**Effects of climate change and landscape-scale forest management on avian communities, abundance, and nest success in the Appalachian Mountains**

Hannah L. Clipp

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Petra B. Wood, Ph.D., Chair

Christopher T. Rota, Ph.D.

Catherine Johnson, Ph.D.

Michael P. Strager, Ph.D.

Division of Forestry and Natural Resources,

Wildlife and Fisheries Resources Program

Morgantown, West Virginia

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**ABSTRACT**

**Effects of climate change and landscape-scale forest management on avian communities, abundance, and nest success in the Appalachian Mountains**

Hannah L. Clipp

[overview of dissertation research]

[Chapter 1]

[Chapter 2]

[Chapter 3]

[Chapter 4]

[Chapter 5]

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**CHAPTER 1**

**Effects of climate and land cover change on forest songbirds of the Appalachian Mountains: A literature review and case study**

Hannah L. Clipp1,2, Christopher T. Rota1, Stephen P. Matthews3, and Petra B. Wood1,2,4

*1West Virginia University Division of Forestry and Natural Resources*

*2West Virginia Cooperative Fish and Wildlife Research Unit*

*3USDA Forest Service Northern Research Station*

*4US Geological Survey*

**Introduction**

**Global climate change effects on birds**

Global climate change refers to the unprecedented rate of increase in Earth’s surface temperature during the 20th and 21st centuries, due primarily to human activity (Karl and Trenberth 2003). Implicated as a factor in declines of avian populations, global climate change can impact birds directly and indirectly (Trautmann 2018). The increasing frequency and intensity of storms can kill migrating birds (Zumeta and Holmes 1978, Newton 2007), while temperature can interact with landscape factors to lower songbird productivity (Cox et al. 2013*a*). Increasing temperatures may also elevate rates of nest predation by snakes and birds (Cox et al. 2013*b*). Furthermore, there is strong evidence that rising temperatures cause phenological mismatches between birds and vegetation budding dates and emergence of or peaks in their insect prey (Visser et al. 2006, Waite and Strickland 2006). In North America, the interval between spring green-up and arrival of migratory passerine species has increased, with certain species unable to keep pace (Mayor et al. 2017). Changes in phenology of migration and breeding are particularly prevalent in response to climate change (Both et al. 2004, 2006, Crick 2004). For instance, arrival dates of Australian and European migratory birds at their breeding grounds are advancing and departure dates from their breeding grounds for some species are delayed (Beaumont et al. 2006, Jonzén et al. 2006). Meanwhile, the clutch initiation dates of a multitude of migratory bird species, including tree swallows (*Tachycineta bicolor*) and pied flycatchers (*Ficedula hypoleuca*), are similarly advancing (Winkler et al. 2002, Both and Visser 2005). These phenological changes can have fitness consequences; species that advance their migration or breeding phenology to track changes in climate may benefit from a longer breeding period and possibly increased recruitment, but species with limited phenological plasticity may be facing an increasing mismatch between timing of food requirements and food availability (Both et al. 2009), lowering reproductive success. For instance, species that advance their egg-laying dates the least in response to increasing spring temperatures over time exhibit the most negative population trends (Franks et al. 2018).

In addition, there is evidence linking global climate change to long-term changes in avian distributions and geographical ranges (Chen et al. 2011). Many bird species in North America and Europe have expanded their wintering and/or breeding ranges northward (Thomas and Lennon 1999, Hitch and Leberg 2007, La Sorte and Thompson III 2007), but both latitudinal and altitudinal shifts have been documented and projected (Pounds et al. 1999, Rodenhouse et al. 2008). High-elevation species are particularly vulnerable to climate change (Siegel et al. 2014). As little as 1° C warming could reduce suitable habitat for certain high-elevation bird species by more than half (Rodenhouse et al. 2008). Meanwhile, low-elevation species are expanding upslope (DeLuca and King 2017). However, along elevational gradients, climate change can cause potentially heterogeneous range shifts, as rising temperature pushes species upslope while increased precipitation pulls them downslope (Tingley et al. 2012). Latitudinal and altitudinal shifts in North American bird distribution are predicted to continue into the future, in conjunction with tree species responses to climate change (Matthews et al. 2011).

Climate change can further affect birds indirectly by altering tree species distributions (Iverson et al. 2008), as well as the frequency, intensity, duration, and timing of forest disturbances, which can alter habitat quality during both breeding and non-breeding seasons (Dale et al. 2001). Thus, it is likely that climate change plays a role in declining forest songbird populations through indirect and synergistic effects, with consequences potentially greatest for long-distance migrants in seasonal habitats (Lemoine and Böhning-Gaese 2003, Both et al. 2010). In fact, migrant passerine species are projected to encounter novel climates throughout most of their annual cycle in the future, which may adversely affect their survival rates (La Sorte et al. 2018). As the climate continues to warm, certain birds may even face extirpation and extinction (Schwartz et al. 2006, Sekercioglu et al. 2008). Alternatively, some species are predicted to expand their distributions, and resident species may benefit from warmer winters (Rodenhouse et al. 2008). Ultimately, changes in bird communities are likely to result from climate change (Rodenhouse et al. 2008, Stralberg et al. 2009), with habitat specialists and cold-associated species more negatively affected by higher temperatures than habitat generalists or southerly distributed species associated with warm temperatures (Pearce-Higgins et al. 2015).

