

CHAPTER 3

RELATING SPATIAL VARIATION IN BIRD PRESENCE-ABSENCE AND ABUNDANCE TO FOREST AND LANDSCAPE VARIABLES AT THE BBS ROUTE LEVEL.

Results

BBS Data Summary

The average abundance (individuals per route) of the 26 bird species I selected for this study ranged from 0.3 (black-billed cuckoo) to 30.5 (red-eyed vireo) during the 2000 FIA inventory cycle (Table 1). Eleven species exhibited significantly decreasing trends in abundance from 1966-2004 ($P \leq 0.01$; Sauer et al. 2005) within the Appalachian bird conservation region (BCR 28) of the North American Bird Conservation Initiative (NABCI). Nine of these species were Partners in Flight (PIF) species of regional concern (Table 2; Panjabi et al. 2005). Six of the species I selected exhibited significantly increasing abundance trends from 1966-2004 ($P \leq 0.03$), and the trend data of the remaining species were inconclusive (Table 2; Sauer et al. 2005). I included 4 short-distance migrants and 6 non-migrants, with most non-migrants limited to the cavity nesting guild (Table 2). Using ANOVA, I detected no year effect in any of the guilds from using the 4-year moving window among states to estimate bird abundance during the 2000 FIA cycle ($P > 0.90$). Seven species had zero detections on less than 5% of the routes within their distribution (Table 1), thus I developed no models of presence-absence for these species. This was an arbitrary cutoff point and selected based on the extremely limited amount of absence data available for these species to train the classification tree and logistic regression models.

Effects of Error Introduced into FIA Plot Locations: Comparing Plot and County Bird-Habitat Relationships

Using the perturbed and swapped plot locations provided in the FIADB to spatially relate the plot-level forest variables to the buffers around the BBS routes affected the relationships detected between bird abundance and the forest variables. Within the 100 m and 1 km buffers around the BBS routes, I detected significantly fewer Pearson's correlations with a $P < 0.05$ between the bird abundances and forest variables calculated at the plot-level versus the county-level (paired t-test, $n = 26$ for all tests, 100 m buffer: $t = 4.25$, $P < 0.001$; 1 km buffer: $t = 2.52$, $P = 0.009$)(Fig. 6). The average correlation coefficients (calculated from their absolute values) also were significantly lower among the plot-level variables than among the county level within both the 100 m ($t = 3.13$, $P < 0.002$) and 1 km buffers ($t = 3.15$, $P < 0.002$)(Fig. 6). Within the 10 km buffers, I detected no differences in the number of correlations with a $P < 0.05$ ($t = 0.04$, $P = 0.482$) or the strength of those correlations ($t = 1.00$, $P = 0.163$) between the bird abundances and the plot and county-level forest variables. With few exceptions (downy woodpecker, great-crested flycatcher, eastern wood pewee, rose-breasted grosbeak), this pattern in the number and strength of the bird abundance-forest variable correlations was consistent for each bird species (Table 7).

The fit of the logistic and CART models relating bird presence-absence and abundance to the forest variables developed using the plot-level variables tended to be poorer than those using the county-level variables. Differences in model performance were scattered among all species and not concentrated in any one guild. At the 100 m buffer scale, where correlation differences of bird abundance to the FIA plot and county forest variables were most pronounced, the regression tree models of bird abundance with the county-level forest variables had a greater

proportional reduction in error (*PRE*, analogous to regression R^2) for 19 of the 26 species than those using the plot-level variables. The county-level regression tree models of abundance accounted for an average difference of 5.7 more percentage point of error. The classification tree models relating bird presence-absence on a BBS route to the county-level forest variables had a greater *PRE* for only 10 of the 19 species, and accounted for an average of 0.9 percentage point more error. For the logistic regression models built using the county-level forest variables, 12 of 19 exhibited greater sensitivity (% correct classification of bird presence) and 13 of 19 greater specificity (% correct classification of absence) relative to those with the plot-level variables. On average, the county-level models had a 4.1 percentage point greater sensitivity and 3.5 percentage point greater specificity over the plot-level models.

Some bird species had considerably better model performance with the county-level forest variables at the 100 m buffer scale and are worth noting. For example, the regression tree model for the downy woodpecker had a *PRE* = 0.069 using the plot-level variables and a *PRE* = 0.332 with the county-level variables. The plot-level model contained 1 landscape variable and no forest variables, even though 4 plot-level forest variables were correlated with downy abundance at $P < 0.05$, while the county-level model contained 2 forest variables and 1 landscape variable. The CART models of chestnut-sided warbler presence-absence and abundance developed using the county-level variables had 20.5 and 29.4 greater *PRE* values than those with the plot-level variables, respectively. The model for presence-absence contained 3 forest variables, the abundance model contained 2 forest variables, and both contained the same landscape variable (CPLAND; Fig. 7a). Both split repetitively on the landscape variable, and none of the forest variables readily described the early successional habitat preferred by this species (Fig. 7a). By contrast, the CART models using the county-level variables contained

fewer repetitive splits, and the abundance model contained 2 forest variables indicative of early successional habitat (SSDIAMAVG and UDIAMAVG; Fig. 7b). Similar patterns in variable selection and model structure between the plot and county-level scales were evident in the CART models for many bird species.

Ability of the Forest and Landscape Variables to Explain Variations in Bird Abundance

Pearson correlation coefficients for single bird abundance-forest variable correlations ranged from -0.589 (DRCTPA and red-bellied woodpecker within the 10 km buffer) to 0.595 (STDSZCD and red-eyed vireo within the 10 km buffer, Appendix L). Summing across the 26 bird species and 3 modeling techniques provided 64 total opportunities for a variable to be included in a model (because correlations among buffers for a given variable were very high, occurrences in more than 1 buffer were considered 1 inclusion). Thirty eight of the 43 forest variables I developed from the FIA data were selected for at least 1 model with a 17% average rate of inclusion for a given variable (Table 9). Two of the variables never selected, SSSW_N and TPA, were highly correlated ($r \geq 0.622$) with others (e.g. SSSW_N to USW_N, TPA to DOMTPA) that tended to have stronger correlations to bird abundance and were selected more frequently (Table 9). The remaining 3 variables were physiographic class codes that described conditions uncommon in the landscape (V13 = deep sands, beaches; V34 = beaver ponds, V39 = other hydric sites; USDA Forest Service 2006), each having no more than 3.2% maximum coverage (< 1% for V13 and V34) and no more than 0.15% average coverage in any given BBS route buffer.

The most frequently selected variables described a range of forest structural characteristics and included tree species diversity indices across all size classes (ALLSW_N) and for dominant trees (DSW_N), the average diameter of understory stems (UDIAMAVG), site

productivity (SITECLCD), the density of dead or rotten-cull trees (DEADTPA, RCTPA, DRCTPA), and 2 physiographic class codes describing mesic flat forest stands outside of flood plains (V21) and mesic rolling uplands (V22, USDA Forest Service 2006). Each of these variables was selected in more than 25% of all models I developed (Table 9).

Coefficients for individual bird abundance-landscape variable correlations ranged from -0.765 (LCAI_CV and red-eyed vireo within the 10 km buffer) to 0.753 (LCAI_MN and red-eyed vireo within the 1 km buffer, Appendix L). Twenty eight of the 29 landscape variables were selected for at least 1 model with an 11% average rate of inclusion for any given variable (Table 10). The 5 variables most frequently selected were specific to the deciduous forest cover class and described the size (CAI_MN, PLAND), shape (LSI, SHAPE_MN) and interspersion (IJI) of deciduous forest patches in the landscape. Each of these variables was selected in at least 18.8% of models developed. The variable never selected (LPI) also described deciduous forest patch size and was strongly correlated with PLAND ($r \geq 0.771$) which had stronger correlations to bird abundance.

CART and Logistic Regression Model Performance

All individual species' models are detailed in Appendix Q

Classification tree models.—The total amount of variation in the presence-absence on BBS routes of the 26 bird species explained by the classification trees among the 3 buffers and multiscale model ranged from 0.250 to 0.811 [classification tree proportional reduction in error (*PRE*), analogous to regression R^2 , Table 11]. The number of variables included in a given model ranged from 3 to 9. Considering only the best models among the 3 buffers and the multiscale model within each species, the lowest *PRE* was 0.432 for the great-crested flycatcher. The average *PRE* across all species and buffer sizes was 0.565, with an average of 5.9 variables

per model. Averaging over the 3 buffers and the multiscale models, models within the cavity guild accounted for the least amount of variation in presence-absence ($\overline{PRE} = 0.465$) and those in the early successional guild accounted for the most variation ($\overline{PRE} = 0.608$; Table 11).

Individual model performance for a given species among the 3 buffer sizes and multiscale models varied among the 4 guilds. For the purposes of this summary, I am characterizing best fit as the model with largest *PRE* and fewest predictor variables when 2 models have equivalent *PRE* values, seeking to balance model fit with parsimony (Burnham and Anderson 2002). Within the cavity, early successional, and mature forest canopy guilds, the models with the best fit were those developed within 100 m or 10 km buffers or the multiscale models (Table 11). Within the mature forest ground-shrub guild, the best models were from the 10 km buffers or the multiscale models. All models developed within the 1 km buffers had a poorer fit than at least 1 other model from another buffer size or the multiscale model. With the exception of the cavity guild, the multiscale models had a greater average *PRE* within each guild than those for a single buffer, but the multiscale models also contained more predictors on average (Table 11).

Regression tree models.— The total amount of variation in bird abundance on BBS routes explained by the regression tree models among the 3 buffers and multiscale models ranged from 0.159 to 0.776 (Table 12). The number of variables included in a given model ranged from 1 to 10. Considering only the best models among the 3 buffers and the multiscale model within each species, the lowest *PRE* was 0.332. The average *PRE* across all species and buffer sizes was 0.527, with an average of 5.3 variables per model. Averaging over the 3 buffers and the multiscale models, models within the cavity guild accounted for the least amount of variation in

bird abundance on the BBS routes ($\overline{PRE} = 0.452$) and those for the mature forest canopy guild accounted for the most variation in abundance ($\overline{PRE} = 0.552$; Table 12).

Individual model performance for a given species among the 3 buffer sizes and multiscale models varied among the 4 guilds. Within the cavity and mature forest ground-shrub guilds, the models with the best fit tended to be the multiscale models (Table 12). Within the early successional and mature forest canopy guilds, the best models were distributed across all buffers and the multiscale models. Similar to the classification trees, the regression trees developed within the 1 km buffers tended to have the poorest overall performance and had the best fit for only 2 species: tufted titmouse and wood thrush. The multiscale models had a greater average *PRE* within each guild than models from any single buffer, but the multiscale models again contained more predictors on average (Table 12).

Logistic regression models.—The individual species models for the 3 buffers and multiscale models selected using AIC_c had model sensitivities that ranged from 0.382 to 0.966, and specificities that ranged from 0.130 to 0.840 (Table 13). The number of variables included models ranged from 2 to 15 (4 - 17 total parameters). Within a given buffer size, several competing models ($\Delta AIC_c < 2$) often existed for a given species (Appendix Q), which was reflected in the low AIC_c weights for the selected models (Table 13). The average sensitivity and specificity across all species and buffer sizes were 0.756 and 0.586, with an average of 7.6 variables per model. Averaging over the 3 buffers and the multiscale models, models within the cavity guild tended to have the poorest fit, indicated by the low rates of specificity (average = 0.255). However, this was likely a function of the small number of routes with no detections available for each of the cavity species (Table 1). The models for the early successional guild had the greatest average levels of sensitivity (0.770) and specificity (0.643), and these values

also tended to be greater within each buffer than those for species in other guilds (Table 13). Individual model performance among most species, characterized by their levels of sensitivity and specificity, tended to be best for the multiscale models. However, these models also tended to have a greater number of parameters and lower AIC weights, indicating a greater level of model uncertainty within the multiscale models (Burnham and Anderson 2002), than those within individual buffer sizes (Table 13).

Examples of Model Performance from 2 Species: Cerulean Warbler and Yellow-Breasted Chat

Cerulean warbler.—The best CART models of cerulean warbler presence-absence and abundance had a *PRE* of 0.598 and 0.776 and were both the multiscale models (Tables 11 and 12). The best logistic regression model is difficult to identify, as each varies slightly in complexity (number of parameters), sensitivity, and specificity. Both the CART and logistic models of presence-absence indicated presence was positively associated with overall tree species diversity (ALLSW_N), the amount of the landscape in deciduous forest cover (PLAND), and increased variability in average tree height (ALLHTCV) at all buffer sizes (Fig. 8; Table 14). The multiscale classification tree model of cerulean presence-absence found presence to be most strongly associated with the percent of deciduous forest cover in the landscape at the 1 km buffer scale (positive relation), and dominant tree species diversity (DSW_N) and average core area of deciduous forest cover (CAI_MN) at the 10 km buffer scale (both negative relationships; Fig. 8d).

All regression tree models of cerulean warbler abundance showed positive associations of abundance with the percent of the landscape in deciduous forest cover (PLAND; Fig. 9); this variable was included in the multiscale model at the 1 km buffer level (Fig. 9d). Abundance also was positively related to the average diameter of dominant trees at the 10 km scale, and

negatively related to the diversity of dominant tree species at the 100 m buffer scale, but only within landscapes having a large percentage of deciduous forest cover and diameters < 30 cm (Fig. 9d).

Yellow-breasted chat.—The best CART models of yellow-breasted chat presence-absence (multiscale model) and abundance (10 km buffer) had a *PRE* of 0.809 and 0.628 (Tables 11 and 12). Both the classification tree and logistic models of presence-absence detected a strong negative relationship of bird presence to the percent of level forestland not in floodplains (V21; Fig. 10 and Table 15). These models also detected a negative association with an increased density of dead and rotten-cull trees per hectare (RCTPA, DEADTPA, DRCTPA) that tended to weaken as buffer size increased. Presence also was negatively associated with the amount of core area present in the landscape (LCAI_AM, negative relationship; CAI_CV and LANDPD, positive relationships). The multiscale CART model of chat presence-absence found presence to be most strongly associated with the absence of level forestland outside of floodplains, increased variability in the amount of core area in the landscape (both at the 10 km buffer scale), and increased density of individual deciduous forest patches (1 km buffer scale; Fig. 10d).

The variables selected by the regression trees of yellow-breasted chat abundance were similar among the 3 buffer sizes and the multiscale model (Fig. 11). Models at all buffer sizes detected a positive relationship of abundance to stands with smaller trees (100 m buffer: SSDIAMAVG, 1 and 10 km buffer: UDIAMAVG, both positive relationship), as well as with stand productivity (SITECLCD) at the 1 and 10 km buffers (Figs. 11b and c). Variables describing deciduous forest patch density (PD; positive relationship), variability in deciduous

patch size (CAI_CV; positive relationship) and overall patch size in the landscape (LCAI_AM; negative relationship) also were present in every model (Fig. 11).

Discussion

Effects of Error Introduced into FIA Plot Locations: Comparing Plot and County Bird-Habitat Relationships

The effect of the error introduced into the FIA plot coordinates on the relationships of bird abundance with the forest variables calculated at the FIA plot level was not surprising. I expected the impacts of this error to be greatest at the 100 m buffer scale. Because of their relatively small spatial scale, these buffers contained the fewest Thiessen polygons (minimal loss of resolution from averaging across polygons) and the buffer radius was 6% that of the circular radius (1.6 km) used to perturb the FIA plots (McRoberts et al. 2005). Because the 10 km radius of the largest buffers was 6.25 times that of the circular radius used to perturb the FIA plots, these buffers contained multiple polygons (resulting in a greater relative loss of resolution from averaging across multiple polygons), and often included data from more than 1 county. The coarser scale of the 10 km buffers served to subsume the effects of the perturbing and swapping such that no difference was detected between the bird-habitat relationships at the 10 km buffer scale using the plot and county-level variables.

At the 100 m and 1 km buffer sizes, however, this error had an obvious impact on the relationships between the FIA variables and bird abundances that was reflected in various ways throughout the analyses. The models using the forest variables calculated at the county-level tended to account for a greater amount of variability in bird abundance and presence-absence on BBS routes than those developed using the plot-level variables. Similar reductions in model fit have been documented in other model-based studies when the spatial scale of the variables being modeled was similar or finer than that of the erroneous coordinates (McRobert et al. 2005).

However, the impact of the perturbed and swapped coordinates was most evident in the regression trees and less so in both the logistic models and classification trees of presence-absence. A greater proportion of the regression trees using the county data had a better fit than the classification trees, and the magnitude of this difference, based on the *PRE* values, was greater in the regression tree models with the county data. This was likely a function of the relationships these models were representing. The presence-absence models were identifying the forest and landscape attributes minimally related to a given species occurrence at a site and thus could include a range of characteristics describing a variety of habitats from minimally acceptable to excellent. The abundance models were developed using only those routes with at least one recorded occurrence and were identifying forest characteristics that improved overall habitat quality as indexed by an increase in abundance, assuming that the habitat was at least minimally acceptable to the species. Forest characteristics influencing species abundance in a given area tend to be more complex and interrelated (Heglund 2002) and thus more prone to the error introduced by the perturbed and swapped plot locations. Also, many of the species that had better model performance with plot-level variables were habitat generalists (e.g. black and white warbler, American redstart, yellow-billed cuckoo) and occur in a broad range of forest characteristics (Hamel 1992, NatureServe 2005).

Also, the unknown nature of this error calls into question the reliability of the bird-habitat relationships identified from the plot-level data. The forest variables developed from the plot data within the 100 m buffers scale should provide the most accurate representation of the forest characteristics immediately present on the ground around the BBS routes (Dungan et al. 2002, Trani 2002), but the error introduced into the coordinates confounds the nature of this representation in ways that cannot be measured. Thus, bird-habitat relationships identified from

these data also contain confounding errors that cannot be precisely quantified, severely limiting their ability to precisely represent real-world interactions. For these reasons, I chose to limit further model development and selection procedures to the models developed using the county-level forest variables.

Ability of the Forest and Landscape Variables to Explain Variations in Bird Abundance

The forest variables I developed from the FIA data for the spatial analyses adequately described several components of forest structure important to bird habitat selection. The majority of forest variables were selected in at least one model, and patterns in variable selection among guilds were evident and tended to follow a guild's general habitat requirements. For example, the average diameter of all understory trees (UDIAMAVG) was selected in 64% of the early successional models, 42% of the mature forest ground-shrub models, 33% of the mature forest canopy models, and 18% of the cavity models. Within the early successional guild, presence and abundance of most species were positively related to smaller diameter understory stems, indicative of early successional habitat, while most species in the mature forest ground-shrub guild exhibited a positive relationship with larger diameter understory stems, indicative of a more developed forest understory.

Interpretation of some frequently selected variables was not always straightforward. For example, variables describing the average diameter and density of standing dead and rotten-cull trees (RCTPA, RCDIAMAVG, DEADTPA, DEADIAMAVG, DRCTPA, DRCDIAMAVG) were frequently selected within the mature-forest ground-shrub guild, but rarely selected within the mature forest canopy guild. These variables likely served to describe heterogeneity and gap structure in a forest stand as well as stand maturity. High densities of dead or rotten-cull stems that are larger in diameter will increase the presence of gaps in the forest canopy. This will

allow more sunlight to reach the forest floor and affect the structure of understory vegetation important to most species in the ground-shrub guild. The density and diameter of these stems also both should increase as trees within the stand mature. While these variables would seem to also describe horizontal structure within the canopy and thus be important to canopy nesters, they were never selected for any of canopy guild models. However, the coefficient of variation in height of all trees (ALLHTCV) also likely served as an index to canopy structure, and it was selected in 77.8% of canopy guild models (Table 9a). Most canopy nesters will prefer more closed canopy habitat and thus exhibit little association with the horizontal gaps the dead and rotten-cull variables represent. Vertical canopy structure within closed canopy stands may be more critical for the canopy guild and was better described by the ALLHTCV variable. For example, cerulean warblers prefer to nest in trees that are taller than the surrounding canopy (Thogmartin et al. 2004, Pashley 2005), and ALLHTCV was included in the classification trees and logistic models with a positive association to cerulean occurrence (Table 14, Fig. 8)

It is important to note that the inclusion of any given variable in a bird-habitat model is not an indication of that variable's importance to that species. Rather, it serves as an index to characteristic(s) within the habitat that are important for meeting the life requisites of the species, and interpreting the biological importance of any variable may not always be obvious and require further research (Welsh et al. 2006). Such considerations are especially true for studies such as this that are exploratory in nature and encompass a large geographic area. Many of the descriptive forest variables I developed could serve as indices to a variety of components for a given species' ecological niche (Heglund 2002), and the large geographic area considered by this study encompasses a tremendous level of ecological variability, further increasing the role a given variable can play in fulfilling the habitat requirements of a given species (Dettmers et al.

2002). Therefore care must be taken in interpreting the biological relevance and importance of the variables identified as important to bird presence and abundance in the models I developed, as they could be serving multiple functions relative to the species' life requisites and other variables present in the model (Heglund 2002, Young and Hutto 2002).

CART and Logistic Regression Model Performance

The overall performance of the CART and logistic regression models in accounting for spatial variability in bird presence-absence and abundance was very good. Many of the CART models I developed accounted for > 50% of the variation in bird presence-absence (Table 11) and abundance (Table 12). Many of the logistic regression models also had sensitivity and specificity rates > 0.50 (Table 13). The bird-habitat relationships identified by these models largely followed those described elsewhere (e.g. Hamel 1992, Lichstein et al. 2002, Thogmartin et al. 2004, Thogmartin and Knutson 2006).

CART model performance between presence-absence and abundance was not always consistent within species, and this was demonstrated by the yellow-breasted chat and cerulean warbler models. The best model of yellow-breasted chat presence-absence (multiscale model) had a $PRE = 0.809$, while the best abundance model (10 km buffer) had a $PRE = 0.628$. Conversely, the best cerulean warbler presence-absence model (multiscale model) had a $PRE = 0.598$, and the PRE of the best abundance model (multiscale model) was 0.776. These situations demonstrate some limitations of the FIA data, in conjunction with the landscape variables, and the scale at which I developed the forest variables to account for different types of bird habitat requirements. For the yellow-breasted chat, the landscape variables in conjunction with a physiographic class code and the site class code were able to identify the edge habitat and early successional forest cover predicting presence of chats at a given site (Fig. 10a, Table 15; Hamel

1992). However, these variables were less effective in characterizing the factors influencing chat abundance at a given site. Some of the variables I developed from the FIA data, such as the seedling-sapling and understory variables, were able to quantify areas of early successional cover preferred by chats and were included in abundance models. However, they were inadequate for further delineating the characteristics within these early successional stands that may influence chat abundance. Cerulean warblers prefer habitats containing forested wetlands and similar mesic sites (Thogmartin et al. 2004). While these characteristics were described in the physiographic class codes I used and selected in the 10 km buffer model, these types of sites tend to be spatially segregated and uncommon in the landscape. The resolution of the county-level values for these variables was likely too coarse to delineate these forested wetlands at the scale which cerulean warblers were responding to their presence in the landscape (MacFaden and Capen 2002, Trani 2002). Also, cerulean warblers may be responding to other physical and environmental characteristics of such sites that were not adequately represented by the physiographic class codes. Within these occupied sites, cerulean abundance increased as diversity and size of dominant trees increased and as the percent deciduous forest cover increased. Thogmartin et al. (2004) also found higher cerulean warbler abundance in landscapes containing drier patches of deciduous forest cover as well as forested wetlands.

In general, the birds with the best model performance were those with specific habitat requirements and well-sampled within the BBS, such as the ovenbird, rose-breasted grosbeak, hooded warbler, and chestnut sided warbler. Poor model performance within a given species could have resulted from one or a combination of factors. For example, Canada warblers have very specific habitat requirements, including mesic sites within mature forest stands containing streams or forested wetlands with dense understory cover (NatureServe 2005), and the models

for them included variables describing mature forest stands and the presence of narrow stream drains. However, this species also had a restricted geographic range within my study area, with an average abundance of 0.5 birds per route and occurrences on 42 of 137 routes (Table 1). Habitat generalists, such as the downy woodpecker and American redstart, also tended to have models with either a poor fit (downy woodpecker) that contained a large number predictors (the logistic model for the American redstart) creating a complex and over-parameterized model (Burnham and Anderson 2002). However, the redstart also demonstrates the utility of using greater than 1 modeling technique. The best CART models for both redstart presence-absence and abundance contained fewer parameters and accounted for a high amount of variability (Tables 11 and 12) relative to the logistic model.

The geographic extent of many bird-habitat studies, especially those examining microhabitat relationships, is relatively small, ranging from a few hectares to a 3-4 state region. These small-scale studies do not readily explain bird-habitat relationships at large spatial scales (Heglund 2002, Hobbs 2003). Dettmers et al. (2002) noted reduced performance in bird-habitat models developed in TN using 4 modeling techniques, including CART and logistic regression, when applied to data from VA and GA. They suggested that regional habitat variation that occurred along the north to south gradient of these states may have contributed to the reduced performance and recommend developing models across broader regions as data permit to better account for spatial variability in habitat structure (Dettmers et al. 2002). The 14 state region of my study encompassed a tremendous range of habitat variation. The BBS, FIA, and NLCD datasets provided consistent and relatively fine-resolution data sources describing bird abundance and habitat across this entire region and likely contributed to the overall performance of the models I developed.

Another problem related to spatial scale is selecting the most ecologically relevant spatial scale at which to conduct studies (Morrison 2002, Trani 2002), coupled with the need to address multiscale habitat selection demonstrated by many bird and other wildlife species (Hagan and Meehan 2002, MacFaden and Capen 2002, Hobbs 2003, Bissonette 2003). Defining the “best” scale(s) at which to conduct bird or any wildlife-habitat study is impractical without knowing the scale(s) at which species are responding to their environment (Hagan and Meehan 2002, Van Horne 2002). It is unlikely that one scale will be universally appropriate for any species and multiscale habitat selection will vary among species (Bissonette 2003). I addressed this problem by developing models at 3 overlapping spatial scales at the finest resolution of my analyses (100 m, 1 km, and 10 km buffers around each BBS route) and then integrating the predictor variables from the best model at each of these scales into a multiscale model. This approach allowed me to assess the relative contribution of each of these scales independently as well as consider habitat selection at multiple scales simultaneously and has been used successfully in other forest bird habitat studies (Thogmartin et al. 2004, Thogmartin and Knutson 2006). The majority of the best CART models tended to be the multiscale models, and many of the multiscale logistic models had greater sensitivity and specificity than their single-scale counter parts. Even for species where the best CART models were within individual buffers, the multiscale analyses still provided insights into how different scales influenced habitat selection. The poorer fit of the multiscale models may have been a function of the coarse resolution of the county-level forest variables and the subsequent loss of finer resolution habitat relationships. Had the forest variables been developed using data from at a finer resolution (e.g. true FIA plot locations), finer scale relationships would be more precisely modeled and improve multiscale model performance. Other studies that used multiscale analyses have repeatedly demonstrated a

multiscale effect on bird-habitat relationships (e.g. Lichstein et al. 2002, MacFaden and Capen 2002, Thogmartin et al. 2004, Thogmartin and Knuston 2006) as well as bird species richness (Mitchell et al. 2006). Bird-habitat relationships at smaller scales tend to account for a greater proportion of variability in bird occupancy and abundance (Lichstein et al. 2002) and the relationships at these scales influenced those at larger scales, making the simultaneous analyses of all scales inherently more informative (MacFaden and Capen 2002, Young and Hutto 2002).

However, even in multiscale studies, the selection of the study scales still tends to be relatively arbitrary and applied universally to all species in spite of differing life history traits and habitat requirements. Varying multiscale approaches have been adapted in more recent wildlife-habitat studies, and while they are improvements over historical single-scale studies, the vexing question remains as to the ecological relevance of the chosen scales (Wiens 2002). Such approaches hold promise for assessing multiscale habitat selection by wildlife, but further research is required to determine appropriate methods of selecting ecologically relevant spatial extents or assessing multiscale selection in general. Variance partitioning using multivariate methods such as canonical correspondence analysis (CCA) have been used with relative success in some studies (e.g. MacFaden and Capen 2002, Miller et al. 2004, Titeux et al. 2004), but such techniques have an array of assumptions that are difficult to adequately address in many wildlife studies (Stauffer 2002). More novel approaches integrating spatial statistics describing components of spatial structure and autocorrelation, such as mantel tests and correlograms (Koenig and Knops 1998, Bjørnstad and Falck 2001), to aid in scale selection or multimodeling (Gross and DeAngelis 2002) also have potential.

