**CHAPTER 4**

**Comparison of avian guild richness, species abundance, and nest success in   
harvested and non-harvested forested landscapes**

**INTRODUCTION**

**Long-term changes in bird populations**

In the forests of the eastern United States, landscapes have been altered significantly in the last century, with tradeoffs associated with different forest bird guilds. Bird species that breed in early-successional forest habitat, such as chestnut-sided warblers (*Setophaga pensylvanica*), eastern towhees (*Pipilo erythrophthalmus*), and yellow-breasted chats (*Icteria virens*), are strongly associated with herbaceous or shrubby areas in the stand initiation/establishment or regeneration phase, with low canopy basal area (Sheehan et al. 2014). In contrast, bird species that breed in mature forest habitat, such as blue-headed vireos (*Vireo* *solitarius*), ovenbirds (*Seiurus aurocapilla*), and wood thrushes (*Hylocichla mustelina*), are associated with late-successional stands in the canopy transition or old-growth/gap dynamics stages, with high canopy basal area (Sheehan et al. 2014). Thus, there are differential benefits to early-successional vs. mature forest birds when there are changes in composition (i.e., amount of different habitat patch types without regard to spatial attributes) and configuration (i.e., spatial characteristics of individual habitat patches, requiring spatial information and usually aggregated across patches at the class or landscape level) of forested landscapes. Historically, such changes in the eastern United States over hundreds of years have comprised a loss of old-growth forests followed more recently by a decrease in age-class diversity and structural complexity within second-growth forests (e.g., Schulte et al. 2007) and loss of early-successional habitats dominated by grass, shrubs, or young trees (Askins 2001, Trani et al. 2001). Concomitantly, there have been severe and widespread population declines in shrubland-dependent species (Litvaitis 1993, Hunter et al. 2001, DeGraaf and Yamasaki 2003), with the removal of early-successional habitat from the landscape thought to be the primary reason driving those trends (Kelley et al. 2008). Thus, optimizing diversity across the forest-associated bird guilds likely calls for mosaic landscapes that contain a variety of forest age classes or successional stages (Loehle et al. 2005, Mitchell et al. 2008).

**Bird responses to harvest intensity**

Increasing variation in composition and configuration within forested landscapes can be accomplished by timber management or silvicultural practices. For instance, harvesting forests can lead to patches that are distinct, more fragmented, less connected, and smaller (Boucher et al. 2015). These forests also contain more edge area and are subjected to more frequent and more severe uniformly-sized disturbance from periodic, repeated harvest regimes. Within stands, even-aged silvicultural systems (e.g., clearcuts) can create homogenous vertical and horizontal structure (Kuuluvainen et al. 1996), but at a landscape scale, timber rotation length can change the age-class distribution of forests, increasing the proportions of early-successional or young forest (Hejl et al. 1995). In contrast, non-harvested forested landscapes (i.e., no timber harvest within >80 years) are usually characterized by occasional large-scale disturbances and frequent small-scale disturbances, which allow for a finer-grained mosaic of different successional phases (Bengtsson et al. 2000). Thus, landscape-scale structural heterogeneity is generally higher in harvested forests managed in an even-aged system whereas within-stand structural heterogeneity might be higher in non-harvested landscapes (Dettki and Esseen 1998), particularly those subject to historic natural disturbance regimes (e.g., fire). Ultimately, harvests increase the availability of early-successional forest habitat, which leads to increased abundance of early-successional and some generalist bird species (Duguay et al. 2001, McDermott and Wood 2009). Especially in forest-dominated landscapes, timber harvest can be a useful management tool to support a diversity of bird species.

Whether within a harvested or non-harvested landscape, birds are sensitive to landscape change in terms of composition. Several studies suggest that songbird abundance in forested landscapes is influenced more by the quantity of different habitats in the landscape rather than the spatial arrangement of those habitats (e.g., Lichstein et al. 2002). Higher proportions of early-successional habitats in harvested landscapes can also result in significantly higher abundances of early-successional and generalist bird species (Drapeau et al. 2000). A study from a harvested forest found that certain forest interior-edge (e.g., black-capped chickadees [*Poecile atricapillus*], dark-eyed juncos [*Junco hyemalis*], eastern towhees) and forest interior (e.g., ovenbirds, black-throated blue warblers [*Setophaga caerulescens*], scarlet tanagers [*Piranga* *olivacea*]) species are sensitive to both landscape composition and landscape configuration metrics, such as contrast-weighted edge density, number of patches, and percent core area (Weakland 2000). Other studies also linked mature forest bird species with landscape composition (Becker et al. 2012), as well as amount of core area, area-weighted mean shape index (i.e., metric of the shape complexity of patches of all cover types derived by measuring the perimeter-to-area ratio weighted by the size of its patches), and interspersion-juxtaposition index (i.e., a measure of the intermixing of cover types relative to the maximum intermixing possible) (Becker 2010).

In addition to the amount of habitat present in the landscape, landscape configuration features, such as habitat patch area, are important predictors of bird abundance (Crozier and Niemi 2003). Other aspects of landscape configuration include core area and edge density. Howell et al. (2000) found that the abundances of Acadian flycatchers (*Empidonax virescens*), red-eyed vireos, scarlet tanagers, and yellow-throated vireos (*Vireo flavifrons*) were all positively associated with mean mature forest patch size; the abundances of Carolina wrens (*Thryothorus ludovicianus*) and northern parulas (*Setophaga americana*) were positively related to mature forest core area; and the abundance of blue-gray gnatcatchers (*Polioptila* *caerulea*) responded negatively to edge density, while abundances of blue jays (*Cyanocitta cristata*), brown-headed cowbirds (*Molothrus ater*), and eastern wood-pewees (*Contopus virens*) responded positively to edge density. Early-successional and shrubland bird abundance is also related positively to patch size of their corresponding habitat (DeGraaf and Yamasaki 2003, Chandler et al. 2009, Lehnen and Rodewald 2009, Shake et al. 2012). For instance, Askins et al. (2007) found that eastern towhees and shrubland generalists are found in higher abundances in larger forest openings. On the other hand, the size of early-successional habitat patches can negatively affect mature forest birds. 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). Another study found that 0.4-ha clearcut openings resulted in the movement of several forest-interior species away from openings and subsequently decreased abundance in and adjacent to openings (Germaine et al. 1997).

Landscape composition and particularly configuration can affect nest success. At a fundamental level, nesting songbird distributions can be dictated by habitat cover within the landscape (Drolet and Desrochers 1999). Composition within forested landscapes further influences avian nesting success by altering interactions between nest predators and nesting birds (Rodewald and Yahner 2001). Configuration can also affect nest survival, as nest predators concentrate near edges (Gates and Gysel 1978), so increased edge density or the abrupt creation of edge due to timber harvest in a managed forest could lower nest success. Nest success of wood thrush in the Monongahela National Forest in West Virginia was found to be positively related to mean shape indices and mean patch fractal dimension of mature forest (both indicative of higher complexity of mature forest patch shapes) and negatively related to an interspersion-juxtaposition index (i.e., measure of the relative interspersion of mature forest patches) and proportion of open habitat (Williams 2002).

Avian population and community processes operate across a broader scale than local patches (Bennett et al. 2004). Patterns of bird species composition and diversity are related to landscape composition, such as proportions of forest types and ages (Drapeau et al. 2000, Carrara et al. 2015), and landscape configuration, such as patch sizes and edge density. Greater landscape age heterogeneity is associated with greater overall species richness (Loehle et al. 2005, Mitchell et al. 2008). In addition, in a study of the effects of group-selection opening size on breeding bird habitat use in a bottomland forest, species richness in 0.06-, 0.13-, 0.26-, and 0.5-ha openings increased as opening size increased, due to the increased use of larger openings by early-successional and edge-associated species (Moorman and Guynn, Jr. 2015). Furthermore, mature forest edge is positively associated with generalist richness but negatively with specialist species richness (Jones et al. 2000). Beyond species richness, landscape changes can ultimately result in shifts in community composition and diversity (i.e., turnover) (Parody et al. 2001), as conversion of guild-specific preferred habitat to less suitable habitat can lead to reductions in guild richness (Aratrakorn et al. 2006, Zurita et al. 2006). In summary, landscape structure may affect forest bird assemblages through effects on both total number of species and on temporal rates of community composition change.