**Land cover change as an additional factor**

Many studies addressing global change are focused on anthropogenic climate change, but it is important to also consider that landscapes have been altered significantly in the last century. Broad-scale trends are spatially and temporally variable, with some regions within the United States (e.g., West Virginia) experiencing stable or increasing trends in forest area within the past five decades (Childs 2005, Morin et al. 2016). However, cumulative historical changes in land cover and use, landscape composition, and landscape configuration over hundreds of years have tended to result in forest habitat loss, fragmentation, and decreased connectivity, which affect forest songbird populations and distributions (Villard et al. 1999). Certain forest songbirds require large tracts of relatively mature forest, which makes them sensitive to landscape change (Moenkkoenen and Welsh 1994). Losses in suitable forest habitat directly lead to subsequent declines or absences of associated forest bird populations (Pimm and Askins 1995, Trzcinski et al. 1999). Conversion of preferred habitat to less suitable habitat can also lead to population declines and reductions in species richness (Gaston et al. 2003, Aratrakorn et al. 2006, Zurita et al. 2006). For instance, urbanization and energy development tend to negatively impact native forest bird populations and communities (Nilon et al. 1995, Rottenborn 1999, Er et al. 2005, Farwell et al. 2016).

Habitat fragmentation, which is a landscape-scale process involving the simultaneous loss of habitat, reduction in habitat patch size, increase in the number of habitat patches, and increased isolation of habitat patches (Fahrig 2003), generally has non-significant or positive relationships with overall abundance and richness (Fahrig 2017, Fahrig et al. 2019). However, it may also have negative effects, particularly for habitat-interior specialist species such as ovenbirds (*Seiurus aurocapillus*) (Bayne et al. 2005), red-eyed vireos (*Vireo olivaceus*) (Keller and Yahner 2007), and cerulean warblers (*Setophaga cerulea*) (Weakland and Wood 2005). For instance, forest-interior and interior-edge guild abundances decreased after specific thresholds in timber harvest within a heavily forested central Appalachian landscape (Becker et al. 2011). Similarly, forest-interior species abundance responded negatively to core forest (i.e., >100 m from a non-forest edge) loss, forest loss, and increased edge density after alteration of landscape structure by mountaintop removal activities (Becker et al. 2015). In fragmented habitat patches, forest-interior songbirds and long-distance migratory birds are subject to increased risk of nest predation and parasitism (Wilcove 1985, Robinson et al. 1995, Hobson and Bayne 2000, Donovan et al. 2012). Distance to edge and edge types also influence nestling growth rates (Kaiser and Lindell 2007). Ultimately, forest-interior songbird populations in severely fragmented landscapes can become extirpated (Temple and Cary 1988). However, the effects of forest fragmentation can vary by species, with some (e.g., edge-associated species) increasing in abundance and others showing no response (Uezu et al. 2005, Becker et al. 2015).

Because landscape change can have significant impacts on bird populations, communities, and distributions, it is worth considering as an additional factor when evaluating avian responses to global climate change. In general, climate change may have greater influence on bird distributions than land cover change, as it likely affects range limits while land cover affects where species occur within those ranges. For instance, Sohl (2014) found that climate variables (i.e., mean annual temperature and precipitation) contributed more than land cover variables to models of 50 North American bird distributions in 2001 and that projected climate change resulted in larger overall range changes than projected land cover change. However, Sohl (2014) concluded that both climate and land cover variables are important for modeling contemporary and potential future species ranges. At regional scales, adding vegetation/land cover in species distribution models can create more refined projections (Pearson et al. 2004, Seoane et al. 2004). For example, including tree species has been demonstrated to improve models for breeding bird species in the eastern United States (Matthews et al. 2011). Furthermore, the importance of including land cover change in projections of future avian ranges on a global scale was highlighted by models that coupled climate and land use change together (Jetz et al. 2007); they projected range reductions in many bird species, with land use change in the tropics responsible for range contractions of species currently not recognized as imperiled.

**Significance of the Appalachian Mountains**

The Appalachian Mountains are a dominant land feature of the eastern United States. They contain a range of elevations and primarily forested habitats, from temperate deciduous forests at lower elevations/latitudes to boreal forests at higher elevations/latitudes. The forest songbird communities in this extensive region reflect that habitat diversity, comprising species from a plethora of families. The Appalachian Mountains are a key component influencing contemporary species’ ranges, and they serve as the southern-most limit of many species’ breeding ranges, such as Canada warblers (*Cardellina canadensis*) and black-throated blue warblers (*Setophaga caerulescens*). Looking forward, the Appalachian Mountains will likely play an important role in shaping future distributions of birds, particularly those whose regional distributions seem to be influenced heavily by elevation and concomitant climatic conditions. As the climate warms over time, the elevational gradient of the Appalachian Mountains may enable them to serve as refugia for bird species (Keppel et al. 2012). However, the Appalachian Mountains region is also experiencing rapid land cover change in some areas, in part due to energy extraction (e.g., coal mines, wells and pipelines for natural gas) or production (e.g., wind turbines) and housing development. Given the significance of the Appalachian Mountains and the potential impact on high-elevation species, there is a clear need to focus on this specific region and assess bird responses to the relative and cumulative effects of global climate change and land cover change. Greater understanding of how avian populations, communities, and species distributions in the Appalachian Mountains have been changing and will change over time will inform conservation and management efforts in this region.

