistanceToCoast	0.22	0.10	0.10	0.09	-0.18	-0.08	-0.27	-0.28	0.20	0.09	0.17	1.00	
RelativeElevation	0.26	0.38	-0.01	-0.16	0.35	0.07	0.18	0.02	0.17	0.40	0.17	0.20	1.00

APPENDIX A (continued). Pearson's Rank Correlation Coefficients for final covariate set. This table is for the BCR27 analysis in fall (n=815).

Covariate	Pasture/Cultivated	Grassland	HardwoodForestEdge	HardwoodForestCore	OpenspaceEdge	OpenspaceCore	DevelopedEdge	DevelopedCore	MeanCanopyHeight	StDevCanopyHeight	MeanFallNDVI	DistanceToCoast	RelativeElevation
Pasture/Cultivated	1.00												
Grassland	0.20	1.00											
HardwoodForestEdge	-0.11	-0.14	1.00										
HardwoodForestCore	-0.23	-0.29	0.54	1.00									
OpenspaceEdge	0.17	0.22	-0.18	-0.36	1.00								
OpenspaceCore	0.00	-0.02	-0.07	-0.08	0.25	1.00							
DevelopedEdge	0.15	0.12	-0.19	-0.26	0.57	0.23	1.00						
DevelopedCore	-0.06	-0.06	-0.16	-0.13	0.27	0.05	0.41	1.00					
MeanCanopyHeight	-0.42	-0.21	0.44	0.50	-0.34	-0.10	-0.40	-0.20	1.00				
StDevCanopyHeight	0.52	0.35	0.03	-0.21	0.35	0.09	0.27	0.08	-0.43	1.00			
MeanFallNDVI	-0.34	-0.15	0.34	0.33	-0.34	-0.13	-0.43	-0.29	0.58	-0.25	1.00		
DistanceToCoast	0.21	0.03	0.09	0.13	-0.12	-0.05	-0.18	-0.18	0.21	0.06	0.03	1.00	
RelativeElevation	0.37	0.27	-0.13	-0.31	0.28	0.04	0.18	0.01	-0.18	0.27	-0.15	0.27	1.00

APPENDIX A (continued). Pearson's Rank Correlation Coefficients for final covariate set. This table is for the BCR31 analysis in fall (n=456).

Covariate	Pasture/Cultivated	Grassland	HardwoodForestEdge	HardwoodForestCore	OpenspaceEdge	OpenspaceCore	DevelopedEdge	DevelopedCore	MeanCanopyHeight	StDevCanopyHeight	FallNDVI	DistanceToCoast	RelativeElevation
Pasture/Cultivated	1.00												
Grassland	0.24	1.00											
HardwoodForestEdge	0.16	0.39	1.00										
HardwoodForestCore	-0.02	0.20	0.67	1.00									
OpenspaceEdge	-0.05	0.30	0.02	-0.10	1.00								
OpenspaceCore	-0.09	0.09	-0.05	-0.11	0.50	1.00							
DevelopedEdge	-0.19	0.18	-0.07	-0.15	0.85	0.39	1.00						
DevelopedCore	-0.30	-0.08	-0.30	-0.28	0.52	0.23	0.72	1.00					
MeanCanopyHeight	-0.07	0.34	0.78	0.79	0.18	0.08	0.13	-0.06	1.00				
StDevCanopyHeight	0.13	0.48	0.66	0.38	0.37	0.22	0.29	0.06	0.67	1.00			
FallNDVI	0.41	0.27	0.59	0.55	-0.10	-0.05	-0.26	-0.40	0.57	0.36	1.00		
DistanceToCoast	0.27	0.12	0.10	-0.01	-0.35	-0.07	-0.44	-0.39	-0.08	0.04	0.18	1.00	
RelativeElevation	0.18	0.39	0.20	0.10	0.39	0.23	0.31	0.21	0.29	0.40	0.23	-0.03	1.00

APPENDIX A (continued). Pearson's Rank Correlation Coefficients for final covariate set. This table is for the entire regional analysis of the spring season (n=1178).

Covariate	Pasture/Cultivated	Grassland	HardwoodForestEdge	HardwoodForestCore	OpenspaceEdge	OpenspaceCore	DevelopedEdge	DevelopedCore	MeanCanopyHeight	StDevCanopyHeight	MeanSpringNDVI	DistanceToCoast	RelativeElevation
Pasture/Cultivated	1.00												
Grassland	0.22	1.00											
HardwoodForestEdge	0.01	0.05	1.00										
HardwoodForestCore	-0.09	-0.11	0.66	1.00									
OpenspaceEdge	0.07	0.30	-0.10	-0.26	1.00								
OpenspaceCore	-0.02	0.04	-0.06	-0.11	0.39	1.00							
DevelopedEdge	0.03	0.11	-0.16	-0.24	0.70	0.32	1.00						
DevelopedCore	-0.19	-0.12	-0.23	-0.20	0.38	0.14	0.58	1.00					
MeanCanopyHeight	-0.24	0.15	0.48	0.49	0.02	-0.11	-0.19	-0.21	1.00				
StDevCanopyHeight	0.29	0.42	0.22	0.01	0.38	0.10	0.26	0.00	0.18	1.00			
MeanSpringNDVI	-0.07	0.18	0.46	0.45	-0.06	-0.13	-0.28	-0.35	0.81	0.20	1.00		
DistanceToCoast	0.16	0.09	0.05	0.07	-0.17	-0.13	-0.29	-0.29	0.14	-0.01	0.16	1.00	
RelativeElevation	0.24	0.38	0.00	-0.13	0.39	0.11	0.23	0.04	0.21	0.40	0.17	0.12	1.00

