**CHAPTER 4**

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

**INTRODUCTION**

**Long-term changes in bird populations**

Prevailing evidence suggests that forest songbird populations in eastern North America have been decreasing in abundance during the past century. Long-term data from annual, nationwide breeding bird surveys indicate that numerous bird species, many of which breed in forests (Robbins et al. 1989), have experienced decreases in their populations throughout the eastern United States since 1966 (Sauer et al. 2020). Additionally, a recent quantitative study using data from multiple and independent monitoring networks demonstrated bird population losses across much of North America since 1970, including a negative change within the range of -15.6% to -19.2% in birds breeding in eastern forests, with 63.5% of those species in decline (Rosenberg et al. 2019).

In the Central Appalachians region of the eastern United States, forest management may contribute to or ameliorate these declines over time, 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 / stand 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). However, a subset of songbirds that breed in mature forest will shift their habitat use to early-successional areas, including regenerating clear-cuts (Vitz and Rodewald 2006, McDermott and Wood 2010, Streby et al. 2011, Major and Desrochers 2012, Stoleson 2013) during the post-breeding period (i.e., after nesting but before migration) (Pagen et al. 2000, Bowen et al. 2007, Chandler et al. 2012). Thus, there are differential benefits to early-successional vs. mature forest birds when forest management actions such as timber harvest alter the composition and configuration of forested landscapes. Here, landscape composition refers to amount of different habitat patch types without regard to spatial attributes (e.g., proportions of individual habitat types), whereas landscape configuration refers to spatial characteristics of individual habitat patches, requiring spatial information and usually aggregated across patches (e.g., mean patch size).

Historically, changes in forested landscapes of 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 forest-associated bird guilds during the breeding and post-breeding seasons likely calls for mosaic landscapes that contain a variety of forest age classes or successional stages (Loehle et al. 2005, Mitchell et al. 2008). Such landscapes can be produced by active forest management involving timber harvest.

**Timber harvest as a forest management tool for bird conservation**

Timber harvest can be used as a landscape-level forest management tool by increasing the variation in composition and configuration of forested landscapes. 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 timber harvest regimes. Within stands, even-aged silvicultural systems (e.g., clear-cuts) 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). However, century-long fire suppression tactics have reduced the amount of large-scale natural disturbances in forests of eastern North America, contributing to an increase in homogenous forest conditions over large scales. In the absence of natural disturbance regimes, timber harvest may be the most feasible source of anthropogenic disturbance for land managers to diversify forest structure.

Timber harvests can increase the availability of early-successional forest habitat, which leads to increased abundance and densities of early-successional and generalist bird species in those areas (King and Degraaf 2000, Duguay et al. 2001, McDermott and Wood 2009). Similarly, higher proportions of early-successional habitats in harvested landscapes can also result in significantly higher abundances of early-successional and generalist bird species in those landscapes (Drapeau et al. 2000). Timber harvests can also increase fragmentation, edge density, and canopy openings within a forest stand or landscape, which could lead to increased abundance of edge-associated species, such as indigo buntings, and gap-dependent species, such as hooded warblers (Greenberg and Lanham 2001). On the other hand, large-scale timber harvest operations may negatively affect mature forest birds that require intact forest-interior / core forest habitat or late-successional (i.e., >80 years old) forest (Lichstein et al. 2002). Forest-interior species are more abundant in mature forest than clearcuts (King and Degraaf 2000, Sheehan et al. 2014) and in landscapes with higher amounts of late-successional forest in the landscape (Lichstein et al. 2002). Thus, abundance of forest-interior and interior-edge species can decrease after reaching specific thresholds in timber harvest within forested landscapes (Becker et al. 2011). Small openings may not necessarily adversely affect mature forest birds (e.g., Greenberg and Lanham 2001), but a study of the breeding bird community in a Vermont hardwood forest found that 0.4-ha clearcuts resulted in the movement of several forest-interior species away from the harvested areas and subsequently decreased abundance in and adjacent to clearcuts (Germaine et al. 1997).

In addition to species abundance, it is critical to consider long-term bird population dynamics because abundance and density metrics alone can be poor indicators of habitat quality (Van Horne 1983, Vickery et al. 1992, Hagan et al. 1996). Reproductive success of avian species in forested landscapes can be affected by timber harvest due to changes in habitat composition and configuration. For example, 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). Composition within forested landscapes further influences avian nesting success by altering interactions between nest predators and nesting birds (Rodewald and Yahner 2001, Rodewald et al. 2001). However, recent studies of nest success within Central Appalachian forests have found little overall effect of various harvest types on productivity (Duguay et al. 2001, Becker et al. 2011, 2012), perhaps because habitat features related to nest survival are spatially variable (Boves et al. 2013*a*, *b*).

Avian population and community processes operate across a broad scale (Bennett et al. 2004), and habitat-associated guilds are thought to respond differently to landscape-scale harvest intensity. 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. In general, greater landscape age heterogeneity produced by higher levels of timber harvest intensity is associated with greater overall species richness (Loehle et al. 2005, Mitchell et al. 2008). Furthermore, landscape changes due to timber harvest can ultimately result in shifts in avian community composition and diversity (Parody et al. 2001, Anderson and Crompton 2002), 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) and increased edge habitat can result in increases in generalist richness but decreases in specialist species richness (Jones et al. 2000). In summary, landscape-scale harvest intensity may differentially affect forest bird assemblages.

**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, which can alter forest composition, configuration, and connectivity on a landscape scale (e.g., Spies et al. 1994). Thus, timber harvest can be potentially used as a landscape-level management 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-scale harvest intensity. Many studies on this topic are traditionally focused on single harvest types or single harvesting events; examine avian responses at control and harvested sites on limited spatial scales; or tend to be short-term (i.e., lasting 1–3 years) and focused on immediate impacts that may not reflect the full temporal response to the management practices under study (Sallabanks et al. 2000, Loehle et al. 2005). By quantifying long-term, landscape-level trends in avian responses to active forest management using multiple harvesting methods and harvesting events (e.g., Perry et al. 2018, Kellner et al. 2019), we can guide management decisions and make recommendations to provide lasting benefits to forest bird species. Thus, it would be valuable to investigate the response of bird communities and populations through time in forested landscapes with varying levels of timber harvest intensity, particularly within the Central Appalachians region.

**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 >60% 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 / 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 / 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 14 focal songbird species, and the nest success of 6 focal songbird species (Table 1).

**METHODS**

**Study area**

Sampling points and nest search plots for this study were spread throughout 2 study areas within the Central Appalachians region (Figures 1–3). I used data from a total of 1,186 sampling points and 50 nest search plots (Figures 2–3), consisting of 166 sampling points and 20 nest search plots in the actively harvested MeadWestvaco Wildlife and Ecosystem Research Forest (WERF), which is located in Randolph County, West Virginia, and 1020 sampling points and 30 nest search plots in the minimally 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. All sampling points used in this study were located in forest stands that experienced varying levels and types of recent or ongoing timber harvest (ranging from no harvest to clear-cutting), and distances between sampling points were at least 200 m.

Research in the actively harvested WERF was conducted from 1996–1998 (Weakland 2000), 2001–2003 (Dellinger 2005), and 2007–2009 (Becker 2010). The WERF encompasses 3,080 ha and was established in 1994 by the Westvaco Corporation to study the effects of industrial forest management practices on ecosystem processes and wildlife within a primarily 70–90 year-old even-aged mature forest. Located within the Central Appalachians (Allegheny Mountains) physiographic province, regional topography within the WERF 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 (Strausbaugh and Core 1977), and elevation ranges 734–1,180 m. Vegetation communities in the WERF are variable across that elevational gradient. 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 was limited to grassy cover along road edges, gas well openings, and log landings.

Research in the minimally harvested MNF was conducted from 1993–1994 (Nichols 1996), 1995–1996 (Duguay 1997), 1996–1997 (DeMeo 1999), 1998–2000 (Williams 2002), and 2001–2009. 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 (Clarkson 1966). Elevation within the MNF ranges 275–1,480 m. In terms of forest composition, the MNF was comprised primarily of 70–100 year-old stands at the start of the study period, 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, sugar maple (*Acer saccharum*), hickory, and tulip-poplar as the dominant species (Madarish et al. 2002). At increasing elevations, there is a transition in stand dominance to northern hardwoods, including American beech, sugar maple, and black cherry (*Prunus serotina*) (Stephenson 1993). 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).

**Harvest history**

During its establishment in 1994, the WERF was comprised of secondary forests that were established by natural regeneration following large-scale logging from 1916–1928 (Keyser and Ford 2005). Timber had been sporadically thinned and harvested since the 1930’s, resulting in numerous logging roads and skidder trails transecting the forest. Since its initial establishment, much of the WERF had 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). Prior to 1997, several timber harvests had been conducted, including diameter-limit harvests, two-age harvests, and regeneration (seed-tree) harvests, but the majority of the WERF remained mature deciduous or mixed forest (Figure 4). From 1997–1998, additional forest stands were harvested using a variety of methods (e.g., diameter-limit harvests, two-age harvests, regeneration harvests, clear-cuts). More stands were harvested throughout the years, and nearly 50% of the WERF had recently experienced some type of harvest by 2003 (Figure 4). In 2007, management shifted to primarily uneven-aged techniques, and by 2009, at least 60% of the WERF had been recently harvested to some degree (Figure 4). Thus, the WERF served as an actively harvested landscape for this study.

The MNF is comprised of mature, second-growth Appalachian hardwood forests. A timber harvest rotation of 100–120 years applies to most areas of the MNF not designated as Wilderness Areas, and the vast majority of the MNF had not been harvested nor majorly disturbed within 50 years prior to the study period. Therefore, most of the sampling points within the MNF were located in relatively intact areas with high (>60%) core area (DeMeo 1999). A small subset of the sampling points was in forest stands in the Cheat and Greenbrier Ranger Districts of the MNF that had experienced two-age harvest or clear-cutting between 1979 and 1986 for a study on the effects of two-age harvests (Miller et al. 2006). However, the area of the harvested stands accounted for <1% of the total area of public lands in the MNF. Thus, the MNF served as a minimally harvested landscape for this study.

**Guild designations**

To compare temporal trends for overall species richness and guild richness in the actively harvested landscape and the minimally harvested landscape, I considered a subset of the 114 total avian species that were detected across all surveys in all years from the 2 study areas. Specifically, I limited the richness analyses to 62 passerine and near-passerine species (see Appendix A for full list) with breeding ranges that encompassed the 2 study areas and that had ≥10 detections. I also excluded wetland-associated songbirds (e.g., red-winged blackbirds [*Agelaius phoeniceus*]) 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 62 songbird species were assigned based on breeding habitat and comprised 4 categories (Appendix A): (1) early-successional / 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).

**Focal species**

To compare temporal trends in focal species abundance in the actively harvested landscape and the minimally harvested landscape, I selected a total of 14 songbird species across the 4 guild designations (Table 1): 3 early-successional / edge-associated species, 4 forest-interior species, 4 forest-gap species, and 3 forest generalist species. Species selection was based on relative frequency; for each guild designation, I included the 3 species with the highest relative frequency. For the forest-interior guild and forest-gap guild, I additionally included a species of regional conservation concern with the highest relative frequency.

To assess temporal trends in focal species nest success in the actively harvested landscape and the minimally harvested landscape, I selected 6 species from the 14 songbird species listed above as focal species for abundance analyses (Table 1): 2 early-successional / edge-associated species, 3 forest-interior species, and 1 forest-gap species. Species selection was based on sample size; these were the 6 species that had sample sizes of at least 70 total nests across the 2 study areas and a minimum of 15 nests from each study area.

**Bird count data**

Avian point count survey data for the 2 study areas were collected in 1996–1998, 2001–2003, and 2007–2009 at 166 WERF sampling points and in 1996–2009 at 1020 MNF sampling points. In the WERF, point count surveys 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 2) 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. In the MNF, point count surveys were conducted along 109 extensive linear transects (up to 2,500 m in length) with 10–12 sampling points per transect (Figure 3). Of the 109 total transects, at least 44 transects were oriented at right angles to contours to capture maximum variation in elevation and landforms.

Avian point count surveys were not completed every year at every sampling point. The number of years of data associated with each sampling point ranged 2–9 years (mean = 5.9 ± 2.5 years) in the WERF and 1–12 years (mean = 4.0 ± 2.8 years) in the MNF. Within a year that avian point count survey data were collected, the number of repeated visits (i.e., replicate surveys) ranged from 1–3 visits (mean = 2.0 ± 0.2 visits) in the WERF and 1–4 visits (mean = 1.3 ± 0.5 visits) in MNF. I included all replicate surveys per sampling point per year in my data analyses, for a total of 14,504 replicate surveys across 4,999 site × year combinations.

At both study areas, 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 all individuals heard or seen. Up to 4 detection covariates were recorded for each survey: date, start time, wind code, and sky code. While date was recorded for all surveys, a subset of surveys was missing start times (68% of MNF data), wind codes (73% of MNF data), or sky codes (73% of MNF data). However, all surveys began within 30 minutes of sunrise and continued until approximately 4 hours after sunrise, and no surveys were conducted on days with rain, heavy fog, or high wind speed, following the guidelines of Ralph et al. (1993).

The 10-minute point count survey was divided into 2 time intervals (i.e., within-survey replicates): 0–5 minutes and >5–10 minutes. Individual birds were only recorded the first time they were observed, following removal sampling methods. For each record, observers indicated the corresponding time interval and distance band (≤50 m or >50 m). To limit detection variability due to distance, I restricted all data analyses to birds detected within 50 m.

**Nest success data**

Avian nest monitoring survey data were collected at the 2 study areas from 1996–1998, 2001–2003, and 2007–2009 from 20 WERF nest search plots and from 1993–1999 at 30 MNF nest search plots (Figures 2–3). Throughout the breeding season, field technicians looked for active nests within the nest search plots. Nests that were located through both systematic searching efforts and opportunistic observations were then monitored from mid-May until mid-July. During the monitoring period, field technicians checked each nest a minimum of every 3–4 days until the nesting attempt was complete and identified as either successful or failed. From the nest monitoring records, I used the following data for each nest location: bird species, success or failure during the incubation period, and success or failure during the brooding period.

Nest search plots varied in size and location among sampling years and between study areas (Figures 2–3). In the WERF, there were 8 45-ha nest search plots during 1996–1998 and 12 20-ha nest search plots during 2001–2003 and 2007–2009. The nest search plots were distributed randomly throughout 3 elevational blocks and encompassed either non-harvested areas with intact, predominantly mature hardwood forest, lightly harvested areas that retained closed canopy conditions, or heavily harvested areas with early-successional vegetation. Due to harvest activity, 4 nest search plots had to be shifted slightly for the 2007–2009 nest monitoring seasons (Figure 2). In the MNF, 31 stands were intensively searched for nests during 1993–1998 (Duguay et al. 2001), with search effort distributed relatively evenly between stands. From 1996 to 1999, nest searches occurred within 40-ha (200-m wide × 2,000-m long, oriented perpendicular to prevailing slopes) plots that were established along 2 transects in each of 5 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% in core forest area (DeMeo 1999). Nest searching protocols followed the methodology of the national BBird program of nest search plot monitoring (Conway and Martin 2000). 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).

My objective was to compare temporal trends in nest success between the actively harvested landscape and the minimally harvested landscape, but the time periods of nest monitoring at the 2 study areas did not fully overlap (WERF: 1996–1998, 2001–2003, and 2007–2009 vs. MNF: 1993–1999). Therefore, I made the following assumptions: (1) trends from MNF data collected from 1993 to 1999 were representative of long-term trends; and (2) there were no outside, unconsidered systemic confounding factors (e.g., stochastic weather extremes, climate change, invasive species introduction) influencing trends from WERF data collected after 1999.

