**CHAPTER 3**

**Multi-species avian occupancy of wildlife openings in a heavily forested landscape**

**Introduction**

**Wildlife use of forest openings**

In forested landscapes and extensive forest stands within the eastern United States, openings (i.e., open patches of area that do not contain mature forest) can serve as habitat and provide food resources for disturbance-dependent, early-successional forest-associated wildlife species. Insects and herbaceous vegetation (i.e., grasses and forbs), which is generally more nutritious and digestible than woody plants, can be more abundant in these openings than beneath a forest canopy (Blake and Hoppes 1986, Martin and Karr 1986, Shure and Phillips 1991). Although forest openings do occur naturally (Askins 2001), wildlife openings (i.e., open or early-successional forest habitat created incidentally or purposefully for target wildlife species) tend to be specifically created and maintained by land managers through timber harvest, grazing, or other active forest management strategies. New wildlife openings are often created along or from log decks, log roads, and utility rights-of-way. To encourage and maintain the herbaceous community, managers use a variety of management actions, including mowing, liming, fertilizing, planting, and burning. In most cases, the purpose of these wildlife openings is to provide habitat specifically for game species (Overcash et al. 1989), including 3 popular game birds --- wild turkeys (*Meleagris gallopavo*), ruffed grouse (*Bonasa umbellus*), and American woodcocks (*Scolopax minor*).

Wild turkeys, ruffed grouse, and American woodcocks vary slightly in their forested habitat preferences, but all three species are known to use herbaceous wildlife openings for mating displays, nesting, brood-rearing, or feeding. Wild turkeys tend to reside in open deciduous or mixed forests with interspersed clearings. Wildlife openings are commonly maintained to improve forest habitat for wild turkeys (Healy and Nenno 1983), as openings can be important to nest site selection and poult feeding activity (Healy 1985, Byrne and Chamberlain 2013). Ruffed grouse and American woodcocks are both associated with early-successional, shrubby deciduous forests (Dessecker and McAuley 2001, Endrulat et al. 2005). Ruffed grouse tend to rely on young stands of trees for both cover and food, with wildlife openings providing brood cover and food for their chicks (Bump et al. 1947, Sharp 1963). American woodcocks use forest openings for mating displays in the spring and roosting in the summer (Roboski and Causey 1981). They also use wildlife openings and other open areas as nocturnal habitat (Straw et al. 1994, Krementz et al. 1995). It is widely believed that the loss of early-successional forest habitat is a primary reason for declines in American woodcock recruitment and in overall population status (Kelley et al. 2008).

Despite plenty of evidence that wild turkeys, ruffed grouse, and American woodcocks use wildlife openings, there is a general lack of published studies for each species that explicitly focus on their responses to a combination of local habitat attributes, size, management, or landscape context of wildlife openings (e.g., Shartell 2016). Results from the few existing studies suggest that local habitat attributes and management may have the greatest influence on species-specific use, but opening size was also mentioned frequently. For instance, wild turkey broods generally benefit from active management (e.g., mowing) that enhances the abundance of herbaceous vegetation in areas <0.5 ha (Healy and Nenno 1983). Similarly, ruffed grouse select for brood habitat with high amounts of herbaceous groundcover, which can be achieved by specific management actions (Jones et al. 2008). In the Cherokee National Forest in Tennessee, management of logging roads converted to linear wildlife openings resulted in greater arthropod availability to ruffed grouse chicks than logging roads not managed for wildlife (Hollifield and Dimmick 1995). In the same study, the abundance of herbaceous vegetation was more important in determining arthropod availability than the successional age of clearcuts. However, forest succession played a role in the amount of herbaceous vegetation and ruffed grouse brood use in 0.1–0.4 ha openings in Pennsylvania (Sharp 1963). Maintenance of 0.1–0.8 ha permanent openings is recommended for food production for ruffed grouse in Manistee National Forest in Michigan (Berner and Gysel 1969), but in central hardwood forests, Thompson and Dessecker (1997) suggested that ruffed grouse would benefit most from 2–16 ha patches of regenerating forest, with interspersion of habitats. For American woodcocks, habitat structure is important in the selection of display sites; opening size and distance to the nearest opening may also have influence (Gutzwiller et al. 1983). Regular disturbance (e.g., cutting trees) is likely important to maintain that structure and appears to increase American woodcock use of clearcut aspen areas (Hale and Gregg 1976). To best benefit American woodcocks, McAuley et al. (1996) and Masse et al. (2014) recommend actively maintaining >25% of the landscape as early-successional habitat, with approximately eight >0.2-ha wildlife openings per 40 ha.