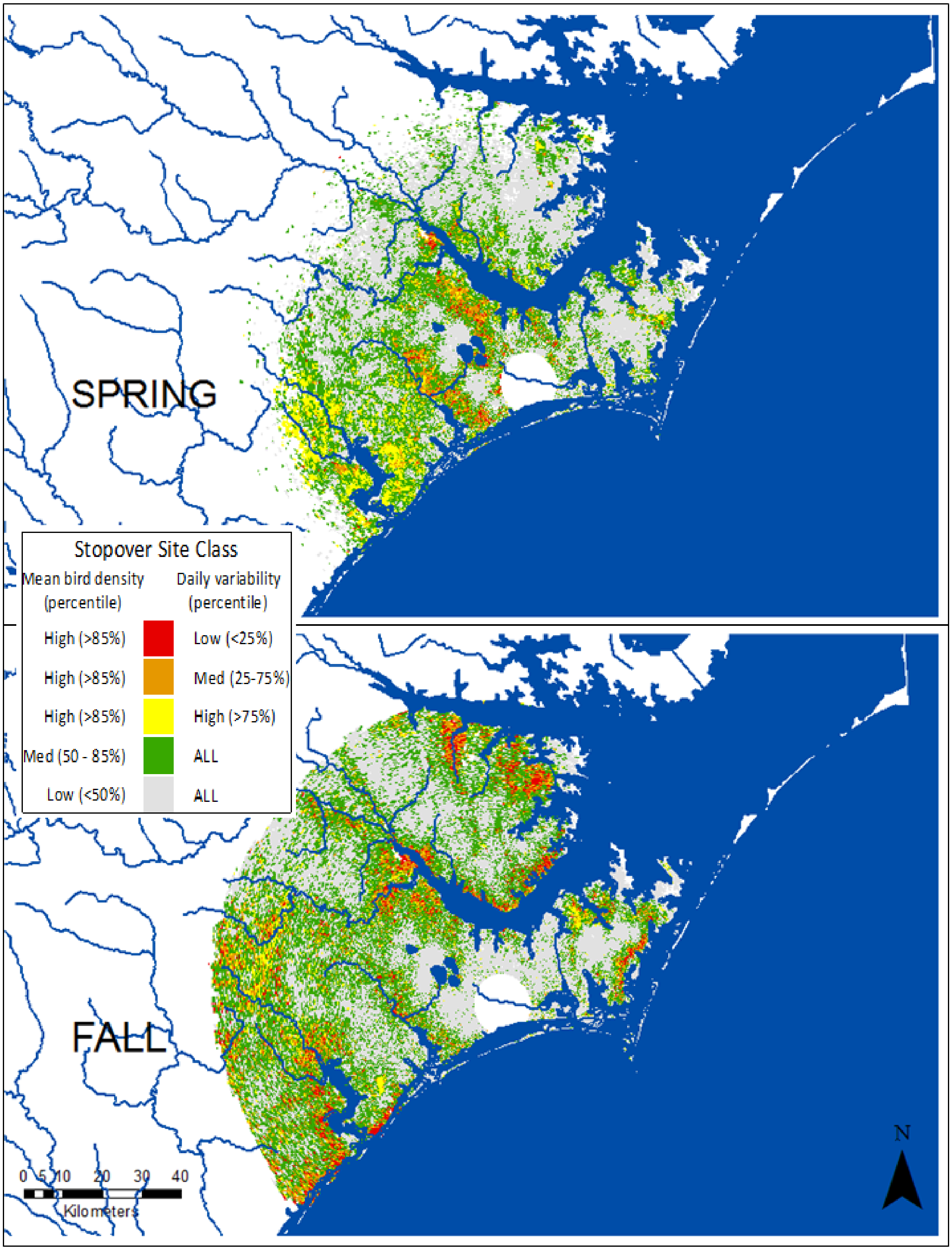
APPENDIX A (continued). Pearson's Rank Correlation Coefficients for final covariate set. This table is for the BCR27 analysis in spring (n=617).

Covariate	Pasture/Cultivated	Grassland	HardwoodForestEdge	HardwoodForestCore	OpenspaceEdge	OpenspaceCore	DevelopedEdge	DevelopedCore	MeanCanopyHeight	StDevCanopyHeight	MeanSpringNDVI	DistanceToCoast	RelativeElevation
Pasture/Cultivated	1.00												
Grassland	0.23	1.00											
HardwoodForestEdge	-0.18	-0.19	1.00										
HardwoodForestCore	-0.27	-0.31	0.59	1.00									
OpenspaceEdge	0.25	0.24	-0.25	-0.42	1.00								
OpenspaceCore	-0.01	-0.05	-0.18	-0.15	0.26	1.00							
DevelopedEdge	0.20	0.13	-0.23	-0.31	0.56	0.27	1.00						
DevelopedCore	0.00	-0.03	-0.16	-0.14	0.25	0.19	0.37	1.00					
MeanCanopyHeight	-0.47	-0.25	0.46	0.48	-0.32	-0.18	-0.42	-0.22	1.00				
StDevCanopyHeight	0.51	0.35	-0.11	-0.28	0.38	0.06	0.36	0.08	-0.52	1.00			
MeanSpringNDVI	-0.34	-0.20	0.51	0.50	-0.34	-0.19	-0.41	-0.27	0.62	-0.27	1.00		
DistanceToCoast	0.11	0.01	0.01	0.11	-0.05	-0.19	-0.18	-0.17	0.25	-0.03	0.09	1.00	
RelativeElevation	0.29	0.21	-0.23	-0.38	0.34	0.03	0.24	0.06	-0.16	0.26	-0.21	0.17	1.00

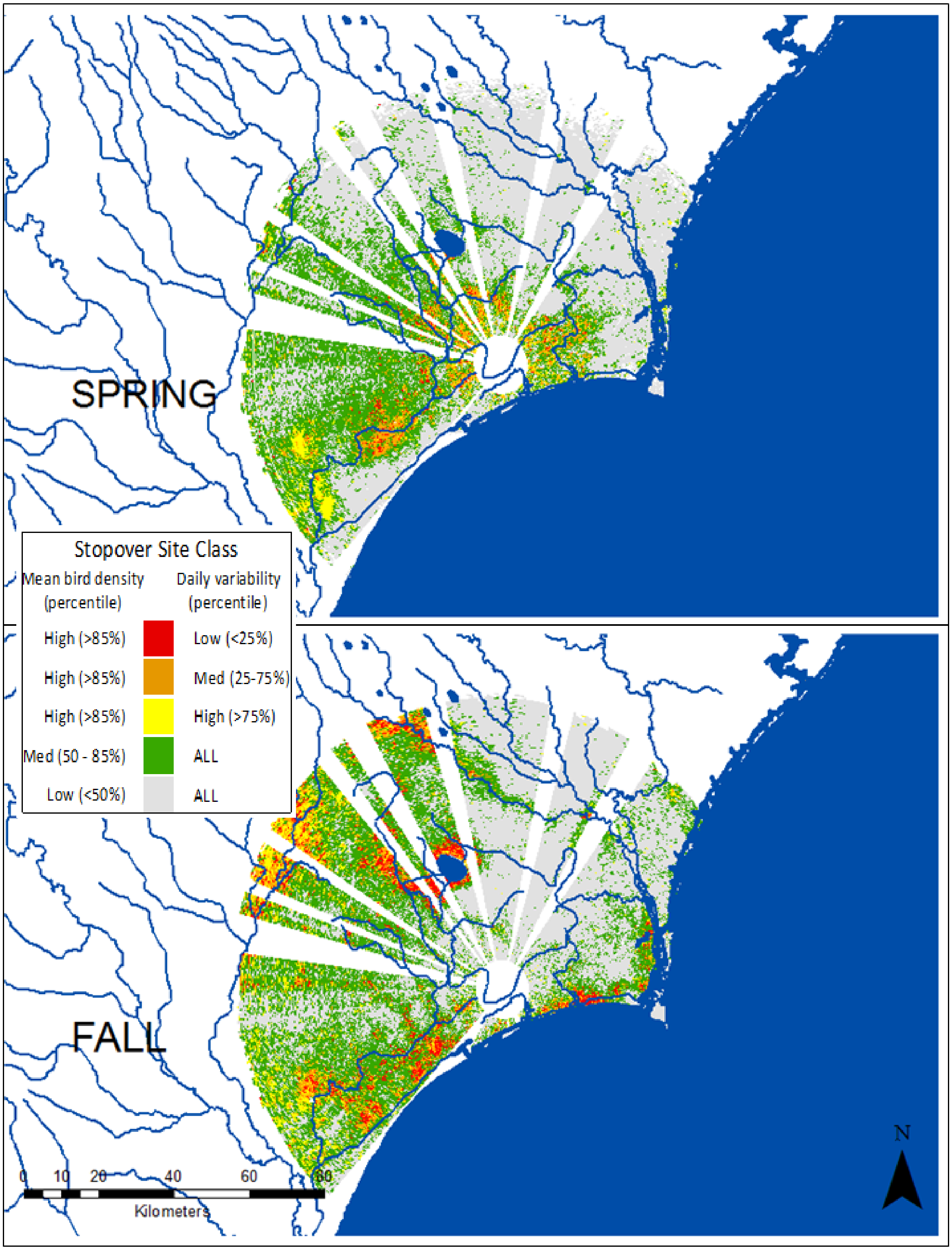
APPENDIX A (continued). Pearson’s Rank Correlation Coefficients for final covariate set. This table is for BCR31 analysis in spring (n=561).