Table 9a. Number of times the county-level forest variables developed from the 2000 FIA inventory were included in the logistic regression and CART models within the cavity and early successional guilds. Data are summarized by modeling approach. The number of potential unique species-model combinations within a guild appears in the parenthesis.

Metric	Cavity (11)				Early successional (11)			
	CART-PA	CART-Abund	Logistic	Rate of inclusion	CART-PA	CART-Abund	Logistic	Rate of inclusion
ALLDIAMAVG	0	0	0	0.000	1	0	0	0.091
ALLDIAMCV	0	0	0	0.000	0	1	0	0.091
ALLHTAVG	0	0	0	0.000	0	0	0	0.000
ALLHTCV	2	1	1	0.364	0	2	1	0.273
ALLSW_N	1	4	1	0.545	3	4	1	0.727
DDIAMAVG	2	1	0	0.273	0	0	0	0.000
DDIAMCV	1	1	1	0.273	0	0	0	0.000
DEADDIAMAVG	0	0	0	0.000	0	1	1	0.182
DEADTPA	0	1	0	0.091	2	1	2	0.455
DHTCV	0	0	0	0.000	0	1	0	0.091
DOMHTAVG	1	0	0	0.091	1	2	0	0.273
DOMTPA	0	1	0	0.091	1	1	0	0.182
DRCDIAMAVG	1	1	0	0.182	0	3	0	0.273
DRCTPA	2	2	2	0.545	2	2	2	0.545
DSW_N	1	1	1	0.273	0	1	0	0.091
RCDIAMAVG	1	3	1	0.455	0	0	0	0.000
RCTPA	0	1	1	0.182	1	1	1	0.273
SITECLCD	1	1	1	0.273	1	3	2	0.545
SSDIAMAVG	1	1	0	0.182	0	2	1	0.273
SSDIAMCV	0	0	0	0.000	0	0	0	0.000
SSSW_N	0	0	0	0.000	0	0	0	0.000
SSTPA	0	1	1	0.182	0	0	0	0.000
STDAGE	1	0	0	0.091	0	0	0	0.000
STDSZCD	0	0	0	0.000	0	0	0	0.000
TPA	0	0	0	0.000	0	0	0	0.000
UDIAMAVG	1	1	0	0.182	3	3	1	0.636
UDIAMCV	0	2	0	0.182	0	0	0	0.000
USW_N	0	0	0	0.000	0	0	0	0.000
UTPA	0	0	0	0.000	0	0	0	0.000
V11	0	1	0	0.091	0	1	1	0.182
V12	0	1	0	0.091	0	0	1	0.091
V13	0	0	0	0.000	0	0	0	0.000
V19	0	1	0	0.091	1	2	1	0.364
V21	0	3	0	0.273	3	2	2	0.636
V22	1	1	0	0.182	2	3	1	0.545
V23	1	2	2	0.455	0	0	0	0.000
V24	1	1	0	0.182	0	1	0	0.091
V25	0	0	0	0.000	0	1	0	0.091
V29	0	0	0	0.000	0	0	0	0.000
V31	1	0	0	0.091	1	1	2	0.364
V32	1	2	1	0.364	0	1	0	0.091
V34	0	0	0	0.000	0	0	0	0.000
V39	0	0	0	0.000	0	0	0	0.000

Table 9b. Number of times the county-level forest variables developed from the 2000 FIA inventory were included in the logistic regression and CART models within the mature forest canopy and ground-shrub guilds. Data are summarized by modeling approach. The number of potential unique species-model combinations within a guild appears in the parenthesis.

Metric	Mature forest canopy (9)				Mature forest ground shrub (33)			
	CART-PA	CART-Abund	Logistic	Rate of inclusion	CART-PA	CART-Abund	Logistic	Rate of inclusion
ALLDIAMAVG	0	2	1	0.333	2	0	1	0.091
ALLDIAMCV	1	0	0	0.111	0	0	0	0.000
ALLHTAVG	1	0	0	0.111	4	4	4	0.364
ALLHTCV	3	2	2	0.778	3	2	3	0.242
ALLSW_N	2	2	2	0.667	4	4	3	0.333
DDIAMAVG	1	3	1	0.556	2	2	3	0.212
DDIAMCV	0	2	0	0.222	0	1	1	0.061
DEADDIAMAVG	0	0	0	0.000	3	2	4	0.273
DEADTPA	0	0	0	0.000	5	3	6	0.424
DHTCV	0	0	0	0.000	0	0	0	0.000
DOMHTAVG	1	1	0	0.222	3	2	1	0.182
DOMTPA	1	1	1	0.333	3	2	3	0.242
DRCDIAMAVG	0	0	0	0.000	1	3	3	0.212
DRCTPA	0	0	0	0.000	3	1	3	0.212
DSW_N	1	3	0	0.444	2	4	4	0.303
RCDIAMAVG	0	0	0	0.000	3	1	2	0.182
RCTPA	0	2	1	0.333	4	3	2	0.273
SITECLCD	1	0	1	0.222	5	2	4	0.333
SSDIAMAVG	0	0	0	0.000	0	1	0	0.030
SSDIAMCV	0	0	0	0.000	1	0	1	0.061
SSSW_N	0	0	0	0.000	0	0	0	0.000
SSTPA	1	1	0	0.222	0	1	0	0.030
STDAGE	0	0	0	0.000	3	2	4	0.273
STDSZCD	1	1	1	0.333	1	1	1	0.091
TPA	0	0	0	0.000	0	0	0	0.000
UDIAMAVG	1	1	1	0.333	5	6	3	0.424
UDIAMCV	1	0	1	0.222	1	2	3	0.182
USW_N	0	1	0	0.111	2	1	0	0.091
UTPA	0	0	0	0.000	1	0	1	0.061
V11	0	0	0	0.000	2	1	2	0.152
V12	0	1	0	0.111	1	4	6	0.333
V13	0	0	0	0.000	0	0	0	0.000
V19	1	2	1	0.444	1	1	2	0.121
V21	0	0	0	0.000	4	6	3	0.394
V22	1	1	0	0.222	3	5	4	0.364
V23	0	0	0	0.000	2	3	3	0.242
V24	0	0	0	0.000	2	2	4	0.242
V25	0	0	0	0.000	2	2	3	0.212
V29	1	0	0	0.111	1	0	2	0.091
V31	0	0	0	0.000	2	1	1	0.121
V32	0	0	0	0.000	0	1	0	0.030
V34	0	0	0	0.000	0	0	0	0.000
V39	0	0	0	0.000	0	0	0	0.000

Table 9c. Number of times the county-level forest variables developed from the 2000 FIA inventory were included in the logistic regression and CART models summarized across all guilds. Data are summarized by modeling approach. There were 64 potential unique species-model combinations across all guilds.

Metric	CART- PA	CART- Abund	Logistic	Total	Rate of inclusion
ALLDIAMAVG	3	2	2	7	0.109
ALLDIAMCV	1	1	0	2	0.031
ALLHTAVG	5	4	4	13	0.203
ALLHTCV	8	7	7	22	0.344
ALLSW_N	10	14	7	31	0.484
DDIAMAVG	5	6	4	15	0.234
DDIAMCV	1	4	2	7	0.109
DEADDIAMAVG	3	3	5	11	0.172
DEADTPA	7	5	8	20	0.313
DHTCV	0	1	0	1	0.016
DOMHTAVG	6	5	1	12	0.188
DOMTPA	5	5	4	14	0.219
DRCDIAMAVG	2	7	3	12	0.188
DRCTPA	7	5	7	19	0.297
DSW_N	4	9	5	18	0.281
RCDIAMAVG	4	4	3	11	0.172
RCTPA	5	7	5	17	0.266
SITECLCD	8	6	8	22	0.344
SSDIAMAVG	1	4	1	6	0.094
SSDIAMCV	1	0	1	2	0.031
SSSW_N	0	0	0	0	0.000
SSTPA	1	3	1	5	0.078
STDAGE	4	2	4	10	0.156
STDSZCD	2	2	2	6	0.094
TPA	0	0	0	0	0.000
UDIAMAVG	10	11	5	26	0.406
UDIAMCV	2	4	4	10	0.156
USW_N	2	2	0	4	0.063
UTPA	1	0	1	2	0.031
V11	2	3	3	8	0.125
V12	1	6	7	14	0.219
V13	0	0	0	0	0.000
V19	3	6	4	13	0.203
V21	7	11	5	23	0.359
V22	7	10	5	22	0.344
V23	3	5	5	13	0.203
V24	3	4	4	11	0.172
V25	2	3	3	8	0.125
V29	2	0	2	4	0.063
V31	4	2	3	9	0.141
V32	1	4	1	6	0.094
V34	0	0	0	0	0.000
V39	0	0	0	0	0.000

Table 10a. Number of times the landscape variables were included in models developed by logistic regression and CART within the cavity and early successional guilds. Data are summarized by modeling approach. The number of potential unique species-model combinations within each guild appears in the parenthesis.

Metric	Cavity (11)				Early successional (11)			
	CART-PA	CART-Abund	Logistic	Rate of inclusion	CART-PA	CART-Abund	Logistic	Rate of inclusion
CAI_AM	1	1	0	0.182	0	0	0	0.000
CAI_CV	0	1	0	0.091	2	2	2	0.545
CAI_MN	2	2	0	0.364	1	1	1	0.273
CPLAND	0	0	0	0.000	0	1	0	0.091
CWED	0	0	0	0.000	0	1	0	0.091
IJI	0	1	0	0.091	0	1	1	0.182
LANDCONTAG	0	1	0	0.091	0	0	0	0.000
LANDCWED	0	0	0	0.000	1	1	0	0.182
LANDIJI	0	1	1	0.182	0	1	1	0.182
LANDLPI	0	0	0	0.000	0	1	0	0.091
LANDLSI	0	0	0	0.000	0	0	0	0.000
LANDPD	0	1	0	0.091	2	0	1	0.273
LANDSHDI	1	1	0	0.182	0	0	0	0.000
LANDSIDE	0	0	0	0.000	0	0	0	0.000
LANDTECI	0	0	0	0.000	0	1	0	0.091
LCAI_AM	0	1	0	0.091	2	2	2	0.545
LCAI_CV	0	0	0	0.000	0	0	0	0.000
LCAI_MN	0	1	0	0.091	0	0	0	0.000
LPI	0	0	0	0.000	0	0	0	0.000
LSHAPE_AM	1	1	0	0.182	0	1	0	0.091
LSHAPE_CV	0	1	0	0.091	0	0	1	0.091
LSHAPE_MN	0	0	0	0.000	0	1	0	0.091
LSI	0	0	1	0.091	0	0	0	0.000
PD	1	0	0	0.091	1	1	1	0.273
PLAND	0	0	0	0.000	0	1	1	0.182
SHAPE_AM	1	2	1	0.364	0	0	0	0.000
SHAPE_CV	1	0	1	0.182	0	0	0	0.000
SHAPE_MN	1	0	1	0.182	1	1	0	0.182
TECI	0	0	0	0.000	0	1	0	0.091

Table 10b. Number of times the landscape variables were included in models developed by logistic regression and CART within the mature forest canopy and ground-shrub guilds. Data are summarized by modeling approach. The number of potential unique species-model combinations within each guild appears in the parenthesis.

Metric	Mature forest canopy (9)				Mature forest ground shrub (33)			
	CART-PA	CART-Abund	Logistic	Rate of inclusion	CART-PA	CART-Abund	Logistic	Rate of inclusion
CAI_AM	1	1	1	0.333	2	2	2	0.182
CAI_CV	0	0	0	0.000	1	1	0	0.061
CAI_MN	1	1	0	0.222	3	2	2	0.212
CPLAND	0	0	0	0.000	0	1	1	0.061
CWED	1	0	0	0.111	3	1	1	0.152
IJI	1	1	1	0.333	2	3	1	0.182
LANDCONTAG	0	0	0	0.000	1	1	0	0.061
LANDCWED	0	0	0	0.000	1	1	0	0.061
LANDIJI	0	0	0	0.000	1	2	1	0.121
LANDLPI	0	0	0	0.000	0	0	0	0.000
LANDLSI	0	1	0	0.111	1	0	1	0.061
LANDPD	0	0	0	0.000	2	1	1	0.121
LANDSHDI	0	0	0	0.000	0	2	0	0.061
LANDSIDE	1	0	1	0.222	0	0	0	0.000
LANDTECI	0	0	0	0.000	0	0	0	0.000
LCAI_AM	0	1	0	0.111	1	1	1	0.091
LCAI_CV	0	2	0	0.222	1	1	1	0.091
LCAI_MN	0	0	0	0.000	3	3	3	0.273
LPI	0	0	0	0.000	0	0	0	0.000
LSHAPE_AM	0	1	1	0.222	2	3	0	0.152
LSHAPE_CV	0	0	0	0.000	1	1	0	0.061
LSHAPE_MN	1	1	0	0.222	3	2	0	0.152
LSI	0	2	0	0.222	4	4	3	0.333
PD	1	2	0	0.333	0	0	0	0.000
PLAND	1	3	1	0.556	3	4	2	0.273
SHAPE_AM	0	0	0	0.000	0	0	0	0.000
SHAPE_CV	0	0	0	0.000	1	0	0	0.030
SHAPE_MN	0	0	0	0.000	4	3	5	0.364
TECI	0	0	0	0.000	0	0	1	0.030

Table 10c. Number of times the landscape variables were included in models developed by logistic regression and CART summarized across all guilds. Data are summarized by modeling approach. There were 64 potential unique species-model combinations across all guilds.

Metric	CART- PA	CART- Abund	Logistic	Total	Rate of inclusion
CAI_AM	4	4	3	11	0.172
CAI_CV	3	4	2	9	0.141
CAI_MN	7	6	3	16	0.250
CPLAND	0	2	1	3	0.047
CWED	4	2	1	7	0.109
IJI	3	6	3	12	0.188
LANDCONTAG	1	2	0	3	0.047
LANDCWED	2	2	0	4	0.063
LANDIJI	1	4	3	8	0.125
LANDLPI	0	1	0	1	0.016
LANDLSI	1	1	1	3	0.047
LANDPD	4	2	2	8	0.125
LANDSHDI	1	3	0	4	0.063
LANDSIDEI	1	0	1	2	0.031
LANDTECI	0	1	0	1	0.016
LCAI_AM	3	5	3	11	0.172
LCAI_CV	1	3	1	5	0.078
LCAI_MN	3	4	3	10	0.156
LPI	0	0	0	0	0.000
LSHAPE_AM	3	6	1	10	0.156
LSHAPE_CV	1	2	1	4	0.063
LSHAPE_MN	4	4	0	8	0.125
LSI	4	6	4	14	0.219
PD	3	3	1	7	0.109
PLAND	4	8	4	16	0.250
SHAPE_AM	1	2	1	4	0.063
SHAPE_CV	2	0	1	3	0.047
SHAPE_MN	6	4	6	16	0.250
TECI	0	1	1	2	0.031

Table 11. Performance of classification tree models relating bird presence-absence on BBS routes to forest and landscape variables calculated within 3 buffers centered on BBS routes and a multiscale model incorporating all 3 buffers. The number of BBS routes used for the model, the number of variables per model, and amount of variation in bird presence-absence explained by the model are given for each buffer size and the multiscale model. The best model (having the maximum *PRE* and minimum number of variables if *PRE* was equal between 2 models) for a give species are highlighted in gray.

Bird species	100 m			1 km			10km			Multiscale			Overall average	
	<i>n</i> routes	<i>n</i> vars	<i>PRE</i>	<i>n</i> routes	<i>n</i> vars	<i>PRE</i>	<i>n</i> routes	<i>n</i> vars	<i>PRE</i>	<i>n</i> routes	<i>n</i> vars	<i>PRE</i>	<i>n</i> vars	<i>PRE</i>
Cavity														
Great-crested flycatcher	226	3	0.250	217	3	0.257	227	4	0.432	226	3	0.307	3	0.312
Pileated woodpecker	169	6	0.566	225	7	0.547	173	5	0.449	169	5	0.528	6	0.523
Red-bellied woodpecker	163	5	0.554	166	5	0.560	221	8	0.633	164	4	0.495	6	0.561
Average		4.7	0.457		5.0	0.455		5.7	0.505		4.0	0.443	4.8	0.465
Early Successional														
Chestnut-sided warbler	140	5	0.659	141	6	0.610	169	5	0.578	169	8	0.659	6	0.627
Prairie warbler	220	6	0.440	221	7	0.432	222	7	0.406	221	8	0.466	7	0.436
Yellow-breasted chat	162	6	0.646	164	6	0.781	171	5	0.751	162	8	0.809	6	0.747
Average		5.7	0.582		6.3	0.608		5.7	0.599		8.0	0.645	6.4	0.608
Mature forest canopy														
Cerulean warbler	170	6	0.528	171	6	0.471	172	6	0.498	170	8	0.598	6	0.524
Pine warbler	145	7	0.620	148	7	0.543	149	8	0.615	147	7	0.612	7	0.598
Average		7.5	0.574		6.5	0.507		6.5	0.559		7.5	0.605	6.7	0.561
Mature forest ground-shrub														
American redstart	159	6	0.629	200	7	0.720	202	5	0.753	200	7	0.719	6	0.705
Black and white warbler	224	4	0.515	172	6	0.652	173	5	0.626	170	7	0.742	6	0.634
Black-billed cuckoo	168	5	0.383	171	4	0.466	172	8	0.525	168	5	0.441	6	0.454
Black-thr. blue warbler	127	5	0.651	129	4	0.548	131	8	0.628	128	5	0.808	6	0.659
Canada warbler	137	4	0.376	137	4	0.508	137	4	0.426	126	6	0.543	5	0.463
Hooded warbler	170	7	0.594	226	8	0.584	227	5	0.594	170	7	0.579	7	0.588
Kentucky warbler	144	6	0.563	147	7	0.603	148	9	0.585	144	7	0.619	7	0.593
Ovenbird	225	7	0.762	226	5	0.727	226	4	0.727	224	6	0.811	6	0.757
Rose-breasted grosbeak	148	7	0.684	149	5	0.526	150	6	0.694	148	6	0.799	6	0.676
Worm eating warbler	208	4	0.347	210	6	0.435	210	5	0.362	209	8	0.468	6	0.403
Yellow-billed cuckoo	169	7	0.434	172	6	0.423	177	6	0.531	170	7	0.473	7	0.465
Average		5.6	0.540		5.6	0.563		5.9	0.586		6.5	0.637	5.9	0.581
Overall average		5.6	0.537		5.7	0.547		5.9	0.573		6.4	0.604	5.9	0.565

Table 12. Performance of regression tree models relating variations in bird abundance to forest and landscape metrics variables calculated within 3 buffers centered on BBS routes and a multiscale model incorporating all 3 buffers. The number of BBS routes used for the model, the number of variables per model, and amount of variation in bird abundance explained by the model are given for each buffer size and the multiscale model. The best model (having the maximum *PRE* and minimum number of variables if *PRE* was equal between 2 models) for a give species are highlighted in gray.

Bird species	100 m			1 km			10km			Multiscale			Overall average	
	<i>n</i> routes	<i>n</i> vars	<i>PRE</i>	<i>n</i> routes	<i>n</i> vars	<i>PRE</i>	<i>n</i> routes	<i>n</i> vars	<i>PRE</i>	<i>n</i> routes	<i>n</i> vars	<i>PRE</i>	<i>n</i> vars	<i>PRE</i>
Cavity														
Downy woodpecker	213	3	0.332	223	2	0.159	223	2	0.216	213	3	0.252	2.5	0.240
Great-crested flycatcher	210	5	0.372	205	5	0.369	211	4	0.333	203	6	0.472	5.0	0.387
Pileated woodpecker	148	5	0.449	199	5	0.469	150	5	0.524	188	7	0.542	5.5	0.496
Red-bellied woodpecker	146	6	0.552	149	8	0.623	201	7	0.609	147	7	0.679	7.0	0.616
Tufted titmouse	167	8	0.531	169	8	0.547	224	8	0.464	169	8	0.542	8.0	0.521
Average		5.4	0.447		5.6	0.433		5.2	0.429		6.2	0.497	5.6	0.452
Early Successional														
Chestnut-sided warbler	88	7	0.615	88	5	0.527	101	5	0.451	88	8	0.615	6.3	0.552
Common yellowthroat	166	6	0.581	167	9	0.613	169	8	0.539	166	10	0.654	8.3	0.597
Eastern towhee	225	8	0.531	224	7	0.510	171	7	0.626	213	8	0.612	7.5	0.570
Prairie warbler	127	4	0.445	128	2	0.258	128	5	0.368	128	4	0.396	3.8	0.367
Yellow-breasted chat	96	5	0.587	98	6	0.592	105	6	0.628	97	5	0.586	5.5	0.598
Average		6.0	0.552		5.8	0.500		6.2	0.522		7.0	0.573	6.3	0.537
Mature forest canopy														
Cerulean warbler	62	4	0.653	62	4	0.647	63	3	0.645	62	3	0.776	3.5	0.680
Eastern wood-pewee	171	5	0.479	227	5	0.361	226	6	0.362	226	5	0.431	5.3	0.408
Pine warbler	46	3	0.517	47	2	0.459	48	3	0.677	46	3	0.533	2.8	0.547
Red-eyed vireo	168	4	0.558	171	5	0.675	174	6	0.568	222	7	0.681	5.5	0.621
Wood thrush	171	4	0.525	225	6	0.540	226	5	0.422	225	7	0.524	5.5	0.503
Average		4.0	0.546		4.4	0.536		4.6	0.535		5.0	0.589	4.5	0.552
Mature forest ground-shrub														
American redstart	133	6	0.598	141	6	0.602	142	5	0.471	133	6	0.617	5.8	0.572
Black and white warbler	150	5	0.490	121	5	0.565	122	6	0.508	120	7	0.645	5.8	0.552
Black-billed cuckoo	87	4	0.553	87	5	0.564	87	3	0.387	87	5	0.585	4.3	0.522
Black-thr. blue warbler	41	3	0.467	41	4	0.463	42	3	0.487	41	4	0.482	3.5	0.475
Canada warbler	42	2	0.302	42	2	0.289	42	1	0.298	38	2	0.433	1.8	0.331

Table 12 continued

Bird species	100 m			1 km			10km			Multiscale			Overall average	
	<i>n</i> routes	<i>n</i> vars	<i>PRE</i>	<i>n</i> routes	<i>n</i> vars	<i>PRE</i>	<i>n</i> routes	<i>n</i> vars	<i>PRE</i>	<i>n</i> routes	<i>n</i> vars	<i>PRE</i>	<i>n</i> vars	<i>PRE</i>
Mature forest ground-shrub														
Hooded warbler	117	4	0.719	155	5	0.709	155	6	0.617	144	5	0.737	5.0	0.696
Kentucky warbler	83	4	0.433	84	6	0.459	84	4	0.456	83	3	0.471	4.3	0.455
Ovenbird	186	8	0.694	187	6	0.595	187	7	0.536	186	7	0.646	7.0	0.618
Rose-breasted grosbeak	112	8	0.690	112	7	0.592	112	6	0.519	113	7	0.630	7.0	0.608
Worm eating warbler	121	4	0.749	122	4	0.598	122	6	0.529	121	4	0.702	4.5	0.645
Yellow-billed cuckoo	140	6	0.428	143	6	0.548	148	6	0.628	140	6	0.554	6.0	0.540
Average		4.9	0.557		5.1	0.544		4.8	0.494		5.1	0.591	5.0	0.546
Overall average		5.0	0.533		5.2	0.513		5.1	0.495		5.7	0.569	5.3	0.527

Table 13. Performance of logistic regression models relating bird presence-absence on BBS routes to forest and landscape variables calculated within 3 buffers centered on BBS routes and a multiscale model incorporating all 3 buffers. For each species the number of reference (no detection) and response (≥ 1 detection during the 4-year window used to estimate abundance) BBS routes used for the model, the number of variables per model (K , includes intercept and error term), Akaike weight (w_i) of the best model selected using AIC_c , and model sensitivity (correct classification rate of presence) and specificity (correct classification rate of absence) are given for each buffer size and the multiscale model.

