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Changes in the Breeding Range of the Broad-Winged Hawk (Buteo platypterus) due to Habitat Fragmentation in the Northern Appalachian Region

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Abstract

The Broad-winged Hawk (BWHA), Buteo platypterus, a small, secretive hawk with distinguishing broad black tail bands, breeds in northeastern North America. The hawks nest in deciduous or mixed forest, often near water, and close to clearings or forest edges. Land conversion and fragmentation alters the landscape and reduces the area of contiguous forest used by BWHA. This study seeks to determine the habitat metrics that may be influencing the apparent breeding range declines of the BWHA at the landscape scale. Landscape characteristics and BWHA presence data from 18,684 Breeding Bird Atlas blocks (each about 25km2) from Ohio, West Virginia, Maryland, Pennsylvania, and New York for two atlas period (1st Atlas: 1980s, 2nd Atlas: 2000s) were analyzed. Logistic regression models revealed block level declines in BWHA presence that were associated with increases in urban, barren, wetland and agricultural land cover. These trends were especially prevalent in low-elevation areas around the region's largest cities: New York, Philadelphia, Baltimore and Washington DC. Alternatively, an increase in predicted presence was associated with increases in core and edge forest, specifically in regions of New York. Availability of forested habitat with large areas of core forest at higher latitudes and elevations appear to be influential in the breeding habitat selection of BWHA and may be suggestive of a climate change influence. Additional research on the relative influence of each of the metrics and the impacts that the range decline may have on BWHA populations is warranted

Keywords

Broad-winged Hawk, Northern Appalachian Mountains, habitat change, Breeding Bird Atlas

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Changes in the breeding range of the Broad-Winged Hawk (*Buteo platypterus*) due to habitat fragmentation in the Northern Appalachian region

by

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A thesis submitted in partial fulfillment of the requirements for the Degree of Bachelor of Science in the Environmental Studies Major.

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I affirm that I have upheld the highest principles of honesty and integrity in my academic work and have not witnessed a violation of the Honor Code. Rachael M Pruitt

May 8, 2017

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ABSTRACT

The Broad-winged Hawk (BWHA), *Buteo platypterus*, a small, secretive hawk with distinguishing broad black tail bands, breeds in northeastern North America. The hawks nest in deciduous or mixed forest, often near water, and close to clearings or forest edges. Land conversion and fragmentation alters the landscape and reduces the area of contiguous forest used by BWHA. This study seeks to determine the habitat metrics that may be influencing the apparent breeding range declines of the BWHA at the landscape scale. Landscape characteristics and BWHA presence data from 18,684 Breeding Bird Atlas blocks (each about $25km^2$) from Ohio, West Virginia, Maryland, Pennsylvania, and New York for two atlas period (1st Atlas: 1980s, 2nd Atlas: 2000s) were analyzed. Logistic regression models revealed block level declines in BWHA presence that were associated with increases in urban, barren, wetland and agricultural land cover. These trends were especially prevalent in low-elevation areas around the region's largest cities: New York, Philadelphia, Baltimore and Washington DC. Alternatively, an increase in predicted presence was associated with increases in core and edge forest, specifically in regions of New York. Availability of forested habitat with large areas of core forest at higher latitudes and elevations appear to be influential in the breeding habitat selection of BWHA and may be suggestive of a climate change influence. Additional research on the relative influence of each of the metrics and the impacts that the range decline may have on BWHA populations is warranted.

INTRODUCTION

Habitat loss and fragmentation are threats to biodiversity throughout the world and are of continued concern to wildlife conservationists (Fahrig 2003). Habitat fragmentation is defined as the division of a certain habitat into several isolated patches, resulting in a reduction of suitable habitat for any given species (Rolstad 1991). The formation of edges, especially in forest habitats, increases inter-specific competition, changes the structure of available habitat, and opens up niches for some species. Forest fragmentation due to conversion to urban developments and agricultural land leads to loss in the area of suitable habitat for forest specialist species, particularly those that avoid forest edges. This alteration of habitat can have negative implications, especially for migratory birds. Migrant species are known to be associated with more natural habitats like forest and wetlands (Flather and Sauer 1996), therefore loss of these habitats may be detrimental to their ability to find appropriate breeding habitat. In contrast, resident species are often habitat generalists, and thus may benefit from fragmentation, or are unaffected by it (Flather and Sauer 1996). Because landscape structure is important for breeding location in migrating birds, the alteration of these landscapes has important ecological consequences.

Landscape change in the Northeastern United States

The Northeastern United States hosts a wide range of land cover types and large tracts of contiguous forest. In particular, the mountainous regions of the Appalachian and Allegheny Mountains are an important region for breeding and migrating birds. The large patches of contiguous forest found throughout these mountain ranges support a high diversity of bird species, making them an important region for observing the impacts of land use change on bird distributions (Abrahams et al. 2015). As part of the Appalachian Mountains Joint Venture, a partnership of organizations working to conserve bird habitat (http://www.amjv.org), this region is especially significant for migratory bird conservation. Most of the native forest in this region was cleared during the 19th century for logging and agriculture but secondary forest growth now dominates in areas that are less suitable for agriculture. However, the implications of forest fragmentation in this diverse region continue to be of concern.

One of the main drivers of land conversion is the increase in urban development (Drummond and Loveland 2010). The Northeast United States contains some of the largest cities in the country,

including the Northeast Megalopolis, which contains almost one fifth of the population of the United States. As populations of these urban centers grew, the urban and exurban expansion has resulted in extensive urban sprawl, which continues to replace forested and natural lands. Estimates of total forest loss between 1973 and 2000 total 10.05 million ha, with a net decline of forest cover of more than 3.70 million ha (Drummond and Loveland 2010). The mid-Atlantic coast region exhibited net forest decline as a result of urban development, while other regions showed a cycle of forest growth and loss (Drummond and Loveland 2010).

A more recent driver of forest fragmentation in the Northeast United States, particularly in Pennsylvania, is the development of infrastructure for oil and natural gas extraction. Exploration for development sites is becoming more prevalent throughout the Allegheny Plateau of Pennsylvania, as well as nearby West Virginia and Ohio (Drohan et al. 2012). The Marcellus Formation, an expansive reserve of economically viable shale gas, encompasses a large portion of the Northern Appalachians. The development of hydraulic fracturing sites fragments forest landscapes through the implementation of access roads, compressor stations and gathering pipelines, in addition to the placement of wells pads that typically span 1.2-2.8 ha (Abrahams et al. 2015). In Pennsylvania, 45% of existing pads are located within forests, of which 23% are in core forest (Drohan et al. 2012). Future development of well pads could result in the loss of 695 ha of core forest in Pennsylvania, resulting in an increase in the area of forest edge (Drohan et al. 2012). In addition to the well pads themselves, an increase in 282 km of roads to new pads will further fragment the landscape, thereby increasing the area of edge forests, which can exacerbate the potential for the spread of invasive species as the forest is disturbed (Drohan et al. 2012).

Broad-winged Hawk

The Broad-winged Hawk (BWHA), *Buteo platypterus*, is a small, secretive hawk that has a breeding range extending from Nova Scotia south through the Appalachian region into Arkansas, west through the Great Lakes region and north of the Canadian border (Kaufman 1996). The smaller stature and distinct broad black tail bands of the Broad-winged Hawk distinguish it from other hawk species. Broad-winged Hawks migrate to Central and South America in the fall and return to North America in the spring to breed. Nesting usually begins in April and ends by mid-September for northern populations but may begin earlier in southern populations (Matray 1974, Fitch 1974). Rosenfield (1984) found that Broad-winged Hawks often reoccupied the same

nesting area in Wisconsin each year. Hawks that return to the same breeding area often rebuild nests from the previous year (Crocoll and Parker 1989). This philopatric behavior suggests that landscape change may lead to the need to alter nesting location due to loss of habitat, potentially causing an alteration of migration behavior.

Broad-winged Hawks most often nest in deciduous or mixed forest, often near water, and close to clearings or forest edges (Kaufman 1996). In northeastern Kansas, Broad-winged Hawks inhabited scrubby and thorny second-growth forest with limestone outcrops adjacent to pastures and old-fields (Fitch 1974). Titus and Mosher (1981) also found that Broad-winged Hawks select nest sites based on proximity to water, and distance to forest opening. In Wisconsin, Rosenfield (1984) found nests within 50 meters of an edge and in areas close to water, including areas with poor drainage. In New York all nests were found less than one kilometer from a water source (Crocoll and Parker 1989). The close proximity to water is most likely due to the higher prey density found near water sources (Titus and Mosher 1981, Crocoll and Parker 1989). Additionally, forest edges and upland openings are thought to be used as primary hunting sites for the Broad-winged Hawk due to prey availability and accessibility (Rosenfield 1984). However, forest fragmentation can lead to a decrease in availability of small vertebrate prey, one of the main food sources of the Broad-winged Hawk (Fitch 1974). The most common prey include voles, mice, small birds and amphibians (Rusch and Doerr 1972). On the local scale, these characteristics are important for nest site selection, but little is known about how habitat change at the landscape scale impacts habitat use. It is commonly noted that contiguous forests provide the best landscape for nest sites of the Broad-winged Hawk (Wilson et al. 2012, Abrahams et al. 2015), but whether they will change their nesting location when these forests become altered is unclear. Determining if land cover change has an impact on the on the breeding range of this species will be valuable information for better understanding its ecology.

Threats to Broad-winged Hawks in the Northeast United States

Breeding bird surveys have already indicated locally losses of Broad-winged Hawks in parts of the Northeastern United States including parts of Maryland (Ellison 2010), New York (McGowen and Corwin 2008), Pennsylvania (Wilson et al. 2012), and Ohio (Rodewald et al. 2016) (Figure 1). Many of these decreases are thought to be associated with increasing fragmentation and urbanization (Wilson et al. 2012). Unlike other species of hawks, the Broad-

winged Hawk is rarely found in small woodlots or in built-up landscapes, therefore competition with larger hawk species for nesting sites may increase as suitable habitat becomes less available (Ellison 2010). While Broad-winged Hawks are currently listed as of least concern by the IUCN, they continue to face pressure from climate change and land conversion (BirdLife International 2012). Preemptive understanding of how habitat change in the Northeast is impacting the Broad-winged Hawk could be beneficial for understanding and managing the habitats of the Broad-winged Hawk and other migratory hawk species in the future. This study examines the landscape metrics that are associated with local changes in the breeding range of the Broad-winged Hawk in the Northern Appalachian Mountains and surrounding areas. I hypothesize that fragmentation, loss of core forest and conversion of land to agriculture are the main drivers of the observed loss of Broad-winged Hawks from some areas since the 1980s.

METHODS

Breeding Bird Atlas Data

I obtained Broad-winged Hawk presence data from the Breeding Bird Atlases for five contiguous states in the Northeastern United States: Pennsylvania, New York, Ohio, West Virginia and Maryland. Breeding Bird Atlas data were collected primarily through volunteer effort and a strict protocol of procedures for data collection is employed. This protocol ideally ensures consistency in coverage among blocks and requires that a significant amount of time is invested in each sampled block (Porter and Jarzyna 2013). Although atlas methodologies are designed to ensure consistent coverage, in reality, coverage is inconsistent. Breeding Bird Atlases are useful for monitoring range shifts of birds because they have relatively even sampling periods, are repeated at ecologically relevant intervals, typically every 20 years, and provide data at the landscape scale (Dickinson et al. 2010). The atlases used in this study are based on approximately 5x5 kilometer (c. 3x3 mile) gridded sampling blocks. The study area encompassed 18,684 atlas blocks equaling 471,590 km^2. Sampling for the first atlas was conducted during the 1980s and the second atlas was conducted during the 2000s (Table 1).

