**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 explain game bird species occupancy of wildlife openings. After identifying which wildlife opening attributes are 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**

Study sites are located throughout the Monongahela National Forest, which encompasses portions of nine counties (Preston, Tucker, Grant, Randolph, Pendleton, Pocahontas, Webster, Nicholas, and Greenbrier) in eastern West Virginia (Figure 5). 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 Monongahela National Forest 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 Monongahela National Forest ranges from 275–1,480 m.

The Monongahela National Forest is comprised primarily of 70–100 year-old stands with high regional tree diversity and four major forest zones (mixed mesophytic, northern hardwoods, red spruce, and dry oaks). Mixed mesophytic forests are present at low elevations (<900 m), with 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 Monongahela National Forest, 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).

**Study design**

Data from the West Virginia Division of Natural Resources (WVDNR) indicate that there are almost 2,200 individual openings, including linear openings, grazing allotments, and those specifically targeting wildlife, in the Monongahela National Forest (Figure 8), ranging 0.009–15 ha (mean = 1.9 ha). Most of these openings were created following timber harvest operations within the past several decades and were subsequently managed by the WVDNR. The purpose of the wildlife openings is to provide habitat to regionally important game species associated with early-successional or open habitat, including white-tailed deer, wild turkey, and American woodcock. The majority (97.1%) are ≤5 ha in size, with 62 >5 ha. More than 80% of the openings are maintained or have a history of maintenance. Active management of wildlife openings consists primarily of mowing, although applying herbicides, liming, fertilizing, and planting are also implemented in select wildlife openings. The density of wildlife openings within the landscape varies, but many wildlife openings are located less than 1 km from the nearest neighboring opening.

For this research, I will include a total of ~275–365 wildlife openings as study sites, with ~60–150 different sites sampled per year over the course of three years (Figure 8). The total number of wildlife openings will depend on the number of field technicians available to collect data each year. Based on size and maintenance status, there are six main “treatments” under consideration: (1) large (5–15 ha), maintained openings, (2) large, unmaintained openings, (3) mid-sized (1–5 ha), maintained openings, (4) mid-sized, unmaintained openings, (5) small (0.02–1 ha), maintained openings, and (6) small, unmaintained openings. Each “treatment” will have 14–70 replicates over the course of the study. The selection of wildlife openings will be constrained by size (0.02–15 ha) and shape (to avoid purely linear openings). Within those constraints, all large openings will be sampled, due the limited number available, while a subset of mid-sized and small, maintained and unmaintained openings will be further selected through stratified random sampling to best ensure geographical variation.

**Focal species**

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

**Guild designations**

To assess avian guild richness at each wildlife opening, I will group avian species into one of four guilds, based on taxa and habitat: game bird, early-successional songbird (i.e., primarily breed or found in grasslands, shrub/scrub, or young forest), edge-associated songbird (i.e., generally breed or found along forest edges, at the interface of early-successional and mature forest, or equally in early-successional and mature forest), or forest-interior songbird (i.e., generally breed or found in the core area of mature forest). To assess multi-species or species-specific occupancy and abundance, focal species for this study will include three regionally important game birds (American woodcock, wild turkey, and ruffed grouse) and selected songbird species belonging to the following three habitat guilds: early-successional, edge-associated, and forest-interior (Table 12). Focal songbird species were chosen based on: (1) occurrence or relative abundance within the study region during the breeding season (e.g., reported in >10% of all completed eBird checklists submitted in June within the past 5 years), or (2) inclusion in the Monongahela National Forest 2017 Regional Forester’s Sensitive Species List, WVDNR Resources Species of Concern list, and/or WV State Wildlife Action Plan.