Bird species	100 m						1 km					
	n reference	n response	K	w_i	Sensitivity	Specificity	n reference	n response	K	w_i	Sensitivity	Specificity
Cavity												
Great-crested flycatcher	16	210	4	0.287	0.938	0.190	16	210	4	0.237	0.934	0.130
Pileated woodpecker	28	199	4	0.366	0.892	0.235	26	199	8	0.163	0.908	0.297
Red-bellied woodpecker	20	201	5	0.221	0.922	0.218	20	201	6	0.258	0.929	0.290
Average			4.3	0.291	0.917	0.214			6.0	0.219	0.924	0.239
Early Successional												
Chestnut-sided warbler	68	101	8	0.255	0.746	0.623	53	88	10	0.344	0.801	0.670
Prairie warbler	95	128	6	0.374	0.638	0.512	94	128	7	0.289	0.653	0.527
Yellow-breasted chat	72	145	8	0.371	0.850	0.697	73	146	7	0.400	0.846	0.693
Average			7.3	0.333	0.745	0.611			8.0	0.344	0.767	0.630
Mature forest canopy												
Cerulean warbler	108	62	10	0.285	0.617	0.780	109	62	7	0.293	0.558	0.749
Pine warbler	119	80	10	0.275	0.561	0.705	101	47	4	0.167	0.416	0.728
Average			10.0	0.280	0.589	0.743			5.5	0.230	0.487	0.739
Mature forest ground-shrub												
American redstart	27	133	9	0.302	0.906	0.538	59	141	16	0.204	0.893	0.745
Black and white warbler	77	150	7	0.471	0.821	0.651	77	150	5	0.187	0.808	0.625
Black-billed cuckoo	83	87	4	0.268	0.605	0.586	84	87	5	0.327	0.609	0.595
Black-thr. blue warbler	86	41	7	0.475	0.640	0.828	100	51	6	0.373	0.556	0.773
Canada warbler	95	42	4	0.362	0.382	0.727	95	42	4	0.319	0.395	0.733
Hooded warbler	53	117	7	0.307	0.772	0.496	71	155	11	0.409	0.805	0.574
Kentucky warbler	77	122	9	0.332	0.747	0.599	63	84	11	0.260	0.761	0.681
Ovenbird	39	186	8	0.231	0.938	0.704	40	187	11	0.298	0.956	0.794
Rose-breasted grosbeak	54	120	11	0.355	0.841	0.647	37	112	8	0.302	0.875	0.621
Worm eating warbler	87	121	8	0.441	0.682	0.558	88	122	6	0.271	0.656	0.523
Yellow-billed cuckoo	34	192	5	0.224	0.871	0.272	34	192	7	0.220	0.872	0.277
Average			7.2	0.343	0.746	0.601			8.2	0.288	0.744	0.631
Overall average			7.1	0.326	0.756	0.556			7.5	0.280	0.749	0.580

Table 13 continued

Bird species	10km						Multiscale					
	<i>n</i> reference	<i>n</i> response	<i>K</i>	<i>w_i</i>	Sensitivity	Specificity	<i>n</i> reference	<i>n</i> response	<i>K</i>	<i>w_i</i>	Sensitivity	Specificity
Cavity												
Great-crested flycatcher	16	211	5	0.356	0.944	0.260	16	210	5	0.975	0.944	0.267
Pileated woodpecker	23	150	7	0.454	0.896	0.321	23	148	8	0.263	0.896	0.333
Red-bellied woodpecker	20	202	5	0.391	0.926	0.251	20	202	6	0.341	0.928	0.272
Average			6.0	0.411	0.922	0.284			6.3	0.526	0.923	0.291
Early Successional												
Chestnut-sided warbler	68	101	8	0.366	0.778	0.671	53	88	9	0.266	0.822	0.704
Prairie warbler	95	128	9	0.318	0.681	0.570	95	128	8	0.297	0.676	0.564
Yellow-breasted chat	72	147	9	0.348	0.880	0.754	73	146	8	0.420	0.867	0.734
Average			8.0	0.405	0.771	0.655			8.3	0.328	0.788	0.667
Mature forest canopy												
Cerulean warbler	109	63	6	0.356	0.508	0.716	108	62	8	0.263	0.576	0.799
Pine warbler	101	48	7	0.374	0.476	0.751	99	47	11	0.272	0.608	0.814
Average			6.5	0.316	0.494	0.735			9.5	0.268	0.592	0.807
Mature forest ground-shrub												
American redstart	63	149	11	0.337	0.859	0.667	26	133	17	0.202	0.940	0.692
Black and white warbler	77	150	7	0.342	0.795	0.601	77	150	7	0.338	0.821	0.652
Black-billed cuckoo	85	87	5	0.369	0.620	0.611	83	87	4	0.336	0.616	0.598
Black-thr. blue warbler	100	51	8	0.373	0.645	0.819	86	41	8	0.224	0.659	0.838
Canada warbler	95	42	4	0.822	0.411	0.740	95	42	4	0.428	0.409	0.739
Hooded warbler	72	155	9	0.311	0.783	0.533	54	117	9	0.248	0.785	0.535
Kentucky warbler	64	84	10	0.475	0.763	0.689	80	122	11	0.237	0.766	0.643
Ovenbird	40	187	7	0.312	0.947	0.752	40	187	11	0.315	0.966	0.840
Rose-breasted grosbeak	38	112	10	0.574	0.867	0.607	54	119	9	0.228	0.827	0.618
Worm eating warbler	88	122	7	0.479	0.658	0.526	87	121	9	0.286	0.696	0.577
Yellow-billed cuckoo	30	187	6	0.331	0.891	0.322	30	186	6	0.331	0.891	0.322
Average			8.1	0.360	0.751	0.631			8.6	0.288	0.761	0.641
Overall average			7.6	0.371	0.754	0.591			8.3	0.330	0.773	0.607

Table 13 Continued

Bird species	Overall average			
	K	w_i	Sensitivity	Specificity
Cavity				
Great-crested flycatcher	4.5	0.464	0.940	0.212
Pileated woodpecker	6.8	0.312	0.898	0.297
Red-bellied woodpecker	5.5	0.303	0.926	0.258
Average	5.6	0.359	0.921	0.255
Early Successional				
Chestnut-sided warbler	8.8	0.308	0.787	0.667
Prairie warbler	7.5	0.320	0.662	0.543
Yellow-breasted chat	8.0	0.385	0.861	0.720
Average	8.1	0.337	0.770	0.643
Mature forest canopy				
Cerulean warbler	7.8	0.299	0.565	0.761
Pine warbler	8.0	0.272	0.515	0.750
Average	7.9	0.286	0.540	0.755
Mature forest ground-shrub				
American redstart	13.3	0.261	0.900	0.661
Black and white warbler	6.5	0.335	0.811	0.632
Black-billed cuckoo	4.5	0.325	0.613	0.598
Black-throated blue warbler	7.3	0.361	0.625	0.815
Canada warbler	4.0	0.483	0.399	0.735
Hooded warbler	9.0	0.319	0.786	0.535
Kentucky warbler	10.3	0.326	0.759	0.653
Ovenbird	9.3	0.289	0.952	0.773
Rose-breasted grosbeak	9.5	0.365	0.853	0.623
Worm eating warbler	7.5	0.369	0.673	0.546
Yellow-billed cuckoo	6.0	0.277	0.881	0.298
Average	7.9	0.3	0.750	0.624
Overall	7.6	0.3	0.756	0.586

Table 14. Predictors from the logistic regression models relating variations in cerulean warbler presence-absence on BBS routes during the 2000 FIA inventory cycle to forest and landscape variables calculated at 3 buffer sizes centered each BBS route. Each model was the best model as selected from an *a priori* set using AIC_c .

Predictor	β	P-value
100 m		
ALLDIAMAVG	-11.107	0.073
DOMTPA	0.641	<0.001
ALLHTCV	2.686	<0.001
SITECLCD	1.627	0.001
ALLSW_N	0.132	0.042
PLAND	0.059	<0.001
IJI	0.042	0.049
LSHAPE_AM	-0.386	0.137
1 km		
STDSZCD	-0.579	0.126
DDIAMAVG	0.573	0.005
ALLHTCV	1.243	0.008
ALLSW_N	0.145	0.008
PLAND	0.059	<0.001
10 km		
DDIAMAVG	0.408	0.038
ALLHTCV	0.858	0.043
ALLSW_N	0.160	0.006
PLAND	0.033	0.015
Multiscale ^a		
V1ALLSW_N	0.155	0.005
V1LSHAPE_AM	-0.376	0.08
V2STDSZCD	-0.663	0.091
V2PLAND	0.069	<0.001
V3DDIAMAVG	0.656	0.007
V3ALLHTCV	10.51	0.029

^a V1 = 100 m buffer, V2 = 1 km buffer, V3 = 10 km buffer

Table 15. Predictors from the logistic regression models relating variations in yellow-breasted chat presence-absence on BBS routes during the 2000 FIA inventory cycle to forest and landscape variables calculated at 3 buffer sizes centered each BBS route. Each model was the best model as selected from an *a priori* set using AIC_c.

Predictor	β	P-value
100 m		
DEADTPA	-0.305	<0.001
RCTPA	-0.542	0.014
LCAI_AM	-0.071	0.002
V21	-35.755	<0.001
V31	-136.097	0.048
SITECLCD	0.614	0.112
1 km		
SITECLCD	0.917	0.011
DRCTPA	-0.310	<0.001
V21	-34.252	<0.001
V31	-158.496	0.030
LCAI_AM	-0.093	<0.001
10 km		
SITECLCD	1.670	0.001
DEADTPA	-0.196	0.067
RCTPA	-0.232	0.418
V21	-56.067	<0.001
CAI_CV	0.011	<0.001
IJI	0.073	0.055
LCAI_AM	-0.720	0.050
Multiscale ^a		
V1LCAI_AM	-0.050	0.015
V2DRCTPA	-0.233	0.003
V3V21	-51.285	<0.001
V3SITECLCD	1.557	0.001
V3CAI_CV	0.008	0.001
V3IJI	0.087	0.015

^a V1 = 100 m buffer, V2 = 1 km buffer, V3 = 10 km buffer

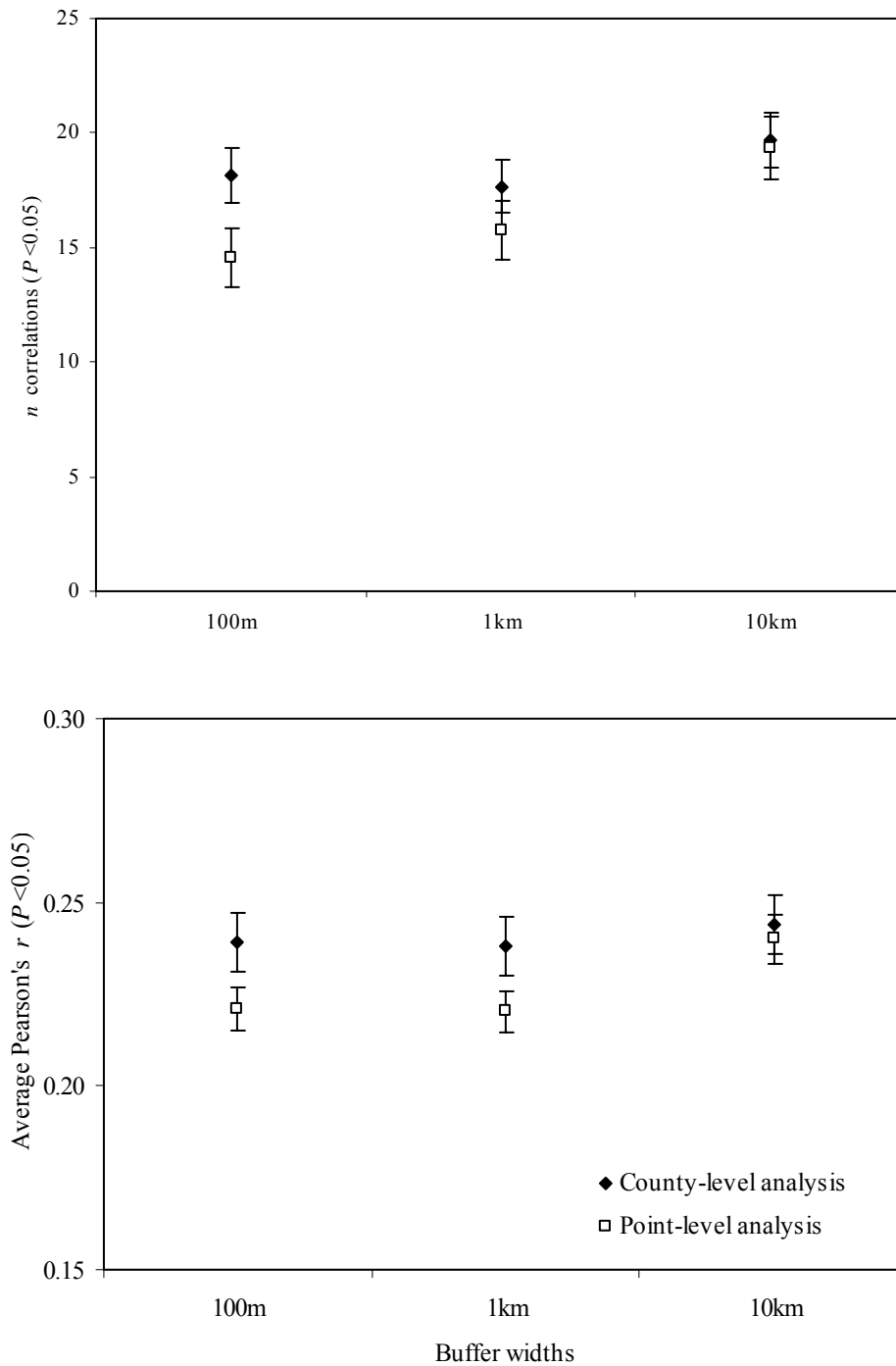


Figure 6. Difference between the average number of significant correlations ($P < 0.05$) and the strength of those correlations (Pearson's r) between the county-level forest metrics and plot-level metrics calculated from the perturbed and swapped FIA plot coordinates. The vertical bars around each point represent standard errors.

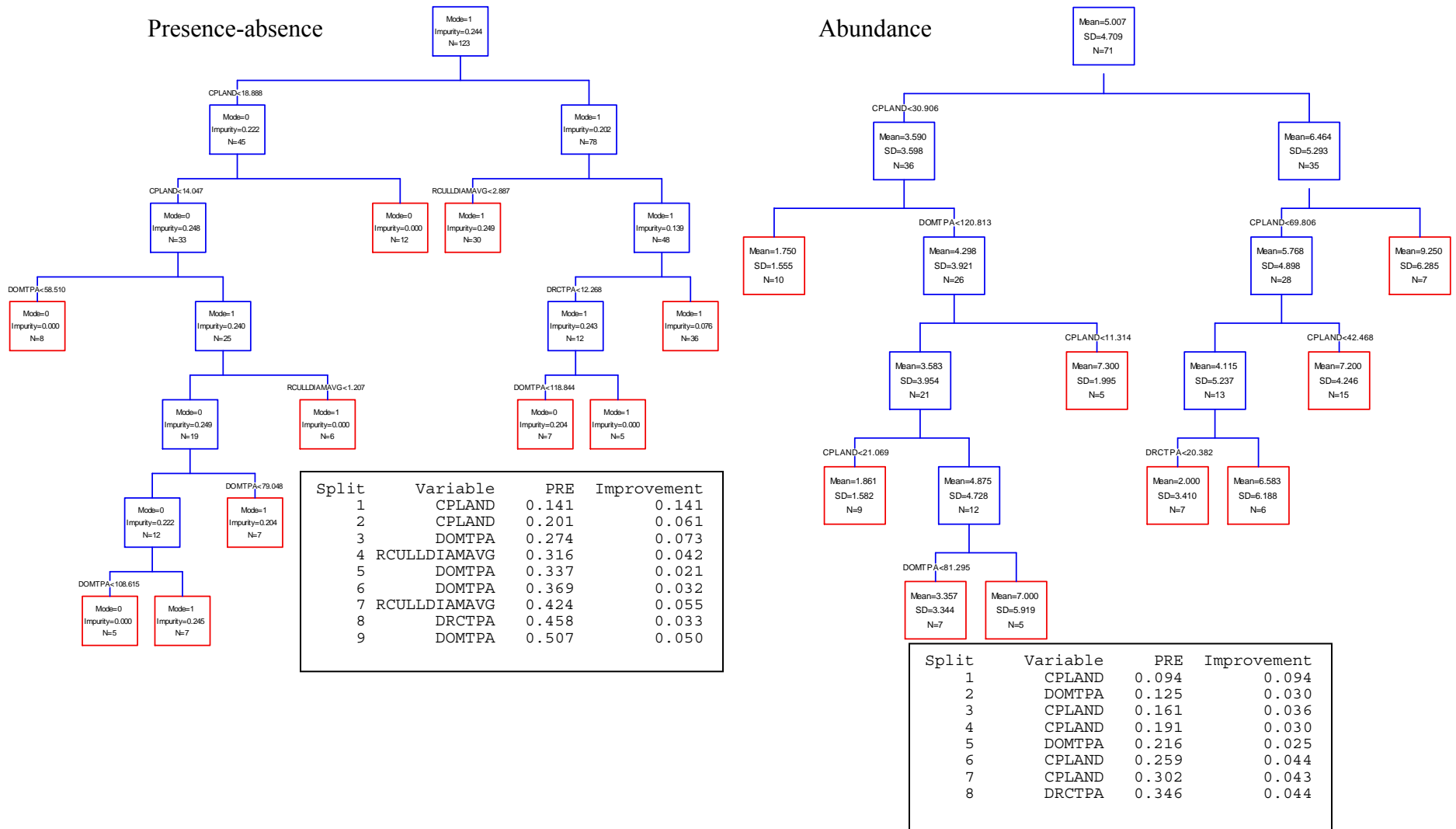


Figure 7a: CART presence-absence and abundance models for the chestnut-sided warbler using forest metrics developed at the FIA plot level. Models are read from top to bottom with the first split explaining the greatest variability and the subsequent splits accounting for further variations in the data. Each node (square) is labeled with the mode (classification tree) or mean (regression tree) of the response variable for that group, a measure of variability around that measure, and the number of samples in that group. Labels along the branches identify the factor creating the split for the underlying nodes.

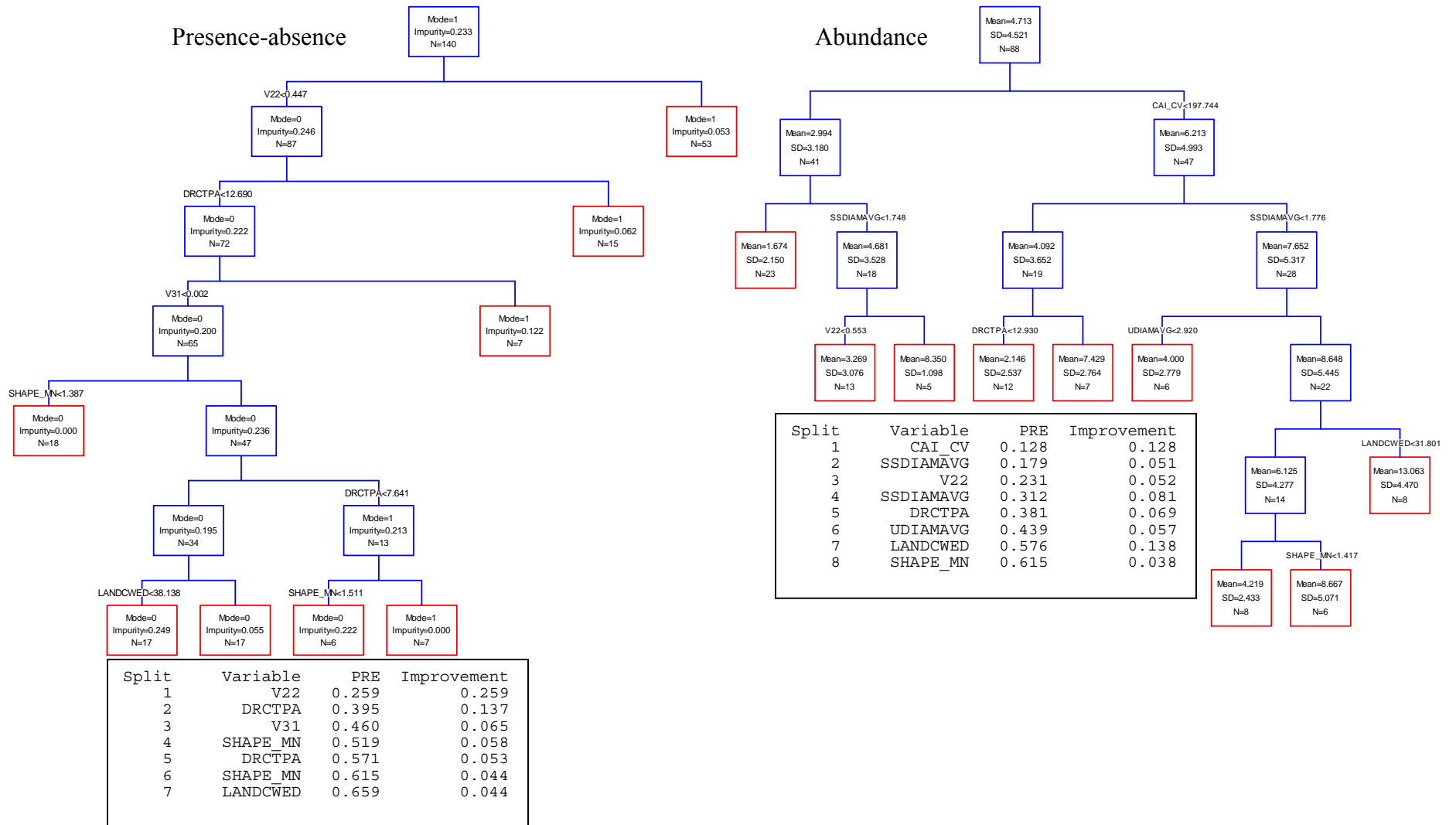


Figure 7b: CART presence-absence and abundance models for the chestnut-sided warbler using forest metrics developed at the FIA county level.

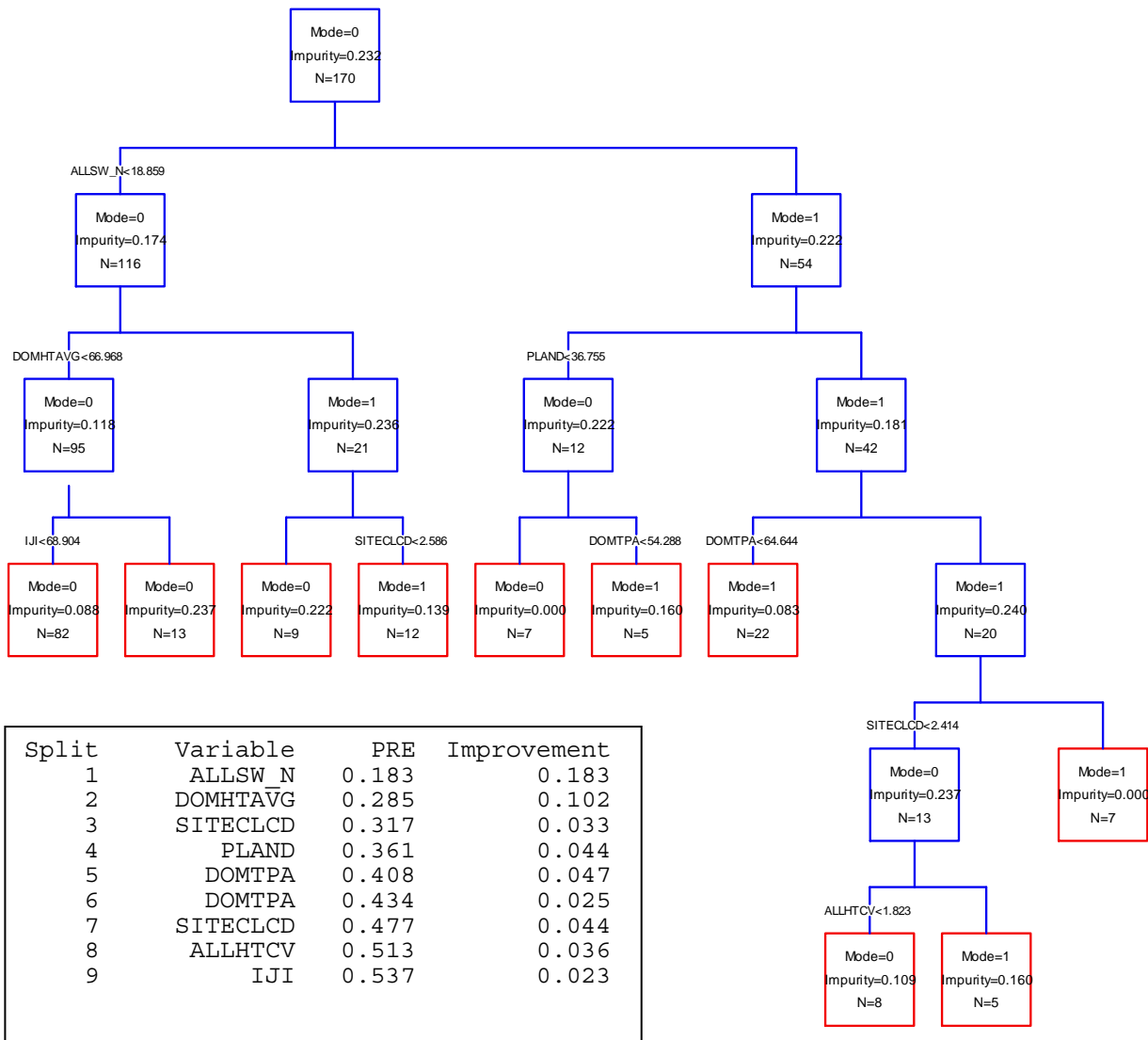


Figure 8a. Classification tree of cerulean warbler presence-absence on BBS routes ($n = 170$) relative to forest and landscape variables calculated within a 100 m buffer around each route.

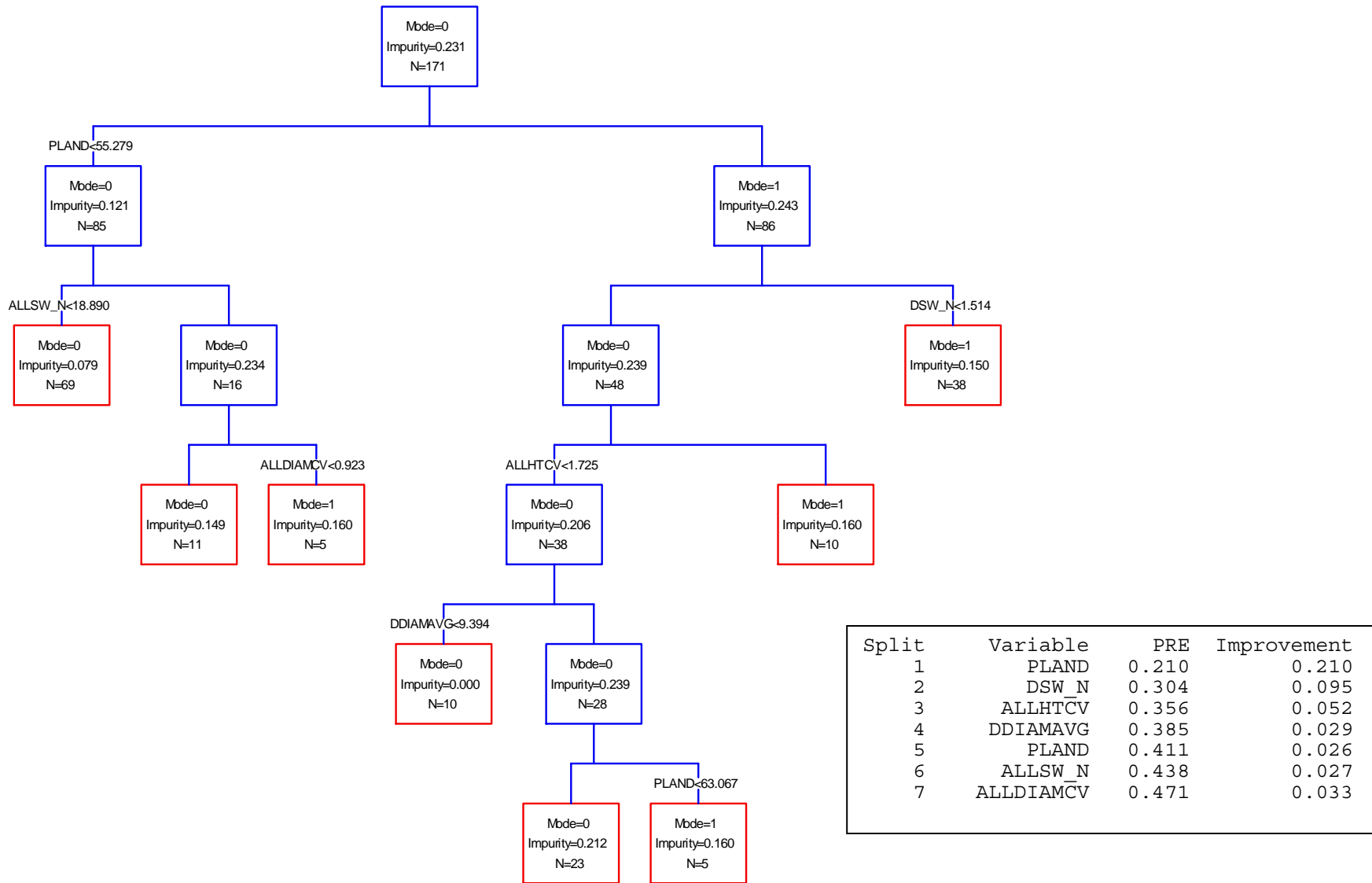


Figure 8b. Classification tree of cerulean warbler presence-absence on BBS routes ($n = 171$) relative to forest and landscape variables calculated within a 1 km buffer around each route.

