**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 generally low vegetation 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 openings that were <0.5 ha in size (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 permanent openings that are 0.1–0.8 ha in size 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. Bird species that breed in early-successional habitat are often restricted by the area of wildlife openings (Margenau et al. 2022). 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). Within forest-dominated landscapes in West Virginia, the width of rights-of-ways and wildlife openings had a negative influence on forest-interior bird species (Margenau et al. 2022). However, McDermott et al. (2011) documented an increase in late-successional bird diversity with size of stands that ranged in age from 15–40 years, such that the highest species diversity was found in the largest stands within their study. In addition to opening size, time since disturbance likely influences breeding songbird abundance and community composition in wildlife openings; if not regularly maintained, then an opening created by timber harvest may cease to provide suitable habitat for early successional breeding specialists after a certain period of time (McDermott et al. 2011). For example, Robinson and Robinson (1999) found that 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. 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 likely 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 a suite of site-level and landscape-level wildlife opening attributes (Table 1) relate to multi-species occupancy of 3 game birds (wild turkey, ruffed grouse, and American woodcock) during the game bird courtship season 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 in wildlife openings (Table 2). 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 (Clarkson 1966). Elevation within the MNF ranges from 275–1,480 m.

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

**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 (USDA Forest Service 2006). 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 and near-passerine species. Although a total of 116 avian species were detected across all surveys, I limited the richness analyses to 66 species (see Appendix A for full list) with breeding ranges that encompassed the study area and that had ≥5 detections. I also excluded wetland-associated songbirds because they were incidental to the focal habitat types, as well as corvids and waterthrushes because they are not well-sampled with breeding songbird point count surveys.

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

**Field data collection**

*In-person sampling methods for game bird species*

I conducted in-person game bird surveys at 64 wildlife openings in 2019 and 251 wildlife openings in 2021, for a total of 315 wildlife openings (Table 3); 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 3). 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 (Table 3), following the U.S. Fish and Wildlife Service American Woodcock Singing Ground Survey protocols (Bergh and Andersen 2019). 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 (Table 3). 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, for a total of 309 wildlife openings (Table 3). 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 (Table 3); this sampling period was intended to minimize overlap with the breeding season (McDermott and Wood 2011, McDermott et al. 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 sight 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 with the variable radius plot method. 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 from the four cardinal directions using a spherical densiometer. 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, such that a sequence comprises multiple photos that are taken within 1 minute of each other. For each wildlife opening, trained data processing assistants recorded the species detected within 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*

Local habitat data associated with each wildlife opening consisted of percent cover of 4 vegetation classes (herb, shrub, sapling, tree), percent canopy cover, canopy height, number of trees, relative basal area, and 3 topographical variables (elevation, aspect, topographical position index [TPI]) (Table 1). From the sight tube vegetation surveys, I calculated percent herb / shrub / sapling / tree cover as the total number of points at which herbs / shrubs / saplings / trees were present divided by the total number of points located within the opening. Because mature forest surrounding small wildlife openings was often within 50 m of the central sampling point, I also calculated percent tree cover outside of the wildlife opening, for which I divided the total number of points outside of the opening at which trees were present by the total number of points in the survey (N = 20). Percent canopy cover, canopy height, number of trees, and basal area were derived from field data collected during the tree plot surveys. Percent canopy cover was calculated as the average of the 4 densiometer values. Canopy height was calculated using trigonometry for a right triangle, given horizontal distance and angle from the base to the apex. Number of trees corresponded to the total number of live trees and dead snags within the tree plot that had a diameter >10 cm. Relative basal area was calculated as the sum of the individual basal area (DBH2 × 0.005454) of all the trees within the tree plot. Mean elevation, mode aspect, and mode TPI within the boundaries of each wildlife opening were calculated or derived using Shuttle Radar Topography Mission digital elevation data. Mode aspect was then converted to a dummy variable where 0 = mode aspect was towards the south or west (i.e., between 135 and 315 degrees) and 1 = mode aspect was towards the north or east (i.e., <135 or >315 degrees), reflecting differences in forest productivity (Desta et al. 2004).

I also calculated habitat data associated with each adjacent forest sampling point, which included percent shrub cover, percent any tree cover, percent canopy cover, basal area, elevation, and aspect. From the sight tube vegetation surveys, I calculated percent shrub cover and percent any tree cover as the total number of points at which shrubs and either saplings or trees were present divided by the total number of points (N = 20). Percent canopy cover and basal area were calculated in the same way as for the wildlife openings. Mean elevation and mode aspect within 50 m of each adjacent forest sampling point were calculated using Shuttle Radar Topography Mission digital elevation data. Mode aspect was then converted to a dummy variable following the same procedure as for the wildlife openings.

*Predictor data – Size and shape*

Size and shape data were derived from a GIS dataset of MNF wildlife openings (Table 1). In addition to the area of each wildlife opening, I calculated the edge-to-area ratio (i.e., perimeter divided by area) and the Polsby-Popper score (*PP*), which is a shape metric that indicates roundness and uses the following equation:

*PP* = 4π × *A* / *m*2

where *A* = area and *m* = perimeter.

*Predictor data – Management*

Management-related data were derived from both the GIS dataset of MNF wildlife openings and field observations, and included opening type, past maintenance status, recent disturbance, mowing frequency, human activity level, and proximity to roads (Table 1). Opening type was a designation by MNF and West Virginia Division of Natural Resources managers that I converted to a dummy variable, where 1 = opening type of “1” (N = 170 wildlife openings) and 0 = all other opening types (N = 155 wildlife openings). An opening type of “1” corresponded to standard maintained wildlife openings, which were intentionally created by managers and characterized as a group by their small sizes, their relatively round (i.e., non-linear) shapes, and being actively maintained or mowed frequently (every 1–2 years). Other opening types included maintained linear openings along Forest Service roads, utility rights-of-way maintained by utility or gas companies, gas well sites, reclaimed strip mines, orchards, hayfields, current or former grazing allotments, savannahs, and beaver meadows. Past maintenance status and recent disturbance were dummy variables indicating whether the wildlife openings had a record of past maintenance by managers and whether there had been a recent disturbance (e.g., exposed bare soil, tilling, mowing). Mowing frequency was how many years elapsed between mowing by managers, ranging from 1–5 years. Human activity level and proximity to roads were 2 more dummy variables, where 0 = no or low levels of human activity or recreation (e.g., wildlife openings that were not easily or readily accessible) and not within 50 m of a public, maintained road, and 1 = moderate to high levels of human activity or recreation (e.g., wildlife openings that were located in areas with designated camping, tourist attractions, hiking trails) and within 50 m of a public, maintained road.

*Predictor data – Landscape context*

Data pertaining to the landscape context of each wildlife opening were derived from multiple GIS datasets and calculated within 1 km (Askins et al. 2007, Shake et al. 2012). Landscape-scale variables included distance to the nearest neighboring wildlife opening, numbers of small / mid-size / large wildlife openings within 1 km, proportion of land with wildlife habitat priority status within 1 km, proportions of regenerating / immature sawtimber / mature sawtimber stands within 1 km, proportions of stands managed with individual tree selection / two-age harvest within 1 km, mode stand age within 1 km, proportions of all forest / dry-oak forest / red spruce forest within 1 km, proportion of agricultural land within 1 km, and proportion of open habitat within 1 km (Table 1). Using the GIS dataset of MNF wildlife openings, distance to the nearest neighboring wildlife opening was measured as the distance from the edge of the focal wildlife opening to the edge of its nearest neighbor and ranged from <1 m to ~2,720 m. For the number of small / mid-size / large wildlife openings within 1 km, I counted all wildlife openings that overlapped with a 1-km buffer around the edge of the focal wildlife opening and tallied them by size category. To calculate the proportion of land with wildlife habitat priority status within 1 km, I used a GIS dataset from the MNF that mapped forest management prescriptions. For proportions of different stand types (e.g., regenerating, immature sawtimber, and mature sawtimber) and different harvest types (e.g., individual tree selection and two-age) within 1 km and for mode stand age within 1 km, I used a GIS dataset from the MNF that mapped forest stands and provided stand-scale attribute information. Finally, I calculated the proportions of different forest types and land cover classes using a 2016 statewide spectral land cover classification for West Virginia with 5 m resolution (Maxwell et al. 2019). This raster map was created using geographic object-based image analysis, random forest machine learning, and National Agriculture Imagery Program orthophotography; it had an overall accuracy of 96.7%, and forest cover was mapped with user’s and producer’s accuracies of 98.0% and 99.4%, respectively (Maxwell et al. 2019). For all forest, I added the proportions of land cover classes 10–18 (other, red spruce, northern hardwood, mixed mesophytic, dry-mesic oak, dry oak / pine, pine oak rock, dry calcareous, and montane red oak forests), and for dry-oak forest, I combined the latter 5 land cover classes (14–18). Agricultural land included land cover classes 20 (hay / pasture) and 21 (cultivated crops), whereas open habitat included land cover classes 19 (low vegetation), 20 (hay / pasture), and 22 (mine grass).

I also calculated landscape-scale data associated with each adjacent forest sampling point, which included distance to the corresponding wildlife opening and proportions of dry-oak, northern hardwoods, and red spruce forest within 50 m. Distance to the wildlife opening was calculated using the GIS dataset of MNF wildlife openings, and proportions of different forest types were derived from WV land cover map (Maxwell et al. 2019).

**Data analysis**

*Modeling occupancy of focal game bird species*

To quantify and compare how wildlife opening attributes influence game bird species in wildlife openings, I estimated the probability of occurrence for wild turkey, ruffed grouse, and American woodcock in multi-species occupancy models (Rota et al. 2016) (see Appendix B for JAGS code). A multi-species occupancy modelling framework incorporates a hierarchical structure that accounts for imperfect detection and increasingly higher-order species interactions (Rota et al. 2016). For example, first-order linear models affect the probability of each species occurring when all others are absent, and second-order linear models affect the probability of two species occurring together.

Within the multi-species occupancy model, I modeled the latent occupancy state of species *sp* at site *s* as a multivariate Bernoulli random variable:

***Z****s* ~ MVB(*Ψs*)

where ***Z****s* = {*z.witus*, *z.rugrs*, *z.amwos*} was a 3-dimensional vector of 1’s and 0’s denoting the latent occupancy state of the 3 game bird species and *Ψs* was an 8-dimensional vector denoting the probability of all possible sequences of 1’s and 0’s that ***Z****s* could attain, such that the sum of all *Ψs* together was 1. The natural parameters *f.witu*, *f.rugr*, *f.amwo*, *f.witu.rugr*, *f.witu.amwo*, and *f.rugr.amwo* were defined as:

I further modeled the conditional occurrence of each game bird species (*f.witu*, *f.rugr*, and *f.amwo*; i.e., the log odds that species *sp* is present when the other 2 species are absent) as a function of 3–16 predictor variables (Tables 1–2). All continuous predictor variables were centered and scaled prior to analysis. Including quadratic relationships for certain variables, the total number of slope coefficients ranged 4–17, depending on the candidate model (Table 2). In addition, because my data included stacked observations across multiple years, I also incorporated a random year effect for each species. For the second-order natural parameters (*f.witu.rugr*, *f.witu.amwo*, and *f.rugr.amwo*), I assumed constant interspecific interactions. When modeling the latent occupancy state of the 3 game bird species, I was also able to incorporate known detections of wild turkey, ruffed grouse, and American woodcock in the wildlife openings outside of survey periods (e.g., an incidental sighting of a wild turkey in the wildlife opening during deployment of the game cameras and ARUs).

Due to multiple types of surveys and sources of data for each game bird species (Table 3), I included 3 detection models for wild turkey, 1 detection model for ruffed grouse, and 2 detection models for American woodcock within the multi-species occupancy model, such that:

*y.witu.pcss,r | z.witus*  ~ *Bernoulli*(*p.witu.pcss,r* × *z.witus*)  
*y.witu.gcs,r | z.witus* ~ *Bernoulli*(*p.witu.gcs,r* × *z.witus*)  
*y.witu.arus,r | z.witus* ~ *Bernoulli*(*p.witu.arus,r* × *z.witus*)  
*y.rugr.pcss,r* *| z.rugrs* ~ *Bernoulli*(*p.rugr.pcss,r* × *z.rugrs*)  
*y.amwo.pcss,r | z.amwos* ~ *Bernoulli*(*p.amwo.pcss,r* × *z.amwos*)  
*y.amwo.arus,r | z.amwos* ~ *Bernoulli*(*p.amwo.arus,r* × *z.amwos*)

where the observed data *y* indicate detection (1) and non-detection (0) of wild turkeys during in-person surveys (*y.witu.pcss,r*), game camera surveys (*y.witu.gcs,r*), or ARU surveys (*y.witu.arus,r*), ruffed grouse during in-person surveys (*y.rugr.pcss,r*), or American woodcocks during in-person surveys (*y.amwo.pcss,r*) or ARU surveys (*y.amwo.arus,r*) at site *s* during survey replicate *r*, and *p.witu.pcss,r*, *p.witu.gcs,r*, *p.witu.arus,r*, *p.rugr.pcss,r*, *p.amwo.pcss,r*, and *p.amwo.arus,r* are the corresponding detection probabilities for the *r*th replicate survey at site *s* corresponding to each species and data source, conditional on the presence of each game bird species at site *s* (e.g., *z.witus* = 1, *z.rugrs* = 1, *z.amwos* = 1). Replicates for the in-person morning surveys for wild turkey and ruffed grouse included 2 within-survey replicates (i.e., two 5-minute time intervals during the 10-minute surveys) across the 2 visits per wildlife opening. For the in-person evening surveys for American woodcock, there were 3 replicates corresponding to the three 2-minute time intervals during the 6-minute surveys. For the game camera and ARU surveys, the number of survey replicates corresponded to the number of days that they were deployed and functioning in the wildlife opening (e.g., a game camera that was deployed for 10 days and was operational that entire time would result in 10 survey replicates).