**Purpose and objectives**

To determine the potential effects of both climate and land cover change on forest songbirds of the Appalachian Mountains, I will conduct a comprehensive review of published literature and present a novel case study. The specific objectives of the review and case study are to: (1) provide a synthesis of documented and predicted changes in forest songbird species distributions, population dynamics, and communities in the Appalachian Mountains in response to climate and land cover change; (2) determine the relative influence of climate change and land cover change on 15 forest songbird distributions in the Appalachian Mountains in the past 20 years; and (3) project future distribution changes based on expected scenarios of climate change and land cover change.

**Review of climate and land cover change in the Appalachian Mountains and associated forest songbird responses**

**Historical (pre-1980) changes in climate and land cover**

[historical changes in climate]

[historical changes in land cover]

**Contemporary (1980–present) changes in climate and land cover**

[contemporary changes in climate]

[contemporary changes in land cover]

**Projected future changes in climate and land cover**

[future changes in climate]

[future changes in land cover]

**Documented and predicted forest songbird responses to changing climate and land cover**

*Species distributions*

[documented]

[predicted]

*Population dynamics*

[documented]

[predicted]

*Communities and species composition*

[documented]

[predicted]

**Case study: influence of climate and land cover change on 15 forest songbird distributions in the Appalachian Mountains**

**Methods**

*Study area*

My study area will comprise the entire Appalachian Mountains range, which encompasses 15 states in the eastern United States (Figure 1), extending from the White Mountains in New Hampshire and Maine to the Talladega Mountains in Alabama and Blue Ridge Mountains in Georgia. The Appalachian Mountains first formed ~480 million years ago during the Ordovician Period. They cover more than 190 million ha and stretch across a latitudinal range of 1,450 km, comprising five main physiographic provinces (New England, Appalachian Plateau, Ridge and Valley, Blue Ridge, and Piedmont) and broadly forming the Appalachian Highlands physiographic division. Elevation ranges from ~200 m to ~2,000 m above sea level. Mean breeding season precipitation and temperature vary widely across latitude and elevation. Tree diversity in the Appalachian Mountains reflects local and regional geology, latitude, elevation, and moisture availability. Red spruce (*Picea rubens*) dominates the conifer communities of the northern latitudes and high elevations. Fraser fir (*Abies fraseri*) accompanies red spruce in highest parts of the southern Appalachian Mountains. At lower latitudes and elevations, deciduous tree communities include mixed mesophytic, northern hardwood, and oak-hickory forests (Turner et al. 2003).

*Focal species*

I will focus on 15 forest songbird species that can be found throughout the Appalachian Mountains or primarily at low or high elevations or latitudes within the study region (Table 1). The species were chosen based on a combination of factors: use of mature forest as primary breeding habitat, classification as a passerine, detectability via roadside surveys, occurrence and general range patterns within just the Appalachian Mountains study region, and conservation status. Among the 15 focal species, I aim to have a diversity of taxonomic groups (>5 families and >10 genera), ranges (e.g., high latitude, low latitude, regionwide), and conservation statuses (>10 species of conservation concern).

Table 1. List of the fifteen focal forest songbird species. The regional range refers to whether the species can be found throughout the Appalachian Mountains (i.e., regionwide) or is found primarily at low or high latitudes or elevations within the study region. Special status refers to inclusion as an Appalachian Mountains Joint Venture Priority Species (AMJV PS), North American Bird Conservation Initiative’s Watch List species (NABCI WL), WV Division of Natural Resources Species of Concern (WVDNR SC), or Monongahela National Forest 2017 Regional Forester’s Sensitive Species (MNF RFSS).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Common Name  (*Scientific Name*)** | **Code** | **Family** | **Regional Range** | **Special Status** |
| Black-throated Blue Warbler  (*Setophaga caerulescens*) | BTBW | Parulidae | High latitude or high elevation | AMJV PS, WVDNR SC |
| Blue-headed Vireo  (*Vireo solitarius*) | BHVI | Vireonidae | High latitude or mid/high elevation | none |
| Canada Warbler  (*Cardellina canadensis*) | CAWA | Parulidae | High latitude or high elevation | AMJV PS, NABCI WL |
| Least Flycatcher  (*Empidonax minimus*) | LEFL | Tyrannidae | High latitude or high elevation | WVDNR SC |
| Nashville Warbler  (*Leiothlypis ruficapilla*) | NAWA | Parulidae | High latitude and high elevation | MNF RFSS |
| Veery  (*Catharus fuscescens*) | VEER | Turdidae | High latitude or high elevation | WVDNR SC |
| Cerulean Warbler  (*Setophaga cerulea*) | CERW | Parulidae | Mid/high latitude and mid elevation | AMJV PS, NABCI WL, WVDNR SC, MNF RFSS |
| Kentucky Warbler  (*Geothlypis formosa*) | KEWA | Parulidae | Mid/low latitude and mid/low elevation | AMJV PS, NABCI WL, WVDNR SC |
| Summer Tanager  (*Piranga rubra*) | SUTA | Cardinalidae | Mid/low latitude and low elevation | AMJV PS, WVDNR SC |
| Swainson’s Warbler  (*Limnothlypis swainsonii*) | SWWA | Parulidae | Mid/low latitude and mid/low elevation | AMJV PS, WVDNR SC |
| Eastern Wood-Pewee  (*Contopus virens*) | EAWP | Tyrannidae | Rangewide | AMJV PS |
| Scarlet Tanager  (*Piranga olivacea*) | SCTA | Cardinalidae | Rangewide | AMJV PS |
| Red-eyed Vireo  (*Vireo olivaceus*) | REVI | Vireonidae | Rangewide | none |
| Worm-eating Warbler  (*Helmitheros vermivorum*) | WEWA | Parulidae | Rangewide | AMJV PS, WVDNR SC |
| Wood Thrush  (*Hylocichla mustelina*) | WOTH | Turdidae | Rangewide | AMJV PS, NABCI WL, WVDNR SC |