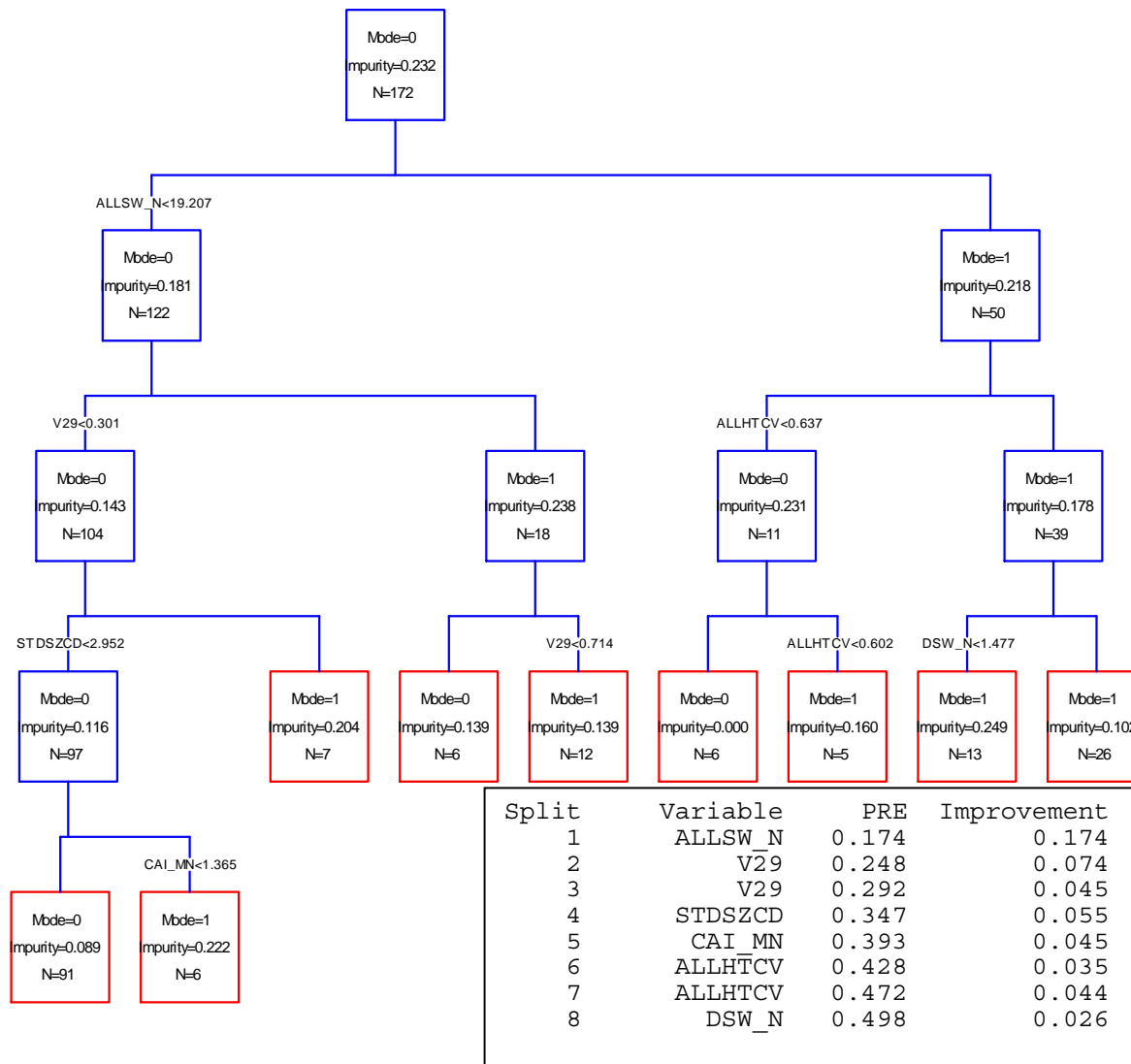


Figure 8c. Classification tree of cerulean warbler presence-absence on BBS routes ($n = 172$) relative to forest and landscape variables calculated within a 10 km buffer around each route.

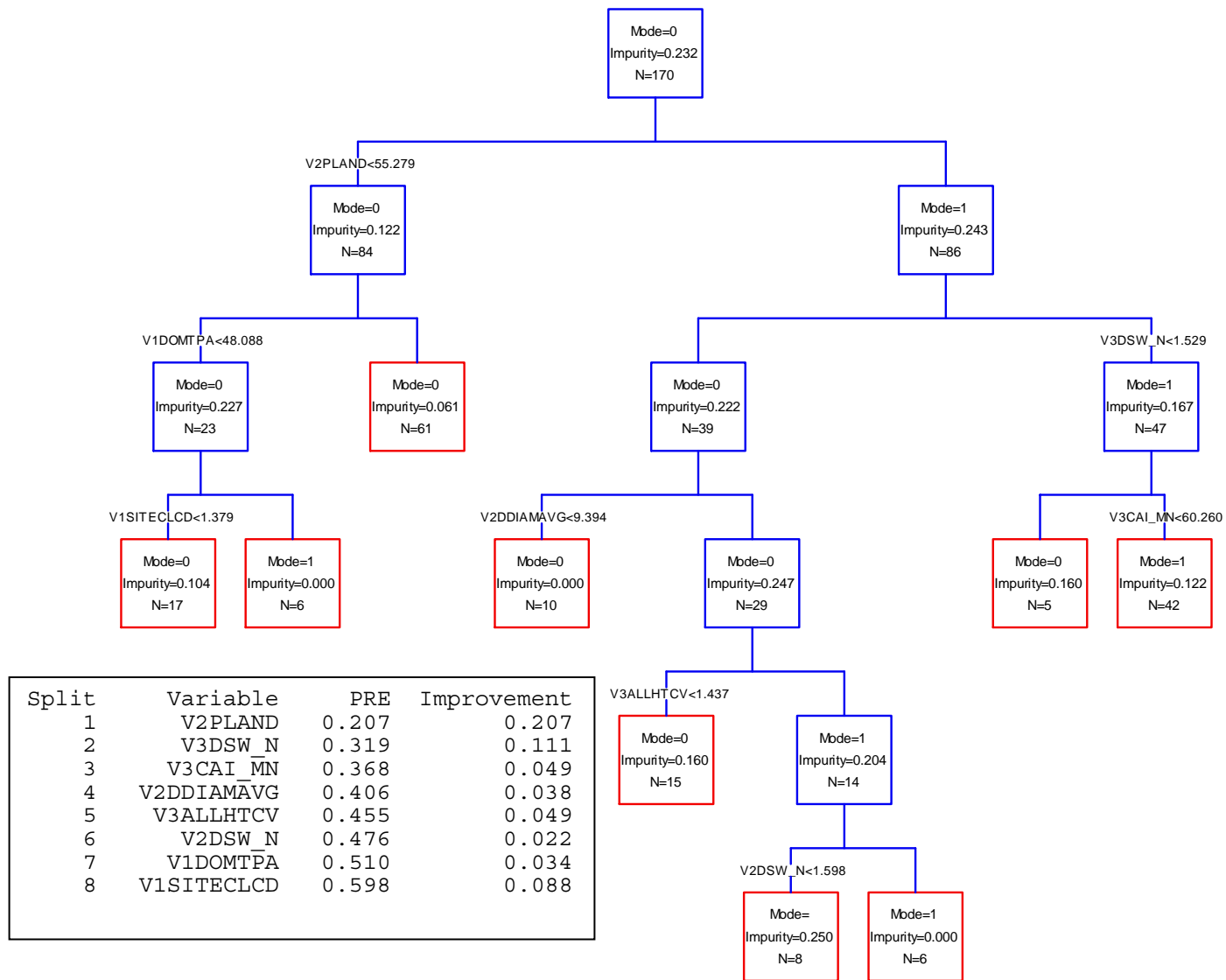


Figure 8d. Classification tree of cerulean warbler presence-absence on BBS routes ($n = 170$) relative to forest and landscape variables calculated within 100 m, 1 km, and 10 km buffers around each route.

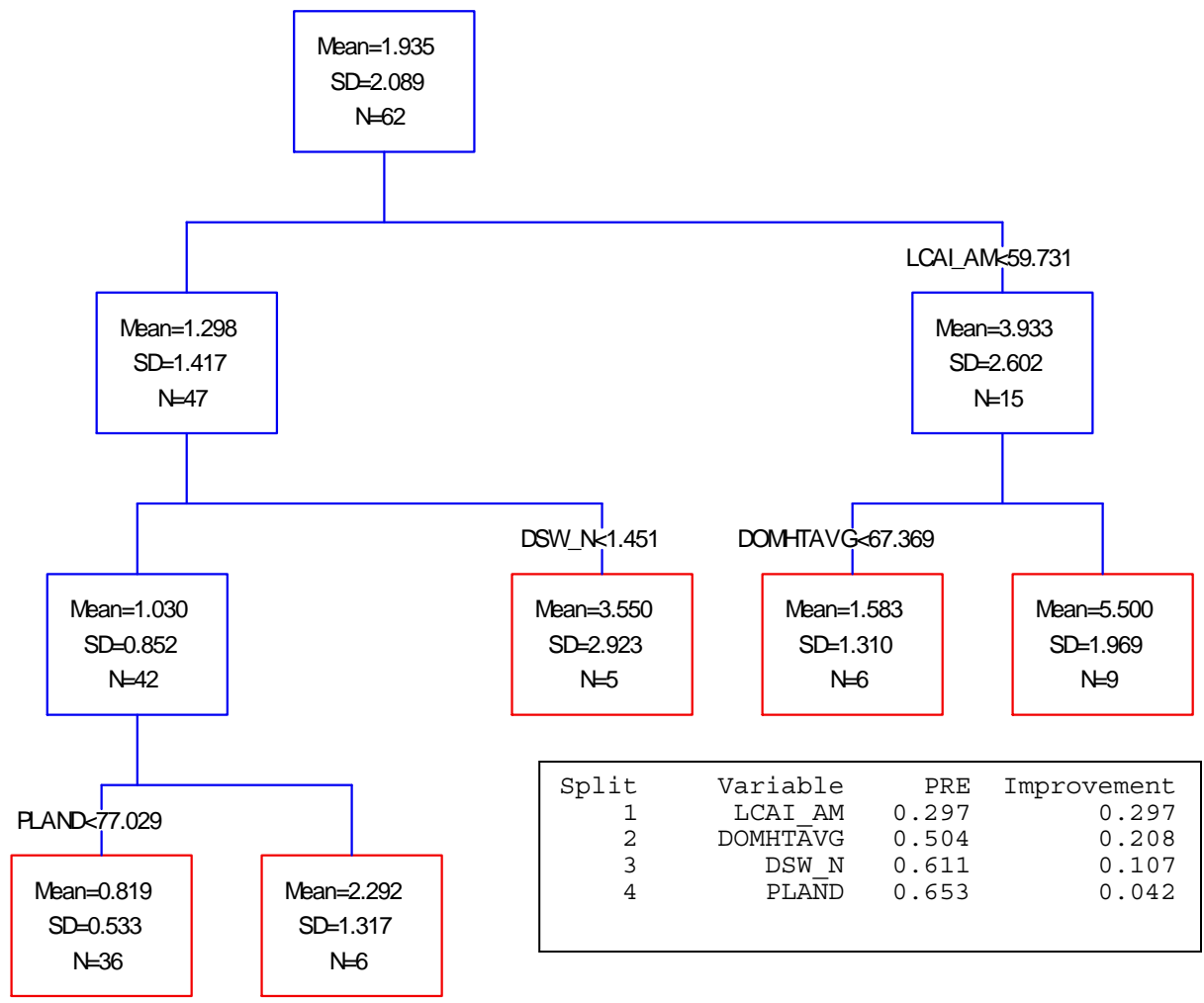


Figure 9a. Regression tree of cerulean warbler abundance on BBS routes ($n = 62$) relative to forest and landscape variables calculated within a 100 m buffer around each route.

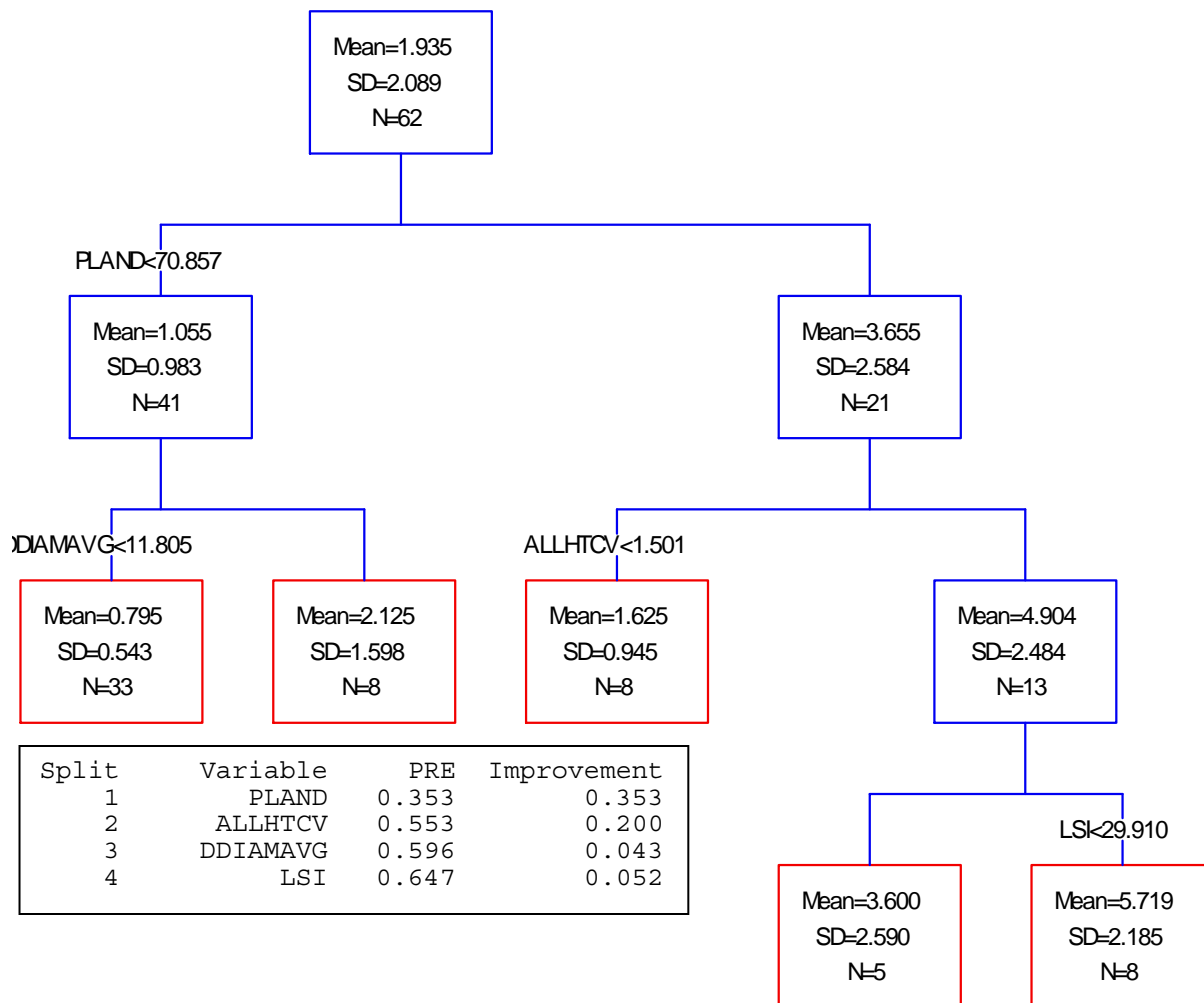


Figure 9b. Regression tree of cerulean warbler abundance on BBS routes ($n = 62$) relative to forest and landscape variables calculated within a 100 m buffer around each route.

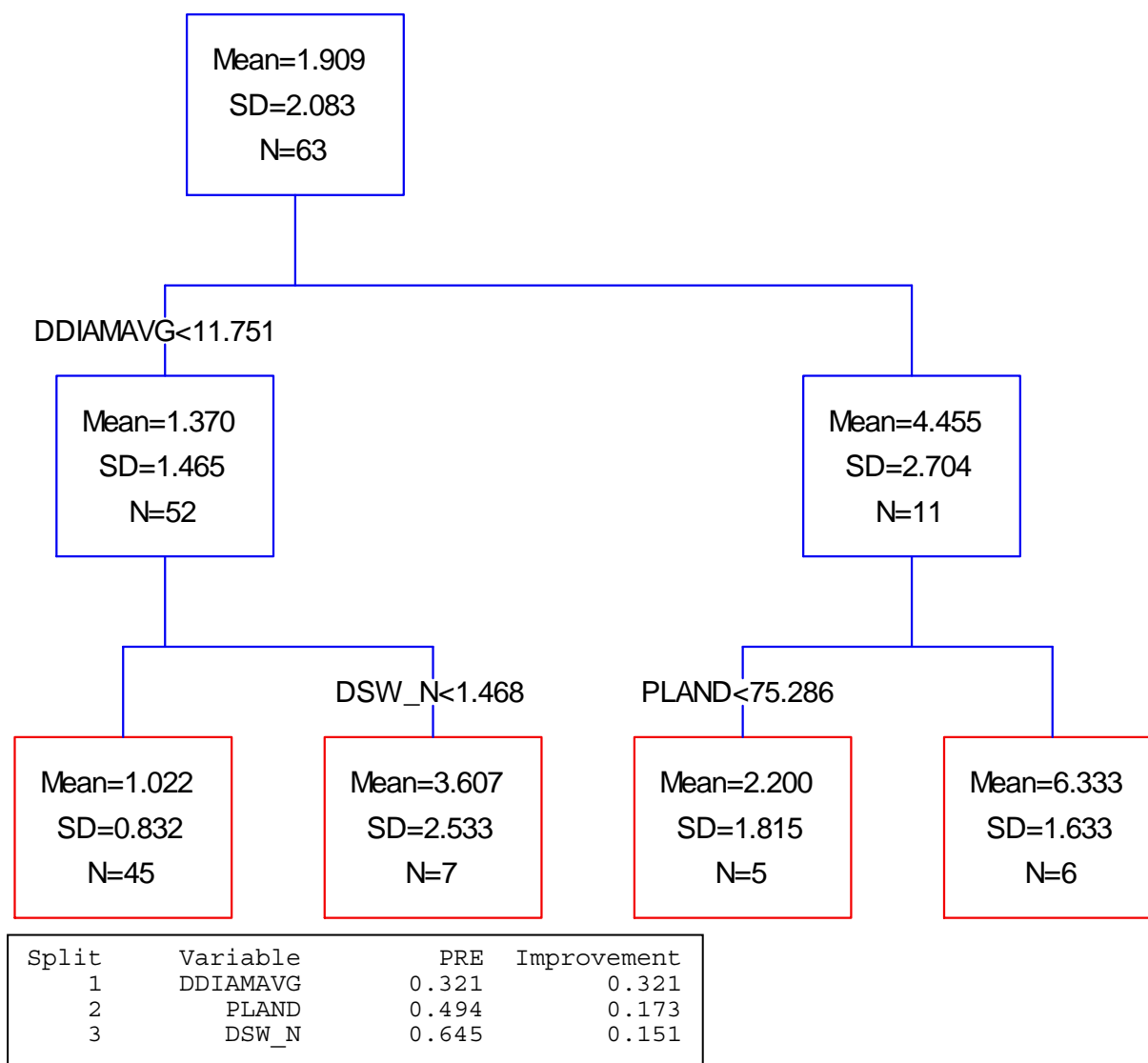


Figure 9c. Regression tree of cerulean warbler abundance on BBS routes ($n = 62$) relative to forest and landscape variables calculated within a 100 m buffer around each route.

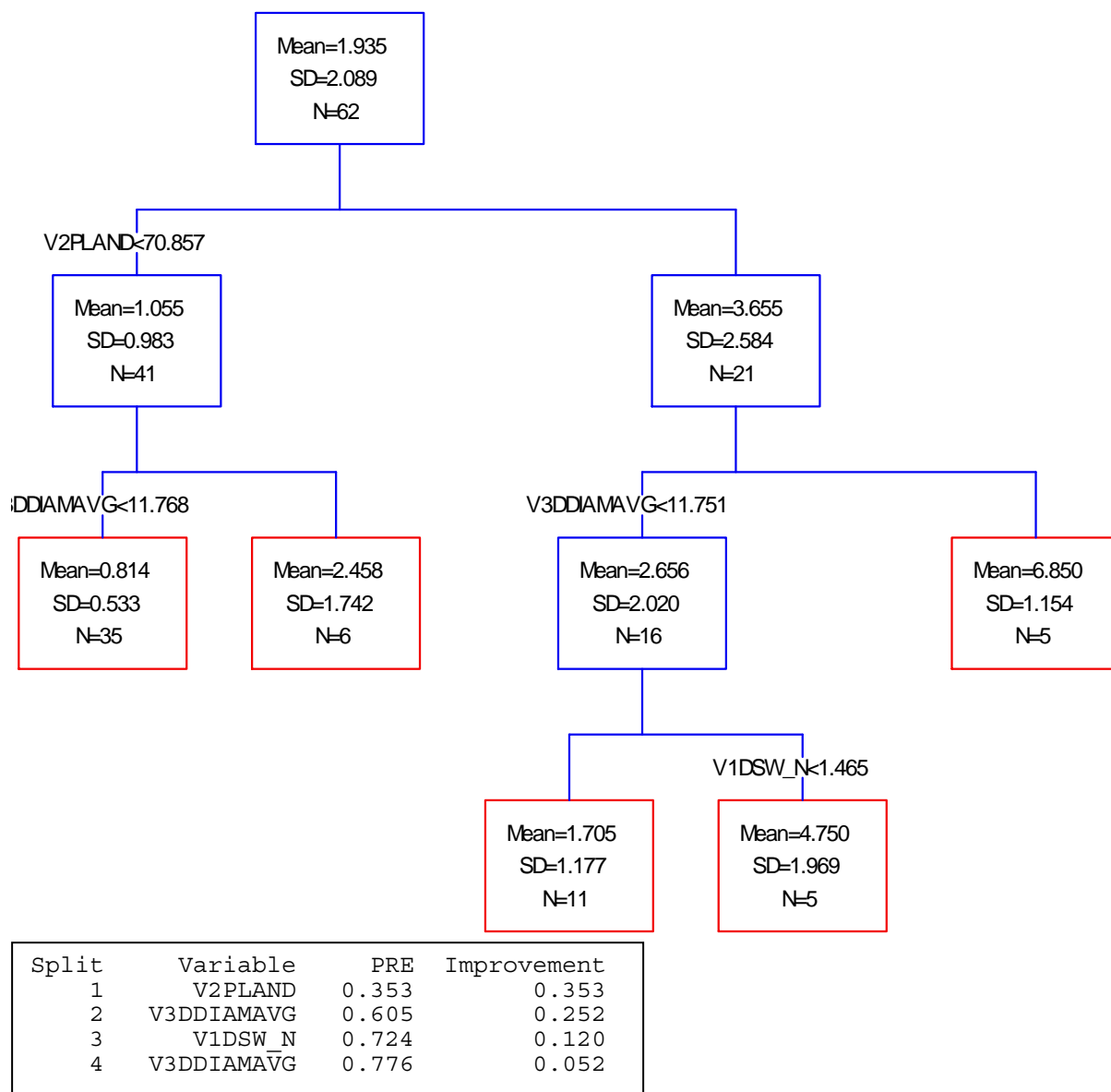


Figure 9d. Regression tree of cerulean warbler abundance on BBS routes ($n = 62$) relative to forest and landscape variables calculated within 100 m (V1), 1 km (V2), and 10 km (V3) buffers around each route.

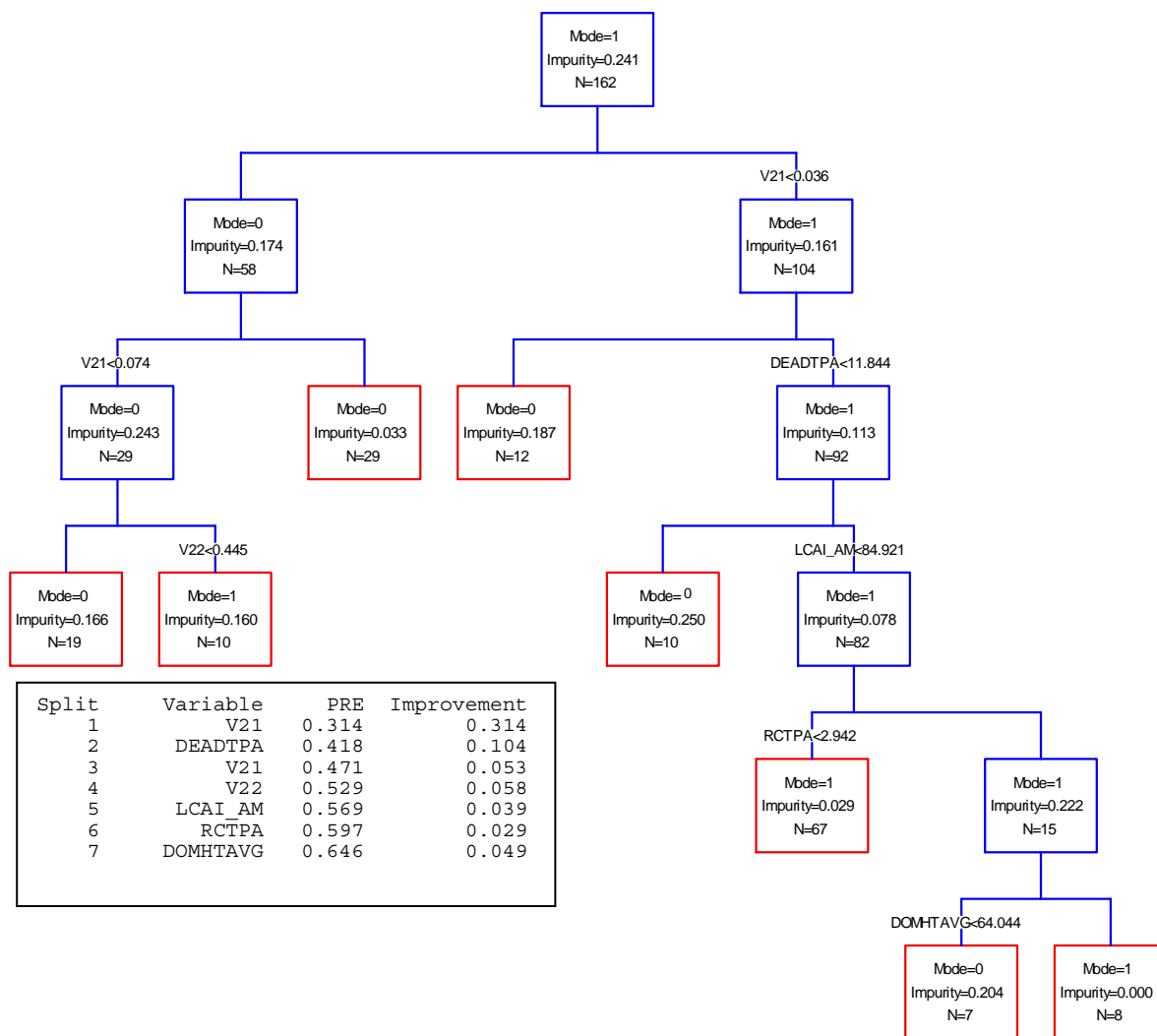


Figure 10a. Classification tree of yellow-breasted chat presence-absence on BBS routes ($n = 162$) relative to forest and landscape variables calculated within a 100 m diameter buffer centered on each route.

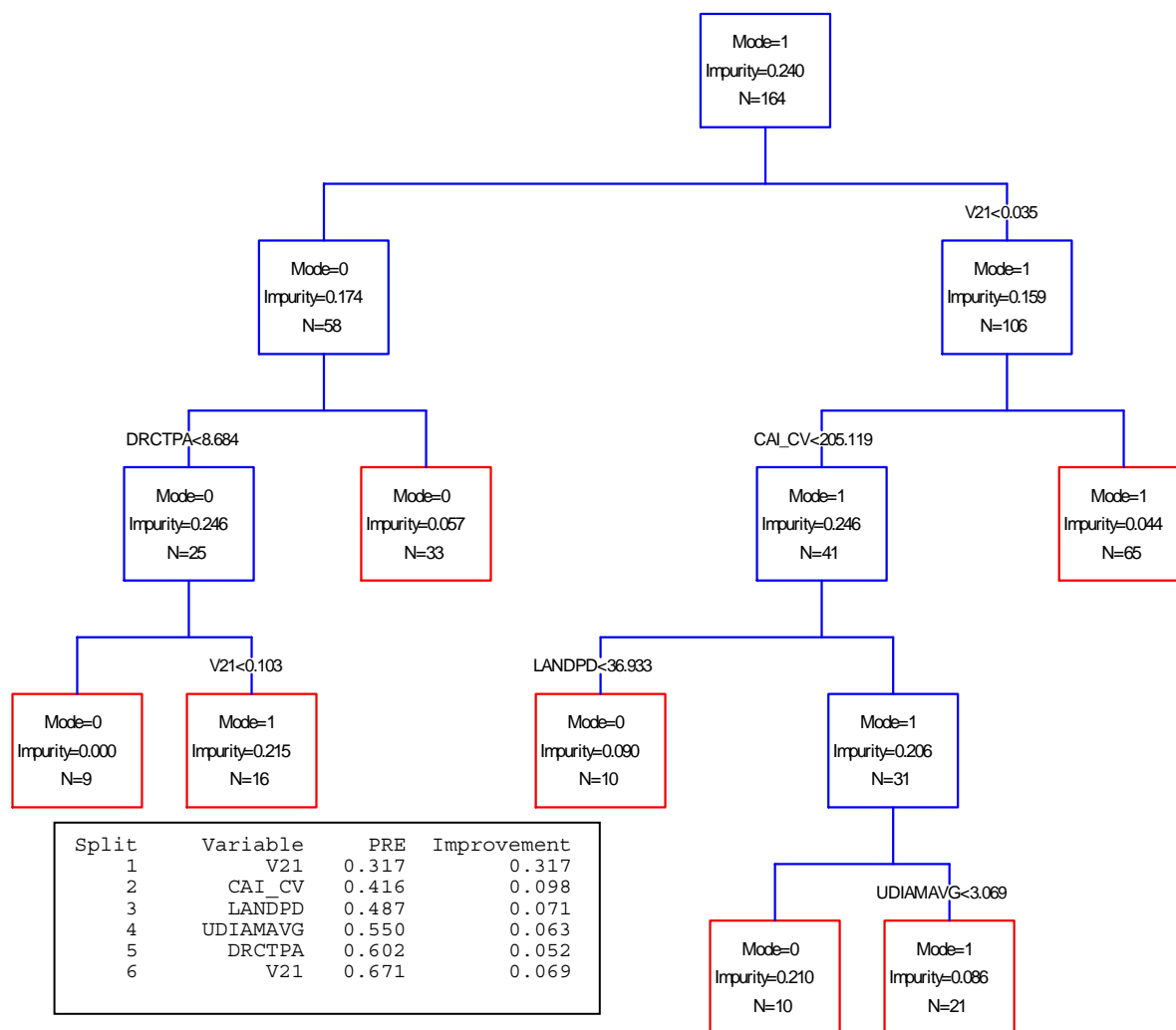


Figure 10b. Classification tree of yellow-breasted chat presence-absence on BBS routes ($n = 164$) relative to forest and landscape variables calculated within a 1 km diameter buffer centered on each route.

