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Distinct forest bird communities are strongly associated with red spruce-northern hardwood ecosystems in Central Appalachia, USA

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A R T I C L E I N F O

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A B S T R A C T

Degraded red spruce (*Picea rubens*)-northern hardwood ecosystems are the focus of restoration efforts across high-elevation landscapes in the Central Appalachian region of the eastern United States. To promote ecosystem function and long-term sustainability of restored forests, it is important to understand the associated biota, including bird communities. Certain bird species could serve as ecological indicators, with potential applications for evaluating restoration efforts. However, contemporary and statistically rigorous studies of red spruce bird communities in this region are lacking, as is a formal analysis of indicator species. The purpose of this study was to use multivariate regression trees and indicator species analyses to determine if bird communities and individual bird species, respectively, are strongly associated with the red spruce-northern hardwood ecosystem in Central Appalachia. Specifically, we assessed those associations with three distinct but complementary sets of forest characteristics, focusing on (1) red spruce and northern hardwood forest types, (2) classes of percent red spruce cover, and (3) red spruce and northern hardwood stand size classes. Community-wide avian point count survey data were collected in mid-May to mid-July 2010–2019 at 645 sampling points located in forest stands throughout the Monongahela National Forest in West Virginia. We found that red spruce and northern hardwood forest types had distinct bird communities within the study area, and that community composition differed among red spruce cover classes. In addition, forest type was more influential on bird community composition than stand size class (poletimber or sawtimber). Eleven indicator species were consistently associated with red spruce forests, whereas fewer species were identified as indicator species for northern hardwood forests. Ultimately, the distinctiveness of the bird community in red spruce forests and strength of those associations highlight the critical need for and importance of restoration efforts targeting red spruce-northern hardwood ecosystems in the Central Appalachians to ensure long-term maintenance of regional avian diversity.

1. Introduction

Habitat or ecosystem restoration is the process of actively assisting in the recovery of natural systems that were previously degraded, damaged, or destroyed (Hobbs and Norton, 1996). To achieve restoration goals, which often incorporate promoting ecosystem function and biodiversity (Strassburg et al., 2020), it is important to understand the biotic communities associated with or even restricted to the focal ecosystem. Species are often strongly associated with specific habitat types or conditions, which is the underlying tenant of the indicator species concept. Indicator species are defined as species that can be used to gain information about environmental conditions due to their niche preferences (McGeoch and Chown, 1998; Carignan and Villard, 2002; Niemi and McDonald, 2004). For example, they can be used to predict site characteristics, assess the condition of the environment, or evaluate the impacts of environmental changes on an ecosystem and potentially diagnose the cause of those changes (Carignan and Villard, 2002; Niemi and McDonald, 2004). Thus, indicator species analyses have many potential applications in the field of restoration ecology.

Restoring degraded forest ecosystems is a common focus of applied forestry research and conservation efforts in the United States and other countries (Keddy and Drummond, 1996; Chazdon, 2008). One example

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of a degraded forest ecosystem receiving extensive attention from both private organizations and government agencies is red spruce (*Picea rubens*) forest communities in the central and southern Appalachian Mountains. Prior to European settlement, West Virginia (located in the Central Appalachians) had an estimated 600,000 ha of subalpine coniferous forests, with red spruce comprising approximately 50% of overstory trees and occurring in conjunction with northern hardwood species such as yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), black cherry (*Prunus serotina*), and eastern hemlock (*Tsuga canadensis*) (Hopkins, 1899). Between 1880 and 1920, red spruce-northern hardwood forest communities were subjected to widespread timber harvest and repeated fires (Rentch et al., 2010). Those large-scale, high-intensity disturbances resulted in a more homogenous landscape in which structurally complex, multi-aged forests formerly dominated by red spruce were replaced by even-aged northern hardwoods, with negligible red spruce regeneration (Schuler et al., 2002). It is estimated that no more than 21,000 ha (and perhaps less than 10,000 ha) of red spruce-dominated forests remain in West Virginia (Griffith and Widmann, 2003; Rentch et al., 2016). Thus, red spruce forests in the Central Appalachians have been considered one of the most at-risk forest systems in the United States (Christensen et al., 1996; Noss et al., 1995), and concerns about the conservation status of these ecosystems have provided impetus for focused research (e.g., Rentch et al., 2007; Rollins et al., 2010) and recent restoration efforts (Rentch et al., 2010).

The Monongahela National Forest (MNF), located in eastern West Virginia, contains the majority of current red spruce forest in the Central Appalachian region (Stephenson and Clovis, 1983; Rentch et al., 2010), with most red spruce forest patches restricted to a fragmented distribution on high peaks and ridgelines (Adams and Stephenson, 1989). In 2006, the MNF revised its Land Management Plan to include passive and active restoration projects on >60,000 ha (USDA Forest Service, 2006). Soon after, the Central Appalachian Spruce Restoration Initiative (CASRI) was established as a partnership among private, state, federal, and non-governmental organizations with a shared desire to restore historic red spruce-northern hardwood ecosystems across high-elevation landscapes of Central Appalachia. Since 2007, CASRI has completed habitat restoration projects across thousands of hectares of land and planted approximately one million trees (K. Barlow, The Nature Conservancy, personal communication).

The primary goal of CASRI is to restore red spruce-northern hardwood forests in portions of their former range, with the scale, connectivity, maturity, and other features that promote full ecosystem function and sustainability over time. A major component of terrestrial ecosystem integrity is providing high quality habitat for wildlife species (Woodley et al., 1993; Keddy and Drummond, 1996; Tierney et al., 2009). Two prominent species that are strongly associated with red spruce forests of eastern West Virginia are the federally threatened Cheat Mountain salamander (*Plethodon nettingi*; Pauley, 2008) and the recently de-listed Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*; Ford et al., 2004). However, the use of these species as indicators of integrity of restored red spruce forests is limited by their highly restricted distributions, associations with mature forest conditions, and sampling difficulty (Menzel et al., 2006; Pauley, 2007; Dillard et al., 2008).

Avian species are often used as ecological indicators of habitat quality or community metrics (e.g., Keddy and Drummond, 1996; Canterbury et al., 2000; Gregory et al., 2003; Loman et al., 2021), and thus may be valuable indicators of red spruce forest integrity. Previous studies have highlighted bird communities in spruce-fir forests of the southern Appalachian Mountains (e.g., Rabenold, 1978), and three published studies have documented the presence of breeding bird species such as Blackburnian warblers (*Setophaga fusca*) and golden-crowned kinglets (*Regulus satrapa*) in red spruce stands within the Central Appalachians (Stewart and Aldrich, 1949; Hall, 1984; Kahler and Anderson, 2010). However, contemporary and statistically rigorous studies are lacking in this region, as is a formal indicator species analysis (e.g., Dufrene and Legendre, 1997).