Covariate	Pasture/Cultivated	Grassland	HardwoodForestEdge	HardwoodForestCore	OpenspaceEdge	OpenspaceCore	DevelopedEdge	DevelopedCore	MeanCanopyHeight	StDevCanopyHeight	MeanSpringNDVI	DistanceToCoast	RelativeElevation
Pasture/Cultivated	1.00												
Grassland	0.29	1.00											
HardwoodForestEdge	0.16	0.30	1.00										
HardwoodForestCore	0.07	0.11	0.72	1.00									
OpenspaceEdge	-0.03	0.31	0.00	-0.14	1.00								
OpenspaceCore	-0.05	0.20	0.01	-0.09	0.50	1.00							
DevelopedEdge	-0.13	0.15	-0.12	-0.19	0.82	0.32	1.00						
DevelopedCore	-0.31	-0.09	-0.28	-0.25	0.48	0.08	0.71	1.00					
MeanCanopyHeight	-0.03	0.20	0.79	0.76	0.19	0.11	0.12	0.00	1.00				
StDevCanopyHeight	0.13	0.32	0.66	0.45	0.34	0.23	0.24	0.06	0.73	1.00			
MeanSpringNDVI	0.33	0.22	0.65	0.61	0.01	0.07	-0.15	-0.32	0.66	0.48	1.00		
DistanceToCoast	0.23	0.13	0.09	0.02	-0.30	-0.09	-0.40	-0.39	-0.10	0.02	0.15	1.00	
RelativeElevation	0.29	0.45	0.21	0.12	0.41	0.24	0.31	0.16	0.32	0.47	0.27	0.02	1.00

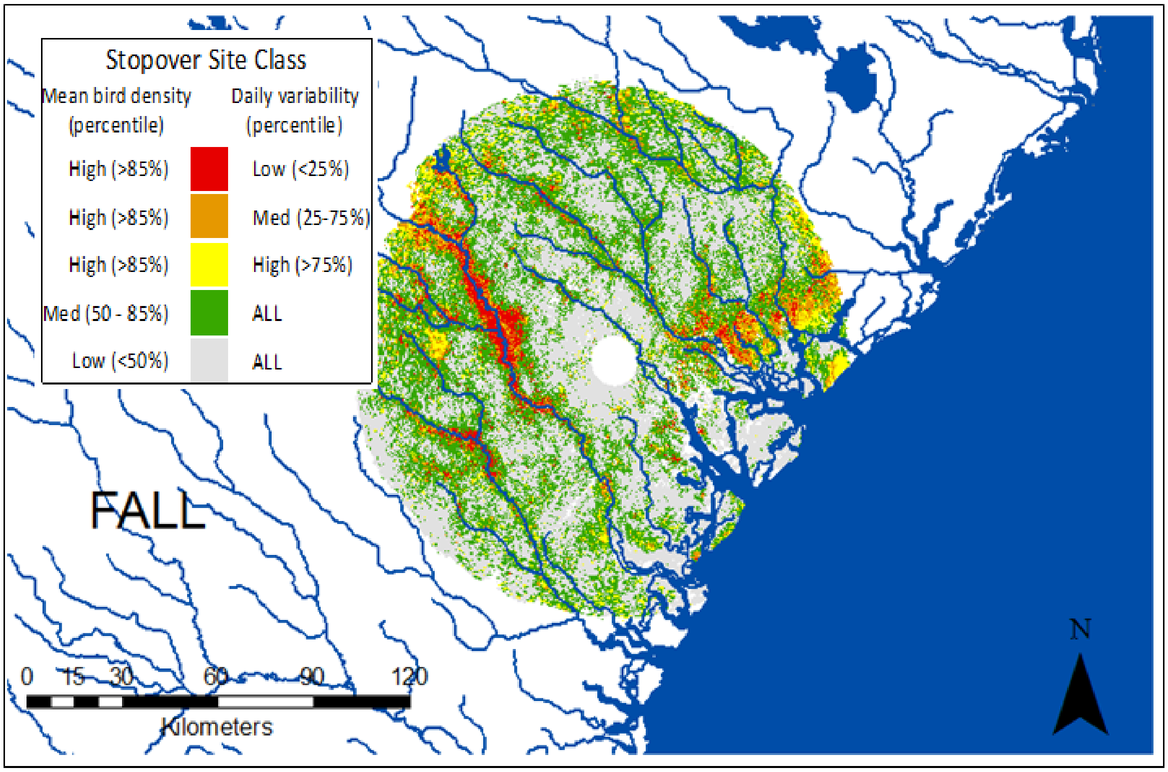
APPENDIX B. Classified bird stopover density during spring (2009 – 2010; n=5 sampling days) and fall (2008 – 2009; n=12 sampling days) from the KMHX station.



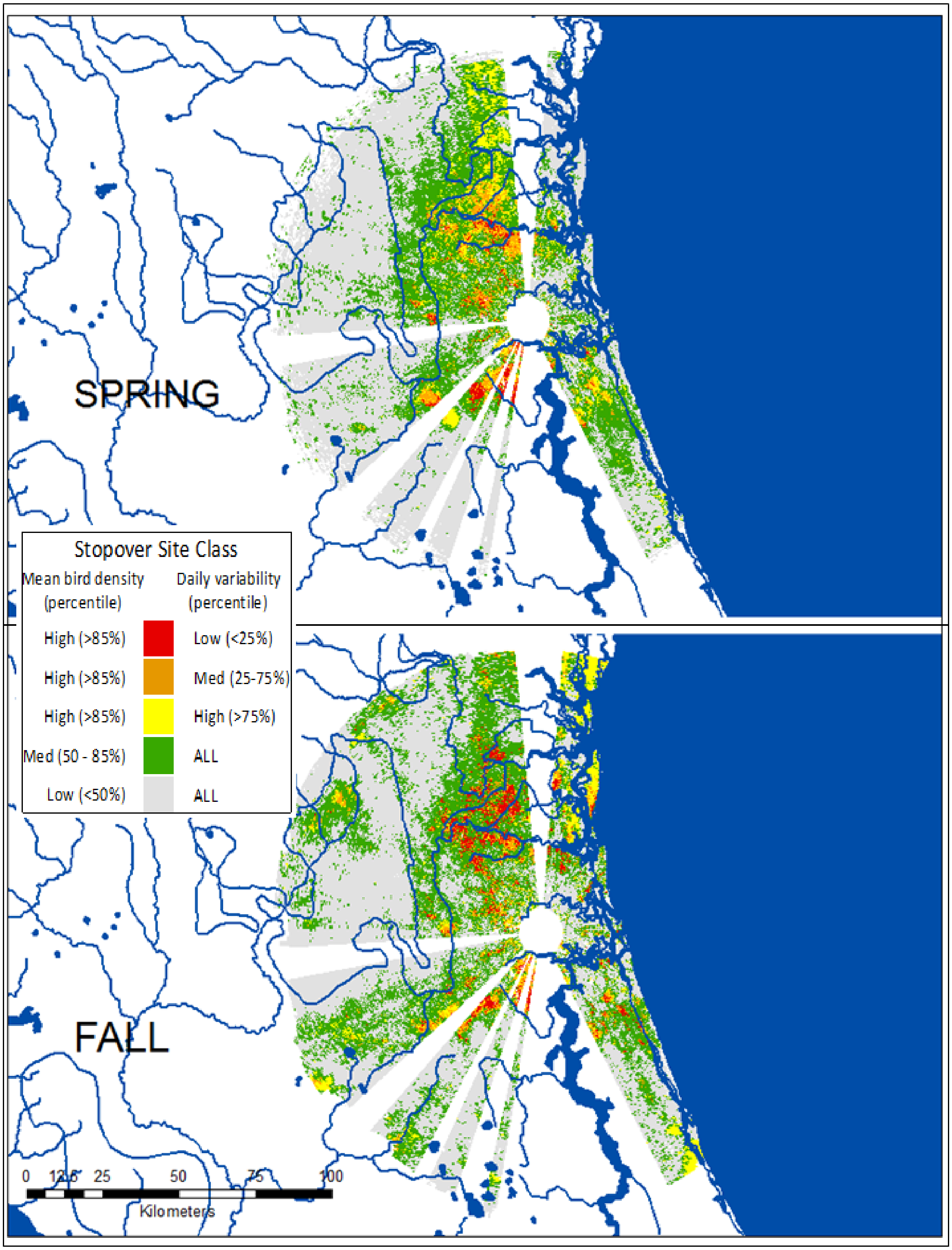
APPENDIX B (continued). Classified bird stopover density during spring (2009 – 2010; n=17 sampling days) and fall (2008 – 2009; n=38 sampling days) from the KLTX station.