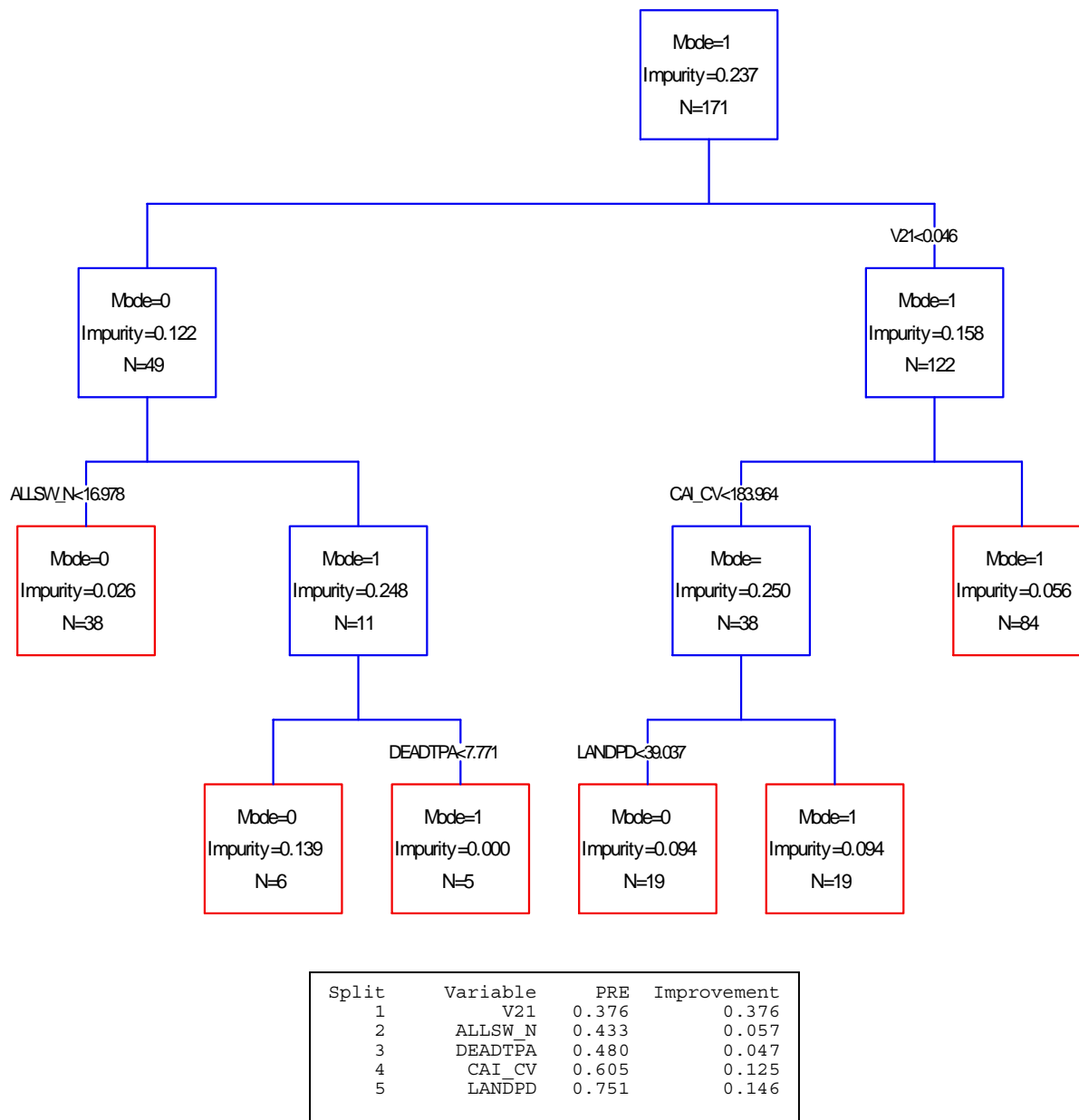


Figure 10c. Classification tree of yellow-breasted chat presence-absence on BBS routes ($n = 171$) relative to forest and landscape variables calculated within a 10 km diameter buffer centered on each route.

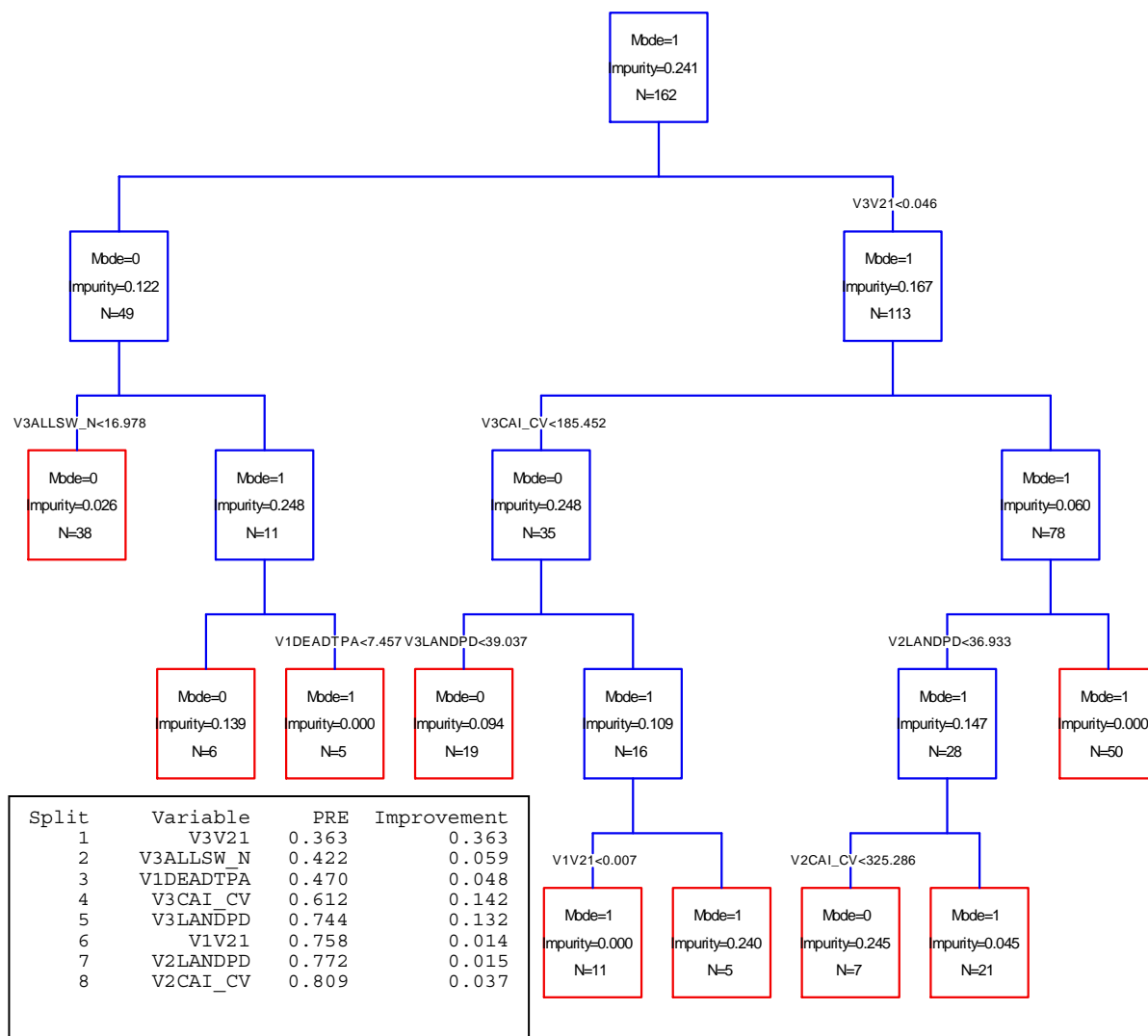


Figure 10d: Classification tree of yellow-breasted chat presence-absence on BBS routes ($n = 162$) relative to forest and landscape variables calculated within 100 m (V1), 1 km (V2), and 10 km (V3) diameter buffers centered on each route.

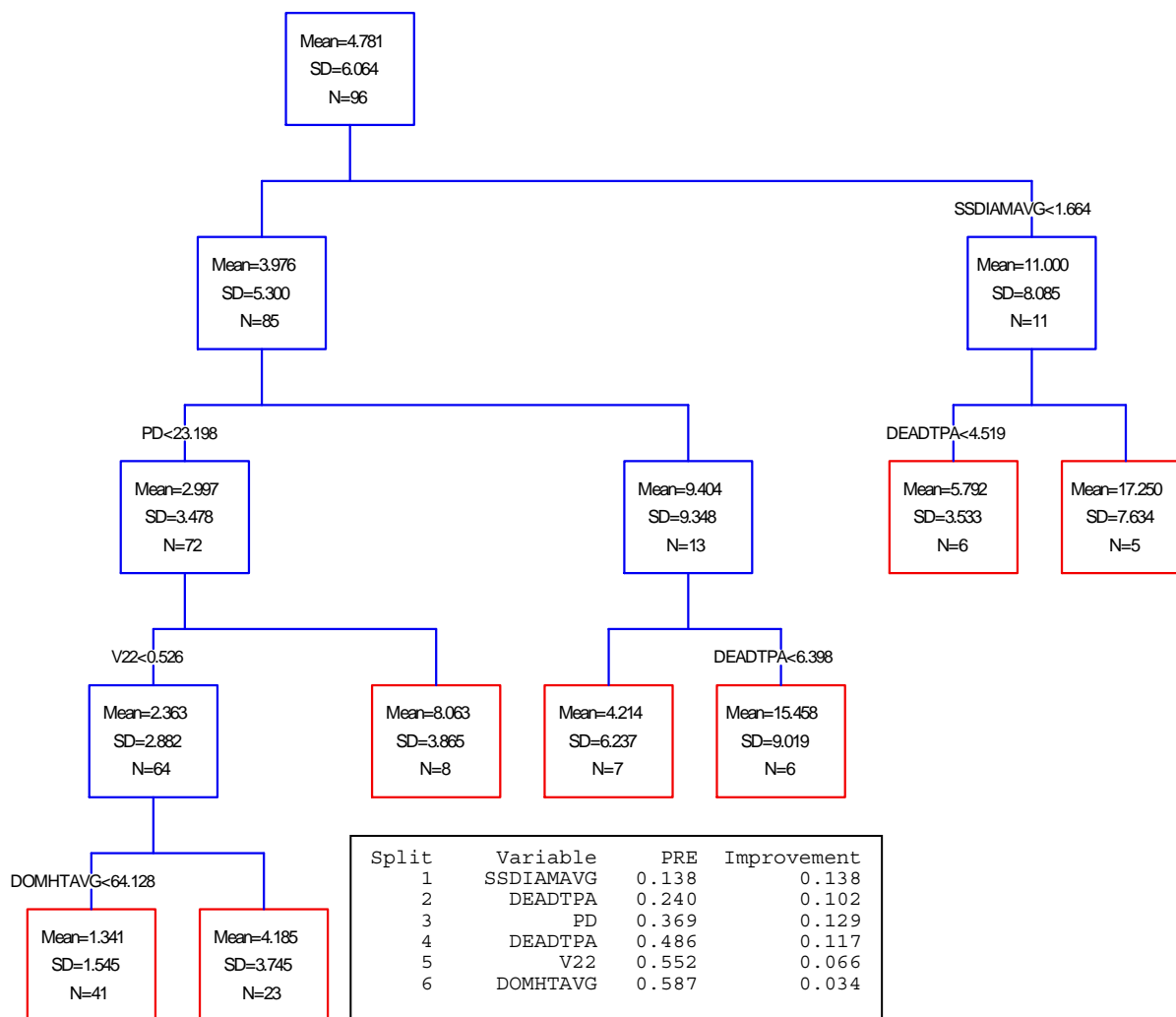


Figure 11a: Regression tree of yellow-breasted chat abundance on BBS routes ($n = 96$) relative to forest and landscape variables calculated within a 100 m diameter buffer centered on each route.

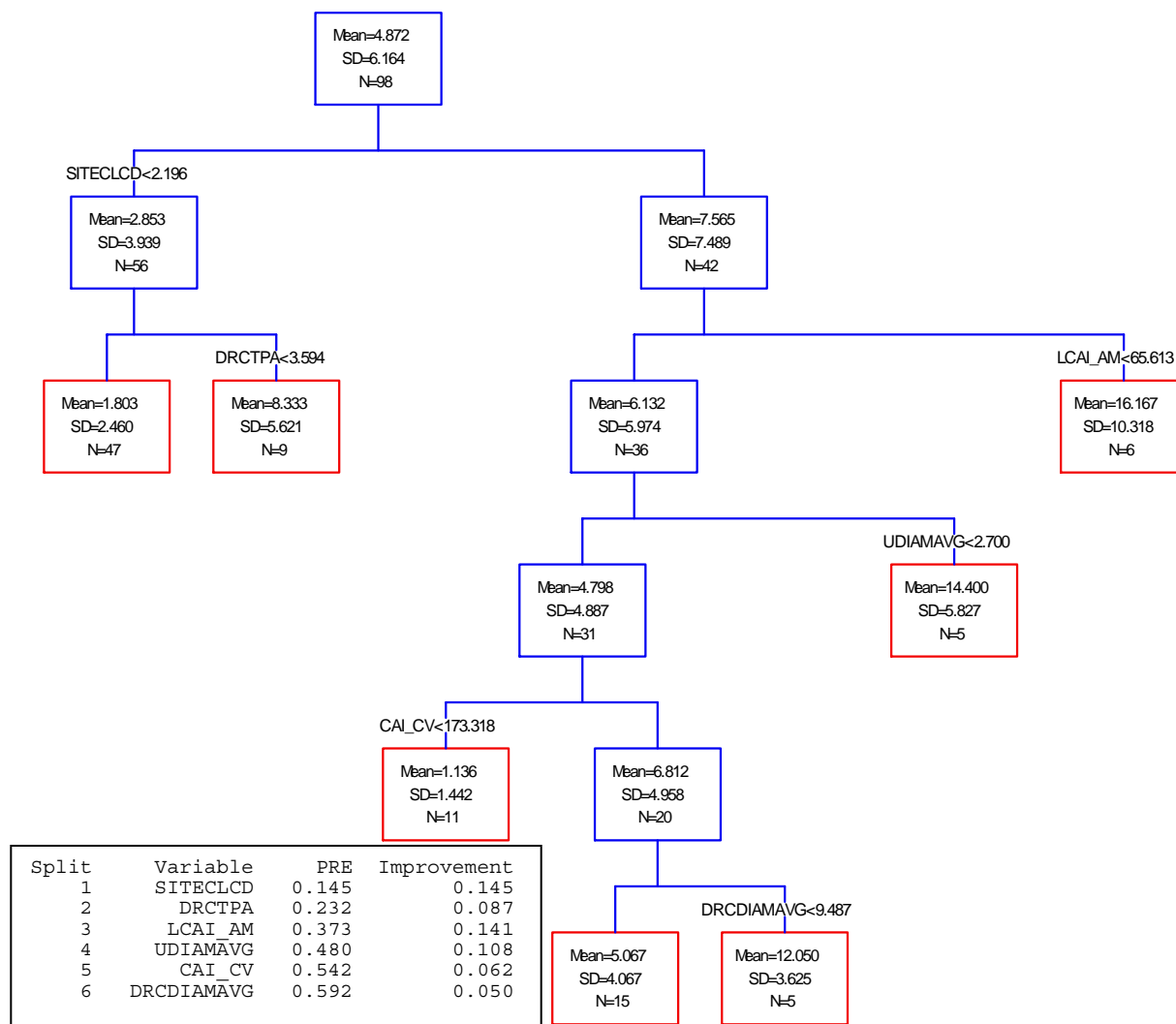


Figure 11b: Regression tree of yellow-breasted chat abundance on BBS routes ($n = 95$) relative to forest and landscape variables calculated within a 1 km diameter buffer centered on each route.

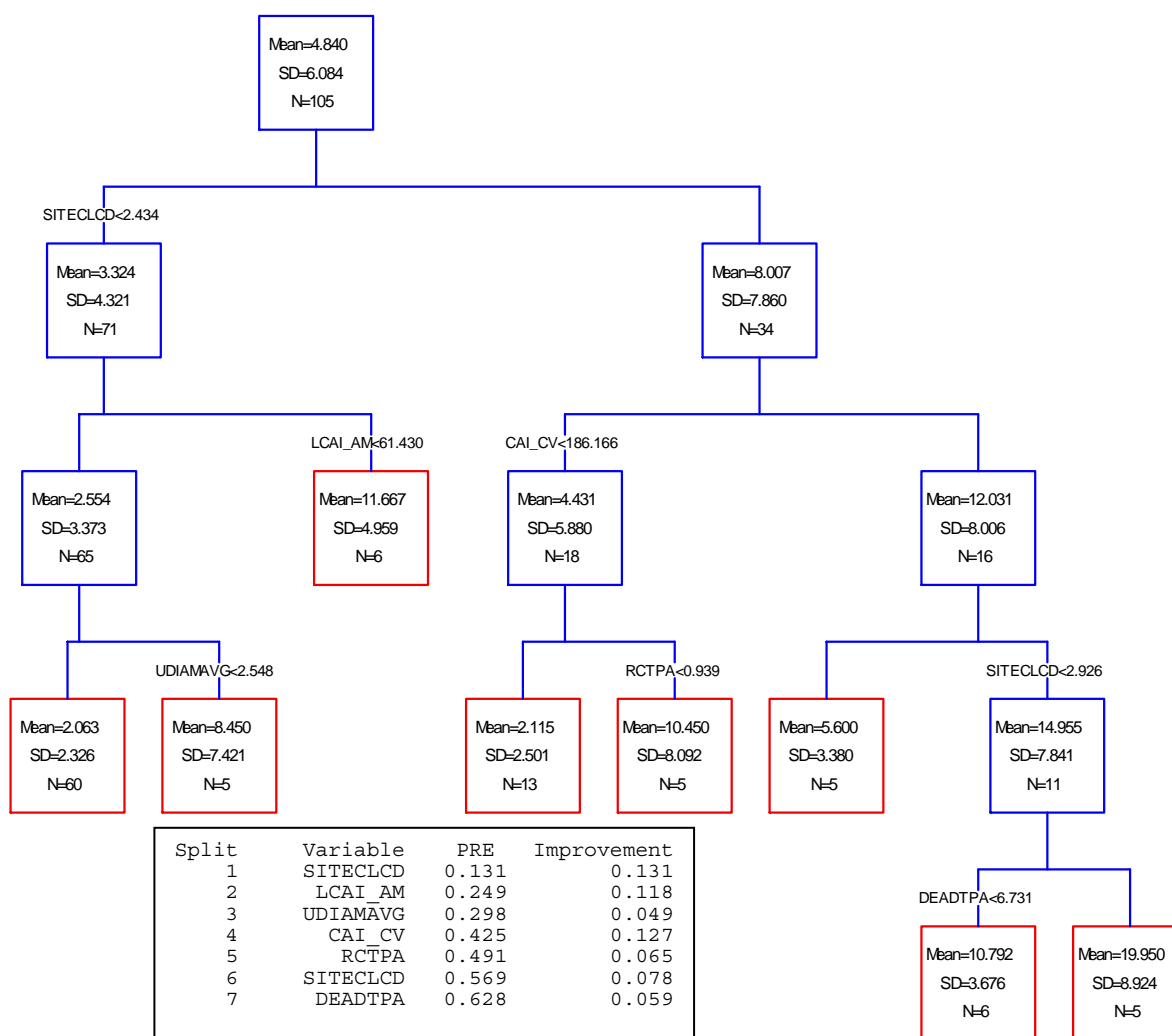


Figure 11c: Regression tree of yellow-breasted chat abundance on BBS routes ($n = 105$) relative to forest and landscape variables calculated within a 10 km diameter buffer centered on each route.

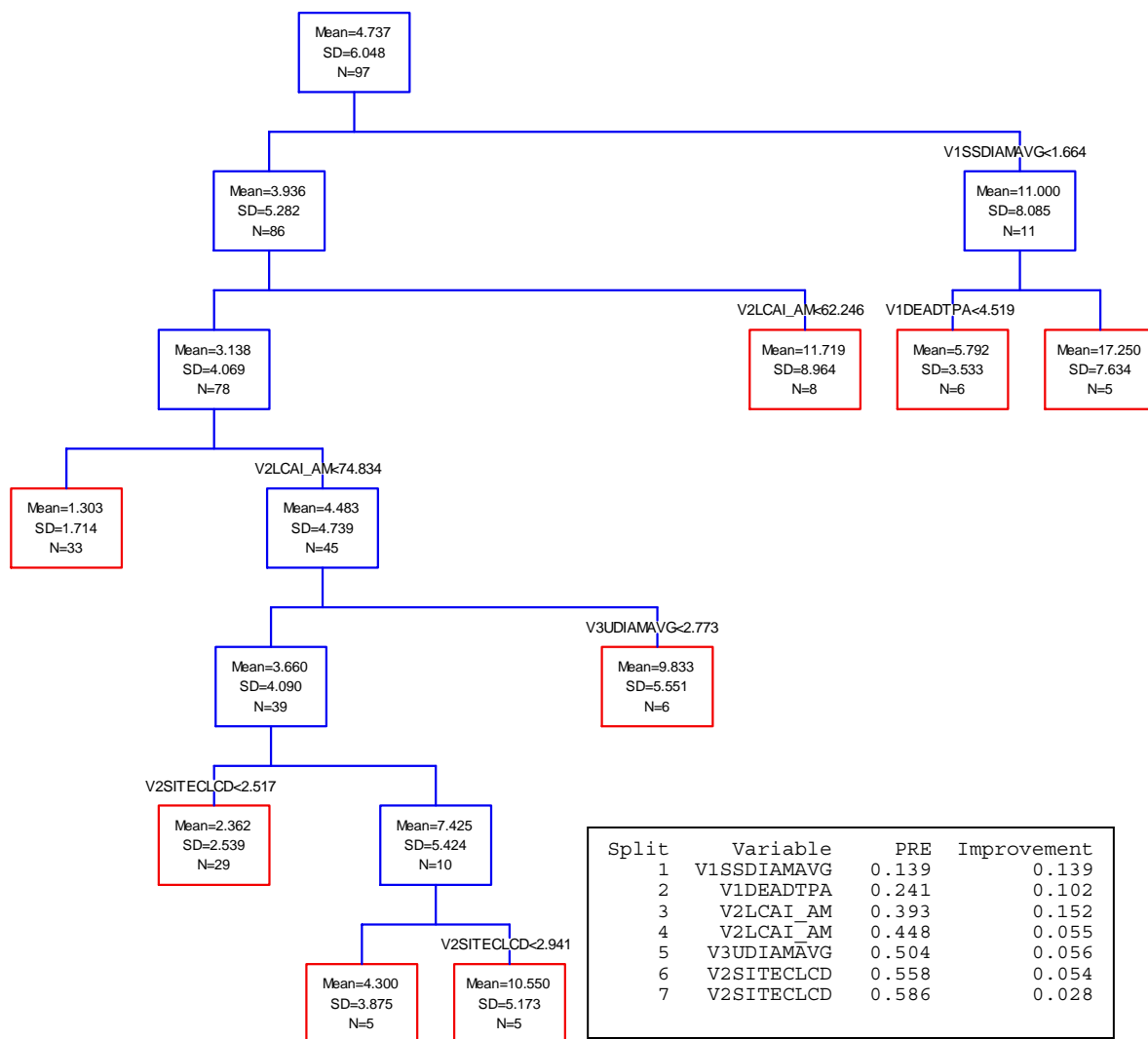


Figure 11d: Regression tree of yellow-breasted chat abundance on BBS routes ($n = 105$) relative to forest and landscape variables calculated within 100 m (V1), 1 km (V2), and 10 km (V3) diameter buffers centered on each route.

CHAPTER 4

**RELATING SPATIAL VARIATION IN BIRD ABUNDANCE TO FOREST
AND LANDSCAPE VARIABLES AT THE FIA UNIT AND
PHYSIOGRAPHIC SECTION SCALES.**

Results

Average abundance of the 26 bird species I selected for this study ranged from 0.23 to 22.99 individuals per route at the FIA unit scale and from 0.17 to 24.78 at the physiographic section scale during the 2000 FIA inventory cycle (Table 16). At both scales, the black-billed cuckoo had the lowest average abundance and red-eyed vireo had the highest. Six species at the FIA unit scale had geographic distributions that excluded some FIA units. Four species at the physiographic section scale had distributions that excluded some sections (Table 16).

Ability of the Forest and Landscape Variables to Explain Variations in Bird Abundance

FIA unit scale.—Pearson correlation coefficients for single bird abundance-forest variable correlations ranged from -0.719 (American redstart with ALLHTAVG) to 0.856 (black and white warbler to STDSZCD). Considering the 26 bird species, 23 of the 43 forest variables I developed from the FIA data were selected in at least 1 model with a 5% average rate of inclusion for any given variable (Tables 17a, b).

The most frequently selected variables described a range of forest structural characteristics and included 1 physiographic class code describing mesic rolling uplands (V22; USDA Forest Service 2006), species diversity of understory size class trees (USW_N), the density and average diameter of rotten-cull stems (RCTPA and RCDIAMAVG), the variability in the diameter of understory stems (UDIAMCV), and the average diameter of dominant trees (DDIAMAVG). Each of these variables was selected in > 15% of the models developed at the

FIA unit scales (Table 17b). With 1 exception each for SSDIAMAVG and ALLDIAMAVG, none of the seedling-sapling age class variables (SSDIAMCV, SSSW_N) or all age-class variables (ALLDIAMCV, ALLHTAVG, ALLHTCV, ALLSW_N) were selected in the models at this scale (Table 17a). The physiographic class codes describing uncommon forest conditions also were not selected.

Coefficients for single bird abundance-landscape variable correlations ranged from -0.751 (black and white warbler with LANDCWED) to 0.701 (American redstart with SHAPE_CV). Ten of the 22 landscape variables were selected in at least 1 model, with a 1.5% average rate of inclusion for any given variable (Tables 18a, b). Of these variables, LSHAPE_CV was the only landscape variable selected in 2 models (Table 18b). The remaining landscape variables were selected only once each.