Explicitly identifying and delineating biotic communities of threatened ecosystems is a critical step in understanding how they function and assessing long-term sustainability of restoration efforts. Because birds are both relatively easy to detect and inexpensive to survey (Ralph et al., 1995; Matsuoka et al., 2014), avian indicators can further serve as a simple, cost- and time-efficient tool for land managers and organizations such as CASRI to evaluate and compare the conditions of existing and restored forests. Therefore, the purpose of this study was to determine if Central Appalachian red spruce and northern hardwood forests have distinct bird communities, and to identify individual bird species that are strong indicators for these forest types. Specifically, we assessed community composition and indicator species for (1) red spruce and northern hardwood forest types, (2) classes of percent red spruce cover, and (3) size classes of red spruce and northern hardwood forest stands. The results of this study will contribute to our understanding of the importance of the red spruce-northern hardwood ecosystem to avian communities and identify specific bird species that could be used as indicators of ecological integrity for restored red spruce forests.

2. Material and methods

2.1. Study area

This study incorporates data collected from 645 sampling points spread throughout public lands within the MNF in West Virginia, which is located in the Central Appalachian region of the eastern United States (Fig. 1). The MNF was established in 1920 and includes 371,906 ha of public lands overseen by the U.S. Forest service within a proclamation boundary of nearly 688,000 ha. 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 (Clarkson, 1966). Elevation within the MNF ranges 275–1480 m.

The MNF is comprised primarily of 70–100 year-old stands with high regional tree diversity and four broad forest zones (Clarkson, 1966). Mixed mesophytic forests are present at low elevations (<900 m), with northern red oak (*Quercus rubra*), hickory (*Carya* spp.), and yellow-poplar (*Liriodendron tulipifera*) as the dominant species. At increasing elevations, there is a transition in stand dominance to northern hardwoods, including American beech, sugar maple, and black cherry. At the highest elevations (>1,150 m), stands of red spruce exist in remnant or actively restored populations of varying size classes. In the eastern MNF, dry oaks (encompassing several finer-scale forest types dominated by oaks and pines) are common in the Ridge and Valley area, consisting of white (*Quercus alba*), chestnut (*Q. montana*), scarlet (*Q. coccinea*), and black (*Q. velutina*) oaks, as well as pines (*Pinus* spp.).

2.2. Data collection

Between 16 May and 15 July in 2010–2019, breeding bird communities were sampled with 10-minute, 50-m radius, stationary point count surveys at the 645 sampling points located throughout the four major forest zones. For all years of data collection, point count surveys were conducted once during the breeding season, beginning within 15 min of sunrise and ending by 1100. Observers, who were skilled in bird identification by sight and sound, recorded the species of all individuals seen or heard during the 10-minute survey period, excluding flyovers. In accordance with standard protocols (Ralph et al., 1995), no surveys were conducted during days with rain, heavy fog, or high wind.

All sampling points were in unharvested forest stands, with >75% mature forest and no open or early-successional habitat within a 50-m radius of the point count survey location, and at least 250 m from the closest neighboring sampling point. Annual efforts were variable and resulted in a total of 1,243 point count surveys conducted across all sampling points and years, with a range of 1–5 years of bird survey data corresponding to individual points (Fig. 1). Twenty-five sampling points

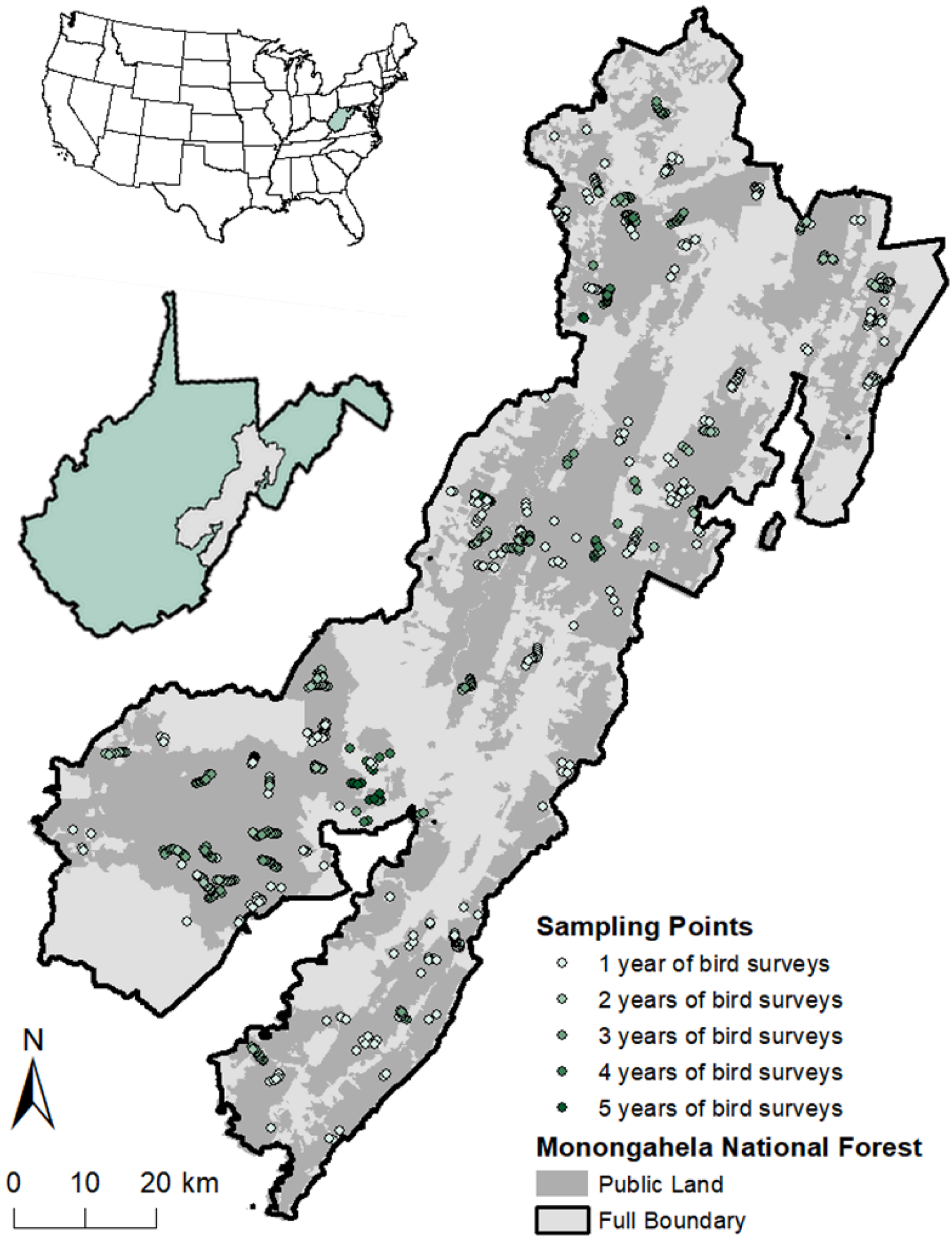

Fig. 1. Spatial map of 645 sampling points surveyed during 2010–2019 within public lands of the Monongahela National Forest in West Virginia, which is located in the Central Appalachian region of the eastern United States.

were surveyed in 5 different years, 34 were surveyed in 4 years, 126 were surveyed in 3 years, 144 were surveyed in 2 years, and 316 were surveyed in a single year.