**Knowledge gap**

Forest managers often aim to balance or combine the economic benefits of timber harvest with the maintenance of wildlife habitat, biodiversity, and ecosystem function. Forest songbirds exhibit varying responses to timber harvest (Thompson et al. 1992, Annand and Thompson III 1997, Robinson and Robinson 1999), which can alter forest composition, configuration, and connectivity on a landscape scale (e.g., Spies et al. 1994). Thus, timber management can be potentially used as a landscape-level tool to promote both early-successional and mature forest songbird populations and diversity (Petit et al. 1995). However, we have an incomplete understanding of how birds respond over time to landscape-level factors. Except for a few recent studies, such as Kellner et al. (2019), previous studies have traditionally focused on forest patches in agricultural landscapes (e.g., Freemark and Merriam 1986, van Dorp and Opdam 1987, McIntyre 1995, Villard et al. 1999, Lee et al. 2002) or in landscapes that are either exclusively harvested or non-harvested (not both simultaneously), or they examined avian responses at control and harvested sites on limited (i.e., stand- and patch-level) scales (e.g., (Crawford et al. 1981, DeGraaf et al. 1998, McDermott et al. 2011), neglecting landscape-level trends. Furthermore, these studies tend to be short-term, lasting 1–3 years, and may not reflect the full temporal response to the management practices under study (Sallabanks et al. 2000, Loehle et al. 2005). Thus, long-term research is needed to investigate the response of bird communities to landscape-level factors in both harvested and non-harvested forests through time. Specifically, I aim to answer the following questions: (1) How do early-successional and forest-interior breeding birds respond to landscape composition and configuration over time, and (2) are those relationships and trends modified by the intensity (i.e., type) of timber harvest in the surrounding landscape?

**Purpose, objectives, and hypotheses**

The purpose of this study was to quantify long-term avian responses to landscape-scale forest management and compare changes over time in avian diversity, abundance, and population dynamics from two Central Appalachian forested landscapes that varied in timber harvest intensity. My specific objectives were to examine the influence and effect of interactions between time and landscape-level timber harvest intensity on breeding season songbird guild richness, focal species abundance, and focal species nest success. I focused on 2 landscapes with diverging forest management prescriptions: (1) an actively harvested landscape with >75% of its area experiencing diameter-limit harvest, two-age harvest, or clear-cutting during the study period (1993–2009), and (2) a minimally harvested landscape with <1% of its area experiencing two-age harvest or clear-cutting approximately 10–15 years prior to the study period.

In this study, I tested the hypothesis that long-term temporal trends in forest songbird communities and populations during the breeding season are mediated by landscape-level forest management. I predicted that trends over time in diversity, abundance, and nest success would vary by guild designation and landscape (i.e., level of timber harvest intensity). For example, in the actively harvested landscape, I expected that early-successional and edge-associated species would respond positively over time, whereas forest-interior and forest-gap species would respond negatively over time. In contrast, in the minimally harvested landscape, I expected that early-successional and edge-associated species would respond negatively over time, while forest-interior and forest-gap species would show little to no response. Taking a holistic approach, I assessed the statistical significance and effect sizes of interactions between time and landscape-level timber harvest intensity for overall species richness, the number of species belonging to 4 habitat guild designations, the abundance of 15 focal songbird species, and the nest success of 6 focal songbird species (Table 1).

**METHODS**

**Study area**

Sampling points for this study were located throughout 3 study regions within the northern, central, and southern Appalachian Mountains (Figure 1). I used data from a total of 1733 sampling points (Figure 2), consisting of 373 sampling points in the Hubbard Brook Experimental Forest (HBEF) in the White Mountains of New Hampshire (~43.9° latitude), 1149 sampling points in the Monongahela National Forest (MNF) in the Allegheny Mountains of West Virginia (~38.5° latitude), and 211 sampling points in the Pisgah and Nantahala National Forests (PNF / NNF; collectively referred to as NCNF hereafter) in the Blue Ridge Mountains of North Carolina (~35.2° latitude). All sampling points used in this study were located in forest stands that had not been harvested in >60 years at the time of sampling, and distances between sampling points were at least 200 m.

My research will incorporate data collected from the intensively managed MeadWestvaco Wildlife and Ecosystem Research Forest (WERF), located in Randolph County, West Virginia (Figure 4), and the less intensively managed and predominantly non-harvested Monongahela National Forest (MNF), which encompasses portions of nine counties (Preston, Tucker, Grant, Randolph, Pendleton, Pocahontas, Webster, Nicholas, and Greenbrier) in eastern West Virginia (Figure 5).

The WERF encompasses 3,080 ha and was established in 1994 to study the effects of industrial forest management practices on ecosystem processes and wildlife. Elevation within the WERF ranges from 734–1180 m, and regional topography consists of narrow valleys with small, high-gradient streams and broad ridges oriented south-southwest to north-northeast (Becker et al. 2011). Annual average precipitation is >160 cm per year.

Vegetation communities in the WERF are variable due to elevation. At high elevations (>1,000 m), red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*) dominate. At mid-elevations (850–1,000 m), northern hardwoods such as red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), and black cherry (*Prunus serotina*) are most prevalent. Meanwhile, low-elevation sites (<850 m) consist of cove hardwood and mixed mesophytic plant communities (northern red oak [*Quercus rubra*], black birch [*Betula lenta*], and tulip-poplar [*Liriodendron tulipifera*]) and xeric oak-hickory communities (black oak [*Quercus velutina*], scarlet oak [*Q. coccinea*], and hickory [*Carya* spp.]). Non-forest cover in the study area is limited to grassy cover along road edges, gas well openings, and log landings. In 1994, the WERF was primarily 70–90 years-old even-aged mature forest, but much of the forest has been actively managed using even-aged timber harvesting through clear-cuts, shelterwood cuts, and uneven-age or partial harvesting via single-tree selection and high-grade harvests of mature sawtimber (Dellinger et al. 2007*b*). In 2007, management shifted to primarily uneven-aged techniques.

The MNF was placed under federal protection in 1920 and encompasses nearly 688,000 ha, of which 54% (371,906 ha) is owned and overseen by the U.S. Forest Service. The MNF stretches across a latitudinal range of nearly 200 km and lies within two physiographic provinces, the Central Appalachians (Allegheny Mountains) and the Ridge and Valley. The eastern section of the Monongahela National Forest, which overlaps the Ridge and Valley physiographic province, lies in the rain shadow of the Allegheny Mountains, so it receives significantly less precipitation (~75 cm/year) compared to the rest of the forest, which experiences 115–150 cm/year. Elevation within the MNF ranges from 275–1480 m.

The MNF is comprised primarily of 70–100 years-old stands with high regional tree diversity and four major forest zones (mixed mesophytic, northern hardwoods, red spruce, and dry oaks). Mixed mesophytic forests are present at low elevations (<900 m), with northern red oak, hickory, and yellow-poplar as the dominant species. At increasing elevations, there is a transition in stand dominance to northern hardwoods, including American beech, sugar maple (*Acer saccharum*), and black cherry (*Prunus serotina*). At the highest elevations (>1,150 m), remnant boreal forest ecosystems consist of red spruce. In the eastern MNF, dry oaks are common in the Ridge and Valley area, consisting of white (*Q. alba*), chestnut (*Q. prinus*), scarlet, and black oaks, as well as pines (*Pinus* spp). The majority of the MNF has not been harvested within the past 30 years, and a 100–120 year timber harvest rotation applies to most areas of the MNF not designated as Wilderness Areas.

Sampling sites for this study were located throughout the Monongahela National Forest (MNF), which encompasses portions of nine counties (Preston, Tucker, Grant, Randolph, Pendleton, Pocahontas, Webster, Nicholas, and Greenbrier) in eastern West Virginia (Figure 1). This area was placed under federal protection in 1920 and encompasses nearly 688,000 ha, of which 54% (371,906 ha) is owned and overseen by the U.S. Forest Service. The MNF stretches across a latitudinal range of nearly 200 km and lies within two physiographic provinces, the Central Appalachians (Allegheny Mountains) and the Ridge and Valley. The eastern section of the Monongahela National Forest, which overlaps the Ridge and Valley physiographic province, lies in the rain shadow of the Allegheny Mountains, so it receives significantly less precipitation (~75 cm/year) compared to the rest of the forest, which experiences 115–150 cm/year (Clarkson 1966). Elevation within the MNF ranges from 275–1,480 m.

