THE RELATIVE EFFECTS OF HABITAT AMOUNT, HABITAT CONFIGURATION, AND URBANIZATION INTENSITY ON FOREST BREEDING BIRDS

by

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ABSTRACT

ALEXANDRA VICTORIA SHOFFNER. The relative effects of habitat amount, habitat configuration, and urbanization intensity on forest breeding birds. (Under the direction of DR. SARA A. GAGNÉ)

It is clear that urbanization causes changes in landscape structure that adversely affect biodiversity. However, the relative impacts of different components of landscape structure remain unclear. Using the 2006 National Land Cover Database and 2010 U.S. Census data, I quantified habitat amount, habitat configuration, and matrix quality in concentric landscapes of ten different radii (ranging from 0.2km to 16km) centered on forested point counts spanning the state of Pennsylvania in order to distinguish the independent impacts of these three aspects of landscape structure. I estimated forest bird abundance, species richness, species evenness, and American robin and Scarlet tanager occurrence from a large and spatially-extensive dataset of point counts collected during the 2nd Pennsylvania Breeding Bird Atlas conducted 2004-2009. I used generalized linear modeling and a multi-model inference approach to determine the relative effects of these three aspects of landscape structure in Pennsylvania landscapes on avian biodiversity in remnant forest. Of the three elements of landscape structure investigated, matrix quality was the most influential predictor of diversity and species occurrence. This research suggests that modifications to the urban and agricultural matrix surrounding forest patches will have more influence on forest birds than attempts to alter forest amount or configuration. These results are expected to be of particular interest to land managers given the emergent intensity of the Marcellus shale gas industry and its impacts on landscape structure in Pennsylvania landscapes.

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CHAPTER 1: INTRODUCTION

The projected doubling of developed land between 2000 and 2025 in the U.S. (Nelson 2006) will be a major contributor to biodiversity loss (Czech et al. 2000). The urbanization of landscapes creates a pattern of remnant habitat patches surrounded by a matrix of residential, commercial, and industrial land uses. Three aspects of landscape structure have important effects on avian diversity in remnant habitat in urban landscapes:

(1) *Habitat amount* is the total area of habitat in a landscape. Declines in biodiversity due to decreasing habitat amount are well-documented and universal across taxa and landscapes (Millennium Ecosystem Assessment 2005). For example, Smith et al. (2011) found that within human-altered landscapes, total habitat amount had strong and consistently positive effects on the presence of forest birds.

(2) *Habitat configuration* is the spatial arrangement of habitat in a landscape, independent of habitat amount. Habitat configuration is fragmentation *per se* (*sensu* Fahrig 2003). Habitat configuration has somewhat unpredictable effects on biodiversity: empirical studies show that the independent effects of configuration on species are generally weak and as likely to be positive as negative (Fahrig 2003). For example, Villard et al. (1999) found that the number of forest fragments had a significant positive effect on Veery (*Catharus fuscescens)* occurrence, whereas fragment mean nearest-neighbor distance had a significant negative effect on Scarlet tanager (*Piranga olivacea*) occurrence.

(3) *Matrix quality* is the degree to which human activities in the matrix disturb natural processes (Gagné et al. 2015). As such, matrix quality is a major determinant of biodiversity in human-dominated landscapes (Prevedello and Vieira 2010). In urban landscapes, matrix quality for forest-dwelling species is inversely proportional to urbanization intensity. For example, native forest bird species abundance in forest patches is lower within urban landscapes than suburban or exurban landscapes (Donnelly and Marzluff 2004).

The independent relative effects of these three aspects of landscape structure on biodiversity are of great interest. Though there is broad support for habitat amount as the strongest determinant of biodiversity (Andren 1994, Fahrig 1997, Fahrig 2003, Radford et al. 2005, Quesnelle et al. 2013), there is less consensus regarding the additional relative effects of habitat configuration and matrix quality on biodiversity. Existing evidence suggests that, after habitat amount, the next most important determinant of biodiversity is either matrix quality (Fahrig 2001, Radford and Bennett 2007) or habitat configuration (Smith et al. 2011).