In addition to game birds, wildlife openings potentially benefit songbird species associated with grasslands, shrub-scrub habitats, and disturbed areas in forested habitats, a habitat guild that has experienced widespread population declines in eastern North America (Hunter et al. 2001, DeGraaf and Yamasaki 2003). However, several attributes of wildlife openings, including size, time since disturbance, and treatment regime, may affect their suitability as early-successional bird habitat. In a study of the effects of group-selection opening size on breeding bird habitat use in a bottomland forest, species richness in 0.06-, 0.13-, 0.26-, and 0.5-ha openings increased as opening size increased, due to the increased use of larger openings by early-successional and edge-associated species (Moorman and Guynn, Jr. 2015). Shrubland bird density may also be related to patch size (Lehnen and Rodewald 2009). To best manage for early-successional forest and shrubland birds, DeGraaf and Yamasaki (2003) recommend that group selection and patch cuts should be at least 0.8 ha, while Chandler et al. (2009) suggest a minimum size of 1.2 ha and Shake et al. (2012) propose >5.5 ha. Opening size may also determine the magnitude of corresponding effects on forest-interior songbirds. One study reported that openings of 0.02–0.04 ha had a minor effect on the forest bird community (Robinson and Robinson 1999), while another found that 0.4-ha clearcut openings resulted in the movement of several forest-interior species away from openings and subsequently decreased abundance in and adjacent to openings (Germaine et al. 1997). In addition to opening size, time since disturbance likely influences breeding songbird abundance and community composition in wildlife openings. Populations of gap-dependent species reached a peak 2–3 years after the creation of 0.02–0.04 ha openings but declined to population levels comparable to those in uncut forest after 5–10 years (Robinson and Robinson 1999). Different successional stages are generally associated with distinct vegetation characteristics and thus local habitat attributes, such as vegetation structure and shrub density, which has been shown to be a primary factor affecting abundance of early-successional bird species (Bulluck and Buehler 2006, Askins et al. 2007, King et al. 2009, McDermott et al. 2011). Management regime (e.g., burning, mowing) may also affect shrubland bird abundance (Chandler et al. 2009), with an optimum post-treatment time of 10–15 years suggested by Schlossberg and King (2009) for shrubland birds in the eastern United States. Although very few studies have addressed the effect of landscape context on use of wildlife openings by early-successional bird species, landscape-level variables such as distance to the nearest opening and land cover composition within 1 km have been found to influence shrubland generalists more than shrubland specialists (Askins et al. 2007) or to have little influence (Shake et al. 2012). Despite the paucity of studies and corresponding evidence, it is likely that landscape-level factors affect avian use of wildlife openings, as they have been found to explain mature forest songbird occupancy and abundance (Villard et al. 1999, Graham and Blake 2001, Lee et al. 2002), grassland bird species richness (Hamer et al. 2006), saltmarsh bird species diversity (Shriver et al. 2004), and waterbird species richness and occurrence (Guadagnin and Maltchik 2006). Based on the effect of landscape characteristics on these other avian species and guilds, I would expect occupancy and species richness of early-successional bird species in a wildlife opening in a landscape with multiple other wildlife openings nearby to be higher than in a landscape with a single isolated wildlife opening.

Use of wildlife openings may not be restricted to early-successional and shrubland birds. Certain songbirds that breed in mature forest shift their habitat use to early-successional areas after nesting but before migration (i.e., during the post-breeding period). Rappole and Ballard (1987) were perhaps the first to report both post-breeding adult and juvenile forest birds moving into early-successional habitats. Since then, a number of mist-netting studies have found that forest-interior songbird species are frequently captured in regenerating clearcuts during the post-breeding season (e.g., Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006, McDermott and Wood 2010, Streby et al. 2011, Chandler et al. 2012, Major and Desrochers 2012, Stoleson 2013). Radio-tagging of ovenbirds (*Seiurus aurocapilla*), wood thrushes (*Hylocichla mustelina*), and scarlet tanagers (*Piranga olivacea*) have also shown that fledglings and adults of these species tend to move into edge and early-successional habitats after breeding in mature forest (Anders et al. 1998, Vega Rivera et al. 1998, 2003, King et al. 2006, Dellinger 2007). Contrary to formerly prevailing assumptions, a subset of forest-interior birds are present in significantly higher densities in early-successional habitats than in surrounding mature forest during the post-breeding season (Pagen et al. 2000, Bowen et al. 2007, Chandler et al. 2012). Thus, early-successional habitat within forested landscapes, such as wildlife openings, may benefit post-breeding forest-interior species in addition to early-successional and edge-associated species (Anders et al. 1998, Pagen et al. 2000, Vitz and Rodewald 2006, Chandler et al. 2012). Supporting this recommendation, forest-interior birds captured in regenerating clearcuts were more advanced in molt and in better condition than those captured in forests (Stoleson 2013). In addition, evidence suggests that food availability is equivalent or greater in early-successional habitats than in mature forest (Keller et al. 2003, Vitz and Rodewald 2006), and vertical structure may provide protection from predators (Vitz and Rodewald 2007). Specifically, post-breeding forest-interior songbirds achieve the highest densities in early-successional habitats with tall, complex vegetation structure (Chandler et al. 2012). However, the shape and size of wildlife openings may also affect use by post-breeding songbirds. One study found that post-breeding individuals avoid the edges and appear to prefer smaller regenerating clearcuts (4–9 ha) over large clearcuts (13–18 ha) (Vitz and Rodewald 2006). Furthermore, post-breeding early-successional, edge-associated, and forest-interior species may exhibit habitat guild-specific responses to wildlife openings created with timber harvest, based on size, amount of edge, and retained basal area (McDermott and Wood 2011). Overall, these handful of studies on the post-breeding songbird use of forest and wildlife openings emphasize the importance of size and vegetation structure, but they fail to address the potential effects of management or landscape context, despite the value of examining both patch- and landscape-level characteristics (Mazerolle and Villard 1999).