The MNF is comprised primarily of 70–100 year-old stands with high regional tree diversity and 4 major forest zones (mixed mesophytic, northern hardwoods, red spruce, and dry oaks) (McCay et al. 1997, DeMeo 1999). Mixed mesophytic forests are present at low elevations (<900 m), with northern red oak (*Quercus rubra*), hickory (*Carya* spp.), and yellow-poplar (*Liriodendron tulipifera*) as the dominant species (Madarish et al. 2002). At increasing elevations, there is a transition in stand dominance to northern hardwoods, including American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and black cherry (*Prunus serotina*) (Stephenson 1993). At the highest elevations (>1,150 m), remnant boreal forest ecosystems are dominated by red spruce (*Picea rubens*). In the eastern MNF, dry oaks are common in the Ridge and Valley area, consisting of white (*Quercus alba*), chestnut (*Q. prinus*), scarlet (*Q. coccinea*), and black (*Q. velutina*) oaks, as well as pines (*Pinus* spp.).

**Guild designations**

To assess climate relationships and temporal trends for overall species richness and guild richness, I used a specific subset of forest songbird species. Although a total of 153 bird species were detected across all surveys in all years from all 3 study regions, I limited the richness analyses to 40 species (see Appendix A for full list) in Order Passeriformes that were mature forest obligates with breeding ranges that overlapped at least 1 of the 3 study regions. I enacted these species restrictions for several reasons: (1) the bird count data were from avian point count surveys, which are primarily designed to detect passerines (i.e., songbirds); (2) this study focused on breeding birds rather than migrants; and (3) by concentrating on bird species with similar breeding habitat requirements or preferences, I sought to minimize differences in species responses due to forest habitat change, since the primary variables of interest were climate factors.

To assess additional impacts on songbird diversity, I considered a subset of passerine and near-passerine species. Although a total of 116 avian species were detected across all surveys, I limited the richness analyses to 66 species (see Appendix A for full list) with breeding ranges that encompassed the study area and that had ≥5 detections. I also excluded wetland-associated songbirds because they were incidental to the focal habitat types, as well as corvids and waterthrushes because they are not well-sampled with breeding songbird point count surveys.

Habitat-related guild designations for the 66 songbird species were assigned based on breeding habitat and comprised 4 categories (Appendix A): (1) early-successional and edge-associated (i.e., primarily breed or found in grasslands, shrub/scrub, or young forest; or along forest edges, such as the interface of early-successional and mature forest); (2) forest-interior (i.e., generally breed or found in the core area of mature forest); (3) forest-gap (i.e., generally breed or found in or near small forest gaps within the core area of mature forest); and (4) forest generalist (i.e., associated with forest but no preference for early-successional vs. mature forest). For early-successional and edge-associated species, the presence of a wildlife opening is required, and for forest-gap species, the presence of gaps in the forest canopy is required.

**Focal species**

To assess climate relationships and temporal trends for focal species belonging to each guild designation, I selected 16 forest songbird species commonly found within the Appalachian Mountains (Table 1). In addition to limiting the focal species by taxonomic order, breeding range, and primary breeding habitat as described above for the richness analyses, I considered only long-distance migrants to keep migration status consistent and selected at least 3 relatively abundant (i.e., >250 detections; Appendix A) species from the 3 taxonomic families (Parulidae, Turdidae, and Tyrannidae) with the most species meeting all the criteria. These selection decisions were made to ensure that models would run efficiently and to compare any potential differences between the 4 guilds within taxonomic families.

**Bird count data**

To calculate bird species occupancy and abundance, I will use bird point count data from the WERF surveyed during 1996–1998, 2001–2003, and 2007–2009 (Figure 6A). Point counts were conducted within a 50-m fixed radius at locations selected systematically from available points on a 241 x 241 m forest inventory grid (Figure 4) established in 1995 by Westvaco Forest Resources (prior to extensive timber harvesting). An average of 110 points were surveyed each year, and locations were mostly consistent across time periods. From the MNF, I will use bird point count data surveyed from 1996 to 2009. During this time period, 1,316 points were sampled at least once. However, only 132 points were sampled at least once during both 1996–1998 and 2007–2009, with a range of 6–12 years of associated point count data.

At both study areas, surveys were conducted from May to July; they began within 15 min of sunrise and continued until approximately 10:00 am. No surveys were conducted during days with rain, heavy fog, or high wind (Ralph et al. 1993). During each point count, observers recorded all individuals seen or heard during a 10-minute period, which was divided into three time intervals (1–3 min, >3–5 min, and >5–10 min). Individuals were recorded only the first time they were observed. Thus, the point counts were conducted in a removal sampling framework, which allows me to estimate detection probability from a single visit each year (Farnsworth et al. 2002, Rota et al. 2009). Point count data included: species, distance band (≤50 m or >50 m), time interval, detection type (song, call, visual, flyover, drumming), and age/sex (if known).

Avian point count survey data were collected at each of the 3 study regions from 1999–2002 and 2005–2019 at 373 HBEF sampling points, from 1993–2013 and 2017–2020 at 1149 MNF sampling points, and from 1997–2018 and 2020 at 211 NCNF sampling points. Avian point count surveys were not collected every year at all sampling points. The number of years of data associated with each sampling points ranged 1–19 years (mean = 17.5 ± 1.6 years) in HBEF, 1–17 years (mean = 4.6 ± 3.9 years) in MNF, and 8–23 years (mean = 17.6 ± 3.3 years) in NCNF. Within a year that avian point count survey data were collected, the number of repeated visits (i.e., replicate surveys) ranged from 1–5 visits (mean = 3.0 ± 0.8 visits) in HBEF and 1–4 visits (mean = 1.2 ± 0.4 visits) in MNF; in NCNF, only 1 avian point count survey was completed per year. I included all replicate surveys per sampling point per year in my data analyses, for a total of 29,610 replicate surveys across 15,494 stacked site × year combinations.

Avian point count surveys were conducted from mid-May to early July (i.e., during the bird breeding season) and consisted of 10-minute stationary counts, during which a single observer recorded the species and number of all birds heard or seen. Surveys began within 30 minutes of sunrise and continued until approximately 4 hours after sunrise. No surveys were conducted on days with rain, heavy fog, or high wind speed, following the guidelines of Ralph et al. (1993). Up to 4 detection covariates were recorded for each survey: date, start time, wind code or wind speed, and sky code. While date was recorded for all surveys, a subset of surveys was missing start times (55% of MNF data, 4% of NCNF data), wind codes or wind speeds (59% of MNF data, 7% of NCNF data), or sky codes (<1% of HBEF data, 60% of MNF data, 7% of NCNF data). For data standardization, any recorded wind speed measurements were converted to wind codes using the Beaufort wind scale.

The 10-minute point count survey was divided into 3 time intervals (i.e., within-survey replicates): 0:00–3:20, 3:21–6:40, and 6:41–10:00 minutes (HBEF); 0:00–3:00, 3:01–5:00, and 5:01–10:00 minutes (MNF); or 0:00–3:59, 4:00–5:59, and 6:00–10:00 minutes (NCNF). For each individual bird that was detected, observers recorded the corresponding time interval and distance band (≤50 m or >50 m). During point count surveys within HBEF, each 3:20-minute interval was treated as a new sampling period (i.e., the presence of an individual bird would be recorded 3 separate times if the bird sang in all 3 time intervals), but observers indicated if a bird appeared for the first time or not during a time interval. During point count surveys within MNF and NCNF, individual birds were only recorded the first time they were observed, following removal sampling methods. To limit detection variability due to distance, I restricted all data analyses to birds detected within 50 m.

**Nest success data**

To estimate nest success of focal species, I will use nest monitoring data from the WERF collected during 1996–1998, 2001–2003, and 2007–2009 (Figure 6B). Throughout the breeding season, field technicians searched six, approximately 20-ha nest plots, which were distributed randomly throughout three elevational blocks and spanned areas of intact, predominantly mature hardwood forest and areas of closed-canopy early-successional vegetation. Nest searching occurred every three days from 6:00 to 13:00 for at least 18 days or 126 person-hours. Nests located through both systematic searching efforts and opportunistic observations were monitored from mid-May until mid-July. During the monitoring period, field technicians checked each nest a minimum of every three days until the nest attempt was complete and identified as either successful or failed. From the nest monitoring data, the following was determined if applicable for each nest: bird species, failure during the incubation period, number of days the nest was observed while in the incubation period, failure during the brooding period, number of days the nest was observed while in the brooding period, ultimate nest failure, total number of days the nest was observed, and the reason why the nest failed (unknown, depredated, abandoned, parasitized by brown-headed cowbirds).