I used a logit link to model relationships between detection probability for each game bird species / data source and up to 6 detection covariates (Table 4). All continuous detection covariates were centered and scaled prior to analysis. For in-person game bird surveys, I also included a species-specific random observer effect, and for the ARU surveys, I incorporated a random ARU type effect to account for possible differences in detection probability among the 3 ARU devices (i.e., Wildlife Acoustics SongMeter SM2+ vs. SM3+ vs. SM4+).

The multi-species occupancy 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 (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 model with a burn-in of 10,000 iterations, thinning rate of 5 iterations, and iteration increment of 5,000; models iteratively ran until reasonable convergence (R̂ ≤ 1.1) was achieved (Gelman et al. 2014), resulting in 3,000–9,000 posterior draws (Appendix C).

*Model comparison to assess competing hypotheses*

To test competing hypotheses and 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, I ran a total of 8 candidate models (Table 2). The first 7 models pertained to local habitat attributes (with 12 vegetation and topographical variables), opening size (with 3 size and shape variables), management (with 6 management-related variables), landscape context (with 16 landscape-scale variables), location (with 16 variables dealing with where the wildlife opening is located within the landscape), construction (with 7 variables dealing with how wildlife openings are constructed within the landscape), and condition (with 14 variables dealing with the status of the wildlife opening itself with no regard to the surrounding landscape). The final model combined the consistently important site-level and landscape-level variables from the first 7 models. To compare the 8 models representing the competing hypotheses, I ranked the models based on their deviance information criterion (DIC) values (Spiegelhalter et al. 2002). DIC is a penalized likelihood method based on the posterior distribution of the deviance statistic. Models with relatively lower DIC values indicate a better fit to the data compared to models with higher DIC values.

*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 D for JAGS code) corresponding to the sampling season and survey location (Table 5), 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). Following the modeling framework of Zipkin et al. (2010), species-specific occurrence and detection processes within each of the hierarchical community models 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).

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 5). 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,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 5). 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.

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 5). 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 D). 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 iterations, 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 (Appendix C).

*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 richness or guild richness as the response variable. 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; Appendix C) 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 up to 19 predictor variables that were important for game bird species (Table 6). 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. 2009) 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 (Table 6). 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 (Table 6). 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**

All 3 game bird species were detected in or adjacent to wildlife openings from the in-person game bird surveys from 15 April to 10 May. During the morning surveys for wild turkey and ruffed grouse at 315 wildlife openings, observers recorded 67 wild turkey detections for 44 wildlife openings and 76 ruffed grouse detections for 44 wildlife openings (Table 3). During the evening surveys for American woodcock at 211 wildlife openings, observers recorded 150 detections of American woodcock for 59 wildlife openings. Only wild turkeys were reliably detected by the game camera surveys. From 142 game camera surveys, there were 50 wild turkey detections at 36 wildlife openings. Both wild turkey and American woodcock were detected by the ARU surveys. From 123 ARU surveys, there were 206 wild turkey detections for 74 wildlife openings and 175 American woodcock detections for 33 wildlife openings. Due to ARU equipment failures and sound file corruption, the total sample size was lower than that of the game camera surveys.

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

The 8 candidate models for multispecies game bird occupancy corresponded to competing hypotheses about 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 in wildlife openings. Based on the DIC values (Table 2), the top model was the MANAGEMENT model with 6 predictor variables relating to management of the wildlife openings. The remaining of the top 4 models included HABITAT, CONDITION, and SIZE. The model with the largest DIC value (i.e., the worst of the 8 candidate models) was the LOCATION model with 16 predictor variables describing where the wildlife opening is located within the landscape.

**Effects of important predictor variables and co-occurrence on game bird occupancy**

Looking at the top candidate model for multi-species game bird occupancy, 2 of the 6 management-related predictor variables had significant influence on at least 1 of the 3 game bird species (Table 7). When the opening type was “1” (i.e., standard maintained openings that tended to be small, round, and actively managed), the probability of marginal ruffed grouse occurrence increased, and the probability of marginal American woodcock occurrence decreased (Figure 4). In addition, when wildlife openings were within 50 m of a public, maintained road, the probability of marginal wild turkey occurrence decreased (Figure 4). In this model, both wild turkeys and ruffed grouse had positive associations with American woodcock presence (Table 7).

The other 3 top candidate models also contained predictor variables that had significant influence on wild turkey, ruffed grouse, and/or American woodcock occupancy. The HABITAT model had 5 significant predictor variables, and ruffed grouse and American woodcock had positive associations with wild turkey presence (Table 7). The probability of marginal wild turkey occurrence peaked at a moderate number of trees in wildlife openings, although the credible intervals were wide at lower and higher numbers of trees; in contrast, ruffed grouse appeared to respond positively to increasing numbers of trees in wildlife openings (Figure 5). The probabilities of both marginal wild turkey occurrence and marginal ruffed grouse occurrence generally increased with elevation, whereas there was a clear peak in probability for American woodcock in wildlife openings at mid-elevations (Figure 5). The probability of marginal American woodcock occurrence further declined with increasing amounts of percent sapling cover within the wildlife opening and percent tree cover outside of the wildlife opening (Figure 5). In the CONDITION model, only 2 predictor variables were significant, and wild turkey and American woodcock had positive co-occurrence (Table 7). Just as in the MANAGEMENT model, the probability of marginal ruffed grouse occurrence increased when the opening type was “1” (Figure 5). In addition, wild turkeys responded positively to increasing canopy height (Figure 5). Finally, in the SIZE model, area was significant predictor variable for ruffed grouse (Table 7), with the highest probability of marginal ruffed grouse occurrence in the largest wildlife openings (Figure 5), and both wild turkeys and ruffed grouse had positive associations with American woodcock presence.

An additional 10 landscape-level predictor variables from the remaining 4 candidate models had significant relationships with at least 1 of the 3 game bird species (Table 8). Although not presented here, their effects were considered in conjunction with the guild richness results (Table 9).

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

A total of 104 species were detected during the breeding bird point count surveys that were conducted within the wildlife openings and in the adjacent forest from 16 May to 10 July. Of those, 66 total species were considered in the guild richness analyses, with 65 species included in the hierarchical community model for breeding songbirds within the wildlife opening and 44 species included in the hierarchical community model for breeding songbirds in the adjacent forest. During the surveys for breeding songbirds at the central sampling points, observers recorded 2,229 detections of the 65 species at 294 of 309 wildlife openings, and during the surveys for breeding songbirds at the adjacent forest sampling points, observers recorded 1,216 detections of the 44 species for 211 of 241 wildlife openings (Table 3). A total of 90 species were detected during the post-breeding bird transect surveys that were conducted along transects within the wildlife openings from 14 July to 5 August. Of those, 65 species were included in the hierarchical community model for post-breeding songbirds. During the transect surveys, observers recorded 1,267 detections of the 65 species at 81 of 82 wildlife openings.

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

A subset of the predictor variables that had significant influence on game bird species occupancy were also important for breeding songbirds in the wildlife openings. Of the 19 predictor variables, 9 had significant relationships with overall species richness, 13 had significant relationships with early-successional and edge-associated guild richness, 7 had significant relationships with forest-interior guild richness, 4 had significant relationships with forest-gap guild richness, and 6 had significant relationships with forest generalist guild richness (Table 10). Mean expected overall species richness and breeding songbird guild richness tended to respond negatively to opening type, percent tree cover outside the wildlife opening, elevation, proportion of both mature and immature sawtimber within 1 km, and proportion of agriculture within 1 km, but tended to respond positively to road proximity and percent sapling cover (Table 10). In addition, 3 of the 4 guilds had a quadratic relationship with area, peaking in mean expected guild richness within larger wildlife openings (Figure 6).

Breeding songbirds in the adjacent forest were significantly influenced by certain predictor variables that were important for game bird species occupancy, but there were fewer overall significant relationships compared to breeding songbirds in the wildlife openings. Of the 19 predictor variables, 5 had significant relationships with overall species richness, 6 had significant relationships with forest-interior guild richness, 4 had significant relationships with forest-gap guild richness, and 4 had significant relationships with forest generalist guild richness (Table 10). Notably, mean expected overall species richness and forest-interior guild richness at adjacent forest sampling points had negative quadratic relationships with wildlife opening size (Figure 6), such that the peak represented the maximum mean expected number of species and corresponded to large wildlife openings, but they responded negatively to the number of large openings within 1 km of the focal wildlife opening (Table 10).

For post-breeding songbirds in wildlife openings, only 3 of the 7 predictor variables included in the post-breeding guild richness models were significant for at least one guild (Table 10). For overall species and most guilds, mean expected richness decreased with elevation, but exhibited negative quadratic relationships with area, such that the peak represented the maximum mean expected number of species and corresponded to large wildlife openings (Figure 6). In addition, mean expected overall species richness and forest generalist guild richness declined with increasing proportions of mature forest within 1 km.

**Discussion**

This study quantified the effects of site-level and landscape-level wildlife opening attributes on multi-species avian occupancy and identified specific characteristics of wildlife openings that support target game birds and a diversity of breeding and post-breeding songbirds. My results supported the hypothesis that management and local habitat attributes best explain game bird species occupancy in wildlife openings. Site-level variables consistently performed better than landscape-level variables. However, a holistic assessment of additional impacts on songbird diversity in wildlife openings highlighted the importance of landscape context. To promote game bird species occurrence in wildlife openings, land managers should primarily focus on management actions and habitat, but to also maximize overall songbird species richness and songbird guild richness during the breeding and post-breeding seasons, it is important to consider elevation, area of the wildlife opening, and proportions of different land cover types in the surrounding landscape.

The 4 candidate multi-species game bird occupancy models with management- and habitat-related predictor variables performed better than the 4 candidate models with landscape-level covariates, suggesting that wild turkey, ruffed grouse, and American woodcock are responding more strongly to site-level factors than to landscape context. This finding from my study builds upon the previous literature focused on game bird species in forest openings. Other studies have also documented game birds using open-canopy, managed areas (Hale and Gregg 1976, Healy and Nenno 1983, Akresh et al. 2022) and highlighted the importance of management and local habitat attributes (Healy 1985, Hollifield and Dimmick 1995, Jones et al. 2008). For example, recommendations for creating and managing ruffed grouse habitat include promoting the growth of young mixed stands with high horizontal and vertical cover provided by high small-stem density (Giroux et al. 2007). My study results regarding wildlife opening size were also congruent with prevailing game bird habitat management recommendations, which often involve creating midsize to large openings in the landscape (Thompson and Dessecker 1997).

Although land managers often focus on game bird species, promoting general biodiversity in wildlife openings is often a secondary goal. My study specifically identified the effects of site-level and landscape-level factors that were important for wild turkey, ruffed grouse, and American woodcock, and then explored their effects on breeding and post-breeding songbird species within and adjacent to the wildlife openings. One interesting trend was the consistency in importance and effects of opening size on breeding and post-breeding songbirds within the wildlife openings. Overall species richness and guild richness either had significant positive linear or negative quadratic relationships, with the maximum mean expected number of species repeatedly occurring between 8 ha and 20 ha across guilds and sampling seasons. Correspondingly, the minimum mean expected number of breeding and post-breeding songbird species within the wildlife openings occurred in small openings (<1 ha). When comparing the 4 habitat guilds, it was also notable that the highest magnitude effects of opening size were on early-successional and edge-associated guild richness. This is consistent with previous studies that correlate early-successional and shrubland guild richness and species abundance with patch size (Chandler et al. 2009, Lehnen and Rodewald 2009, Moorman and Guynn, Jr. 2015).