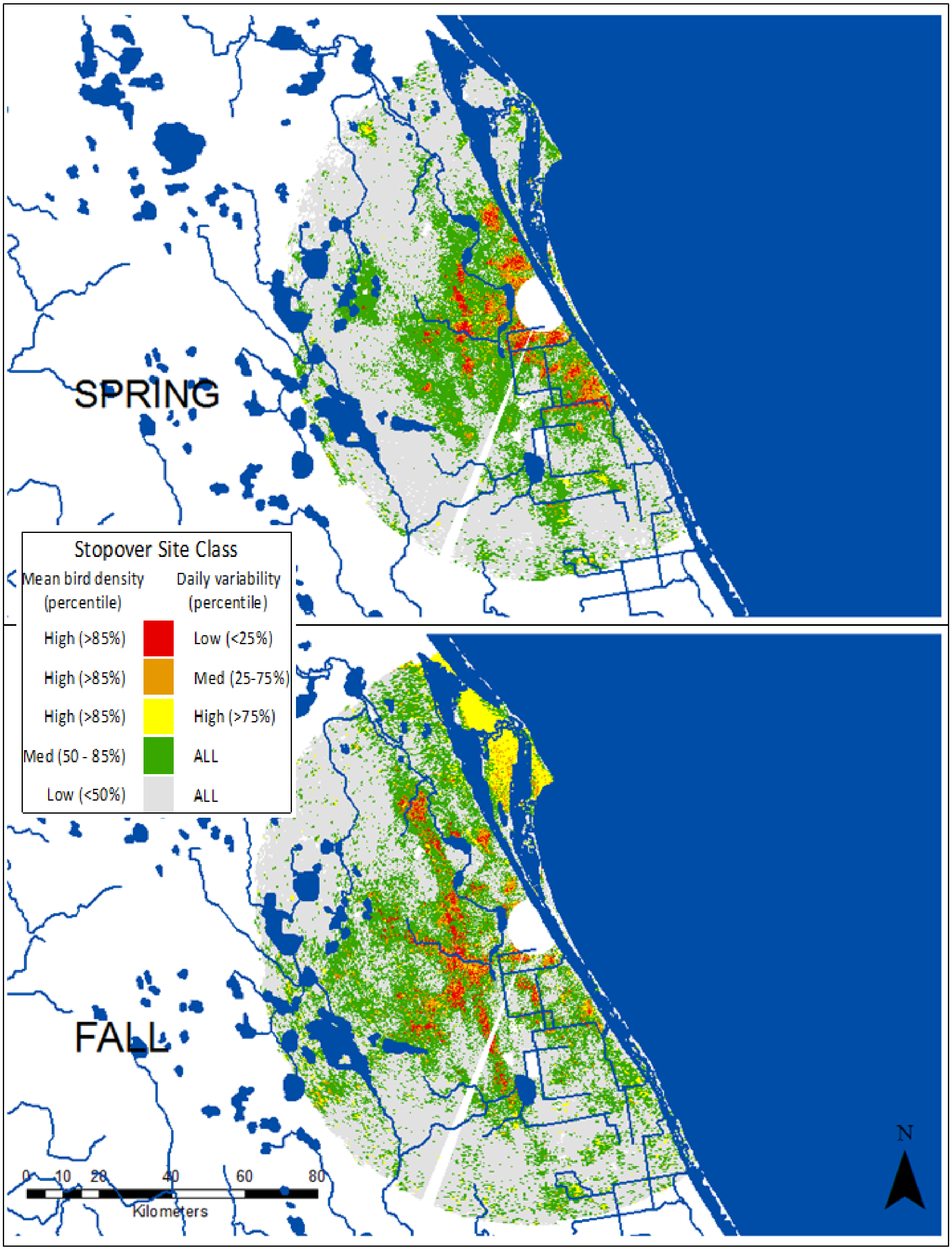
APPENDIX B (continued). Classified bird stopover density during fall (2008 – 2009; n=24 sampling days) from the KCLX station. Insufficient data prevented an analysis of spring at KCLX.