From the MNF, I will use nest monitoring data collected from 1993 to 1999. From 1993 to 1996, 31 stands in the MNF were intensively searched for nests from mid-May to late June, with search effort distributed relatively evenly between stands (Duguay et al. 2001). From 1996 to 1999, nest searches occurred within 40-ha (200-m wide x 2,000-m long, oriented perpendicular to prevailing slopes) plots that were established along two transects in each of five 2,500-ha study areas that were randomly located within the mixed mesophytic vegetation zone of the MNF; the study areas ranged from 42–81% core forest area (DeMeo 1999). Nest searching protocols followed the methodology of the national BBird program of nest search plot monitoring (BBird 1996). In 1998 and 1999, additional nests (outside the established nest search plots) in the northwestern region of the MNF (within Tucker and Randolph counties) were located through behavioral cues and systematic searches of likely nesting habitat (Williams 2002). In all years, once nests were located, they were revisited at 3–4 day intervals from late May to early August until the nestlings fledged or the nest was terminated. On each visit, the number of eggs or nestlings was recorded, and notes were taken on parental location and behavior.

Although the time periods of nest monitoring at the two study areas do not fully overlap (WERF: 1996–1998, 2001–2003, and 2007–2009 vs. MNF: 1993–1999), I will still be able to assess and make inferences concerning nest success trends over time in relation to landscape-level factors in both the harvested (WERF) and predominantly non-harvested (MNF) landscapes. However, I will be making the following assumptions: (1) trends from MNF data collected from 1993 to 1999 are representative of long-term trends; and (2) there is no outside, unconsidered systemic confounding factor (e.g., stochastic weather extremes, climate change, invasive species introduction) influencing trends from WERF data collected after 1999. At the least, I can address the question of nest success patterns across a gradient of harvest intensity within the landscape.

For the abundance analysis, I will focus on common (>2.0% of total detections) Nearctic-Neotropical migrant species associated with forests (Table 5), including five forest-interior species: black-throated blue warbler (*Setophaga caerulescens*), blue-headed vireo, red-eyed vireo, veery (*Catharus fuscuscens*) and wood thrush; four early-successional (including edge-associated) species: eastern towhee, chestnut-sided warbler, indigo bunting (*Passerina cyanea*), cedar waxwing (*Bombycilla cedrorum*); one generalist: American robin (*Turdus migratorius*); and one species of particular conservation concern: cerulean warbler (also a forest-interior species). The focal species for nest success analysis are the seven species of those incorporated in the abundance analysis with at least 30 nests (>4.0% of total nests) detected and monitored in both study areas (Table 5): American robin (WERF: 35, MNF: ≥23), blue-headed vireo (WERF: 32, MNF: ≥36), eastern towhee (WERF: 44, MNF: ≥24), indigo bunting (WERF: 65, MNF: ≥25), red-eyed vireo (WERF: 30, MNF: ≥56), veery (WERF: 66, MNF: ≥32), and wood thrush (WERF: 38, MNF: ≥128).

**Environmental data**

I will use historic site and stand data to quantify the following local habitat-level metrics for each point count and nest location (Table 6): percent canopy cover, dominant forest age class (early-successional forest: ages 0–9; early mid-successional forest: ages 10–29; late mid-successional forest: ages 30–49; late-successional forest: ages >50) within 50 m, and dominant forest type (mixed mesophytic, northern hardwoods, dry oaks, and red spruce) within 50 m. Additional nest-only local site data includes distance to the nearest edge and percent ground cover within 5-m radius of nest. Topographical data will consist of elevation, aspect, and slope position, which will be derived from 10-m resolution, 1/3 arc-second digital elevation models (at a scale of 1:24,000) downloaded from USGS’s The National Map. Although these variables are not the focus of this research, I am including them in my analyses to control for local effects on occupancy, abundance, and nest success.

I will use historic stand-level data and land cover maps digitized by Williams (2002) from 1-m resolution Digital Ortho Quarterquad photos taken by the National Aerial Photography Program between 1997–1999 and GIS/R analysis (e.g., “landscapemetrics” package) to quantify the following landscape composition metrics (Table 6): proportion of non-forest and each forest age class (early-successional, early mid-successional, late mid-successional, and late-successional forest) within 1 km, number of forest age classes within 1 km, evenness of forest age classes within 1 km, Shannon diversity index of forest age classes within 1 km, and dominant harvest intensity (non-harvested: no harvest within 40 years; non-intensive: selection harvest within 40 years; moderately intensive: shelterwood or two-age harvest within 40 years; highly intensive: clearcut within 40 years) within 1 km; and landscape configuration metrics: log-transformed patch (i.e., forest stand) size, log-transformed core patch area (using a 100-m buffer), patch density within 1 km, mean shape index (a measure of patch shape complexity), area-weighted mean shape index (a measure of the shape complexity of patches of all cover types by measuring the perimeter-to-area ratio weighted by the size of its patches; see Table 7 for edge weights), mean patch fractal dimension (another measure of mean patch shape complexity), percent core area of each forest age class (using a 100-m buffer) within 1 km, mean Euclidean nearest-neighbor distance, contrast-weighted edge density, index of dispersion (i.e., ratio of the variance to mean nearest neighbor distance), interspersion-juxtaposition index (a measure of the contagion or distribution of patches), and connectance index (a measure of overall connectivity based on the pairwise connections between patches). Forest composition and configuration metrics will be calculated for each point count and nest location.

The full set of site covariates included year of data collection, latitude, elevation, 4 focal climate variables, and 4 environmental variables that were included to control for their known effects (Table 2). Latitude corresponded to the location of the sampling point. Mean elevation within 50 m of each sampling point was calculated using Shuttle Radar Topography Mission digital elevation data (Table 2).

**Data analysis**

*Determining overall species and guild richness from a hierarchical community model*

For my analyses, I am treating each point count and nest location in space and time as independent, with landscapes defined as the area within a 1-km radius around each point location. In the following models, I will incorporate a random point effect and include year and interactions with dominant harvest intensity within 1 km as covariates, so that I can discern temporal and harvest-related trends.

To quantify how landscape composition and configuration (while controlling for local habitat-level and topographical metrics) relate to forest songbird guild richness and annual community turnover, I will construct a hierarchical community/multi-species occupancy model (Iknayan et al. 2014) within a Bayesian framework, with occurrence data for all species as the response variable. I will integrate the detection process into this community model to explicitly account for the effects of survey-, site-, species-, or individual-level factors affecting detectability. Detection covariates will include observer (as a random effect), ordinal day, time since sunrise, wind speed, and sky code, while site covariates will include the variables listed in Table 6. I will employ model selection using the Watanabe-Akaike Information Criterion (WAIC; a fully Bayesian information criterion analogous to Akaike Information Criterion [Gelman et al. 2014, Hooten and Hobbs 2015]) to compare candidate models incorporating time and landscape composition and configuration metrics that reflect my competing hypotheses. Ultimately, the hierarchical community/multi-species occupancy model incorporates undetected and rare species in a biologically oriented, process-driven way (Iknayan et al. 2014) and allows me to derive detection-corrected guild richness (i.e., the number of species in a certain guild present at a point in a given year) (Dorazio et al. 2006). I can similarly calculate species turnover (i.e., the probability that a species selected at random from the community at time *t* is not present at the community at time *t*–1; (Nichols et al. 1998). I will then propagate uncertainty (Kery and Royle 2016) and use posterior samples to determine if there are differences in guild richness and species turnover across the years among differing levels of harvest intensity within the landscape and along a continuous gradient of selected landscape composition and configuration metrics (similar to the analysis of Russell et al. [2009]).

To calculate overall species richness and guild richness at each sampling point in each year of the study, I estimated the individual species occupancy of the 40 forest songbird species simultaneously in a hierarchical community model (see Appendix B for JAGS code) and then derived the corresponding sums for all species and each guild designation (Zipkin et al. 2010). The hierarchical community model facilitated a multi-species approach to estimating individual species occurrence probabilities (Dorazio and Royle 2005, Dorazio et al. 2006). Following the modeling framework of Zipkin et al. (2010), species-specific occurrence and detection processes within the hierarchical community model were related to one another through a community-level hierarchical component, which assumed that each of the species parameters were random effects, governed by “hyper-parameters” (i.e., drawn from a community-level distribution). Linking individual species occurrence probabilities through this community-level hierarchical component leads to improved precision of species-specific estimates (Kéry and Royle 2008, Zipkin et al. 2009).