**Knowledge gap**

Although wildlife openings are primarily meant to provide habitat and food resources for disturbance-dependent, early-successional game species, they may also benefit a myriad of forest-associated avifauna, including species of high regional conservation concern (Chandler et al. 2009). Yet those benefits are likely dependent upon certain wildlife opening attributes and vary among species and guilds. A research question that has been frequently addressed is the size of an opening needed to provide habitat for early-successional birds (Askins et al. 2007). However, there is a clear knowledge gap concerning which other wildlife opening attributes are important considerations for holistic management for entire avian communities. Most studies consider a limited number of local-scale characteristics of openings created incidentally by timber harvest operations and their corresponding effects on species-specific and, to a lesser extent, community-level responses of breeding songbirds. Only a handful of additional studies focus on the use of openings by game birds (e.g., Sharp 1963, Healy and Nenno 1983, Shartell 2016) or post-breeding songbirds (e.g., Chandler et al. 2012) but never both simultaneously and rarely in conjunction with breeding songbirds. Instead of approaching the question of management piecemeal by season, species, guild, taxon group, or opening characteristic, we need to comprehensively investigate how to optimize wildlife openings to attract a full spectrum of avian species throughout spring and summer, maximize richness across guilds and taxa groups, and minimize negative effects to the forest-interior breeding bird community. Understanding the sympatric use of wildlife openings by game birds, breeding songbirds, and post-breeding songbirds in response to site-level and landscape-level wildlife opening attributes is critical for land managers to design and maintain wildlife openings that simultaneously support game bird populations and promote a diverse suite of songbirds.

**Purpose, objectives, and hypotheses**

The purpose of this research was to identify the characteristics of wildlife openings that support target game birds and a diversity of breeding and post-breeding songbirds. My objectives were to quantify how wildlife opening attributes relate to multi-species occupancy of 3 game birds (wild turkey, ruffed grouse, and American woodcock) and songbird guild richness during the breeding and post-breeding seasons.

In this study, I first tested competing hypotheses to determine whether local habitat attributes, opening size, management, landscape context, or a combination of site-level and landscape-level factors best explained game bird species occupancy of wildlife openings (Table 1). After identifying which wildlife opening attributes were important for the 3 target game bird species, I then evaluated the effects of those variables on breeding and post-breeding songbird communities within the wildlife openings and on breeding songbird communities in mature forest habitat adjacent to the wildlife openings. To holistically assess impacts on songbird diversity, I considered 4 habitat guilds (Appendix A): early-successional and edge-associated species, forest-interior species, forest-gap species, and forest generalist species.

**METHODS**

**Study area**

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

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

**Sampling design**

There are records of ~2,200 individual openings within the MNF (Figure 2), ranging in size from 0.01 ha former log landings to 113 ha former mine lands and ranging in shape from linear cuts to sprawling grazing allotments. A subset of these openings, generally 0.02–20 ha (mean = 2.0 ha), were created or managed to benefit target wildlife species. Within the past several decades, many of the wildlife openings were constructed either opportunistically or systematically following timber harvest, gas well activity, or other human disturbances, and then subsequently managed or maintained by MNF or West Virginia Division of Natural Resources staff. The purpose of the wildlife openings is generally to provide habitat to regionally important game species associated with early-successional or open habitat, including white-tailed deer (*Odocoileus virginianus*), wild turkey, and American woodcock. The majority (>96%) of these wildlife openings are ≤5 ha in size, and approximately 80% of the openings are actively maintained or have a history of maintenance. Active management of wildlife openings consists primarily of mowing, although applying herbicides, liming, fertilizing, planting, and grazing are also implemented in select wildlife openings. The density of wildlife openings within the landscape varies, but many wildlife openings are located <1 km from the nearest neighboring opening.

For this study, I used stratified random sampling based on size and maintenance status to select a total of 335 wildlife openings as sampling sites (Figure 2). They ranged in size from 0.04 ha to 21.53 ha (mean = 1.56 ha), with 236 small (<1 ha) wildlife openings, 71 mid-sized (1–5 ha) wildlife openings, and 28 large (>5 ha) wildlife openings. Of those, 76 of the small wildlife openings, 28 of the mid-sized wildlife openings, and 18 of the large wildlife openings were not maintained or had no history of maintenance.