**Environmental data**

The full set of site covariates for the guild richness analyses and focal species abundance analyses included year of data collection, landscape-scale harvest intensity, an interaction between year and landscape-scale harvest intensity, and 9 environmental variables that were included to control for their known effects (Table 2). Landscape-scale harvest intensity was a dummy variable where 1 = actively harvested landscape (i.e., WERF) and 0 = minimally harvested landscape (i.e., MNF). The first 3 controlling environmental variables were topographical factors: elevation, aspect, and topographical position index (TPI). Mean elevation, mode aspect, and mode TPI within 50 m of each sampling point were calculated or derived using Shuttle Radar Topography Mission digital elevation data. The next controlling environmental variable was stand age. To calculate mode stand age within 50 m of each sampling point, I used GIS datasets from the WERF and from the MNF that mapped forest stands in each study area and provided stand-scale attribute information. The 5 remaining controlling environmental variables were proportions of landcover classifications, including 3 forest types (all forest [i.e., any type of mature forest], mixed forest, and conifer forest) within 50 m of each sampling point, shrub cover within 50 m of each sampling point, and all forest (i.e., any type of mature forest) within 1 km of the sampling point. Note that the proportion of deciduous forest within 50 m of each sampling point was highly correlated (r > 0.70) to the proportion of all forest within 50 m and was thus excluded from analyses. To determine land cover proportions, I downloaded the 2001, 2004, 2006, and 2008 National Land Cover Databases (NLCD), which all have a resolution of 30 m (Jin et al. 2019). All calculations were made using land cover data from the closest year available (i.e., I used the 2001 NLCD data for surveys conducted in 2002 or earlier, 2004 NLCD data for surveys conducted in 2003 or 2004, 2006 NLCD data for surveys conducted in 2005–2007, and 2008 NLCD data for surveys conducted in 2008 or 2009).

**Data analysis**

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

To calculate overall species richness and guild richness at each sampling point in each year sampled, I estimated the individual species occupancy of the 62 passerine and near-passerine species (Appendix A) 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 9 site covariates, which consisted of elevation, aspect, TPI, stand age, proportion of all forest / mixed forest / conifer forest / shrub within 50 m, and proportion of all forest within 1 km (Table 2). All continuous site covariates were centered and scaled prior to analysis. In addition, the hierarchical community model incorporated a random site effect to account for repeated observations at each sampling point over the course of multiple years.

Given the observed data *Ys,y,r,sp*, where *r* is a within-survey replicate (i.e., 5-minute time interval during the 10-minute 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 detection probability of species *sp* for the *r*th replicate at sampling point *s* in year *y*, given that species *sp* is present at sampling point *s* in year *y*. 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 also incorporated a species-specific random observer effect in the hierarchical community model.

Because a subset of avian point count surveys conducted in the MNF lacked data pertaining to time, wind code, or sky code, I imputed those detection covariate values. I assumed that time since sunrise was a Gaussian random variable, and that the wind and sky dummy variables were Bernoulli random variables. 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. 2014).

Ultimately, 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 62 passerine and near-passerine species, as in the following equation:

Similarly, I derived guild-specific richness by summing the occupancy of the subset of songbird species that belonged to each habitat guild designation (Appendix A).

I constructed the hierarchical community model in 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 0.1 and rate parameter of 0.1, 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 0.01 (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 of 5,000 iterations for the hierarchical community model, with a burn-in of 3,000 iterations and thinning rate of 2 iterations, 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 an interaction between time and landscape-level harvest intensity as a predictor variable. 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 topographical and habitat factors and an interaction between year and landscape-level harvest intensity. All continuous predictor variables were centered and scaled prior to analysis. The total number of slope coefficients was 14 (resulting in a ratio of ~85 sites to 1 slope coefficient; Bolker et al. 2008), corresponding to year, landscape-level harvest intensity, year × landscape-level harvest intensity, elevation, aspect, aspect squared, TPI, stand age, stand age squared, proportion of all forest within 50 m, proportion of mixed forest within 50 m, proportion of conifer forest within 50 m, proportion of shrub within 50 m, and proportion of all forest within 1 km. All of the generalized linear mixed effects models also incorporated a random site effect for log expected richness to account for repeated observations at each sampling point over the course of multiple years.

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 landscape-level harvest intensity over time for abundance of individual focal species*

To quantify and compare temporal trends in the abundance of specific focal species during the breeding season, I estimated the abundance of 14 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 topographical and habitat factors and an interaction between year and landscape-level harvest intensity. All continuous predictor variables were centered and scaled prior to analysis. The total number of slope coefficients was 14, corresponding to same site covariates as for the generalized linear mixed effects models. The stacked N-mixture models also incorporated a random site effect for log expected count to account for repeated observations at each sampling point over the course of multiple years.

For the detection model within the hierarchical stacked N-mixture model, I assumed that the observed count was a binomial random variable and modeled the probability of detection for each within-survey replicate, using the same methods 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 from the MNF 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 15,000–51,000 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 6,000 or 9,000 posterior draws.

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

To quantify and compare temporal trends in nest success of specific focal species during the breeding season, I estimated the overall probability of nest success of 6 songbird species (Table 1) independently in conditional binomial models (see Appendix E for JAGS code). I assumed that observed nest success was a Bernoulli random variable and modeled both the probability of nest success during the incubation period and the probability of nest success during the brooding period, which was conditional upon nest success during the incubation period. Thus, given the observed nest success data *Ys,sp,1:2*, where *Ys,sp,1* = 1 if the nest of species *sp* at nest location *s* survived the incubation period (and *Ys,sp,1* = 0 if not) and *Ys,sp,2* = 1 if the nest of species *sp* at nest location *s* survived the brooding period and successfully fledged at least 1 offspring (and *Ys,sp,2* = 0 if not), I defined the nest success model as:

*Ys,sp,1* ~ *Bernoulli*(*p.incubations,sp*)  
*Ys,sp,2* ~ *Bernoulli*(*p.broodings,sp*) × *Ys,sp,1*

where *p.incubations,sp* is the probability of nest success during the incubation period and *p.incubations,sp* is the probability of nest success during the brooding period, dependent upon the nest fate during the incubation period. The probability of overall nest success (*p.overalls,sp*) for species *sp* at nest location *s* was then calculated as the product of the probabilities of nest success during the incubation and brooding periods, as in the following equation:

*p.overalls,sp = p.incubations,sp* × *p.broodings,sp*

For both the probabilities of nest success during the incubation and brooding periods, I further used a logit link to model their relationships with 5 site covariates, which consisted of year, landscape-level timber harvest intensity, an interaction between year and landscape-level timber harvest intensity, a dummy variable for harvest history within the nest search plot (0 = no recent harvest; 1 = recent harvest), and a dummy variable for whether the nest search plot was dominated by mature forest (0 = no; 1 = yes). I also incorporated a species-specific and period-specific random nest search plot effect in the conditional binomial model.

The conditional binomial 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, and Gaussian prior distributions had a mean of 0 and precision of 0.01 (Appendix E). 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 9,000–30,000 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 6,000 or 9,000 posterior draws.

*Determining significance of interactions*

For all of the guild richness models, focal species abundance models, and focal species nest success models, relationships with individual variables were considered significant when the 95% credible intervals of their slope coefficient values did not overlap zero (Tables 3–4, Figures 5–7). Similarly, interactions between year and landscape-scale harvest intensity were considered significant when the 95% credible intervals of their effective slope coefficient values did not overlap zero (Table 5, Figures 8–10). I defined an effective slope coefficient as the effect of a 1-unit change in time given specific levels of landscape-scale harvest intensity (i.e., actively harvested landscape vs. minimally harvested landscape).

**RESULTS**

**Linear relationships with overall species and guild richness**

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

Guild richness model results indicated a significant interaction between year and landscape-scale harvest intensity for overall species richness and early-successional / edge-associated guild richness, forest-interior guild richness, and forest-gap richness (Table 3). Looking at overall species richness, the effective slope coefficients for year were significant in the both levels of landscape-scale harvest intensity, revealing a significant increase over time in overall species richness in the actively harvested landscape and a significant decrease in overall species richness over time in the minimally harvested landscapes (Table 5, Figure 8). Early-successional / edge-associated guild richness, forest-interior guild richness, and forest-gap richness followed similar trends, but their respective effective slope coefficients for year were significant for only one level of landscape-scale harvest intensity. Both early-successional / edge-associated guild richness and forest-gap guild richness were significantly increasing over time in the actively harvested landscape, and forest-interior guild richness was significantly decreasing over time in the minimally harvested landscape. Forest generalist guild richness did not exhibit a significant change over time at either level of landscape-scale harvest intensity.

**Linear relationships with focal species abundance**

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

Focal species abundance model results indicated a significant interaction between year and landscape-scale harvest intensity for 7 of the 14 total focal songbird species, including 2 of the 3 early-successional / edge-associated species, 3 of the 4 forest-interior species, and 2 of the 4 forest-gap species (Table 3). Looking at the 2 early-successional / edge-associated species, their effective slope coefficients for year were significant at only one level of landscape-scale harvest intensity, such that chestnut-sided warbler abundance was significantly decreasing over time in the minimally harvested landscape, while indigo bunting (*Passerina cyanea*) abundance was significantly increasing over time in the actively harvested landscape (Table 5, Figure 9). Interestingly, the third early-successional / edge-associated species (eastern towhee) showed increasing abundance over time in both landscapes, with a higher rate of increase in the actively harvested landscape. Of the 3 forest-interior species and 2 forest-gap species with a significant interaction, 4 species had effective slope coefficients for year that were significant at only one level of landscape-scale harvest intensity; black-throated green warbler (*Setophaga virens*), red-eyed vireo, and veery (*Catharus fuscescens*) abundance decreased over time in the minimally harvested landscape, while hooded warbler (*Setophaga citrina*) abundance increased over time in the actively harvested landscape. For both dark-eyed juncos (*Junco hyemalis*) and American redstarts (*Setophaga ruticilla*), their effective slope coefficients for year were significant for both levels of landscape-scale harvest intensity, such that dark-eyed junco and American redstart abundance was significantly increasing in the actively harvested landscape and significantly decreasing in the minimally harvested landscape. Wood thrushes, cerulean warblers (*Setophaga cerulea*), and the 3 forest generalist species did not exhibit a significant change in abundance over time at either level of landscape-scale harvest intensity.

**Linear relationships with focal species nest success**

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

Focal species nest success model results indicated a significant interaction between year and landscape-scale harvest intensity for only 1 of the 6 focal songbird species, with a difference in indigo bunting nest success during the incubation period over time between the actively harvested landscape and minimally harvested landscape (Table 3). Two other species also had significant differences between the 2 landscapes for nest success during the incubation period. Both wood thrush and red-eyed vireo had significant slope coefficients for year at only one level of landscape-scale harvest intensity, such that the probability of red-eyed vireo nest success during the incubation period decreased over time in the minimally harvested landscape, while the probability of wood thrush nest success during the incubation period decreased over time in the actively harvested landscape. Furthermore, for wood thrush nest success during the overall nesting period, effective slope coefficients for year were significantly negative during the later years of the study period at one level of landscape-scale harvest intensity, such that the probability of overall nest success for wood thrushes declined over time during 2004–2007 in the actively harvested landscape (Table 6, Figure 10). Eastern towhees, dark-eyed juncos, and veeries did not exhibit a significant change in nest success during any nesting period over time at either level of landscape-scale harvest intensity.

**DISCUSSION**

This study quantified the effects of landscape-scale forest management on changes in avian diversity, abundance, and population dynamics over time, using 2 Central Appalachian forested landscapes that varied in timber harvest intensity as focal study areas. My results supported the hypothesis that long-term temporal trends in forest songbird communities and populations during the breeding season are mediated by landscape-level forest management. Guild richness and focal species abundance tended to be consistently higher in the actively harvested landscape, and trends in guild richness and abundance over time were consistently positive in the actively harvested landscape and negative in the minimally harvested landscape. In particular, early-successional / edge-associated species and forest-gap species were found in higher numbers and exhibited positive temporal trends in the actively harvested landscape. However, a holistic assessment that included trends in reproductive success highlighted long-term declines in nest success for a forest-interior species of regional conservation concern within the actively harvested landscape but not the minimally harvested landscape. Thus, there are important trade-offs to consider when using landscape-scale forest management to promote songbird communities and populations in forested landscapes.

Landscape-scale harvest intensity influenced changes over time in overall species richness and guild richness. As predicted, early-successional / edge-associated guild richness increased over time in the actively harvested landscape. Overall species richness and forest-gap guild richness also increased over time in the actively harvested landscape. Within the actively harvested landscape, a combination of clear-cut harvests, heavy partial harvests, and light partial harvests were applied, which created early-successional habitat and canopy gaps, so it makes sense that the number of early-successional / edge-associated species and forest-gap species increased over time. These results are also consistent with previous studies that document higher species diversity and species richness in harvested forest stands compared to non-harvested mature forest (Hagan et al. 1997, King and Degraaf 2000). Contrary to my original predictions, forest-interior guild richness decreased over time in the minimally harvested landscape, while early-successional / edge-associated guild richness and forest-gap guild richness did not significantly change. Declining forest-interior guild richness in the minimally harvested landscape may be due to increasing homogenization of forest stands over time and a need for some amount of early-successional habitat within the landscape during the post-breeding season (Stoleson 2013). However, it is also important to note that although changes in the number of species were statistically significant, the differences in modeled responses across the entire study period were generally ≤1 species, with a maximum 20% increase in early-successional / edge-associated guild richness in the actively harvested landscape and a maximum 10% decrease in forest-interior guild richness in the minimally harvested landscape. Thus, differences between the 2 levels of landscape-scale harvest intensity may not have had much biological significance.

Focal species exhibited consistent diverging trends in abundance over time corresponding to landscape-scale harvest intensity, and changes in abundance followed similar patterns as changes in guild richness. As predicted, 2 of the 3 early-successional / edge-associated species increased over time in the actively harvested landscape and 1 decreased over time in the minimally harvested landscape. Half of the focal forest-gap species also increased in abundance over time in the actively harvested landscape. Just as with the corresponding guild richness results, these findings are consistent with the habitats being transformed or modified by clear-cut harvests, heavy partial harvests, and light partial harvests in the actively harvested landscape. A multitude of previous studies found similar results in how the abundance of early-successional / edge-associated species and forest-gap species responds to timber harvest (e.g., Hagan et al. 1997, Becker et al. 2011). In contrast, trends in forest-interior and forest-gap species defied my initial expectations. Of the 4 forest-interior species, 3 decreased in abundance over time in the minimally harvested landscape, and 1 of the species increased in abundance over time in the actively harvested landscape. Similarly, 2 of the 4 forest-gap species decreased in abundance over time in the minimally harvested landscape. It is possible that homogenization of forest structure as stands age and/or the lack of nearby appropriate post-breeding habitat could explain those declining trends (Stoleson 2013). As with the guild richness results, statistically significant differences may have limited biological impact, as the differences in modeled responses in abundance across the entire study period were generally ≤1 individual for most species. However, maximum percent changes in focal species abundance did include a 230% increase in a forest-gap species in the actively harvested landscape and a 100% decrease in an early-successional / edge-associated species in the minimally harvested landscape. Thus, landscape-level harvest intensity tended to have a higher proportional effect size on individual focal species than on guild richness.

In addition to species diversity and abundance, it is critical to consider landscape-scale harvest intensity impacts on long-term bird population dynamics, such as changes in reproductive success, because abundance and density metrics alone can be poor indicators of habitat quality (Van Horne 1983, Vickery et al. 1992, Hagan et al. 1996). Looking at focal species nest success, there was substantial uncertainty in trends over time, as indicated by wide credible intervals and lack of statistical significance. Wood thrushes had the highest sample size of the 6 focal songbird species, and there were notable significant declines in nest success during both the incubation and overall nesting periods within the actively harvested landscape. This result echoed the findings of Becker (2010), who tracked nest success in the WERF and used a similar dataset spanning 1996–1998, 2001–2003, and 2007–2009. Becker (2010) found few differences in nest success among harvest types within the WERF, but wood thrush nest success significantly declined from 1996–1998 to 2007–2009. Another study also measured nest success of wood thrushes in the Monongahela National Forest in West Virginia and found that nest success was positively associated with mature forest patches and negatively related to open habitat occurring in the landscape (Williams 2002). Indeed, decreasing nest success of a forest-interior species in the actively harvested landscape, which had higher edge density created by roads and higher intensity harvests, is consistent with expected negative edge effects, such as increased nest predator presence and movement (Gates and Gysel 1978).

Overall, songbird diversity and abundance tended to slightly increase over time in the actively harvested landscape and tended to slightly decrease over time in the minimally harvested landscape. The positive trends in the actively harvested landscape were likely due to increased habitat diversity, both spatially and structurally. Clear-cutting and heavily partial harvests can create breeding and post-breeding habitat for early-successional / edge-associated species and post-breeding habitat for forest-interior and forest-gap species. Light partial harvests can additionally create breeding habitat for forest-gap species. However, the reproductive success of an area-sensitive forest-interior species declined over time in the actively harvested landscape, indicating a potential conservation issue. Possible mitigating actions include matching harvest intensity to levels of natural disturbance (Drapeau et al. 2000), reducing the amount of edge from roads and timber harvests, and keeping overall area of harvested forest stands below a specified threshold within the landscape (Becker et al. 2011).