Occurrence *Zs,y,sp* was defined as a binary variable in which *Zs,y,sp* = 1 if species *sp* occurs within 50 m of sampling point *s* in year *y*. The occurrence state was assumed to be the outcome of a Bernoulli random variable, denoted by:

*Zs,y,sp* ~ *Bernoulli*(*Ψs,y,sp*)

where *Ψs,y,sp*is the probability that species *sp* occurs at sampling point *s* in year *y*. I further used a logit link to model linear relationships between occurrence probability (*Ψs,y,sp*) and 6 site covariates, which consisted of latitude, elevation, aspect, TPI, dominant forest type, and proportion of forest. All continuous site covariates were centered and scaled prior to analysis.

Due to missing detection data and inconsistencies in time intervals of avian point count survey periods among the 3 study regions, I had to customize the species-specific detection model within the hierarchical community model. Given the observed data *Ys,y,r,sp*, where *r* is a within-survey replicate (i.e., time interval during the point count survey period) across all survey replicates (i.e., repeated visits to the sampling point during the sampling year), I defined the detection model for species *sp* at sampling point *s* in year *y* during replicate *r* as:

*Ys,y,r,sp* ~ *Bernoulli*(*ps,y,r,sp* × *Zs,y,sp*)

where *ps,y,r,sp* is the probability of detecting species *sp* at least once during the *r*th within-survey replicate at sampling point *s* in year *y*, given that species *sp* is present at sampling point *s* in year *y*. Note that the detection probability (*p*) was calculated in such a way as to handle uneven timing (ranging 2–5 minutes) among the within-survey replicates, which corresponded to the 3 time intervals during the avian point count survey period; I initially modeled detection probability of species *sp* at sampling point *s* in year *y* during replicate *r* for 1 minute (*p1*) and then I used an approach similar to the logistic exposure model (Shaffer 2004) to calculate the probability that an individual is detected at least once during the full time interval *t* of the within-survey replicate *r* (e.g., 2, 3, or 5 minutes), using the following equation:

*ps,y,r,sp* = 1 – (1 – *p1s,y,r,sp*)*t*

I further used a logit link to model linear relationships between detection probability (*ps,y,r,sp*) and 4 detection covariates, which consisted of ordinal day (centered and scaled prior to analysis), time since sunrise (measured as decimal hours and centered and scaled prior to analysis), a dummy variable for wind (0 = wind codes of 0, 1, or 2; 1 = wind codes >2), and a dummy variable for sky (0 = sky codes of 0, 1, or 2; 1 = sky codes >2). I imputed study region-specific detection covariates for avian point count surveys that were lacking data on time, wind code, or sky code. I assumed that time since sunrise was a Gaussian random variable with region-specific prior mean and variance, and that the wind and sky dummy variables were Bernoulli random variables with region-specific probabilities of success. Imputation was informed by the observed data and accounted for uncertainty, with values drawn from a posterior distribution of each detection variable (Gelman et al. 1995).

The hierarchical community model yielded species-specific estimates of latent occupancy (*Zs,y,sp*) for species *sp* at each sampling point *s* in each year *y* based on observed data from replicate surveys. I then derived the overall species richness for each sampling point in each year by summing the occupancy of the 40 forest songbird species, as in the following equation:

Similarly, I derived guild-specific richness by summing the occupancy of the subset of forest songbird species that belonged to each guild designation.

I was able to integrate distinct detection processes and explicitly account for the effects of different sampling methods in each study region within the hierarchical community model by using a Bayesian framework, implemented with Markov chain Monte Carlo methods. For all community-level and species-specific parameters, I used prior distributions which were meant to provide little information; all gamma prior distributions, often used for variance parameters, had a shape parameter of 1 and rate parameter of 1, and all Gaussian prior distributions, such as for the community-level slope coefficients for each site covariate, had a mean of 0 and precision of either 0.1 or 1 (Appendix B). I fit the models in JAGS (Plummer 2003) using the “jagsUI” package (Kellner and Meredith 2021) in Program R (R Core Team 2022). I used the “jags” function to run 3 chains for the hierarchical community model with a burn-in of 2,500 iterations, thinning rate of 1 iteration, and iteration increment of 1,000, which resulted in 3,000 posterior draws and reasonable convergence (R̂ ≤ 1.1) (Gelman et al. 2014).

*Determining relationships with harvest intensity over time for overall species and guild richness*

After I derived detection-corrected overall species and guild richness from the hierarchical community model, I then incorporated those estimates into corresponding generalized linear mixed effects models, with overall species or guild richness as the response variable and incorporating the 4 climate variables as predictor variables. To propagate uncertainty from the original hierarchical community model results, I ran 3,000 iterations of the generalized linear mixed effects models for overall species richness and for each guild designation, cycling through the values from each of the 3,000 posterior draws. In result, the models yielded a posterior distribution of 3,000 for each slope coefficient, from which I derived the mean and 95% credible intervals. Thus, the estimated effects on overall species and guild richness were calculated as derived quantities (Kery and Royle 2016).

For each generalized linear mixed effects model, I assumed the number of species at each site in each year (i.e., overall species richness or guild richness) to be a Poisson random variable and used a log link to model relationships with controlling habitat factors and interactions between year, elevation, and mean temperature (used as an index for latitude). All continuous predictor variables were centered and scaled prior to analysis. The total number of slope coefficients was 25 (resulting in a ratio of ~620 sites to 1 slope coefficient; Bolker et al. 2008), corresponding to 9 single site covariates (year, latitude, elevation, mean temperature, SD temperature, current precipitation, previous precipitation, dominant forest type, and proportion of forest), 11 two-way interactions (latitude × year, latitude × elevation, latitude × mean temperature, latitude × SD temperature, latitude × current precipitation, latitude × previous precipitation, elevation × year, elevation × mean temperature, elevation × SD temperature, elevation × current precipitation, and elevation × previous precipitation), and 5 three-way interactions (latitude × elevation × year, latitude × elevation × mean temperature, latitude × elevation × SD temperature, latitude × elevation × current precipitation, latitude × elevation × previous precipitation). Because my data included repeated observations at each sampling point over the course of multiple years, all of the generalized linear mixed effects models also incorporated a random site effect for log expected richness.

I fit all generalized linear mixed effects models using the “lme4” package (Bates et al. 2015) in Program R (R Core Team 2022). Specifically, I used the “glmer” function with family = “poisson”, optimizer = “bobyqa” (i.e., a specific optimizing function used by the model), and nAGQ = 0. The nAGQ is the number of points per axis for evaluating the adaptive Gauss-Hermite approximation to the log-likelihood. A value of zero uses a form of parameter estimation for generalized linear mixed effects models by optimizing the random effects and the fixed-effects coefficients in the penalized iteratively reweighted least squares step.

*Determining relationships with harvest intensity over time for abundance of individual focal species*

To quantify relationships among abundance of focal species and landscape composition and configuration (while controlling for local habitat-level and topographical metrics), I will use dynamic n-mixture models (Dail and Madsen 2011) and WAIC model selection for each species, with repeated counts of the focal species as the response variable and incorporating interactions with harvest intensity. Detection covariates will include observer (as a random effect), ordinal day, time since sunrise, wind speed, and sky code. For both this and the following analysis, the candidate models will incorporate time and landscape composition and configuration metrics (Table 6) that reflect my competing hypotheses.

To quantify and compare how temperature, precipitation, and other temporal factors influence specific focal species during the breeding season across latitudes and elevations, I estimated the abundance of 16 forest songbird species (Table 1) independently in stacked N-mixture models (Royle 2004) (see Appendix C for JAGS code). For the abundance model within the hierarchical stacked N-mixture model, I assumed that species count was a Poisson random variable and used a log link to model relationships with controlling habitat and topographical factors and interactions between year, elevation, and latitude. All continuous predictor variables were centered and scaled prior to analysis. The total number of slope coefficients was 27, corresponding to 11 single site covariates (year, latitude, elevation, mean temperature, SD temperature, current precipitation, previous precipitation, aspect, TPI, dominant forest type, and proportion of forest) and the same 11 two-way interactions and 5 three-way interactions as in the generalized linear mixed effects models. Because my data included repeated observations at each sampling point over the course of multiple years, the stacked N-mixture models also incorporated a random site effect for log expected count.

Due to missing detection data and inconsistencies in time intervals of avian point count survey periods among the 3 study regions, I had to customize the detection model within the hierarchical stacked N-mixture model. I assumed that the observed count was a binomial random variable and modeled the adjusted probability of detection for the full time interval of each within-survey replicate, using the same methods and equation as for the hierarchical community model. I further used a logit link to model linear relationships between detection probability and 4 detection covariates, which consisted of ordinal day (centered and scaled prior to analysis), time since sunrise (measured as decimal hours and centered and scaled prior to analysis), a dummy variable for wind (0 = wind codes of 0, 1, or 2; 1 = wind codes >2), and a dummy variable for sky (0 = sky codes of 0, 1, or 2; 1 = sky codes >2). I used the same methods as for the hierarchical community model to impute study region-specific detection covariates for avian point count surveys that were lacking data on time, wind code, or sky code.