**Focal game bird species and songbird guild designations**

Taking land manager goals into consideration, my research primarily focused on the 3 regionally important upland game bird species in the Central Appalachians region: wild turkey, ruffed grouse, and American woodcock. To assess additional impacts on songbird diversity, I considered a subset of passerine species. Although a total of 116 avian species were detected across all surveys, I limited the richness analyses to 66 species (see Appendix A for full list) in Order Passeriformes with breeding ranges that encompassed the study area and that had <5 detections. I also excluded wetland-associated songbirds because they were incidental to the focal habitat types, as well as corvids and waterthrushes because they are not well-sampled with breeding songbird point count surveys.

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

**Field data collection**

*In-person sampling methods for game bird species*

I conducted in-person game bird surveys at 65 wildlife openings in 2019 and 251 wildlife openings in 2021; sampling occurred between 15 April and 10 May to overlap with the peak courtship / breeding period for the 3 game bird species (Schumacher 2002, US Fish and Wildlife Service 2011). For the in-person game bird surveys, I randomly generated a single sampling point within each wildlife opening that was >80 m from the forest edge (if possible); for the smallest wildlife openings (<1 ha), the point was located in the approximate center of the opening (Figure 3).

Wild turkeys and ruffed grouse were sampled simultaneously at 315 wildlife openings with repeated 10-minute morning modified drumming (Hansen et al. 2011) / gobbling surveys (Table 2). Each wildlife opening was surveyed twice during the game bird courtship period within a single sampling year (2019 or 2021). Surveys commenced at sunrise and were concluded within 4 hours after sunrise. The 10-minute survey was split into 2 equal time intervals: 0–5 minutes and >5–10 minutes. For each wild turkey or ruffed grouse, the observer noted the species and time interval(s) during which it was detected. Observers also recorded the survey date, start time, temperature, maximum wind speed, maximum ambient noise level (dB), precipitation status, and sky code. Maximum wind speed was measured with a Kestrel 1000 anemometer, and maximum ambient noise was measured with a sound level meter for 1 minute. Sky codes ranged from 0 to 4 and were adapted from the U.S. Weather Bureau and Breeding Bird Survey protocols (U.S. Geological Survey 1998) to measure general sky conditions. No surveys were conducted during mornings with moderate to heavy precipitation or consistent high wind speed (>5.8 m/s).

American woodcocks were sampled at 211 wildlife openings with a single 6-minute evening modified singing-ground survey, following the 2017 Conservation Effects Assessment Project survey protocols. Surveys began 22 minutes after sunset when the sky had <75% cloud cover and 15 minutes after sunset when the sky was overcast (≥75% cloud cover). All surveys were completed by 38 minutes after the start time. The 6-minute survey was split into 3 equal time intervals: 0–2 minutes, >2–4 minutes, and >4–6 minutes. For each American woodcock, the observer noted the time interval(s) during which it was detected. Observers also recorded the survey date, start time, temperature, maximum wind speed, maximum ambient noise level (dB), precipitation status, and sky condition (percent cloud cover). No surveys were conducted during evenings with precipitation, consistent high wind speed is high (>5.8 m/s), or temperatures below 4° C.

*Remote sampling methods for game bird species*

To increase overall detection probabilities of the 3 game bird species, I deployed game cameras and autonomous recording units (ARUs) for up to 11 days during the game bird courtship period in a total of 145 wildlife openings. Together, game cameras and ARUs can collect large amounts of comparable data to in-person surveys in a cost‐effective, efficient, and standardized manner (Digby et al. 2013, Darras et al. 2018). At each wild opening, a single game camera (Bushnell Trophy Cam HD or Reconyx Hyperfire) and a single ARU (Wildlife Acoustics SongMeter SM2+, Wildlife Acoustics SongMeter SM3+, or Wildlife Acoustics SongMeter SM4+) were set up together within 50 m of the in-person game bird survey point (Figure 3). The ARUs were attached at a height of ~1.5 m to a tree or shrub and pointed in a direction that faced the in-person game bird survey point, minimized auditory obstruction, and maximized potential auditory detections (Darras et al. 2018). Game cameras were secured to the same tree or shrub at ~40 cm above the ground. They were oriented parallel with the ground and pointed in a direction that faced the in-person game bird survey point, minimized visual obstruction, and maximized potential visual detections. For every game camera and ARU pair, I noted the type of game camera and ARU, and measured the distance (m) to the central game bird survey point.