Ultimately, based on my results, land managers can maximize both game bird occurrence and breeding / post-breeding songbird diversity in wildlife openings by establishing relatively large (8–20 ha), actively managed wildlife openings in mid-elevation (800–1200 m) areas away from roads. Within the wildlife openings, it would be best to have trees present but reduce percent sapling cover and canopy height. Considering the surrounding landscape, it might be beneficial to have small and large openings within 1 km but to avoid landscapes with high proportions of mature sawtimber, mature forest, dry-oak forest, and agriculture. To avoid negatively impacting the breeding bird community in adjacent forest, it would be prudent to consider limiting the maximum size of wildlife openings to ≤15 ha and increasing the spacing between large wildlife openings created in the landscape. Previous studies have found that larger openings can have more negative effects on forest-interior songbirds (Germaine et al. 1997, Moorman and Guynn, Jr. 2015). It is also important to note that my study focused on guild richness based on individual species occurrence. Forest-interior guild species may respond differently to wildlife opening characteristics in terms of survival and nest success. For example, forest-interior species generally avoid edge conditions for nesting (Kroodsma 1984), and several studies have demonstrated higher predation and parasitism rates of nests located along or near forest edges (e.g., Brittingham and Temple 1983, Wilcove 1985, Andren and Angelstam 1988, Yahner and Scott 1988).

**Conclusions**

Here, I establish that game bird species occupancy in wildlife openings in heavily forested landscape may be best explained by management actions and local habitat attributes. The results of this study are valuable for understanding how to best manage wildlife openings and their surrounding forest matrices for target game bird species and a diversity of songbird species in both the breeding and post-breeding seasons. My findings indicate that it may be feasible to manage wildlife openings for the mutual benefit of these different species groups. I further present a set of management recommendations to maximize occurrence of wild turkey, ruffed grouse, and American in concurrence with breeding and post-breeding songbird occurrence within wildlife openings, with considerations for minimizing negative impacts to breeding songbirds in adjacent forests. These actions be applied by private landowners, non-governmental organizations, and government agencies to simultaneously meet management goals and promote diverse forest ecosystems.

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**Tables**

Table 1. List of site covariates corresponding to the wildlife openings, organized by category.

|  |  |  |  |
| --- | --- | --- | --- |
| **Category** | **Site Covariate** | **Description** | **Data Source** |
| Local Habitat | Percent Herb | Percentage reflecting the total number of vegetation survey points at which herbs / shrubs / saplings / trees were present divided by the total number of points located within the wildlife opening | Sight tube vegetation surveys |
| Percent Shrub |
| Percent Sapling |
| Percent Tree |
| Percent Tree Outside Opening | Percentage reflecting the total number of vegetation survey points outside of the wildlife opening at which trees were present divided by the total number of points in the survey (N = 20) |
| Canopy Cover | Percentage reflecting the average of 4 densiometer measurements of forest overstory density | Tree plot surveys |
| Canopy Height | Height (m) of an average intermediate tree within the wildlife opening |
| Number Trees | Total number of live trees and dead snags with >10 cm diameter located within the tree plot; index of relative tree density |
| Basal Area | Sum of the individual basal areas of all the trees within the tree plot; index of relative basal area |
| Elevation | Mean elevation within boundaries of wildlife opening | Shuttle Radar Topography Mission digital elevation data |
| Aspect | Mode aspect within boundaries of wildlife opening |
| TPI | Mode topographical position index (TPI) value within boundaries of wildlife opening |
| Size | Area | Area (ha) of wildlife opening | GIS dataset of MNF wildlife openings |
| Edge:Area Ratio | Ratio of total edge distance (m) to area (ha) of wildlife opening |
| Roundness | Shape metric; also known as the Polsby-Popper score |

Table 1. Continued.

|  |  |  |  |
| --- | --- | --- | --- |
| **Category** | **Site Covariate** | **Description** | **Data Source** |
| Management | Opening Type | Dummy variable where 1 = opening type of “1” (i.e., standard maintained wildlife openings that were intentionally created by managers and tended to be small, round, and actively managed) and 0 = all other opening types (e.g., reclaimed strip mines, grazing allotments, gas well sites) | GIS dataset of MNF wildlife openings (supplemented by field observations) |
| Past Maintenance | Dummy variable where 1 = record of past maintenance by managers and 0 = no record |
| Recent Disturbance | Dummy variable where 1 = disturbance involving exposing bare soil, tilling, or mowing within past 5 years and 0 = no disturbance |
| Mowing Frequency | Number of elapsed years between mowing by managers |
| Human Activity | Dummy variable where 1 = moderate to high levels of human activity or recreation and 0 = no or low levels of human activity or recreation |
| Road Proximity | Dummy variable where 1 = within 50 m of a public, maintained road and 0 = not within 50 m of a public, maintained road |
| Landscape Context | Distance to Nearest Opening | Distance (m) from the edge of the focal wildlife opening to the edge of its nearest neighbor | GIS dataset of MNF wildlife openings |
|  | Number Small Openings | Number of small (<1 ha) / midsize (1–5 ha) / large (>5 ha) wildlife openings that intersected a 1-km buffer around the edge of the focal wildlife opening |
|  | Number Midsize Openings |
|  | Number Large Openings |
|  | Proportion Wildlife Priority | Proportion of land designated as having “wildlife habitat priority” status within 1 km of the edge of the wildlife opening | GIS dataset of MNF forest management prescriptions |

Table 1. Continued.

|  |  |  |  |
| --- | --- | --- | --- |
| **Category** | **Site Covariate** | **Description** | **Data Source** |
| Landscape Context | Proportion Regenerating Stand | Proportion of different stand types (regenerating / immature sawtimber / mature sawtimber) within 1 km of the edge of the wildlife opening | GIS dataset of MNF forest stands |
| Proportion Immature Sawtimber |
| Proportion Mature Sawtimber |
| Proportion Individual Tree Selection | Proportion of different harvest types (individual tree selection / two-age harvest) within 1 km of the edge of the wildlife opening |
| Proportion Two-Age Harvest |
| Stand Age | Mode stand age within 1 km of the edge of the wildlife opening |
| Proportion Forest | Proportion of all mature forest within 1 km of the edge of the wildlife opening | WV land cover map |
| Proportion Oaks | Proportion of dry-oak forest within 1 km of the edge of the wildlife opening |
| Proportion Red Spruce | Proportion of red spruce forest within 1 km of the edge of the wildlife opening |
| Proportion Agriculture | Proportion of agriculture (including hay / pasture and cultivated crops) within 1 km of the edge of the wildlife opening |
| Proportion Open | Proportion of open habitat (including low vegetation, hay / pasture, and mine grass) within 1 km of the edge of the wildlife opening |

Table 2. List of 8 candidate models (representing competing hypotheses that seek to explain game bird species occupancy of wildlife openings) with corresponding list of predictor variables (and total number of slope coefficients), and deviance information criterion (DIC) value, in order from lowest to highest DIC value.

|  |  |  |  |
| --- | --- | --- | --- |
| **Candidate Model** | **Predictor Variables (N Coefficients)** | **DIC** | **ΔDIC** |
| MANAGEMENT | Opening Type + Past Maintenance + Recent Disturbance + Mowing Frequency + Human Activity + Road Proximity (6) | 2800 | --- |
| HABITAT | Percent Herb + Percent Shrub + Percent Sapling + (Percent Tree)2 + Percent Tree Outside Opening + (Canopy Cover)2 + Canopy Height + (Number Trees)2 + Basal Area + (Elevation)2 + Aspect + TPI (16) | 2832 | 32 |
| CONDITION | Opening Type + Past Maintenance + Recent Disturbance + Mowing Frequency + Human Activity + Percent Herb + Percent Shrub + Percent Sapling + (Percent Tree)2 + Percent Tree Outside Opening + (Canopy Cover)2 + Canopy Height + (Number Trees)2 + Basal Area (17) | 2839 | 39 |
| SIZE | (Area)2 + Edge:Area Ratio + Roundness (4) | 2862 | 62 |
| LANDSCAPE | Distance to Nearest Opening + Number Small Openings + Number Midsize Openings + Number Large Openings + Proportion Wildlife Priority + Proportion Regenerating Stand + Proportion Immature Sawtimber + Proportion Mature Sawtimber + Proportion Individual Tree Selection + Proportion Two-Age Harvest + (Stand Age)2 + Proportion Forest + Proportion Oaks + Proportion Red Spruce + Proportion Agriculture + Proportion Open (17) | 2952 | 152 |
| COMBINED | Opening Type + (Elevation)2 + (Area)2 + Number Total Openings + Proportion Wildlife Priority + Proportion Mature Sawtimber + Proportion Forest + Proportion Agriculture (10) | 2961 | 161 |
| CONSTRUCTION | Distance to Nearest Opening + Number Small Openings + Number Midsize Openings + Number Large Openings + (Area)2 + Edge:Area Ratio + Roundness (8) | 2992 | 192 |
| LOCATION | Road Proximity + (Elevation)2 + Aspect + TPI + Proportion Wildlife Priority + Proportion Regenerating Stand + Proportion Immature Sawtimber + Proportion Mature Sawtimber + Proportion Individual Tree Selection + Proportion Two-Age Harvest + (Stand Age)2 + Proportion Forest + Proportion Oaks + Proportion Red Spruce + Proportion Agriculture + Proportion Open (18) | 3032 | 232 |

Table 3. List of the various data sources for game bird and breeding / post-breeding songbird occurrence, with survey type, target species, sampling period, total sample size (number of wildlife openings or adjacent forest sampling points), number of between-survey replicates (i.e., visits), number of within-survey replicates (i.e., time intervals within total survey period), maximum number of total sampling replicates, total number of replicates with detections of the target species from the corresponding survey type, and number of wildlife openings where the target species was detected during the corresponding survey type.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Survey Type** | **Species** | **Sampling Period** | **Sample Size** | **Visits** | **Time Intervals** | **Replicates** | **Detections** | **Openings with Detections** |
| Morning game bird survey | WITU / RUGR | 15 April – 10 May | 315 | 2 | 2 | 4 | WITU = 67  RUGR = 76 | WITU = 44  RUGR = 44 |
| Evening game bird survey | AMWO | 15 April – 10 May | 211 | 1 | 3 | 3 | 150 | 59 |
| Game camera survey | WITU | 15 April – 10 May | 142 | 1 | 1–11 (mean: 7.6 days) | 11 | 50 | 36 |
| ARU survey | WITU / AMWO | 15 April – 10 May | 123 | 1 | 1–11 (mean: 6.6 days) | 11 | WITU = 206 AMWO = 175 | WITU = 74 AMWO = 33 |
| Point count survey (in wildlife opening) | Breeding songbirds (N = 65) | 16 May – 10 July | 309 | 1 | 2 | 2 | 2,229 | 294 |
| Point count survey (in adjacent forest) | Breeding songbirds (N = 44) | 16 May – 10 July | 241 | 1 | 2 | 2 | 1,216 | 211 |
| Transect survey | Post-breeding songbirds | 14 July – 5 August | 82 | 2 | N/A | 2 | 1,267 | 81 |

Table 4. List of detection covariates corresponding to each survey type.

|  |  |  |
| --- | --- | --- |
| **Survey Type** | **Detection Covariate** | **Description** |
| Morning / evening game bird survey | Day | Numeric day of year (where 1 = 1 January) |
| Time Since Sunrise / Sunset | Number of elapsed hours since local sunrise or sunset time |
| Wind | Dummy variable where 1 = wind codes exceeding “1” and 0 = wind codes of either “0” or “1” |
| Precipitation | Dummy variable where 1 = light precipitation and 0 = no precipitation |
| Temperature | Dummy variable where 1 = temperatures ≤7.2 or ≥18.3 °C and 0 = temperatures between 7.2 and 18.3 °C |
| Noise | Maximum noise level (dB) during survey |
| Observer | Numeric designation for each unique observer; used for random effects |
| Game camera / ARU survey | Day | Numeric day of year (where 1 = 1 January) |
| Distance to Center | Distance (m) to the central survey point |
| Game Camera Type | Type of game camera (0 = Bushnell Trophy Cam HD, 1 = Reconyx Hyperfire) |
| ARU Type | Numeric designation for each type of ARU (1 = Wildlife Acoustics SongMeter SM2+, 2 = SM3+, 3 = SM4+); used for random effects |
| Point count survey (in wildlife opening or adjacent forest) | Day | Numeric day of year (where 1 = 1 January) |
| Time Since Sunrise | Number of elapsed hours since local sunrise time |
| Wind Speed | Maximum wind speed (m/s) during survey |
| Sky | Dummy variable where 1 = sky codes exceeding “1” and 0 = sky codes of either “0” or “1” |
| Precipitation | Dummy variable where 1 = light precipitation and 0 = no precipitation |
| Temperature | Dummy variable where 1 = temperatures ≤7.2 or ≥21.7 °C and 0 = temperatures between 7.2 and 21.7 °C |
| Noise | Maximum noise level (dB) during survey |
| Observer | Numeric designation for each unique observer; used for random effects |
| Transect survey | Total Survey Time | Number of elapsed hours from start time to end time of survey |