While my results are specific to my 2 study areas, they may reflect broad temporal trends for forested landscapes within the Central Appalachians and therefore provide valuable insight to applying landscape-scale forest management in this region. It would be interesting to supplement my findings with an investigation of long-term trends in landscapes across a more extensive spectrum of timber harvest intensity levels in terms of total area harvested and harvest types. Furthermore, I can only speculate at the finer-scale reasons for diverging temporal trends in the actively harvested landscape and minimally harvested landscape. More research is needed to understand the specific mechanisms driving varying temporal trends in species communities and populations in different landscapes.

**Conclusions**

Here, I establish that landscape-scale harvest intensity can influence trends in songbird diversity, abundance, and reproductive success over time. The results of this study are valuable for understanding how to balance the management of forested landscapes for a diversity of breeding songbird species with different habitat associations, and for predicting long-term effects of landscape-scale forest management on those species. My findings indicate that there are distinct benefits and potential negative consequences associated with varying levels of landscape-scale harvest intensity. Actively harvested landscapes may promote overall species richness, as well as the number (i.e., richness) and abundance of early-successional / edge-associated species and forest-gap species, but there may be long-term negative effects on nest success of area-sensitive forest-interior species. Minimally harvested landscapes may be valuable for certain species of regional conservation concern associated with intact mature forests, but in my study, forest-interior guild richness and many of the forest-interior and forest-gap species were declining in the minimally harvested landscape, indicating a potential issue in landscape-scale management for those species. Based on my results, I advocate for a goal-oriented, science-based approach to landscape-scale forest management to be applied by private landowners, non-governmental organizations, and government agencies. Timber harvest operations can benefit a subset of songbird guilds and species without impacting much of the songbird community, but land managers should be aware of potential negative effects to certain species and be willing to implement mitigation plans that may be necessary to achieve their specific management goals. Furthermore, this study emphasizes the value of maintaining minimally harvested landscapes to support species of regional conservation concern that require extensive stands of mature forest.

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**Tables**

Table 1. List of the common name, scientific name, 4-letter species code, and habitat-related guild designation of the 14 songbird species used in the focal species analyses. The habitat-related guild designation indicates the primary breeding habitat of the species, such that: species in the early-successional / 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. All 14 species were focal species for assessing temporal trends in abundance, and 6 species (with bolded common names and 4-letter species codes) were focal species for assessing temporal trends in nest success. 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** | **Guild** |
| Chestnut-sided warbler | *Setophaga pensylvanica* | CSWA | ESEA |
| **Eastern towhee\*** | *Pipilo erythrophthalmus* | **EATO** | ESEA |
| **Indigo bunting\*** | *Passerina cyanea* | **INBU** | ESEA |
| Black-throated green warbler | *Setophaga virens* | BTNW | INT |
| **Dark-eyed junco** | *Junco hyemalis* | **DEJU** | INT |
| **Red-eyed vireo** | *Vireo olivaceus* | **REVI** | INT |
| **Wood thrush**\* | *Hylocichla mustelina* | **WOTH** | INT |
| American redstart | *Setophaga ruticilla* | AMRE | GAP |
| Cerulean warbler\* | *Setophaga cerulea* | CERW | GAP |
| Hooded warbler\* | *Setophaga citrina* | HOWA | GAP |
| **Veery** | *Catharus fuscescens* | **VEER** | GAP |
| American robin | *Turdus migratorius* | AMRO | GEN |
| Black-capped chickadee\* | *Poecile atricapillus* | BCCH | GEN |
| White-breasted nuthatch | *Sitta carolinensis* | WBNU | GEN |

Table 2. List, detailed description, and data source of the 11 site covariates used in the guild richness and focal species abundance analyses, comprising 2 focal variables, 3 topographical variables, and 6 habitat variables.

|  |  |  |
| --- | --- | --- |
| **Variable** | **Description (Unit)** | **Data Source (resolution)** |
| Year | Year of data collection; variable type: discrete; range: 1996–2009 | Bird survey data |
| Landscape-scale Harvest Intensity | Harvest intensity at the landscape level, corresponding to study area; variable type: dummy; 1 = actively harvested (i.e., WERF), 0 = minimally harvested (i.e., MNF) |
| Elevation | Mean elevation (m) within 50 m of each sampling point; variable type: continuous; range: 353–1,395 m | Shuttle Radar Topography Mission digital elevation data (~20–25 m), Consultative Group on International Agricultural Research – Consortium for Spatial Information |
| Aspect | Mode aspect (degrees) within 50 m of each sampling point; variable type: continuous; bounded between 0 and 360 degrees |
| 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: -3.500–2.375 |
| Stand Age | Mode stand age within 1 km of the edge of the wildlife opening; variable type: discrete; range: 0–180 years | GIS datasets of WERF and MNF forest stands |
| Proportion All Forest | Proportion of any type of mature forest cover (including deciduous, mixed, and coniferous) / mixed forest cover / coniferous forest cover / shrub cover within 50 m of the sampling point; variable type: continuous; bounded between 0 and 1 | 2001 / 2004 / 2006 / 2008 National Land Cover Database (30 m), U.S. Geological Survey |
| Proportion Mixed Forest |
| Proportion Conifer Forest |
| Proportion Shrub |
| Proportion All Forest within 1 km | 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 |

Table 3. Statistical significance (indicated by bold type) of slope coefficients for the predictor variables (YR = year, LSHI = landscape-scale harvest intensity, YR×LSHI = interaction between year and landscape-scale harvest intensity, EL = elevation, ASP = aspect, ASP2 = aspect squared, TPI = topographic position index, AGE = stand age, AGE2 = stand age squared, PAF = proportion of all forest within 50 m, PMF = proportion of mixed forest within 50 m, PCF = proportion of conifer forest within 50 m, PS = proportion of shrub cover within 50 m, and PAFkm = proportion of all forest within 1 km) corresponding to overall species richness (ALL), guild (ESEA = early-successional / edge-associated, INT = forest-interior, GAP = forest-gap, and GEN = forest generalist) richness, and focal songbird species abundance (see Table 1 for species codes), arranged by guild designation.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Response** | **YR** | **LSHI** | **YR×LSHI** | **EL** | **ASP** | **ASP2** | **TPI** | **AGE** | **AGE2** | **PAF** | **PMF** | **PCF** | **PS** | **PAFkm** |
| ALL | **-0.018** | **0.084** | **0.049** | **-0.222** | **-0.022** | -0.006 | 0.004 | -0.004 | **0.012** | **0.032** | **-0.056** | 0.000 | 0.012 | -0.009 |
| ESEA | 0.003 | **0.131** | **0.069** | **-0.426** | -0.015 | -0.024 | -0.002 | **-0.046** | 0.018 | -0.036 | **-0.188** | -0.012 | **0.027** | **-0.058** |
| CSWA | **-0.425** | **1.490** | **0.614** | -0.138 | 0.127 | -0.064 | -0.116 | -0.072 | 0.052 | -0.077 | **-0.341** | -0.179 | **0.098** | 0.006 |
| EATO | **0.378** | **1.467** | 0.285 | **-0.414** | -0.067 | -0.139 | 0.080 | -0.189 | -0.006 | **-0.161** | **-0.176** | -0.092 | 0.018 | 0.091 |
| INBU | 0.039 | **0.810** | **0.458** | **-0.689** | -0.078 | -0.095 | 0.065 | -0.147 | **0.088** | -0.146 | **-0.446** | -0.114 | -0.033 | -0.060 |
| INT | **-0.034** | **0.090** | **0.036** | **-0.088** | **-0.025** | 0.003 | -0.005 | **0.025** | 0.005 | **0.039** | 0.017 | **0.028** | -0.004 | 0.017 |
| BTNW | **-0.205** | **0.499** | **0.361** | **0.302** | **-0.075** | 0.018 | 0.033 | 0.005 | -0.024 | **0.081** | **-0.084** | **-0.173** | -0.008 | **0.093** |
| DEJU | **-0.273** | **1.870** | **0.825** | **0.563** | -0.013 | **0.103** | **-0.074** | **0.091** | 0.030 | **-0.098** | **0.137** | -0.004 | -0.013 | 0.026 |
| REVI | **-0.292** | **0.247** | **0.425** | **-0.217** | 0.034 | -0.006 | 0.007 | **-0.052** | -0.019 | **0.095** | **-0.214** | **-0.324** | 0.012 | **0.104** |
| WOTH | -0.087 | -0.181 | 0.238 | **-0.798** | 0.011 | -0.081 | -0.010 | 0.018 | -0.043 | -0.086 | **-0.277** | -0.180 | **-0.166** | 0.038 |
| GAP | -0.020 | **0.098** | **0.075** | **-0.318** | 0.007 | -0.009 | -0.001 | -0.014 | 0.013 | **0.112** | **-0.083** | **-0.081** | 0.019 | -0.008 |
| AMRE | **-0.275** | **-0.628** | **1.092** | **-0.578** | -0.039 | 0.025 | -0.014 | 0.011 | 0.040 | **0.269** | **-0.555** | **-0.274** | 0.057 | **0.175** |
| CERW | -0.093 | **-2.624** | -0.958 | **-0.348** | -0.039 | 0.146 | 0.142 | 0.122 | -0.072 | **0.952** | **-0.455** | 0.005 | -0.228 | 0.189 |
| HOWA | -0.179 | **1.164** | **0.692** | **-0.818** | 0.093 | -0.142 | -0.018 | 0.005 | 0.028 | 0.100 | -0.106 | -0.202 | 0.054 | 0.126 |
| VEER | **-0.301** | **1.612** | 0.292 | 0.115 | **0.102** | 0.050 | -0.009 | -0.052 | 0.033 | **0.142** | **-0.109** | **-0.173** | 0.031 | -0.016 |
| GEN | 0.000 | 0.079 | 0.033 | **-0.329** | **-0.043** | -0.006 | **0.045** | -0.016 | 0.009 | 0.017 | **-0.157** | **-0.075** | -0.019 | 0.013 |
| AMRO | 0.079 | **0.839** | 0.117 | -0.098 | 0.041 | 0.063 | 0.037 | -0.016 | 0.032 | **-0.189** | **-0.172** | -0.073 | -0.065 | -0.032 |
| BCCH | -0.052 | 0.536 | 0.248 | 0.005 | -0.068 | -0.005 | **0.107** | -0.080 | **0.047** | -0.085 | **0.273** | 0.070 | -0.069 | 0.109 |
| WBNU | 0.122 | -0.057 | -0.089 | **-0.358** | -0.025 | -0.080 | **0.152** | 0.067 | 0.000 | -0.071 | **-0.479** | -0.149 | -0.023 | **0.136** |

Table 4. Statistical significance (indicated by bold type) of slope coefficients for the predictor variables (YR = year, LSHI = landscape-scale harvest intensity, YR×LSHI = interaction between year and landscape-scale harvest intensity, HH = harvest history of nest search plot, and MF = nest search plot located in mature forest) corresponding to the probability of nest success during the incubation and brooding periods. Focal species (see Table 1 for species codes) are arranged by habitat-related guild designation (ESEA = early-successional / edge-associated, INT = forest-interior, and GAP = forest-gap).

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Species** | **Guild** | **Incubation Period** | | | | | **Brooding Period** | | | | |
| **YR** | **LSHI** | **YR×LSHI** | **HH** | **MF** | **YR** | **LSHI** | **YR×LSHI** | **HH** | **MF** |
| EATO | ESEA | 0.217 | -0.773 | -0.501 | 0.785 | -1.402 | 1.458 | -1.347 | -2.006 | 1.528 | 0.446 |
| INBU | ESEA | 2.211 | -0.330 | **-3.336** | 1.476 | -1.150 | -2.766 | 1.886 | 4.840 | 1.047 | 1.577 |
| DEJU | INT | -1.391 | 1.516 | 1.560 | 0.893 | 0.360 | -4.751 | 0.050 | 4.700 | 0.631 | 1.194 |
| REVI | INT | -1.150 | -0.692 | 1.888 | -0.518 | 0.043 | -0.459 | -2.115 | 1.647 | -0.266 | -0.025 |
| WOTH | INT | 0.081 | **-1.099** | -0.968 | 0.434 | -0.415 | -0.748 | 1.184 | 2.320 | **-1.427** | -0.797 |
| VEER | GAP | -0.548 | -0.100 | 0.539 | -0.664 | -0.744 | 1.022 | -0.469 | -4.535 | 4.768 | -2.662 |

Table 5. Statistical significance (indicated by bold type) of the effective slope coefficients for year on overall species richness (ALL), guild (ESEA = early-successional / edge-associated, INT = forest-interior, GAP = forest-gap, and GEN = forest generalist) richness, focal songbird species abundance (see Table 1 for species codes), and focal songbird species nest success in an actively harvested landscape and minimally harvested landscape. Model type is denoted such that GR = guild richness, FSA = focal species abundance, FSNS-I = focal species nest success during the incubation period, and FSNS-B = focal species nest success during the brooding period.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Guild** | **Species** | **Model** | **Actively Harvested** | **Minimally Harvested** |
| ALL |  | GR | **0.030** | **-0.018** |
| ESEA |  | GR | **0.072** | 0.003 |
|  | CSWA | FSA | 0.188 | **-0.425** |
|  | EATO | FSA | **0.663** | **0.378** |
|  |  | FSNS-I | -0.285 | 0.217 |
|  |  | FSNS-B | -0.548 | 1.458 |
|  | INBU | FSA | **0.497** | 0.039 |
|  |  | FSNS-I | -1.125 | 2.211 |
|  |  | FSNS-B | 2.074 | -2.766 |
| INT |  | GR | 0.002 | **-0.034** |
|  | BTNW | FSA | 0.156 | **-0.205** |
|  | DEJU | FSA | **0.552** | **-0.273** |
|  |  | FSNS-I | 0.169 | -1.391 |
|  |  | FSNS-B | -0.051 | -4.751 |
|  | REVI | FSA | 0.134 | **-0.292** |
|  |  | FSNS-I | 0.738 | **-1.150** |
|  |  | FSNS-B | 1.188 | -0.459 |
|  | WOTH | FSA | 0.150 | -0.087 |
|  |  | FSNS-I | **-0.887** | 0.081 |
|  |  | FSNS-B | 1.572 | -0.748 |
| GAP |  | GR | **0.055** | -0.020 |
|  | AMRE | FSA | **0.817** | **-0.275** |
|  | CERW | FSA | -1.051 | -0.093 |
|  | HOWA | FSA | **0.513** | -0.179 |
|  | VEER | FSA | -0.010 | **-0.301** |
|  |  | FSNS-I | -0.010 | -0.548 |
|  |  | FSNS-B | -3.513 | 1.022 |
| GEN |  | GR | 0.033 | 0.000 |
|  | AMRO | FSA | 0.195 | 0.079 |
|  | BCCH | FSA | 0.196 | -0.052 |
|  | WBNU | FSA | 0.032 | 0.122 |