[a priori predictions]

*Data compilation*

I will obtain data for the 15 individual bird species from the North American Breeding Bird Survey (BBS; Sauer et al. 2013) for the years 1997 (when data at the individual stop-level is first available) to 2017. The BBS is a long-term, large-scale, international avian monitoring program initiated in 1966 to track the status and trends of North American bird populations; it is coordinated by the U.S. Geological Survey's Patuxent Wildlife Research Center and Environment Canada's Canadian Wildlife Service. Following a rigorous protocol, BBS data are collected by thousands of participants along >300 randomly established roadside survey routes throughout the Appalachian Mountains (Figure 1). Each survey route is approximately 40 km long, with 50 stops separated by ~800 m. At each stop, a 3-minute point count is conducted. During the count, every bird seen within a 400-m radius or heard is recorded. Surveys start one-half hour before local sunrise and continue for 5 hours. For this case study, I will use all BBS routes with at least one year of data during the 20-year period (O’Connor et al. 1996). For each qualifying BBS route, I will further discard those with run types of 0 (signifying routes that do not meet BBS criteria). Of those remaining, I will calculate the annual occurrence of each species at each stop along each route (1 = present, 0 = absent).

The independent variables used as potential predictors of 1997–2017 bird species occurrence will include: 1997–2017 climate conditions, 1997–2017 proportions of land cover, elevation, slope position, and aspect. The independent variables used as potential predictors of bird species occurrence in 2100 will include: future projected climate conditions, future projected proportions of land cover, elevation, slope position, and aspect. I will obtain the same climate and land cover variables from two different sources. For historical climate conditions, I will download temperatures and precipitation from the PRISM Climate Group. I will then calculate mean July temperature, mean May to September temperature, total annual precipitation, and total May to September precipitation for each BBS stop. For future climate conditions, I will consider long-term (30-yr averages), downscaled, monthly data from three general circulation model outputs: the HadleyCM3 (HCM3; Pope et al. 2000), the Geophysical Fluid Dynamics Laboratory model (GFDL; Delworth et al. 2006), and the Parallel Climate Model (PCM; Washington et al. 2000). I will further consider two fossil fuel emission scenarios: the A1fi, which assumes that current emission trends continue for several decades without modification and incorporates an emphasis on fossil fuels, and the B1, which assumes that emissions will be greatly reduced. Ultimately, I will average the three circulation models for each emission scenario to yield an average high and average low emission set of climate predictors. In addition to the two averages, I will model the coolest scenario (PCM-B1) and warmest scenario (HCM3-A1fi) to represent the average and extreme possible outcomes from the climate analysis. These four scenarios all project a warmer, wetter eastern United States, with the higher emissions scenarios resulting in much greater increases in temperature by 2100 (Iverson et al. 2008). For historical land cover, I will quantify the proportion of three land cover categories (deciduous and mixed forest, coniferous forest, and developed land) within a 400-m buffer around each BBS stop using land cover data from the 2001, 2004, 2006, 2008, 2011, 2013, and 2016 National Land Cover Databases, which all have a resolution of 30 m (Homer et al. 2015). For each year, I will use land cover data from the closest year available (e.g., I will use the 2001 data for surveys conducted between 1997 and 2002). For future land cover, I will perform the same calculations of land cover proportions using projections produced by the U.S. Geological Survey (USGS) Earth Resources Observation and Science Center (Sohl et al. 2007). The Earth Resources Observation and Science Center used a modeling framework that forecasts scenarios of land cover change out to 2100 based on three emissions scenarios: A1b, which assumes that current emission trends continue for several decades without modification and incorporates a balanced emphasis on all energy sources; A2, which assumes that current emission trends continue without modification and with regionally oriented economic development; and B1 (same as described above). Corresponding to the future climate change scenarios, I will use the high (A1b) and low (B1) emissions scenarios for projecting land cover change. Elevation, slope position, and aspect will be derived from 10-m resolution, 1/3 arc-second digital elevation models downloaded from USGS’s The National Map.

correlation

Table 2. List of variables with detailed descriptions including units and identification of data sources including the spatial resolution of the dataset, organized by time period (1997–2017 vs. 2100).