Table 5. List of the 3 hierarchical community models organized by sampling season and sampling point location, along with their corresponding number of species (N) and site / detection covariates (with corresponding total number of slope coefficients).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Sampling Season** | **Location** | **N** | **Site Covariates**  **(N Coefficients)** | **Detection Covariates**  **(N Coefficients)** |
| Breeding season (16 May – 10 July) | Wildlife opening | 65 | Percent Herb +  (Percent Shrub)2 +  (Percent Tree)2 +  Recent Distribution +  Basal Area + Elevation + Aspect + Area +  Edge:Area Ratio + Proportion Forest + Proportion Oaks + Proportion Red Spruce + Proportion Open (15) | Day +  (Time Since Sunrise)2 + Wind Speed + Sky + Precipitation + Temperature + Noise (8) |
| Breeding season (16 May – 10 July) | Adjacent forest | 44 | Distance to Wildlife Opening + (Percent Shrub)2 + (Percent Any Tree)2 + (Canopy Cover)2 + Basal Area + Elevation + Aspect + Proportion Oaks + Proportion Northern Hardwoods + Proportion Red Spruce (13) | Day +  (Time Since Sunrise)2 + Precipitation + Noise (5) |
| Post-breeding season (14 July –  5 August) | Wildlife opening | 65 | Percent Shrub + Percent Tree + Recent Disturbance + Elevation + Area + Edge:Area Ratio + Proportion Forest (7) | Total Survey Time (1) |

Table 6. List of the 3 sets of guild richness models, organized by sampling season and sampling point location, along with the corresponding number of guilds (N) and site covariates (with corresponding total number of slope coefficients). All breeding season guild richness models had the same set of site covariates.

|  |  |  |  |
| --- | --- | --- | --- |
| **Sampling Period** | **Location** | **N** | **Site Covariates (N Coefficients)** |
| Breeding season (16 May – 10 July) | Wildlife opening | 4 | Opening Type + Road Proximity + Percent Sapling + Percent Tree Outside Opening + Canopy Height + Number Trees + (Elevation)2 + (Area)2 + Number Small Openings + Number Midsize Openings + Number Large Openings + Proportion Wildlife Priority + Proportion Immature Sawtimber + Proportion Mature Sawtimber + Proportion Individual Tree Selection + Stand Age + Proportion Forest + Proportion Oaks + Proportion Agriculture (21) |
| Breeding season (16 May – 10 July) | Adjacent forest | 3 |
| Post-breeding season (14 July –  5 August) | Wildlife opening | 4 | Opening Type + (Elevation)2 + (Area)2 + Proportion Wildlife Priority + Proportion Mature Sawtimber + Proportion Forest + Proportion Agriculture (9) |

Table 7. Slope coefficient values and significance (bold type) associated with the full set of predictor variables from the top 4 candidate multi-species game bird occupancy models (MANAGEMENT, HABITAT, CONDITION, SIZE). Predictor variables are organized by category (management, local habitat, and size).

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Predictor Variable** | **MANAGEMENT** | | | **HABITAT** | | | **CONDITION** | | | **SIZE** | | |
| WITU | RUGR | AMWO | WITU | RUGR | AMWO | WITU | RUGR | AMWO | WITU | RUGR | AMWO |
| Opening Type | -0.473 | **1.745** | **-0.820** | --- | --- | --- | 0.091 | **1.961** | -0.780 | --- | --- | --- |
| Past Maintenance | -0.329 | 0.513 | 0.683 | --- | --- | --- | 0.683 | 0.587 | 0.532 | --- | --- | --- |
| Recent Disturbance | 0.687 | 0.240 | 0.553 | --- | --- | --- | 0.549 | 0.265 | 0.455 | --- | --- | --- |
| Mowing Frequency | 0.151 | -0.486 | 0.091 | --- | --- | --- | 0.377 | -0.504 | 0.212 | --- | --- | --- |
| Human Activity | 1.219 | 0.847 | 0.360 | --- | --- | --- | 1.156 | 0.894 | 0.331 | --- | --- | --- |
| Road Proximity | **-1.483** | -0.314 | -0.135 | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Percent Herb | --- | --- | --- | -0.974 | 0.292 | 0.140 | -0.485 | 0.268 | 0.280 | --- | --- | --- |
| Percent Shrub | --- | --- | --- | 0.290 | 0.286 | 0.403 | 0.875 | 0.245 | 0.298 | --- | --- | --- |
| Percent Sapling | --- | --- | --- | -0.079 | -0.489 | **-0.666** | 0.423 | -0.457 | -0.510 | --- | --- | --- |
| Percent Tree | --- | --- | --- | 0.603 | -0.088 | 0.046 | -0.128 | -0.109 | -0.107 | --- | --- | --- |
| Percent Tree Squared | --- | --- | --- | 0.945 | -0.131 | -0.018 | 1.032 | -0.162 | -0.015 | --- | --- | --- |
| Percent Tree Outside Opening | --- | --- | --- | 1.102 | 0.394 | **-0.611** | 0.872 | 0.291 | -0.319 | --- | --- | --- |
| Canopy Cover | --- | --- | --- | -0.446 | 0.137 | -0.623 | 0.662 | -0.110 | -0.182 | --- | --- | --- |
| Canopy Cover Squared | --- | --- | --- | 0.832 | -0.097 | 0.247 | 0.908 | 0.004 | 0.032 | --- | --- | --- |
| Canopy Height | --- | --- | --- | 1.282 | -0.128 | -0.147 | **1.711** | -0.311 | -0.332 | --- | --- | --- |
| Number Trees | --- | --- | --- | **2.548** | 0.469 | 0.124 | 2.217 | 0.577 | -0.176 | --- | --- | --- |
| Number Trees Squared | --- | --- | --- | 0.543 | 0.167 | 0.010 | 0.361 | 0.143 | 0.005 | --- | --- | --- |
| Basal Area | --- | --- | --- | 0.496 | -0.094 | -0.048 | 0.882 | -0.201 | 0.223 | --- | --- | --- |
| Elevation | --- | --- | --- | **1.129** | **0.691** | **0.601** | --- | --- | --- | --- | --- | --- |
| Elevation Squared | --- | --- | --- | -0.216 | -0.389 | **-1.358** | --- | --- | --- | --- | --- | --- |
| Aspect | --- | --- | --- | -0.219 | 0.080 | -0.006 | --- | --- | --- | --- | --- | --- |
| TPI | --- | --- | --- | -1.197 | -0.548 | -0.169 | --- | --- | --- | --- | --- | --- |

Table 7. Continued.

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Predictor Variable** | **MANAGEMENT** | | | **HABITAT** | | | **CONDITION** | | | **SIZE** | | |
| WITU | RUGR | AMWO | WITU | RUGR | AMWO | WITU | RUGR | AMWO | WITU | RUGR | AMWO |
| Area | --- | --- | --- | --- | --- | --- | --- | --- | --- | -0.833 | **-2.347** | 0.464 |
| Area Squared | --- | --- | --- | --- | --- | --- | --- | --- | --- | 0.644 | **0.918** | -0.037 |
| Edge:Area Ratio | --- | --- | --- | --- | --- | --- | --- | --- | --- | 0.118 | -0.389 | -0.074 |
| Roundness | --- | --- | --- | --- | --- | --- | --- | --- | --- | -0.008 | -0.268 | 0.260 |
| WITU × RUGR | -1.388 | | | **-2.470** | | | -1.032 | | | -1.122 | | |
| WITU × AMWO | **2.344** | | | **1.785** | | | **2.816** | | | **2.060** | | |
| RUGR × AMWO | **1.092** | | | 0.652 | | | 1.004 | | | **0.986** | | |

Table 8. Slope coefficient values and significance (bold type) associated with the full set of predictor variables from the bottom 4 candidate multi-species game bird occupancy models (LANDSCAPE, COMBINED, CONSTRUCTION, LOCATION). Predictor variables are organized by category (landscape context, management, local habitat, and size).

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Predictor Variable** | **LANDSCAPE** | | | **COMBINED** | | | **CONSTRUCTION** | | | **LOCATION** | | |
| WITU | RUGR | AMWO | WITU | RUGR | AMWO | WITU | RUGR | AMWO | WITU | RUGR | AMWO |
| Distance to Nearest Opening | 1.324 | 0.243 | -0.333 | --- | --- | --- | 0.605 | -0.090 | -0.312 | --- | --- | --- |
| Number Small Openings | 1.529 | **0.683** | 0.236 | --- | --- | --- | 0.124 | 0.120 | 0.346 | --- | --- | --- |
| Number Midsize Openings | 0.763 | -0.088 | 0.042 | --- | --- | --- | 1.098 | 0.186 | **-0.679** | --- | --- | --- |
| Number Large Openings | 1.495 | -0.074 | -0.350 | --- | --- | --- | **2.034** | 0.115 | -0.228 | --- | --- | --- |
| Number Total Openings | --- | --- | --- | 0.124 | 0.021 | -0.008 | --- | --- | --- | --- | --- | --- |
| Proportion Wildlife Priority | -0.062 | 0.730 | **0.777** | 0.172 | 0.539 | 0.225 | --- | --- | --- | -0.464 | 0.652 | 0.295 |
| Proportion Regenerating Stand | -0.684 | -0.333 | -0.213 | --- | --- | --- | --- | --- | --- | -0.677 | -0.192 | -0.294 |
| Proportion Immature Sawtimber | 1.453 | **0.728** | -0.125 | --- | --- | --- | --- | --- | --- | 0.435 | 0.406 | -0.377 |
| Proportion Mature Sawtimber | **-1.839** | -0.498 | 0.263 | --- | --- | --- | --- | --- | --- | **-2.460** | -0.407 | 0.232 |
| Proportion Individual Tree Selection | **-1.614** | -0.271 | 0.232 | **-1.781** | -0.396 | 0.314 | --- | --- | --- | -0.979 | 0.247 | 0.201 |
| Proportion Two-Age Harvest | -0.058 | 0.188 | 0.295 | --- | --- | --- | --- | --- | --- | 0.743 | 0.143 | -0.021 |
| Stand Age | -0.074 | -0.381 | **-1.026** | --- | --- | --- | --- | --- | --- | -0.220 | -0.284 | -1.012 |
| Stand Age Squared | 1.002 | -0.504 | 0.183 | --- | --- | --- | --- | --- | --- | 0.735 | -0.570 | 0.125 |
| Proportion Forest | 0.073 | -0.470 | **-1.002** | -0.799 | -0.735 | **-0.648** | --- | --- | --- | -0.286 | -0.577 | **-0.796** |
| Proportion Oaks | **-2.519** | -0.660 | -0.389 | --- | --- | --- | --- | --- | --- | -1.408 | 0.197 | -0.158 |
| Proportion Red Spruce | -0.455 | -0.303 | 0.425 | --- | --- | --- | --- | --- | --- | -1.795 | -0.594 | 0.184 |
| Proportion Agriculture | -0.336 | 0.623 | **-1.546** | 1.173 | 0.791 | -0.690 | --- | --- | --- | 0.685 | 1.092 | **-1.209** |
| Proportion Open | 1.071 | -0.038 | -0.137 | --- | --- | --- | --- | --- | --- | -0.571 | -0.237 | -0.264 |

Table 8. Continued.

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Predictor Variable** | **LANDSCAPE** | | | **COMBINED** | | | **CONSTRUCTION** | | | **LOCATION** | | |
| WITU | RUGR | AMWO | WITU | RUGR | AMWO | WITU | RUGR | AMWO | WITU | RUGR | AMWO |
| Opening Type | --- | --- | --- | -0.930 | **2.218** | -0.666 | --- | --- | --- | --- | --- | --- |
| Road Proximity | --- | --- | --- | --- | --- | --- | --- | --- | --- | -1.339 | -0.245 | 0.518 |
| Elevation | --- | --- | --- | **2.093** | **1.312** | 0.246 | --- | --- | --- | **2.318** | **1.438** | 0.685 |
| Elevation Squared | --- | --- | --- | -1.277 | -0.069 | **-1.249** | --- | --- | --- | -0.787 | -0.219 | **-1.253** |
| Aspect | --- | --- | --- | --- | --- | --- | --- | --- | --- | 1.015 | 0.659 | -0.003 |
| TPI | --- | --- | --- | --- | --- | --- | --- | --- | --- | -0.764 | -0.352 | -0.265 |
| Area | --- | --- | --- | -0.420 | -0.591 | 0.597 | -2.000 | **-2.294** | 0.399 | --- | --- | --- |
| Area Squared | --- | --- | --- | 0.286 | 0.478 | 0.020 | **1.301** | **0.941** | -0.008 | --- | --- | --- |
| Edge:Area Ratio | --- | --- | --- | --- | --- | --- | -0.005 | -0.379 | -0.303 | --- | --- | --- |
| Roundness | --- | --- | --- | --- | --- | --- | 0.253 | -0.178 | 0.195 | --- | --- | --- |
| WITU × RUGR | **-2.187** | | | -1.144 | | | -1.464 | | | -0.398 | | |
| WITU × AMWO | **2.140** | | | 2.798 | | | **2.455** | | | 2.109 | | |
| RUGR × AMWO | 0.897 | | | 0.875 | | | **1.171** | | | 0.704 | | |