Table 6. Statistical significance (indicated by bold type) of the effective slope coefficients for year on overall nest success of focal songbird species (see Table 1 for species codes) in an actively harvested landscape (AHL) and minimally harvested landscape (MHL) during the years in the study period. Effective slope coefficients for overall nest success in each year and for each level of landscape-scale harvest intensity (LSHI) were determined by calculating the change in estimated probability of nest success during the entire nesting period from one year to the next. Habitat-related guild designation (ESEA = early-successional / edge-associated, INT = forest-interior, GAP = forest-gap, and GEN = forest generalist) of each species is noted in parentheticals.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Species** | **LSHI** | **1993** | **1994** | **1995** | **1996** | **1997** | **1998** | **1999** | **2000** | **2001** | **2002** | **2003** | **2004** | **2005** | **2006** | **2007** |
| EATO  (ESEA) | AHL | -0.015 | -0.017 | -0.018 | -0.018 | -0.019 | -0.019 | -0.018 | -0.017 | -0.016 | -0.014 | -0.013 | -0.011 | -0.009 | -0.008 | -0.006 |
| MHL | 0.040 | 0.047 | 0.048 | 0.041 | 0.032 | 0.022 | 0.015 | 0.010 | 0.007 | 0.005 | 0.003 | 0.002 | 0.001 | 0.000 | 0.000 |
| INBU  (ESEA) | AHL | 0.035 | 0.044 | 0.053 | 0.053 | 0.037 | 0.011 | -0.015 | -0.035 | -0.048 | -0.054 | -0.056 | -0.054 | -0.049 | -0.043 | -0.037 |
| MHL | 0.079 | 0.095 | 0.077 | 0.008 | -0.069 | -0.099 | -0.085 | -0.060 | -0.042 | -0.029 | -0.021 | -0.016 | -0.012 | -0.009 | -0.007 |
| DEJU (INT) | AHL | 0.006 | 0.005 | 0.005 | 0.004 | 0.003 | 0.002 | 0.001 | 0.000 | -0.001 | -0.002 | -0.003 | -0.003 | -0.004 | -0.004 | -0.005 |
| MHL | -0.021 | -0.042 | -0.075 | -0.118 | -0.156 | -0.113 | -0.057 | -0.027 | -0.013 | -0.007 | -0.005 | -0.003 | -0.002 | -0.002 | -0.001 |
| REVI  (INT) | AHL | 0.014 | 0.018 | 0.024 | 0.031 | 0.040 | 0.049 | 0.055 | 0.055 | 0.050 | 0.042 | 0.034 | 0.028 | 0.022 | 0.018 | 0.014 |
| MHL | -0.017 | -0.030 | -0.047 | -0.064 | -0.077 | -0.080 | -0.074 | -0.063 | -0.051 | -0.040 | -0.031 | -0.024 | -0.019 | -0.015 | -0.012 |
| WOTH  (INT) | AHL | 0.028 | 0.025 | 0.013 | -0.009 | -0.028 | -0.039 | -0.042 | -0.041 | -0.037 | -0.033 | **-0.028** | **-0.024** | **-0.020** | **-0.017** | **-0.014** |
| MHL | -0.005 | -0.009 | -0.014 | -0.019 | -0.024 | -0.029 | -0.033 | -0.035 | -0.035 | -0.033 | -0.031 | -0.028 | -0.025 | -0.022 | -0.020 |
| VEER  (GAP) | AHL | -0.011 | -0.019 | -0.031 | -0.046 | -0.063 | -0.074 | -0.076 | -0.067 | -0.049 | -0.032 | -0.019 | -0.012 | -0.008 | -0.006 | -0.004 |
| MHL | 0.030 | 0.033 | 0.030 | 0.017 | -0.002 | -0.017 | -0.024 | -0.026 | -0.025 | -0.022 | -0.020 | -0.017 | -0.015 | -0.013 | -0.011 |

**FIGURES**

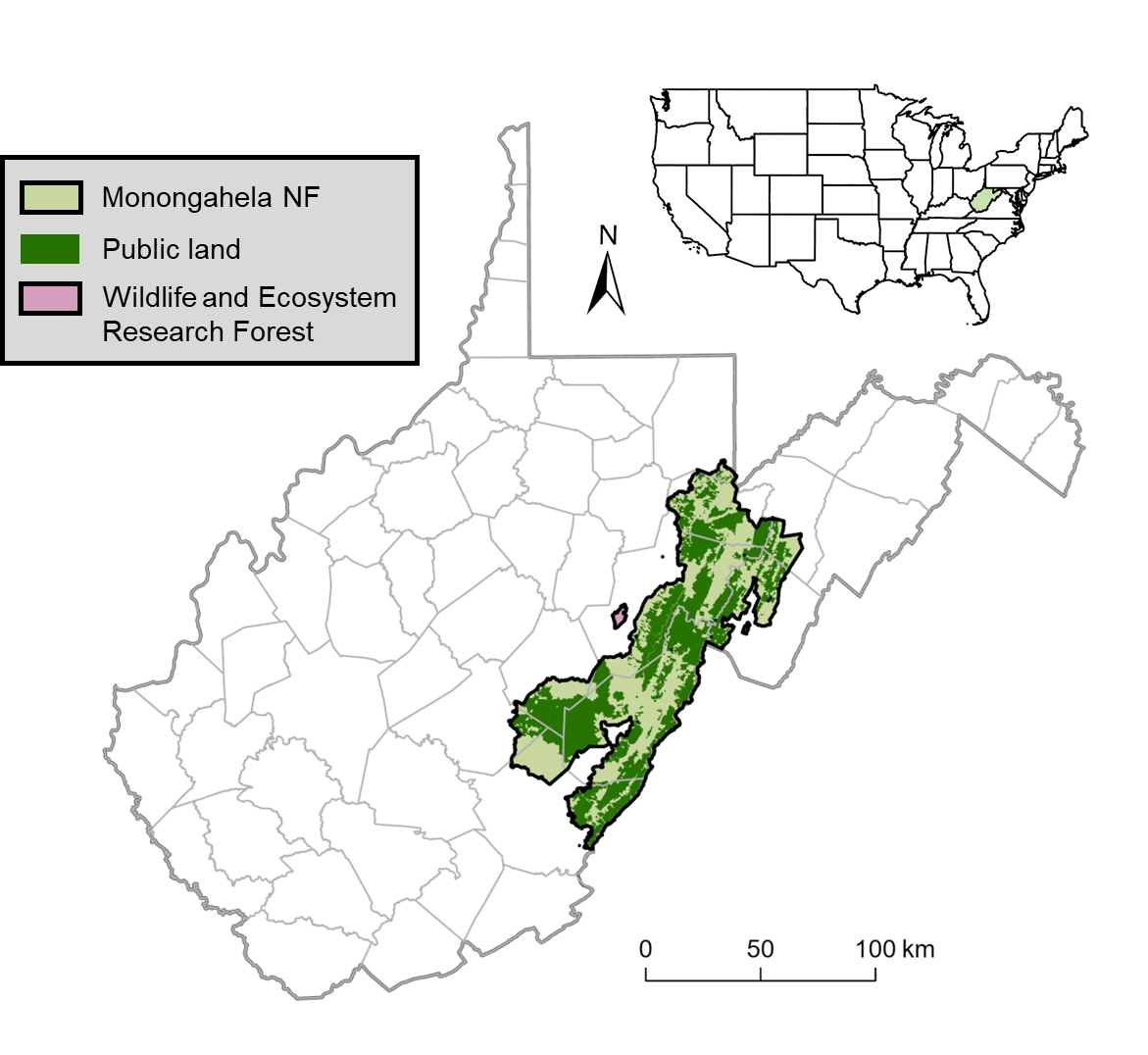


Figure 1. Sampling sites and nest search plots for this study were located in 2 study areas in West Virginia: (1) the MeadWestvaco Wildlife and Ecosystem Research Forest, which was established in 1994 by the Westvaco Corporation and comprises 3,080 ha; and (2) the Monongahela National Forest (NF), which encompasses portions of nine counties (delineated by gray lines) and comprises nearly 688,000 ha, of which 54% (371,906 ha) is public land (dark green).

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Description automatically generated

Figure 2. Locations of the sampling points and nest search plots within the MeadWestvaco Wildlife and Ecosystem Research Forest (WERF) in 1996–1998, 2001–2003, and 2007–2009.

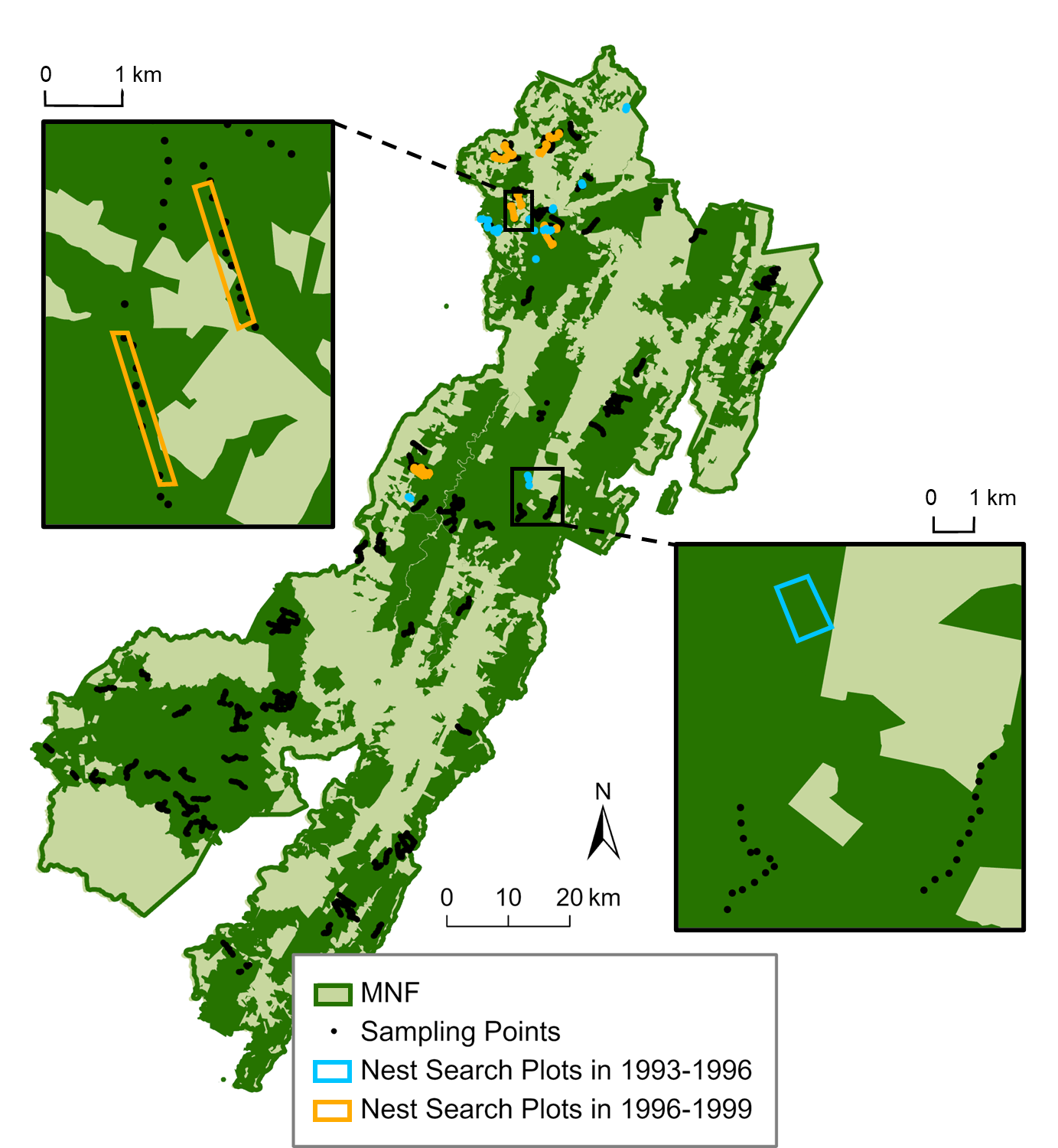


Figure 3. Locations of the sampling points and nest search plots within the public lands (dark green) of the Monongahela National Forest (MNF) in 1993–1996 and 1996–1999.



Figure 4. Timber harvest history of the actively harvested MeadWestvaco Wildlife and Ecosystem Research Forest (WERF) during 1996–1998, 2001–2003, and 2007–2009. Heavy partial harvest methods included shelterwood cuts, two-age harvests, and regeneration (seed-tree) harvests, whereas light partial harvest methods included diameter-limit harvests and single-tree selection.