We assigned categorical forest types, red spruce cover classes, and stand-specific red spruce and northern hardwood size classes to each sampling point. Seven forest type categories (Fig. 2A) were derived from 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). Each sampling point was assigned the dominant (i.e., mode) forest type within a 50-m radius of the point count location. We assumed that the forest type was static across the 10 years (i.e., 2010–2019) of the study and therefore did not consider year when designating the forest type.

Red spruce cover classes (Fig. 2B) and stand-specific size classes

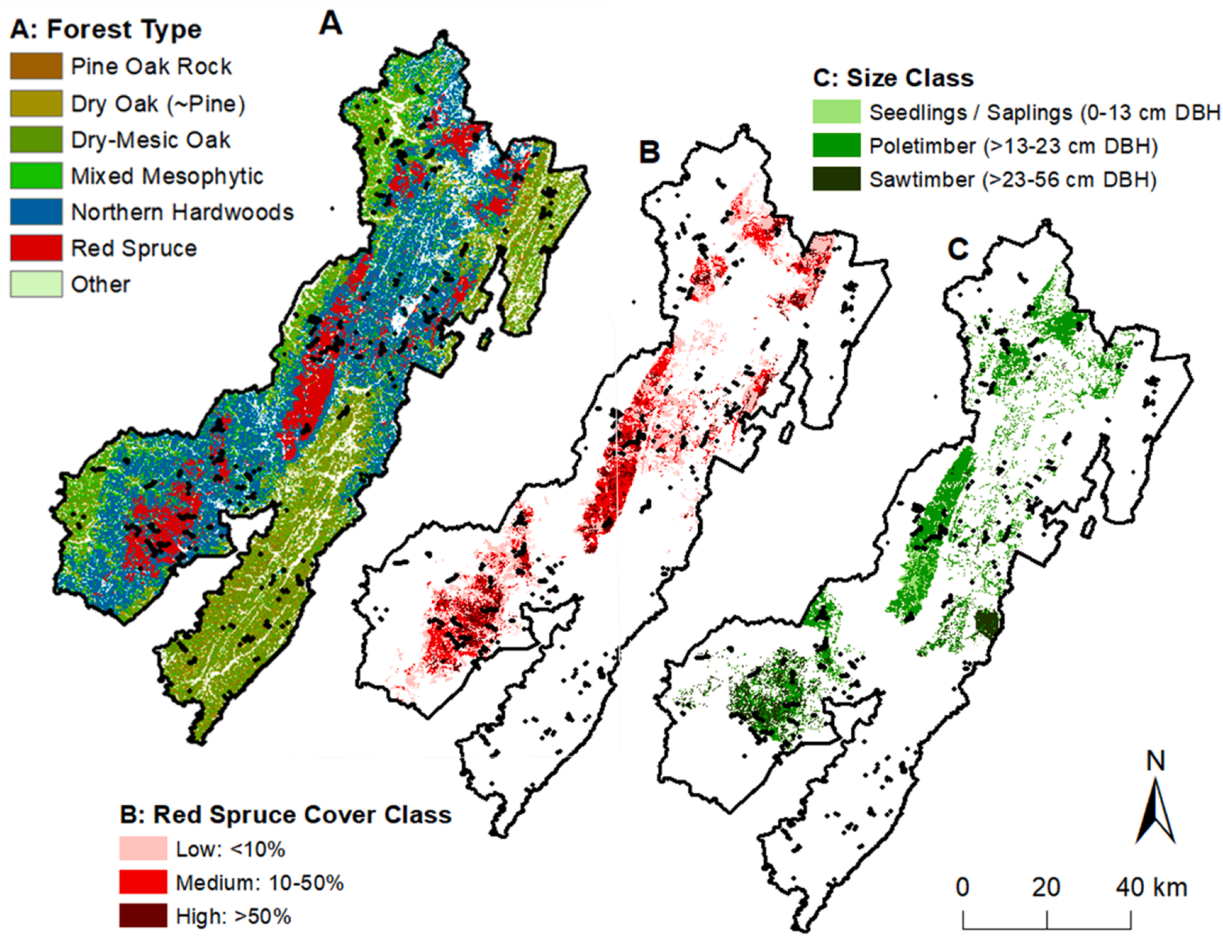

Fig. 2. Predictor values within the boundary of the Monongahela National Forest, West Virginia, of (A) 7 forest types from the 2016 West Virginia land use and land cover map based on National Agriculture Imagery Program orthophotography (Maxwell et al. 2019), (B) 3 classes of percent red spruce cover from the 2013 West Virginia red spruce cover map (Byers et al. 2013), and (C) 3 size classes from the 2013 West Virginia red spruce cover map. The 645 sampling points are also plotted in each map as black points. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Fig. 2C) were both determined from a 2013 red spruce cover map of polygons representing forest stands (Byers et al., 2013). This map was created by biologists from the West Virginia Division of Natural Resources and MNF, who employed a combination of aerial photo interpretation, habitat suitability modeling, and collection of ground truth data from a total of 6,000 points. The minimum mapping unit is 0.4 ha, and the median polygon size is 4.0 ha. The four red spruce cover classes consist of: (1) no (0%) cover; (2) low (<10%) cover, representing sparse young red spruce regeneration, northern hardwood stands with widely scattered red spruce canopy trees, or recent red spruce restoration plantings; (3) medium (10–50%) cover, representing northern hardwood forest with a moderate red spruce component or young red spruce regenerating under northern hardwood forest; and (4) high (>50%) cover, representing mature spruce forest or >40 years-old red spruce plantations. Size class is available for a subset of the polygons and is based on diameter of tree stems at breast height (DBH). The three size classes are seedlings/saplings ($0 < \text{DBH} \leq 13$ cm), poletimber ($13 < \text{DBH} \leq 23$ cm), and sawtimber ($23 < \text{DBH} \leq 56$ cm). Due to the relatively coarse resolution of the polygons, each sampling point was assigned the red spruce cover class and size class of the polygon intersecting with the point count location, which corresponded to the mode class within 50 m. As with forest type, we assumed that the red spruce cover class and size class for each sampling location was accurately reflected by the 2013 map, as there was a maximum difference of only 6 years and general field observations supported those classifications.