All game cameras were equipped with an infrared flash; with highly sensitive trigger times and quick trigger times, the game cameras were able to record animals passing in front of them without the addition of bait. Each game camera was set on maximum trigger sensitivity and recorded multiple photographs per trigger, re‐triggering immediately if the animal was still in view. The ARUs were programmed to record from 3 hours before sunset to 1 hour after sunset and from 1 hour before sunrise to 6 hours after sunrise, which encompasses the time that >90% of all wild turkey gobbles occur (Colbert et al. 2015) and overlaps the in-person game bird survey time period.

*Communitywide avian point count surveys for breeding songbird species*

I conducted breeding songbird surveys between 16 May and 10 July at 63 wildlife openings in 2019, 134 wildlife openings in 2020, and 112 wildlife openings in 2021. Breeding songbirds were sampled with 10-minute unlimited radius stationary point count surveys at 2 sampling points associated with each wildlife opening --- a central point at the same location as the game bird sampling point and an adjacent forest point that was randomly generated between 150 m and 300 m from the perimeter of the wildlife opening, >100 m from any other edges or significant canopy disturbance (to avoid possible edge effects; Germaine et al. 1997, Hobson and Bayne 2000*b*), and at least 200 m from the central point (Figure 3).

Each sampling point was visited once. Surveys began within 15 minutes of sunrise and continued until approximately 4 hours after sunrise. The 10-minute survey was split into 2 equal time intervals: 0–5 minutes and >5–10 minutes. For each individual, the observer noted the species, time interval(s) during which it was detected, and distance band (≤50 m or >50 m). Observers also recorded the survey date, start time, temperature, maximum wind speed, maximum ambient noise level (dB), precipitation status, and sky code. No surveys were conducted on mornings with rain, heavy fog, or consistent high wind speed, following the guidelines of Ralph et al. (1993).

*Communitywide avian transect surveys for post-breeding songbird species*

I conducted post-breeding songbird surveys at a subset of 82 wildlife openings between 14 July and 5 August to minimize overlap with the breeding season (McDermott et al. 2011, McDermott and Wood 2011) and fall migration. Post-breeding songbirds were sampled twice with transect surveys at wildlife openings where at least 1 game bird species had been detected. Post-breeding songbirds were surveyed along 4–8 transect segments per wildlife opening (Figure 3), based on opening size (e.g., 4 for small [<1 ha] openings, 6 for mid-sized [1–5 ha] openings, and 8 for large [>5 ha] openings). To maximize spatial representation, I randomly selected locations for the start points of each transect within the wildlife opening, while ensuring a minimum distance of 15–50 m between points, based on opening size (15 m for small openings, 30 m for mid-sized openings, and 50 m for large openings).

Transect surveys started 30 minutes after sunrise and continued until ~4 hours after sunrise. A single observer walked along the segments connecting the transect start points and recorded all birds detected visually or auditorily within or along the edge of the wildlife opening, excluding individuals recorded during a previous segment to avoid double-counting birds and excluding individuals that were in the adjacent forest surrounding the wildlife opening. For each transect survey, observers also recorded the total time elapsed. Transect surveys were not conducted in inclement weather (e.g., moderate or heavy precipitation, fog) or other conditions that would limit visual and auditory observation of birds.

*Vegetation surveys*

At every sampling point, I conducted a tree plot survey and a site tube vegetation survey. During the tree plot survey, I collected data pertaining to canopy height, basal area, canopy position, and canopy cover. To measure canopy height, I used a clinometer to find the angle to the apex and base of a codominant tree and then measured the horizontal distance (m) to the base with a rangefinder. Trees were sampled using the variable radius plot method, which yields results for tree basal area and distribution that are comparable to the fixed 11.3-m radius plot method (Piqué et al. 2011). Using a Jim-Gem Cruz-All with a basal area factor of 10, I identified all tree stems that qualified for the tree plot survey and recorded the species, diameter at breast height (DBH; measured with a Biltmore stick), and canopy position for each tree. For canopy position, I used a categorical classification that separates trees into five distinct classes: suppressed, intermediate, codominant, dominant, and open growth (for trees in non-forested sites, such as wildlife openings) (Jennings et al. 1999). Forest overstory density (i.e., percent canopy cover) was measured using a spherical densiometer, taking the average count from the four cardinal directions. To measure vegetative cover and structure at the sampling points, I used the sight tube method. For these surveys, a sight tube was used to determine the presence of 4 vegetation classes (herb, shrub, sapling, tree) at 5 points located 10 m apart in each cardinal direction, resulting in systematic estimates of vegetative cover at 20 points within a 50-m radius plot. For each of the 20 points for the sight tube survey, observers recorded whether it was located within the wildlife opening or not.

**Data compilation and processing**

*Processing images from game cameras and sound files from ARUs*

Images from the game cameras were processed using eMammal software, which groups photos into sequences based on the time elapsed between photos. Trained data processing assistants recorded species, wildlife opening ID, and date detected for each photo sequence. Sound files from the ARUs were processed using RavenPro 1.6 software. I semi-automated the initial screening process and used a Band-Limited Energy Detector with specific frequency and duration parameters to produce a selection of candidate vocalizations of wild turkey and American woodcock for trained data processing assistants to confirm. For each verified detection of wild turkey or American woodcock vocalizations, data processing assistants recorded the species, wildlife opening ID, and date detected.