Table 9. Overall summary of the significance, direction, and magnitude of effects of predictor variables on game bird occupancy (1 = WITU, 2 = RUGR, 3 = AMWO) and guild richness (ALL = all species, ESEA = early-successional and edge-associated songbirds, INT = forest-interior songbirds, GAP = forest-gap songbirds, GEN = forest generalist songbirds). Cell colors indicate a non-significant (gray) or significant negative (blue) / positive (yellow) / quadratic (green) relationship resulting in a change of ≥0.10 in probability of marginal occurrence for game bird species or of ≥1 species for songbird guild richness.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Predictor Variable** | **Game Birds** | | | **Breeding Birds (Opening)** | | | | | | **Breeding Birds (Forest)** | | | | | **Post-breeding Birds** | | | | | |
| 1 | 2 | 3 | ALL | ESEA | INT | GAP | GEN | ALL | | INT | GAP | GEN | ALL | | ESEA | INT | GAP | GEN |
| Opening Type |  |  |  |  |  |  |  |  |  | |  |  |  |  | |  |  |  |  |
| Road Proximity |  |  |  |  |  |  |  |  |  | |  |  |  | --- | | --- | --- | --- | --- |
| Percent Sapling |  |  |  |  |  |  |  |  |  | |  |  |  | --- | | --- | --- | --- | --- |
| Percent Tree Outside Opening |  |  |  |  |  |  |  |  |  | |  |  |  | --- | | --- | --- | --- | --- |
| Canopy Height |  |  |  |  |  |  |  |  |  | |  |  |  | --- | | --- | --- | --- | --- |
| Number Trees |  |  |  |  |  |  |  |  |  | |  |  |  | --- | | --- | --- | --- | --- |
| Elevation |  |  |  |  |  |  |  |  |  | |  |  |  |  | |  |  |  |  |
| Area |  |  |  |  |  |  |  |  |  | |  |  |  |  | |  |  |  |  |
| Number Small Openings |  |  |  |  |  |  |  |  |  | |  |  |  | --- | | --- | --- | --- | --- |
| Number Midsize Openings |  |  |  |  |  |  |  |  |  | |  |  |  | --- | | --- | --- | --- | --- |
| Number Large Openings |  |  |  |  |  |  |  |  |  | |  |  |  | --- | | --- | --- | --- | --- |
| Proportion Wildlife Priority |  |  |  |  |  |  |  |  |  | |  |  |  |  | |  |  |  |  |
| Proportion Mature Sawtimber |  |  |  |  |  |  |  |  |  | |  |  |  |  | |  |  |  |  |
| Proportion Immature Sawtimber |  |  |  |  |  |  |  |  |  | |  |  |  | --- | | --- | --- | --- | --- |
| Proportion Individual Tree Selection |  |  |  |  |  |  |  |  |  | |  |  |  | --- | | --- | --- | --- | --- |
| Stand Age |  |  |  |  |  |  |  |  |  | |  |  |  | --- | | --- | --- | --- | --- |
| Proportion Forest |  |  |  |  |  |  |  |  |  | |  |  |  |  | |  |  |  |  |
| Proportion Oaks |  |  |  |  |  |  |  |  |  | |  |  |  | --- | | --- | --- | --- | --- |
| Proportion Agriculture |  |  |  |  |  |  |  |  |  | |  |  |  |  | |  |  |  |  |

Table 10. Slope coefficient values and significance (bold type) associated with the full set of predictor variables from the 14 guild richness models. Predictor variables are organized by category (management, local habitat, size, and landscape context).

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Predictor Variable** | **Breeding Birds (Opening)** | | | | | **Breeding Birds (Forest)** | | | | **Post-breeding Birds** | | | | |
| ALL | ESEA | INT | GAP | GEN | ALL | INT | GAP | GEN | ALL | ESEA | INT | GAP | GEN |
| Opening Type | **-0.076** | -0.057 | -0.061 | 0.091 | **-0.266** | -0.053 | -0.015 | -0.098 | -0.136 | 0.000 | 0.027 | -0.024 | 0.003 | 0.048 |
| Road Proximity | 0.055 | **0.097** | -0.066 | **0.383** | 0.036 | 0.005 | 0.021 | -0.033 | -0.082 | --- | --- | --- | --- | --- |
| Percent Sapling | **0.032** | **0.030** | 0.032 | 0.007 | 0.054 | 0.024 | -0.014 | 0.038 | **0.118** | --- | --- | --- | --- | --- |
| Percent Tree Outside Opening | **-0.116** | **-0.166** | -0.043 | 0.036 | -0.048 | 0.046 | 0.034 | **0.177** | -0.107 | --- | --- | --- | --- | --- |
| Canopy Height | **-0.036** | 0.013 | **-0.136** | **0.199** | -0.033 | -0.040 | -0.042 | 0.005 | **-0.135** | --- | --- | --- | --- | --- |
| Number Trees | 0.005 | **-0.076** | **0.102** | -0.045 | 0.021 | **-0.082** | **-0.110** | -0.145 | 0.051 | --- | --- | --- | --- | --- |
| Elevation | **-0.149** | **-0.262** | 0.003 | **-0.313** | -0.083 | -0.061 | 0.027 | **-0.645** | -0.190 | **-0.130** | **-0.254** | 0.067 | **-0.629** | **-0.300** |
| Elevation Squared | -0.026 | **-0.092** | **0.067** | -0.090 | -0.022 | **0.055** | **0.053** | 0.043 | 0.032 | 0.012 | -0.025 | 0.022 | -0.093 | -0.011 |
| Area | **0.221** | **0.277** | **0.198** | 0.014 | **0.285** | **0.175** | **0.193** | 0.253 | 0.014 | **0.248** | **0.337** | **0.189** | **0.294** | **0.279** |
| Area Squared | **-0.020** | **-0.024** | **-0.024** | 0.013 | **-0.042** | **-0.031** | **-0.038** | -0.023 | -0.007 | **-0.042** | **-0.047** | **-0.039** | -0.061 | **-0.051** |
| Number Small Openings | 0.011 | 0.005 | -0.018 | 0.080 | **0.094** | 0.016 | -0.009 | **0.205** | 0.023 | --- | --- | --- | --- | --- |
| Number Midsize Openings | -0.008 | **0.053** | -0.043 | -0.058 | **-0.114** | 0.002 | -0.025 | 0.026 | 0.038 | --- | --- | --- | --- | --- |
| Number Large Openings | 0.018 | -0.001 | 0.031 | -0.077 | **0.111** | **-0.118** | **-0.117** | -0.157 | -0.114 | --- | --- | --- | --- | --- |
| Proportion Wildlife Priority | 0.034 | 0.028 | 0.008 | 0.049 | 0.035 | 0.016 | 0.009 | -0.095 | 0.101 | 0.009 | -0.006 | -0.019 | 0.059 | 0.062 |
| Proportion Mature Sawtimber | **-0.077** | -0.013 | **-0.170** | **0.116** | **-0.252** | -0.029 | -0.013 | 0.091 | **-0.161** | -0.019 | -0.033 | -0.011 | -0.034 | 0.001 |
| Proportion Immature Sawtimber | **-0.067** | **-0.072** | **-0.082** | -0.046 | -0.016 | 0.005 | -0.009 | 0.048 | 0.048 | --- | --- | --- | --- | --- |
| Proportion Individual Tree Selection | 0.020 | **0.055** | -0.023 | 0.081 | -0.069 | -0.013 | 0.018 | -0.105 | **-0.177** | --- | --- | --- | --- | --- |
| Stand Age | 0.007 | **-0.039** | **0.110** | -0.006 | -0.019 | 0.023 | 0.023 | 0.027 | 0.071 | --- | --- | --- | --- | --- |
| Proportion Forest | -0.015 | **-0.049** | 0.056 | 0.058 | -0.072 | **-0.047** | **-0.060** | 0.015 | -0.016 | **-0.042** | -0.041 | -0.018 | -0.053 | **-0.103** |
| Proportion Oaks | -0.047 | **-0.108** | -0.067 | 0.159 | 0.120 | -0.022 | 0.009 | **-0.383** | 0.004 | --- | --- | --- | --- | --- |
| Proportion Agriculture | **-0.045** | **-0.057** | -0.073 | -0.039 | -0.019 | -0.030 | **-0.053** | 0.017 | 0.042 | 0.012 | 0.040 | 0.006 | -0.027 | 0.004 |

**Figures**

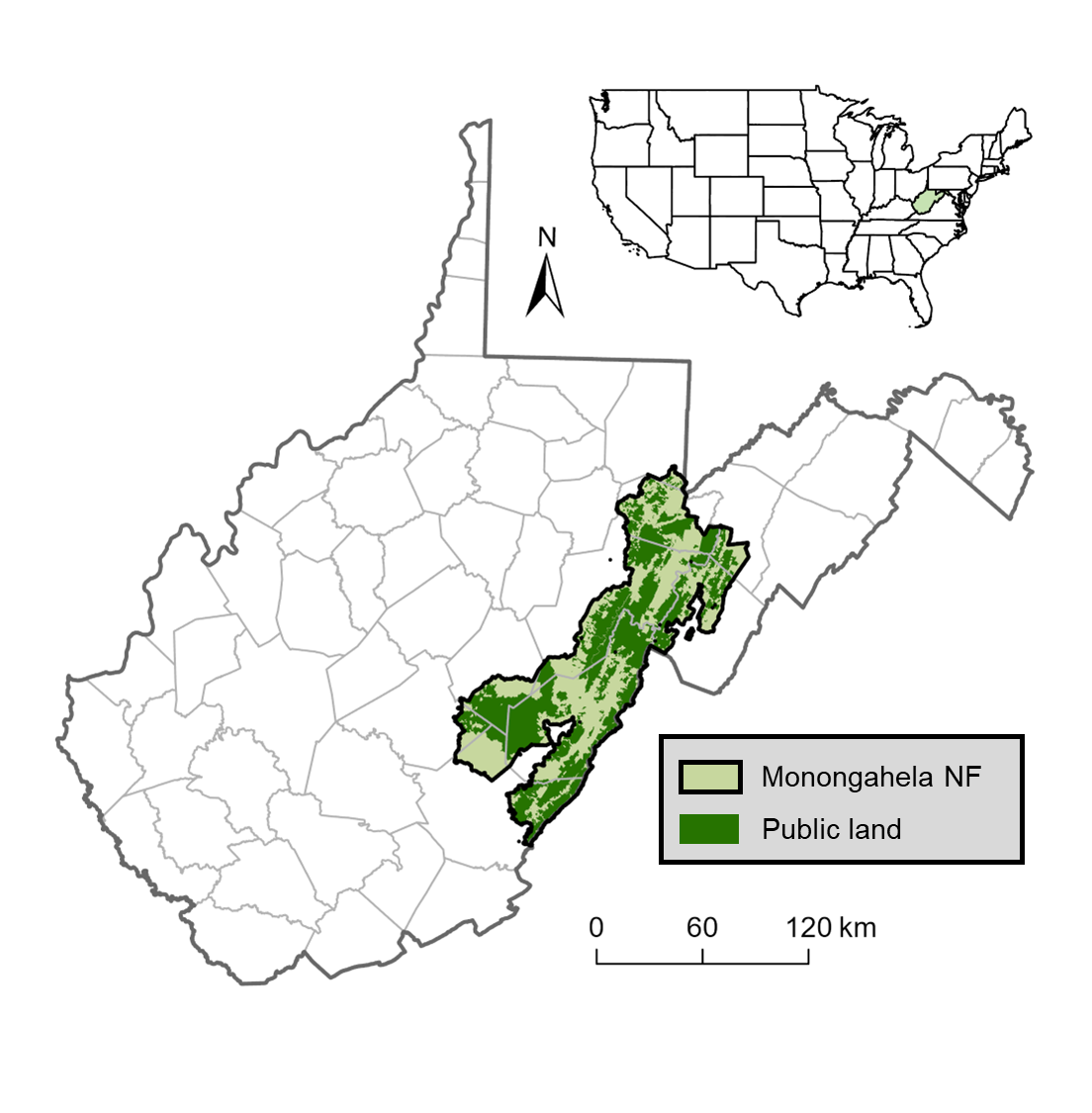


Figure 1. Sampling sites for this study were located throughout the Monongahela National Forest (NF), which encompasses portions of nine counties (delineated by gray lines) in eastern West Virginia. The National Forest encompasses nearly 688,000 ha, of which 54% (371,906 ha) is public land (dark green).