Landscape Metrics

I used ArcMap 10.3.1 (ESRI, Redlands, CA) to calculate landscape metrics within each atlas block for both atlas periods (Appendix, Table 5). I used land cover data (National Land Cover Database) for the period closest to the middle of the atlas surveys for the second atlas (MD, NY,

PA: 2006; WV, OH: 2011) (Fry et al. 2011, Homer et al. 2015) and 1992 land cover data for the first atlas, since it is the earliest land cover data available. The National Land Cover database uses a 16-class land cover classification scheme at a spatial resolution of 30 meters for 2001 and later. Land cover data for 1992 uses a 21 class system at a 30 meter spatial resolution. Because 1992 land cover data were not compatible with more recent land cover products, I used the retrofit land cover change product to determine 1992 land cover values in order to maintain a comparable classification scheme (Fry et al. 2009). I tabulated the area of each of the 7 broad categories of land cover within each block: water, urban, barren, forest, shrubland/grassland, agriculture, and wetlands. I computed the Shannon diversity index of the 7 broad land cover types within each block (Flather and Sauer 1996).

I used the Landscape Fragmentation Tool (LFT) geoprocessing package (Shapiro et al. 2016) which uses morphological image processing to differentiate forest land cover into core and edge classifications (Vogt et al. 2007). Morphological image processing uses pixel-level classification to differentiate forest type using morphological operators of erosion, dilation, and skeletonization. Erosion shrinks, dilator expands and the direction is defined by a geometric object of fixed shape and size, called a structuring element. The process identifies forest as different classifications by taking into account the pixels that surround it using cell neighborhoods defined by the structuring element. By systematically removing pixels that have been defined, the remaining pixels can be appropriated to a determined category. The LFT identifies four forest classes: core forest is far from non-forest boundaries, patch forest is forest that is too small to contain core forest, perforated forest are the boundaries between core forest and small patches of non-forest and edge forest are the boundaries of forest surrounding large areas of non-forest (Vogt et al. 2007). The four categories determined by the LFT were then grouped into two forest classes: (1) core and inner edge, and (2) patch and outer edge. Tests of the tool revealed that 7x7 cell neighborhoods resulted in forest edge bands of approximately 90 meters, consistent with definitions of edge forest as forest further than 100 m from a forest edge. The area for each of the three defined classes (non-forest, core and edge) was tabulated for each block. I converted the core forest raster to polygon and conducted summary statistics to determine the number of core forest patches per block and the area of the largest patch of core forest that was intersected by the block. The core to edge ratio, a commonly employed measure

of forest fragmentation, was determined by dividing the area of core by the total area of forest (Imre 2006). I derived topography for the study region from a digital elevation model (DEM; USGS, http://nationalmap.gov/elevation.html). The mean, maximum, minimum and range elevation were tabulated for each block.

Statistical Analysis

Because survey coverage was variable, both spatially and temporally, and the detection of birds is a function of observer effort, I included a proxy of survey effort as a covariate in my models (Sadoti et al. 2013). Because actual survey effort (e.g. total hours spent in each block) was not available for every atlas dataset, I used recorded species richness as my proxy measure (Figure 2A, 2C). A positive linear trend was seen between the species richness and the proportion of blocks that had observations of Broad-winged Hawks, indicating the relationship between the number of species recorded and the likelihood of hawk detection (Figure 2B, 2D). To correct for the variation in sampling effort (i.e. low sampling effort in Ohio and West Virginia), I used a regression model with landscape metrics as explanatory variables to predict the number of species for blocks with little or no sampling effort. For these predictions of species richness, I restricted the analysis to blocks that likely had comprehensive survey coverage—those in which 70 or more species were recorded. Because I had 17 candidate landscape metric covariates, I used Stepwise AIC in Program R (R Core team, 2013) in order to determine the best fit model with a retained subset of landscape metrics that were associated with species richness.

Spatial regression using package INLA in Program R (Blangiardo et al. 2013) was conducted to predict the number of species per block. Package INLA uses integrated nested Laplace approximation to efficiently perform computationally expensive Bayesian inference. I used a Besag-York-Mollie (BYM) specification (Blangiardo and Cameletti 2015) to account for spatial autocorrelation in the data, and provide spatially specific predictions in all blocks in which fewer than 70 species were recorded. The model of species richness took the form:

$$n_i = b_0 + \sum_j \beta_j z_{ij} + u_i + v_i$$

Where *n* is the number of species in block $_i$, b_0 is the intercept, *z* are $_j$ landscape covariates with linear effects *ß*, $u_i$is the spatially structured residual using an iCAR specification, and v_i are unstructured residuals. To account for gaps between blocks within the study area (i.e. non-contiguity of block boundaries along some state lines), I used Voronoi tessellation of atlas blocks as the spatial structure. I used these methods to create maps of predicted species richness across all blocks in both the first and second atlases.

I performed a spatial logistic regression using package INLA to model probability of block occupancy of Broad-winged Hawks in the first atlas and the second atlas respectively. The presence of Broad-winged Hawk was included as the criteria value and landscape metrics for the respective time period were included as the explanatory variables. Similar to the total species prediction analysis, I used a stepAIC model to reduce candidate landscape metrics to a smaller subset for inclusion in the spatial models. The predictions were back transformed to correct for varying survey effort by including the greatest value for species richness between the predicted and actual number of species as in place of the actual value used in the regression equation. The spatial models took the same form as those used to predict species richness, but the probability of Broad-winged Hawk presence *y* in block $_i$ follows a Bernoulli distribution, and predicted species richness is included as a covariate $S_{i:}$

$$y_i \sim \text{Binomial}(\pi_i n_i)$$

$$n_i = \text{logit}(\pi_i) = b_0 + S_i + \sum_j \beta_j z_{ij} + u_i + v_i$$

I calculated the difference between the probability of Broad-winged Hawk block occupancy in the first atlas and the second atlas and changes in landscape metrics between the two time periods. I used the same spatial regression modeling procedure as used to predict species richness and probability of Broad-winged Hawk presence to identify landscape metrics that were associated with changes in the probability of Broad-winged Hawk presence. Predicted changes in Broad-winged Hawk presence were approximately normally distributed (mean = -0.128, standard deviation= 0.173), so were modeled using Gaussian likelihood model.

Evaluating Model performance

I calculated Area under the Receiver Operator Curve (AUC) values for the predicted Broad-winged Hawk presence to determine the effectiveness of my models. Because the original data included a large number of false negatives (blocks with little or no survey effort), I also calculated AUC for blocks for which survey effort was comprehensive (70 or more species recorded). I denote these two measures as AUC_{all} and AUC_{70}, respectively. AUC was calculated from a test sample of 10% of available data, i.e. 1,868 for AUC_{all}, and 615 and 861 for AUC_{70} in the first atlas and second atlases respectively.

RESULTS

Changes in land cover between atlas periods

Changes in land cover reflect a general conversion of forest to other land cover types within the study area. Forested land decreased by 3,584 km^2 or an average of 0.19 km^2 per block between the two atlas periods. This net loss of forest cover was almost entirely attributable to a loss of core forest (-3,577 km^2), while the area of edge forest was virtually unchanged (-42.6km^2). The number of core patches, area of agriculture and area of wetlands also showed an overall decrease between atlas periods. In contrast, the area of urban land increased by 5,657 km^2 or an average of 0.30 km^2 per block. The area of barren land also increased in amount by 345 km^2, or an average of 0.018 km^2 per block, between the two atlas periods. Land cover diversity showed an overall increase.

Survey Effort Correction

Non-spatial models of species richness identified 11 landscape metrics that were associated with species richness for both atlas periods (Appendix, Table 6). The spatial model revealed significantly positive trends between the number of species and area of the block, core to edge forest ratio and the Shannon diversity index in the first atlas. Core to edge forest ratio, and Shannon diversity index were positively associated with species richness in the second atlas. Spatial models showed significant negative relationships between species richness and area of urban land, area of barren land and area of agricultural land in both atlas periods (Table 2). The model predicted a mean species richness of 79.2 species per block in the first atlas (s.d. = 3.5), and 79.1 species in the second atlas (s.d. = 4.4). The highest species richness was predicted in Northeast Ohio and regions of New York in both atlas periods (Figure 3 and 4). Lower species

richness was predicted throughout West Virginia in the second atlas than the first atlas (Figure 3 and 4). Expanded regions of high species richness were seen in the second atlas throughout New York (Figure 4).

Broad-winged Hawk Presence Predictions

Non-spatial models identified 11 landscape metrics associated with Broad-winged Hawk presence in both atlas periods, although there was some variation between them (Appendix, Table 7 and 8). Of these metrics, five were consistent between the atlas periods: species richness, area of edge forest, area of wetlands, area of agricultural land, and size of the largest patch of core forest intersecting the block. Spatial models revealed that species richness, area of edge forest, number of core patches, size of the largest patch of core forest intersecting the block, area of barren land, area of forest land and mean elevation had significant positive trends, while area of agricultural land and the Shannon diversity index had significant negative trends in the first atlas (Appendix, Table 7). Spatial models for the second atlas showed significantly positive trends in the species richness, area of core forest, area of edge forest, number of core patches, size of the largest core patch intersected, area of wetlands and maximum elevation. Significantly negative trends were noted between area of agricultural land and presence of Broad-winged Hawks (Appendix, Table 8).

Change in Broad-winged Hawk Presence

Changes in probability of Broad-winged Hawk occurrence were positively associated with change in core forest area, change in edge forest area, change in the number of core forest patches, the change in core to edge forest ratio, change in the largest core forest patch that was intersected by the block and mean elevation (Table 3). Changes in probability of occurrence were negatively associated with area of edge forest found in the first atlas, area of forest found in the first atlas, maximum elevation, and change in area of water, urban, barren, agriculture, and wetlands (Table 3). My model showed a substantial area of reduced Broad-winged Hawk occurrence in central Maryland/southeast Pennsylvania, and in southwest West Virginia (Figure 5). There was also a striking pattern of reduced probability of Broad-winged Hawks occurrence at lower elevations between atlas periods (Figure 6N and 6P).

Predicted changes in Broad-winged Hawk occupancy suggests that range size of the Broad-winged Hawk has declined by 12.8% between the 1980s and 2000s. This indicates that Broad-winged Hawks have been predicted to be lost from more blocks than they persisted in or more recently inhabited and suggests a decline in distribution. Although these models do not show the relative importance of each variable in this decline, there are indications that changes in land use have likely affected the local distribution of Broad-winged Hawks in parts of the study region.

Relationship between change and significant variables

If a large area of edge forest was found in the first atlas, it is less likely that a Broad-winged Hawk will be found in that block during the second atlas (Figure 6A). Increases in the number of core forest patches showed positive trends in the model but the simple relationship between change in the number of patches and average change of predictions indicates a negative trend, variation which is likely a reflection of the nature of multiple regression analysis (Figure 6B). Increasing the core to edge ratio (i.e. increasing the area of core forest) indicates an increase in the probability of presence of Broad-winged Hawks (Figure 6C). As more patches were found within a block, the probability of a Broad-winged Hawk occupying that block decreased. The negative trends seen in the other significant land cover variables—barren, wetland and water—indicate that conversion to these land cover is likely to reduce the probability of Broad-winged Hawk presence (Figure 6E, 6G, 6J). The change in area of urban land cover shows a negative trend indicating that increasing urbanization results in a lower probability of Broad-winged Hawk occupancy (Figure 6F). Change in area of agriculture shows a negative trend based on the regression coefficient but is positively related to the predicted change in probability (Figure 6H). Change in area of core forest, shows a positive trend between an increase in core forest area and increasing probability of occupancy of Broad-winged Hawks (Figure 6K).