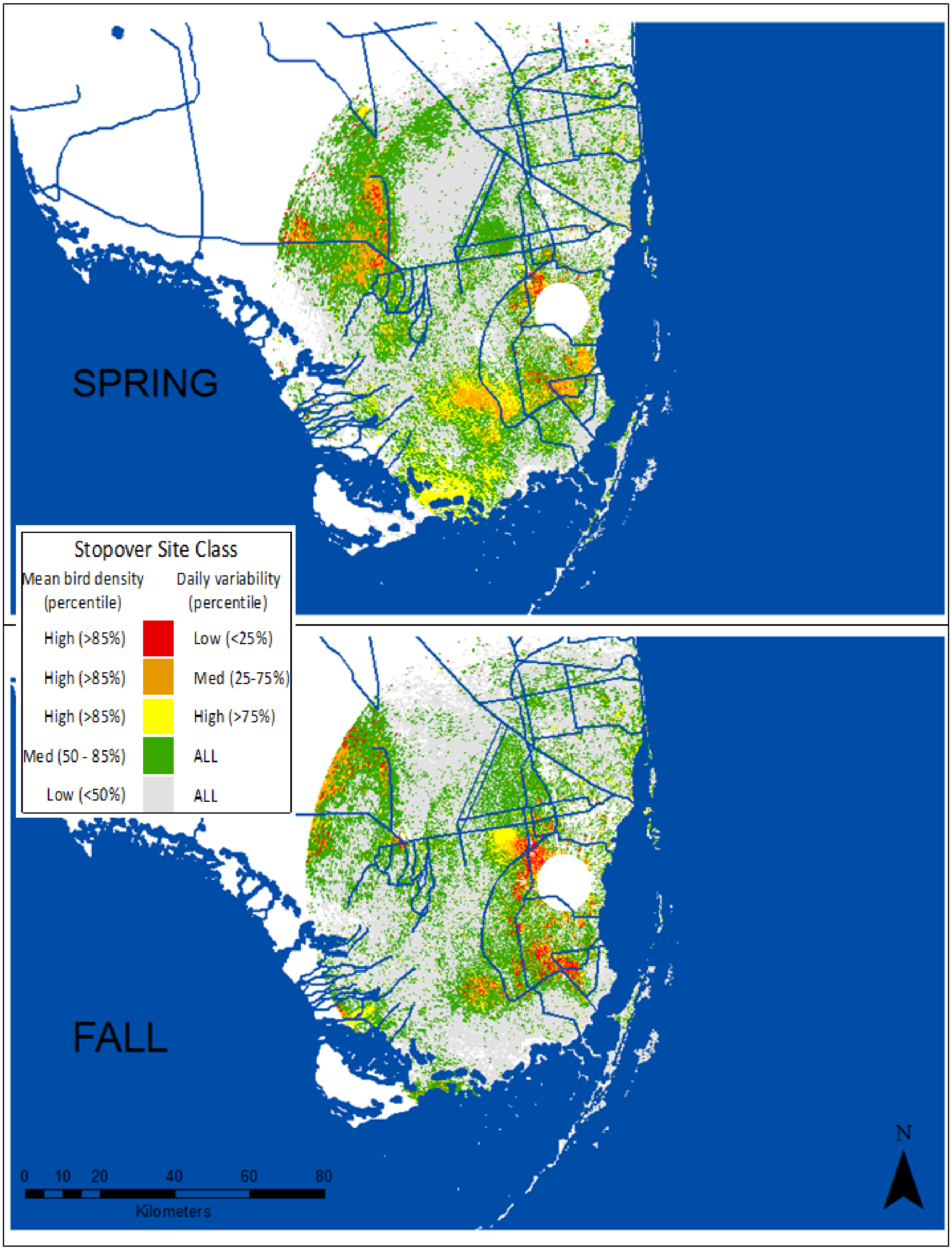
APPENDIX B (continued). Classified bird stopover density during spring (2009 – 2010; n=12 sampling days) and fall (2008 – 2009; n=27 sampling days) from the KJAX station.



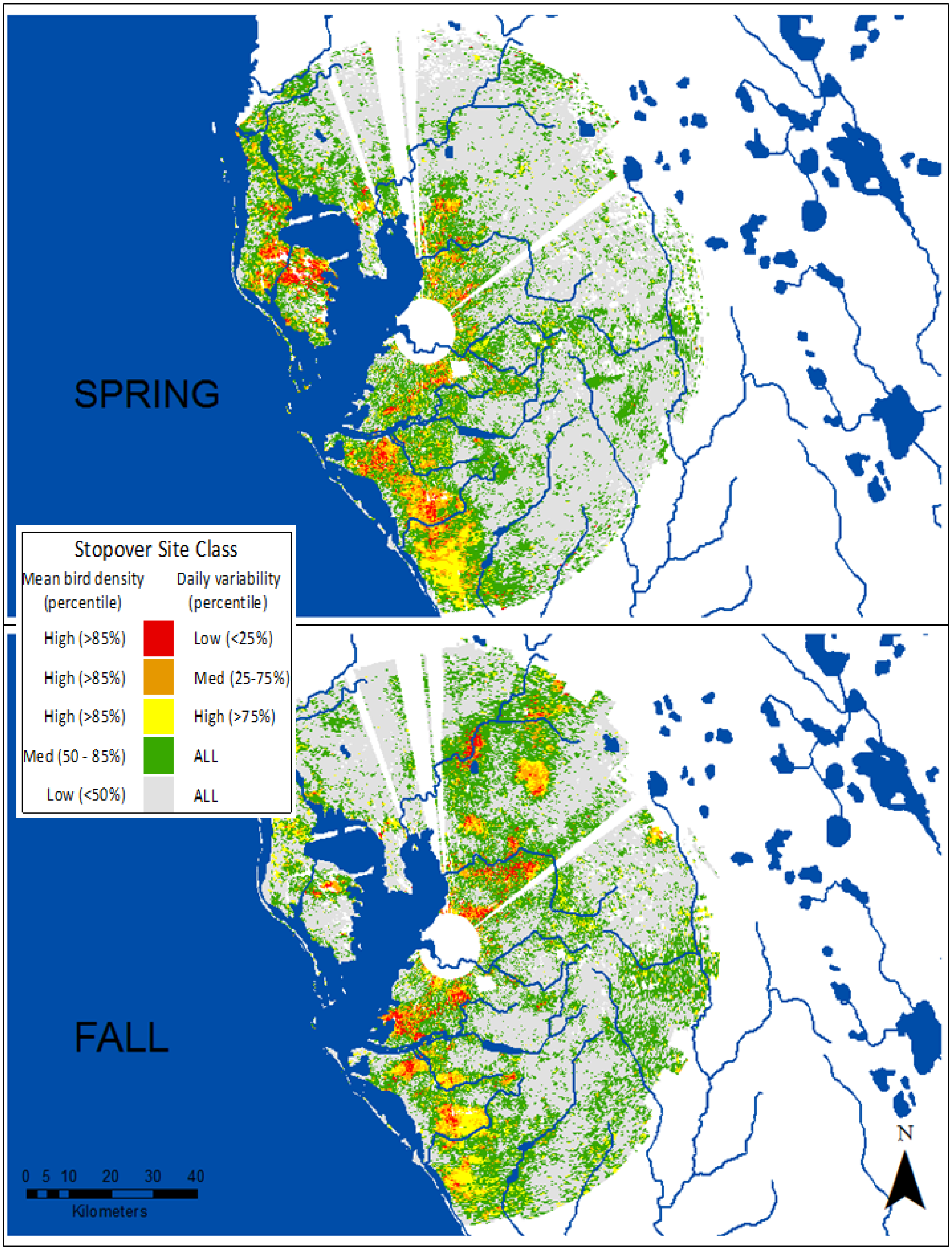
APPENDIX B (continued). Classified bird stopover density during spring (2009 – 2010; n=23 sampling days) and fall (2008 – 2009; n=22 sampling days) from the KMLB station.