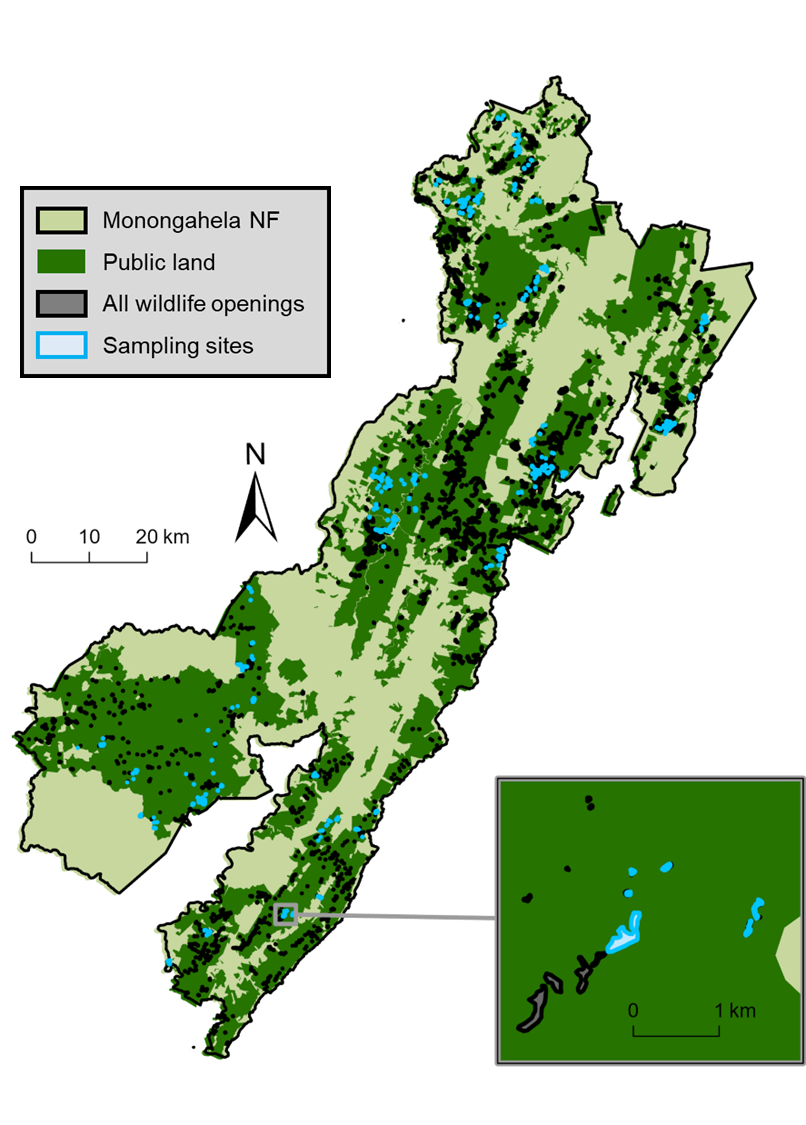


Figure 2. Locations of all recorded wildlife openings (N = ~2,200) and the study sampling sites (N = 335) within the Monongahela National Forest (NF), West Virginia.

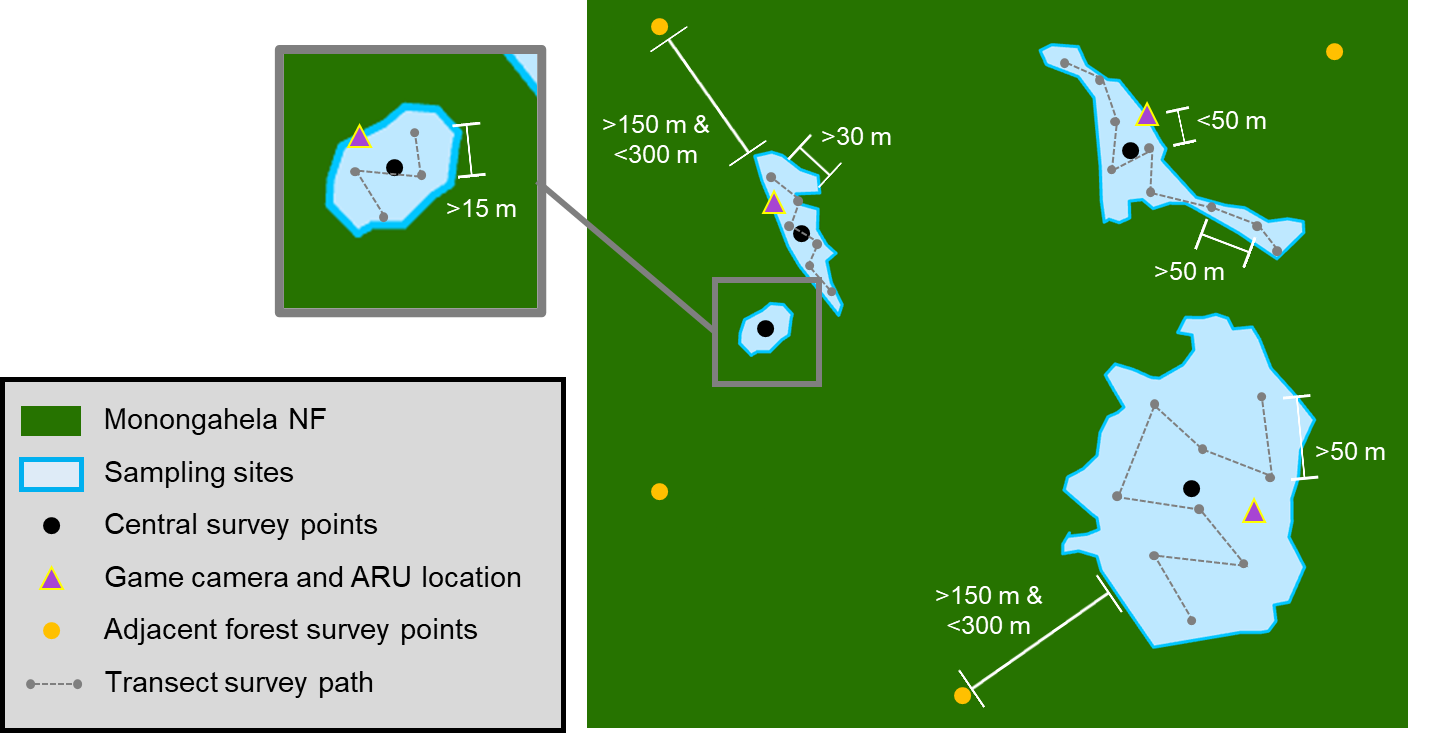


Figure 3. Diagram of a small (<1 ha) wildlife opening (inset), a midsize (1–5 ha) wildlife opening (top left), and 2 large (>5 ha) wildlife openings (right) within the Monongahela National Forest (NF), with their central survey points (black circles), game camera and acoustic recording unit (ARU) survey points (purple triangle), adjacent forest survey points (gold circles), and transect survey points (gray circles) and segments (dashed gray lines). White line segments and labels indicate minimum or maximum distances, such that: game camera and ARU survey points are located within 50 m of the central survey point; adjacent forest survey points are located between 150 and 300 m from the edge of their corresponding wildlife opening; transect segments in small openings are >15 m, transect segments in midsize openings are >30 m, and transect segments in large wildlife openings are >50 m.

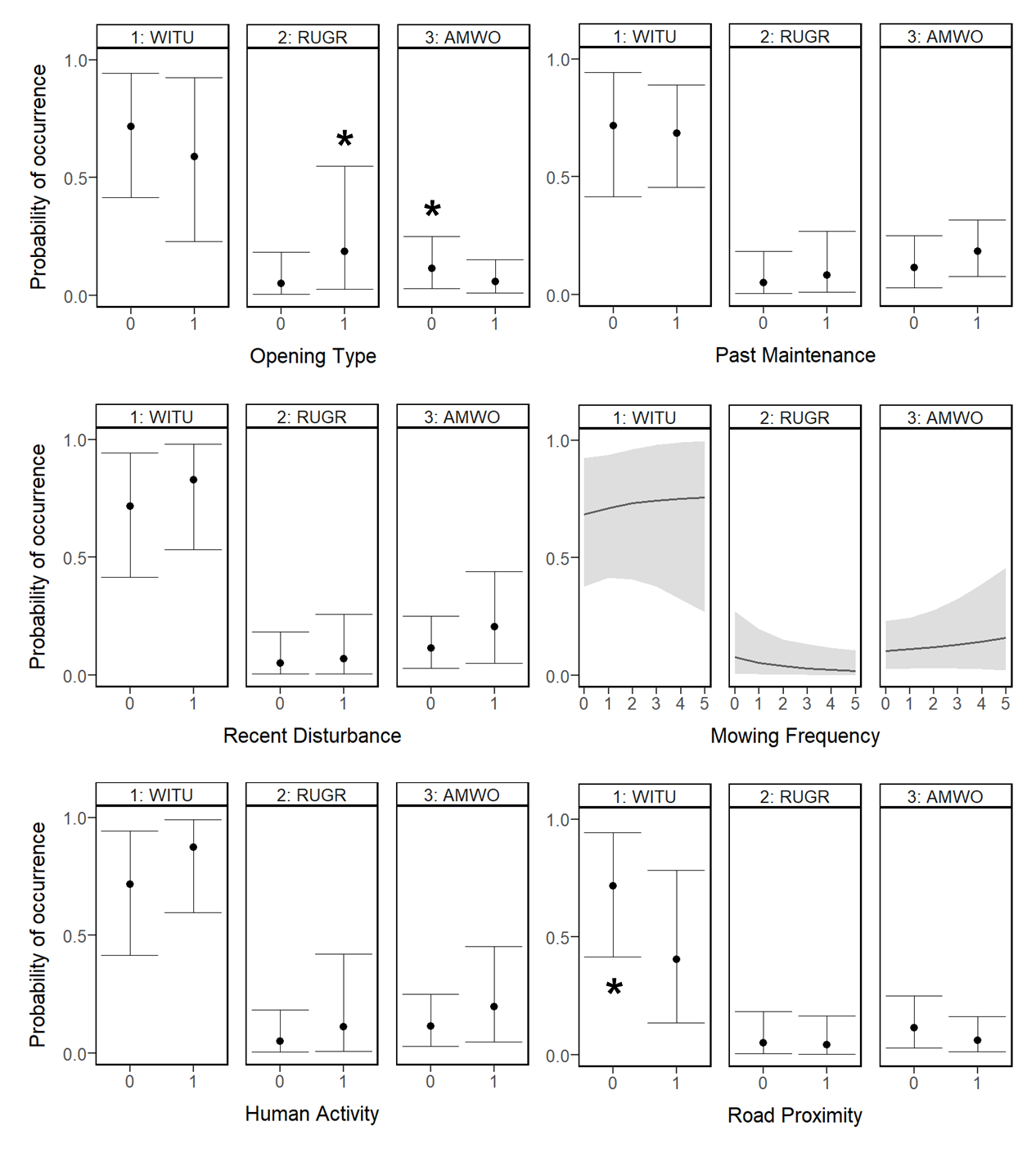


Figure 4. Effects of the 6 predictor variables (Tables 1–2) in the MANAGEMENT candidate model of multi-species game bird occupancy. Bold asterisks indicate significant relationships between the predictor variable and the probability of marginal occurrence of wild turkey (1: WITU), ruffed grouse (2: RUGR), or American woodcock (3: AMWO), with the asterisk aligned with the condition resulting in higher probability of marginal occurrence.