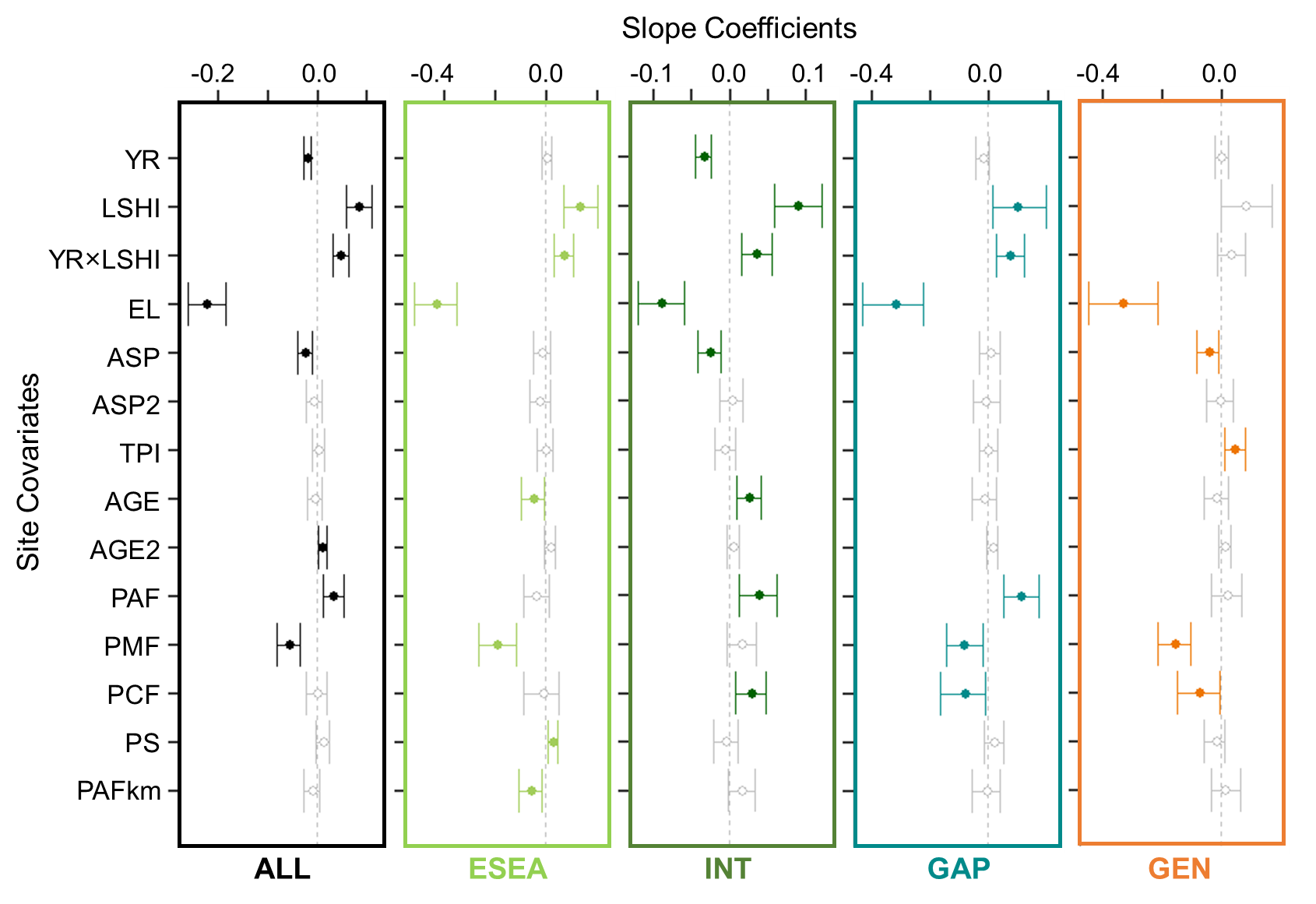
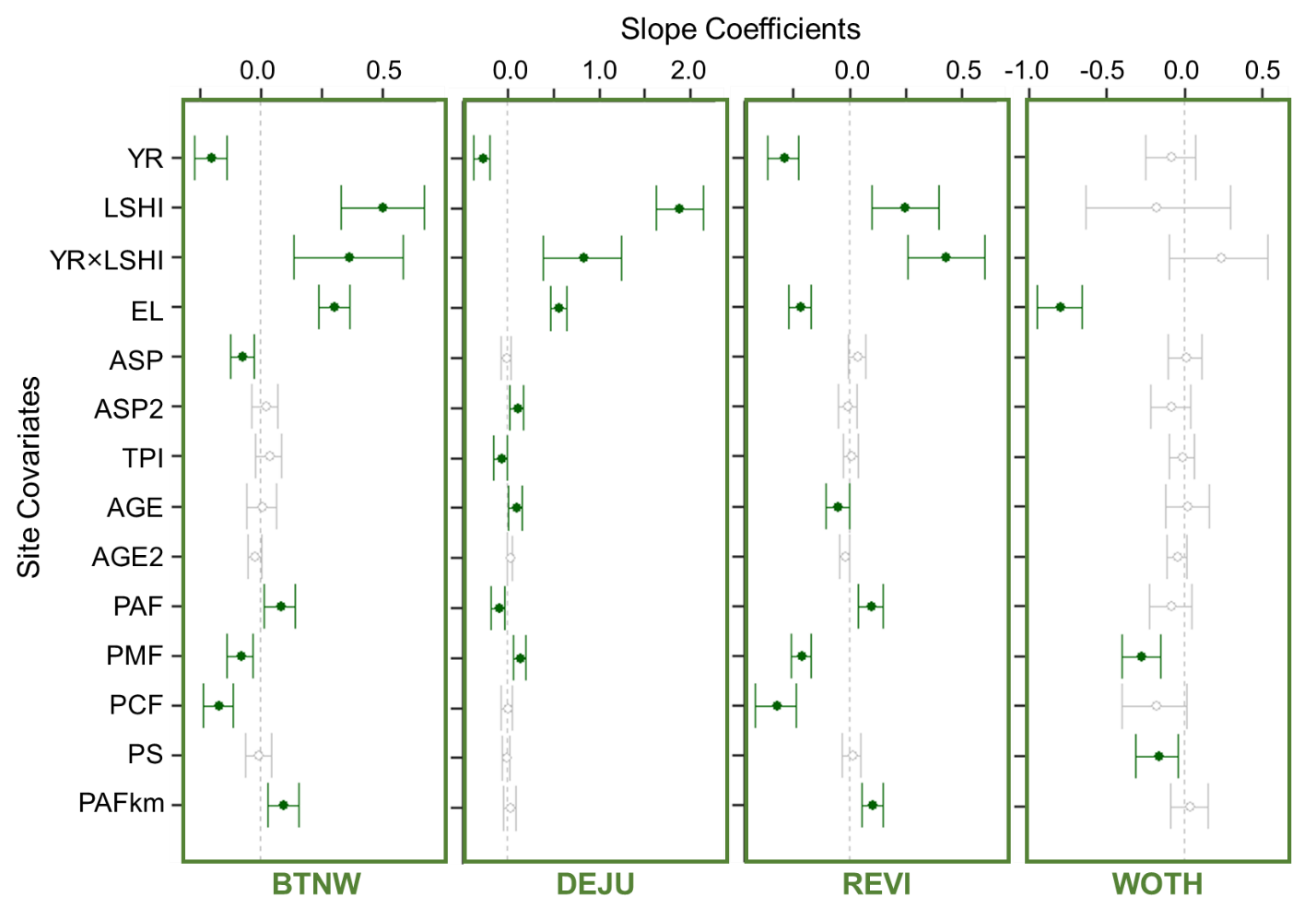
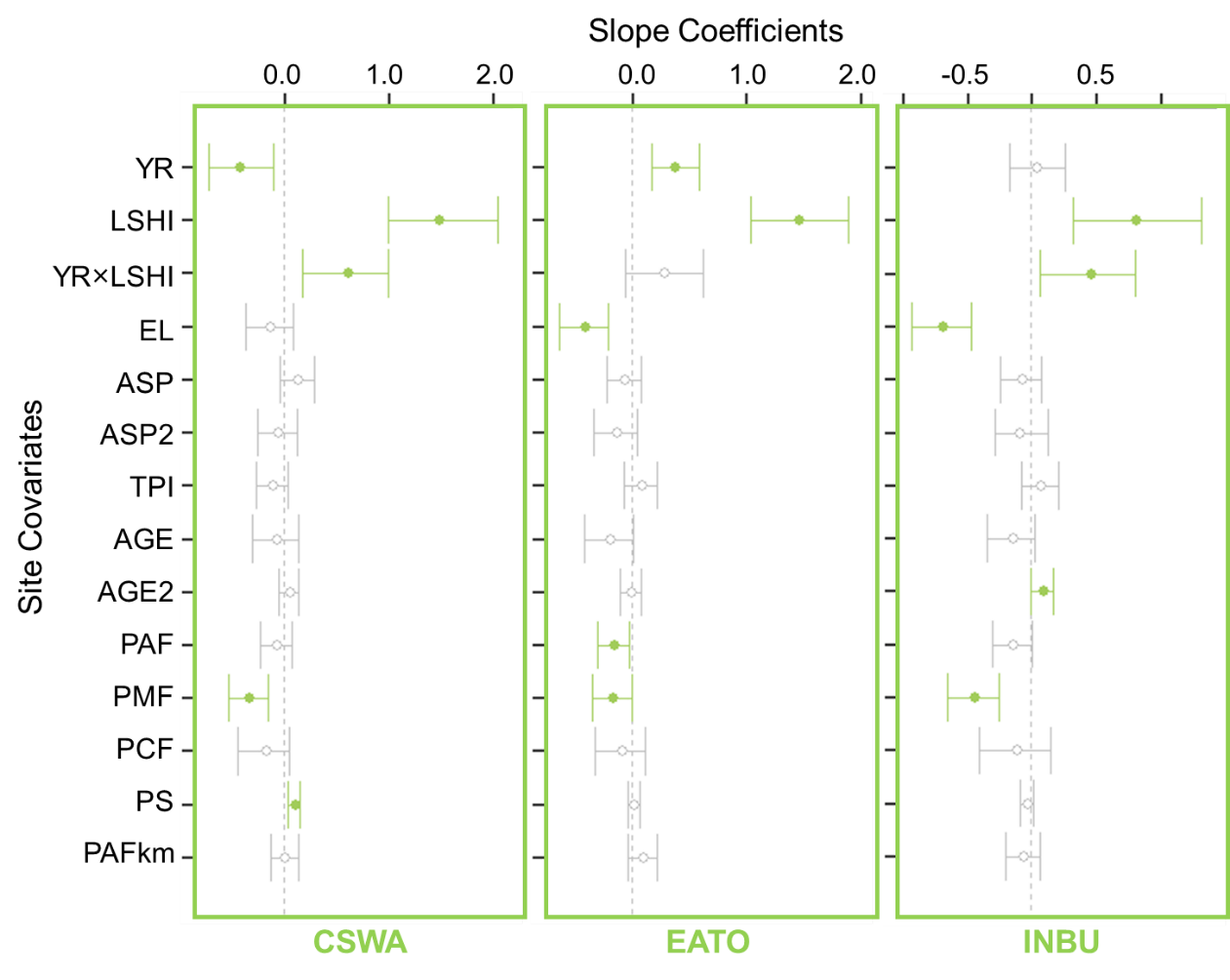


Figure 5. Whisker plots for overall species richness (ALL) and guild (ESEA = early-successional / edge-associated, INT = forest-interior, GAP = forest-gap, and GEN = forest generalist) richness (see Appendix A for guild designations and associated forest songbird species), displaying the slope coefficients of the predictor variables (i.e., site covariates; YR = year, LSHI = landscape-scale harvest intensity, YR×LSHI = interaction between year and landscape-scale harvest intensity, EL = elevation, ASP = aspect, ASP2 = aspect squared, TPI = topographic position index, AGE = stand age, AGE2 = stand age squared, PAF = proportion of all forest within 50 m, PMF = proportion of mixed forest within 50 m, PCF = proportion of conifer forest within 50 m, PS = proportion of shrub cover within 50 m, and PAFkm = proportion of all forest within 1 km). Points are located at the mean values for the posterior distributions and the corresponding whiskers encompass the 95% credible intervals. Solid colored points with closed circles and non-gray whiskers indicate statistical significance (i.e., credible intervals do not overlap zero).



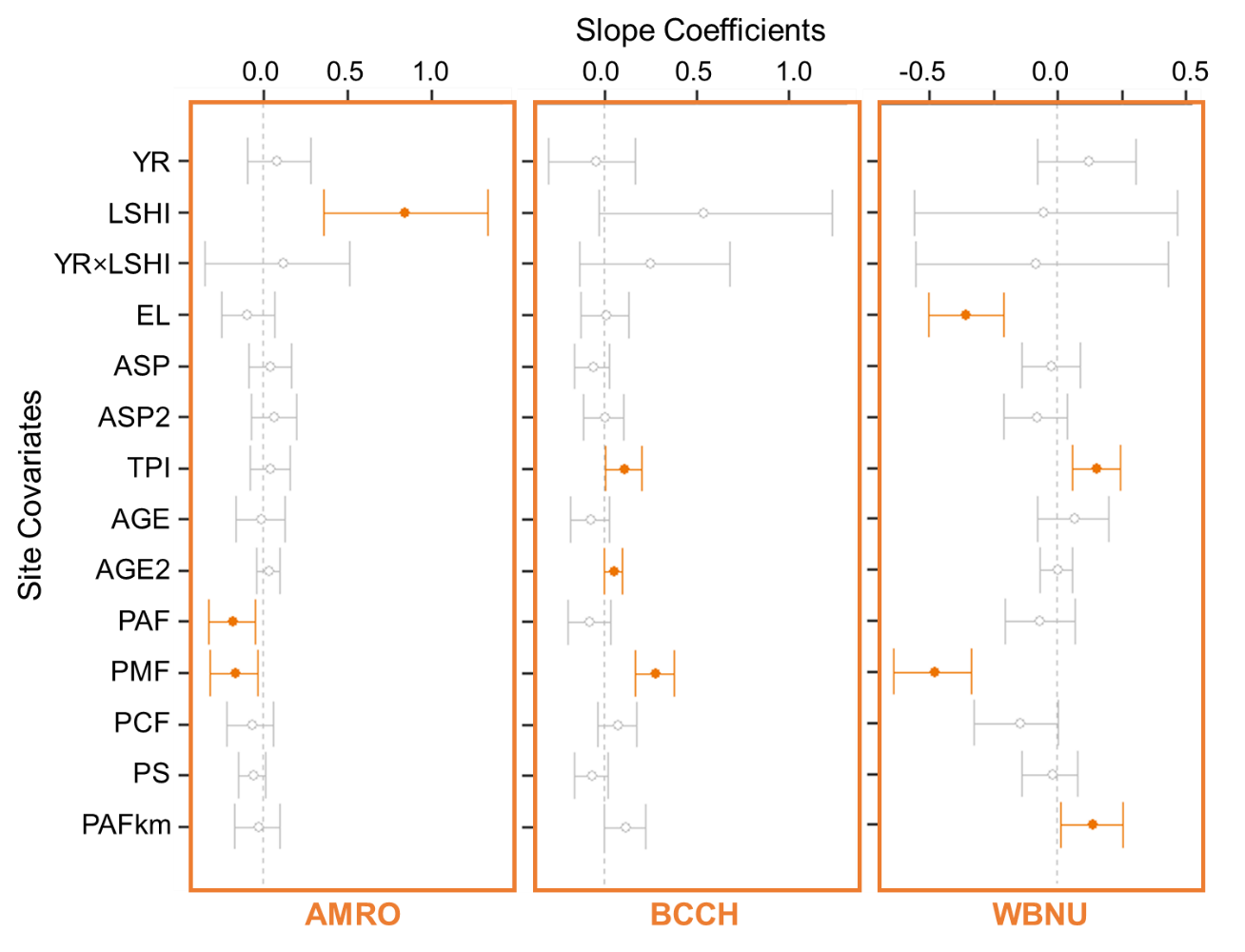
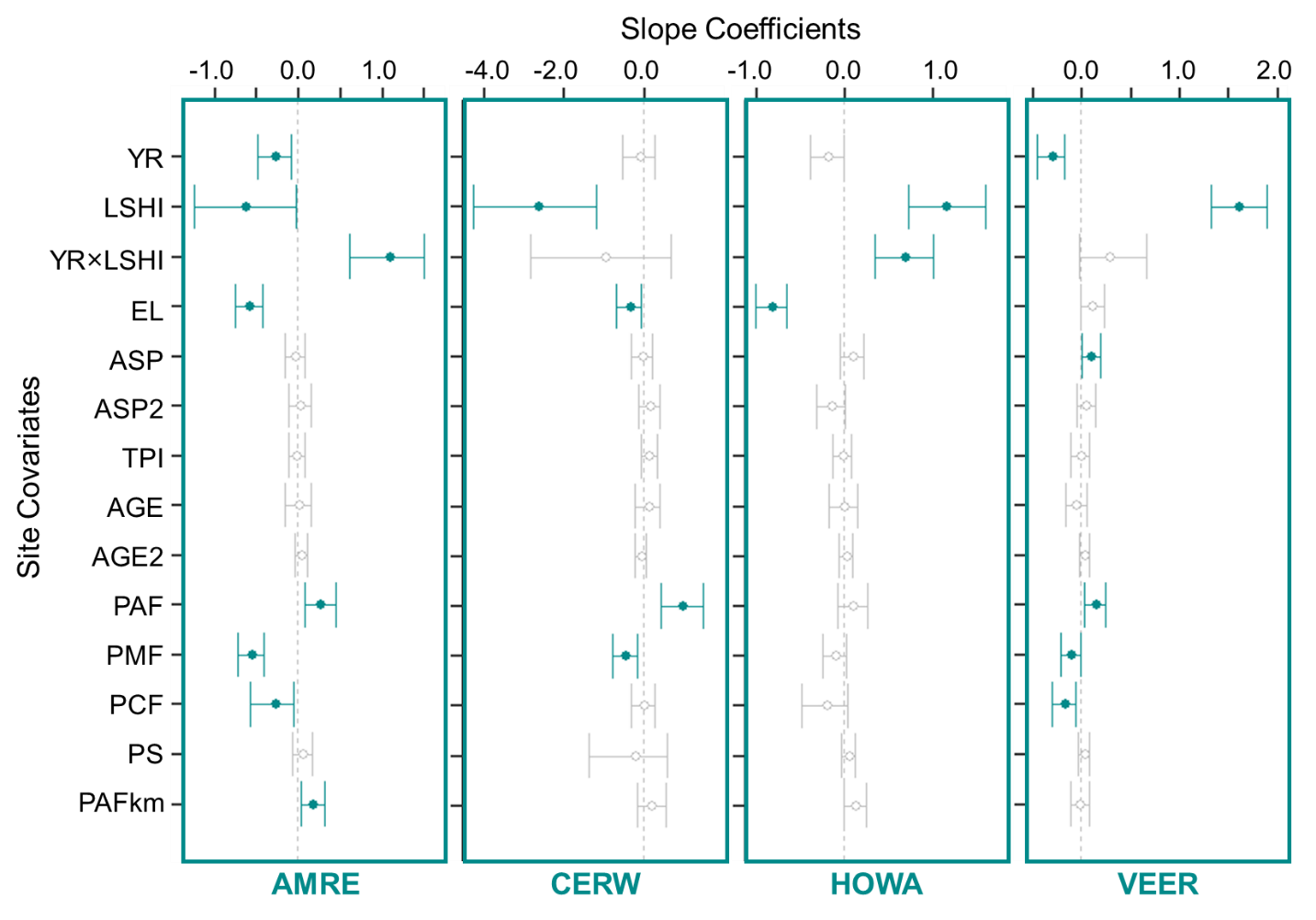


Figure 6. Whisker plots for each focal species for abundance analyses (Table 1), displaying the slope coefficients of the predictor variables (i.e., site covariates; YR = year, LSHI = landscape-scale harvest intensity, YR×LSHI = interaction between year and landscape-scale harvest intensity, EL = elevation, ASP = aspect, ASP2 = aspect squared, TPI = topographic position index, AGE = stand age, AGE2 = stand age squared, PAF = proportion of all forest within 50 m, PMF = proportion of mixed forest within 50 m, PCF = proportion of conifer forest within 50 m, PS = proportion of shrub cover within 50 m, and PAFkm = proportion of all forest within 1 km). Points are located at the mean values for the posterior distributions and the corresponding whiskers encompass the 95% credible intervals. Solid colored points with closed circles and non-gray whiskers indicate statistical significance (i.e., credible intervals do not overlap zero). Color of the 4-letter species code and plot elements indicates the species’ guild designation (light green = early-successional or edge-associated guild, dark green = forest-interior guild, teal = forest-gap guild, and orange = forest generalist guild).