The stacked N-mixture models were constructed in a Bayesian framework, implemented with Markov chain Monte Carlo methods. For all model parameters, I used prior distributions which were meant to provide little information; gamma prior distributions had shape and rate parameters of 0.01 or 0.1, and Gaussian prior distributions had a mean of 0 and precision of 0.01 (Appendix C). I fit the models in JAGS (Plummer 2003) using the “jagsUI” package (Kellner and Meredith 2021) in Program R (R Core Team 2022). I used the “autojags” function to run 3 chains for each model with a burn-in of 2,000–21,000 iterations (Appendix D), thinning rate of 3 iterations, and iteration increment of 3,000; models iteratively ran until reasonable convergence (R̂ ≤ 1.1) was achieved (Gelman et al. 2014), resulting in 3,000 posterior draws.

*Determining relationships with harvest intensity over time for nest success of individual focal species*

To quantify relationships among nest success of focal species and landscape composition and configuration (while controlling for local habitat-level and topographical metrics), I will use a nest survival model that calculates daily nest survival rates (Dinsmore et al. 2002) and has been established as an improved approach over simple Mayfield constant-nest-survival estimates or logistic regression (Shaffer 2004). These models will allow me to assess relationships between the nest survival of each focal species and each of the predictor variables (Table 6) relative to my competing hypotheses.

*Determining significance of interactions*

For all of the guild richness models and focal species abundance models, relationships with individual variables were considered significant when the 95% credible intervals of their slope coefficient values did not overlap zero (Table 3, Figures 3–4). Similarly, interactions with latitude and elevation (Tables 4–5, Figures 3–4) were considered significant when the 95% credible intervals of their effective slope coefficient values did not overlap zero (Tables 6–7). I defined an effective slope coefficient as the effect of a 1-unit change in 1 predictor variable given specific levels of the 2 interacting variables (i.e., northern vs. central vs. southern latitudes and low vs. mid vs. high elevations).

**RESULTS**

**Effects of harvest intensity over time on overall species and guild richness**

**Effects of harvest intensity over time on focal species abundance**

**Effects of harvest intensity over time on focal species nest success**

**DISCUSSION**

[summary of key results]

[breakdown of key result concerning guild richness; reference to previous literature]

[breakdown of key result concerning focal species abundance; reference to previous literature]

[breakdown of key result concerning focal species nest success; reference to previous literature]

[holistic summation combining consistent results across guild richness, abundance, and nest success]

**Conclusions**

[repeat key result and put in context of why important; state conservation / management implications]

**Acknowledgments**

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**Literature Cited**

**Tables**

Table 1. List of the common name, scientific name, 4-letter species code, taxonomic family, and climate-related guild designation of the 16 forest songbird species used in the focal species analyses. Climate-related guild designations for the 40 forest songbird species were assigned based on their ranges within the Appalachian Mountains and comprised 4 mutually exclusive categories (Appendix A): north (only found in the Northern or Central Appalachians study regions), south (only found in the Southern or Central Appalachians study regions), trailing (found in all 3 study regions in the Appalachian Mountains but with trailing-edge populations that are limited to higher elevations in the Central or Southern Appalachians study regions), and general (found throughout all 3 study regions in the Appalachian Mountains). An asterisk following the common name indicates a species of regional conservation concern (i.e., listed as an Appalachian Mountains Joint Venture Priority Species or North American Bird Conservation Initiative’s Watch List species).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Common Name** | **Scientific Name** | **Code** | **Family** | **Guild** | | |
| Blackpoll warbler\* | *Setophaga striata* | BLPW | Parulidae | | north |
| Swainson's thrush | *Catharus ustulatus* | SWTH | Turdidae | | north |
| Yellow-bellied flycatcher\* | *Empidonax flaviventris* | YBFL | Tyrannidae | | north |
| Acadian flycatcher\* | *Empidonax virescens* | ACFL | Tyrannidae | | south |
| Hooded warbler\* | *Setophaga citrina* | HOWA | Parulidae | | south |
| Worm-eating warbler\* | *Helmitheros vermivorum* | WEWA | Parulidae | | south |
| Blackburnian warbler\* | *Setophaga fusca* | BLBW | Parulidae | | trailing |
| Black-throated blue warbler | *Setophaga caerulescens* | BTBW | Parulidae | | trailing |
| Black-throated green warbler | *Setophaga virens* | BTNW | Parulidae | | trailing |
| Canada warbler\* | *Cardellina canadensis* | CAWA | Parulidae | | trailing |
| Least flycatcher | *Empidonax minimus* | LEFL | Tyrannidae | | trailing |
| Veery | *Catharus fuscescens* | VEER | Turdidae | | trailing |
| American redstart | *Setophaga ruticilla* | AMRE | Parulidae | | general |
| Northern parula\* | *Setophaga americana* | NOPA | Parulidae | | general |
| Ovenbird | *Seiurus aurocapilla* | OVEN | Parulidae | | general |
| Wood thrush\* | *Hylocichla mustelina* | WOTH | Turdidae | | general |

Table 2. List of temporal (N = 1), spatial (N = 2), climate (N = 4), topographical (N = 2), and habitat (N = 2) variables with detailed descriptions including units, identification of data sources including the spatial resolution of the dataset, and notes on the type of variable and its corresponding range in values.

|  |  |  |
| --- | --- | --- |
| **Variable** | **Description (Unit)** | **Data Source (resolution)** |
| Year | Year of data collection; variable type: discrete; range: 1993–2020 | Bird survey data |
| Latitude | Latitude (decimal degrees) of the sampling point; variable type: continuous; range: 35.00585–43.95997 | Bird survey data |
| Elevation | Mean elevation (m) within 50 m of each sampling point; variable type: continuous; range: 240–1881 m | Shuttle Radar Topography Mission digital elevation data (~20–25 m), Consultative Group on International Agricultural Research – Consortium for Spatial Information |
| Mean Temperature | Average of daily mean temperatures (degrees Celsius) from 15 May–30 June (i.e., breeding season) during the year of data collection within 50 m of the sampling point; variable type: continuous; range: 12.2–24.0 °C | PRISM Climate Group daily temperatures (4 km) |
| SD Temperature | Standard deviation of daily mean temperatures (degrees Celsius) from 15 May–30 June (i.e., breeding season)  during the year of data collection within  50 m of the sampling point; variable type: continuous; range: 1.3–5.7 °C | PRISM Climate Group daily temperatures (4 km) |
| Current Precipitation | Sum of daily total precipitation (mm) from 15 May–30 June (i.e., breeding season) during the year of data collection within  50 m of the sampling point; variable type: continuous; range: 42–808 mm | PRISM Climate Group daily precipitation (4 km) |
| Previous Precipitation | Sum of daily total precipitation (mm) from 15 May–30 June (i.e., breeding season) from the year prior to the year of data collection within 50 m of the sampling point; variable type: continuous; range:  42–808 mm | PRISM Climate Group daily precipitation (4 km) |

Table 2. Continued.

|  |  |  |
| --- | --- | --- |
| **Variable** | **Description (Unit)** | **Data Source (resolution)** |
| Aspect | Mode aspect (degrees) within 50 m of each sampling point; variable type: continuous; bounded between 0 and 360 degrees | Shuttle Radar Topography Mission digital elevation data (~20–25 m), Consultative Group on International Agricultural Research – Consortium for Spatial Information |
| Topographical Position Index (TPI) | Mode TPI within 50 m of each sampling point; higher positive values indicate ridges, lower positive values indicate upper to mid slopes, values near 0 indicate flat areas, higher negative values indicate lower slopes, and lower negative values indicate valleys; variable type: continuous; range: -4.125–4.625 | Shuttle Radar Topography Mission digital elevation data (~20–25 m), Consultative Group on International Agricultural Research – Consortium for Spatial Information |
|  |  |  |
| Dominant Forest Type | Forest type (deciduous or mixed / coniferous) occupying the greatest proportion of area within 50 m of the sampling point; variable type: dummy; 1 = deciduous forest; 0 = not deciduous forest (i.e., mixed and coniferous forest) | National Land Cover Database (30 m), U.S. Geological Survey |
| Proportion Forest | Proportion of any type of mature forest cover (including deciduous, mixed, and coniferous) within 1 km of the sampling point; variable type: continuous; bounded between 0 and 1 | National Land Cover Database (30 m), U.S. Geological Survey |
|  |  |  |

Table 3. Statistical significance (indicated by bold type) of slope coefficients for the 10 linear predictor variables (YR = year, LAT = latitude, EL = elevation, ASP = aspect, TPI = topographic position index, DFT = dominant forest type, PF = proportion forest, MT = mean temperature, SDT = SD temperature, CP = current precipitation, PP = previous precipitation) corresponding to overall species richness (ALL), the 4 guild designations (NORTH, SOUTH, TRAILING, and GENERAL), and the 16 focal forest songbird species (see Table 1 for species codes), arranged by guild designation.