|  |  |  |  |
| --- | --- | --- | --- |
| **Period** | **Variable** | **Description (Unit)** | **Data Source (resolution)** |
| --- | Latitude | Latitude (decimal degrees) of the starting point of the Breeding Bird Survey route (also the center of the sampling hexagon) or of the central point of a hexagonal grid cell | North American Breeding Bird Survey route data, U.S. Geological Survey |
| --- | Elevation | Median elevation (m) within sampling hexagon or within hexagonal grid cell | Shuttle Radar Topography Mission digital elevation data (~20–25 m), Consultative Group on International Agricultural Research – Consortium for Spatial Information |
| 1997–2017 | Mean May-June temperature | Mean (°C) of mean monthly temperatures in May within sampling hexagon and mean monthly temperatures in June within sampling hexagon | PRISM Climate Group monthly temperatures (4 km) |
| Temperature difference | Difference (°C) between mean March-April temperature (calculated as described above but for March and April) and mean May-June temperature |
| March-April precipitation | Mean (mm) of total monthly precipitation in March within sampling hexagon and total monthly precipitation in April within sampling hexagon | PRISM Climate Group monthly precipitation (4 km) |
| May-June precipitation | Mean (mm) of total monthly precipitation in May within sampling hexagon and total monthly precipitation in June within sampling hexagon |
| Deciduous and mixed forest | Proportion of each land cover class within the sampling hexagon | National Land Cover Database (30 m), U.S. Geological Survey |
| Conifer forest |
| Developed land |
| Future (2100) | Mean May-June temperature | Mean (°C) of area-weighted mean monthly temperatures in May within hexagonal grid cell and area-weighted mean monthly temperatures in June within hexagonal grid cell | Long-term (30-yr average), downscaled, monthly temperature data from three general circulation model outputs and two representative concentration pathways (10 km), U.S. Forest Service Northern Research Station |
| Temperature difference | Difference (°C) between mean March-April temperature (calculated as described above but for March and April) and mean May-June temperature |
| March-April precipitation | Mean (mm) of area-weighted mean total precipitation in March within hexagonal grid cell and area-weighted mean monthly precipitation in April within hexagonal grid cell | Long-term (30-yr average), downscaled, monthly precipitation data from three general circulation model outputs and two representative concentration pathways (10 km), U.S. Forest Service Northern Research Station |
| May-June precipitation | Mean (mm) of area-weighted mean total precipitation in May within hexagonal grid cell and area-weighted mean monthly precipitation in June within hexagonal grid cell |
| Deciduous and mixed forest | Proportion of each land cover class within the hexagonal grid cell | Conterminous United States projections from the Forecasting Scenarios of land (FORE-SCE) use model (250 m), U.S. Geological Survey |
| Conifer forest |
| Developed land |

*Data analysis*

I will model the 15 focal species simultaneously with a single joint species distribution model (Pollock et al. 2014). The response variable will be occurrence (1 or 0) at a stop, and the predictor variables will include: mean July temperature, mean May to September temperature, total annual precipitation, and total May to September precipitation; proportions of deciduous and mixed forest, coniferous forest, urban/developed land, and other non-forest land within 400 m; and mean elevation, mode slope position, and mode aspect within 400 m. The route will be treated as a random effect to account for possible pseudoreplication.

Model fit

Variable importance will be determined by looking at whether credible intervals overlap 0. I will assess the relative influence of climate and land cover variables for each species by comparing the amount of climate vs. land cover change that is required to result in the same specified change in occupancy. I will then use the top model to predict species occurrence historically (based on climate and land cover data from 2000) and in 2100 (based on the four different combinations of future climate and land cover scenarios) to a 1 km x 1 km grid covering the study area. I will quantify differences in area and mean-center of spatial distribution between the historical (2000) and future (2100) distributions for each species. The change in area is a measure of gains or losses in the area of suitable habitat. Meanwhile, the change in mean-center for the occurrence of each species will be calculated with the spatial statistic tool “Mean Center” within ArcGIS. The coordinates of the mean-center will be used to calculate distance and direction of potential movement of suitable habitat, by species and by scenario. In addition, I will test for significant directional movement from random of the mean-centers using the Rayleigh test of random circular distribution (Matthews et al. 2011).

Statistical significance

**Results**

*Models*

Table 3. Measures of prevalence based on North American Breeding Bird Survey data from routes surveyed in 1997–2017, model type and model fit, the number of iterations in the posterior distribution, and statistical significance of predictor variables for the six cold-associated species. Route-level occurrence across years is the total number of routes where at least one individual was detected across the 50 stops, whereas total count across years is the total number of individuals detected across all routes and years. The model type refers to whether a negative binomial model with spatial random effects (spatial) vs. with site-level random effects (nonspatial) was used for that species. Model fit was assessed using squared Pearson residuals. Predictor variables (latitude, elevation, interaction between latitude and elevation, mean May-June temperature, difference between mean March-April temperature and mean May-June temperature, mean total March-April precipitation, mean total May-June precipitation, proportions of deciduous and mixed forest, conifer forest, and developed land) are marked with an X if the credible interval of their beta coefficient did not overlap zero (which indicates statistical significance) and with a 0 if their beta coefficient did overlap zero.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | **VEER** | **BHVI** | **LEFL** | **BTBW** | **CAWA** | **NAWA** |
| Route-level occurrence across years | 1,590 | 1,768 | 1,352 | 857 | 411 | 77 |
| Total count across years | 11,441 | 6,995 | 5,299 | 3,016 | 1,041 | 109 |
| Model type | spatial | spatial | spatial | spatial | spatial | spatial |
| Model fit | 0.679 | 0.313 | 0.452 | 0.725 | 0.410 | 0.727 |
| Iterations | 6,000 | 15,000 | 21,000 | 18,000 | 15,000 | 18,000 |
| Latitude | X | X | X | X | X | 0 |
| Elevation | X | X | X | X | X | 0 |
| Latitude x Elevation | X | 0 | X | X | X | --- |
| May-June temperature | 0 | 0 | 0 | 0 | 0 | 0 |
| Temperature difference | 0 | X | X | 0 | 0 | 0 |
| March-April precipitation | 0 | X | X | 0 | 0 | 0 |
| May-June precipitation | X | 0 | 0 | 0 | 0 | 0 |
| Deciduous and mixed forest | 0 | 0 | X | X | 0 | 0 |
| Conifer forest | 0 | X | 0 | 0 | 0 | 0 |
| Developed land | X | 0 | 0 | X | 0 | 0 |