2.3. *Statistical analyses*

2.3.1. *Bird data*

Because our study was focused on primarily forest birds, we first removed all species that are almost exclusively associated with non-forest habitats (e.g., waterfowl, waterbirds, grassland birds). We also removed species that are not sampled well with point count surveys (e.g., raptors, corvids), as well as species that were detected at <10 sampling points or for which <10 individuals were detected, as such rare species would not be meaningful in our subsequent analyses. For each of the remaining species ($N = 56$; Supplementary Material Appendix Table A.1.), we calculated the maximum number of individuals of that species across years at each sampling point. For instance, if there was one red-eyed vireo (*Vireo olivaceus*) detected at a site in 2015 and two detected at that same site in 2019, the maximum count across years would be two red-eyed vireos. By removing species with known sampling issues and using maximum counts across years (which are likely closer to true abundance than the average) from fixed-radius surveys (Hutto, 2016), we were able to reduce detectability bias in our count data.

2.3.2. *Community-level associations*

We used multivariate regression trees (MRTs) to assess the strength of bird community composition differences among forest types, red spruce cover classes, and stand-specific size classes by delineating sampling points (i.e., sites) into clusters, such that each cluster is characterized by species occurrence or abundance (De'ath, 2002). A MRT is the multivariate equivalent to a univariate classification and regression tree, which seeks to minimize the sum of squared distances among sites for each node on the tree, given a single response variable and multiple predictors. A MRT does this using the multivariate mean (i.e., sum of squared Euclidean distances from the node centroid). Thus, a MRT is a statistical tool that can be used to explore and describe relationships between multispecies occupancy or abundance data and continuous or categorical environmental characteristics. Specifically, MRTs form clusters by hierarchically splitting the sites into groups based on consistency in species composition. Each split is defined by a simple rule based on environmental values, and the splits are chosen to minimize the dissimilarity of sampling points within clusters. The strongest split will be the first split and weak splits will not be supported. Cross-validation is used to optimize the size of the regression tree.

We created three sets of MRTs to group sampling points into clusters based on the GIS-derived categorical forest types, red spruce cover classes, and stand-specific size classes. We used the "MRT" function in the "MVPARTwrap" package (Ouellette and Legendre, 2013) in Program R, with the default option of 10-fold cross-validation. For categorical forest types and red spruce cover classes, we used all 645 sampling points and determined the optimal size of the regression tree by minimizing cross-validated relative error. Because only 28 of the 170 total sampling points with associated size class data were located in forest types other than red spruce and northern hardwoods, we used the subset of sampling points that fell in either the red spruce or northern hardwood forest types for analysis of the stand size classes. After reducing the sample size, there were only two sampling points in stands classified as seedlings/saplings, so we further limited the stand size analysis to just poletimber- and sawtimber-sized stands. Therefore, for stand-specific size classes, we ultimately used a subset of 140 sampling points and determined the optimal size of the regression tree by minimizing cross-validated relative error.

2.3.3. Species-level associations

We used indicator species analyses to identify individual bird species that were strongly associated with specific forest types, cover classes, and size classes. Indicator species analysis is a community-level statistical technique to identify species that are strongly associated with a specific subset of sites from the full sample set, which may span a spectrum of habitat or environmental conditions or states (Dufrene and Legendre, 1997; De Cáceres et al., 2010). The first step of an indicator species analysis is to model site associations with environmental data based on the bird communities at each site, which we accomplished with the MRTs. The second step of an indicator species analysis is to delineate which species are strongly associated with the different environmental attributes. To do this, we derived indicator values for species from the three sets of clusters produced by the MRTs. Indicator values are a function of abundance and frequency of occurrence, such that species with the highest indicator values have both high abundance and frequent occurrence at sites within a cluster, whereas species with the lowest indicator values have both low abundance and rare occurrence. Species with intermediate indicator values may have either high abundance or high frequency of occurrence, but not both, or they may have both intermediate abundance and intermediate frequency of occurrence. In all cases, the calculation of indicator values incorporates only the within-species abundance distribution (Dufrene and Legendre, 1997).

Corresponding to the three MRTs, we ran three indicator species analyses using the "indval" function in the "labdsv" package (Roberts, 2019) in Program R. This function yields a list of species and their corresponding cluster (i.e., the cluster for which each species has its maximum indicator value), relative abundance of species in that cluster across all clusters, relative frequency of species within that cluster across all sites within that cluster, indicator value (i.e., product of relative abundance and relative frequency in the cluster), and p-value (i.e., probability of obtaining a more extreme [i.e., higher] indicator value when randomly permuting the data compared to the observed data; De Cáceres et al., 2010). For example, a relative abundance of 0.500 would indicate that 50% of the individuals of a species were detected within a cluster, and a relative frequency of 0.500 would indicate that a species was detected in 50% of the sites within a cluster.

3. Results

Approximately half of the 645 sampling points (N = 367) were assigned forest types of either red spruce (N = 123) or northern hardwoods (N = 244), with 55 sampling points in areas of high (>50%) red spruce cover and 59 in areas of medium (10–50%) cover. During the point count surveys conducted from 2010 to 2019, observers detected a total of 4,745 individuals from 56 forest-associated bird species that qualified for our analyses (Supplementary Material Appendix Table A.1.). The five most frequently occurring or widespread of those species (i.e., occupying >25% of the sampling points) were black-throated green warblers (*Setophaga virens*), blue-headed vireos (*Vireo solitarius*), red-eyed vireos, magnolia warblers (*Setophaga magnolia*), and dark-eyed juncos (*Junco hyemalis*). The same five species were also the most abundant (N > 240 individuals), based on total maximum counts across years.

3.1. Forest type

The first MRT grouped the 645 sampling points using the assigned forest type as the environmental variable and resulted in four clusters, as determined by minimizing cross-validated relative error (Fig. 3; residual error: 0.954, cross-validation error: 0.967, standard error for the cross-validated relative error: 0.061). Red spruce and northern hardwood forests were separated out in the first and second splits, respectively. In the final split, the MRT lumped together mixed mesophytic and other forests, distinguishing them from pine oak rock, dry oak (~pine), and dry-mesic oak forests.