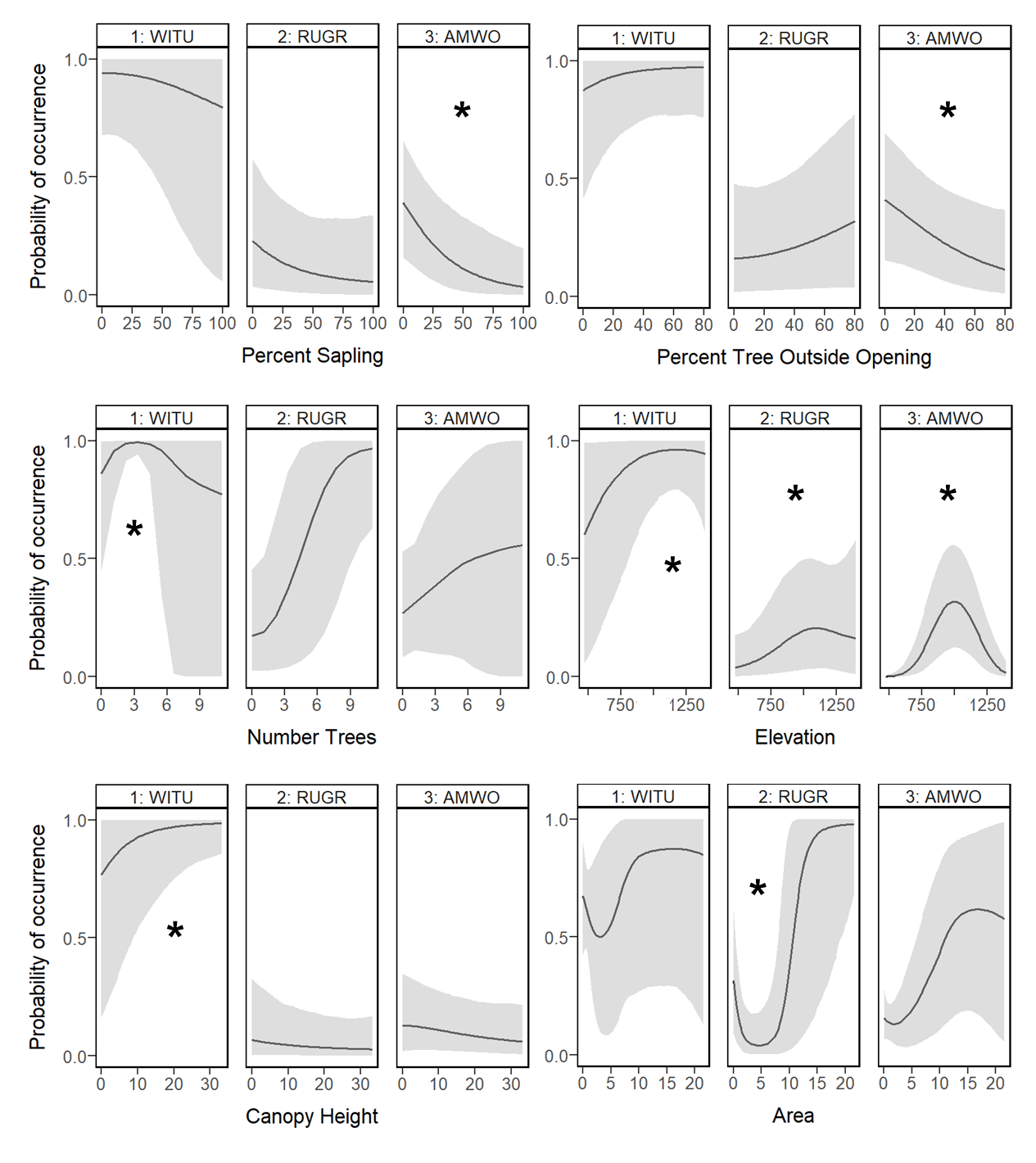


Figure 5. Effects of the significant predictor variables (Tables 1–2, 7) in the HABITAT, CONDITION, and SIZE candidate models of multi-species game bird occupancy. Bold asterisks indicate significant relationships between the predictor variable and the probability of marginal occurrence of wild turkey (1: WITU), ruffed grouse (2: RUGR), or American woodcock (3: AMWO).

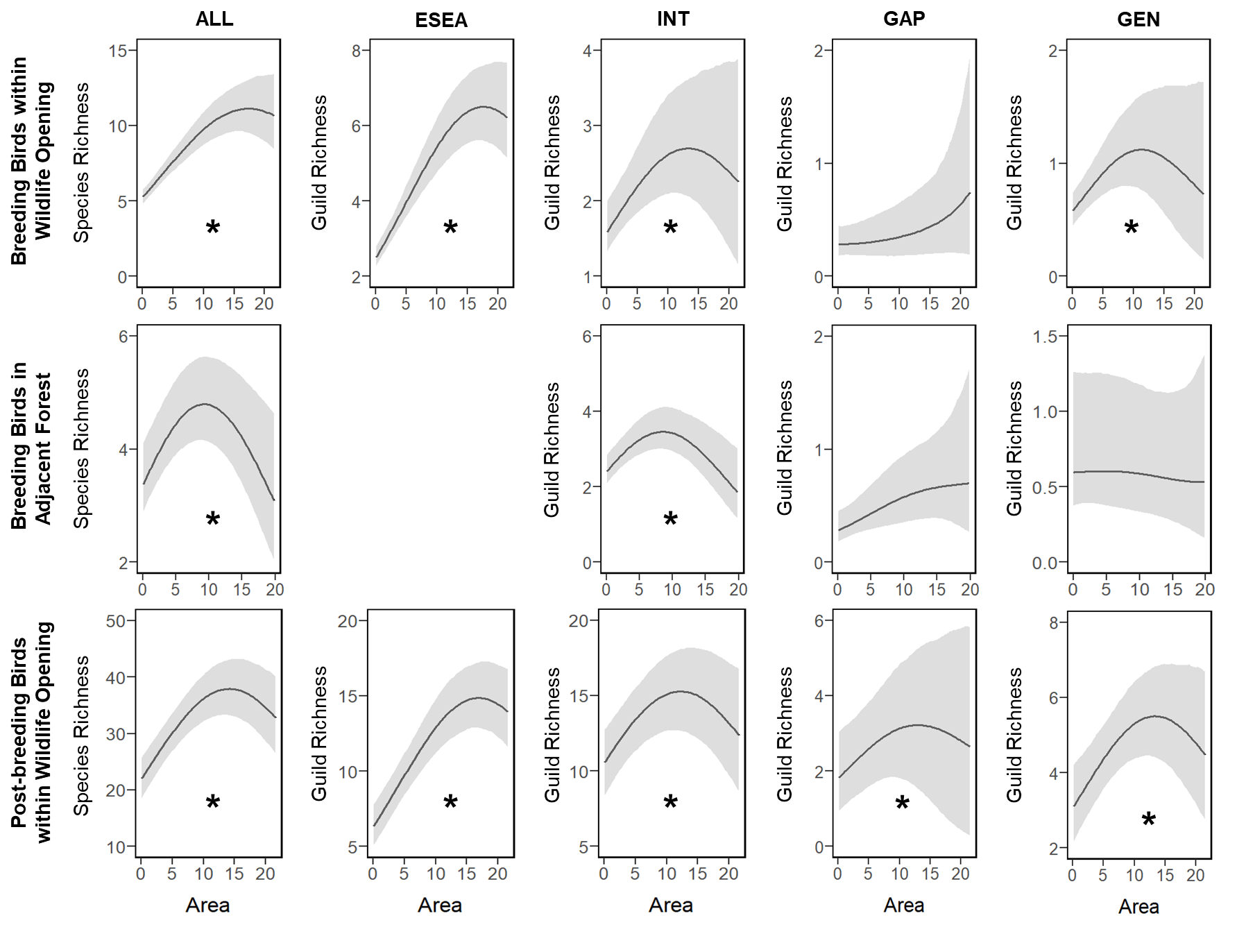


Figure 6. Effects of wildlife opening size (i.e., area in ha) on mean expected overall (ALL) species richness (first column), early-successional and edge-associated (ESEA) guild richness (second column), forest-interior (INT) guild richness (third column), forest-gap (GAP) guild richness (fourth column), and forest generalist (GEN) guild richness (fifth column) during the breeding season within the wildlife opening (first row) and in the adjacent forest (second row), as well as during the post-breeding season within the wildlife opening (third row). Bold asterisks indicate significant relationships between area and the mean expected number of species.

**APPENDICES**

**Appendix A**

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

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

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

Table A1. Continued.

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

Table A1. Continued.

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

Table A1. Continued.

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

**Appendix B**

JAGS model code for the multi-species game bird occupancy analyses.

model{

### PRIOR DISTRIBUTIONS

# SITE COVARIATES - INTERCEPT (alpha0)

alpha0.witu ~ dunif(-10, 10) #WITU

alpha0.rugr ~ dunif(-10, 10) #RUGR

alpha0.amwo ~ dunif(-10, 10) #AMWO

# SITE COVARIATES - SLOPE COEFFICIENTS (alpha)

for(sitecov in 1:n.sitecovs){

alpha.witu[sitecov] ~ dlogis(0, 1) #WITU

alpha.rugr[sitecov] ~ dlogis(0, 1) #RUGR

alpha.amwo[sitecov] ~ dlogis(0, 1) #AMWO

}

# RANDOM YEAR EFFECT (rye) - for modeling natural parameters

tau.rye.witu ~ dgamma(0.1, 0.1) #WITU

tau.rye.rugr ~ dgamma(0.1, 0.1) #RUGR

tau.rye.amwo ~ dgamma(0.1, 0.1) #AMWO

for (year in 1:n.years) {

rye.witu[year] ~ dnorm(alpha0.witu, tau.rye.witu)

rye.rugr[year] ~ dnorm(alpha0.rugr, tau.rye.rugr)

rye.amwo[year] ~ dnorm(alpha0.amwo, tau.rye.amwo)

}

# CO-OCCURENCE - for each two-way combination of game bird species

alpha.witu.rugr ~ dlogis(0, 1) #WITU+RUGR

alpha.witu.amwo ~ dlogis(0, 1) #WITU+AMWO

alpha.rugr.amwo ~ dlogis(0, 1) #RUGR+AMWO

# DETECTION COVARIATES - INTERCEPT (beta0)

beta0.witu.pcs ~ dunif(-10, 10) #WITU in-person point count survey

beta0.rugr.pcs ~ dunif(-10, 10) #RUGR in-person point count survey

beta0.amwo.pcs ~ dunif(-10, 10) #AMWO in-person point count survey

beta0.witu.gc ~ dunif(-10, 10) #WITU game camera survey

beta0.witu.aru ~ dunif(-10, 10) #WITU acoustic recording unit survey

beta0.amwo.aru ~ dunif(-10, 10) #AMWO acoustic recording unit survey

# DETECTION COVARIATES - SLOPE COEFFICIENTS (beta)

for(detcov in 1:n.detcovs.witu.rugr.pcs){

beta.witu.pcs[detcov] ~ dlogis(0, 1) #WITU in-person point count survey

beta.rugr.pcs[detcov] ~ dlogis(0, 1) #RUGR in-person point count survey

}

for(detcov in 1:n.detcovs.amwo.pcs){

beta.amwo.pcs[detcov] ~ dlogis(0, 1) #AMWO in-person point count survey

}

for(detcov in 1:n.detcovs.gc){

beta.witu.gc[detcov] ~ dlogis(0, 1) #WITU game camera survey

}

for(detcov in 1:n.detcovs.aru){

beta.witu.aru[detcov] ~ dlogis(0, 1) #WITU ARU survey

beta.amwo.aru[detcov] ~ dlogis(0, 1) #AMWO ARU survey

}

# RANDOM OBSERVER EFFECT (roe)

tau.roe.witu ~ dgamma(0.1, 0.1) #WITU

tau.roe.rugr ~ dgamma(0.1, 0.1) #RUGR

tau.roe.amwo ~ dgamma(0.1, 0.1) #AMWO

for (observer in 1:n.observers.witu.rugr) {

roe.witu[observer] ~ dnorm(beta0.witu.pcs, tau.roe.witu)

roe.rugr[observer] ~ dnorm(beta0.rugr.pcs, tau.roe.rugr)

}

for (observer in 1:n.observers.amwo) {

roe.amwo[observer] ~ dnorm(beta0.amwo.pcs, tau.roe.amwo)

}

# RANDOM ARU TYPE EFFECT (rate)

tau.rate.witu ~ dgamma(0.1, 0.1) #WITU

tau.rate.amwo ~ dgamma(0.1, 0.1) #AMWO

for (aru.type in 1:n.aru.types) {

rate.witu[aru.type] ~ dnorm(beta0.witu.aru, tau.rate.witu)

rate.amwo[aru.type] ~ dnorm(beta0.amwo.aru, tau.rate.amwo)

}

### LIKELIHOOD

for(site in 1:n.sites){

# NATURAL PARAMETERS

f.witu[site] <- inprod(alpha.witu[1:n.sitecovs],

sitecov.matrix[site, 1:n.sitecovs]) + rye.witu[year.id[site]]

f.rugr[site] <- inprod(alpha.rugr[1:n.sitecovs],

sitecov.matrix[site, 1:n.sitecovs]) + rye.rugr[year.id[site]]

f.amwo[site] <- inprod(alpha.amwo[1:n.sitecovs],

sitecov.matrix[site, 1:n.sitecovs]) + rye.amwo[year.id[site]]

f.witu.rugr[site] <- alpha.witu.rugr

f.witu.amwo[site] <- alpha.witu.amwo

f.rugr.amwo[site] <- alpha.rugr.amwo

# PROBABILITY OF EACH COMBINATION OF 1 AND 0

Psi[site, 1] <- exp(f.witu[site] + f.rugr[site] + f.amwo[site] +

f.witu.rugr[site] + f.witu.amwo[site] + f.rugr.amwo[site]) \* no.extra.detections.vector[site]

Psi[site, 2] <- exp(f.witu[site] + f.rugr[site] + f.witu.rugr[site]) \*

no.extra.detections.vector[site]

Psi[site, 3] <- exp(f.witu[site] + f.amwo[site] + f.witu.amwo[site]) \*

no.extra.detections.vector[site]

Psi[site, 4] <- exp(f.witu[site]) \* no.extra.detections.vector[site]

Psi[site, 5] <- exp(f.rugr[site] + f.amwo[site] + f.rugr.amwo[site]) \*

no.extra.detections.vector[site]

Psi[site, 6] <- exp(f.rugr[site]) \* no.extra.detections.vector[site]

Psi[site, 7] <- exp(f.amwo[site]) \* no.extra.detections.vector[site]

Psi[site, 8] <- 1 \* no.extra.detections.vector[site]

Psi.WITU[site, 1] <- exp(f.witu[site] + f.rugr[site] + f.amwo[site] +

f.witu.rugr[site] + f.witu.amwo[site] + f.rugr.amwo[site]) \* known.witu.vector[site]