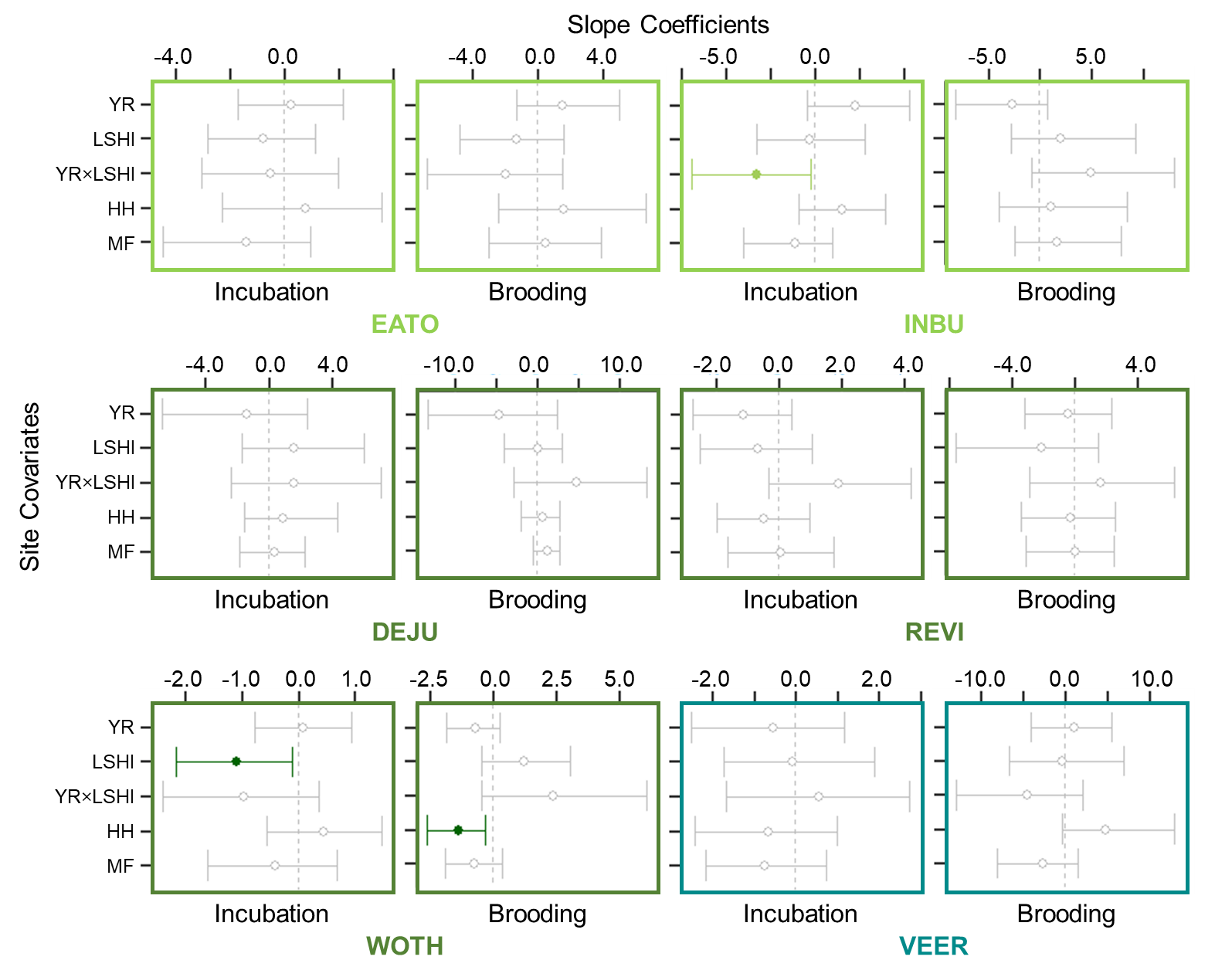


Figure 7. Whisker plots for each focal species for nest success analyses (Table 1), displaying the slope coefficients of the predictor variables (i.e., site covariates; YR = year, LSHI = landscape-scale harvest intensity, YR×LSHI = interaction between year and landscape-scale harvest intensity, HH = harvest history of nest search plot, and MF = nest search plot located in mature forest) for nest success during the incubation and brooding periods, respectively. Points are located at the mean values for the posterior distributions and the corresponding whiskers encompass the 95% credible intervals. Solid colored points with closed circles and non-gray whiskers indicate statistical significance (i.e., credible intervals do not overlap zero). Color of the 4-letter species code and plot elements indicates the species’ guild designation (light green = early-successional or edge-associated guild, dark green = forest-interior guild, teal = forest-gap guild, and orange = forest generalist guild).

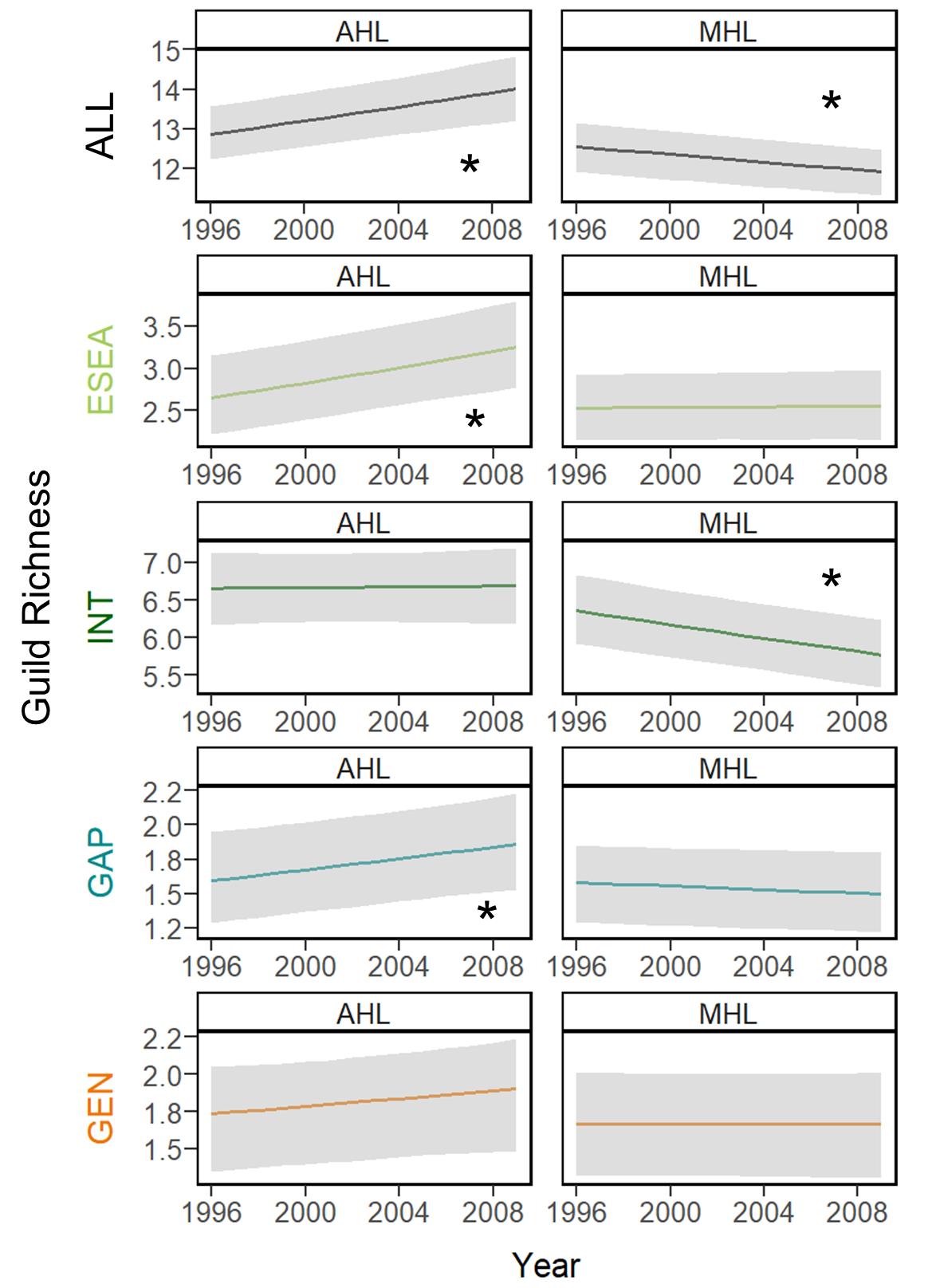
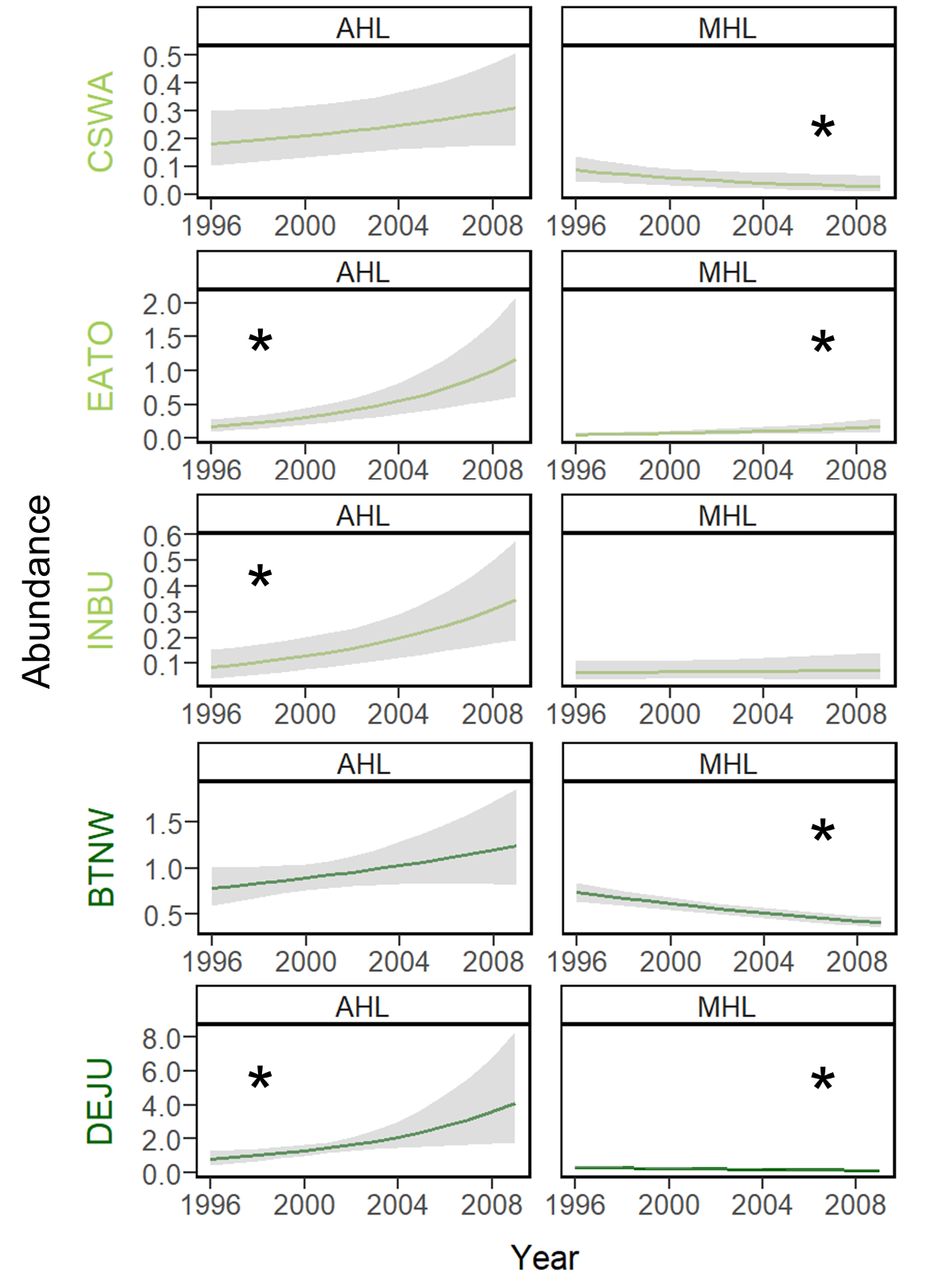


Figure 8. Plots of the change over time in overall species richness (ALL) and guild (ESEA = early-successional / edge-associated, INT = forest-interior, GAP = forest-gap, and GEN = forest generalist) richness (see Appendix A for guild designations and associated forest songbird species) within an actively harvested landscape (AHL) and minimally harvested landscape (MHL). An asterisk indicates a significant trend, where the 95% credible interval of the effective slope coefficient for year does not overlap 0.





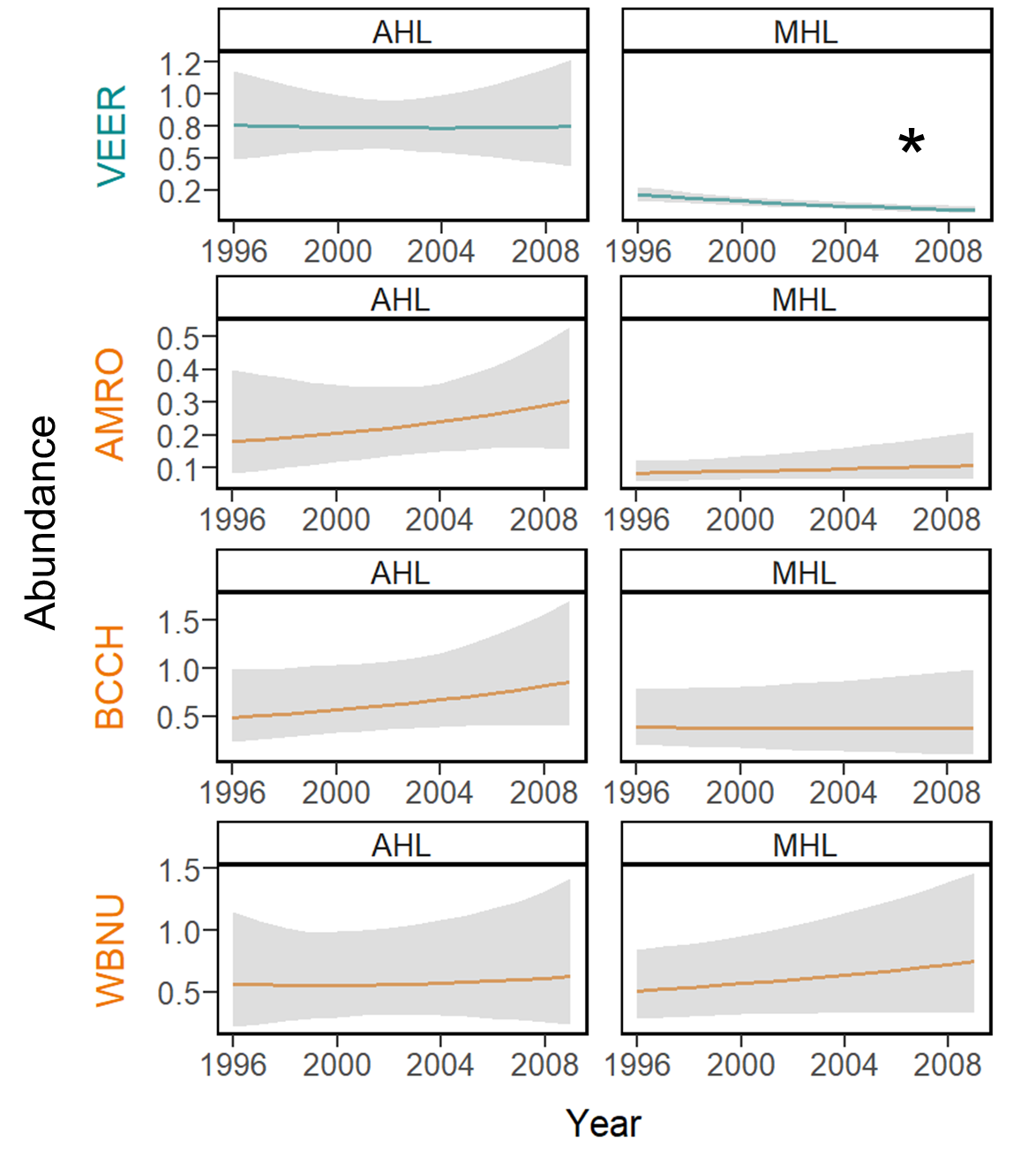
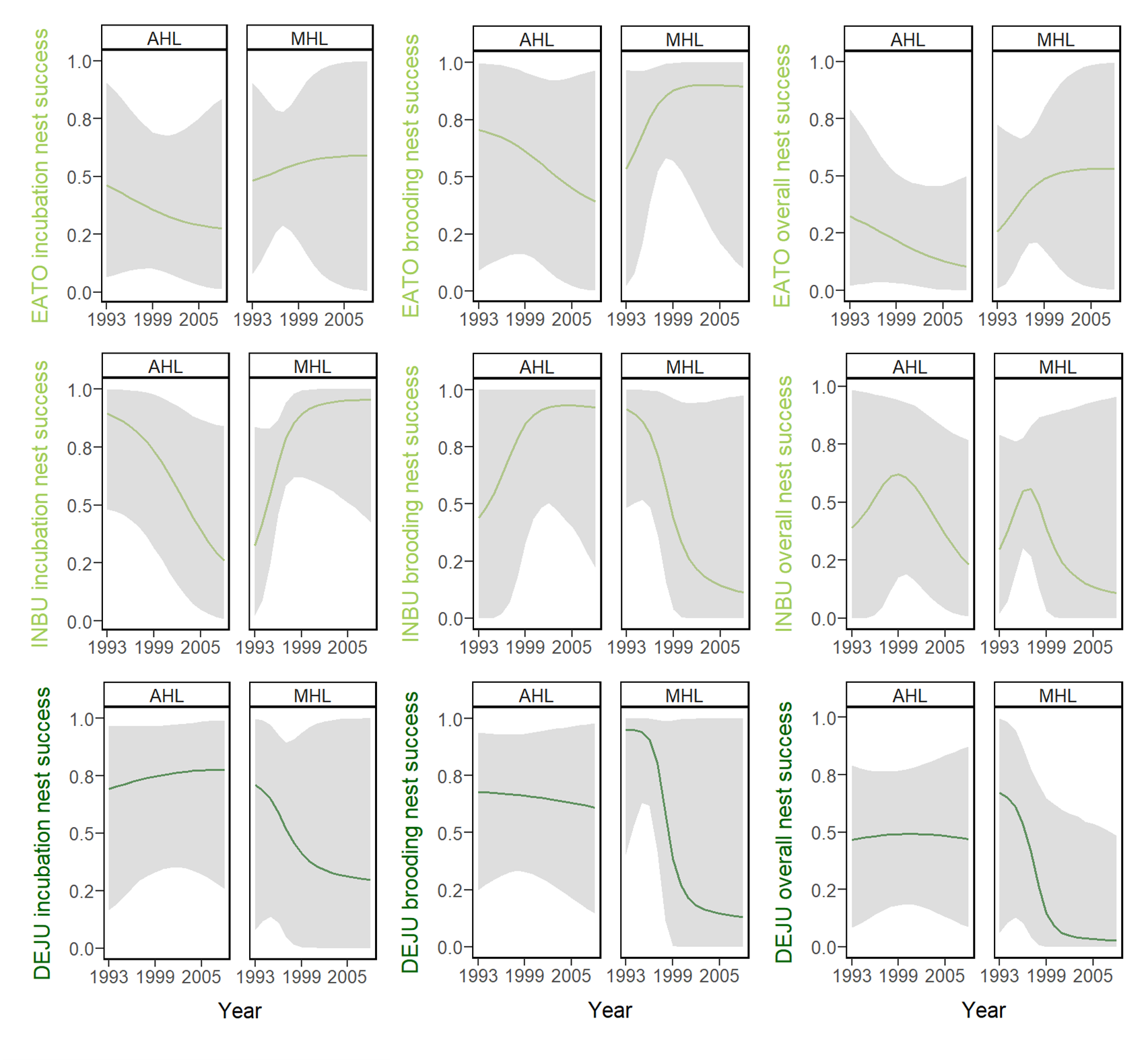