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

Climate-related guild designations for the 40 forest songbird species were assigned based on their ranges within the Appalachian Mountains and comprised 4 mutually exclusive categories (Appendix A): north, south, trailing, and general. Species in the north guild were only found in the Northern or Central Appalachians study regions, whereas species in the south guild were only found in the Southern or Central Appalachians study regions. Species in the trailing guild could be found in all 3 study regions in the Appalachian Mountains but had trailing-edge populations that were limited to higher elevations in the Central or Southern Appalachians study regions. In contrast, species in the general guild were found throughout all 3 study regions in the Appalachian Mountains.

**Data collection**

In-person game bird surveys will be conducted from April 15 to May 10 in 2019–2021 to capture peak courtship/breeding period (Schumacher 2002, US Fish and Wildlife Service 2011) at a total of 65 wildlife openings in 2019 and 60–150 wildlife openings in both 2020 and 2021. American woodcocks will be sampled with 6-minute evening modified singing-ground surveys, while ruffed grouse and wild turkeys will be sampled simultaneously with 10-minute morning modified drumming/gobbling surveys. Using game cameras and autonomous recording units, a total of 72 wildlife openings per year will be surveyed for game birds, with 40 overlapping with the in-person surveys, resulting in an additional 32 wildlife openings sampled per year. A single game bird sampling point per wildlife opening will be randomly generated >80 m from the forest edge (if possible); for the smallest wildlife openings (<1 ha), the point will be approximately in the center of the opening.

American woodcocks will be surveyed once per year following the 2017 Conservation Effects Assessment Project survey protocols. Surveys will begin 22 minutes after official sunset when the sky is clear or has <75% cloud cover and 15 minutes after official sunset when the sky is overcast (>75% cloud cover). All surveys will be completed by 38 minutes after the start time. No surveys will be conducted if there is any precipitation, wind speed is high (>10 mph), or temperatures are below 4° C (40° F). Prior to the survey start time, the observer will record: wildlife opening ID (name/number), date (month/day/year), observer initials, sunset time, sky condition (% cloud cover), temperature, ambient noise level (dB), precipitation, wind speed (mph), UTM coordinates, and survey start time. Maximum wind speed will be measured with a Kestrel 1000 anemometer, and maximum ambient noise will be measured with a sound level meter for one minute. The survey itself will be a total of 6 minutes, which is split into three 2-minute periods. During the survey, the observer will listen for peenting woodcock and, for each bird, indicate presence within the wildlife opening when first heard (1 = within wildlife opening, 0 = outside of wildlife opening), estimate distance from the observer (in distance bands: 0–20 m, >20–50 m, >50–100 m, >100 m) when first heard, and mark the time period in which the bird was detected. At the conclusion of the 6 minutes, observers will record the survey end time. Furthermore, observers will make a note if there were American woodcock at the site that were not observed during the survey.

Ruffed grouse occupancy will be quantified twice per year using a modified drumming survey method (Hansen et al. 2011). Surveys will start one-half hour before sunrise and end 4 hours after sunrise. No surveys will be conducted if there is moderate to heavy precipitation or wind speed is high (>10 mph). Prior to the survey start time, the observer will record: wildlife opening ID (name/number), date (month/day/year), observer initials, temperature, ambient noise level (dB), precipitation, sky code, wind speed (mph), UTM coordinates, and survey start time. Maximum wind speed will be measured with a Kestrel 1000 anemometer, and maximum ambient noise will be measured with a sound level meter for one minute. Sky codes range from 0 to 4 and are adapted from the U.S. Weather Bureau and Breeding Bird Survey protocols (U.S. Geological Survey 1998) to measure general sky conditions. The survey will be a total of 10 minutes, which is split into three intervals: 0–3 minutes, >3–5 minutes, and >5–10 minutes. Ruffed grouse typically drum every 2–4 minutes during the breeding season (McBurney 1989) and can be heard from distances of nearly 400 m (Bump et al. 1947). Wild turkey will be surveyed simultaneously with ruffed grouse. During the 10-minute survey, the observer will listen and look for drumming ruffed grouse and gobbling wild turkeys. For each bird detected, the observer will record the species, presence within the wildlife opening when first heard (1 = within wildlife opening, 0 = outside of wildlife opening), estimated distance from the observer (in distance bands: 0–20 m, >20–50 m, >50–100 m, >100 m) when first heard, and the time period in which the bird was detected. At the conclusion of the 10 minutes, observers will record the survey end time. Furthermore, observers will make a note if there were ruffed grouse or wild turkey at the site that were not observed during the survey.