Table 4. Measures of prevalence based on North American Breeding Bird Survey data from routes surveyed in 1997–2017, model type and model fit, the number of iterations in the posterior distribution, and statistical significance of predictor variables for the four warm-associated species. Route-level occurrence across years is the total number of routes where at least one individual was detected across the 50 stops, whereas total count across years is the total number of individuals detected across all routes and years. The model type refers to whether a negative binomial model with spatial random effects (spatial) vs. with site-level random effects (nonspatial) was used for that species. Model fit was assessed using squared Pearson residuals. Predictor variables (latitude, elevation, interaction between latitude and elevation, mean May-June temperature, difference between mean March-April temperature and mean May-June temperature, mean total March-April precipitation, mean total May-June precipitation, proportions of deciduous and mixed forest, conifer forest, and developed land) are marked with an X if the credible interval of their beta coefficient did not overlap zero (which indicates statistical significance) and with a 0 if their beta coefficient did overlap zero.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **KEWA** | **SUTA** | **CERW** | **SWWA** |
| Route-level occurrence across years | 1,317 | 826 | 904 | 114 |
| Total count across years | 3,575 | 3,078 | 2,761 | 183 |
| Model type | spatial | spatial | spatial | spatial |
| Model fit | 0.647 | 0.839 | 0.448 | 0.616 |
| Iterations | 3,000 | 15,000 | 3,000 | 18,000 |
| Latitude | X | X | 0 | 0 |
| Elevation | X | X | X | 0 |
| Latitude x Elevation | --- | 0 | --- | --- |
| May-June temperature | X | X | X | 0 |
| Temperature difference | X | X | X | 0 |
| March-April precipitation | 0 | 0 | 0 | 0 |
| May-June precipitation | X | X | 0 | X |
| Deciduous and mixed forest | X | X | X | X |
| Conifer forest | 0 | X | X | X |
| Developed land | 0 | 0 | 0 | 0 |

Table 5. Measures of prevalence based on North American Breeding Bird Survey data from routes surveyed in 1997–2017, model type and model fit, the number of iterations in the posterior distribution, and statistical significance of predictor variables for the five climate generalist species. Route-level occurrence across years is the total number of routes where at least one individual was detected across the 50 stops, whereas total count across years is the total number of individuals detected across all routes and years. The model type refers to whether a negative binomial model with spatial random effects (spatial) vs. with site-level random effects (nonspatial) was used for that species. Model fit was assessed using squared Pearson residuals. Predictor variables (latitude, elevation, interaction between latitude and elevation, mean May-June temperature, difference between mean March-April temperature and mean May-June temperature, mean total March-April precipitation, mean total May-June precipitation, proportions of deciduous and mixed forest, conifer forest, and developed land) are marked with an X if the credible interval of their beta coefficient did not overlap zero (which indicates statistical significance) and with a 0 if their beta coefficient did overlap zero.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | **REVI** | **WOTH** | **SCTA** | **EAWP** | **WEWA** |
| Route-level occurrence across years | 4,481 | 4,412 | 4,034 | 3,933 | 1,274 |
| Total count across years | 140,488 | 56,553 | 34,152 | 20,348 | 3,648 |
| Model type | nonspatial | nonspatial | nonspatial | nonspatial | spatial |
| Model fit | 0.317 | 0.211 | 0.413 | 0.459 | 0.519 |
| Iterations | 3,000 | 3,000 | 3,000 | 3,000 | 6,000 |
| Latitude | X | X | X | X | X |
| Elevation | X | X | X | X | X |
| Latitude x Elevation | --- | --- | --- | --- | --- |
| May-June temperature | 0 | X | X | X | 0 |
| Temperature difference | X | X | 0 | X | 0 |
| March-April precipitation | X | X | 0 | 0 | X |
| May-June precipitation | 0 | X | 0 | X | 0 |
| Deciduous and mixed forest | X | X | X | X | X |
| Conifer forest | 0 | 0 | 0 | X | 0 |
| Developed land | X | X | X | 0 | 0 |

FIGURE – whisker plots of beta coefficients

FIGURE – relationships with each variable

*Variable importance*

*Relative influence of climate vs. land cover variables*

(amount of climate vs. land cover change that is required to result in the same specified change in expected count)

[birds for which climate > land cover]

[birds for which land cover > climate]