These trends show that Broad-winged Hawks are sensitive to land cover change and suggests that that they may be impacted more so by forest conversion than fragmentation. Of the 10 significant land cover change variables, 5 are non-forest land cover variables that are negatively associated with the change in predicted presence of Broad-winged Hawks. The other metrics indicate a positive association with increases forest area.

Model Verification

Area under the Receiver Operator Curves (AUC) for the models of Broad-winged Hawk distribution in the first and second atlases suggests that the model was good at predicting Broad-winged Hawk occurrence (AUC_{all}; Table 4). AUC for blocks with good observer coverage (and hence, lower false negative rates), suggest that the models performed well (AUC_{70}; Table 4).

DISCUSSION

Effects of land use and land use change on Broad-winged Hawks

The overall decrease of the range of the Broad-winged Hawk in the Northern Appalachian region appears to be associated with increases in non-forest land cover. Land cover metrics with a significant positive relationship with change in probability of Broad-winged Hawk presence are related to forest composition. A number of metrics point to the association of Broad-winged Hawk occupancy with large tracts of contiguous forest. The positive relationship of the change in the largest core forest patch also indicates an association with large tracts of contiguous forest. In addition, the positive association observed between an increase in the core to edge ratio since the 1980s and increases in the probability of presence of Broad-winged Hawks suggests that large areas of core forest are a key metric in the distribution of this species. Core forest has increased through much of northern New York and more locally, generally at higher elevations, further south (Figure 7), the same areas in which the probability of occupancy of Broad-winged Hawks has been maintained or increased in probability since the 1980s (Figure 5). Because a large portion of the overall decrease in forest is accounted for in changes in core forest, the changes in total forest area show similar trends (Appendix, Figure 9 and 10).

The positive association between change in the area of edge forest and probability of presence indicates that some increase in edge is likely not detrimental to nesting site selection. This species may be able to cope with increasing edge forest as long as there are also large tracts of core forest in the region. Rusch and Doerr (1972) report observations of Broad-winged Hawk presence along edges of large contiguous forest patches in New York. Since Broad-winged Hawks are known to forage along forest edges, it is possible that they may be finding more food resources with increasing edge forest area. Broad-winged Hawks consume small mammals including voles and other small vertebrates that are often found in clearings (Rusch and Doerr 1972). It should also be noted that increasing edge forest area may not, by itself, be an indication

of increasing forest fragmentation, but could also result from reforestation of small patches and woodlots, which would nearly all be classified as edge forest. Similarly, the positive relationship between number of core forest patches and presence of Broad-winged Hawks is open to multiple interpretations. For instance, an increase in number of core patches may be due to increased fragmentation, but could also be due to merging of small forest patches. The positive association of these forest landscape metrics suggests that area forest itself, regardless of whether it is fragmented, is likely a major driver of Broad-winged Hawk distribution at the atlas block scale.

Although this analysis does not definitively determine the drivers related to change in Broad-winged Hawk distribution in specific regions (i.e. the drivers acting in Maryland may be different than drivers of the change observed in southwest West Virginia), some trends are apparent. Increased urbanization is most apparent in central and eastern Maryland and southeast Pennsylvania (Figure 8). Jantz et al (2005) described an increase in urban area in the Chesapeake Bay watershed of more than 20% between 1990 and 2000, particularly around Washington, DC, Baltimore, MD and Philadelphia, PA. They found a greater percentage of land was converted from agriculture to urban land cover than from forest to urban land. This differentiation was not made in my study, but the analysis of the effects of different land conversion types may warrant future analyses. A negative association between the presence of Broad-winged Hawks and increasing urbanization points toward avoidance of breeding in increasingly urban areas by this species of hawk. Bosakowski and Smith (1997) suggested that in New Jersey, Broad-winged Hawks were less sensitive to urbanization than other species, such as the Red Shouldered Hawk, but noted that they preferred regions of contiguous forest. The majority of landscape metrics associated with loss of Broad-winged Hawks were related to changes in non-forest land cover types. These associations suggest that increases in non-forest land cover in the study region are contributing to shifts in occupancy of the Broad-winged Hawk.

It is likely that the shift in range is not attributed to solely one agent; rather a combination of habitat loss, fragmentation, prey availability, climate, or other biotic factors may have an influence on habitat suitability. It is important to note that the relative contribution of each of the landscape metrics was not differentiated in this analysis and further analysis of degree of influence may be beneficial for better understanding the principal drivers of distribution change.

Elevation

The positive relationship between mean elevation and the change in occupancy suggests that land cover may not be the sole or primary driver in the change in Broad-winged Hawk distribution. However because urbanization and forest loss are especially prevalent in lower elevations areas, like the Chesapeake Bay region, it is difficult to tease out the potentially separate effects of topography and land cover. Loss of climatically-sensitive organisms from low elevations has been widely attributed to climate change, but the response of Broad-winged Hawks to climate change has not been thoroughly studied. Studies of other migrant species have reported northerly shifts in range in response to climate change (Tingley et al. 2009, Zuckerberg et al. 2009). Zuckerberg et al (2009) reported most species having little elevational shift in responses to climate changes, suggesting a greater latitudinal than elevational response. Rodenhouse et at (2008) predicted changes in species abundance based on climate change variables and found significant changes in presence of neotropical migrants in the Northeastern United States. The pattern of decreased Broad-winged Hawk occurrences in the southern and lower elevation regions of my study area, and increased occurrence at higher elevations and in more northern latitudes are suggestive of an influence of climate change on this species' distribution. Further analysis of how climate change may be playing a role in the range decline of migrant species in the Northern Appalachian region should be considered.

Limitations

The mismatch of time periods between NLCD data and the first Breeding Bird Atlas data (1992 land cover versus 1980s bird data) introduces some bias to the analysis, namely that change in land-cover may have been underestimated. The secretive nature of the Broad-winged Hawk may have led to a large number of false negatives in the atlas data set. While I attempted to overcome this issue assuming a linear relationship between effort (number species reported in each block) and the probability of detecting Broad-winged Hawks, I acknowledge that this approach is simplistic, and that the actual relationship between species richness and hawk detection may be non-linear, and may vary regionally. While these limitations are not trivial, the tremendous amount of data available on this species through the combined ten atlas projects confers some confidence that the spatial patterns observed are genuine.

Conservation implications and recommendations

Preserving large tracts of contiguous forest, especially at higher elevations will become increasingly important to support forest dependent migrant species. A shift in range and decrease of suitable habitat may lead to increased competition between other larger hawk species and the Broad-winged Hawk for nesting sites (Ellison 2010). Since there is an association with large core forest fragments, these areas should continue to be the focus on conservation strategies. Reducing the conversion of forest to non-forested land is also an important and influential component of habitat conservation. A better understanding of how changes in the landscape are altering the habitat choices of the Broad-wing Hawk, as well as other species, is important for ensuring that these habitats are present in future landscapes. Determination of regions where the greatest threats are may help resource managers to preserve and better define bird conservation areas. Many questions still remain regarding the area of land that is necessary for persistence of Broad-winged Hawks, the most relevant drivers of the range shift and the impacts that shifts may have on Broad-winged Hawk populations. Further analysis is warranted to support conclusions of the drivers defined in this study. Additionally, similar methodology could be applied to other migratory species to determine important metrics related to their breeding range and may be especially important for species that may be in decline.

Future analysis will focus on using an Information Criterion approach (e.g. WAIC; Link and Sauer 2016) to compare suites of models of change in Broad-winged Hawk distribution. This will allow direct comparisons of competing hypotheses for the observed change in Broad-winged Hawk distribution and attempt to answer the question: is change most associated with habitat loss, habitat fragmentation, correlates of climate (elevation and latitude), or combinations of all of these factors?

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TABLES AND FIGURES

Table 1. The number of blocks sampled for each state of the study region and the dates of sampling for the first and second atlas periods.

State	No. blocks	1st Atlas dates	Citation	2nd Atlas dates	Citation
Maryland	1,294	1983-87	Robbins, Chandler S., senior ed. (1996). *Atlas of the breeding birds of Maryland and the District of Columbia*. Univ. Pittsburgh Press. 479 p.	2002-06	W. G. Ellison, ed. (2010). *Atlas of the Breeding Birds of Maryland and the District of Columbia*, Johns Hopkins University Press, Baltimore, MD, USA, 2nd edition. 520 p.
New York	5,332	1980-85	Andrle, Robert F., and Janet R. Carroll, eds. 1988. *The atlas of breeding birds in New York State*. Cornell Univ. Press, Ithaca. 551 p.	2000-05	McGowan, K.J. and K. Corwin, eds. 2008. *The Second Atlas of Breeding Birds in New York State*: 2000-2005. Cornell Univ. Press, Ithaca, NY. 688 p.
Ohio	4,447	1982-87	Peterjohn, Bruce G., and Daniel L. Rice, eds. 1991. *The Ohio breeding bird atlas*. Ohio Dept. of Natural Resources, Division of Natural Areas and Preserves, Columbus, Ohio. 416 p.	2006-11	Rodewald, Paul, Matthew Shumar, Aaron Boone, David Slager, and Jim McCormac, eds. 2016. *Second Atlas of Breeding Birds in Ohio*. Pennsylvania State University Press, University Park, PA. 600 p
Pennsylvania	4,937	1985-89	Brauning, Daniel W., ed. 1992. At*las of breeding birds in Pennsylvania*. Univ. Pittsburgh Press. 484 p.	2004-09	Wilson, A., D. Brauning, and R. Mulvihill, eds. 2012. *Second Atlas of Breeding Birds in Pennsylvania*. Pennsylvania State University Press, University Park, PA. 586 p.
West Virginia	2,653	1984-89	Buckelew, Albert R. Jr., and George A. Hall, eds. 1994. *West Virginia Breeding Bird* Atlas. Univ. Pittsburgh Press 215 p.	2009-14	In prep. (unpublished data)

Table 2. Significant metrics in the spatial model of species richness for the 1st Atlas (top) and 2nd Atlas (bottom). **Bold**: 95% CI does not overlap zero.

		95% Credible Interval	
	Parameter estimate	Lower	Upper
(Intercept)	**71.6766**	**69.1905**	**74.1604**
Area of block	**0.1953**	**0.1075**	**0.283**
Count of Core Patches	-0.0071	-0.0157	0.0015
Ratio of Core to Edge Forest	**2.0933**	**0.4905**	**3.695**
Largest forest patch intersecting block	0	-0.0001	0.0001
Area of Water	0.0934	-0.095	0.2817
Area of Urban	**-0.3546**	**-0.4637**	**-0.2456**
Area of Barren	**-1.1019**	**-2.145**	**-0.0597**
Area of Agriculture	**-0.2577**	**-0.3463**	**-0.1691**
Mean elevation	-0.0041	-0.009	0.0007
Max elevation	0.0022	-0.0017	0.0061
Shannon Diversity Index	**14.0614**	**11.2947**	**16.826**

		95% Credible Interval	
	Parameter estimate	Lower	Upper
(Intercept)	67.7219	66.1449	69.2976
Count of Core Patches	**-0.0178**	**-0.0268**	**-0.0088**
Ratio of Core to Edge Forest	**5.3055**	**3.7072**	**6.9024**
Largest forest patch intersecting block	-0.0454	-0.1992	0.1083
Area of Water	**0.3813**	**0.2266**	**0.5357**
Area of Barren	**-1.0432**	**-1.7238**	**-0.3632**
Area of Forest	**0.1928**	**0.107**	**0.2785**
Area of Grasslands	0.1323	-0.145	0.4093
Area of Wetlands	**0.8219**	**0.6757**	**0.9681**
Mean elevation	0.0006	-0.0021	0.0034
Minimum Elevation	0.0001	-0.0004	0.0006
Shannon Diversity Index	**15.6884**	**13.1087**	**18.2658**

Table 3. Landscape metrics included in the Broad-winged Hawk presence models for the change in Broad-winged Hawk Presence between the first and second atlas. **Bold**: 95% CI does not overlap zero.