*Predictor data – Local habitat*

X

*Predictor data – Size and shape*

X

*Predictor data – Management*

X

*Predictor data – Landscape context*

X

Using ArcGIS software, I will calculate the following metrics: aspect, elevation, slope position, area of wildlife opening (ha), edge-to-area ratio, total area of wildlife openings or other early-successional habitat (ha) within 1 km, distance to nearest wildlife opening or other early-successional habitat (m), and juxtaposition of different opening sizes within 1 km (i.e., an index incorporating size and quantity of surrounding wildlife openings). Area and distance variables will be calculated from shapefiles provided by the WVDNR and confirmed with aerial photography. Additional predictor variables will include the age of the wildlife opening (i.e., years since creation), successional age of the wildlife opening (i.e., years since creation if unmaintained or years since maintenance if maintained), proportion of intensive harvest (i.e., clearcut) within 1 km, proportion of non-intensive harvest (i.e., shelterwood, single selection, group selection) within 1 km, proportion of no harvest within 1 km, and maintenance (none vs. mowing vs. mowing and planting vs. other). All landscape-level factors will be calculated within 1 km (Askins et al. 2007, Shake et al. 2012).

The full set of site covariates included year of data collection, latitude, elevation, 4 focal climate variables, and 4 environmental variables that were included to control for their known effects (Table 2). Latitude corresponded to the location of the sampling point. Mean elevation within 50 m of each sampling point was calculated using Shuttle Radar Topography Mission digital elevation data (Table 2). The focal climate variables consisted of mean breeding season (i.e., 15 May to 30 June) temperature during the year of data collection (hereafter mean temperature), standard deviation of mean breeding season temperature (hereafter SD temperature), and mean total breeding season precipitation during the year of data collection and during the previous year (hereafter current precipitation and previous precipitation, respectively). All climate data were calculated from PRISM Climate Group daily temperature and precipitation data (Daly et al. 2008) corresponding to 15 May through 30 June of each survey year. The 4 additional environmental variables consisted of aspect, topographic position index (TPI), dominant (i.e., occupying the greatest proportion of area within 50 m of the sampling point) forest type (deciduous, mixed, or coniferous), and proportion of any type of mature forest cover within 1 km of the sampling point. Mode aspect and mode TPI within 50 m of each sampling point were derived from Shuttle Radar Topography Mission digital elevation data. To determine the dominant forest type and proportion of forest cover, I downloaded the 2001, 2004, 2006, 2008, 2011, 2013, 2016, and 2019 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, 2008 NLCD data for surveys conducted in 2008 or 2009, 2011 NLCD data for surveys conducted in 2010–2012, 2013 NLCD data for surveys conducted in 2013 or 2014, 2016 NLCD data for surveys conducted in 2015–2017, and 2019 NLCD data for surveys conducted in 2018 or later).

**Data analysis**

*Modeling occupancy of focal game bird species*

To relate wildlife opening attributes with multi-species occupancy of a specific subset of game birds, breeding songbirds, and post-breeding songbirds (see Table 12) within wildlife openings (from which single-species occupancy can be obtained), I will model the occurrence probabilities of focal species as a function of wildlife opening attributes. I will include the three years of focal species occurrence data from game bird surveys, central point count surveys, and transect surveys in a stacked joint species distribution model, constructed in a Bayesian framework, where the focal game bird, breeding songbird, and post-breeding songbird species will serve as potentially interacting species within the model (Pollock et al. 2014). I will perform model selection with WAIC on a set of candidate models corresponding to the site-level predictor variables (Table 11) to determine which wildlife opening attributes influence the probability that the focal species occur together, as well as the marginal (single-species) occupancy of specific shrubland, edge-associated, and forest-interior species within wildlife openings during the post-breeding period.

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

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

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

*Model comparison to assess competing hypotheses*

X

*Determining importance and assessing effects of predictor variables on game bird species*

To identify predictor variables that had significant influence on at least 1 of the 3 game bird species, I assessed variable importance by looking at whether the 95% credible intervals of the slope coefficient values overlapped zero; if the 95% credible intervals did not overlap zero, the variable was considered important. I further evaluated the marginal effects of important site covariates on the 3 game bird species by plotting the estimated probability of marginal species occurrence for wild turkey, ruffed grouse, and American woodcock across the full range of the variable, while holding the other variables constant.