*Projected historic (2000) distribution*

FIGURE – historic with BBS raw data

*Projected future (2100) distributions*

FIGURE – historic and 4 future

Table 6. Mean and standard deviation (SD) of growing season (March-April) and breeding season (May-June) temperatures (°C) and precipitation (mm) predicted by the six combinations of three general circulation models (Community Climate System Model [CCSM], Geophysical Fluid Dynamics Laboratory model [GFDL], and Hadley GEM2-ES [HAD] model) and two representative concentration pathways (RCP) that correspond to lower (4.5) and higher (8.5) levels of greenhouse gas emissions, as well as the averages of the three general circulation models for each RCP.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **March-April Temperature** | | **May-June Temperature** | | **March-April Precipitation** | | **May-June Precipitation** | |
| **Climate scenario** | *Mean* | *SD* | *Mean* | *SD* | *Mean* | *SD* | *Mean* | *SD* |
| CCSM-4.5 RCP | 9.90 | 3.09 | 20.75 | 2.14 | 102.42 | 17.65 | 112.10 | 8.86 |
| CCSM-8.5 RCP | 11.87 | 3.07 | 22.86 | 2.18 | 114.95 | 22.41 | 111.30 | 13.65 |
| GFDL-4.5 RCP | 11.02 | 2.86 | 22.05 | 1.92 | 122.34 | 21.90 | 130.67 | 14.81 |
| GFDL-8.5 RCP | 13.62 | 2.68 | 23.84 | 1.91 | 129.21 | 17.32 | 133.89 | 14.19 |
| HAD-4.5 RCP | 11.87 | 2.91 | 21.71 | 2.08 | 117.11 | 23.28 | 113.44 | 10.90 |
| HAD-8.5 RCP | 13.43 | 2.85 | 23.81 | 2.44 | 124.18 | 17.97 | 117.94 | 10.95 |
| Average 4.5 RCP | 10.93 | 2.95 | 21.50 | 2.05 | 113.96 | 20.73 | 118.73 | 10.83 |
| Average 8.5 RCP | 12.97 | 2.87 | 23.50 | 2.17 | 122.78 | 18.63 | 121.04 | 10.50 |

Average 4.5 scenario across circulation models

(average the three circulation models for 4.5 emission scenario)

Average 8.5 scenario across circulation models

(average the three circulation models for 8.5 emission scenario)

Coolest scenario (PCM 4.5-B1)

Warmest scenario (HCM3 4.5-A1B – Hadley)

*Projected differences in distribution*

[Differences in total count]

[Differences in area]

[Differences in mean center of spatial distribution] - FIGURE

Table 7. Total projected count of individuals across the entire study region (“Count”) in 2000 and 2100, based on the four climate scenarios (coolest: CCSM-4.5 RCP, average of lower emissions: Avg 4.5 RCP, average of higher emissions: Avg 8.5 RCP, and warmest: GFDL-8.5 RCP), as well as the percent change from 2000 to 2100 (“%”). An asterisk by the percent change value indicates a statistically significant difference between years.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **2000** | **CCSM-4.5 RCP** | | **Avg 4.5 RCP** | | **Avg 8.5 RCP** | | **GFDL-8.5 RCP** | |
| **Species** | *Count* | *Count* | *%* | *Count* | *%* | *Count* | *%* | *Count* | *%* |
| VEER | 1,179 | 1,015 | -13.91 | 1,014 | -13.99 | 1,098 | -6.87 | 1,100 | -6.7 |
| BHVI | 711 | 696 | -2.11 | 695 | -2.25 | 762 | +7.17\* | 736 | +3.52 |
| LEFL | 348 | 374 | +7.47\* | 375 | +7.76\* | 379 | +8.91\* | 391 | +12.36\* |
| BTBW | 471 | 416 | -11.68 | 417 | -11.46 | 410 | -12.95 | 408 | -13.38 |
| CAWA | 2,048 | 2071 | +1.12 | 2,072 | +1.17 | 1,855 | -9.42 | 1,891 | -7.67 |
| NAWA |  |  |  |  |  |  |  |  |  |
| KEWA | 110 | 108 | -1.82\* | 108 | -1.82\* | 109 | -0.91\* | 109 | -0.91\* |
| SUTA | 1,393 | 1,206 | -13.42\* | 1,244 | -10.70\* | 1,189 | -14.64\* | 1,236 | -11.27\* |
| CERW | 72 | 71 | -1.39 | 71 | -1.39 | 71 | -1.39 | 72 | 0.00 |
| SWWA | 1 | 1 | 0.00 | 1 | 0.00 | 1 | 0.00 | 1 | 0.00 |
| REVI | 8,057 | 8,057 | 0.00 | 8,057 | 0.00 | 8,057 | 0.00 | 8,059 | +0.02 |
| WOTH | 3,550 | 3,551 | +0.03 | 3,541 | -0.25\* | 3,544 | -0.17\* | 3,525 | -0.70\* |
| SCTA | 1,839 | 1,838 | -0.05 | 1,837 | -0.11 | 1,837 | -0.11 | 1,833 | -0.33 |
| EAWP | 1,194 | 1,195 | +0.08 | 1,194 | 0.00 | 1,194 | 0.00 | 1,192 | -0.17 |
| WEWA | 197 | 198 | +0.51 | 197 | 0.00 | 197 | 0.00 | 195 | -1.02\* |