	Parameter estimate	95% Credible Interval	
		Lower	Upper
(Intercept)	**-0.1374**	**-0.1446**	**-0.1302**
Area of Core 1st Atlas	0.0022	-0.0015	0.0059
∆ Area of Core	**0.0042**	**0.0023**	**0.0061**
∆ Area of Edge	**0.0066**	**0.0033**	**0.0099**
Area of Edge 1st Atlas	**-0.0064**	**-0.0102**	**-0.0026**
∆ Count of Core Patches	**0.0002**	**0.0002**	**0.0003**
∆ Ratio of Core to Edge Forest	**0.02**	**0.0166**	**0.0235**
∆ Largest forest patch intersecting block	**0.009**	**0.0063**	**0.0117**
∆ Area of Water	**-0.0218**	**-0.0319**	**-0.0118**
∆ Area of Urban	**-0.0106**	**-0.0132**	**-0.0081**
∆ Area of Barren	**-0.0177**	**-0.0225**	**-0.0128**
Area of Forest 1st Atlas	**-0.006**	**-0.0097**	**-0.0024**
∆ Area of Agriculture	**-0.0198**	**-0.0219**	**-0.0178**
∆ Area of Wetlands	**-0.0027**	**-0.0047**	**-0.0007**
Maximum elevation	**-0.0001**	**-0.0002**	**-0.0001**
Mean elevation	**0.0003**	**0.0003**	**0.0003**

Table 4: Model performance as measured by Area under the Recover Operator Curve (AUC) for models of BWHA occurrence in first and second atlas, based on 10% of all blocks (AUC_{all}) and only blocks with good coverage, i.e. where 70 or more species were document (AUC_{70}).

Model and evaluation method	Test sample size	AUC
AUCall first Atlas	1,868 (10% of 18,684 blocks)	0.7970
AUC70 first atlas	615 (10% of 6,153 blocks)	0.8528
AUCall second Atlas	1,868 (10% of 18,684 blocks)	0.8406
AUC70 second atlas	861 (10% of 8,614 blocks)	0.8848

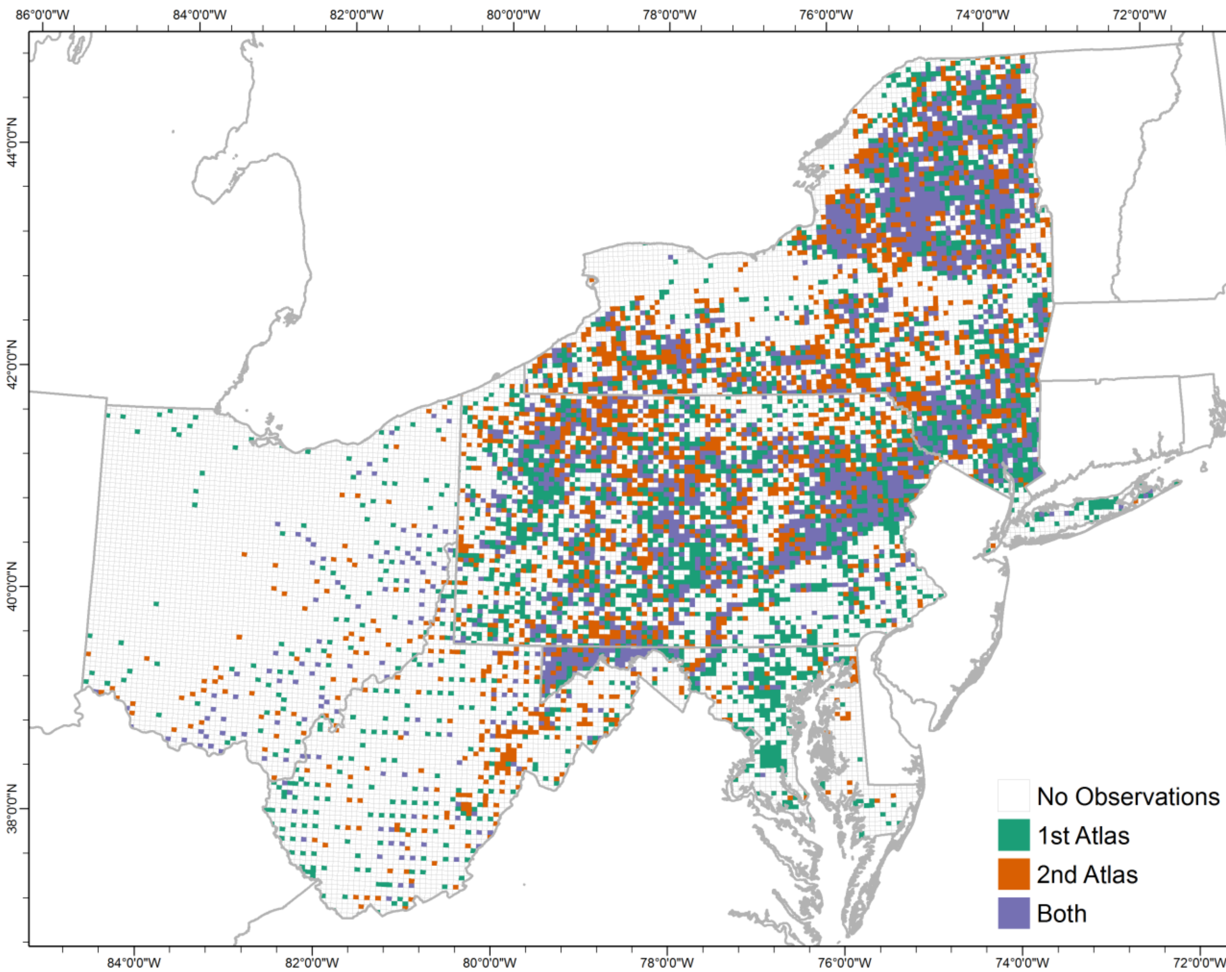


Figure 1. Observations of Broad winged Hawks from the 1st (1980s) and 2nd (2000s) breeding bird atlases.

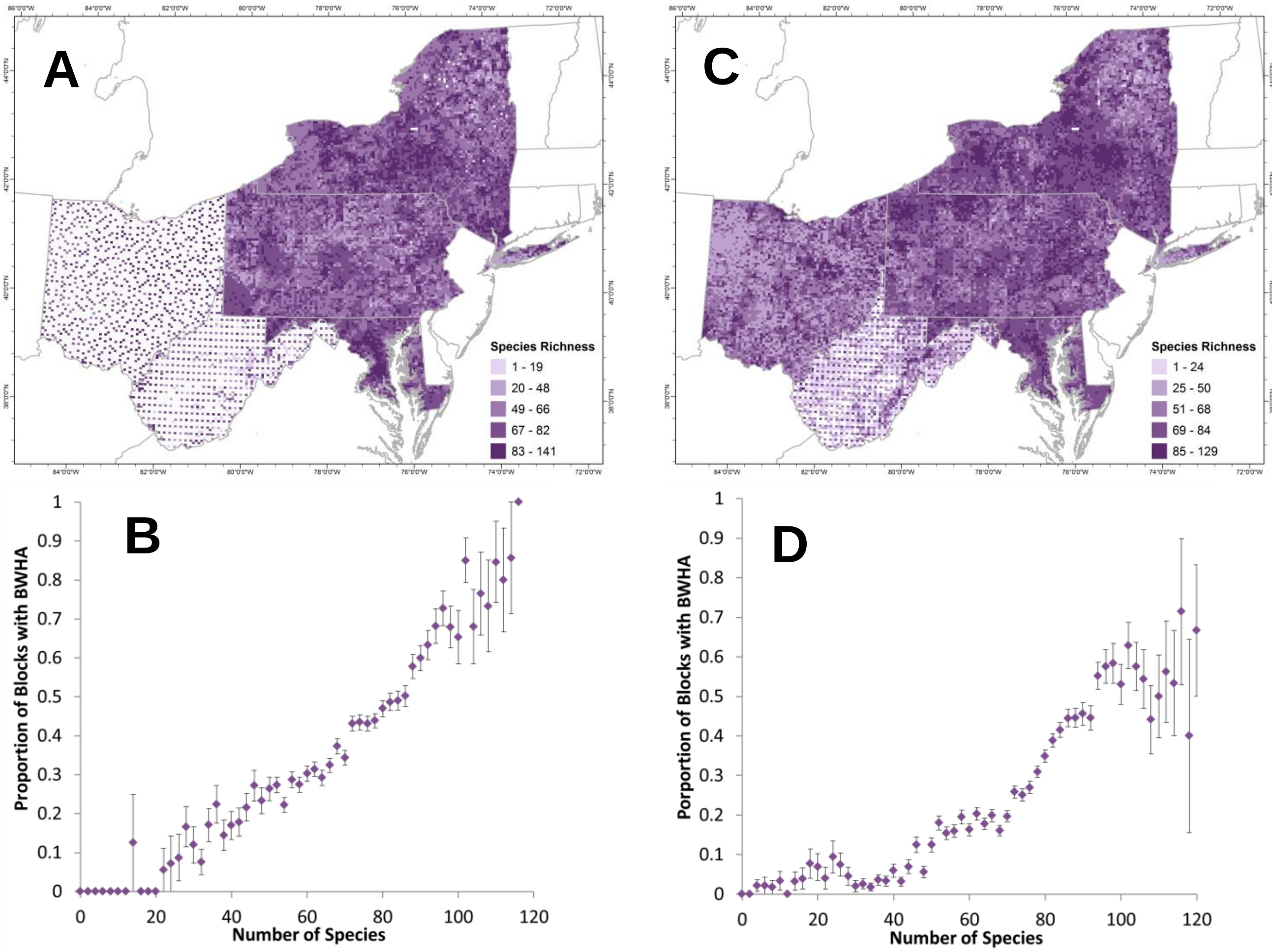


Figure 2. Top: number of species observed per block in the 1st (A) and 2nd Atlases (B), and bottom: relationship between numbers of species detected and proportion of blocks in which Broad-winged Hawks were detected in 1st (C) and 2nd Atlases (D).