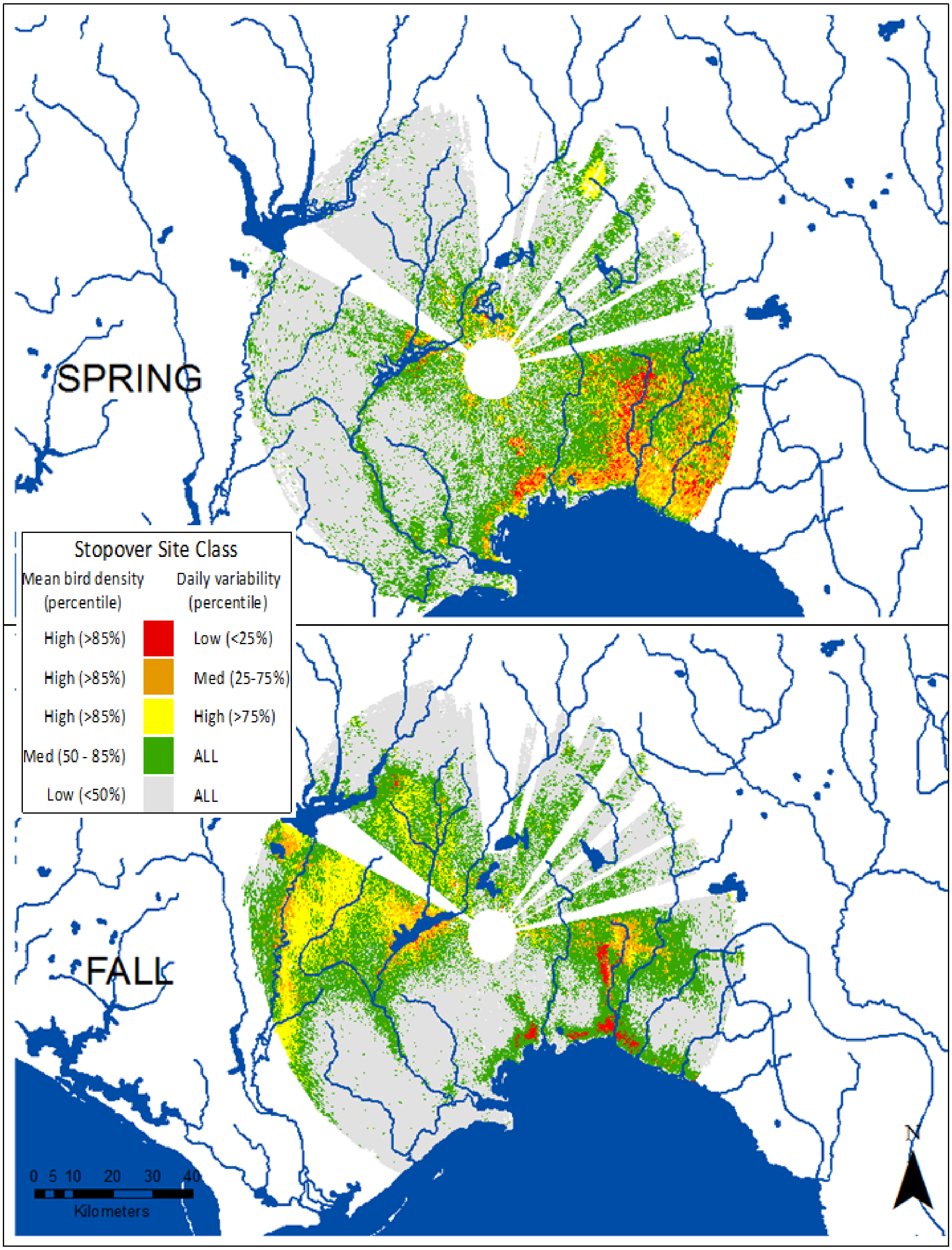
APPENDIX B (continued). Classified bird stopover density during spring (2009 – 2010; n=13 sampling days) and fall (2008 – 2009; n=12 sampling days) from the KAMX station.



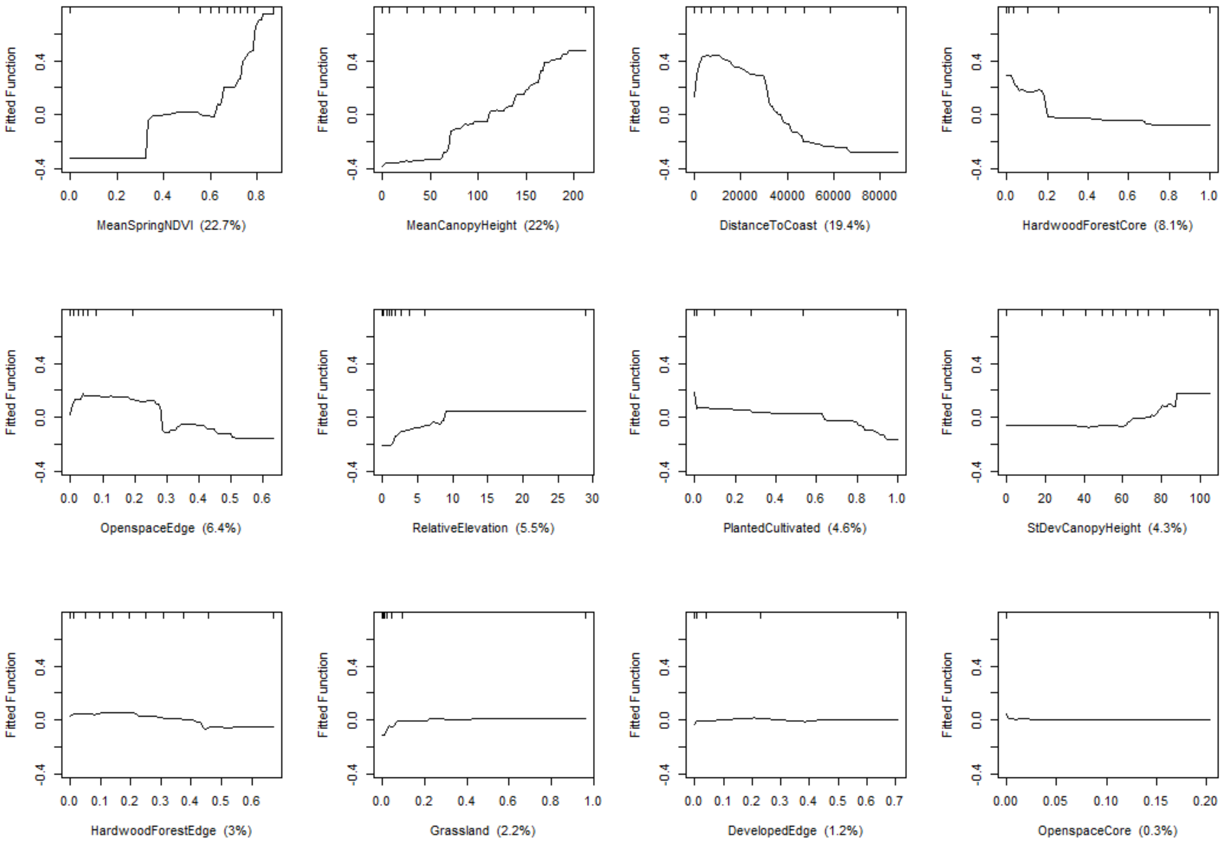
APPENDIX B (continued). Classified bird stopover density during spring (2009 – 2010; n=10 sampling days) and fall (2008 – 2009; n=17 sampling days) from the KTBW station.