Figure 9. Plots of the change over time in focal songbird species abundance (see Table 1 for species codes) within an actively harvested landscape (AHL) and minimally harvested landscape (MHL). Color of the 4-letter species code and plot elements indicates the species’ guild designation (light green = early-successional or edge-associated guild, dark green = forest-interior guild, teal = forest-gap guild, and orange = forest generalist guild). An asterisk indicates a significant trend, where the 95% credible interval of the effective slope coefficient for year does not overlap 0.



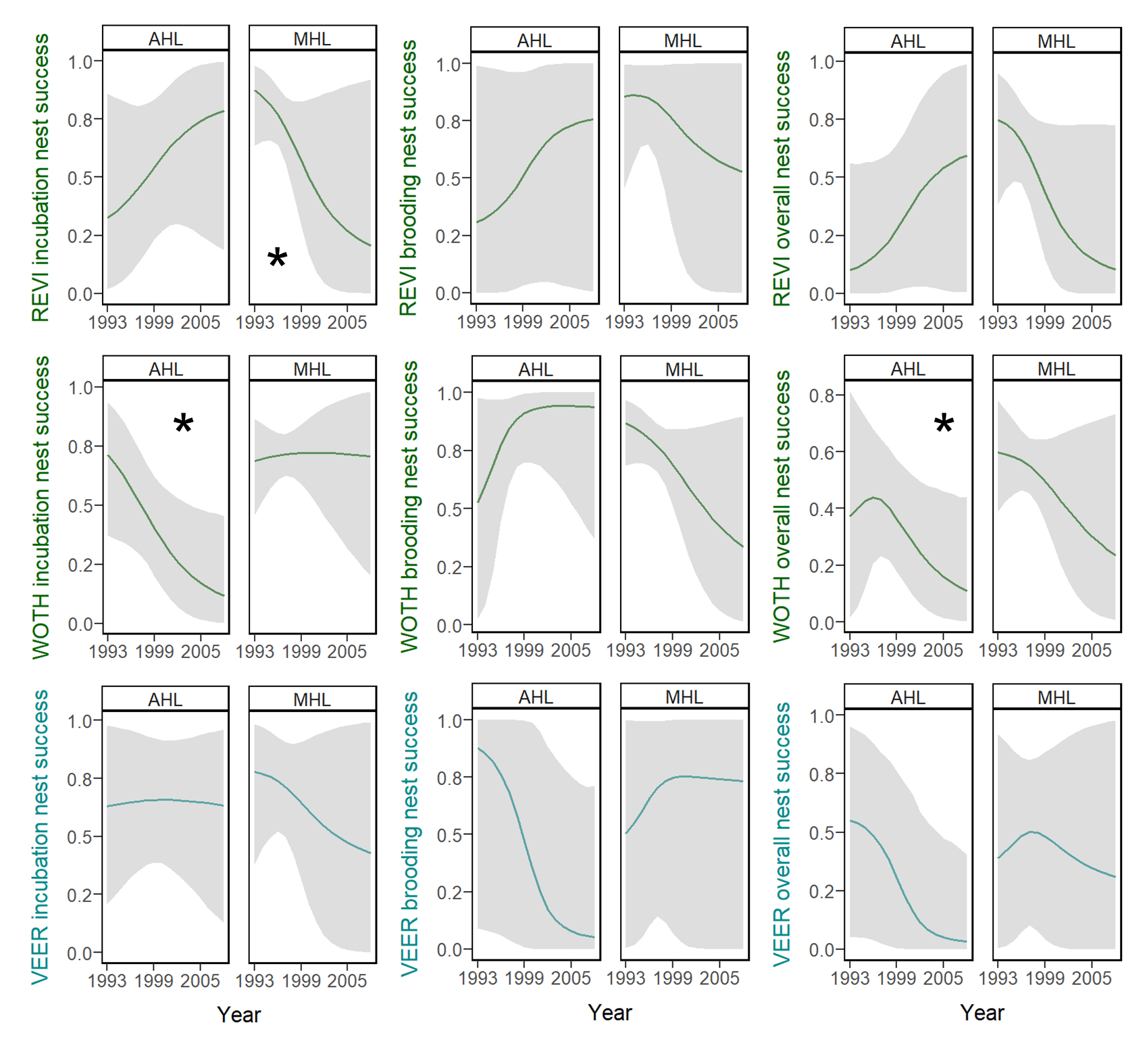


Figure 10. Plots of the change over time in focal songbird species nest success (see Table 1 for species codes) during the incubation period, brooding period, and overall nesting period within an actively harvested landscape (AHL) and minimally harvested landscape (MHL). Color of the 4-letter species code and plot elements indicates the species’ guild designation (light green = early-successional or edge-associated guild, dark green = forest-interior guild, and teal = forest-gap guild). An asterisk indicates a significant trend, where the 95% credible interval of the effective slope coefficient for year does not overlap 0.

**APPENDICES**

**Appendix A**

Table of the 62 passerine and near-passerine species considered in the guild richness analyses.

Table A1. List of the common name, scientific name, 4-letter species code, relative frequency, taxonomic family, habitat-related guild designation, and focal species status of all 62 passerine and near-passerine 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 in the study. The habitat-related guild designation indicates the primary breeding habitat of the species, such that: species in the early-successional / 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** | **Focal Species** |
| Chestnut-sided Warbler  (*Setophaga pensylvanica*) | CSWA | 600 | Parulidae | ESEA | 1 |
| Eastern Towhee  (*Pipilo erythrophthalmus*) | EATO | 718 | Passerellidae | ESEA | 1 |
| Indigo Bunting  (*Passerina cyanea*) | INBU | 589 | Cardinalidae | ESEA | 1 |
| American Goldfinch  (*Spinus tristis*) | AMGO | 89 | Fringillidae | ESEA | 0 |
| Brown-headed Cowbird  (*Molothrus ater*) | BHCO | 163 | Icteridae | ESEA | 0 |
| Blue-winged Warbler  (*Vermivora cyanoptera*) | BWWA | 110 | Parulidae | ESEA | 0 |
| Carolina Wren  (*Thryothorus ludovicianus*) | CARW | 14 | Troglodytidae | ESEA | 0 |
| Cedar Waxwing  (*Bombycilla cedrorum*) | CEDW | 216 | Bombycillidae | ESEA | 0 |
| Chipping Sparrow  (*Spizella passerina*) | CHSP | 40 | Passerellidae | ESEA | 0 |
| Common Yellowthroat  (*Geothlypis trichas*) | COYE | 60 | Parulidae | ESEA | 0 |
| Eastern Phoebe  (*Sayornis phoebe*) | EAPH | 16 | Tyrannidae | ESEA | 0 |

Table A1. Continued.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Common Name**  **(*Scientific Name*)** | **Species Code** | **Relative Frequency** | **Taxonomic Family** | **Guild** | **Focal Species** |
| Field Sparrow  (*Spizella pusilla*) | FISP | 34 | Passerellidae | ESEA | 0 |
| Gray Catbird  (*Dumetella carolinensis*) | GRCA | 132 | Mimidae | ESEA | 0 |
| Mourning Dove  (*Zenaida macroura*) | MODO | 17 | Columbidae | ESEA | 0 |
| Mourning Warbler  (*Geothlypis philadelphia*) | MOWA | 42 | Parulidae | ESEA | 0 |
| Northern Cardinal  (*Cardinalis cardinalis*) | NOCA | 24 | Cardinalidae | ESEA | 0 |
| Song Sparrow  (*Melospiza melodia*) | SOSP | 75 | Passerellidae | ESEA | 0 |
| Yellow-billed Cuckoo  (*Coccyzus americanus*) | YBCU | 64 | Cuculidae | ESEA | 0 |
| Black-throated Green Warbler  (*Setophaga virens*) | BTNW | 2458 | Parulidae | INT | 1 |
| Dark-eyed Junco  (*Junco hyemalis*) | DEJU | 1719 | Passerellidae | INT | 1 |
| Red-eyed Vireo  (*Vireo olivaceus*) | REVI | 3135 | Vireonidae | INT | 1 |
| Wood Thrush  (*Hylocichla mustelina*) | WOTH | 610 | Turdidae | INT | 1 |
| Acadian Flycatcher  (*Empidonax virescens*) | ACFL | 708 | Tyrannidae | INT | 0 |
| Black-and-white Warbler  (*Mniotilta varia*) | BAWW | 641 | Parulidae | INT | 0 |
| Blackburnian Warbler  (*Setophaga fusca*) | BLBW | 608 | Parulidae | INT | 0 |
| Black-throated Blue Warbler  (*Setophaga caerulescens*) | BTBW | 1162 | Parulidae | INT | 0 |
| Blue-headed Vireo  (*Vireo solitarius*) | BHVI | 1636 | Vireonidae | INT | 0 |
| Brown Creeper  (*Certhia americana*) | BRCR | 150 | Certhiidae | INT | 0 |
| Canada Warbler  (*Cardellina canadensis*) | CAWA | 558 | Parulidae | INT | 0 |
| Golden-crowned Kinglet  (*Regulus satrapa*) | GCKI | 437 | Regulidae | INT | 0 |
| Hairy Woodpecker  (*Leuconotopicus villosus*) | HAWO | 318 | Picidae | INT | 0 |
| Hermit Thrush  (*Catharus guttatus*) | HETH | 384 | Turdidae | INT | 0 |

Table A1. Continued.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Common Name**  **(*Scientific Name*)** | **Species Code** | **Relative Frequency** | **Taxonomic Family** | **Guild** | **Focal Species** |
| Least Flycatcher  (*Empidonax minimus*) | LEFL | 71 | Tyrannidae | INT | 0 |
| Magnolia Warbler  (*Setophaga magnolia*) | MAWA | 1153 | Parulidae | INT | 0 |
| Ovenbird  (*Seiurus aurocapilla*) | OVEN | 788 | Parulidae | INT | 0 |
| Pileated Woodpecker  (*Dryocopus pileatus*) | PIWO | 168 | Picidae | INT | 0 |
| Pine Warbler  (*Setophaga pinus*) | PIWA | 79 | Parulidae | INT | 0 |
| Purple Finch  (*Haemorhous purpureus*) | PUFI | 35 | Fringillidae | INT | 0 |
| Red-breasted Nuthatch  (*Sitta canadensis*) | RBNU | 198 | Sittidae | INT | 0 |
| Rose-breasted Grosbeak  (*Pheucticus ludovicianus*) | RBGR | 443 | Cardinalidae | INT | 0 |
| Scarlet Tanager  (*Piranga olivacea*) | SCTA | 1084 | Cardinalidae | INT | 0 |
| Swainson's Thrush  (*Catharus ustulatus*) | SWTH | 126 | Turdidae | INT | 0 |
| Winter Wren  (*Troglodytes hiemalis*) | WIWR | 541 | Troglodytidae | INT | 0 |
| Worm-eating Warbler  (*Helmitheros vermivorum*) | WEWA | 237 | Parulidae | INT | 0 |
| Yellow-rumped Warbler  (*Setophaga coronata*) | YRWA | 83 | Parulidae | INT | 0 |
| American Redstart  (*Setophaga ruticilla*) | AMRE | 568 | Parulidae | GAP | 1 |
| Cerulean Warbler  (*Setophaga cerulea*) | CERW | 125 | Parulidae | GAP | 1 |
| Hooded Warbler  (*Setophaga citrina*) | HOWA | 580 | Parulidae | GAP | 1 |
| Veery  (*Catharus fuscescens*) | VEER | 1070 | Turdidae | GAP | 1 |
| Eastern Wood-Pewee  (*Contopus virens*) | EAWP | 314 | Tyrannidae | GAP | 0 |
| Great-crested Flycatcher  (*Myiarchus crinitus*) | GCFL | 90 | Tyrannidae | GAP | 0 |
| Northern Parula  (*Setophaga americana*) | NOPA | 113 | Parulidae | GAP | 0 |
| Yellow-throated Vireo  (*Vireo flavifrons*) | YTVI | 44 | Vireonidae | GAP | 0 |

Table A1. Continued.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Common Name**  **(*Scientific Name*)** | **Species Code** | **Relative Frequency** | **Taxonomic Family** | **Guild** | **Focal Species** |
| American Robin  (*Turdus migratorius*) | AMRO | 533 | Turdidae | GEN | 1 |
| Black-capped Chickadee  (*Poecile atricapillus*) | BCCH | 702 | Paridae | GEN | 1 |
| White-breasted Nuthatch  (*Sitta carolinensis*) | WBNU | 449 | Sittidae | GEN | 1 |
| Blue-gray Gnatcatcher  (*Polioptila caerulea*) | BGGN | 147 | Polioptilidae | GEN | 0 |
| Downy Woodpecker  (*Picoides pubescens*) | DOWO | 206 | Picidae | GEN | 0 |
| Northern Flicker  (*Colaptes auratus*) | NOFL | 134 | Picidae | GEN | 0 |
| Red-bellied Woodpecker  (*Melanerpes carolinus*) | RBWO | 51 | Picidae | GEN | 0 |
| Tufted Titmouse  (*Baeolophus bicolor*) | TUTI | 195 | Paridae | GEN | 0 |
| Yellow-bellied Sapsucker  (*Sphyrapicus varius*) | YBSA | 24 | Picidae | GEN | 0 |

**Appendix B**

JAGS model code for the guild richness analyses.

model {

### PRIORS

# COMMUNITY-LEVEL MODEL PARAMETERS (OCCUPANCY)

community.occupancy.a ~ dlogis(0,1) #this assumes a logistic prior

community.occupancy.tau ~ dgamma(0.1, 0.1)