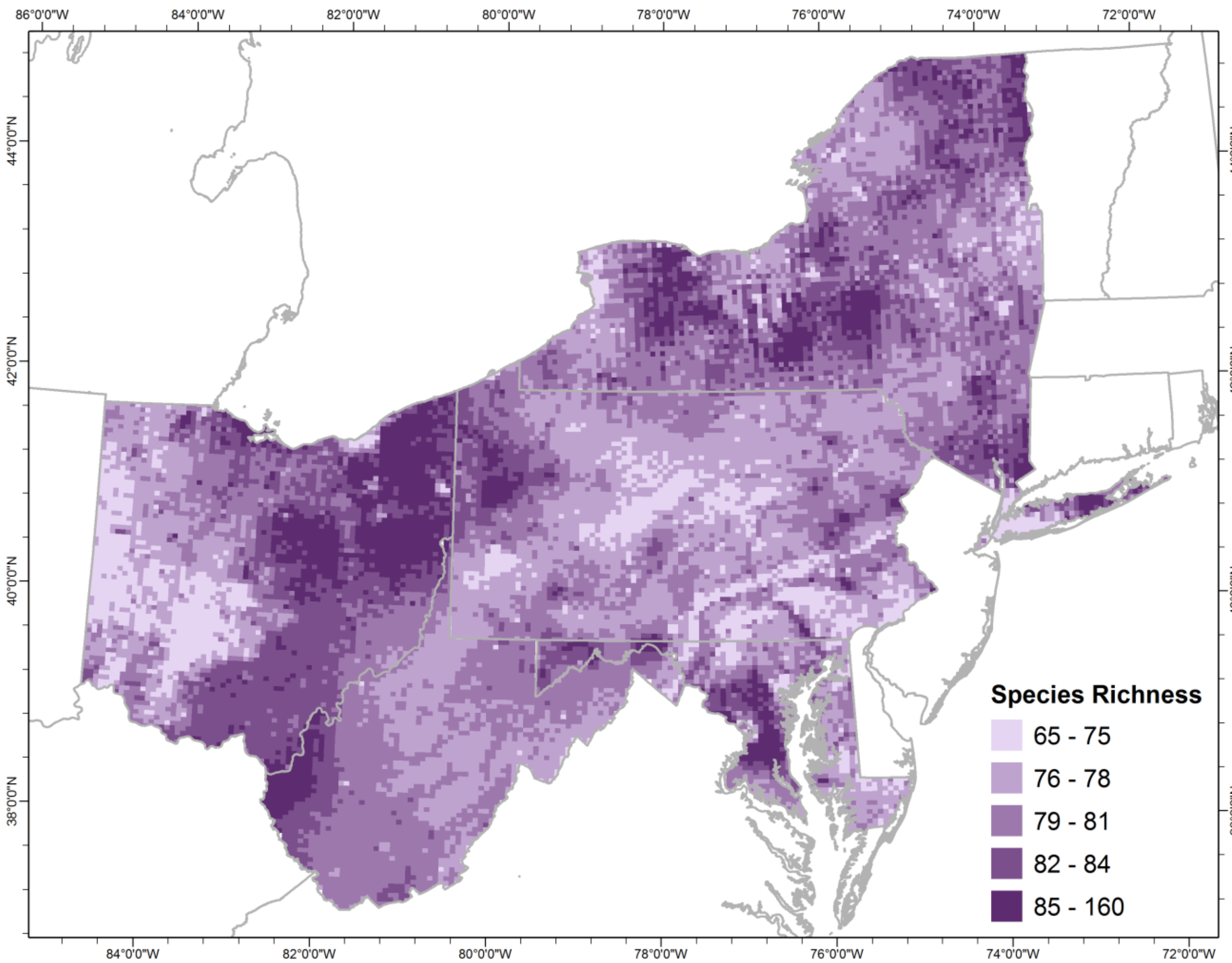


Figure 3. The predicted number of species for the 1st Atlas period (1980s) based on the spatial model using landscape metrics as a predictor of number of species.

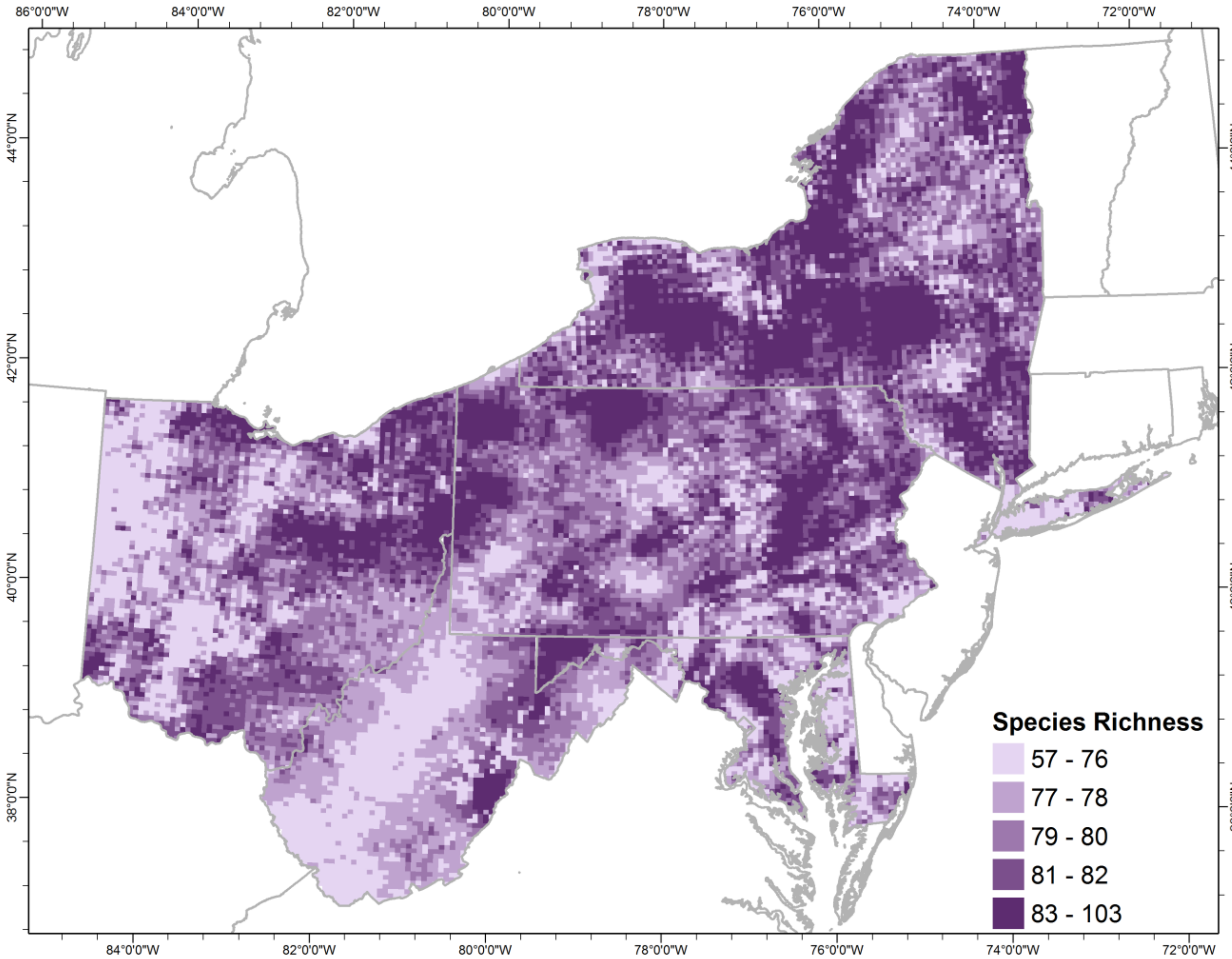


Figure 4. The predicted number of species per block for the 2nd Atlas period (2000s) based on the spatial model using landscape metrics as a predictor of number of species.