In addition to in-person field surveys, I will use autonomous recording units (Wildlife Acoustics SongMeter SM2+, Wildlife Acoustics SongMeter SM3+, Wildlife Acoustics SongMeter SM4+) during the same survey period (April 15 to May 10) to increase detection probabilities of the three game bird species. Autonomous sound recorders 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). I will deploy the autonomous recording units in 24 wildlife openings at a time for a period of 7–8 days. They will be set up within 50 m of the in-person game bird survey points. I will attach them at a height of ~1.5 m to the nearest tree/shrub (or to a pole that I will erect in the absence of suitable attachment substrate) and pointed in a direction that faces the in-person game bird survey point, minimizes auditory obstruction, and maximizes potential auditory detections (Darras et al. 2018). I will program the autonomous recording units to record from three hours before sunset to an hour after sunset and from an 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 survey time span. For all three years, 40 sampling periods using the autonomous recording units will overlap with the in-person game bird surveys. When the field season is finished, I will enlist the help of paid and volunteer undergraduates to search recordings for wild turkey gobbling, ruffed grouse drumming, and American woodcock peenting by visually using a spectrogram to process audio files. If possible, I will try to automate the initial screening process and use a recognizer file to produce a list of candidate vocalizations for me to confirm.

Game cameras (Bushnell Trophy Cam HD, Reconyx Hyperfire) will be used as a third sampling method for the game birds. Bushnell and Reconyx camera traps are equipped with an infrared flash; with highly sensitive trigger times and quick trigger times, the game cameras can record animals passing in front without the addition of bait. I will deploy the game cameras in 24 wildlife openings at a time for a period of 7–8 days (i.e., the same deployment schedule and sites as the autonomous recording units). I will set up a single game camera at the same location as the autonomous recording units (i.e., within 50 m of the in-person game bird survey points); I will attach the cameras ~40 cm above the ground to the same tree/shrub/pole as the autonomous recording unit and ensure that the camera is oriented parallel with the ground and pointed in a direction that faces the in-person game bird survey point, minimizes visual obstruction, and maximizes potential visual detections. Cameras will be set on maximum trigger sensitivity and record multiple photographs per trigger, re‐triggering immediately if the animal is still in view. For all three years, 40 sampling periods using the game cameras will overlap with the in-person game bird surveys and use of the autonomous recording units. When the field season is finished, I will enlist the help of paid and volunteer undergraduate students to use eMammal software to identify wild turkeys, ruffed grouse, American woodcock, and other wildlife species in camera trap images.

All breeding songbird surveys will be conducted from May 15 to July 10 in 2019–2021, with sites at lower elevation surveyed by the end of June. Breeding songbirds will be sampled with 10-minute unlimited radius stationary point counts at a total of 65 wildlife openings in 2019 and 60–150 different wildlife openings in both 2020 and 2021. I will conduct three point counts (central, edge, and adjacent forest) per wildlife opening (Figure 8). The central point count will be at the same location as the game bird sampling point, which was either randomly generated >80 m from the forest edge or the approximate center of the opening for the smallest wildlife openings (<1 ha). The edge point count location will be randomly generated along the perimeter of the wildlife opening and at least 200 m from the central point count. Similarly, the adjacent forest point count location will be randomly generated between 150 m and 300 m from the perimeter of the wildlife opening, 150 m from any other edges/canopy disturbance (to avoid possible edge effects; Germaine et al. 1997, Hobson and Bayne 2000*b*), and at least 200 m from the central and edge point count locations. For wildlife openings that are so small that the edge point count is not spatially feasible (i.e., >200 m from the central point count), I will only conduct point counts at the central and adjacent forest locations.