Table 4. Statistical significance (indicated by bold type) of effective slope coefficients for the two temperature variables, mean temperature (MT) and SD temperature (SDT), on overall species richness (ALL), the 4 guild designations (NORTH, SOUTH, TRAILING, and GENERAL), and the 16 focal forest songbird species (see Table 1 for species codes) at low, mid, and high elevations (EL) in northern, central, and southern latitudes (LAT) within the Appalachian Mountains.

**FIGURES**

Figure 1. Location and extent of the 3 study regions in the Appalachian Mountains (shaded in gray): Hubbard Brook Experimental Forest (EF) in the White Mountains of New Hampshire (i.e., Northern Appalachians); Monongahela National Forest (NF) in the Allegheny Mountains of West Virginia (i.e., Central Appalachians); and Pisgah and Nantahala National Forests (NF) in the Blue Ridge Mountains of North Carolina (i.e., Southern Appalachians).

Figure 2. Locations and elevations (m) of the 373 sampling points in the Hubbard Brook Experimental Forest (EF) (i.e., Northern Appalachians study region); 1,149 sampling points in the Monongahela National Forest (NF) (i.e., Central Appalachians study region); and 211 sampling points in the Pisgah and Nantahala National Forests (NF) (i.e., Southern Appalachians study region).

Figure 3. Locations of the nest search plots.

Figure 4. Whisker plots for overall species richness and guild richness (see Appendix A for guild designations and associated forest songbird species), displaying the slope coefficients of the predictor variables (i.e., site covariates), which consisted of year, latitude, elevation, mean breeding season (i.e., 15 May to 30 June) temperature during the year of data collection (Mean Temp), standard deviation of breeding season temperature (SD Temp), total breeding season precipitation during the year of data collection (Current Precip), total breeding season precipitation during the previous year (Previous Precip), dominant forest type within 50 m as deciduous forest (Forest Type), and proportion of any type of forest cover within 1 km (Proportion Forest). Points are located at the mean values for the posterior distributions and the corresponding whiskers encompass the 95% credible intervals. Black points with closed circles and black whiskers indicate statistical significance (i.e., credible intervals do not overlap zero).

Figure 5. Plots of year x study area interaction for overall species richness and guild richness

Figure 6. Whisker plots for each focal species (Table 1), displaying the slope coefficients of the predictor variables (i.e., site covariates), which consisted of year, latitude, elevation, mean breeding season (i.e., 15 May to 30 June) temperature during the year of data collection (Mean Temp), standard deviation of breeding season temperature (SD Temp), total breeding season precipitation during the year of data collection (Current Precip), and total breeding season precipitation during the previous year (Previous Precip), aspect, topographic position index (TPI), dominant forest type within 50 m as deciduous forest (Forest Type), proportion of any type of forest cover within 1 km (Proportion Forest),. Points are located at the mean values for the posterior distributions and the corresponding whiskers encompass the 95% credible intervals. Black points with closed circles and black whiskers indicate statistical significance (i.e., credible intervals do not overlap zero). Color of the 4-letter species code indicates its guild designation (dark blue = north guild, red = south guild, light blue = trailing guild, and orange = general guild), and the bird silhouette indicates its taxonomic family (warbler, thrush, or flycatcher).

Figure 7. Plots of year x study area interaction for focal species abundance

Figure 6. Whisker plots for each focal species (Table 1),

Figure 8. Plots of year x study area interaction for focal species nest success

**APPENDICES**

**Appendix A**

Table of the 66 forest songbird species considered in the guild richness analyses.

Table A1. List of the common name, scientific name, 4-letter species code, relative frequency, taxonomic family, guild designation, and corresponding hierarchical community model (1 = breeding songbirds within the wildlife opening, 2 = breeding songbirds in the adjacent forest, 3 = post-breeding songbirds within the wildlife opening) of all 66 forest songbird species considered for the guild richness analyses. Relative frequency is the number of detections across all breeding bird point count surveys from all sampling points (within the wildlife opening and in the adjacent forest) and all post-breeding bird transect surveys. The guild designation indicates the primary breeding habitat of the species, such that: species in the early-successional and edge-associated (ESEA) guild breed in open habitat, shrub/scrub, or young forest, or along forest edges, such as the interface of early-successional and mature forest; species in the forest-interior (INT) guild breed in the core area of mature forest; species in the forest-gap (GAP) guild breed in or near small forest gaps within the core area of mature forest; and species in the forest generalist (GEN) guild are associated with forest but have no preference for early-successional vs. mature forest.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Common Name**  **(*Scientific Name*)** | **Species Code** | **Relative Frequency** | **Taxonomic Family** | **Guild** | **Model** |
| American Goldfinch  (*Spinus tristis*) | AMGO | 192 | Fringillidae | ESEA | 1+3 |
| Brown Thrasher  (*Toxostoma rufum*) | BRTH | 11 | Mimidae | ESEA | 1+3 |
| Brown-headed Cowbird  (*Molothrus ater*) | BHCO | 42 | Icteridae | ESEA | 1+3 |
| Carolina Wren  (*Thryothorus ludovicianus*) | CARW | 148 | Troglodytidae | ESEA | 1+3 |
| Cedar Waxwing  (*Bombycilla cedrorum*) | CEDW | 513 | Bombycillidae | ESEA | 1+3 |
| Chestnut-sided Warbler  (*Setophaga pensylvanica*) | CSWA | 184 | Parulidae | ESEA | 1+3 |
| Chipping Sparrow  (*Spizella passerina*) | CHSP | 212 | Passerellidae | ESEA | 1+3 |
| Common Yellowthroat  (*Geothlypis trichas*) | COYE | 355 | Parulidae | ESEA | 1+3 |
| Eastern Bluebird  (*Sialia sialis*) | EABL | 5 | Turdidae | ESEA | 3 |
| Eastern Phoebe  (*Sayornis phoebe*) | EAPH | 28 | Tyrannidae | ESEA | 1+3 |

Table A1. Continued.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Common Name**  **(*Scientific Name*)** | **Species Code** | **Relative Frequency** | **Taxonomic Family** | **Guild** | **Model** |
| Eastern Towhee  (*Pipilo erythrophthalmus*) | EATO | 487 | Passerellidae | ESEA | 1+3 |
| Field Sparrow  (*Spizella pusilla*) | FISP | 229 | Passerellidae | ESEA | 1+3 |
| Gray Catbird  (*Dumetella carolinensis*) | GRCA | 148 | Mimidae | ESEA | 1+3 |
| House Wren  (*Troglodytes aedon*) | HOWR | 49 | Troglodytidae | ESEA | 1+3 |
| Indigo Bunting  (*Passerina cyanea*) | INBU | 553 | Cardinalidae | ESEA | 1+3 |
| Mourning Dove  (*Zenaida macroura*) | MODO | 45 | Columbidae | ESEA | 1+3 |
| Mourning Warbler  (*Geothlypis philadelphia*) | MOWA | 26 | Parulidae | ESEA | 1+3 |
| Northern Cardinal | NOCA | 67 | Cardinalidae | ESEA | 1+3 |
| Song Sparrow  (*Melospiza melodia*) | SOSP | 107 | Passerellidae | ESEA | 1+3 |
| Yellow Warbler  (*Setophaga petechia*) | YEWA | 5 | Parulidae | ESEA | 1+3 |
| Yellow-billed Cuckoo  (*Coccyzus americanus*) | YBCU | 42 | Cuculidae | ESEA | 1+3 |
| Acadian Flycatcher  (*Empidonax virescens*) | ACFL | 79 | Tyrannidae | INT | 1+2+3 |
| Black-and-white Warbler  (*Mniotilta varia*) | BAWW | 166 | Parulidae | INT | 1+2+3 |
| Blackburnian Warbler  (*Setophaga fusca*) | BLBW | 130 | Parulidae | INT | 1+2+3 |
| Black-throated Blue Warbler  (*Setophaga caerulescens*) | BTBW | 210 | Parulidae | INT | 1+2+3 |
| Black-throated Green Warbler  (*Setophaga virens*) | BTNW | 838 | Parulidae | INT | 1+2+3 |
| Blue-headed Vireo  (*Vireo solitarius*) | BHVI | 423 | Vireonidae | INT | 1+2+3 |
| Brown Creeper  (*Certhia americana*) | BRCR | 18 | Certhiidae | INT | 1+2+3 |
| Canada Warbler  (*Cardellina canadensis*) | CAWA | 39 | Parulidae | INT | 1+2+3 |
| Dark-eyed Junco  (*Junco hyemalis*) | DEJU | 430 | Passerellidae | INT | 1+2+3 |
| Golden-crowned Kinglet  (*Regulus satrapa*) | GCKI | 184 | Regulidae | INT | 1+2+3 |
| Hairy Woodpecker  (*Leuconotopicus villosus*) | HAWO | 65 | Picidae | INT | 1+2+3 |