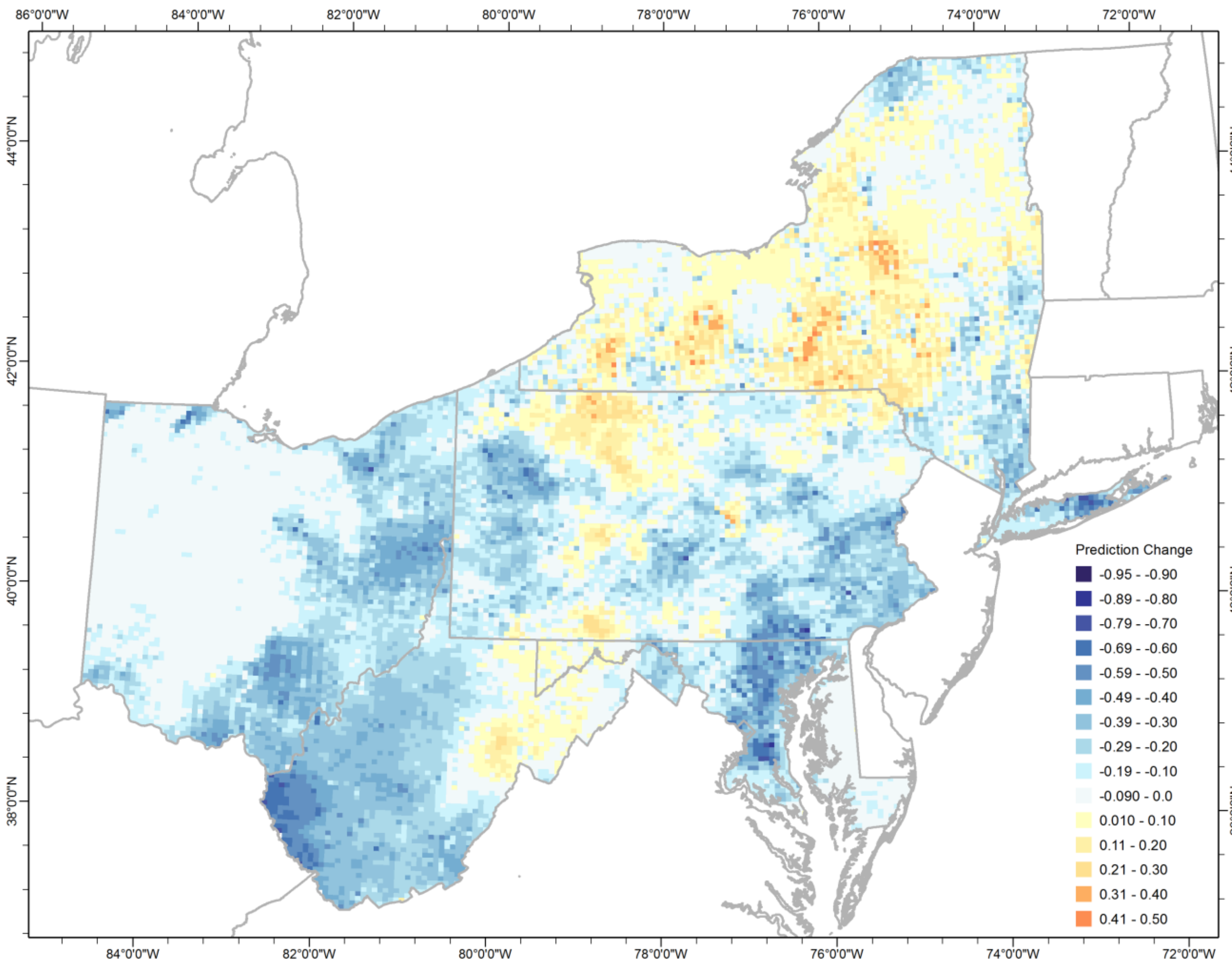
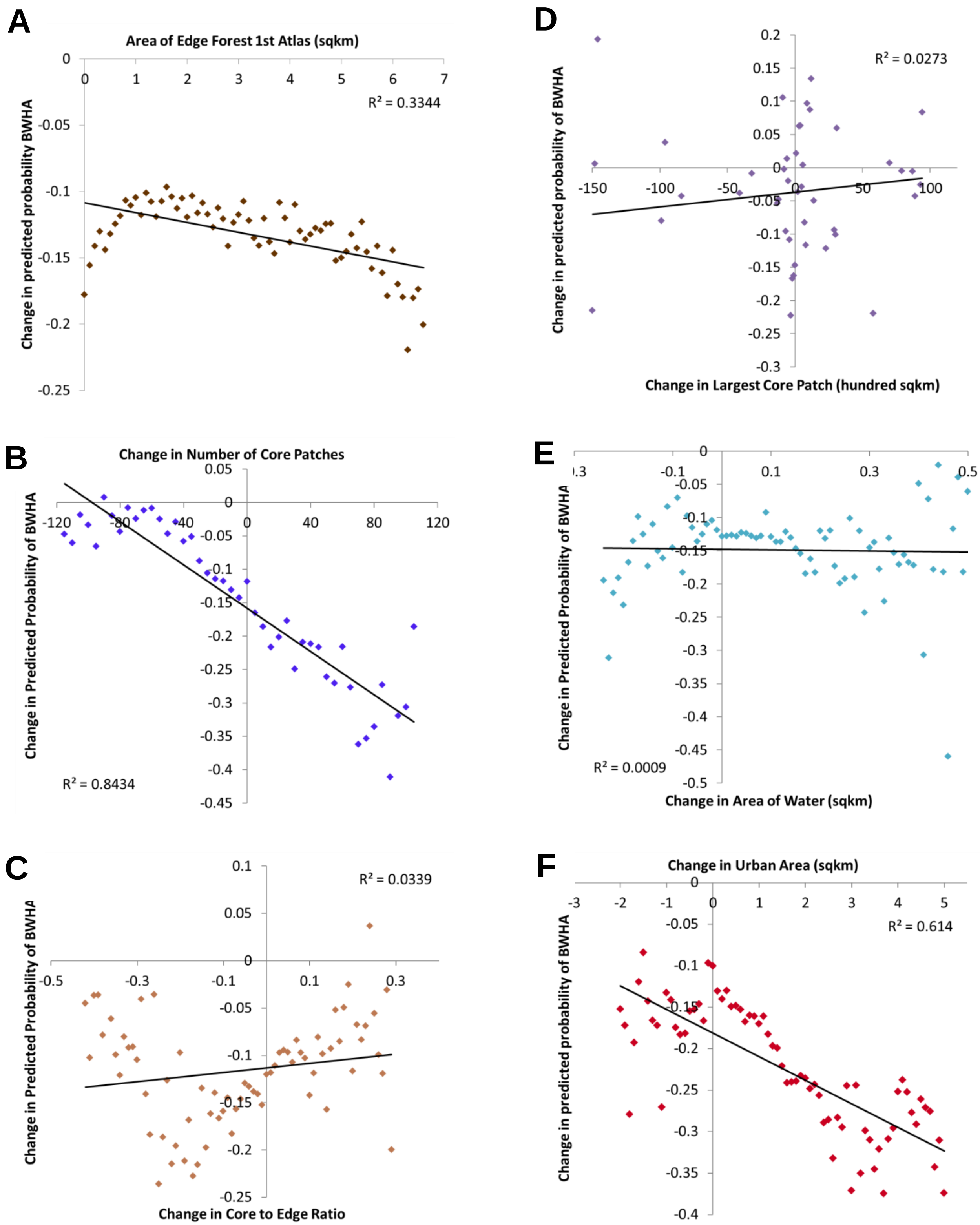
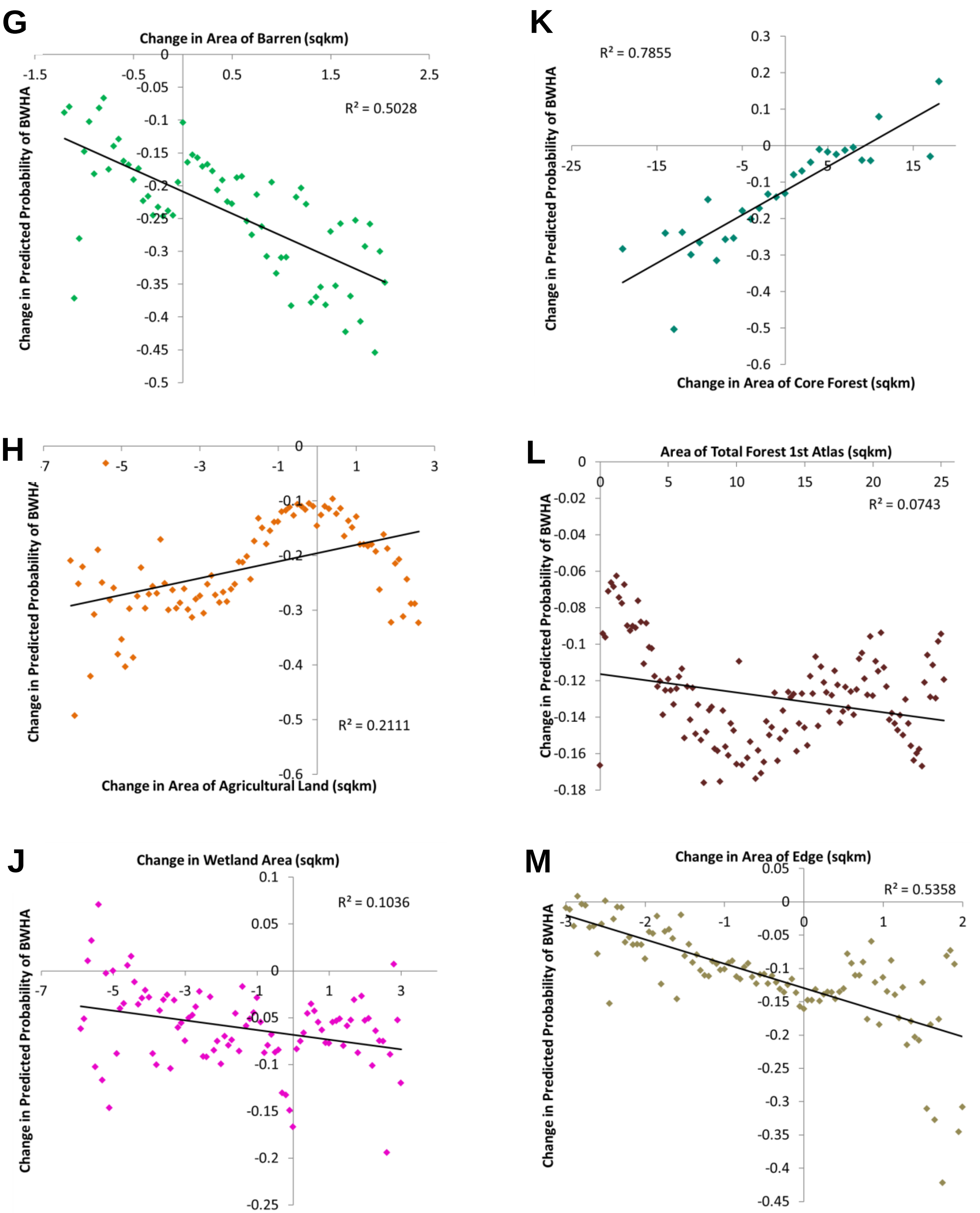


Figure 5. The change in predicted probability of BWHA presence between the 1st (1980s) and 2nd (2000s) atlases. Positive values (warm colors) represent an increase in probability while negative values (blues) represent a decrease in probability.


A
Area of Edge Forest 1st Atlas (sqkm)
Change in predicted probability BWHA
R² = 0.3344
B
Change in Number of Core Patches
Change in Predicted Probability of BWHA
R² = 0.8434
C
Change in Predicted Probability of BWHA
R² = 0.0339
Change in Core to Edge Ratio
D
Change in predicted probability of BWHA
R² = 0.0273
Change in Largest Core Patch (hundred sqkm)
E
Change in Predicted Probability of BWHA
R² = 0.0009
Change in Area of Water (sqkm)
F
Change in Urban Area (sqkm)
Change in predicted probability of BWHA
R² = 0.614


G
Change in Area of Barren (sqkm)
Change in Predicted Probability of BWHA
R² = 0.5028
K
R² = 0.7855
Change in Predicted Probability of BWHA
Change in Area of Core Forest (sqkm)
H
Change in Predicted Probability of BWHA
R² = 0.2111
Change in Area of Agricultural Land (sqkm)
L
Area of Total Forest 1st Atlas (sqkm)
R² = 0.0743
Change in Predicted Probability of BWHA
J
Change in Wetland Area (sqkm)
R² = 0.1036
Change in Predicted Probability of BWHA
M
Change in Area of Edge (sqkm)
R² = 0.5358
Change in Predicted Probability of BWHA

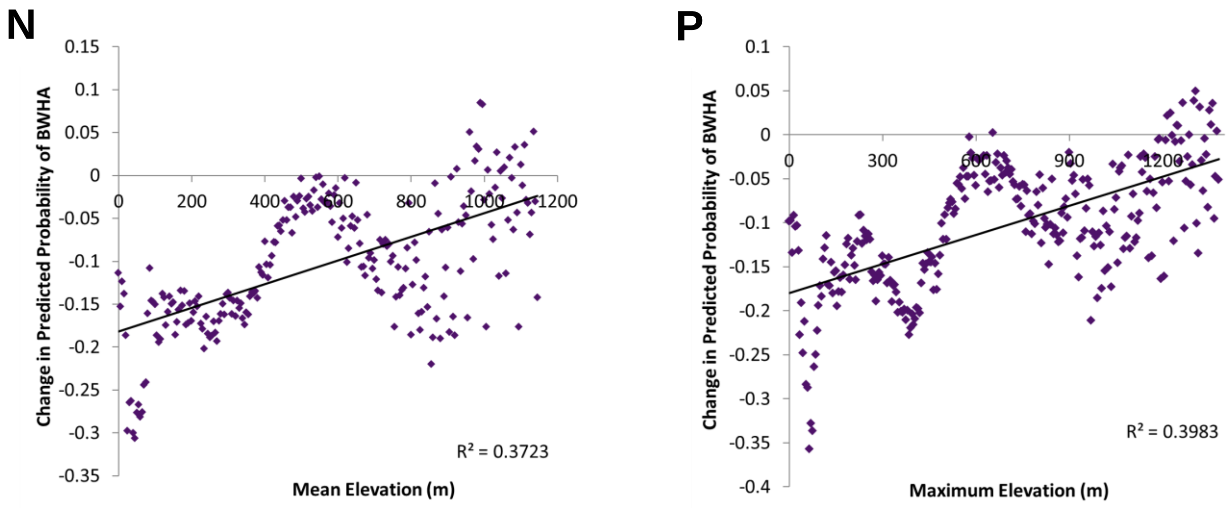


Figure 6. Simple relationships between significant metrics determined by the final spatial change model to the change in the average predicted probability of the presence of BWHA per block. (A) Area of edge forest in the 1st Atlas in 0.1 km^2 bins; regression coefficient of -0.0064. (B) Change in number of core forest patches per block in 5 patch bins; regression coefficient 0.0002. (C) Change of core to edge forest ratio in 0.01 bins; regression coefficient 0.02. (D) Change of area of largest core forest patch that intersects with the block in 1.0 km^2 bins; regression coefficient 0.009. (E) Change of area of water in 0.01 km^2 bins; regression coefficient -0.0218. (F) Change of area of urban in 0.1 km^2 bins; regression coefficient -0.0106. (G) Change of area of barren in 0.05 km^2 bins; regression coefficient -0.0177. (H) Change in area of agriculture in 0.1 km^2 bins; regression coefficient -0.0198. (J) Change in area of wetlands in 0.1 km^2 bins; regression coefficient -0.0027. (K) Change in area of core forest in 1.0 km^2 bins; regression coefficient 0.0042. (L) Area of total forest in the 1st Atlas in 0.02km^2 bins; regression coefficient -0.006. (M) Change in area of edge forest in 0.05km^2 bins; regression coefficient 0.0066. (N) Mean Elevation in 5.0 m bins; regression coefficient 0.0003. (P) Maximum elevation in 5.0 m bins; regression coefficient -0.0001.