Physiographic section scale.— Pearson correlation coefficients for single bird abundance-forest variable correlations ranged from -0.841 (tufted titmouse with V21) to 0.883 (American redstart with RCTPA, Appendix N). Totaling across the 22 bird species included in this analysis, 17 of the 43 forest variables I developed from the FIA data were selected in at least 1 model with a 3.4% average rate of inclusion for any given variable (Tables 17a, b).

The most frequently selected variables included the physiographic class code describing flatwoods outside of flood plains (V21; USDA Forest Service 2006), the density of rotten-cull stems (RCTPA), the variability in the diameter of understory stems (UDIAMCV), the average diameter of dominant trees (DDIAMAVG), and the site productivity class code (SITECLCD). Each of these variables was selected in > 13.6% of the models developed at this scale (Table 17b). None of the seedling-sapling variables were selected in the models at this scale. The

physiographic class codes describing uncommon forest conditions and the variables describing tree diameter and height attributes across all size classes also were not selected.

Coefficients for single bird abundance-landscape variable correlations ranged from -0.793 (black and white warbler with LANDCWED) to 0.820 (pine warbler with LANDPD). Only 3 of the 22 landscape variables (LPI, LANDPD, and LSHAPE_AM) were selected for models with a 0.5% average rate of inclusion across all variables (Tables 18a, b). No landscape variables were selected in greater than 1 model (Table 18b).

Model Performance

FIA unit scale.— The total amount of variation in bird abundance among FIA units explained by the CART models (*PRE*) ranged from 0.055 (Canada warbler) to 0.854 (red-bellied woodpecker), with an average *PRE* across all species of 0.541 (Table 19). The number of variables included in a given model ranged from 1 to 4, with an average of 2.4 variables per model. Models within the mature forest ground-shrub guild had the greatest range in *PRE* (0.055 - 0.776) and accounted for the least amount of variation in bird abundance on average among FIA units (average *PRE* = 0.486). Models for the mature forest canopy guild had the smallest range in *PRE* (0.411-0.759) and accounted for the most variation in abundance (average *PRE* = 0.597; Table 19).

Physiographic section.— Three species within the mature forest ground-shrub guild (black-throated blue warbler, Canada warbler, and rose-breasted grosbeak) and 1 within the early successional guild (chestnut-sided warbler) were not detected in ≥ 1 physiographic section and no models were developed for these species at this scale. The total amount of variation (R^2) in bird abundance among physiographic sections explained by the GLMs selected using AIC_c ranged 0.277 (wood thrush) to 0.872 (yellow-billed cuckoo), with an average R^2 across all species of

0.663 (Table 19). The number of parameters in a model ranged from 3 to 5 (1 - 3 predictor variables), with an average of 3.7 parameters per model. The AIC_c weights of the selected models ranged from 0.400 to 0.963. Eleven species had competing models ($\Delta AIC_c < 2$) (Appendix Q) and thus they tended to have relatively lower AIC_c weights (Table 19; Burnham and Anderson 2002). Only one variable each was significantly correlated with cerulean warbler, Kentucky warbler, and wood thrush abundances at this scale and available for model development. Thus these models were not subjected to AIC_c selection (Table 19).

Models within the mature forest canopy guild had the greatest range in R^2 values (0.277-0.859) and also accounted for the least amount of variation in bird abundance on average among FIA units ($R^2 = 0.524$). Models for the cavity guild had the smallest range in R^2 (0.470 - 0.757) and the cavity (average $R^2 = 0.647$) and mature forest ground-shrub (average $R^2 = 0.648$, range = 0.314 – 0.872) guilds accounted for the greatest variation in abundance (Table 19).

Examples of Model Performance from 2 Species: Cerulean Warbler and Yellow-Breasted Chat

Cerulean warbler.—The regression tree relating variations in cerulean warbler abundance among FIA unit to forest and landscape variables had a $PRE = 0.411$ and contained 1 landscape (LPI) and 2 forest variables (V29 and DDIAMAVG; Fig. 12). Cerulean warbler abundance was greatest in FIA units where contiguous deciduous forest composed at least 50% of the unit and large portions of these forests were mesic stands (Fig. 12). They were least prevalent in units containing less than 50% of contiguous deciduous forests that were dominated by smaller diameter trees (DBH < 24.2 cm).

At the physiographic section scale, the GLM relating cerulean abundance to the forest and landscape metrics contained 1 landscape variable ($R^2 = 0.348$, $F_{1, 14} = 7.474$, $P = 0.016$;

Table 20). Cerulean abundance was positively related to the percent of the landscape in contiguous deciduous forest cover.

Yellow-breasted chat.—The yellow-breasted chat regression tree had a $PRE = 0.754$ and contained 4 forest variables (DRCDIAMAVG, RCTPA, USW_N, and V22; Fig. 13). Yellow-breasted chats were most abundant in units containing smaller diameter (DBH < 24.3 cm) dead and rotten-cull trees. If units were dominated by larger diameter dead and rotten-cull stems, chat abundance remained relatively high if the unit had a low density of rotten-cull trees (< 4 stems/ha) and > 20% of the unit was in mesic rolling uplands associated with small streams. Chats were least abundant in units having densities of rotten-cull trees > 4 stems/ha and greater understory tree species diversity (Fig. 13).

At the physiographic section scale, the GLM selected using AIC_c ($w_i = 0.772$) contained 2 forest variables ($R_{adj}^2 = 0.683$, $F_{2,13} = 17.131$, $P < 0.001$; Table 20). Chat abundance was negatively associated with the density of rotten-cull trees and the proportion of stands in mesic flatwoods outside of floodplains.

Discussion

Changing the resolution of the bird abundance, forest, and landscape variables to the larger FIA unit and physiographic section scales had several notable effects on the individual variables and nature of the bird-habitat relationships identified at these scales that merit consideration when interpreting the results. Observational scales influence the characteristics of a variable's distribution, its mean, variance, relationships among other variables, and interpretations of those relationships (Dungan et al. 2002, Hobbs 2003). The broad spatial extent of an FIA unit (mean size = 2,153,798 ha, range = 276,157 – 9,515,172 ha) or physiographic section (mean size = 3,815,669 ha, range = 985,663 – 8,325,904 ha) allowed for an inherently

large amount of local variability to exist in both response (bird abundance) and predictor (forest and landscape metrics) variables at their finest resolution (BBS route and FIA plot) within these regions. However, increasing an observational and analytical scale from small to broad and correspondingly decreasing the measurement resolution of the variables from fine to coarse typically reduces (but can increase) this variability, changing the strength and nature of the relationships among variables detected at smaller scales (Dungan et al. 2002, Trani 2002).

In this case, treating FIA units and physiographic sections as sample units and averaging bird abundance across routes within individual units and sections reduced the overall variability in average abundance relative to that observed among BBS routes (Tables 1 and 16). The landscape variables developed at these scales were calculated using NLCD imagery resampled from a 30 m to a 400 m (16 ha) pixel size. This reduced resolution created a more generalized representation of landcover by eliminating patches smaller than the 400 m pixel size and reducing the overall patch density in the landscape (Trani 2002). The 400 m pixel resolution also prevented calculation of core area metrics at these scales because the maximum edge depth for delineating core area (100 m) was less than the pixel size. Because the forest variables developed from FIA data could be effectively interpolated to these larger scales using the expansion factors (U.S. Forest Service 2006) rather than averaged across sample plots, the variability in many of the forest variables actually increased at these scales relative to the county-level values (see Appendices C and D). These differences in resolution between the 2 suites of predictor variables may confound the interactions between them as well as their relationships with bird abundance (Van Horne 2002, Bissonette 2003) in ways that are difficult to quantify (Dungan et al. 2002).

Broad regional-scale analyses such as these typically assess species' presence-absence as a function of the distribution of general habitat characteristics measured at coarse scales (Heglund 2002). The availability of consistent abundance data at these scales, the coarse nature and/or broad extent of the predictor variables included in the models, and the ability to relate the biological significance of models to life-history requirements of the species being modeled limit their interpretation and applicability (Heglund 2002). For example, the forest variables at these scales represent the range of forest characteristics present across a given unit or section. However, the distribution of BBS routes within these regions was neither uniform nor consistent relative to a unit or section's size and configuration. Therefore the forest variables may include information from regions not sampled by the BBS, or, for bird species with restricted geographic distributions, information from areas where they do not occur. The inclusion of such data can obscure bird-habitat relationships and create misleading results (Young and Hutto 2002). GIS analyses involving landscape patterns (e.g. patch size and shape) are most effective when the scale of the analyses match the scale(s) at which a species responds to the landscape (Trani 2002, Van Horne 2002). Interpreting the biological meaning of relationships identified at large scales based on coarse-resolution variables is difficult given the range of ecological processes such relationships may represent (Van Horne 2002, Young and Hutto 2002). Finally, using FIA units and physiographic sections as sample units reduced the sample sizes available for these analyses, a typical result of such increases in spatial scale (Trani 2002).

The inclusion of a variable in these models may reflect its ability to be extrapolated to coarser scales and still retain meaningful information regarding bird-habitat relationships (Trani 2002). However, any relationships identified in the models developed at these scales should serve only as indices to broad patterns that may be exerting influence on a species at the

population-level across the region (MacFaden and Capen 2002, Van Horne 2002) and should be validated against those identified at smaller scales (Heglund 2002). More refined interpretations of the biological context of such relationships should be limited to models developed at smaller scales using data at a finer resolution (Young and Hutto 2002).

Relationships of the Forest Variables Developed from FIA Data and Landscape Variables to Variations in Bird Abundance

Some general patterns in variable selection in the models were evident among guilds. The majority of the variables selected within the early successional guild described characteristics of early successional cover and included species diversity (USW_N) and variability in stem diameter (UDIAMCV) of understory species, the overall diameter of trees in the stand (STDSZCD), and the density and diameter of dead and rotten-cull trees (RCTPA, DEADDIAMAVG, DRCDIAMAVG; Table 17a). The dead and rotten-cull tree variables tended to be negatively related to abundance and likely served as indices of stand maturity. As forest stands mature, both the density and diameter of standing dead and rotten-cull trees should increase (Healy 2002). Many variables selected for models within the mature forest ground-shrub guild described characteristics of the forest understory, including average diameter and variability in the diameter of understory stems (UDIAMAVG, UDIAMCV), understory species diversity (USW_N), and the density and diameter of rotten-cull trees in the stand (RCTPA, RCDIAMAVG; Table 17a). As with the models at the BBS-route scale, the rotten-cull variables likely served as an index to heterogeneity and gap structure in a forest stand.

The impact of landscape patterns on bird abundance appears to be reduced at these scales based on the relatively few landscape variables included in any of the models (Tables 18a, b). This may be an artifact of the coarser resolution of the NLCD imagery I used to develop the

landscape variables for these analyses. The landscape patterns described by these variables may be too generalized to be associated with variations in bird abundance. However, it may also imply that structural habitat characteristics rather than landscape patterns were the primary components influencing variations in bird abundance at these scales. Flather and Sauer (1996) found that landscape structure measured at coarse resolutions was poorly associated with forest bird abundance trends in the eastern U.S., and studies incorporating variables describing both habitat structure and landscape patterns have demonstrated a heavier influence of habitat structure over landscape patterns on bird abundance (Lichstein et al. 2002, MacFaden and Capen 2002). However, landscape pattern did appear to have relatively greater influence on bird abundance within the mature forest canopy guild as indicated by the rates of selection between the forest and landscape variables (Table 18a). Any individual landscape variable had a 5.4% chance at random for selection in a mature forest canopy species model while a forest variable had a 2.8% random chance of selection. A possible explanation for this may be that the developed canopy structure required by this guild can occur in a variety of forest stands and age classes, and therefore landscape-level attributes affecting deciduous forest patches served as better predictors of abundance than the forest variables. The habitat requirements of the other guilds, notably the early successional and ground-shrub nesters, were driven by a more diverse range of specific structural attributes described by the forest variables but not captured by the general landscape metrics.

Model Performance

The overall performance of the regression trees and GLMs in explaining variability in bird abundance among FIA units and physiographic sections was very good. The bird-habitat relationships identified by these models, though typically very general, largely followed those

described elsewhere (e.g. Hamel 1992, Thogmartin et al. 2004, NatureServe 2005). At both scales most of the models I developed accounted for > 50% of the variation in bird abundance (Table 19), and many of them accounted for as much or more variability in abundance than the regression trees relating bird abundance to the forest and landscape variables developed at the BBS route scale (Table 12). Tobalske (2002) obtained similar increases in model fit between bird presence-absence and habitat variables measured at coarser resolutions. Such increases were likely a result of the reduction in the variability among bird-habitat relationships more apparent at finer resolutions and smaller scales and the ability of coarse-resolution variables to encompass a broader range of ecological processes and potentially account for a broader range of habitat requirements (Van Horne 2002, Young and Hutto 2002).

Some notable exceptions to this trend included the cerulean, Canada, and black-throated blue warblers. The model performance for these species at the FIA unit scale (*PRE* for cerulean, Canada, and black-throated blue = 0.411, 0.055, and 0.113, respectively) and for the cerulean warbler at the physiographic section ($R^2 = 0.348$) scales was considerably poorer relative to the best regression tree models developed at the BBS route level (*PRE* for cerulean, Canada, and black-throated blue = 0.776, 0.433, and 0.487, respectively). All 3 of these species have relatively complex and hierarchical habitat requirements relative to many of the other species. The Canada and black-throated blue warbler share similar habitat preferences, selecting mesic areas within deciduous forests having a dense shrub layer often composed of rhododendron (*Rhododendron* spp.) or mountain laurel (*Kalmia latifolia*) typically associated with moist stream drains or forested wetlands (Hamel 2002, NatureServe 2005). Cerulean warblers prefer deciduous stands either along ridges or in mesic sites, especially forested wetlands, containing some tall trees emerging from the overall canopy (Thogmartin et al. 2004, Pashley 2005). These

requirements were better represented in whole at smaller scales, while the variables selected in their models at the FIA unit and physiographic section scales incorporate only those components detectable at these scales. At the FIA unit scale the regression trees for both the Canada and black-throated blue warblers included 1 forest variable that described the percent of the landscape in small drains or wet strands of forest land without a well-defined stream channel (V32). The cerulean warbler regression tree contained a landscape variable describing the percent of the landscape in contiguous deciduous forest cover (LPI) and a forest variable describing the percent of mesic forest stands (V29, Fig. 12), and the GLM at the physiographic section scale included only the LPI variable. These 3 species had some of the lowest average abundance estimates of the species I modeled (Table 16), and the Canada and black-throated blue warblers had restricted geographic distributions, occurring within relatively small portions of FIA units and physiographic sections. These characteristics also likely contributed to their reduced model performance.

The models of yellow-breasted chat abundance at both scales included the density of rotten-cull trees (RCTPA), and the regression tree also included the average diameter of dead and rotten cull stems (Fig. 13, Table 20). Both of these variables were negatively associated with chat abundance and were likely indices of stand maturity as discussed previously, with a greater density of rotten-cull stems and larger diameter of dead or rotten-cull stems occurring in more mature stands. It was interesting that these variables were selected over others that would seem to better describe the early successional characteristics preferred by chats (e.g. the seedling-sapling and understory diameter variables and the stand age variable, Table 3). One explanation is that the average diameter and density of standing dead and rotten-cull trees was more sensitive to changes in the successional progression of forest stands. High densities of

seedling-saplings and understory stems that are small in diameter, the characteristics of these variables that would best describe early successional cover, can also occur in a variety of successional stages within a given stand. An increase in both the density and diameter of standing dead and rotten cull stems tends to be associated with an increase in stand maturity. No clear trends were evident in seedling-sapling and rotten-cull stem densities (stems/ha) relative to increasing chat abundance (Fig. 14). However, seedling-sapling density did increase to a point as the density of dominant trees increased, while no similar trend in the densities of rotten-cull to dominant stems was evident (Fig. 15). This reinforces the notion that the seedling-sapling density variable was likely a poor indicator of early successional cover. The models for the chat also included 2 physiographic class code variables describing rolling uplands (V22) at the FIA unit scale and flatwoods outside of flood plains (V21) at the physiographic section scale. Chat abundance increased with increasing amount of rolling uplands but decreased with greater flatwoods (Fig. 13, Table 20). The interpretation of these variables was unclear. It is possible that the forest stands contained within rolling upland class code tended to contain more early successional habitat than those in the flatwoods class code, but I have no explanation for why this may be so.

While applicability and interpretive strength of the regression tree and GLMs developed at these larger scales is limited, they may serve as indices to those habitat components exerting the greatest influences on bird abundance at these regional scales. Such relationships should be validated against more reliable models developed at smaller scales with finer resolution data, but they do demonstrate how the broad extent of the BBS and FIA databases allows for the potential to provide information explaining spatial variations in bird abundance at regional scales.

Table 16. Bird abundance (individuals/route) data averaged across the FIA units and physiographic sections within the study area during the 2000 FIA inventory cycle for the 26 bird species selected for this study.

Species	FIA unit scale					Physiographic section scale				
	# units in spp range	Avg. count	Min	Max	C.V.	# sections in spp range	Avg. count	Min	Max	C.V.
Cavity										
Downy woodpecker	30	2.41	1.03	4.63	0.387	16	2.68	1.40	5.33	0.355
Great-crested flycatcher	30	2.36	0.54	6.96	0.578	16	2.67	1.11	8.00	0.676
Pileated woodpecker	30	2.01	0.21	5.14	0.653	16	2.14	0.31	3.83	0.562
Red-bellied woodpecker	30	4.28	0.26	11.15	0.777	16	4.81	0.31	11.00	0.742
Tufted titmouse	30	11.04	0.79	20.81	0.445	16	12.08	3.28	19.85	0.399
Early Successional										
Chestnut-sided warbler	23	2.00	0.0	7.89	1.198	14	2.01	0	8.41	1.320
Common yellowthroat	30	10.48	0.42	29.64	0.726	16	10.44	2.23	28.60	0.658
Eastern towhee	30	9.03	1.43	27.90	0.621	16	9.18	3.17	19.83	0.525
Prairie warbler	30	1.19	0.06	4.75	1.103	16	1.22	0.03	3.40	0.863
Yellow-breasted chat	30	4.13	0.0	15.07	1.059	16	5.07	0	14.71	0.876
Mature forest canopy										
Cerulean warbler	30	0.63	0	3.44	1.579	16	0.70	0.02	4.06	1.590
Eastern wood-pewee	30	4.00	0.9	8.55	0.540	16	4.01	0.79	7.93	0.464
Pine warbler	30	1.17	0	8.16	1.574	16	1.94	0	12.33	1.726
Red-eyed vireo	30	22.99	3.6	56.31	0.577	16	24.78	5.29	47.12	0.530
Wood thrush	30	10.14	2.66	27.99	0.687	16	10.01	2.26	24.78	0.646
Mature forest ground-shrub										
American redstart	30	2.12	0	8.09	1.094	16	2.35	0	9.56	1.137
Black and white warbler	30	1.27	0	6.02	1.084	16	1.46	0.07	4.09	0.896
Black-billed cuckoo	30	0.23	0	1.95	1.672	16	0.17	0	0.83	1.335
Black-thr. blue warbler	22	0.74	0	5.55	1.752	13	0.71	0	4.00	1.785
Canada warbler	22	0.35	0	2.39	1.742	11	0.33	0	1.51	1.349
Hooded warbler	30	3.24	0	17.58	1.176	16	3.45	0.04	10.49	1.012
Kentucky warbler	28	1.32	0.03	3.65	0.865	16	1.49	0	4.41	0.963
Ovenbird	30	7.73	0.01	19.36	0.733	16	7.79	0.11	15.89	0.765
Rose-breasted grosbeak	23	1.20	0	4.04	1.108	14	1.21	0	4.55	1.195
Worm eating warbler	29	1.09	0	5.22	1.076	16	1.11	0.02	4.09	1.024
Yellow-billed cuckoo	30	2.38	0.15	6.25	0.781	16	2.57	0.19	5.98	0.710

Table 17b. Number of times that forest variables calculated at the FIA unit and physiographic section scales with data from the 2000 FIA inventory were selected in the regression trees (FIA unit) and GLMs (physiographic section) and their rate of selection. Data are for all guilds summarized by scale of the analyses. Variables not selected within any guild were omitted from the table for brevity.

Metric	FIA unit		Phys. section	
	# times selected	Rate of selection	# times selected	Rate of selection
ALLDIAMAVG	1	0.038	0	0.000
ALLSW_N	3	0.115	2	0.091
DDIAMAVG	4	0.154	3	0.136
DDIAMCV	0	0.000	1	0.045
DEADDIAMAVG	1	0.038	1	0.045
DEADTPA	1	0.038	1	0.045
DOMTPA	1	0.038	0	0.000
DRCDIAMAVG	1	0.038	0	0.000
DRCTPA	1	0.038	1	0.045
DSW_N	0	0.000	1	0.045
RCDIAMAVG	4	0.154	1	0.045
RCTPA	5	0.192	3	0.136
SITECLCD	2	0.077	3	0.136
SSDIAMAVG	1	0.038	0	0.000
STDAGE	1	0.038	0	0.000
STDSZCD	2	0.077	1	0.045
UDIAMAVG	1	0.038	2	0.091
UDIAMCV	4	0.154	3	0.136
USW_N	5	0.192	0	0.000
V19	1	0.038	2	0.091
V21	0	0.000	5	0.227
V22	5	0.192	1	0.045
V23	0	0.000	1	0.045
V24	1	0.038	0	0.000
V29	2	0.077	0	0.000
V31	3	0.115	0	0.000
V32	1	0.038	0	0.000

Table 18a. Number of times that landscape variables calculated at the FIA unit and physiographic section scales calculated from NLCD imagery resampled to a 400m resolution were included in the regression trees (FIA unit) and GLMs (physiographic section). Data are summarized by bird species guild and modeling approach. Variables not selected within any guild were omitted from the table for brevity.

Metric	Cavity		Early successional		Mature forest canopy		Mature forest ground shrub	
	FIA unit	Phys. section	FIA unit	Phys. section	FIA unit	Phys. section	FIA unit	Phys. section
Deciduous class								
CWED	0	0	1	0	0	0	0	0
LPI	0	0	0	0	1	1	0	0
PD	0	0	0	0	1	0	0	0
PLAND	0	0	0	0	0	0	1	0
SHAPE_AM	0	0	0	0	1	0	0	0
Landscape								
LANDCWED	1	0	0	0	0	0	0	0
LANDIJI	1	0	0	0	0	0	0	0
LANDPD	0	0	0	0	0	1	0	0
LANDSIDE	0	0	0	0	1	0	0	0
LSHAPE_AM	0	0	0	0	0	0	0	1
LSHAPE_CV	0	0	0	0	1	0	1	0
LSHAPE_MN	0	0	0	0	1	0	0	0

Table 18b. Number of times that landscape variables calculated at the FIA unit and physiographic section scales calculated from NLCD imagery resampled to a 400m resolution were selected in the regression trees (FIA unit) and GLMs (physiographic section) and their rate of selection. Data are for all guilds summarized by scale of the analyses. Variables not selected within any guild were omitted from the table for brevity.

Metric	FIA unit		Phys. section	
	# times selected	Rate of selection	# times selected	Rate of selection
Deciduous class				
CWED	1	0.038	0	0.000
LPI	1	0.038	1	0.045
PD	1	0.038	0	0.000
PLAND	1	0.038	0	0.000
SHAPE_AM	1	0.038	0	0.000
Landscape				
LANDCWED	1	0.038	0	0.000
LANDIJI	1	0.038	0	0.000
LANDPD	0	0.000	1	0.045
LANDSIDE	1	0.038	0	0.000
LSHAPE_AM	0	0.000	1	0.045
LSHAPE_CV	2	0.077	0	0.000
LSHAPE_MN	1	0.038	0	0.000

Table 19. Performance of the regression trees at the FIA unit scale and GLMs at the physiographic section scale relating bird abundance to forest and landscape variables. The number of FIA units or physiographic sections included in the model, the number of variables (regression tree) or parameters (GLM) per model, and amount of variation in bird presence-absence explained by the model are given for each scale. The Akaike weight (w_i) of the best model selected using AIC_c also is given for the GLMs. Weight values highlighted in gray indicate these had competing models ($\Delta AIC_c < 2$).

Bird species	FIA unit scale			Physiographic section scale			
	# FIA units	# variables	<i>PRE</i>	# Physiographic sections	K^a	w_i	R^2
Cavity							
Downy woodpecker	30	3	0.474	16	4	0.400	0.470
Great-crested flycatcher	29	3	0.579	16	3	0.529	0.622
Pileated woodpecker	30	3	0.621	16	5	0.697	0.757
Red-bellied woodpecker	28	3	0.854	16	3	0.635	0.679
Tufted titmouse	30	4	0.631	16	3	0.748	0.707
Average		3.2	0.632		3.6	0.602	0.647
Early Successional							
Chestnut-sided warbler	23	1	0.569	No model developed ^b			
Common yellowthroat	30	3	0.725	16	5	0.686	0.732
Eastern towhee	30	1	0.382	16	3	0.692	0.372
Prairie warbler	30	1	0.379	15	4	0.721	0.730
Yellow-breasted chat	29	4	0.754	16	4	0.772	0.683
Average		2.0	0.562		4.0	0.718	0.629
Mature forest canopy							
Cerulean warbler	30	3	0.411	16	3	N/A ^c	0.348
Eastern wood-pewee	30	2	0.569	16	4	0.751	0.473
Pine warbler	29	2	0.625	16	4	0.580	0.859
Red-eyed vireo	28	3	0.759	16	3	0.686	0.661
Wood thrush	29	3	0.622	16	3	N/A	0.277
Average		2.6	0.597		3.4	0.672	0.524

^aThis value includes the intercept and error terms

^bThese species did not occur in every physiographic section due to their limited geographic distribution. No models were developed for them due to limited sample size.

^cOnly 1 variable each was significantly correlated ($P < 0.05$) with these species, negating the need for model selection procedures

Table 19 continued

Bird species	FIA unit scale			Physiographic section scale			
	# FIA units	# variables	<i>PRE</i>	# Physiographic sections	<i>K</i> ^a	<i>w_i</i>	<i>R</i> ²
Mature forest ground-shrub							
American redstart	28	3	0.596	16	3	0.532	0.765
Black and white warbler	29	2	0.686	15	4	0.561	0.797
Black-billed cuckoo	30	3	0.450	16	4	0.606	0.729
Black-thr. blue warbler	22	1	0.113	No model developed ^b			
Canada warbler	22	1	0.055	No model developed ^b			
Hooded warbler	28	3	0.436	16	4	0.963	0.652
Kentucky warbler	28	1	0.453	16	3	N/A ^c	0.336
Ovenbird	28	3	0.776	16	4	0.676	0.722
Rose-breasted grosbeak	18	1	0.643	No model developed ^b			
Worm eating warbler	27	3	0.594	16	3	0.563	0.314
Yellow-billed cuckoo	30	4	0.548	15	4	0.890	0.872
Average		2.3	0.486		3.6	0.684	0.648
Overall average		2.5	0.550		3.7	0.668	0.663

^aThis value includes the intercept and error terms

^bThese species did not occur in every physiographic section due to their limited geographic distribution. No models were developed for them due to limited sample size.

^cOnly 1 variable each was significantly correlated ($P < 0.05$) with these species, negating the need for model selection procedures

Table 20. Predictors from the GLMs relating cerulean warbler and yellow-breasted chat abundance among physiographic sections during the 2000 FIA inventory cycle to forest and landscape variables calculated at the physiographic section scale.