Table 8. Total number of occupied hexagonal grid cells (i.e., projected to contain at least one individual; “Cells”) across the entire study region in 2000 and 2100, based on the four climate scenarios (coolest: CCSM-4.5 RCP, average of lower emissions: Avg 4.5 RCP, average of higher emissions: Avg 8.5 RCP, and warmest: GFDL-8.5 RCP), as well as the percent change from 2000 to 2100 (“%”). An asterisk by the percent change value indicates a statistically significant difference between years.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **2000** | **CCSM-4.5 RCP** | | **Avg 4.5 RCP** | | **Avg 8.5 RCP** | | **GFDL-8.5 RCP** | |
| **Species** | *Cells* | *Cells* | *%* | *Cells* | *%* | *Cells* | *%* | *Cells* | *%* |
| VEER | 135 | 134 | -0.74 | 134 | -0.74 | 134 | -0.74 | 134 | -0.74 |
| BHVI | 142 | 142 | 0.00 | 142 | 0.00 | 143 | 0.70 | 143 | 0.70 |
| LEFL | 108 | 108 | 0.00 | 108 | 0.00 | 108 | 0.00 | 108 | 0.00 |
| BTBW | 55 | 57 | +3.64 | 58 | 5.45 | 58 | +5.45 | 58 | +5.45 |
| CAWA | 75 | 76 | +1.33 | 76 | 1.33 | 74 | -1.33 | 74 | -1.33 |
| NAWA |  |  |  |  |  |  |  |  |  |
| KEWA | 63 | 63 | 0.00 | 63 | 0.00 | 63 | 0.00 | 63 | 0.00 |
| SUTA | 80 | 78 | -2.5 | 78 | -2.5 | 77 | -3.75 | 78 | -2.5 |
| CERW | 2 | 2 | 0.00 | 2 | 0.00 | 2 | 0.00 | 2 | 0.00 |
| SWWA | 0 | 0 | 0.00 | 0 | 0.00 | 0 | 0.00 | 0 | 0.00 |
| REVI | 346 | 346 | 0.00 | 346 | 0.00 | 346 | 0.00 | 346 | 0.00 |
| WOTH | 346 | 346 | 0.00 | 346 | 0.00 | 346 | 0.00 | 346 | 0.00 |
| SCTA | 346 | 346 | 0.00 | 346 | 0.00 | 346 | 0.00 | 346 | 0.00 |
| EAWP | 346 | 346 | 0.00 | 346 | 0.00 | 346 | 0.00 | 346 | 0.00 |
| WEWA | 154 | 153 | -0.65 | 153 | -0.65 | 153 | -0.65 | 151 | -1.95 |

Table 9. Distance (km) and angle (degree, where 0 is directly east and 90 is directly north) of the shift in count-weighted mean-center of the projected distribution from 2000 to 2100, based on the four climate scenarios (coolest: CCSM-4.5 RCP, average of lower emissions: Avg 4.5 RCP, average of higher emissions: Avg 8.5 RCP, and warmest: GFDL-8.5 RCP). An asterisk by the distance value indicates a statistically significant difference between years.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **CCSM-4.5 RCP** | | **Avg 4.5 RCP** | | **Avg 8.5 RCP** | | **GFDL-8.5 RCP** | |
| **Species** | *Distance* | *Angle* | *Distance* | *Angle* | *Distance* | *Angle* | *Distance* | *Angle* |
| VEER | 1,111 | 211 | 1,114 | 211 | 1,921 | 215 | 1,828 | 215 |
| BHVI | 71 | 53 | 89 | 50 | 46 | 61 | 84 | 52 |
| LEFL | 250 | 41 | 233 | 42 | 283 | 39 | 313 | 35 |
| BTBW | 407 | 45 | 416 | 45 | 513 | 46 | 528 | 46 |
| CAWA | 32 | 254 | 66 | 238 | 74 | 47 | 20 | 34 |
| NAWA |  |  |  |  |  |  |  |  |
| KEWA | 71 | 46 | 71 | 40 | 24 | 67 | 37 | 17 |
| SUTA | 72 | 19 | 62 | 21 | 82 | 10 | 67 | 9 |
| CERW | 154 | 29 | 59 | 24 | 75 | 28 | 57 | 10 |
| SWWA | 70 | 33 | 61 | 43 | 82 | 59 | 257 | 48 |
| REVI | 15 | 208 | 10 | 216 | 11 | 219 | 28 | 220 |
| WOTH | 31 | 197 | 34 | 45 | 13 | 130 | 51 | 35 |
| SCTA | 16 | 206 | 9 | 61 | 8 | 130 | 31 | 53 |
| EAWP | 32 | 200 | 6 | 79 | 17 | 181 | 9 | 21 |
| WEWA | 44 | 219 | 9 | 203 | 12 | 157 | 38 | 55 |

**Discussion and conclusions**

It is important to note that my model projections assume that: (1) historical predictor-response relationships remain constant through time; (2) the predictors used are comprehensive and ecologically relevant to birds; (3) the models of bird-habitat associations are able to capture the distribution of a species rather than spurious spatial associations; (4) biotic interactions with species not incorporated into the model do not change the outcomes; and (5) there are no major changes in forest dynamics. Violations of any of these assumptions could lead to model deficiencies. Thus, these models are meant to provide a general, broad-scale perspective, supporting some of the documented and predicted trends from the literature review, and should not be examined or interpreted at fine scales.

[climate groups – trends]

Data was aggregated at a broad scale

Limitation in developed land cover (inherent error in classification, potential issues with mixed habitat)

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**Literature Cited**

**Tables**

Table 2. For analysis of historical land cover in Chapter 1 (potential effects of climate and land cover change on forest songbirds of the Appalachian Mountains), I will combine the various land cover categories from the 2001, 2004, 2006, 2008, 2011, 2013, and 2016 National Land Cover Databases (NLCD) into five different land cover classes.

|  |  |
| --- | --- |
| **Land Cover Class** | **NLCD Land Cover Categories** |
| Deciduous and Mixed Forest | Deciduous Forest  Mixed Forest  Woody Wetlands |
| Coniferous Forest | Evergreen Forest |
| Urban/Developed | Developed, Open Space  Developed, Low Intensity  Developed, Medium Intensity  Developed, High Intensity |
| Non-Forest | Grassland/Herbaceous  Shrub/Scrub  Pasture/Hay  Cultivated Crops  Emergent Herbaceous Wetlands |
| Non-Habitat | Open Water  Barren Land (Rock/Sand/Clay)  Perennial Ice/Snow  Unconsolidated Shore |

**Figures**

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Figure 1. Location and extent of the Appalachian Mountains study region (shaded tan) in the eastern United States.