The indicator species analysis for the four forest type clusters indicated that 12 and 5 species were statistically significant ($p < 0.05$) indicators for the clusters corresponding to red spruce and northern hardwood forests, respectively (Table 1). Golden-crowned kinglets and magnolia warblers had the highest indicator values for the red spruce cluster, but the more uncommon purple finches (*Haemorhous purpureus*) and yellow-rumped warblers (*Setophaga coronata*) had the highest relative abundance values. For the northern hardwoods cluster, black-throated green warblers had the highest indicator value, but northern flickers (*Colaptes auratus*) had the highest relative abundance value.

Based on the MRT and indicator species analysis results, the forest bird community composition of the cluster corresponding to red spruce forests was distinct from the other three clusters in that it was dominated by species considered significant indicators for red spruce, with very low relative proportions of significant indicator species for dry oak and pine forests or mixed mesophytic and other forests (Fig. 3). In contrast, the forest bird community composition of the cluster corresponding to northern hardwood forests was similar to those of the mixed mesophytic and other forest cluster (Fig. 3).

3.2. Red spruce cover class

The second MRT grouped the 645 sampling points using red spruce cover class as the environmental variable and resulted in four clusters, as determined by minimizing cross-validated relative error (Fig. 4; residual error: 0.954, cross-validation error: 0.963, standard error for the cross-validated relative error: 0.060). No (0%) cover and high (>50%) red spruce cover were separated out in the first and second splits, respectively. In the final split, the MRT distinguished low (<10%) and medium (10–50%) cover.

After running the indicator species analysis for the four red spruce cover class clusters, 8 and 5 species were statistically significant ($p <$

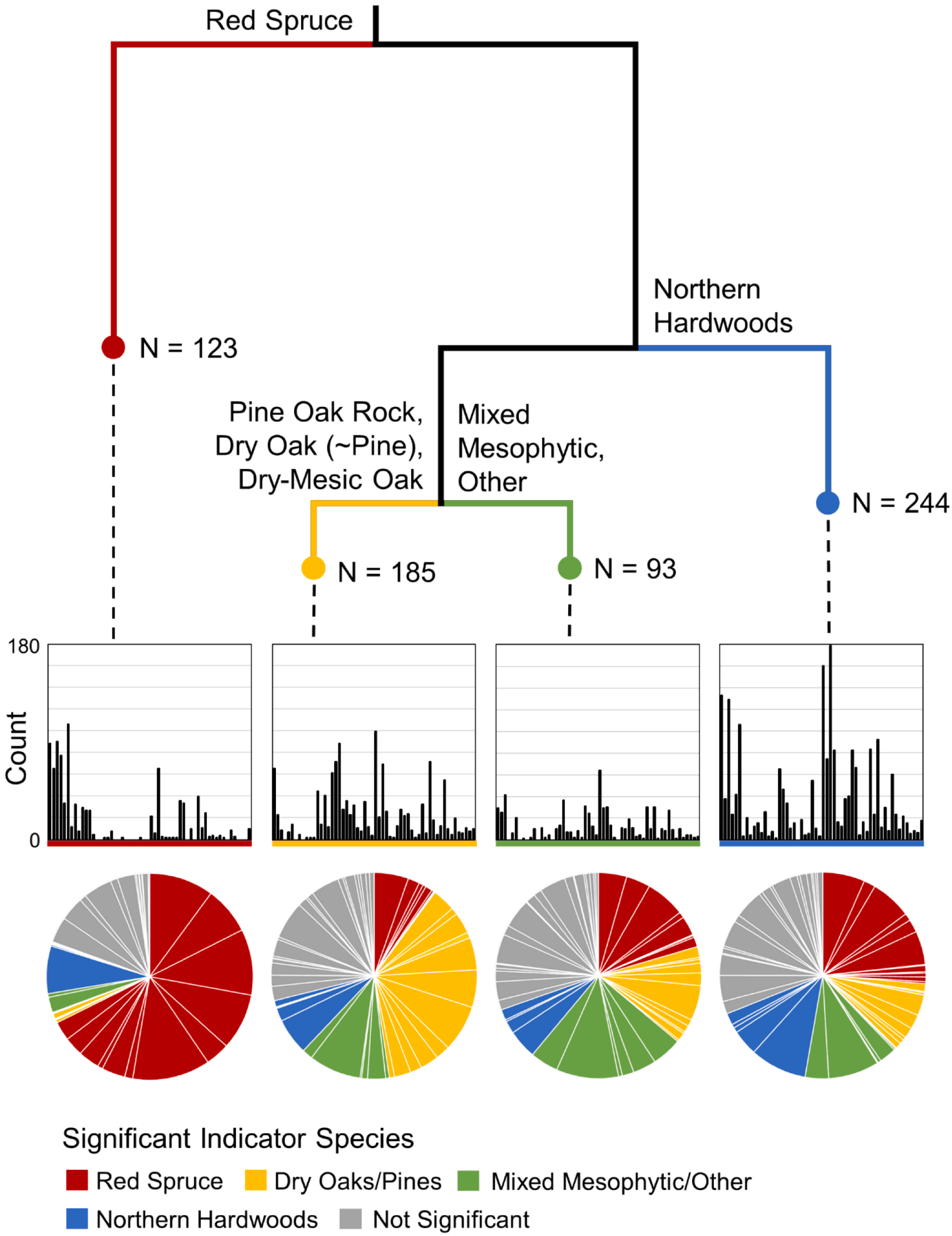

Fig. 3. Multiple regression decision tree and associated bar plots and pie graphs for the four clusters grouping 645 sampling points in the Monongahela National Forest, West Virginia, based on seven forest types. N is the number of sample points in each cluster. Bar plots for each cluster portray the maximum total counts across years for individual bird species summed across all sampling points within the cluster; from left to right, the individual bars correspond to the order of the 56 species listed in Supplementary Material Appendix Table A.2. Color-coded pie graphs for each of the four clusters portray the relative composition of significant ($p < 0.05$) indicator species identified by the indicator species analysis, with each slice representing a single species, the size of the slice representing the total maximum count of that species across years summed across all sampling points within the cluster, and the color of the slice representing the cluster for which that species had a significant indicator value. Proceeding clockwise from the top, the individual slices of the pie graph correspond to the order of the 56 species listed in Supplementary Material Appendix Table A.2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
List of forest bird species identified by an indicator species analysis as significant ($p < 0.05$) indicator species for two clusters corresponding to the red spruce and northern hardwoods forest types, respectively. A total of four clusters were delineated by a multiple regression tree analysis grouping 645 sampling points in the Monongahela National Forest, West Virginia, based on forest type (Fig. 3). Scientific names for the bird species are in Supplementary Material Appendix Table A.1. Relative abundance (RelA) of the species in that cluster across all clusters, relative frequency (RelF) of the species within that cluster across all sites within that cluster, and indicator values (IndVal; the product of relative abundance and relative frequency in that cluster) are provided for each species. The p-value is the probability of obtaining a more extreme [i.e., higher] indicator value when randomly permuting the data compared to the observed data.