Psi.WITU[site, 2] <- exp(f.witu[site] + f.rugr[site] + f.witu.rugr[site])

\* known.witu.vector[site]

Psi.WITU[site, 3] <- exp(f.witu[site] + f.amwo[site] + f.witu.amwo[site])

\* known.witu.vector[site]

Psi.WITU[site, 4] <- exp(f.witu[site]) \* known.witu.vector[site]

Psi.WITU[site, 5] <- 0

Psi.WITU[site, 6] <- 0

Psi.WITU[site, 7] <- 0

Psi.WITU[site, 8] <- 0

Psi.RUGR[site, 1] <- exp(f.witu[site] + f.rugr[site] + f.amwo[site] +

f.witu.rugr[site] + f.witu.amwo[site] + f.rugr.amwo[site]) \* known.rugr.vector[site]

Psi.RUGR[site, 2] <- exp(f.witu[site] + f.rugr[site] + f.witu.rugr[site])

\* known.rugr.vector[site]

Psi.RUGR[site, 3] <- 0

Psi.RUGR[site, 4] <- 0

Psi.RUGR[site, 5] <- exp(f.rugr[site] + f.amwo[site] + f.rugr.amwo[site])

\* known.rugr.vector[site]

Psi.RUGR[site, 6] <- exp(f.rugr[site]) \* known.rugr.vector[site]

Psi.RUGR[site, 7] <- 0

Psi.RUGR[site, 8] <- 0

Psi.AMWO[site, 1] <- exp(f.witu[site] + f.rugr[site] + f.amwo[site] +

f.witu.rugr[site] + f.witu.amwo[site] + f.rugr.amwo[site]) \* known.amwo.vector[site

Psi.AMWO[site, 2] <- 0

Psi.AMWO[site, 3] <- exp(f.witu[site] + f.amwo[site] + f.witu.amwo[site])

\* known.amwo.vector[site

Psi.AMWO[site, 4] <- 0

Psi.AMWO[site, 5] <- exp(f.rugr[site] + f.amwo[site] + f.rugr.amwo[site])

\* known.amwo.vector[site]

Psi.AMWO[site, 6] <- 0

Psi.AMWO[site, 7] <- exp(f.amwo[site]) \* known.amwo.vector[site]

Psi.AMWO[site, 8] <- 0

Psi.WITU.RUGR[site, 1] <- exp(f.witu[site] + f.rugr[site] + f.amwo[site]

+ f.witu.rugr[site] + f.witu.amwo[site] + f.rugr.amwo[site]) \* known.witu.rugr.vector[site]

Psi.WITU.RUGR[site, 2] <- exp(f.witu[site] + f.rugr[site] +

f.witu.rugr[site]) \* known.witu.rugr.vector[site]

Psi.WITU.RUGR[site, 3] <- 0

Psi.WITU.RUGR[site, 4] <- 0

Psi.WITU.RUGR[site, 5] <- 0

Psi.WITU.RUGR[site, 6] <- 0

Psi.WITU.RUGR[site, 7] <- 0

Psi.WITU.RUGR[site, 8] <- 0

Psi.TOTAL[site,1] <- Psi[site,1] + Psi.WITU[site,1] + Psi.RUGR[site,1] +

Psi.AMWO[site,1] + Psi.WITU.RUGR[site,1]

Psi.TOTAL[site,2] <- Psi[site,2] + Psi.WITU[site,2] + Psi.RUGR[site,2] +

Psi.AMWO[site,2] + Psi.WITU.RUGR[site,2]

Psi.TOTAL[site,3] <- Psi[site,3] + Psi.WITU[site,3] + Psi.RUGR[site,3] +

Psi.AMWO[site,3] + Psi.WITU.RUGR[site,3]

Psi.TOTAL[site,4] <- Psi[site,4] + Psi.WITU[site,4] + Psi.RUGR[site,4] +

Psi.AMWO[site,4] + Psi.WITU.RUGR[site,4]

Psi.TOTAL[site,5] <- Psi[site,5] + Psi.WITU[site,5] + Psi.RUGR[site,5] +

Psi.AMWO[site,5] + Psi.WITU.RUGR[site,5]

Psi.TOTAL[site,6] <- Psi[site,6] + Psi.WITU[site,6] + Psi.RUGR[site,6] +

Psi.AMWO[site,6] + Psi.WITU.RUGR[site,6]

Psi.TOTAL[site,7] <- Psi[site,7] + Psi.WITU[site,7] + Psi.RUGR[site,7] +

Psi.AMWO[site,7] + Psi.WITU.RUGR[site,7]

Psi.TOTAL[site,8] <- Psi[site,8] + Psi.WITU[site,8] + Psi.RUGR[site,8] +

Psi.AMWO[site,8] + Psi.WITU.RUGR[site,8]

# LATENT OCCUPANCY STATE

Z[site] ~ dcat(Psi.TOTAL[site, 1:8])

z.witu[site] <- (Z[site] == 1) + (Z[site] == 2) + (Z[site] == 3) +

(Z[site] == 4)

z.rugr[site] <- (Z[site] == 1) + (Z[site] == 2) + (Z[site] == 5) +

(Z[site] == 6)

z.amwo[site] <- (Z[site] == 1) + (Z[site] == 3) + (Z[site] == 5) +

(Z[site] == 7)

# DETECTION PROCESS FOR WITU AND RUGR POINT COUNT SURVEYS (pcs)

for(replicate in 1:n.replicates.witu.rugr.pcs[site]){

# CONDITIONAL DETECTION PROBABILITY

logit(p.witu.pcs[site, replicate]) <-

inprod(beta.witu.pcs[1:n.detcovs.witu.rugr.pcs],

detcov.array.witu.rugr.pcs[site, replicate, 1:n.detcovs.witu.rugr.pcs]) + roe.witu[observer.id.witu.rugr[site, replicate]]

logit(p.rugr.pcs[site, replicate]) <-

inprod(beta.rugr.pcs[1:n.detcovs.witu.rugr.pcs], detcov.array.witu.rugr.pcs[site, replicate, 1:n.detcovs.witu.rugr.pcs]) + roe.rugr[observer.id.witu.rugr[site, replicate]]

# DETECTION MODEL

y.witu.pcs[site, replicate] ~ dbern(z.witu[site] \* p.witu.pcs[site,

replicate])

y.rugr.pcs[site, replicate] ~ dbern(z.rugr[site] \* p.rugr.pcs[site,

replicate])

} # END REPLICATE LOOP FOR WITU AND RUGR POINT COUNT SURVEYS (pcs)

# DETECTION PROCESS FOR AMWO POINT COUNT SURVEYS (pcs)

for(replicate in 1:n.replicates.amwo.pcs[site]){

# CONDITIONAL DETECTION PROBABILITY

logit(p.amwo.pcs[site, replicate]) <-

inprod(beta.amwo.pcs[1:n.detcovs.amwo.pcs], detcov.matrix.amwo.pcs[site, 1:n.detcovs.amwo.pcs]) + roe.amwo[observer.id.amwo[site]]

# DETECTION MODEL

y.amwo.pcs[site, replicate] ~ dbern(z.amwo[site] \* p.amwo.pcs[site,

replicate])

} # END REPLICATE LOOP FOR AMWO POINT COUNT SURVEYS (pcs)

# DETECTION PROCESS FOR GAME CAMERA SURVEYS (gc)

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

# CONDITIONAL DETECTION PROBABILITY

logit(p.witu.gc[site, replicate]) <- beta0.witu.gc +

inprod(beta.witu.gc[1:n.detcovs.gc], detcov.matrix.gc[site, 1:n.detcovs.gc])

# DETECTION MODEL

y.witu.gc[site, replicate] ~ dbern(z.witu[site] \* p.witu.gc[site,

replicate])

} # END REPLICATE LOOP FOR GAME CAMERA SURVEYS (gc)

# DETECTION PROCESS FOR ACOUSTIC RECORDING UNIT SURVEYS (aru)

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

# CONDITIONAL DETECTION PROBABILITY

logit(p.witu.aru[site, replicate]) <-

inprod(beta.witu.aru[1:n.detcovs.aru], detcov.matrix.aru[site, 1:n.detcovs.aru]) + rate.witu[aru.type.id[site]]

logit(p.amwo.aru[site, replicate]) <-

inprod(beta.amwo.aru[1:n.detcovs.aru], detcov.matrix.aru[site, 1:n.detcovs.aru]) + rate.amwo[aru.type.id[site]]

# DETECTION MODEL

y.witu.aru[site, replicate] ~ dbern(z.witu[site] \* p.witu.aru[site,

replicate])

y.amwo.aru[site, replicate] ~ dbern(z.amwo[site] \* p.amwo.aru[site,

replicate])

} # END REPLICATE LOOP FOR ACOUSTIC RECORDING UNIT SURVEYS (aru)

} # END SITE LOOP

}

**Appendix C**

Table of model information associated with the multi-species game bird occupancy candidate models and hierarchical community models.

Table C1. List of the 8 multi-species game bird occupancy candidate models (HABITAT, SIZE, MANAGEMENT, LANDSCAPE, LOCATION, CONSTRUCTION, CONDITION, COMBINED) and 3 hierarchical community models (HCM 1 = breeding songbirds within wildlife openings, HCM 2 = breeding songbirds in the adjacent forest, HCM 3 = post-breeding songbirds within wildlife openings), with corresponding model information that includes the number of chains (Chains), total iterations (Total), burn-in (Burn), thinning rate (Thin), and resulting posterior iterations (Posterior).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model** | **Chains** | **Total** | **Burn-In** | **Thin** | **Posterior** | |
| HABITAT | 3 | 20,000 | 10,000 | 5 | 6,000 |
| SIZE | 3 | 25,000 | 10,000 | 5 | 9,000 |
| MANAGEMENT | 3 | 20,000 | 10,000 | 5 | 6,000 |
| LANDSCAPE | 3 | 25,000 | 10,000 | 5 | 9,000 |
| LOCATION | 3 | 20,000 | 10,000 | 5 | 6,000 |
| CONSTRUCTION | 3 | 20,000 | 10,000 | 5 | 6,000 |
| CONDITION | 3 | 25,000 | 10,000 | 5 | 9,000 |
| COMBINED | 3 | 25,000 | 10,000 | 5 | 9,000 |
| HCM 1 | 3 | 15,000 | 10,000 | 5 | 3,000 |
| HCM 2 | 3 | 25,000 | 10,000 | 5 | 9,000 |
| HCM 3 | 3 | 15,000 | 10,000 | 5 | 3,000 |

**Appendix D**

JAGS model code for the guild richness analyses

model {

### PRIORS

# COMMUNITY-LEVEL MODEL PARAMETERS (OCCUPANCY)

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

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

# COMMUNITY-LEVEL MODEL PARAMETERS (DETECTION)

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

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

# COMMUNITY-LEVEL PARAMETERS FOR SITE COVARIATE SLOPE COEFFICIENTS

for (sitecov in 1:n.sitecovs) {

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

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

}

# COMMUNITY-LEVEL PARAMETERS FOR DETECTION COVARIATE SLOPE COEFFICIENTS

for (detcov in 1:n.detcovs) {

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

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

}

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

for (species in 1:n.species) {

# INTERCEPTS

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

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

# SLOPE COEFFICIENTS FOR SITE COVARIATES

for (sitecov in 1:n.sitecovs) {

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

tau.alpha[sitecov])

}

# RANDOM YEAR EFFECT

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

for (year in 1:n.years) {

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

tau.rye[species])

}

# SLOPE COEFFICIENTS FOR DETECTION COVARIATES

for (detcov in 1:n.detcovs) {

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

}

# RANDOM OBSERVER EFFECT

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

for (observer in 1:n.observers) {

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

tau.roe[species])

}

}

# NOTES: Loop over all species.

### LIKELIHOOD

for (species in 1:n.species) {

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

for (site in 1:n.sites){

# OCCUPANCY MODEL

logit(psi[site, species]) <-

inprod(alpha[species, 1:n.sitecovs],

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

random.year.effect[species, year.id[site]]

# ESTIMATING OCCUPANCY

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

# Loop to estimate detection

for (replicate in 1:n.replicates) {

# DETECTION MODEL

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

inprod(beta[species, 1:n.detcovs],

detcov.array[site, replicate, 1:n.detcovs]) +

random.observer.effect[species, observer.id[site]]

# ESTIMATING PROBABILITY OF DETECTION

mu.p[site, replicate, species] <- p[site, replicate, species] \*

Z[site, species]

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

species])

} # end replicate loop

} #end site loop

} #end species loop

### DERIVED QUANTITIES

# Loop to determine site-level richness estimates

for (site in 1:n.sites) {

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

es.ea.guild.richness[site] <- inprod(Z[site, 1:n.species],

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

forest.interior.guild.richness[site] <- inprod(Z[site, 1:n.species],

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

forest.gap.guild.richness[site] <- inprod(Z[site, 1:n.species],

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

generalist.guild.richness[site] <- inprod(Z[site, 1:n.species],

generalist.guild[1:n.species])

} #end site loop

}