Each breeding songbird point count location will be sampled only one time per year to maximize the number of points surveyed annually. Surveys will begin within 15 minutes of sunrise and continue until approximately 10:30 am (depending on bird activity). No surveys will be conducted on days with rain, heavy fog, or high wind speed, following guidelines of Ralph et al. (1993). Prior to the survey start time, the observer will record: wildlife opening ID (name/number), point count location (central, edge, adjacent forest), date (month/day/year), observer initials, temperature, ambient noise level (dB), precipitation, sky code, wind speed (mph), UTM coordinates, and survey start time. Maximum wind speed will be measured with a Kestrel 1000 anemometer, and maximum ambient noise will be measured with a sound level meter for one minute. Sky codes range from 0 to 4 and are adapted from the U.S. Weather Bureau and Breeding Bird Survey protocols (U.S. Geological Survey 1998) to measure general sky conditions. Surveys will not be conducted when sky conditions are more severe than code 3. During each survey, I will record all individuals seen or heard during a 10-minute period. Avian sampling protocols will be consistent with those used by the U.S. Forest Service. The 10-minute point count is divided into three time intervals: 1–3, >3–5, and >5–10 minutes. Each individual bird will be assigned a new row and will be recorded for each time interval it is observed. In addition, I will record the distance band (≤50 m or >50 m), detection type (song, call, visual, flyover, or drumming), and age/sex (male, female, adult, juvenile, unknown). After the 10-minute period ends, observers will record the survey end time.

All post-breeding songbird surveys will be conducted from July 15 to August 1 in 2019–2021, to minimize overlap with the breeding season (McDermott et al. 2011, McDermott and Wood 2011) and fall migration. Post-breeding songbirds will be sampled twice with transect surveys. Due to the short sampling period, I am sampling a subset of the total sites. These sites will be selected based primarily on detections of game birds (i.e., I will not survey sites with no game birds detected) and secondarily by size (i.e., I will aim for an equal number of the three size “treatments”). I will survey birds along 4–8 transect segments per wildlife opening (4 for small openings, 6 for mid-sized openings, and 8 for large openings). To maximize spatial representation, I will randomly select locations for the start points of each transect within the wildlife opening, while ensuring a minimum distance of 15–50 m between points (15 m for small openings, 30 m for mid-sized openings, and 50 m for large openings).

Transect surveys will begin 30 minutes after sunrise and continue until ~10:30 am. The observer will walk along the segments connecting the transect start points and record all birds detected visually or aurally from within each segment, excluding individuals recorded during a previous segment to avoid double-counting birds. If possible, observers will note the sex (male vs. female vs. unknown) and age (hatch-year vs. after-hatch-year vs. unknown) of every observed individual based on plumage or other identifying characteristics. For each transect survey, observers will also record the following: wildlife opening ID (name/number), date (month/day/year), observer initials, temperature, sky code (U.S. Geological Survey 1998), maximum wind speed (mph; measured with Kestrel 1000 anemometer), UTM coordinates of the start and end points, and starting and ending times for each transect segment. Transect surveys will not be conducted in inclement weather (e.g., moderate or heavy precipitation, fog) or other conditions that would limit visual observation of birds.