Forest Type	Species	RelA	RelF	IndVal	P-Value
Red spruce	Golden-crowned kinglet	0.869	0.561	0.488	0.001
Red spruce	Magnolia warbler	0.545	0.667	0.363	0.001
Red spruce	Blackburnian warbler	0.495	0.504	0.250	0.001
Red spruce	Dark-eyed junco	0.419	0.545	0.229	0.001
Red spruce	Blue-headed vireo	0.372	0.520	0.194	0.001
Red spruce	Yellow-rumped warbler	0.876	0.203	0.178	0.001
Red spruce	Red-breasted nuthatch	0.695	0.228	0.158	0.001
Red spruce	Swainson's thrush	0.756	0.203	0.154	0.001
Red spruce	Hermit thrush	0.503	0.228	0.115	0.001
Red spruce	Winter wren	0.548	0.187	0.103	0.001
Red spruce	Purple finch	0.879	0.081	0.072	0.001
Red spruce	Red crossbill	0.776	0.049	0.038	0.005
Northern hardwoods	Black-throated green warbler	0.375	0.471	0.177	0.001
Northern hardwoods	Chestnut-sided warbler	0.536	0.164	0.088	0.001
Northern hardwoods	Rose-breasted grosbeak	0.442	0.115	0.051	0.044
Northern hardwoods	Northern flicker	0.784	0.045	0.035	0.011
Northern hardwoods	Mourning warbler	0.619	0.053	0.033	0.034

0.05) indicators for the clusters corresponding to high and medium red spruce cover, respectively (Table 2). Golden-crowned kinglets and Blackburnian warblers had the highest indicator values for the high cover cluster, but the less frequently occurring purple finches and yellow-rumped warblers had the highest relative abundance values. For the medium cover cluster, magnolia and black-throated green warblers had the highest indicator values and were among the top three species with the highest relative abundance values. Meanwhile, there were only two significant indicator species, Canada warblers (*Cardellina canadensis*) and brown creepers (*Certhia americana*), for the low cover cluster.

Based on the MRT and indicator species analysis results, nearly half of the forest bird community of the cluster corresponding to high red spruce cover was composed of species considered significant indicators for that cluster, with very low relative proportions of significant indicator species for no or low cover (Fig. 4). The forest bird community composition of the cluster corresponding to medium red spruce cover also had the second highest proportion of significant indicator species for high cover and the second lowest proportion of indicator species for no cover (Fig. 4). As expected from the MRT, the most similar communities were those of the low and medium cover clusters.

3.3. Stand size class

The third MRT grouped the subset of 140 sampling points in either red spruce or northern hardwood forest based on forest type and size class (poletimber: $13 < \text{DBH} \leq 23$ cm vs. sawtimber: $23 < \text{DBH} \leq 56$ cm) and resulted in two clusters, as determined by minimizing cross-validated relative error (residual error: 0.978, cross-validation error: 1.01, standard error for the cross-validated relative error: 0.049). The two forest types were split without distinguishing between size classes.

After running the indicator species analysis for the two clusters, 3 and 6 species were statistically significant ($p < 0.05$) indicators for the clusters corresponding to poletimber- and sawtimber-sized red spruce stands and poletimber- and sawtimber-sized northern hardwood stands, respectively (Table 3). Blackburnian warblers and golden-crowned kinglets had the highest indicator values for the poletimber- and sawtimber-sized red spruce cluster, but the less frequently occurring yellow-rumped warblers had the highest relative abundance values. For the poletimber- and sawtimber-sized northern hardwood cluster, black-throated green warblers had the highest indicator value and highest relative frequency value.

4. Discussion

Our results provide evidence that a clearly distinct forest bird community is associated with red spruce forests in the Central Appalachians, a formerly degraded and currently threatened ecosystem that is the focus of intensive regional restoration efforts. Using several site-level categories to explore different habitat aspects resulted in a cohesive story wherein there were consistently significant indicator species that were strongly associated with red spruce across multiple analyses. The avian community composition in the red spruce forest type differed from the other forest types, and the amount but not size of red spruce was influential. However, we emphasize that our size class analysis was restricted to poletimber- and sawtimber-sized stands, and thus we are unable to make inferences for seedling/sapling or old growth size classes.

From the three sets of indicator species analyses, a total of eleven forest bird species were identified as significant indicator species for red spruce forests. Twelve species were associated with the red spruce forest type in the first indicator species analysis (Table 1), but certain species were strongly and consistently associated with red spruce forests in additional indicator species analyses. For example, three species were identified as significant indicator species across all three sets of analyses; golden-crowned kinglets, Blackburnian warblers, and yellow-rumped warblers were associated with the red spruce forest type (Table 1), high (>50%) amounts of red spruce cover (Table 2), and specifically poletimber- and sawtimber-sized red spruce forests (Table 3). Meanwhile, 8 of the 12 species were significant indicator species for the red spruce forest type (Table 1) and either high or medium (10–50%) amounts of red spruce cover (Table 2). Although magnolia warblers, dark-eyed juncos, and blue-headed vireos had the highest indicator values for the medium cover class (which included young red spruce regenerating under a northern hardwood canopy), they also had high relative abundance and relative frequency at sites with high red spruce cover. Red crossbills (*Loxia curvirostra*) were the twelfth significant indicator species for the red spruce forest type (Table 1), but unlike the other eleven species, they were not strongly associated with a specific cover class. In addition, we note that red crossbills have low value as an indicator species despite their significant association with red spruce forest because their populations tend to be irruptive, with abundance potentially fluctuating between years due to factors unrelated to habitat quality or condition (Bailey and Rucker, 2021).

Fewer species were identified as indicator species for northern hardwood forests, with less consistency across analyses and generally weaker associations (i.e., lower indicator values) compared to red spruce forests. Of the five significant indicator species associated with the northern hardwood forest type (Table 1), only black-throated green warblers were also associated with the cluster corresponding to medium red spruce cover class (Table 2), which generally consisted of northern hardwoods with a moderate red spruce component, and with the cluster corresponding to poletimber- and sawtimber-sized northern hardwood forests (Table 3). Overall, two species (black-throated green warblers and mourning warblers [*Geothlypis philadelphia*]) were identified as significant indicator species for northern hardwoods across at least two sets of analyses.