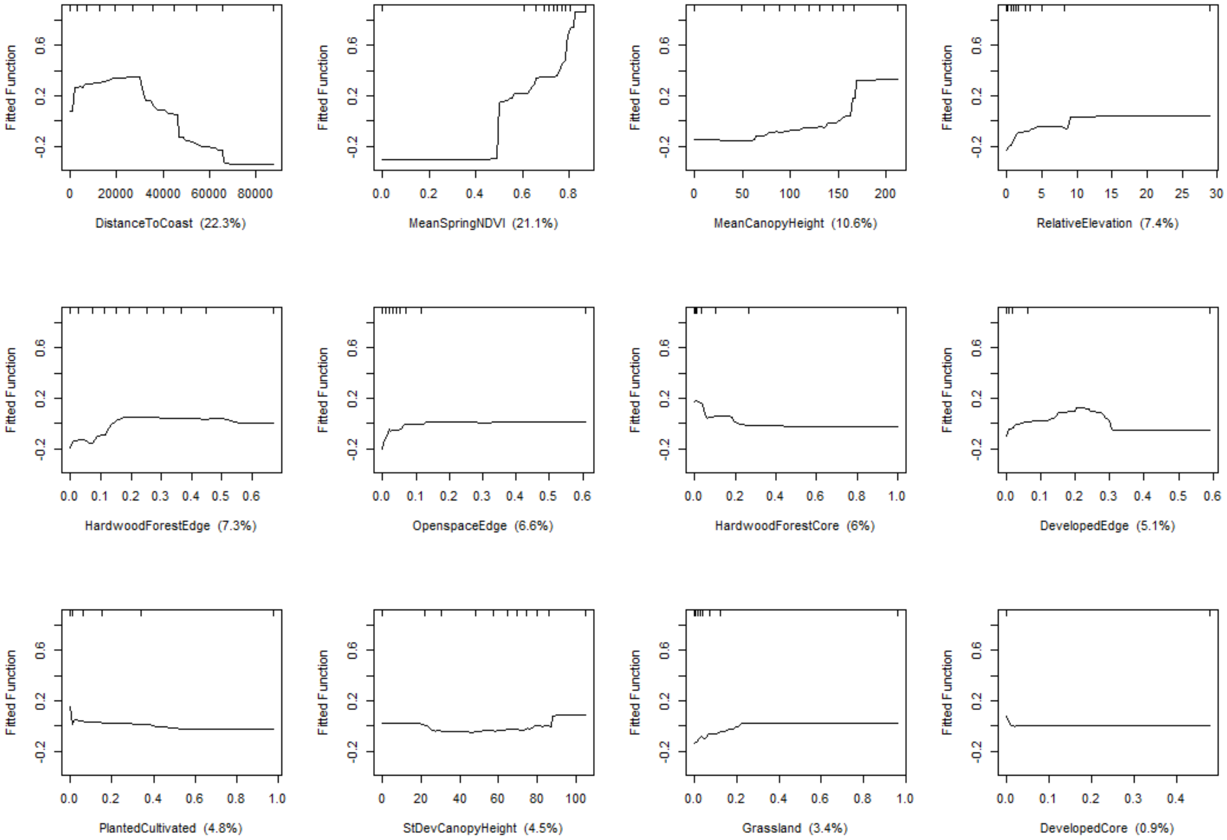
APPENDIX B (continued). Classified bird stopover density during spring (2009 – 2010; n=13 sampling days) and fall (2008 – 2009; n=23 sampling days) from the KTLH station.



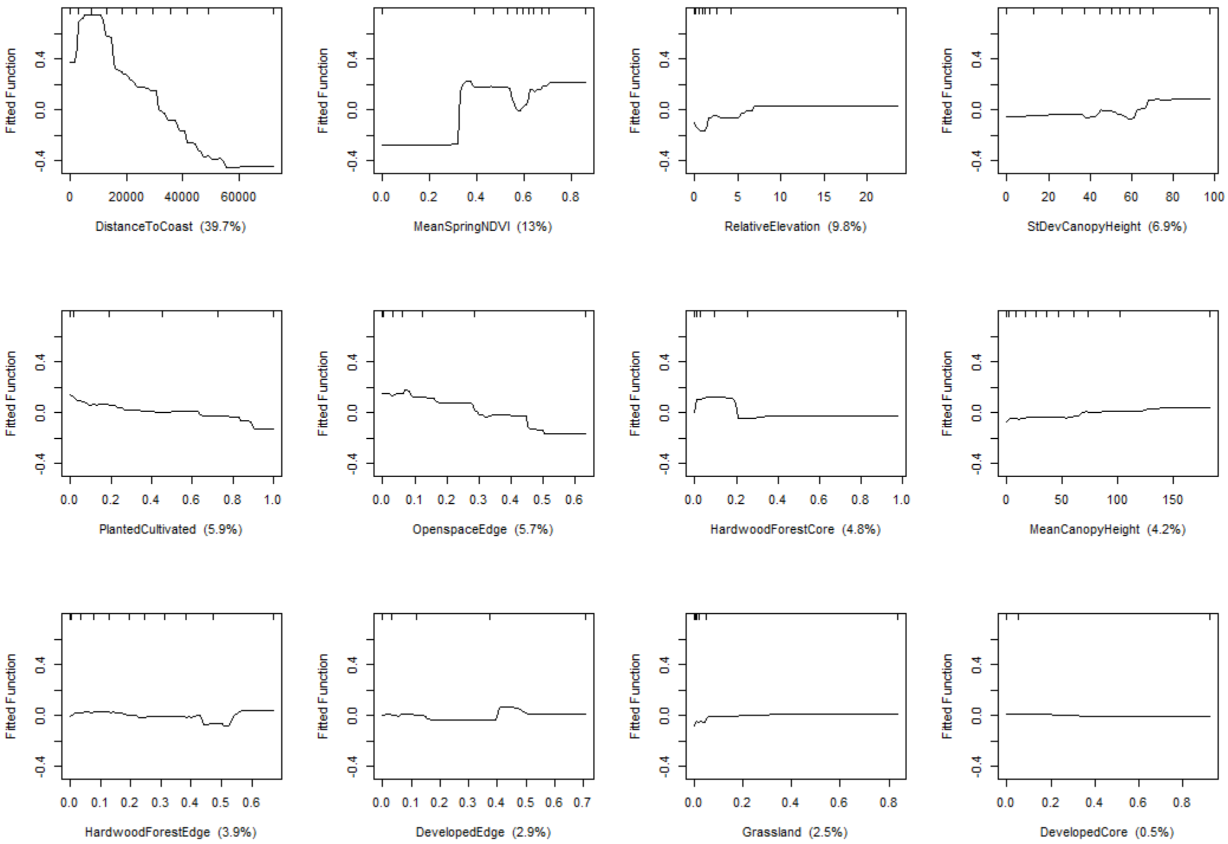
APPENDIX C. Partial dependence plots of top twelve variables for predicting mean bird density in spring at the entire region scale. For explanation of the variables and their units, see Table 2. Y axes are centered to have zero mean over the data distribution. Rug plots at inside top of plots show distribution of sites across that variable, in deciles. Values in parentheses denote relative contribution of the variable to the model.