Predictors	β	P-value
Cerulean warbler		
LPI	0.010	0.016
Yellow-breasted chat		
RCTPA	-0.479	0.012
V21	-11.728	0.006

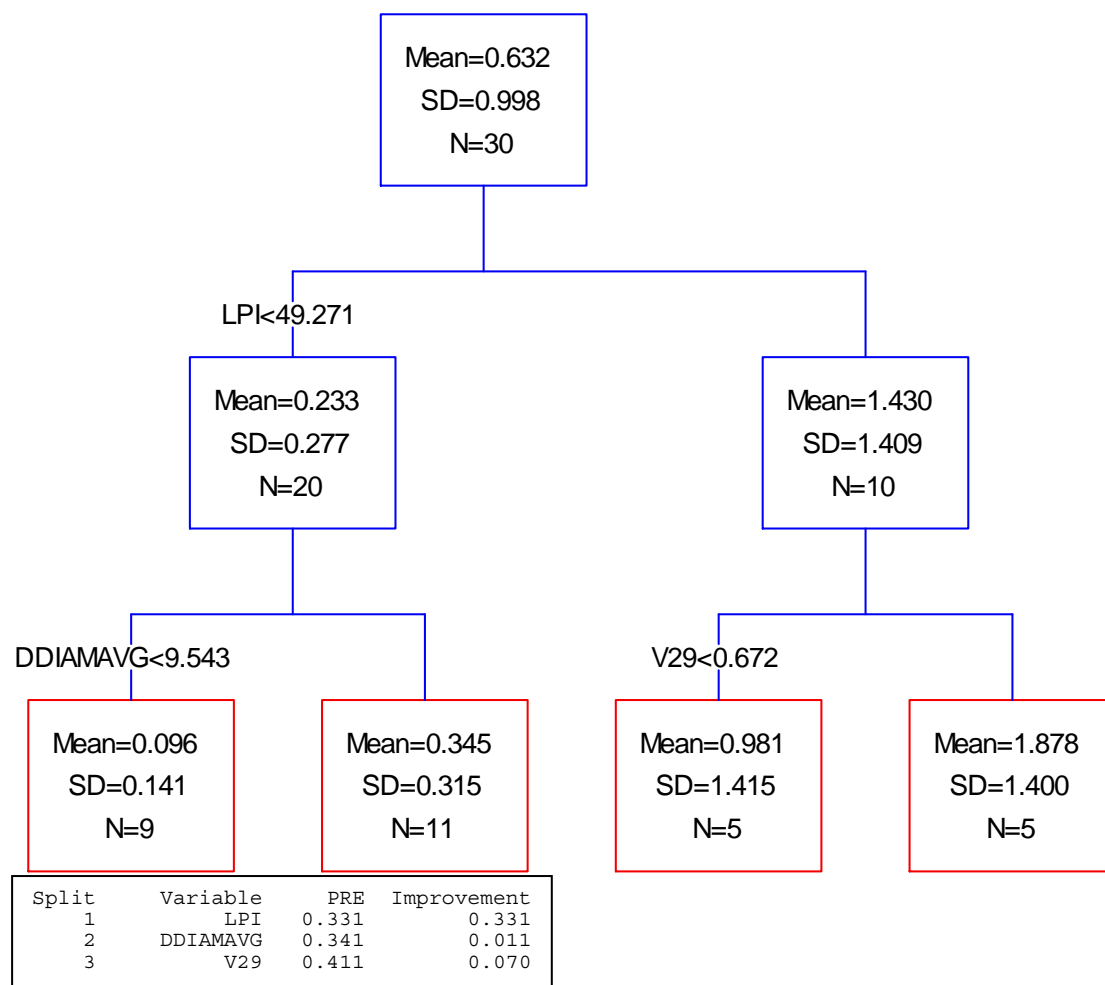


Figure 12. Regression tree relating variations in cerulean warbler abundance averaged across individual FIA survey units ($n = 30$) to forest and landscape variables calculated at the FIA unit scale. Models are read from top to bottom with the first split explaining the greatest variability and the subsequent splits accounting for further variations in the data. Each node (square) is labeled with the mode (classification tree) or mean (regression tree) of the response variable for that group, a measure of variability around that measure, and the number of samples in that group. Labels along the branches identify the factor creating the split for the underlying nodes.

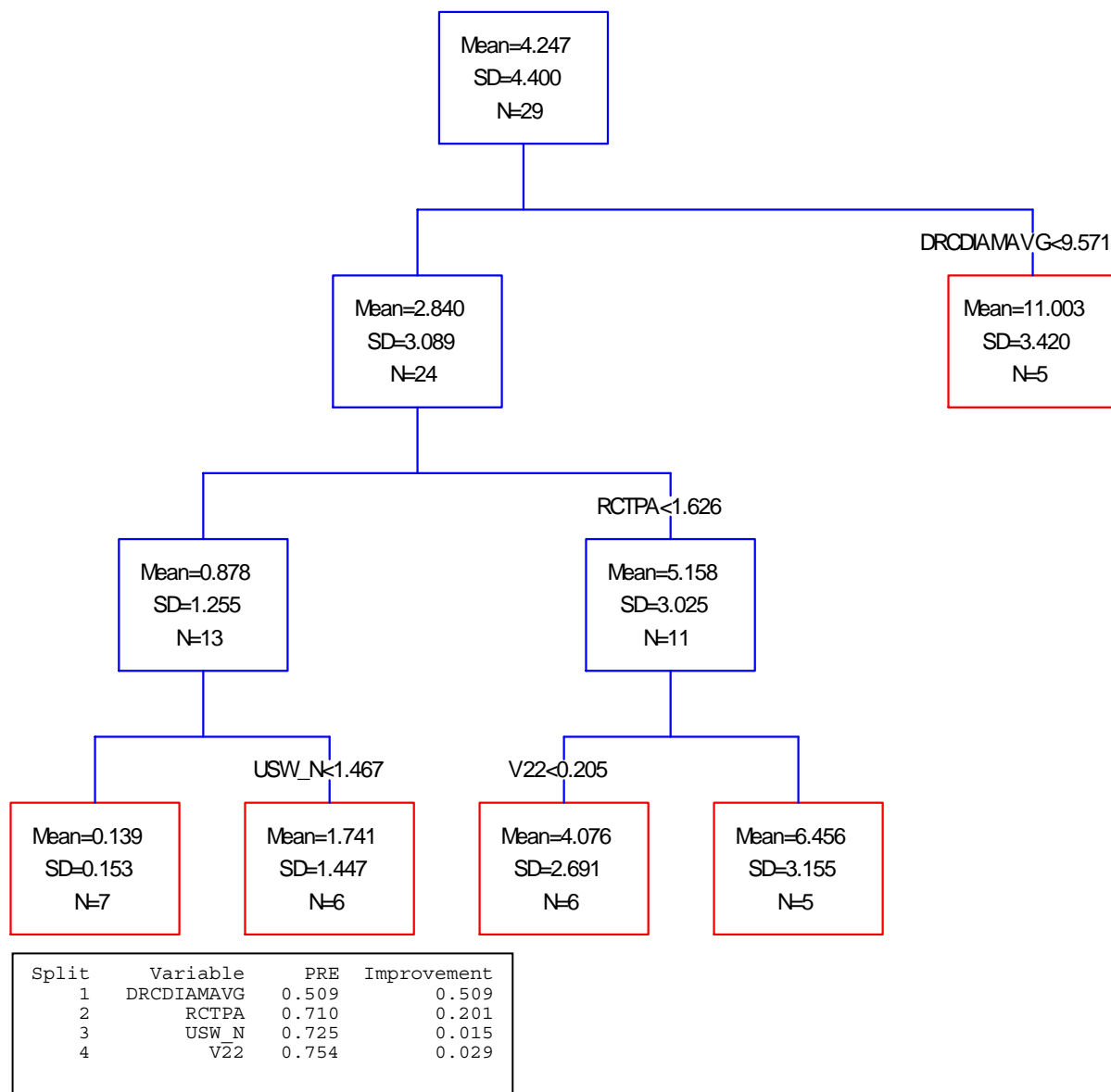


Figure 13. Regression tree relating variations in yellow-breasted chat abundance averaged across individual FIA survey units ($n = 29$) to forest and landscape variables calculated at the FIA unit scale.

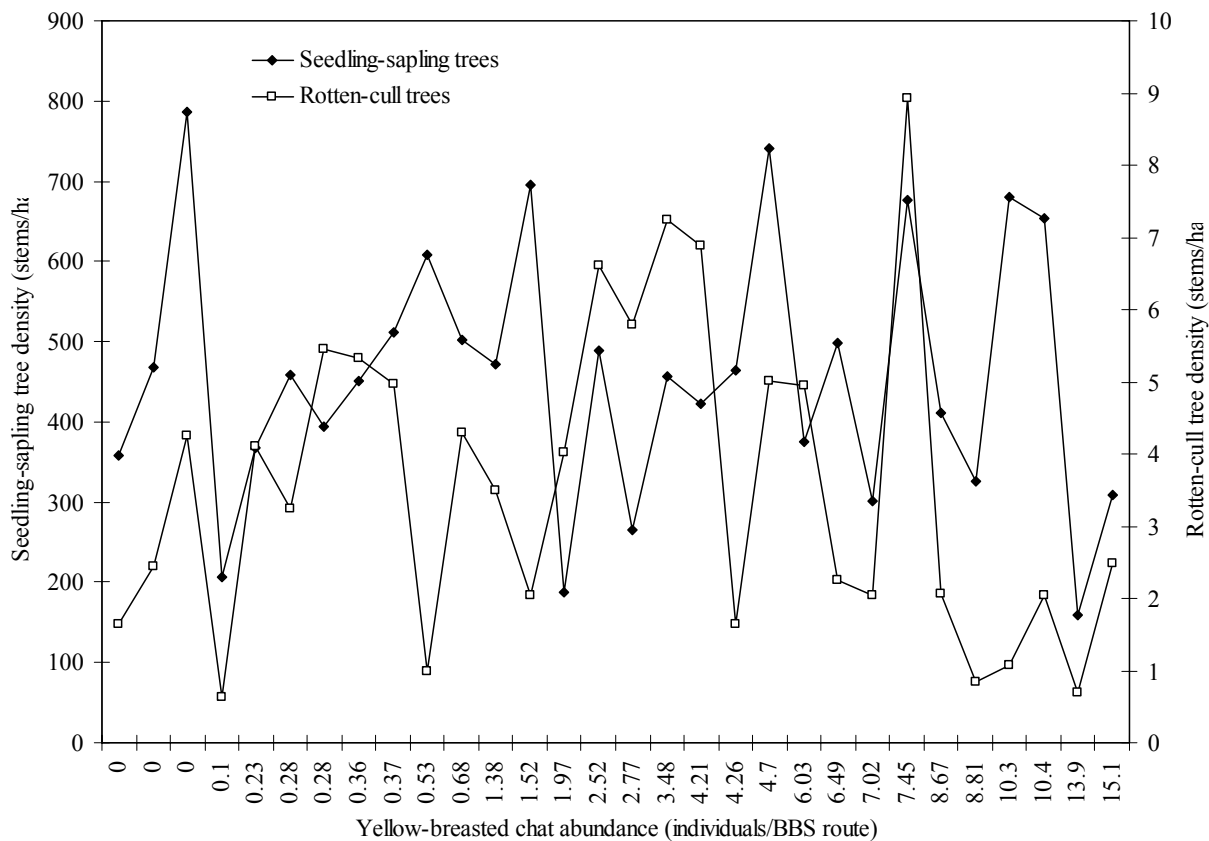


Figure 14. The average densities of seedling-sapling and rotten-cull trees relative to the average abundance of yellow-breasted chats at the FIA unit scale during the 2000 FIA inventory cycle.

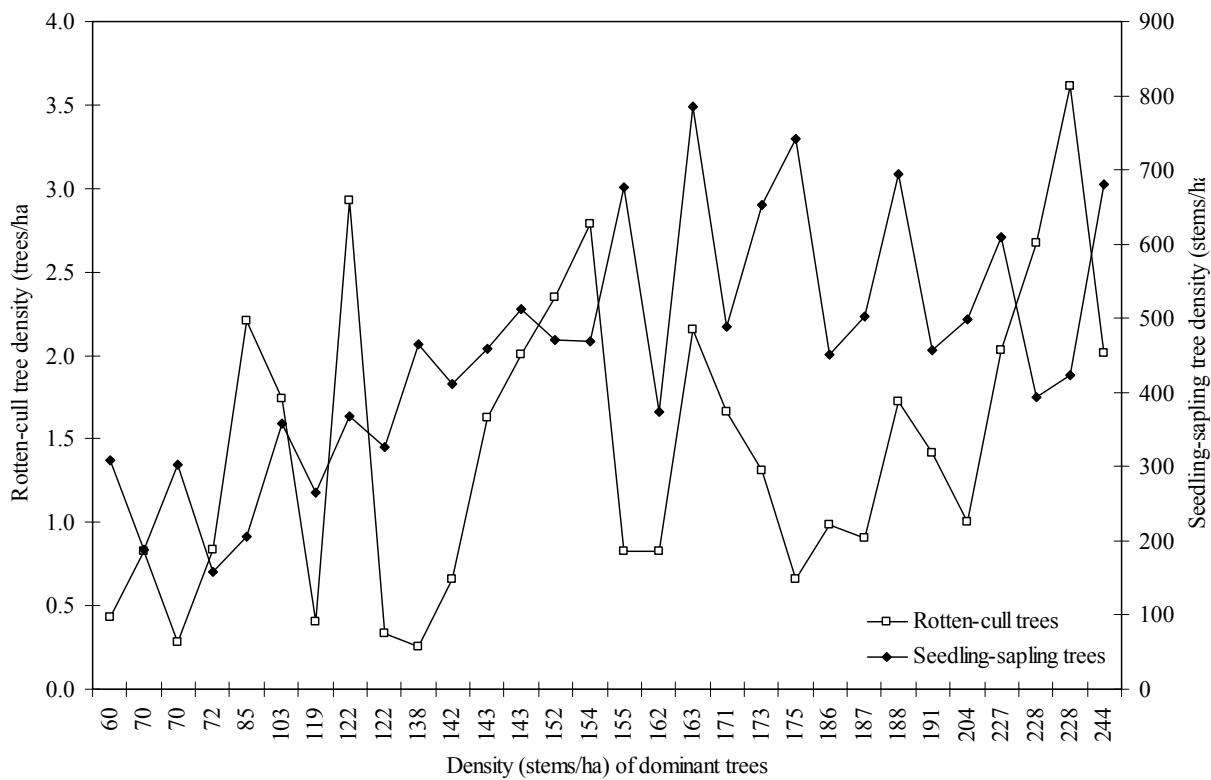


Figure 15. The average densities of seedling-sapling and rotten-cull trees relative to the average density of dominant trees at the FIA unit scale during the 2000 FIA inventory cycle.

CHAPTER 5

RELATING AVERAGE ANNUAL BIRD ABUNDANCE TO ANNUAL CHANGES IN FOREST VARIABLES

Results

Average annual abundance between 1966 and 2000 of the 26 bird species ranged from 0.31 (cerulean warbler) to 25.46 (red-eyed vireo) individuals per route per year across the 11 FIA units in MD, NY, PA, and WV included in this analysis (Table 21). Eight species (black-billed cuckoo, black-throated blue warbler, Canada warbler, cerulean warbler, pileated woodpecker, pine warbler, prairie warbler, and worm-eating warbler) had an average annual abundance less than 1 (Table 21). Most of these species had relatively low abundances during the 2000 FIA inventory cycle (Table 1) with the exception of the pileated woodpecker, which exhibited a significantly increasing trend in abundance (1.7%/year, $P < 0.01$) from 1966 to 2004 in the Appalachian BCR (Table 2). The number of routes sampled on the BBS varied annually and increased over the 1966 to 2000 time period within the 4 states considered in this analysis (Fig. 16). The annual abundance of 16 bird species was highly correlated ($|r| \geq 0.50$) with the number of BBS routes sampled in a given year (Table 21).

Relationships of the Forest Variables Developed from FIA Statistical Report Data to Annual Variations in Bird Abundance

Pearson correlation coefficients for single bird abundance-forest variable correlations ranged from -0.964 (red-bellied woodpecker with %SoftWood) to 0.972 (ovenbird with %Saw, Appendix O). Across the 26 bird species, 8 of the 13 forest variables I developed from the FIA statistical report data were included in at least 1 model (Table 22). However, because all forest variables exhibited significant multicollinearity (all $|r| \geq 0.595$, $P < 0.001$, Table 23), I

developed only 1 model per species using the forest variable with the greatest correlation to bird abundance. The variables most frequently included were % of land area in forestland (%ForCover) and % of timberland in sawtimber stands (%Saw, Table 22). Also, the number of BBS routes sampled annually was strongly correlated (all $|r| \geq 0.549$) with all but 1 forest metric (SoftWDPoleVol/ha, Table 23). Black-billed cuckoo annual abundance was not significantly correlated with any of the forest variables ($|r| \leq 0.173$, $P \geq 0.321$), and no model was developed for this species.

Model Performance

The total amount of variation (R_{adj}^2) in annual bird abundance explained by the GLMs ranged from 0.050 (yellow-billed cuckoo) to 0.952 (red-bellied woodpecker), with an average R_{adj}^2 across all species of 0.620 (Table 24). When considering the sequential sums of squares (type I) in the GLM, a significant ($P < 0.05$) amount of variation in bird abundance was accounted for by the number of BBS routes sampled annually in 21 of 25 models. After accounting for this route effect, 20 of these 21 species still exhibited a significant effect ($P < 0.05$) of habitat on average annual abundance (Table 24). However, when developing the beta coefficients using the regression analyses (type III sequential sums of squares), the estimated effect of the number of routes sampled on annual abundance appeared minimal as indicated by the small β values and was significantly different from zero ($P < 0.05$) in only 3 of the 25 models (Table 24).

Discussion

Several limiting factors must be considered when interpreting these models. I was able to develop a limited suite of variables from the FIA statistical reports; linear interpolation was applied to those variables between successive FIA cycles to develop their annual estimates; there

was substantial multicollinearity among all forest variables; the forest variables were developed at a coarse resolution and broad spatial extent; and the 4-state region considered for this analysis was relatively small and limited to the northern portion of my study area.

I addressed the first 2 factors above in chapter 2, and they both contributed to the multicollinearity among the variables developed from the statistical report data. The range of compatible data was limited to 4 states and described very general components of forest cover and volume that were related hierarchically and ecologically. For example, it is logical that as the percent of forest cover in the landscape increases (%ForCover) the percent of hardwood cover within that forest cover also will increase (%HardWood, Table 23). It is also critical to recognize that these variables were driven by a temporal as well as spatial component, and many of the intercorrelations reflect temporal changes in forest characteristics (Luppold and McWilliams 2000). For example, the proportion of timberland in poletimber stands increased between the 1965 and '75 inventory cycles, and then declined through 2000 (Fig. 17). The initial increase corresponded to a conversion of abandoned pastureland to forest that occurred during that time period (Bones 1978, Considine and Frieswyk 1982), with the subsequent decline after this land-use conversion slowed and poletimber stands matured into sawtimber stands. However, poletimber volume on timberland declined slightly between the '65 and '75 inventory cycles and then increased through 2000 in spite of the decline in the proportion of poletimber stands in timberland (Fig. 17). Such increases were likely a function of accretion as pole trees within those stands aged. Corresponding increases in sawtimber volume at an increasing rate between the 1975 and 2000 inventories were a function of both ingrowth from maturing pole stems and accretion within existing sawtimber stands (Fig. 17, Luppold and McWilliams 2000).

Actual estimates of these variables were limited to 4 points in time corresponding to each inventory cycle. The values for the remaining 31 years, 87% of the data points included in this analysis, were interpolated between those cycles. Therefore, annual variability among these metrics was reduced considerably, decreasing their resemblance to real-world patterns and increasing their likelihood of intercorrelation. Such strong multicollinearity among the forest variables limits the applicability of the bird-habitat relationships developed from these variables in 2 ways. First, I was able to include only one variable per model, limiting the range of habitat characteristics described by the models. Second, in spite of what appear to be ecologically meaningful (though general) relationships described by the models, many of the selected variables could be exchanged for others with little change in model fit.

The statistical report data I used to develop these forest variables were at the FIA unit scale, and then I developed average annual values across the 11-unit region. Therefore, these variables suffer many of the shortcomings discussed in chapter 4 regarding analyses at broad spatial scales. The broad extent of the variables limits their ability to relate biological significance of the models to a species' life-history requirements (Heglund 2002, Van Horne 2002). The distribution of the BBS routes within the 11-unit region was neither uniform nor consistent temporally or spatially. Thus the forest variables included information from areas not sampled by the BBS, and for bird species with restricted geographic distributions, provided information from areas where they are absent. The inclusion of such data can obscure bird-habitat relationships and create misleading results (Young and Hutto 2002).

The trends in abundance from 1965 to 2000 within the 4-state region of these analyses differed from those throughout the entire Appalachian BCR for some bird species. For example, ovenbird abundance declined from 1965 to 2000 in the Appalachian BCR (Table 2) but actually

increased within MD (0.7%/yr, $P = 0.07$), NY (2.4%/yr, $P < 0.01$), PA (2.7%/yr, $P < 0.01$), and WV (2.3%/yr, $P = 0.02$) during the same time range (Sauer et al. 2001). The bird-habitat relationships described by these models were a function of both the general habitat characteristics and the trends in bird abundance specific to this 4-state region and may not be applicable to other states or regions.

Relationships of the Forest Variables Developed from FIA Statistical Report Data to Annual Variations in Bird Abundance

In spite of the multicollinearity among the forest variables, some notable patterns in bird-habitat relationships did seem apparent. It is important to note that, with the exception of the percent of forest cover (%ForCover), the remaining variables describe characteristics within forested stands. The variables selected for 8 of the 10 models within the mature forest ground-shrub guild were those within forested stands (Table 22), indicating that structural characteristics within forested stands may exert a stronger influence on abundance within this guild than presence of general forest cover. Within the early successional guild, eastern towhee and yellow-breasted chat abundance declined as %ForCover increased or as the proportion of timberland in nonstocked or seedling-sapling stands (%NonSawPole) declined. Cerulean warbler abundance was most strongly and negatively associated with the proportion of nonstocked or seedling-sapling stands within timberland, which may serve as an index to forest fragmentation. Other studies have documented similar negative associations of ceruleans to decreases in forest patch size and increases in fragmentation (Thogmartin et al. 2004, NatureServe 2005). Pileated woodpecker abundance was most strongly and positively associated with the total volume of softwood trees per hectare (TotalSoftWDVol/ha), and coniferous stands tend to be their preferred habitat in the northern portions of their range (NatureServe 2005).

Wood thrush abundance was most strongly and negatively associated with increases in the volume per hectare of softwood trees in pole diameter classes (SoftWDPoleVol/ha). Within mature forested stands, the trees comprising this volume would likely be most prevalent in the forest understory, and wood thrushes tend to be most abundant in mature deciduous or coniferous stands with well developed deciduous understories (Hamel 2002, NatureServe 2005).

Model Performance

Eighteen of the 25 models I developed accounted for > 50% of the variation in bird abundance (Table 24). As with the models developed at the FIA unit and physiographic sections scales for the spatial analyses, many of these models accounted for as much or more variability in abundance than the regression trees relating bird abundance to the forest and landscape variables developed at the BBS route scale (Table 12). Such increases in R^2 were likely a result of the reduction in the variability among bird-habitat relationships more apparent at finer resolutions and smaller scales and the ability of coarse-resolution variables to encompass a broader range of ecological processes and potentially account for a broader range of habitat requirements (Van Horne 2002, Young and Hutto 2002). Also, variability in bird abundance through time tended to be less than that across space, even at the comparable spatial scales of these analyses and those discussed in chapter 4 (Tables 16 and 22, Heglund 2002). In these analyses, bird abundance CV ranged from 0.15-0.86. For the spatial analyses abundance CV ranged from 0.35 to 1.75 at the FIA unit scale and 0.36 to 1.79 at the physiographic section scale. This relatively small level of variation likely acted to further improve model fit.

The variable and increasing number of BBS routes sampled through time appears to have had a minimal influence on the abundance estimates. Though the number of routes was a significant covariate in many of the models, the effect size (as indicated by the slope of the

coefficient) on abundance was very small and rarely significant ($P > 0.05$, Table 24). The small effect size was, in part, a function of the differing measurement scales between bird abundance (typically ranging only a few individuals, Table 21) and number of routes (ranging over 100 routes). However, annual abundance patterns of several species deviated strongly from those of BBS route quantity. For example, the number of BBS routes sampled remained relatively constant between 1973 and 1984, but ovenbird abundance continued to increase during this time (Fig. 16). Abundance of eastern wood-pewees declined between 1986 and 2000 while the number of BBS routes sampled increased considerably (Fig. 16). Such departures seem to indicate annual bird abundance estimates were affected little by sampling effort and were responding to other factors, such as habitat.

Because the majority of the forest variables I developed for these analyses exhibited consistent linear trends with little variability through time, the models with the poorest fit tended to be for species with no definitive trend in annual abundance and/or high variability in abundance estimates (e.g. Canada and Kentucky warbler, downy woodpecker, black and yellow-billed cuckoos).

These models may serve as indices to those habitat components exerting the greatest influences on bird abundance trends through time at regional scales. However, because the relationships identified in these models were limited by the habitat and bird abundance trends specific to the 4-state region encompassed by these analyses, their applicability outside this is limited. Also, the multicollinearity of the forest variables precludes inferences regarding specific habitat-abundance relationships. As with the models discussed in chapter 4, further interpretation of these relationships should be based on more reliable models developed at smaller scales with finer resolution data. As the FIA continues to accumulate data using the new

pseudo-annual survey methodology, its usefulness as a tool for developing more detailed models of annual bird abundance estimates to forest habitat at finer scales will improve considerably.

Table 21. Average annual bird abundance (count/route/year) data from 1966 to 2000 across the 11 FIA units in NY, PA, MD, and WV that were included in the temporal analysis for the 26 bird species selected for this study.

Species	Avg. count	Minimum	Maximum	C.V.	Pearson <i>r</i> with # BBS routes
Cavity					
Downy woodpecker	2.31	1.33	3.14	0.198	0.334
Great-crested flycatcher	2.99	1.68	3.93	0.197	0.442
Pileated woodpecker	0.72	0.17	1.71	0.592	0.629
Red-bellied woodpecker	1.11	0.03	3.21	0.857	0.792
Tufted titmouse	5.54	2.19	9.66	0.425	0.727
Early successional					
Chestnut-sided warbler	2.84	1.75	4.48	0.261	0.521
Common yellowthroat	19.39	12.67	24.27	0.188	0.606
Eastern towhee	11.25	7.74	16.92	0.206	-0.173
Prairie warbler	0.50	0.13	0.88	0.328	0.586
Yellow-breasted chat	1.42	0.56	3.14	0.390	-0.763
Mature forest canopy					
Cerulean warbler	0.31	0.06	0.69	0.422	0.521
Eastern wood-pewee	5.15	2.70	7.19	0.215	0.324
Pine warbler	0.32	0.00	0.93	0.750	0.681
Red-eyed vireo	25.46	13.86	38.04	0.300	0.694
Wood thrush	15.37	11.69	21.35	0.150	-0.229
Mature forest ground-shrub					
American redstart	3.77	2.35	5.91	0.283	0.673
Black and white warbler	1.46	0.89	2.33	0.265	0.520
Black-billed cuckoo	0.71	0.24	1.39	0.395	-0.083
Black-thr. blue warbler	0.38	0.07	0.96	0.764	0.752
Canada warbler	0.39	0.17	0.75	0.365	-0.004
Hooded warbler	1.13	0.26	2.40	0.564	0.746
Kentucky warbler	1.03	0.45	2.38	0.380	0.063
Ovenbird	8.04	3.58	14.87	0.489	0.750
Rose-breasted grosbeak	2.56	1.52	3.98	0.229	0.379
Worm eating warbler	0.50	0.19	1.23	0.618	0.714
Yellow-billed cuckoo	1.67	0.37	3.13	0.352	0.272

Table 22. Number of times that forest variables developed using the FIA statistical report data from the 1965, '75, '89, and 2000 inventory cycles were included in the GLMs. Data are summarized by bird species guild. Variables not selected within any guild were omitted from the table for brevity.

Variable	Cavity	Early successional	Mature forest canopy	Mature forest ground shrub	Total times selected	Rate of selection
%ForCover	1	4	2	2	9	0.360
%HardWood	0	0	1	0	1	0.040
%NonSawPole	1	0	1	0	2	0.080
%Pole	0	0	0	2	2	0.080
%Saw	2	0	0	3	5	0.200
SoftwoodPoleVol/ha	0	0	1	1	2	0.080
TotalSoftWDVol/ha	1	0	0	1	2	0.080
HDWDPoleVol/Ha	0	1	0	1	2	0.080

Table 23. Pearson r values among the number of BBS routes and the forest variables developed using the FIA statistical report data from the 1965, '75, '89, and 2000 inventory cycles.