*Determining overall species and guild richness from hierarchical community models*

To calculate overall species richness and guild richness within each wildlife opening during the breeding and post-breeding seasons and in the adjacent forest during the breeding season, respectively, I estimated individual songbird species occupancy simultaneously in 3 hierarchical community models (see Appendix B for JAGS code) corresponding to the sampling season and survey location (Table), and then derived the corresponding sums for all species and each guild designation (Zipkin et al. 2010). I included 65 songbird species in the hierarchical community models for breeding and post-breeding songbirds within the wildlife opening and 44 songbird species in the hierarchical community model for breeding songbirds within 50 m of the adjacent forest sampling point (Appendix A).

Hierarchical community models facilitate a multi-species approach to estimating individual species occurrence probabilities (Dorazio and Royle 2005, Dorazio et al. 2006). In each hierarchical community model, occurrence *Zs,sp* was defined as a binary variable in which *Zs,sp* = 1 if species *sp* occurs at site *s*. The occurrence state was assumed to be the outcome of a Bernoulli random variable, denoted by:

*Zs,sp* ~ *Bernoulli*(*Ψs,sp*)

where *Ψs,sp*is the probability that species *sp* occurs at site *s*. I further used a logit link to model linear relationships between occurrence probability (*Ψs,sp*) and 7–15 biologically relevant site covariates (Table). All continuous site covariates were centered and scaled prior to analysis. In addition, because my data included stacked observations across multiple years, each of the hierarchical community models also incorporated a random year effect.

Given the observed data *Ys,r,sp*, where *r* is a survey replicate, I defined the detection model for species *sp* at site *s* during replicate *r* as:

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

Where *ps,y,r,sp* is the detection probability of species *sp* for the *r*th replicate at site *s*, given that species *sp* is present at site *s*. I further used a logit link to model linear relationships between detection probability (*ps, r,sp*) and 1–7 detection covariates (Table). I also incorporated a species-specific random observer effect in the hierarchical community models for breeding songbirds within the wildlife opening and in the adjacent forest.

Finally, following the modeling framework of Zipkin et al. (2010), species-specific occurrence and detection processes within the 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).

Each hierarchical community model yielded species-specific estimates of latent occupancy (*Zs,sp*) for species *sp* at each site *s* based on observed data from replicate surveys. I then derived the overall species richness for each site by summing the occupancy of all the songbird species under consideration, as in the following equation:

where *N* = 65 or *N* = 44, depending on the sampling season and survey location (Table). Similarly, I derived guild-specific richness by summing the occupancy of the subset of songbird species that belonged to each guild designation.

All hierarchical community models were constructed in a Bayesian framework and 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 had a shape parameter of 0.1 and rate parameter of 0.1, and all Gaussian prior distributions had a mean of 0 and precision of 0.1 (Appendix B). I fit the models in JAGS (Plummer 2003) using the “jagsUI” package (Kellner and Meredith 2021) in Program R (R Core Team 2022). I used the “autojags” function to run 3 chains for each hierarchical community model with a burn-in of 10,000 iterations, thinning rate of 5 iteration, and iteration increment of 5,000. The models iteratively ran until reasonable convergence (R̂ ≤ 1.1) was achieved (Gelman et al. 2014), resulting in 3,000–9,000 posterior draws (Table).

*Determining relationships between overall species and guild richness and important predictor variables for game bird species*

After I derived detection-corrected overall species and guild richness within each wildlife opening during the breeding and post-breeding seasons and in the adjacent forest during the breeding season from the corresponding hierarchical community model, I then incorporated those estimates into generalized linear mixed effects models, with overall species or guild richness as the response variable and incorporating up to 19 site covariates as predictor variables (Table). To propagate uncertainty from the original hierarchical community model results, I ran 3,000–9,000 iterations (corresponding to the total number of posterior draws; Table) of the generalized linear mixed effects models for overall species richness and for each guild designation, cycling through the values from each of the posterior draws. In result, the models yielded a posterior distribution of 3,000–9,000 values 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 within each wildlife opening or within 50 m of each adjacent forest sampling point (i.e., overall species richness or guild richness) to be a Poisson random variable and used a log link to model relationships with important predictor variables for game bird species. All continuous predictor variables were centered and scaled prior to analysis. The total number of slope coefficients was 21 for breeding songbird guild richness within the wildlife opening and in the adjacent forest (resulting in a ratio of ~11–15 sites to 1 slope coefficient; Bolker et al. 2008) and 9 for post-breeding songbird guild richness within the wildlife opening (resulting in a ratio of 9 sites to 1 slope coefficient). The full set of site covariates (N = 19) comprised all of the predictor variables that were determined to be important for at least 1 of the 3 game bird species in at least 1 of the candidate models, including: area (quadratic), elevation (quadratic), opening type, proximity to road, percent sapling cover, percent tree cover outside of the wildlife opening, canopy height, number of trees, number of small openings within 1 km, number of mid-size openings within 1 km, number of large openings within 1 km, proportion of land with wildlife habitat priority status within 1 km, proportion of mature sawtimber stands within 1 km, proportion of immature sawtimber stands within 1 km, proportion of individual tree selection stands within 1 km, proportion of all mature forest within 1 km, proportion of dry-oak forest within 1 km, proportion of agricultural land within 1 km, and mode stand age within 1 km. The subset of site covariates (N = 7) used for modeling post-breeding songbird guild richness consisted of the predictor variables that were determined to be important for ≥2 game bird species or in ≥2 candidate multi-species game bird species occupancy models, including: area (quadratic), elevation (quadratic), opening type, proportion of land with wildlife habitat priority status within 1 km, proportion of mature sawtimber stands within 1 km, proportion of all mature forest within 1 km, and proportion of agricultural land within 1 km. Because my data included stacked observations across multiple years, all of the generalized linear mixed effects models also incorporated a random year effect for log expected richness. I fit all generalized linear mixed effects models using “glmer” function from the “lme4” package (Bates et al. 2015) in Program R (R Core Team 2022).