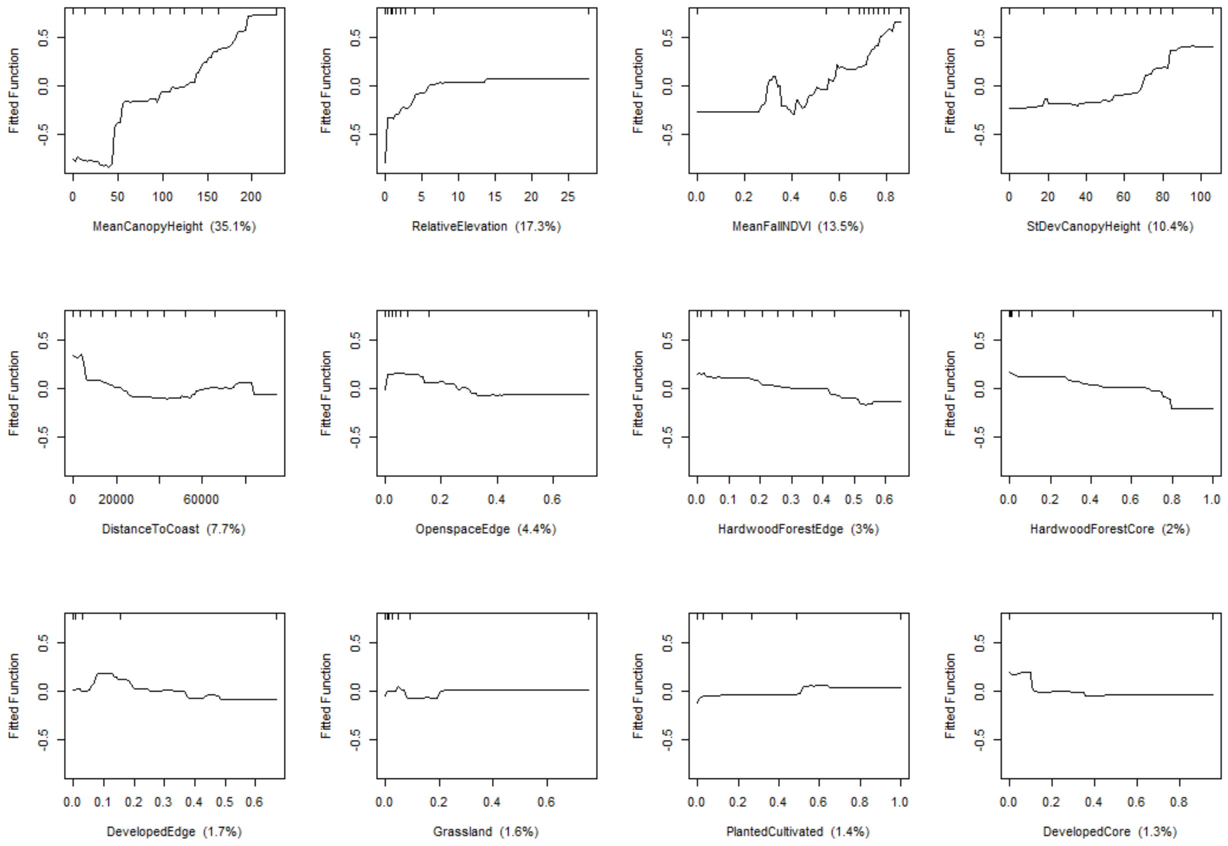
APPENDIX C (continued). Partial dependence plots of top twelve variables for predicting mean bird density in spring for BCR 27. For explanation of the variables and their units, see Table 2. Y axes are centered to have zero mean over the data distribution. Rug plots at inside top of plots show distribution of sites across that variable, in deciles. Values in parentheses denote relative contribution of the variable to the model.



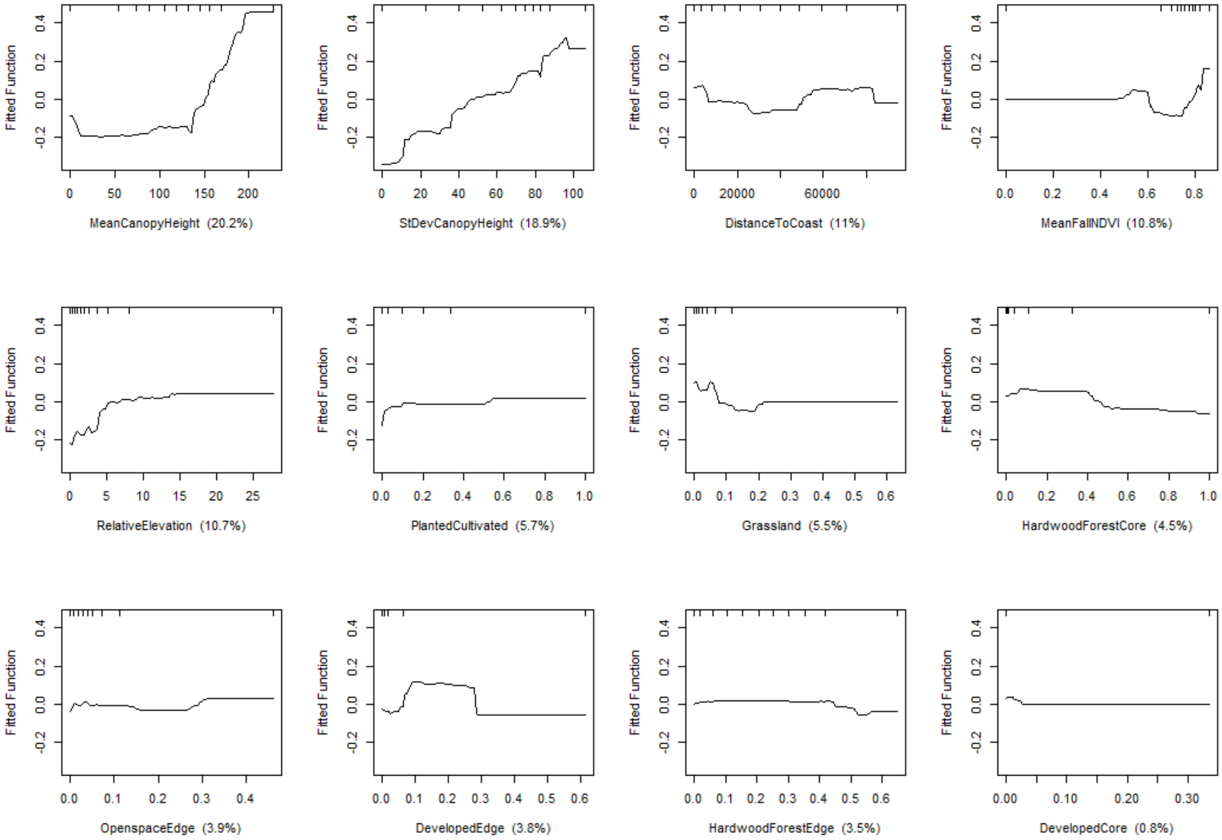
APPENDIX C (continued). Partial dependence plots of top twelve variables for predicting mean bird density in spring for BCR 31. For explanation of the variables and their units, see Table 2. Y axes are centered to have zero mean over the data distribution. Rug plots at inside top of plots show distribution of sites across that variable, in deciles. Values in parentheses denote relative contribution of the variable to the model.



APPENDIX C (continued). Partial dependence plots of top twelve variables for predicting mean bird density in fall at the entire region scale. For explanation of the variables and their units, see Table 2. Y axes are centered to have zero mean over the data distribution. Rug plots at inside top of plots show distribution of sites across that variable, in deciles. Values in parentheses denote relative contribution of the variable to the model.



APPENDIX C (continued). Partial dependence plots of top twelve variables for predicting mean bird density in fall for BCR 27. For explanation of the variables and their units, see Table 2. Y axes are centered to have zero mean over the data distribution. Rug plots at inside top of plots show distribution of sites across that variable, in deciles. Values in parentheses denote relative contribution of the variable to the model.



APPENDIX C (continued). Partial dependence plots of top twelve variables for predicting mean bird density in fall for BCR 31. For explanation of the variables and their units, see Table 2. Y axes are centered to have zero mean over the data distribution. Rug plots at inside top of plots show distribution of sites across that variable, in deciles. Values in parentheses denote relative contribution of the variable to the model.