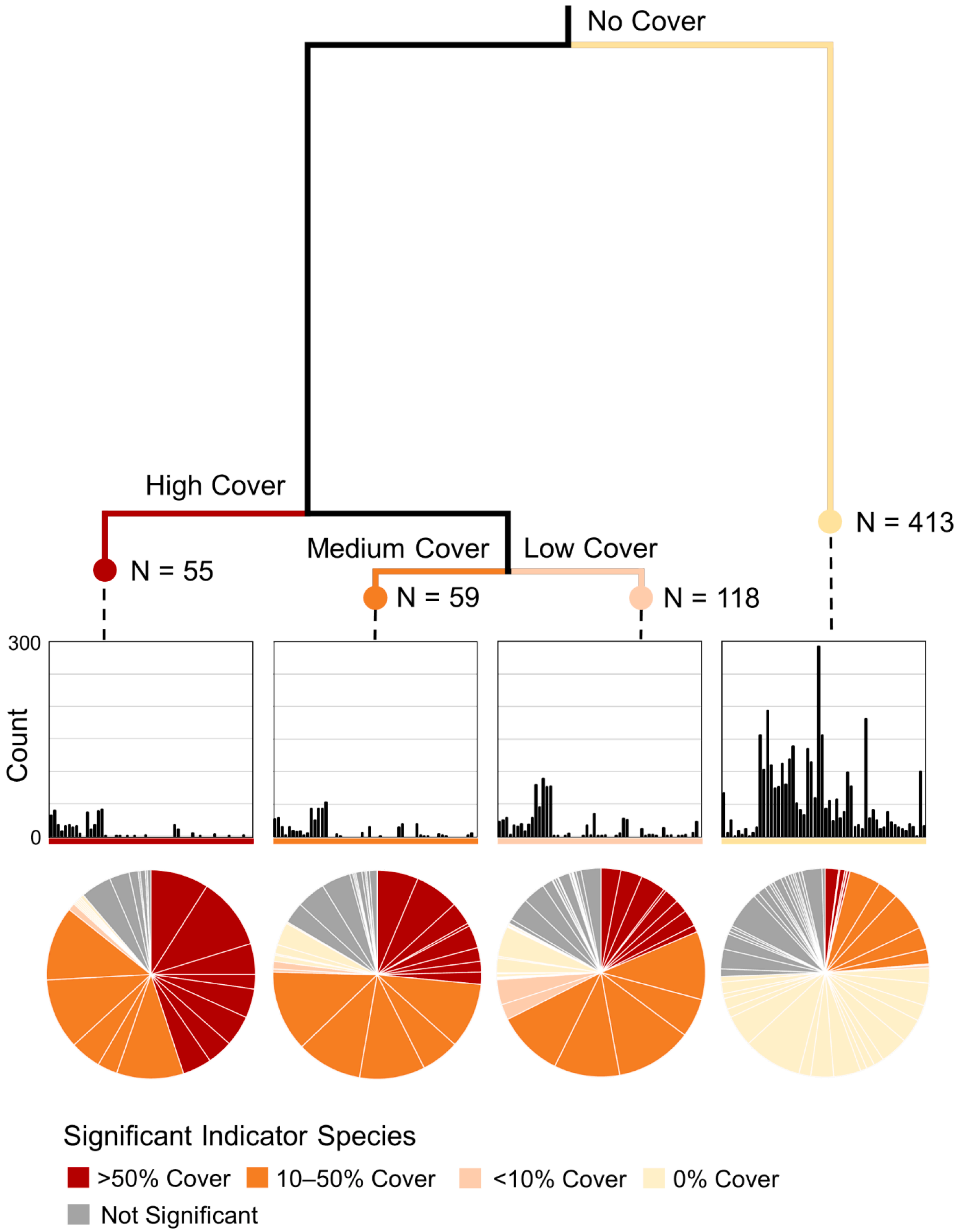

Fig. 4. Multiple regression decision tree and associated bar plots and pie graphs for the four clusters grouping 645 sampling points in the Monongahela National Forest, West Virginia, based on four red spruce cover classes (no cover: 0%, low: <10%, medium: 10–50%, high: >50%). N is the number of sample points in each cluster. Bar plots for each cluster portray the maximum total counts across years for individual bird species summed across all sampling points within the cluster; from left to right, the individual bars correspond to the order of the 56 species listed in Supplementary Material Appendix Table A.3. Color-coded pie graphs for each of the four clusters portray the relative composition of significant ($p < 0.05$) indicator species identified by the indicator species analysis, with each slice representing a single species, the size of the slice representing the total maximum count of that species across years summed across all sampling points within the cluster, and the color of the slice representing the cluster for which that species had a significant indicator value. Proceeding clockwise from the top, the individual slices of the pie graph correspond to the order of the 56 species listed in Supplementary Material Appendix Table A.3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
List of forest bird species identified by an indicator species analysis as significant ($p < 0.05$) indicator species for three clusters corresponding to high (>50%), medium (10–50%), and low (<10%) red spruce cover, respectively. A total of four clusters were delineated by a multiple regression tree analysis grouping 645 sampling points in the Monongahela National Forest, West Virginia, based on red spruce cover classes (Fig. 4). Scientific names for the bird species are in Supplementary Material Appendix Table A.1. Relative abundance (RelA) of the species in that cluster across all clusters, relative frequency (RelF) of the species within that cluster across all sites within that cluster, and indicator values (IndVal; the product of relative abundance and relative frequency in cluster) are provided for each species. The p-value is the probability of obtaining a more extreme [i.e., higher] indicator value when randomly permuting the data compared to the observed data.

Cover Class	Species	RelA	RelF	IndVal	P-Value
High	Golden-crowned kinglet[a]	0.503	0.691	0.348	0.001
High	Blackburnian warbler[a]	0.417	0.527	0.220	0.001
High	Yellow-rumped warbler[a]	0.586	0.273	0.160	0.001
High	Swainson's thrush[a]	0.519	0.255	0.132	0.001
High	Winter wren[a]	0.452	0.236	0.107	0.001
High	Red-breasted nuthatch[a]	0.409	0.255	0.104	0.006
High	Purple finch[a]	0.702	0.145	0.102	0.001
High	Hermit thrush[a]	0.355	0.255	0.091	0.018
Medium	Magnolia warbler[a]	0.363	0.712	0.258	0.001
Medium	Black-throated green warbler[b]	0.322	0.627	0.202	0.003
Medium	Dark-eyed junco[a]	0.310	0.542	0.168	0.005
Medium	Blue-headed vireo[a]	0.298	0.525	0.156	0.044
Medium	Black-throated blue warbler	0.338	0.356	0.120	0.039
Low	Canada warbler	0.674	0.161	0.109	0.001
Low	Brown creeper	0.557	0.127	0.071	0.008

[a] Species that was a significant indicator for red spruce forest in previous analyses.
[b] Species that was a significant indicator for northern hardwood forest in previous analyses.