I will conduct two types of site-level vegetation surveys for each wildlife opening, with the aim to collect data that is compatible with historical data (e.g., DeMeo 1999) but also addresses the habitat attributes in which I am interested. First, following morning point count surveys (May 15 to July 10) or until August 1, I will conduct tree plot surveys centered at the central, edge, and adjacent forest-interior bird count locations. Each tree plot will be surveyed once and include data on canopy height, basal area, canopy position, and canopy cover. To measure canopy height, I will use a clinometer to find the angle to the apex and base of a codominant tree and then measure the horizontal distance to the base with a rangefinder. Trees will be sampled using the variable radius plot method, which should yield accurate results for tree basal area and distribution 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, all tree stems that fall within the plot with be recorded. Borderline trees will be included and measured; I will later determine if they should be counted or not by comparing the tree’s distance with the effective sampling radius for a tree of that size. The species, diameter at breast height (DBH; measured with a Biltmore stick), and canopy position for each tree will be recorded. For dead trees, the species will be denoted as “snag”. Canopy position is a categorical classification that separates trees into five distinct classes: suppressed, intermediate, codominant, dominant, and open growth (for trees in otherwise non-forested landscapes) (Jennings et al. 1999). Forest overstory density (i.e., percent canopy cover) will be measured using a spherical densiometer, taking the average count from the four cardinal directions. Second, I will conduct vegetative cover surveys once at each central, edge, and adjacent forest-interior bird count location using the sight tube method. Specifically, I will use sight tubes to estimate vegetative cover at 20 sampling points within a 50-m radius plot centered at the point count location. The 20 sampling points will consist of 5 sampling points located 10 m apart in each cardinal direction. At each sampling point, the observer will look through the sight tube straight up and down (e.g., simulating a line that extends from the ground into space) and record the vegetation classes (tree, sapling, shrub, herb) that intersect the sight tube crosshairs.

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).

**Environmental data**

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*

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

To relate wildlife opening attributes to avian guild richness within wildlife openings, I will designate a guild (game bird, early-successional songbird, edge-associated songbird, or forest-interior songbird) for all species detected during modified singing-ground surveys, drumming/gobbling surveys, autonomous acoustic monitoring, game camera trapping, central point count surveys, and transect surveys. For each guild, I will include the three years of corresponding bird survey data for all species in that guild in a stacked hierarchical community/multi-species occupancy model (Iknayan et al. 2014), constructed in a Bayesian framework. I will integrate the detection process into these community models to explicitly account for the effects of survey-, site-, species-, or individual-level factors affecting detectability. For these and all following models (including those below addressing different objectives), I will consider observer, ordinal day, time since sunrise, wind speed, and sky code as detection covariates. The hierarchical community/multi-species occupancy model incorporates undetected species in a biologically oriented, process-driven way (Iknayan et al. 2014) and will yield the detection-corrected guild richness associated with each wildlife opening (Dorazio et al. 2006). I will further model those derived estimates of guild richness, after propagating the uncertainty (Kery and Royle 2016), as a function of the site-level predictor variables (Table 11) using Poisson regression. I will then employ model selection using the Watanabe-Akaike Information Criterion (WAIC), a fully Bayesian information criterion analogous to Akaike Information Criterion (Gelman et al. 2014, Hooten and Hobbs 2015), to identify and describe relationships with the predictor variables.

To calculate overall species richness and guild richness at each sampling point in each year of the study, I estimated the individual species occupancy of the 40 forest songbird species simultaneously in a hierarchical community model (see Appendix B for JAGS code) and then derived the corresponding sums for all species and each guild designation (Zipkin et al. 2010). The hierarchical community model facilitated a multi-species approach to estimating individual species occurrence probabilities (Dorazio and Royle 2005, Dorazio et al. 2006). Occurrence *Zs,y,sp* was defined as a binary variable in which *Zs,y,sp* = 1 if species *sp* occurs within 50 m of sampling point *s* in year *y*. The occurrence state was assumed to be the outcome of a Bernoulli random variable, denoted by:

*Zs,y,sp* ~ *Bernoulli*(*Ψs,y,sp*)

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

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

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

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

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

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

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).

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

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

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

*Determining relationships with climate factors and temporal trends for overall species and guild richness*

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

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

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

*Determining significance and effect size of predictor variables*

**RESULTS**

**Variation in effects of temperature across latitudinal and elevational gradients**

Overall

**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.