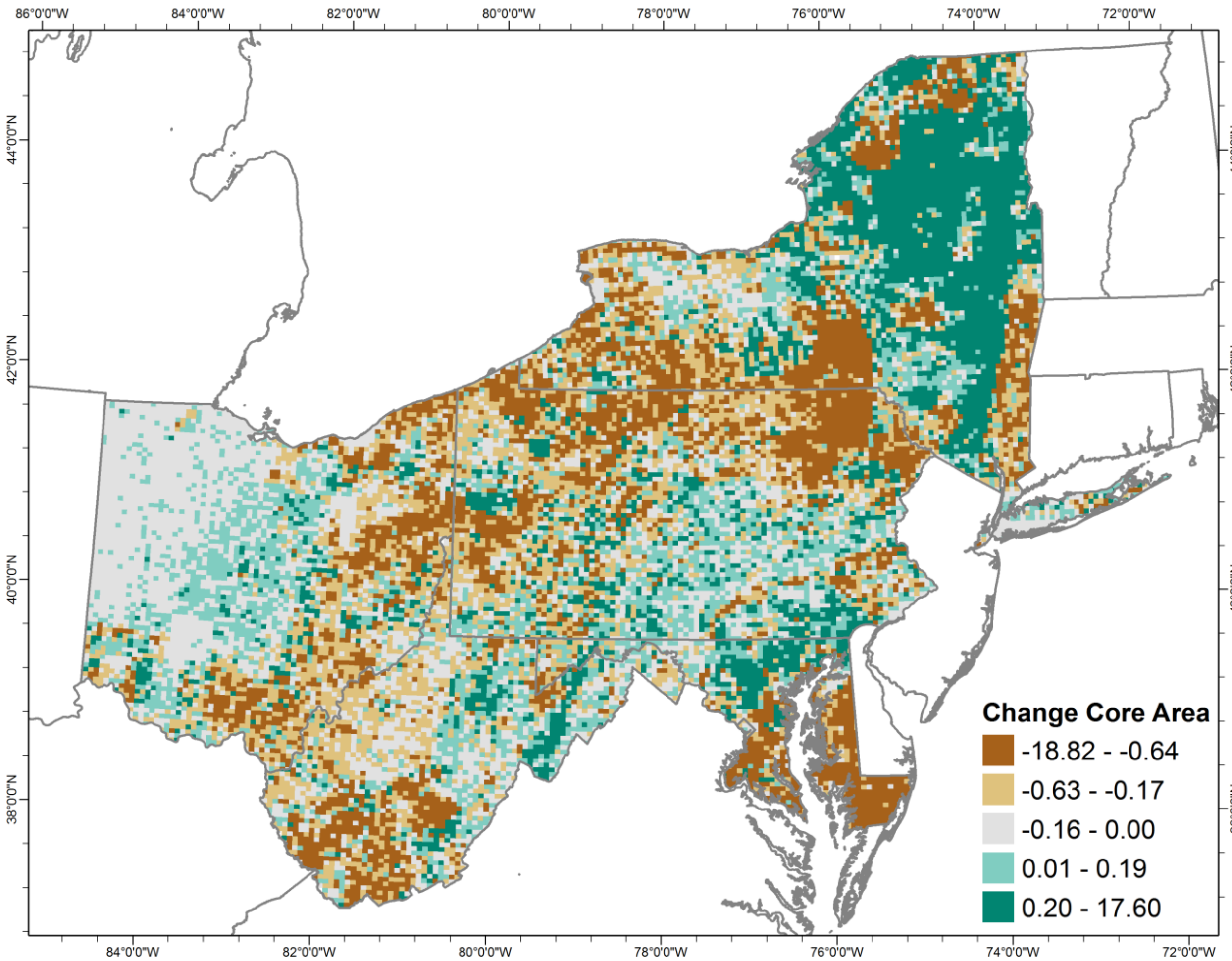


Figure 7. Change in area of core forest land cover between the 1st (1980s) and 2nd (2000s) Atlas periods in square kilometers.

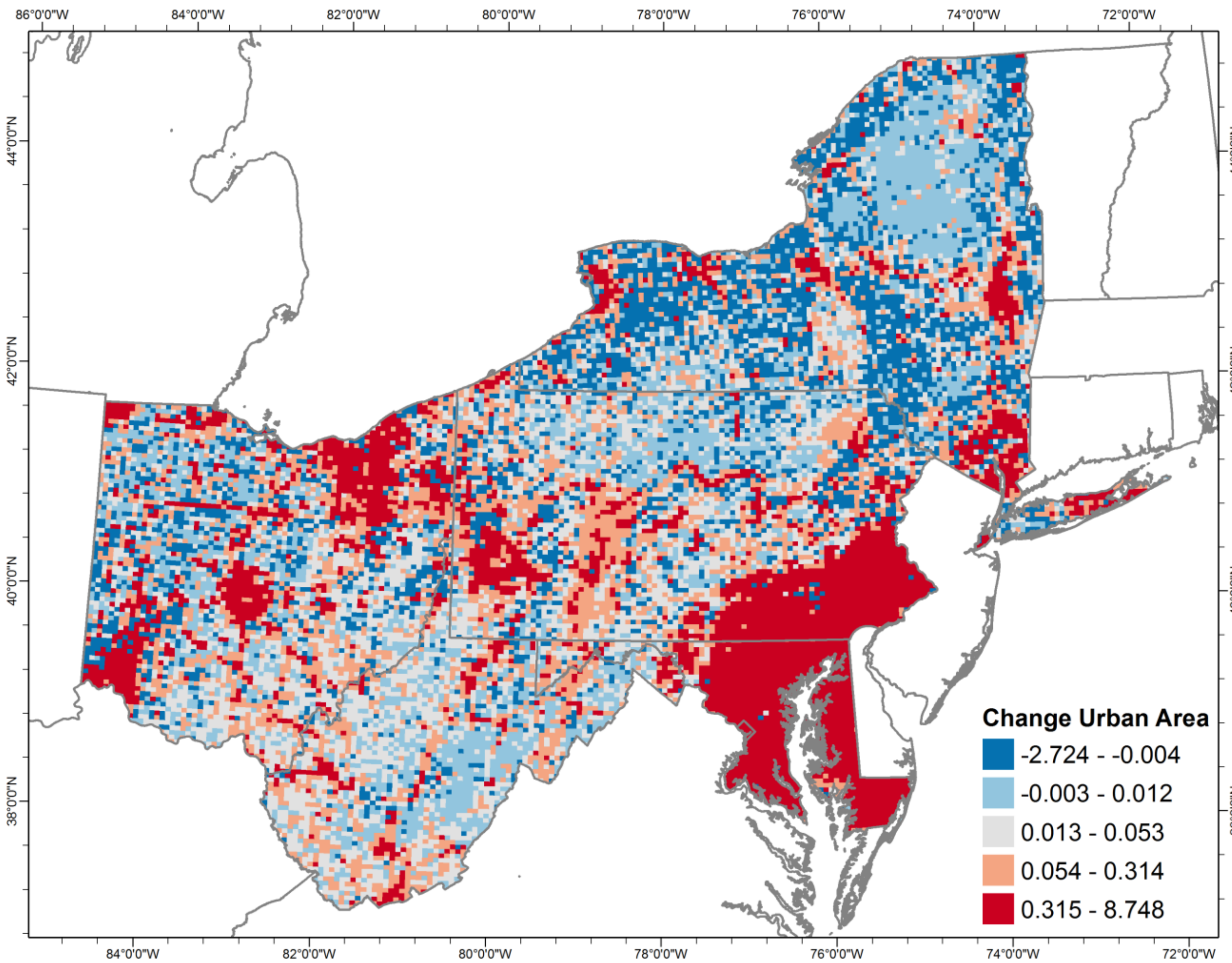


Figure 8. Change in area of urban land cover between the 1st (1980s) and 2nd (2000s) Atlas periods in square kilometers.

APPENDIX

Table 5. Definitions of metrics tested as landscape variables.

Variable	Definition
Core	Area of core forest, defined as forest greater than 100 meters from a forest edge. A combination of core and inner edge forest derived from the LFT.
Edge	Area of edge forest, defined as forest within 100 meters of a forest edge. A combination of patch and outer edge forest derived from the LFT.
Core Ratio	The ratio of core area to total forest area
Count Core Patches	The number of core forest patches
Intersected Patch	The largest patch of core forest that is intersected by block but may not be completely contained within the block.
Land Cover (Open Water, Urban, Barren, Grassland/Shrub, Agriculture, Wetland)	The areas of land cover for each land cover type defined by the NLCD.
Elevation (mean, maximum, minimum, range)	The elevation from a Digital Elevation model from USGS

Table 6. Metrics determined by the non-spatial model for species richness in the 1st Atlas (top) and the 2nd Atlas (bottom).

	Estimate	Std. Error	t value	Pr(>|t|)	Significance
(Intercept)	73.9400	1.0600	69.7430	< 2e-16	***
Area of block	0.1061	0.0381	2.7860	0.0054	**
Count of Core Patches	-0.0113	0.0035	-3.2290	0.0013	**
Ratio of Core to Edge Forest	1.0710	0.7188	1.4900	0.1363	
Largest forest patch intersecting block	-0.0001	0.0000	-2.8790	0.0040	**
Area of Water	0.1895	0.0900	2.1060	0.0353	*
Area of Urban	-0.1264	0.0452	-2.8010	0.0051	**
Area of Barren	-2.0440	0.4887	-4.1830	0.0000	***
Area of Agriculture	-0.1530	0.0357	-4.2920	0.0000	***
Mean elevation	0.0027	0.0018	1.5010	0.1333	
Max elevation	-0.0024	0.0015	-1.5440	0.1227	
Shannon Diversity Index	12.5600	1.1240	11.1760	< 2e-16	***

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

	Estimate	Std. Error	t value	Pr(>|t|)	Significance
(Intercept)	69.85762	0.591308	118.141	< 2e-16	***
Count of Core Patches	-0.02162	0.004093	-5.282	1.31E-07	***
Ratio of Core to Edge Forest	4.333041	0.793931	5.458	4.96E-08	***
Largest forest patch intersecting block	-0.22024	0.053641	-4.106	4.07E-05	***
Area of Water	0.388996	0.075801	5.132	2.93E-07	***
Area of Barren	-1.28645	0.343763	-3.742	0.000184	***
Area of Forest	0.079129	0.041909	1.888	0.059044	.
Area of Grasslands	0.382714	0.104103	3.676	0.000238	***
Area of Wetlands	0.360267	0.0536	6.721	1.91E-11	***
Mean elevation	0.006574	0.000723	9.096	< 2e-16	***
Minimum Elevation	0.000391	0.000258	1.518	0.129142	
Shannon Diversity Index	14.95376	1.139159	13.127	< 2e-16	***

Signif. code 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table 7. Metrics included in the non-spatial (top) and spatial (bottom) models for BWHA in the 1st Atlas.

	Estimate	Std. Error	z value	Pr(>|z|)	Significance
(Intercept)	-4.6720	0.1643	-28.4390	< 2e-16	***
Species Richness (survey effort)	0.0630	0.0013	47.0660	< 2e-16	***
Area of Edge Forest	0.1040	0.0239	4.3520	0.0000	***
Count of Core Patches	0.0069	0.0007	9.5040	< 2e-16	***
Largest forest patch intersecting block	0.0000	0.0000	3.8390	0.0001	***
Area of Water	0.0401	0.0176	2.2720	0.0231	*
Area of Barren	0.3865	0.0896	4.3140	0.0000	***
Area of Forest	0.0453	0.0061	7.3990	0.0000	***
Area of Grassland	-0.1518	0.0279	-5.4350	0.0000	***
Area of Agriculture	-0.1086	0.0071	-15.3960	< 2e-16	***
Area of Wetlands	0.0415	0.0129	3.2220	0.0013	**
Mean Elevation	-0.0026	0.0004	-7.1640	0.0000	***

Signif. code s: 0 ‘***’ 0.001 ‘**’ 0.01 ‘* ’ 0.05 ‘. ’ 0.1 ‘ ’ 1

		95% Confidence Interval	
	Parameter estimate	Lower	Upper
(Intercept)	**-6.5245**	**-7.0483**	**-6.012**
Species Richness (survey effort)	**0.0762**	**0.0725**	**0.08**
Area of Edge Forest	**0.1064**	**0.0467**	**0.1662**
Count of Core Patches	**0.003**	**0.0009**	**0.0051**
Largest forest patch intersecting block	**0.0000**	**0.0000**	**0.0000**
Area of Water	-0.0154	-0.0624	0.0304
Area of Barren	**0.2965**	**0.0732**	**0.5223**
Area of Forest	**0.0608**	**0.044**	**0.0778**
Area of Grassland	-0.0529	-0.134	0.0277
Area of Agriculture	**-0.1176**	**-0.1371**	**-0.0983**
Area of Wetlands	-0.0016	-0.0452	0.0417
Mean Elevation	**0.0018**	**0.0007**	**0.0029**
Maximum Elevation	-0.0007	-0.0016	0.0001
Shannon Diversity Index	**-1.371**	**-2.2247**	**-0.517**

Bold: 95% CI does not overlap zero.