Table 3
List of forest bird species identified by an indicator species analysis as significant ($p < 0.05$) indicator species for two clusters corresponding to poletimber (PT)- and sawtimber (ST)-sized red spruce stands and poletimber- and sawtimber-sized northern hardwood stands, respectively. The two clusters were delineated by a multiple regression tree analysis grouping 140 sampling points in the Monongahela National Forest, West Virginia, based on stand size classes. Scientific names for the bird species are in Supplementary Material Appendix Table A.1. Relative abundance (RelA) of the species in that cluster across all clusters, relative frequency (RelF) of the species within that cluster across all sites within that cluster, and indicator values (IndVal; the product of relative abundance and relative frequency in cluster) are provided for each species. The p-value is the probability of obtaining a more extreme [i.e., higher] indicator value when randomly permuting the data compared to the observed data.

Size Class	Species	RelA	RelF	IndVal	P-Value
PT + ST red spruce	Blackburnian warbler[a,c]	0.778	0.538	0.419	0.001
PT + ST red spruce	Golden-crowned kinglet[a,c]	0.687	0.571	0.392	0.003
PT + ST red spruce	Yellow-rumped warbler[a,c]	0.850	0.220	0.187	0.013
PT + ST northern hardwoods	Black-throated green warbler[b,d]	0.621	0.612	0.380	0.015
PT + ST northern hardwoods	Red-eyed vireo	0.703	0.224	0.158	0.046
PT + ST northern hardwoods	Veery	0.881	0.122	0.108	0.014
PT + ST northern hardwoods	Ovenbird	0.867	0.102	0.088	0.019
PT + ST northern hardwoods	White-breasted nuthatch	1.000	0.061	0.061	0.044
PT + ST northern hardwoods	Mourning warbler[b]	1.000	0.061	0.061	0.042

[a] Species that was a significant indicator for red spruce forest in previous analyses.
[b] Species that was a significant indicator for northern hardwood forest in previous analyses.
[c] Species that was a significant indicator for high (>50%) red spruce cover in previous analyses.
[d] Species that was a significant indicator for medium (10–50%) red spruce cover in previous analyses.

The selection of species repeatedly identified as significant and strong indicators for red spruce or northern hardwood forests is consistent with their individual natural histories and underscores the importance of these forest types to regional biodiversity. All of the red spruce-associated species are known to breed in coniferous or mixed forests, with yellow-rumped warblers, red-breasted nuthatches (*Sitta canadensis*), magnolia warblers, and red crossbills usually restricted to just coniferous or mixed forests in the eastern USA (Billerman et al., 2020). Meanwhile, black-throated green warblers and mourning warblers are generally associated with boreal forests, but they tend to breed in mixed hardwood forests in the Central Appalachians (Billerman et al., 2020). Furthermore, the West Virginia populations of all the aforementioned indicator species are considered trailing-edge populations in the eastern United States, meaning they are persisting at or near the margins or limits of the species' overall range (Merker and Chandler, 2020). Trailing-edge populations contribute to regional biodiversity and species-level genetic diversity (Hampe and Petit, 2005; Ferrari et al., 2018), so habitats that support their persistence are valuable for conservation, especially when many trailing-edge bird populations are predicted to be at risk from global climate change (Cahill et al., 2014; Rushing et al., 2020). Indeed, a few of the red spruce indicator species are of regional conservation concern, despite being common enough in the bird surveys for inclusion in our analyses. Swainson's thrush (*Catharus ustulatus*), Blackburnian warbler, and red crossbill are listed in the West Virginia State Wildlife Action Plan, and both Blackburnian warbler and red crossbill are also listed as Appalachian Mountains Joint Venture priority species.

Our results are consistent with previous studies in the Central Appalachian Mountains region. Although their surveys were conducted more than 70 years ago, Stewart and Aldrich (1949) frequently detected Blackburnian warblers, magnolia warblers, golden-crowned kinglets, black-throated green warblers, blue-headed vireos, and dark-eyed juncos in red spruce-northern hardwood forest stands. From point count surveys conducted from 1996 to 1997 in the MNF, Demeo (1999) recorded black-throated green warblers as one of the ten most abundant species in the northern hardwood sites and Blackburnian warblers, dark-eyed juncos, golden-crowned kinglets, magnolia warblers, blue-headed vireos, and winter wrens (*Troglodytes hiemalis*) among the ten most abundant species in the red spruce sites. More recently in 2000–2001, Kahler and Anderson (2010) recorded Swainson's thrushes and red crossbills only in red spruce stands within their study area. Also consistent with our results, Blackburnian warblers, golden-crowned kinglets, dark-eyed juncos, magnolia warblers, and red-breasted nuthatches had significantly higher relative abundance in red spruce than northern or central hardwood forests (Kahler and Anderson, 2010). The consistency of bird-habitat associations across long temporal scales is supported by a long-term bird population study in a Central Appalachians second-growth red spruce forest, which found that bird species composition showed little change over 36 years (Hall, 1984).

Ultimately, this study identifies significant indicator species associated with red spruce and northern hardwood forests, with considerations for the amount of red spruce cover and stand size classes. Our results can be used to directly guide the actions and restoration efforts (e.g., tree planting) of the Central Appalachian Spruce Restoration Initiative, its partners, and similar organizations. The findings of this study provide a baseline for the current outcome of red spruce-northern hardwood ecosystem restoration pertaining to forest bird species in the Central Appalachians, as well as measurable goals in terms of the amount of red spruce cover needed to support birds associated with red spruce forest. In addition, these indicator species represent a simple and easily obtained metric (i.e., abundance from point count surveys) that can be used to support assessments of ongoing and future restoration efforts. Thus, this study has implications for future qualitative and quantitative measures of success for restoration of the red spruce-northern hardwood ecosystem in Central Appalachia. Moreover, the distinctiveness of the bird community in red spruce forests and strength of those associations highlight the critical need for and importance of red spruce restoration efforts to ensure long-term maintenance of regional avian diversity.

CRediT authorship contribution statement

Hannah L. Clipp: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Donald J. Brown:** Conceptualization, Methodology, Writing – review & editing. **Christopher T. Rota:** Funding acquisition, Resources, Writing – review & editing. **Petra B. Wood:** Funding acquisition, Resources, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108568.

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