*Determining importance and assessing effects of predictor variables on guild richness*

To identify predictor variables that had significant influence on overall species and guild richness within the wildlife opening during the breeding and post-breeding seasons and in the adjacent forest during the breeding season, I assessed variable importance by looking at whether the 95% credible intervals of the slope coefficient values overlapped zero; if the 95% credible intervals did not overlap zero, the variable was considered important. I further evaluated the marginal effects of important site covariates on overall species and guild richness within and adjacent to the wildlife openings by plotting the estimated number of species across the full range of the variable, while holding the other variables constant.

**RESULTS**

**Detection of game bird species during surveys**

**Comparison of multi-species game bird occupancy models**

Table of model selection with DIC values

**Effects of important predictor variables on game bird occupancy**

Table with values / significance of full set of predictor variables from all candidate models

Table with summary of effects of each variable for each game bird

Figures of marginal effects on marginal occurrence

**Detection of breeding and post-breeding songbird species during surveys**

**Effects of important predictor variables on breeding and post-breeding songbird guild richness**

Table with values / significance of full set of predictor variables

Table with summary of effects of each variable for each guild

Figures of marginal effects on guild richness

**Discussion**

This study quantified the effects of climate factors on forest songbird communities and species abundance during the breeding season across latitudinal and elevational gradients within the Appalachian Mountains. I also investigated concurrent long-term temporal trends beyond climate change and determined how they were mediated by latitude and elevation. Model results supported the hypothesis that the effects of climate change on forest songbird communities during the breeding season are mediated by latitude and elevation. Relationships with climate factors and long-term temporal trends varied by climate-related guild designation, latitude, and elevation, such that the different guilds showed distinct trends that varied among regions and along elevational gradients within the Appalachian Mountains. Because temperatures are expected to rise and precipitation patterns will be altered in the future due to climate change (Trenberth 2011, Rogers et al. 2016, Fernandez and Zegre 2019), it is critical to incorporate this new understanding of dynamic relationships with climate factors across latitudinal and elevational gradients to improve region-specific predictions of how climate change will affect cold-associated, warm-associated, and climate generalist species. In addition, variation in temporal trends among guild designations, latitudes, and elevations indicates the need for additional research and conservation efforts for certain climate-related guilds in specific regions.

**Conclusions**

Here, I establish that the influence of temperature and precipitation on guild richness and abundance of forest songbirds breeding in the Appalachian Mountains is mediated by latitude and elevation. The results of this study are valuable for understanding historical effects of changing climate factors and improving predictions of future climate change impacts on forest songbirds in the Appalachian Mountains by verifying and delineating the dynamic nature of the relationships with temperature and precipitation across latitudinal and elevational gradients. They will also help to inform forest songbird conservation efforts in the Appalachian Mountains because they quantify the regional effects of temperature and precipitation on climate-related guilds and forest songbird species and identify specific latitudes and elevations at which they are at the highest risk from climate change and other temporal factors. Based on my models, climate mitigation strategies for forest songbirds in the Appalachian Mountains are most needed for northern guild species and the Northern Appalachians.

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**Literature Cited**

**Tables**

Table 1. List of the common name, scientific name, 4-letter species code, taxonomic family, and climate-related guild designation of the 16 forest songbird species used in the focal species analyses.

**Figures**

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

**APPENDICES**

**Appendix A**

Table of the 40 forest songbird species considered in the guild richness analyses.

Table A1. List of the common name, scientific name, 4-letter species code, relative frequency, taxonomic family, and guild designation of all 40 forest songbird species considered for the guild richness analyses. Relative frequency is the number of detections across all point count surveys from all sampling points in all 3 study regions. The guild designation indicates the extent of the species’ range within the Appalachian Mountains, such that: species in the north guild are only found in the Northern or Central Appalachians; species in the south guild are only found in the Southern or Central Appalachians; species in the trailing guild have trailing-edge populations that are found throughout the Appalachian Mountains but are limited to higher elevations in the Southern Appalachians; and species in the general guild are found throughout the Appalachian Mountains.