# COMMUNITY-LEVEL MODEL PARAMETERS (DETECTION)

community.detection.b ~ dlogis(0,1) #this assumes a logistic prior

community.detection.tau ~ dgamma(0.1, 0.1)

# COMMUNITY-LEVEL PARAMETERS FOR SITE COVARIATE SLOPE COEFFICIENTS

for (sitecov in 1:n.sitecovs) {

mu.alpha[sitecov] ~ dnorm(0, 0.01)

tau.alpha[sitecov] ~ dgamma(0.1, 0.1)

}

# COMMUNITY-LEVEL PARAMETERS FOR DETECTION COVARIATE SLOPE COEFFICIENTS

for (detcov in 1:n.detcovs) {

mu.beta[detcov] ~ dnorm(0, 0.01)

tau.beta[detcov] ~ dgamma(0.1, 0.1)

}

# SPECIES-SPECIFIC PRIORS FROM THE COMMUNITY-LEVEL PRIOR DISTRIBUTIONS

for (species in 1:n.species) {

# INTERCEPTS

alpha0[species] ~ dnorm(community.occupancy.a, community.occupancy.tau)

beta0[species] ~ dnorm(community.detection.b, community.detection.tau)

# SLOPE COEFFICIENTS FOR SITE COVARIATES

for (sitecov in 1:n.sitecovs) {

alpha[species, sitecov] ~ dnorm(mu.alpha[sitecov],

tau.alpha[sitecov])

}

# RANDOM SITE EFFECT

tau.rse[species] ~ dgamma(0.1, 0.1)

for (site in 1:n.sites) {

random.site.effect[species, site] ~ dnorm(alpha0[species],

tau.rse[species])

}

# SLOPE COEFFICIENTS FOR DETECTION COVARIATES

for (detcov in 1:n.detcovs) {

beta[species, detcov] ~ dnorm(mu.beta[detcov], tau.beta[detcov])

}

# RANDOM OBSERVER EFFECT

tau.roe[species] ~ dgamma(0.1, 0.1)

for (observer in 1:n.observers) {

random.observer.effect[species, observer] ~ dnorm(beta0[species],

tau.roe[species])

}

}

# NOTES: Loop over all species.

# PARAMETERS FOR IMPUTATION OF DETECTION COVARIATES

# WIND CODE

wind.prob ~ dbeta(1, 1)

# SKY CODE

sky.prob ~ dbeta(1, 1)

### LIKELIHOOD

# IMPUTATION OF DETECTION COVARIATES

for (site in 1:n.sites){

for (year in 1:n.years[site]) {

for (replicate in 1:n.replicates[site, year]) {

time.array[site, year, replicate] ~ dnorm(0, 1)

wind.array[site, year, replicate] ~ dbern(wind.prob)

sky.array[site, year, replicate] ~ dbern(sky.prob)

}

}

}

# NOTES: Loop over sites, years, and replicates.

for (species in 1:n.species) {

# Loop to estimate Z (true occurrence) for each species at each site

for (site in 1:n.sites){

for (year in 1:n.years[site]) {

# OCCUPANCY MODEL

logit(psi[site, year, species]) <- inprod(alpha[species,

1:n.sitecovs],

sitecov.array[site, year, 1:n.sitecovs]) +

random.site.effect[species, site]

# ESTIMATING OCCUPANCY

Z[site, year, species] ~ dbern(psi[site, year, species])

# Estimate detection of each species at each site during each

# sampling replicate

# Loop over each replicate for each site (variable number of

# replicates depending on site and year; n.visits x 2 replicates)

for (replicate in 1:n.replicates[site, year]) {

# DETECTION MODEL

logit(p[site, year, replicate, species]) <- beta[species, 1] \*

day.array[site, year, replicate] +

beta[species, 2] \*

time.array[site, year, replicate] +

beta[species, 3] \*

time.array[site, year, replicate] \* time.array[site, year, replicate] +

beta[species, 4] \*

wind.array[site, year, replicate] +

beta[species, 5] \*

sky.array[site, year, replicate] +

random.observer.effect[species,

observer.id.array[site, year, replicate]]

# ESTIMATING PROBABILITY OF DETECTION

mu.p[site, year, replicate, species] <- p[site, year,

replicate, species] \*

Z[site, year, species]

Y[site, year, replicate, species] ~ dbern(mu.p[site, year,

replicate, species])

} # end replicate loop

} #end year loop

} #end site loop

} #end species loop

### DERIVED QUANTITIES

# Loop to determine site-level richness estimates for the whole community

# and for subsets or assemblages of interest

for (site in 1:n.sites) {

for (year in 1:n.years[site]) {

site.species.richness[site, year] <- sum(Z[site, year, 1:n.species])

es.ea.guild.richness[site, year] <- inprod(Z[site, year,

1:n.species],

es.ea.guild[1:n.species])

forest.interior.guild.richness[site, year] <- inprod(Z[site, year,

1:n.species],

forest.interior.guild[1:n.species])

forest.gap.guild.richness[site, year] <- inprod(Z[site, year,

1:n.species],

forest.gap.guild[1:n.species])

generalist.guild.richness[site, year] <- inprod(Z[site, year,

1:n.species],

generalist.guild[1:n.species])

}

} #end site loop

}

**Appendix C**

JAGS model code for the focal species abundance analyses.

model {

### PRIORS

for (species in 1:n.species) {

# INTERCEPTS

alpha0[species] ~ dnorm(0, 0.01) #intercept for abundance model

beta0[species] ~ dnorm(0, 0.01) #intercept for detection model

# SLOPE COEFFICIENTS FOR SITE COVARIATES

for (alpha.index in 1:n.alphas) {

alpha[species, alpha.index] ~ dnorm(0, 0.01)

}

# RANDOM SITE EFFECT

tau.rse[species] ~ dgamma(0.01, 0.01) #for random site effects

for (site in 1:n.sites){

random.site.effect[species, site] ~ dnorm(alpha0[species],

tau.rse[species])

}

# NOTES: Loop over the number of unique sites

# SLOPE COEFFICIENTS FOR DETECTION COVARIATES

for (detcov in 1:n.detcovs) {

beta[species, detcov] ~ dnorm(0, 0.01)

}

# RANDOM OBSERVER EFFECT

tau.roe[species] ~ dgamma(0.01, 0.01)

for (observer in 1:n.observers) {

random.observer.effect[species, observer] ~ dnorm(beta0[species],

tau.roe[species])

}

}

# NOTES: Loop over each focal species.

# PARAMETERS FOR IMPUTATION OF DETECTION COVARIATES

# TIME

time.mu ~ dnorm(0, 0.01)

time.tau ~ dgamma(0.1, 0.1)

# NOTE: Normal distribution.

# WIND CODE

wind.prob ~ dbeta(1, 1)

# SKY CODE

sky.prob ~ dbeta(1, 1)

### LIKELIHOOD

# IMPUTATION OF DETECTION COVARIATES

for (site in 1:n.sites){

for (year in 1:n.years[site]) {

for (visit in 1:n.visits[site, year]) {

time.array[site, year, visit] ~ dnorm(time.mu, time.tau)

wind.array[site, year, visit] ~ dbern(wind.prob)

sky.array[site, year, visit] ~ dbern(sky.prob)

}

}

}

# NOTES: Loop over sites, years, and visits.

# ESTIMATE ABUNDANCE AND DETECTION PROBABILITY

for (species in 1:n.species) {

# Loop to estimate N (true abundance) for each species at each site

for (site in 1:n.sites) {

for (year in 1:n.years[site]) {

# ABUNDANCE MODEL

log(lambda[site, year, species]) <- alpha[species, 1] \*

sitecov.array[site, year, 1] +

alpha[species, 2] \*

sitecov.array[site, year, 2] +

alpha[species, 3] \*

sitecov.array[site, year, 3] +

alpha[species, 4] \*

sitecov.array[site, year, 4] +

alpha[species, 5] \*

sitecov.array[site, year, 4] \*

sitecov.array[site, year, 4] +

alpha[species, 6] \*

sitecov.array[site, year, 5] +

alpha[species, 7] \*

sitecov.array[site, year, 6] +

alpha[species, 8] \*

sitecov.array[site, year, 6] \*

sitecov.array[site, year, 6] +

alpha[species, 9] \*

sitecov.array[site, year, 7] +

alpha[species, 10] \*

sitecov.array[site, year, 8] +

alpha[species, 11] \*

sitecov.array[site, year, 9] +

alpha[species, 12] \*

sitecov.array[site, year, 10] +

alpha[species, 13] \*

sitecov.array[site, year, 11] +

alpha[species, 14] \*

sitecov.array[site, year, 1] \*

sitecov.array[site, year, 2] +

random.site.effect[species, site]

# sitecov.array: 1 = study area, 2 = year, 3 = elevation,

# 4 = aspect, 5 = TPI, 6 = stand age, 7 = proportion all forest,

# 8 = proportion mixed forest, 9 = proportion conifer forest,

# 10 = proportion shrub, 11 = proportion all forest within 1 km

# ESTIMATING ABUNDANCE

N[site, year, species] ~ dpois(lambda[site, year, species])

for (visit in 1:n.visits[site, year]) {

# OBSERVATION PROBABILITY

Y[site, year, visit, 1, species] ~ dbin(p[site, year, visit,

1, species],

N[site, year, species])

z[site, year, visit, 1, species] <- N[site, year, species] –

Y[site, year, visit, 1,

species]

for (i in 2:n.replicates) {

Y[site, year, visit, i, species] ~ dbin(p[site, year,

visit, i,

species],

z[site, year, visit, i-1,

species])

z[site, year, visit, i, species] <- N[site, year, species]

- sum(Y[site, year,

visit, 1:i,

species])

}

# Loop to estimate detection each species at each site

for (replicate in 1:n.replicates) {

# DETECTION MODEL

logit(p[site, year, visit, replicate, species]) <-

beta[species, 1] \* day.array[site, year, visit] +

beta[species, 2] \* time.array[site, year, visit] +

beta[species, 3] \* time.array[site, year, visit] \*

time.array[site, year, visit] +

beta[species, 4] \* wind.array[site, year, visit] +

beta[species, 5] \* sky.array[site, year, visit] +

random.observer.effect[species,

observer.id.array[site, year,

visit]]

}

# NOTES: Loop over each replicate for each site.

} # end visit loop

} # end year loop

} # end site loop

} # end species loop

}

**Appendix D**

Table of model information for overall species richness, the 4 habitat-related guild designations considered in the guild richness analyses, the 14 focal songbird species considered in the species abundance analyses, and the 6 focal songbird species considered in the species nest success analyses.

Table D1. List of the 4 habitat-related guild designations and 14 focal songbird species (see Table 1 for species codes), with corresponding information for the hierarchical community model (HCM), focal species abundance (FSA) models, and focal species nest success (FSNS) models that includes the number of chains (Chains), total iterations (Total), burn-in (Burn), thinning rate (Thin), and resulting posterior iterations (Posterior). The habitat-related guild designation indicates the primary breeding habitat of the species (see Appendix A for precise definitions) and includes 4 categories: early-successional / edge-associated (ESEA), forest-interior (INT), forest-gap (GAP), and forest generalist (GEN).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Guild** | **Species** | **Model** | **Chains** | **Total** | **Burn-In** | **Thin** | **Posterior** |
| ALL |  | HCM | 3 | 5,000 | 3,000 | 2 | 3,000 |
| ESEA | | HCM | 3 | 5,000 | 3,000 | 2 | 3,000 |
|  | CSWA | FSA | 3 | 21,000 | 15,000 | 3 | 6,000 |
|  | EATO | FSA | 3 | 26,000 | 20,000 | 3 | 6,000 |
|  |  | FSNS | 3 | 12,000 | 6,000 | 3 | 6,000 |
|  | INBU | FSA | 3 | 16,000 | 10,000 | 3 | 6,000 |
|  |  | FSNS | 3 | 30,000 | 21,000 | 3 | 9,000 |
| INT | | HCM | 3 | 5,000 | 3,000 | 2 | 3,000 |
|  | BTNW | FSA | 3 | 15,000 | 9,000 | 3 | 6,000 |
|  | DEJU | FSA | 3 | 15,000 | 9,000 | 3 | 6,000 |
|  |  | FSNS | 3 | 15,000 | 6,000 | 3 | 9,000 |
|  | REVI | FSA | 3 | 15,000 | 9,000 | 3 | 6,000 |
|  |  | FSNS | 3 | 12,000 | 6,000 | 3 | 6,000 |
|  | WOTH | FSA | 3 | 21,000 | 15,000 | 3 | 6,000 |
|  |  | FSNS | 3 | 9,000 | 3,000 | 3 | 6,000 |
| GAP | | HCM | 3 | 5,000 | 3,000 | 2 | 3,000 |
|  | AMRE | FSA | 3 | 16,000 | 10,000 | 3 | 6,000 |
|  | CERW | FSA | 3 | 51,000 | 45,000 | 3 | 6,000 |
|  | HOWA | FSA | 3 | 16,000 | 10,000 | 3 | 6,000 |
|  | VEER | FSA | 3 | 15,000 | 9,000 | 3 | 6,000 |
|  |  | FSNS | 3 | 12,000 | 6,000 | 3 | 6,000 |
| GEN | | HCM | 3 | 5,000 | 3,000 | 2 | 3,000 |
|  | AMRO | FSA | 3 | 39,000 | 30,000 | 3 | 9,000 |
|  | BCCH | FSA | 3 | 26,000 | 20,000 | 3 | 6,000 |
|  | WBNU | FSA | 3 | 39,000 | 30,000 | 3 | 9,000 |

**Appendix E**

JAGS model code for the focal species nest success analyses.

model {

### PRIORS

# INTERCEPTS

ISM.alpha0 ~ dnorm(0, 0.01) #intercept for incubation success model (ISM)

BSM.alpha0 ~ dnorm(0, 0.01) #intercept for brooding success model (BSM)

# SLOPE COEFFICIENTS FOR SITE COVARIATES

for (alpha.index in 1:n.alphas) {

ISM.alpha[alpha.index] ~ dnorm(0, 0.01) #for incubation success model

BSM.alpha[alpha.index] ~ dnorm(0, 0.01) #for brooding success model

}

# RANDOM PLOT EFFECT

ISM.tau.rpe ~ dgamma(0.01, 0.01) #for incubation success model

BSM.tau.rpe ~ dgamma(0.01, 0.01) #for brooding success model

for (nest.plot in 1:n.nest.plots){

ISM.random.plot.effect[nest.plot] ~ dnorm(ISM.alpha0, ISM.tau.rpe)

BSM.random.plot.effect[nest.plot] ~ dnorm(BSM.alpha0, BSM.tau.rpe)

}

# NOTES: Loop over the number of nest search plots

### LIKELIHOOD

for (nest in 1:n.nests){

Y[nest, 1] ~ dbern(p.incubation[nest])

Y[nest, 2] ~ dbern(p.brooding[nest] \* Y[nest, 1])

# NOTE: probability of nest success during brooding period is

# conditional on nest success during incubation period

logit(p.incubation[nest]) <- ISM.alpha[1] \* sitecov.matrix[nest, 1] +

ISM.alpha[2] \* sitecov.matrix[nest, 2] +

ISM.alpha[3] \* sitecov.matrix[nest, 3] +

ISM.alpha[4] \* sitecov.matrix[nest, 4] +

ISM.alpha[5] \* sitecov.matrix[nest, 1] \*

sitecov.matrix[nest, 2] +

ISM.random.plot.effect[nest.plot.index[nest]]

# sitecov.matrix: 1 = study area, 2 = year, 3 = nest search plot with

# harvest history, 4 = nest search plot in mature forest

logit(p.brooding[nest]) <- BSM.alpha[1] \* sitecov.matrix[nest, 1] +

BSM.alpha[2] \* sitecov.matrix[nest, 2] +

BSM.alpha[3] \* sitecov.matrix[nest, 3] +

BSM.alpha[4] \* sitecov.matrix[nest, 4] +

BSM.alpha[5] \* sitecov.matrix[nest, 1] \*

sitecov.matrix[nest, 2] +

BSM.random.plot.effect[nest.plot.index[nest]]

# sitecov.matrix: 1 = study area, 2 = year, 3 = nest search plot with

# harvest history, 4 = nest search plot in mature forest

p.overall[nest] <- p.incubation[nest] \* p.brooding[nest]

} # end nest loop

}