Table 8. Metrics included for Non-spatial (top) and spatial (bottom) models for Broad-winged Hawk Presence in 2nd Atlas.

	Estimate	Std. Error	z value	Pr(>|z|)	Significance
(Intercept)	-6.7740	0.2303	-29.4150	< 2e-16	***
Species Richness (survey effort)	0.0625	0.0015	41.5470	< 2e-16	***
Area of Core Forest	0.0547	0.0087	6.2600	0.0000	***
Area of Edge Forest	0.2198	0.0236	9.2990	< 2e-16	***
Ratio of Core to Edge Forest	0.5433	0.1306	4.1620	0.0000	***
Largest forest patch intersecting block	0.0000	0.0000	8.5760	< 2e-16	***
Area of Urban	-0.0400	0.0099	-4.0550	0.0001	***
Area of Agriculture	-0.1508	0.0096	-15.6290	< 2e-16	***
Area of Wetlands	0.0588	0.0130	4.5390	0.0000	***
Mean Elevation	-0.0008	0.0003	-2.3370	0.0195	*
Maximum Elevation	0.0021	0.0003	7.2490	0.0000	***
Shannon Diversity Index	-0.9313	0.3117	-2.9880	0.0028	**

Signif. code 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

		95% Confidence Interval	
	Parameter estimate	Lower	Upper
(Intercept)	-8.4456	-9.0198	-7.8835
Species Richness (survey effort)	6.2137	5.8242	6.6117
Area of Core Forest	0.0643	0.0437	0.0851
Area of Edge Forest	0.1684	0.1047	0.2322
Count of Core Patches	0.0033	0.0008	0.0059
Ratio of Core to Edge Forest	0.2617	-0.0435	0.5678
Largest forest patch intersecting block	0.0947	0.0574	0.1321
Area of Water	-0.0002	-0.0464	0.0448
Area of Barren	-0.0546	-0.2281	0.1157
Area of Agriculture	-0.127	-0.1483	-0.1059
Area of Wetlands	0.065	0.0173	0.1121
Maximum Elevation	0.0009	0.0004	0.0014
Shannon Diversity Index	-0.7445	-1.6315	0.1433

Bold: 95% CI does not overlap zero.

Table 9. Metrics determined as significant by the non-spatial model for change in predictions of Broad-winged Hawk presence between the 1st and 2nd atlases.

Coefficients: Non-Spatial BWHA Change

	Estimate	Std. Error	t value	Pr(>|t|)	Significance
(Intercept)	-0.1426	0.0036	-39.5540	< 2e-16	***
Δ Area of Core	-0.0124	0.0013	-9.7370	< 2e-16	***
Area of Core 1st Atlas	-0.0222	0.0038	-5.8170	0.0000	***
Δ Area of Edge	-0.0269	0.0026	-10.2200	< 2e-16	***
Area of Edge 1st Atlas	-0.0216	0.0039	-5.5420	0.0000	***
Δ Count of Core Patches	-0.0012	0.0001	-18.9030	< 2e-16	***
Δ Ratio of Core to Edge Forest	0.0206	0.0036	5.6610	0.0000	***
Δ Largest forest patch intersecting block	0.0154	0.0026	5.8390	0.0000	***
Δ Area of Water	-0.0367	0.0099	-3.6880	0.0002	***
Δ Area of Urban	-0.0635	0.0020	-31.7080	< 2e-16	***
Δ Area of Barren	-0.0938	0.0049	-19.0500	< 2e-16	***
Area of Forest 1st Atlas	0.0139	0.0038	3.6620	0.0003	***
Δ Area of Agriculture	-0.0256	0.0015	-16.5340	< 2e-16	***
Δ Area of Wetlands	-0.0095	0.0013	-7.2200	0.0000	***
Mean elevation	0.0001	0.0000	5.8250	0.0000	***
Maximum elevation	0.0002	0.0000	10.9570	< 2e-16	***

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

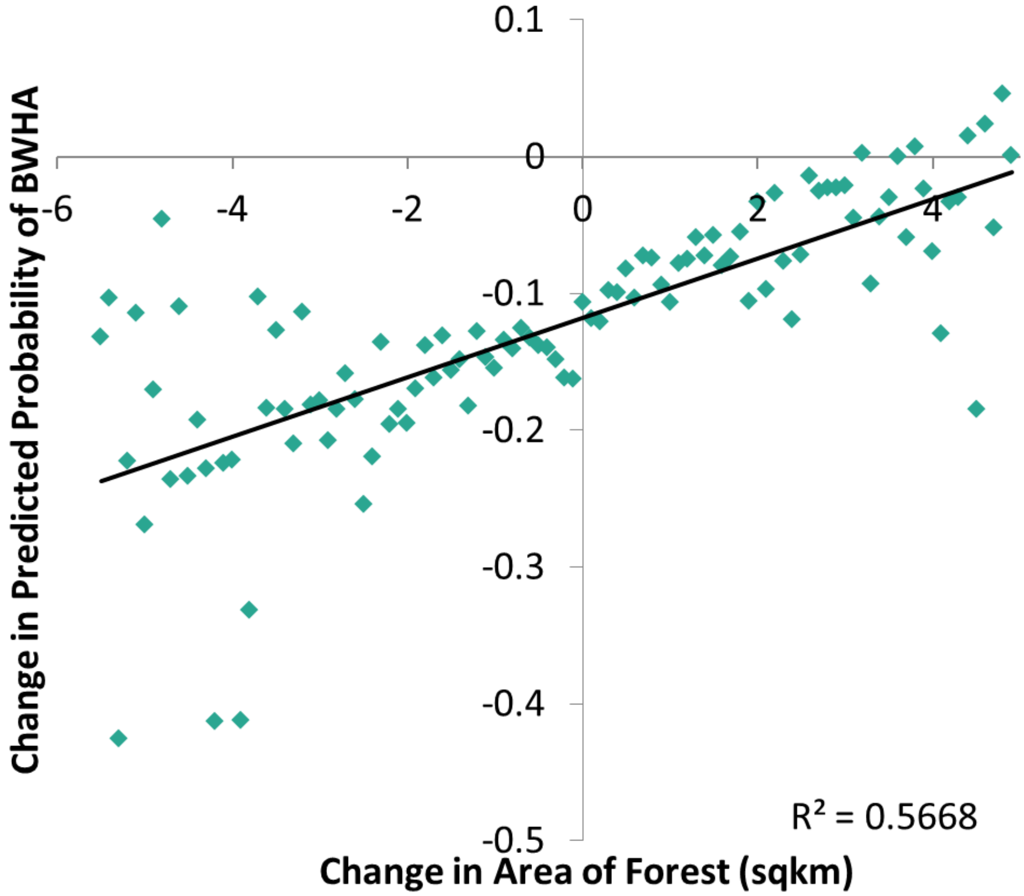


Figure 9. Simple relationship between change in the total area of forest per block between the first and second atlas in $0.1km^2$ bins and the average change in predicted probability of BWHA occupancy.

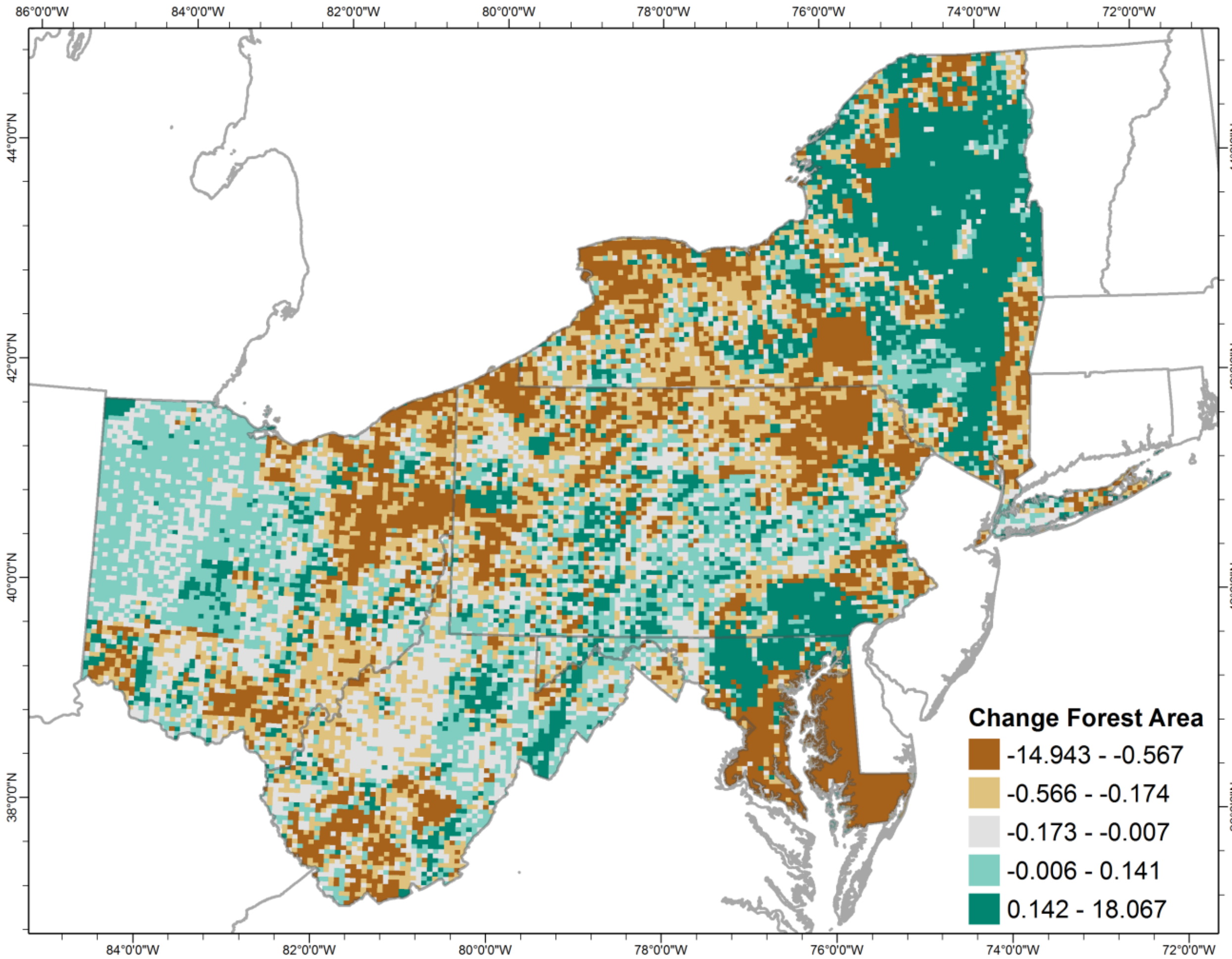


Figure 10. Change in area of forest land cover between the 1st (1980s) and 2nd (2000s) Atlas periods in square kilometers.