Forest variable	# BBS routes	%ForCover	%SoftWood	%HardWood	%Saw	%Pole	%NonSawPole
%ForCover	0.805						
%SoftWood	-0.818	-0.904					
%HardWood	0.821	0.890	-0.999				
%Saw	0.724	0.931	-0.951	0.937			
%Pole	-0.549	-0.621	0.864	-0.866	-0.846		
%NonSawPole	-0.733	-0.961	0.931	-0.915	-0.993	0.778	
SoftWDPoleVol/ha	0.432	0.595	-0.786	0.779	0.848	-0.967	-0.787
SoftWDSawVol/ha	0.724	0.922	-0.957	0.945	0.999	-0.863	-0.989
HDWDPoleVol/ha	0.730	0.731	-0.952	0.961	0.853	-0.937	-0.801
HDWDSawVol/ha	0.770	0.800	-0.980	0.985	0.896	-0.920	-0.855
TotalSoftWDVol/ha	0.712	0.907	-0.955	0.944	0.998	-0.881	-0.983
TotalHDWDVol/ha	0.763	0.783	-0.974	0.980	0.884	-0.922	-0.840
TotalVol/ha	0.764	0.792	-0.977	0.983	0.892	-0.924	-0.849

Table 23 continued.

Forest variable	SoftWDPoleVol/ha	SoftWDSawVol/ha	HDWDPoleVol/ha	HDWDSawVol/ha	TotalSoftWDVol/ha	TotalHDWDVol/ha
SoftWDSawVol/ha	0.860					
HDWDPoleVol/ha	0.829	0.869				
HDWDSawVol/ha	0.821	0.909	0.994			
TotalSoftWDVol/ha	0.878	0.999	0.878	0.914		
TotalHDWDVol/ha	0.819	0.897	0.997	1.000	0.903	
TotalVol/ha	0.825	0.905	0.996	1.000	0.911	1.000

Table 24. Parameters from the GLMs relating average annual bird abundance (count/route) across 11 FIA units in NY, PA, MD, and WV from 1966 to 2000 to average annual values of the forest variables developed from FIA statistical report data. Values for the forest variables were developed from the 1965, '75, '89, and 2000 inventory cycles and then interpolated between cycles to create the annual values.

Predictors	Seq SS	F	P-value	R_{adj}^2	β	SE	P-value
Cavity							
Downy woodpecker							
# routes	0.790	5.75	0.023	0.278	-0.0026	0.0032	0.435
%Saw	1.911	13.90	0.001		4.439	1.191	0.001
Great-crested flycatcher							
# routes	0.195	16.02	<0.001	0.514	-0.00113	0.0011	0.312
%ForCover	0.267	21.93	<0.001		17.675	3.774	<0.001
Pileated woodpecker							
# routes	0.744	70.89	<0.001	0.831	-0.00001	0.00085	0.989
TotalSoftWoodVol/ha	0.925	93.97	<0.001		0.0062	0.0006	<0.001
Red-bellied woodpecker							
# routes	4.037	442.58	<0.001	0.952	0.00252	0.00098	0.015
%Saw	2.158	236.56	<0.001		5.169	0.336	<0.001
Tufted titmouse							
# routes	2.667	250.77	<0.001	0.927	0.0018	0.00091	0.057
%NonSawPole	1.957	183.96	<0.001		-5.377	0.396	<0.001
Early Successional							
Chestnut-sided warbler							
# routes	0.290	17.04	<0.001	0.511	0.00001	0.00112	0.993
HDWDPoleVol/ha	0.347	20.43	<0.001		0.00063	0.00014	<0.001
Common yellowthroat							
# routes	0.459	71.93	<0.001	0.828	-0.00158	0.00079	0.056
%ForCover	0.597	93.57	<0.001		26.443	2.734	<0.001
Eastern towhee							
# routes	5.469	2.02	0.165	0.498	0.05798	0.01635	0.001
%ForCover	91.208	33.72	<0.001		-326.820	56.280	<0.001
Prairie warbler							
# routes	0.008	16.95	<0.001	0.312	0.00288	0.00143	0.052
%ForCover	0.586	0.46	0.501		3.261	4.790	0.501
Yellow-breasted chat							
# routes	6.100	69.07	<0.001	0.746	-0.00493	0.00299	0.109
%ForCover	1.867	23.83	<0.001		-48.282	-9.890	<0.001
Mature forest canopy							
Cerulean warbler							
# routes	0.158	20.19	<0.001	0.543	-0.00003	0.00078	0.967
%NonSawPole	0.174	22.22	<0.001		-1.6047	0.3404	<0.001
Eastern wood-pewee							
# routes	4.368	7.17	0.012	0.503	-0.01885	0.00776	0.021
%ForCover	17.773	29.18	<0.001		144.270	26.710	<0.001
Pine warbler							
# routes	0.911	83.82	<0.001	0.812	-0.00007	0.00137	0.962
%HardWood	0.704	64.74	<0.001		30.746	3.821	<0.001

Table 24. Continued

Predictors	Seq SS	F	P-value	R_{adj}^2	β	SE	P-value
Mature forest canopy							
Red-eyed vireo							
# routes	1.506	179.12	<0.001	0.915	-0.00178	0.00091	0.06
%ForCover	1.582	188.25	<0.001		43.048	3.138	<0.001
Wood thrush							
# routes	9.510	3.70	0.063	0.517	0.00596	0.0111	0.595
SoftWDPoleVol/ha	89.167	34.73	<0.001		-0.51424	0.08726	<0.001
Mature forest ground-shrub							
American redstart							
# routes	0.661	82.73	<0.001	0.833	-0.00034	0.00062	0.584
%Saw	0.711	88.89	<0.001		2.869	0.304	<0.001
Black and white warbler							
# routes	0.204	22.74	<0.001	0.608	0.00047	0.00054	0.387
%Pole	0.288	32.10	<0.001		-8.130	1.435	<0.001
Black-thr. blue warbler							
# routes	0.771	176.19	<0.001	0.893	0.00089	0.00052	0.095
TotalSoftWDVol/ha	0.478	109.12	<0.001		0.00480	0.00046	<0.001
Canada warbler							
# routes	<0.001	<0.00	0.981	0.201	-0.00146	0.00097	0.143
%Pole	0.173	10.56	0.003		-5.937	1.824	0.003
Hooded warbler							
# routes	1.489	88.73	<0.001	0.806	0.00104	0.0009	0.253
%Saw	0.911	54.24	<0.001		3.248	0.441	<0.001
Kentucky warbler							
# routes	0.013	0.52	0.476	0.226	-0.00126	0.00100	0.214
SoftWDPoleVol/ha	0.277	11.42	0.002		0.03163	0.00936	0.002
Ovenbird							
# routes	3.095	293.08	<0.001	0.942	0.00006	0.00071	0.934
%Saw	2.769	262.19	<0.001		5.663	0.350	<0.001
Rose-breasted grosbeak							
# routes	1.674	8.45	0.007	0.423	-0.00612	0.00358	0.094
%ForCover	3.649	18.42	<0.001		70.570	16.440	<0.001
Worm eating warbler							
# routes	0.599	105.95	<0.001	0.839	0.00040	0.00054	0.471
HDWDPoleVol/ha	0.416	73.57	<0.001		0.00075	0.00009	<0.001
Yellow-billed cuckoo							
# routes	0.869	2.64	0.114	0.050	0.00048	0.00461	0.917
%ForCover	0.376	1.14	0.293		22.660	21.190	0.293

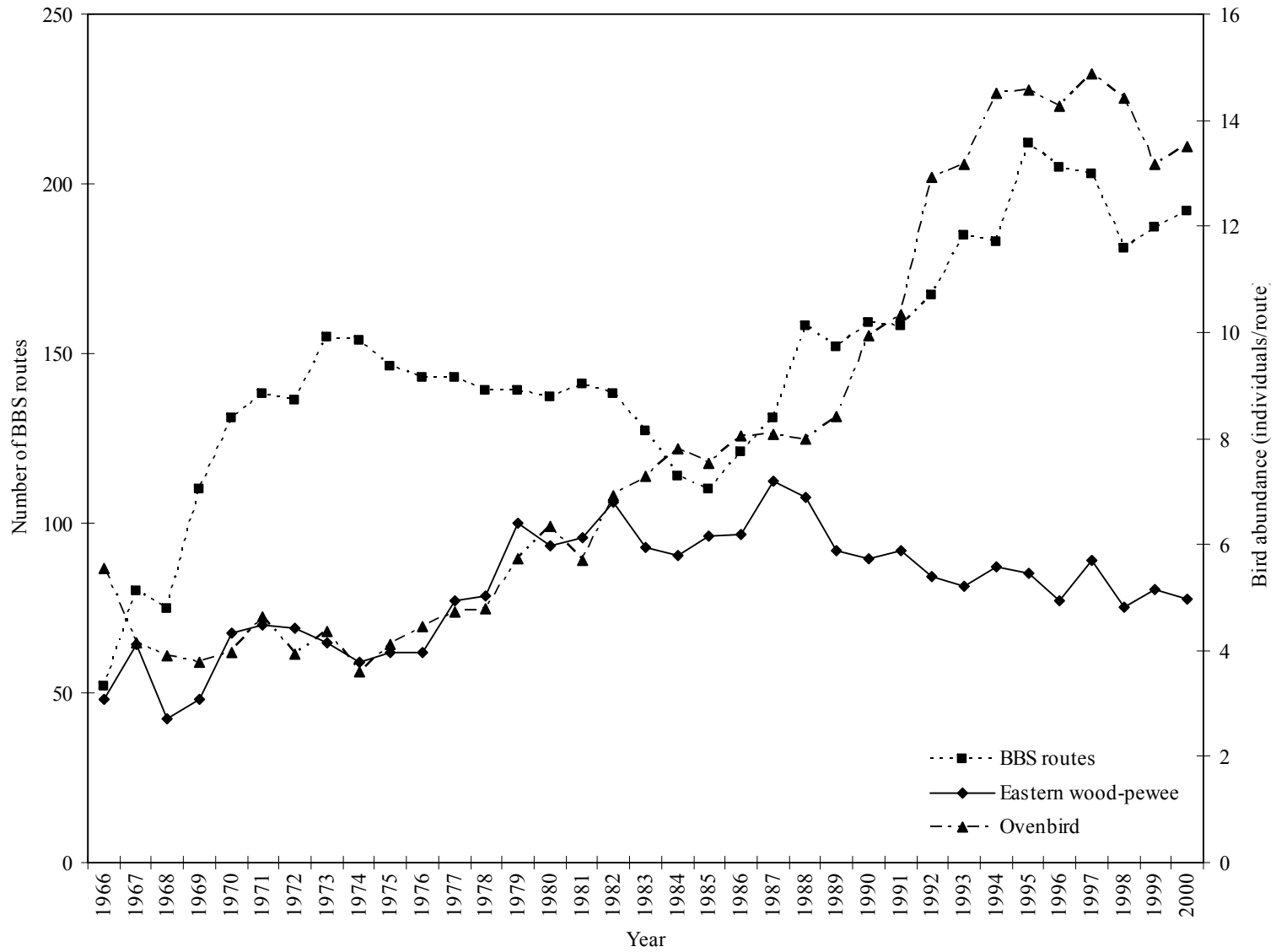


Figure 16. The number of BBS routes sampled per year and annual abundance estimates for eastern wood-pewees and ovenbirds from 1965 to 2000 within the 11 FIA units of MD, NY, PA, and WV included in this study.

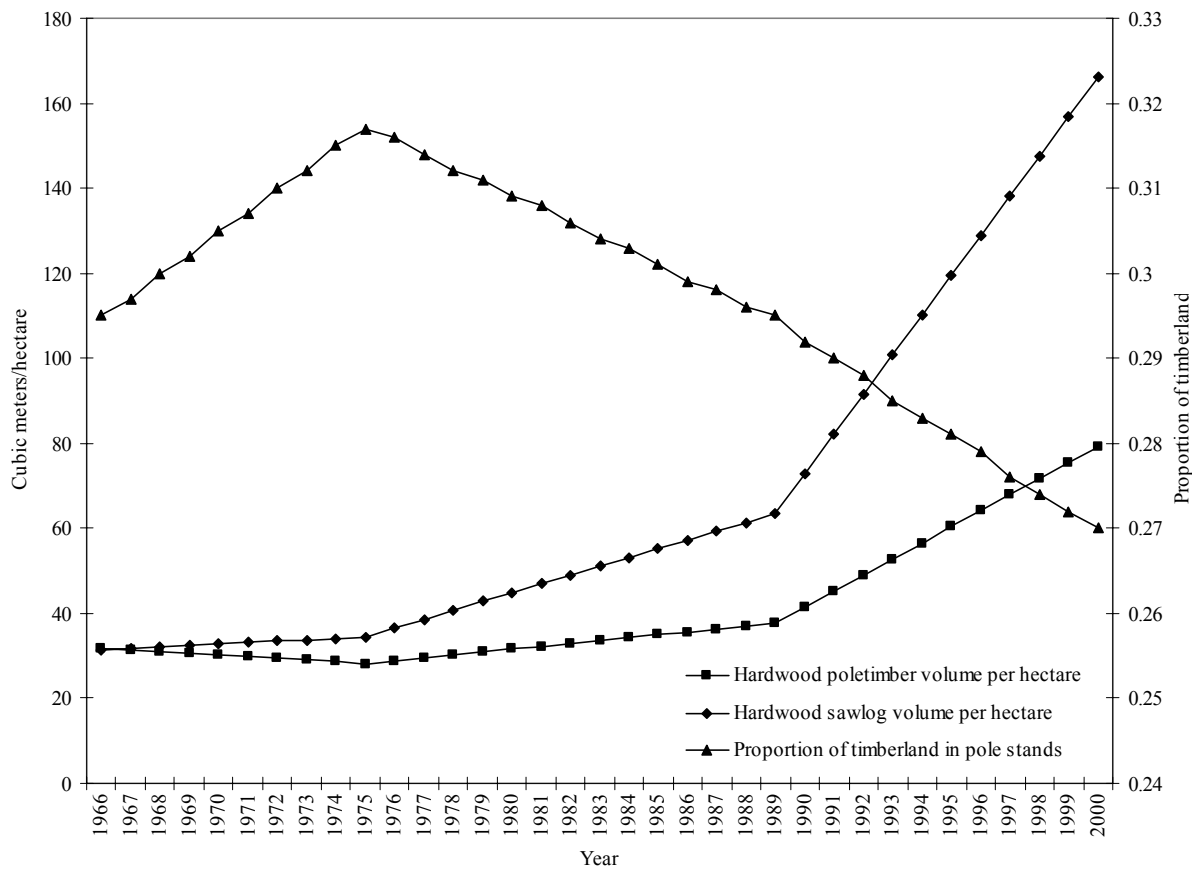


Figure 17. Annual estimates of 3 forest variables within the 11 FIA units of MD, NY, PA, and WV developed for the temporal analyses. Actual estimates for each variable were calculated in 1965, 1975, 1989, and 2000 corresponding to the FIA inventory cycles. The remaining values were linearly interpolated between those cycles.

Summary and Conclusions

Using measures of bird presence-absence and abundance developed from the BBS, forest variables developed from the FIA, and landscape variables developed from NLCD imagery, I was able to produce a suite of models describing bird-habitat relationships at multiple spatial scales.

The models developed at the BBS route level described bird-habitat relationships at the finest resolution possible, given the properties of the data over the 14 state extent of my study area. Many of the CART models accounted for more than 50% of the variation in bird presence-absence (Table 11) and abundance (Table 12). The logistic regression models had sensitivity and specificity rates greater than 0.50 (Table 13). By incorporating the variables selected for the models developed within each buffer (100 m, 1 km, and 10 km) around the BBS routes into a multiscale model, I was able to further improve the performance of many of the models and gain additional insight regarding the contribution of multiscale influences on bird-habitat relationships. The majority of the best CART models tended to be the multiscale models, and many of the multiscale logistic models had greater sensitivity and specificity than their single-scale counter-parts (Tables 11-13). The relatively fine resolution and extensive coverage of the BBS, FIA, and NLCD datasets coupled with the overlapping multiscale approach of these analyses allowed me to incorporate levels of variation in both habitat and bird occurrence and abundance into my models that likely represented a more comprehensive range of ecological variability in the bird-habitat relationships relative to studies conducted at smaller scales and/or using data at coarser resolutions.

At the FIA unit and physiographic section scales, the regression trees accounted for an average of 54.1% of the variability in bird abundance among FIA units, and the GLMs accounted

for an average of 66.3% of the variability among physiographic sections (Table 19). However, increasing the observational and analytical scale to the FIA unit and physiographic section decreased the measurement resolution of the bird abundance and landscape variables, and the bird-habitat relationships identified by the coarser variables at these larger scales can encompass a range of ecological processes. This limits the applicability and interpretive strength of the models developed at these scales, but they may serve as indices to those habitat components exerting the greatest influences on bird abundance at these broader scales.

The GLMs relating average annual bird abundance to annual estimates of forest variables developed using statistical report data from the 1965, '75, '89, and 2000 FIA inventories explained an average of 62.0% of the variability in annual bird abundance estimates (Table 24). However, these relationships were a function of both the general habitat characteristics and the trends in bird abundance specific to the 4-state region (MD, NY, PA, and WV) used for these analyses and may not be applicable to other states or regions. The small suite of variables available from the FIA statistical reports and the multicollinearity among all forest variables further limits the applicability of these models. As with those developed at the FIA unit and physiographic sections scales, these models may serve as general indices to the habitat components exerting the greatest influences on bird abundance trends through time at regional scales.

The inclusion of variables describing habitat structure developed from the FIA data (e.g. stem densities within age classes and species diversity indices) and landscape characteristics developed from both the FIA data (e.g. the physiographic class codes) and NLCD imagery (e.g. patch size and shape, edge characteristics) contributed to my success in developing the bird-habitat models for this study. With the continued advancement in GIS and remote sensing

technologies, the current trend is to rely heavily or entirely on remotely sensed imagery for developing wildlife-habitat models (Van Horne 2002, Wiens 2002, Seoane et al. 2004). This practice may be appropriate for studies conducted over large geographic extents where the study objective is the assessment of coarse spatial patterns. However, it has limitations when the objectives involve assessing relationships that are best considered at fine resolutions and/or are a function of structural components within the habitat. Indeed, many recent studies that modeled wildlife-habitat relationships derived their suite of habitat variables entirely from remotely sense data (e.g. Flather and Sauer 1996, Vernier et al. 2002, Prather et al. 2006). As remotely sensed imagery and the techniques for deriving data from it continue to improve, it is tempting to rely solely on the maps developed from such imagery in developing wildlife-habitat models. Doing so may give the perception that such data adequately represent any suite of habitat characteristics we may wish to study (Van Horne 2002). However, even the best imagery and the information derived from it is limited by resolution, measurement error, ground-truthing (or lack of), compatibility among different types of imagery and data, and a myriad of other constraints (Dungan et al. 2002, Henebry and Merchant 2002, Trani 2002, Van Horne 2002, Wiens 2002).

Perhaps 2 of the most important considerations are, first, that data derived from GIS analyses often are pattern rather than process based, and the variables defining a given map pixel may not be related to those directly affecting the study animal (Van Horne 2002). Second, while the use of maps describing vegetation structure and landscape characteristics can describe wildlife distributions and other life-history characteristics with some success, there will likely always be a finite level of detail regarding habitat structure that can be derived from remotely sensed imagery (Seona et al. 2004). The importance of microhabitat structure in bird-habitat relationships has been well documented (e.g., Thompson et al. 1995, Hunter et al. 2001, Jobes et

al. 2004, Hanowski et al. 2006). Therefore, inclusion of variables that describe habitat structure derived from ground data should always improve wildlife-habitat modeling when describing such relationships is an objective of the study. The forest variables I derived using the FIA data, in conjunction with the landscape variables, were successful in explaining considerable variability in bird presence-absence and abundance, and models for some species included only variables developed from the FIA data (e.g. yellow-billed cuckoo logistic and classification tree models at the 100m buffer BBS route level).

I developed 43 forest variables from the FIA data and 29 landscape variables from the NLCD imagery; many of these variables were redundant and exhibited varying levels of multicollinearity. Many common modeling techniques assume independence among predictor variables (e.g. logistic regression, GLM), and a common practice in studies containing a large suite of intercorrelated variables is to reduce them to groups of independent variables using multivariate techniques such as principal components (PCA) or canonical correlation analysis (CCA, e.g. Cumming and Vernier 2002, MacFaden and Capen 2002). This approach can simplify the suite of predictor variables to a more manageable group and may be appropriate when the modeling objectives are to describe general patterns over broad regions or rescale fine resolution datasets to match those at coarser resolutions (Cumming and Vernier 2002). However, when the objective is to describe specific wildlife-habitat relationships and/or predict abundance patterns, I suggest these procedures can potentially confound the wildlife-habitat relationships they are attempting to describe and inhibit model performance in 2 ways. The first relates to the spatial and temporal scales of the model parameters and the documented effects they have on the outcome of a model (Dungan et al. 2002, Trani 2002, Bissonette 2003). In many modeling studies (this one not withstanding), the parameters included in a given model are

developed from data sources existing at varying scales and resolutions, all of which are integrated into a single data set with little or no consideration or understanding of how these differing scales might affect the model results (Dungan et al. 2002, Wiens 2002). Using PCA or other multivariate techniques to further reduce data from differing scales without carefully considering scaling and resolution effects may further confound wildlife-habitat relationships (Cumming and Vernier 2002, Henebry and Merchant 2002, Trani 2002). The second concern involves relating model results back to the ecology of the animal being studied. A central issue of wildlife-habitat modeling is interpreting the biological meaning between the dependent and predictor variables in the model (Heglund 2002, Young and Hutto 2002, Wiens 2002). The factors driving the ecological importance of a variable for a given species tend to be process-driven (Heglund 2002, Young and Hutto 2002) and may be very different from the factors, which are likely pattern-driven, creating the multicollinearity among several variables. The variable groupings created by PCA or similar methods can sometimes be ambiguous and interpreting the meanings of such groupings can be subjective. A species may respond differently to individual variables in spite of the multicollinearity they exhibit as a group; these responses may vary over space and/or through time as habitat characteristics change and interact (Wiens 2002). Thus an inspection of these interrelations on more of an individual basis can lead to a better understanding of the observed relationships and how an organism is responding to its habitat (De'ath and Fabricius 2000, Young and Hutto 2002). This consideration is especially true for overlapping multiscale analyses where relationships among predictor variables as well as between the predictor and response variables may vary across scales.

The ability to integrate the BBS and FIA databases and develop bird-habitat models from these datasets has several positive implications regarding development and use of wildlife-

habitat models. Natural resource managers recognize the need to develop management plans over broad regions (e.g. multiple physiographic sections), and wildlife-habitat models play an integral role in this process. For example, bird-habitat models have been integrated with timber harvest models to assess the effects of forest management and timber harvest schedules on bird species richness and habitat quality (Larson et al. 2004, Loehle et al. 2006). Wisconsin implemented landscape-scale management efforts for grassland bird species based on habitat models that incorporated an overlapping multiscale approach similar to that of this study (Sample et al. 2003). The models developed from this study could be readily integrated into similar regional management plans. The form of the CART models is analogous to a dichotomous key and could be readily adapted into a decision tree or rule-based system for evaluating management options on bird presence-absence and abundance (Hobbs 2003). The hierarchical nature of the models I developed, from the broadest scale at the physiographic section to the smallest scale at BBS route level, could be used as a consistent means of evaluating management among regions as well as at varying scales within a region. Because the models at the finest resolution (BBS route) were developed across such a broad geographic extent, and those at the largest scale were derived from the same data generalized to that scale, this should facilitate efficient and relatively precise comparisons of the bird-habitat relationships they describe among scales (Cumming and Vernier 2002). Therefore, they could be used to assess region-wide objectives and activities as well as assess specific within-region management strategies. The FIA data include several variables describing management activities such as timber harvests and stand disturbances that I did not incorporate into the models I developed. Further study is needed to assess the utility of these variables in wildlife-habitat modeling, but

they could potentially serve to evaluate the effects of specific forest management practices or other phenomenon, such as insect outbreaks, on bird-habitat relationships.

A common criticism of wildlife-habitat models is they describe correlative relationships that tend to be driven by patterns in the data and provide little insight regarding the ecological processes underlying the identified relationships (Heglund 2002). This issue is becoming more prevalent with the development of large-scale analyses coupled with an increasing awareness of the interrelation and confounding effects of measurement scale (temporal and spatial) and ecological scale (the scale at which an organism is responding to its environment; Heglund 2002, Hobbs 2003, Araújo and Guisan 2006). Researchers have advocated that wildlife-habitat research proceed in a hierarchical fashion where the wildlife-habitat relationships described by models are used to formulate hypotheses for experiment-based studies examining the causes of the relationships (Hobbs 2003, Bennett and Adams 2004, Welsh et al. 2006). Because BBS data are gathered during the breeding season, patterns of occupancy and abundance in these data should, in theory, be related to breeding habitat and thus have implications for reproductive success. The broad extent, relatively fine resolution, and multiscale components of the models I developed at the individual BBS route scale, coupled with examining habitat relationships relative to both occupancy and abundance, may serve as a foundation for such a hierarchical approach.

The adoption of the semi-annual inventory cycles within the FIA and integration of the Forest Health Monitoring program into the FIA provide a further resource for such work using a BACI-style (before-after, control-impact) research approach (Bennett and Adams 2004). The FIA collects data regarding natural stand disturbances (e.g. insect outbreaks, storm damage), timber harvesting, and other activities that impact forest characteristics. The fine resolution of

these data coupled with their broad spatial extent provides a foundation of information that could be used to assess cause-effect relationships applicable across broad regions (Bennett and Adams 2004). The results of such work, either experimentally based, developed from BACI-style research, or a combination of both strategies, could be used to refine or modify wildlife-habitat models by assessing the importance of model parameters and the ecological validity of the wildlife-habitat relationships they describe.

Ecosystem functions take place at a variety of scales and wildlife-habitat relationships are a part of that functionality, responding to changes in the system occurring over both space and time (Dunning et al. 1992). A landscape perspective is required to understand species distribution across complex and stochastic ecosystems (Dunning et al. 1992), recognizing that the realized niche (Hutchinson 1957) of a given species will vary constantly across space and time as resources, competition, predator abundance, and other components affecting that niche change (Heglund 2002, Araújo and Guisan 2006), and multiple combinations of resources may equally fulfill the niche. Wildlife-habitat models, regardless of their spatial and/or temporal extent, are still only capturing ‘snapshot’ relationships that inadequately assess dynamic processes such as population cycles, variable or pulsed resource availability (e.g. mast production), or lag effects in a population’s response to the environment (Heglund 2002, Araújo and Guisan 2006). This tremendous environmental complexity implies that no model or experiment will completely describe all elements of how an animal relates to its habitat to meet its life history requirements, thus requiring a paradigm shift in how natural resource researchers and managers view approach their work (Henebry and Scott 2002, Wiens 2002, Hobbs 2003, Cadenasso et al. 2006). This includes basing management plans on multiple lines of evidence developed from multiple models using several techniques over numerous temporal and spatial

scales. The relationships described by these models should both serve as a source of further experimental research and be refined based on the results of such experimental work. This integrated feedback incorporates an adaptive management approach, allowing for effective evaluation of management and conservation efforts (Hobbs 2003, Cadenasso et al. 2006). The framework for such work needs to be that of cooperative efforts among several agencies (e.g. multi-agency joint ventures such as the NABCI), that recognize the need to manage populations over broad regions. This will facilitate the sharing of ideas, information, and resources, making complex and large-scale conservation efforts more feasible. I feel that using resources such as the FIA, BBS, and NLCD, and taking a meta-analysis style approach to addressing wildlife conservation issues in a broad context is an integral step in achieving these changes.

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