Table A1. Continued.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Common Name**  **(*Scientific Name*)** | **Species Code** | **Relative Frequency** | **Taxonomic Family** | **Guild** | **Model** |
| Hermit Thrush  (*Catharus guttatus*) | HETH | 234 | Turdidae | INT | 1+2+3 |
| Least Flycatcher  (*Empidonax minimus*) | LEFL | 78 | Tyrannidae | INT | 1+2+3 |
| Magnolia Warbler  (*Setophaga magnolia*) | MAWA | 226 | Parulidae | INT | 1+2+3 |
| Ovenbird  (*Seiurus aurocapilla*) | OVEN | 410 | Parulidae | INT | 1+2+3 |
| Pileated Woodpecker  (*Dryocopus pileatus*) | PIWO | 116 | Picidae | INT | 1+2+3 |
| Pine Warbler  (*Setophaga pinus*) | PIWA | 7 | Parulidae | INT | 1+2+3 |
| Purple Finch  (*Haemorhous purpureus*) | PUFI | 10 | Fringillidae | INT | 1+2+3 |
| Red Crossbill  (*Loxia curvirostra*) | RECR | 93 | Fringillidae | INT | 1+2+3 |
| Red-breasted Nuthatch  (*Sitta canadensis*) | RBNU | 156 | Sittidae | INT | 1+2+3 |
| Red-eyed Vireo  (*Vireo olivaceus*) | REVI | 895 | Vireonidae | INT | 1+2+3 |
| Rose-breasted Grosbeak  (*Pheucticus ludovicianus*) | RBGR | 49 | Cardinalidae | INT | 1+2+3 |
| Scarlet Tanager  (*Piranga olivacea*) | SCTA | 219 | Cardinalidae | INT | 1+2+3 |
| Swainson's Thrush  (*Catharus ustulatus*) | SWTH | 41 | Turdidae | INT | 1+2+3 |
| Winter Wren  (*Troglodytes hiemalis*) | WIWR | 109 | Troglodytidae | INT | 1+2+3 |
| Wood Thrush  (*Hylocichla mustelina*) | WOTH | 182 | Turdidae | INT | 1+2+3 |
| Worm-eating Warbler  (*Helmitheros vermivorum*) | WEWA | 23 | Parulidae | INT | 1+2+3 |
| Yellow-rumped Warbler  (*Setophaga coronata*) | YRWA | 35 | Parulidae | INT | 1+2+3 |
| American Redstart  (*Setophaga ruticilla*) | AMRE | 128 | Parulidae | GAP | 1+2+3 |
| Black-billed Cuckoo  (*Coccyzus erythropthalmus*) | BBCU | 6 | Cuculidae | GAP | 1+3 |
| Eastern Wood-Pewee  (*Contopus virens*) | EAWP | 201 | Tyrannidae | GAP | 1+2+3 |
| Great-crested Flycatcher  (*Myiarchus crinitus*) | GCFL | 12 | Tyrannidae | GAP | 1+2+3 |

Table A1. Continued.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Common Name**  **(*Scientific Name*)** | **Species Code** | **Relative Frequency** | **Taxonomic Family** | **Guild** | **Model** |
| Hooded Warbler  (*Setophaga citrina*) | HOWA | 145 | Parulidae | GAP | 1+2+3 |
| Northern Parula  (*Setophaga americana*) | NOPA | 38 | Parulidae | GAP | 1+2+3 |
| Veery  (*Catharus fuscescens*) | VEER | 266 | Turdidae | GAP | 1+2+3 |
| Yellow-throated Vireo  (*Vireo flavifrons*) | YTVI | 16 | Vireonidae | GAP | 1+2 |
| American Robin  (*Turdus migratorius*) | AMRO | 343 | Turdidae | GEN | 1+2+3 |
| Black-capped Chickadee  (*Poecile atricapillus*) | BCCH | 482 | Paridae | GEN | 1+2+3 |
| Blue-gray Gnatcatcher  (*Polioptila caerulea*) | BGGN | 33 | Polioptilidae | GEN | 1+2+3 |
| Downy Woodpecker  (*Picoides pubescens*) | DOWO | 80 | Picidae | GEN | 1+2+3 |
| Northern Flicker  (*Colaptes auratus*) | NOFL | 66 | Picidae | GEN | 1+2+3 |
| Red-bellied Woodpecker  (*Melanerpes carolinus*) | RBWO | 100 | Picidae | GEN | 1+2+3 |
| Tufted Titmouse  (*Baeolophus bicolor*) | TUTI | 170 | Paridae | GEN | 1+2+3 |
| White-breasted Nuthatch  (*Sitta carolinensis*) | WBNU | 89 | Sittidae | GEN | 1+2+3 |
| Yellow-bellied Sapsucker  (*Sphyrapicus varius*) | YBSA | 90 | Picidae | GEN | 1+2+3 |

**Appendix B**

JAGS model code for the guild richness analyses

**Appendix C**

JAGS model code for the focal species abundance analyses

**Appendix D**

JAGS model code for the focal species nest success analyses

**Appendix E**

Table of model information for overall species richness, the 4 guild designations, and the 16 focal forest songbird species considered in the guild richness and focal species analyses.

Table E1. List of the 4 guild designations and 16 focal forest songbird species (sorted by guild and family), with corresponding model information that includes the number of chains (Chains), total iterations (Total), burn-in (Burn), thinning rate (Thin), and resulting posterior iterations (Posterior).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Guild** | **Family** | **Species** | **Chains** | **Total** | **Burn-In** | **Thin** | **Posterior** |
| ALL |  |  | 3 | 3,500 | 2,500 | 1 | 3,000 |
| NORTH | |  | 3 | 3,500 | 2,500 | 1 | 3,000 |
|  | Parulidae | BLPW | 3 |  |  | 3 |  |
|  | Turdidae | SWTH | 3 |  |  | 3 |  |
|  | Tyrannidae | YBFL | 3 |  |  | 3 |  |
| SOUTH | |  | 3 | 3,500 | 2,500 | 1 | 3,000 |
|  | Parulidae | HOWA | 3 |  |  | 3 |  |
|  | Parulidae | WEWA | 3 |  |  | 3 |  |
|  | Tyrannidae | ACFL | 3 |  |  | 3 |  |
| TRAILING | |  | 3 | 3,500 | 2,500 | 1 | 3,000 |
|  | Parulidae | BLBW | 3 | 11,000 | 2,000 | 3 | 9,000 |
|  | Parulidae | BTNW | 3 | 11,000 | 2,000 | 3 | 9,000 |
|  | Parulidae | BTBW | 3 | 11,000 | 2,000 | 3 | 9,000 |
|  | Parulidae | CAWA | 3 | 26,000 | 20,000 | 3 | 6,000 |
|  | Turdidae | VEER | 3 | 19,000 | 10,000 | 3 | 9,000 |
|  | Tyrannidae | LEFL | 3 | 29,000 | 20,000 | 3 | 9,000 |
| GENERAL | |  | 3 | 3,500 | 2,500 | 1 | 3,000 |
|  | Parulidae | AMRE | 3 |  |  | 3 |  |
|  | Parulidae | NOPA | 3 |  |  | 3 |  |
|  | Parulidae | OVEN | 3 | 11,000 | 2,000 | 3 | 9,000 |
|  | Turdidae | WOTH | 3 | 36,000 | 30,000 | 3 | 6,000 |