Of the empirical studies that have compared the relative effects of these three aspects of landscape structure (Diekotter et al. 2007, Guadagnin and Maltchik 2007, Haynes et al. 2007, Radford and Bennett 2007, Smith et al. 2011, Quesnelle et al. 2013), few have included urban landscapes. Urban areas comprised 1% and 8% of the study areas investigated by Smith et al. (2011) and Quesnelle et al. (2013) respectively, but it was not specified in either methodology if the actual landscapes measured from within those study areas had any significant urban component. Most landscapes are characterized by either an artificial matrix (Diekotter et al. 2007, Haynes et al. 2007) or a primarily agricultural matrix (Guadagnin and Maltchik 2007, Radford and Bennett 2007, Smith et al. 2011). Therefore, there is a need for research investigating the relative impacts of habitat amount, habitat configuration, and matrix quality in urban landscapes.

Given the paucity of knowledge about the relative impacts of different aspects of landscape structure on biodiversity in urban landscapes, I address the following research question: What are the relative effects of habitat amount, habitat configuration, and matrix quality on forest breeding bird abundance, species richness, species evenness, and the occurrence of individual species?

Based on the evidence to date, I hypothesize that habitat amount will have the largest effects, followed by matrix quality and habitat configuration, in that order.

I will quantify habitat amount, habitat configuration, and urbanization intensity in landscapes of multiple sizes across the state of Pennsylvania. For each landscape, I will estimate avian biodiversity and species occurrence using point count data from the 2nd Pennsylvania Breeding Bird Atlas (Wilson et al. 2012). Using generalized linear modeling and a multi-model inference approach, I will determine the relative independent effects of each of the three landscape structure predictors on avian diversity.

CHAPTER 2: METHODS

2.1. Study Area

Pennsylvania has an area of 119,283 km^2 and includes three Bird Conservation Regions. The majority of the state is classified as the Appalachian Mountains region, characterized by forested mountains and lower-elevation agriculture (U.S. NABCI Committee 2000). The Lower Great Lakes region occurs in the northwest and consists of agriculture and lakeshore habitat, and the Piedmont region occurs in the southeast and is highly urbanized. The state has two major urban centers, Philadelphia and Pittsburgh, at its southeast and southwest corners, respectively. The state's population is approximately 12.7 million, over half of which is concentrated in the Philadelphia and Pittsburgh metropolitan areas (Pennsylvania Governor's Center for Local Government Services 2010).

Pennsylvania's forest cover has undergone drastic change over the last several hundred years. Prior to European settlement, the state was predominantly forest; by the early 20th century, forest extent was between 20% (Wilson et al. 2012) and 35% (Cuff et al. 1989). By 2005, forests regenerated to cover 63.9% of the state, followed by agriculture (23.4%) and developed land (9.6%; Pennsylvania Governor's Center for Local Government Services 2010). Between 1992 and 2005, developed land in Pennsylvania more than doubled, despite population growth of only 4.5% (Pennsylvania Governor's Center for Local Government Services 2010). These increases in developed land come primarily at the expense of open land and agricultural land. Total forest cover has remained constant in the state for the past half-century, but forest cover is locally dynamic; i.e., forest to urban conversion is occurring at the same rate that agricultural land and open spaces are being afforested (Pennsylvania Governor's Center for Local Government Services 2010, Wilson et al. 2012).

2.2. Second Pennsylvania Breeding Bird Atlas

Data collection for the Second Pennsylvania Breeding Bird Atlas (2nd PBBA) occurred from 2004 to 2009. The state was divided into 57 regions from pages in the DeLorme Pennsylvania Atlas and Gazetteer (DeLorme 2003) and further subdivided into 4937 'blocks.' Blocks are defined as one-sixth of a standard U.S. Geological Survey 7.5 minute topographic map, and in Pennsylvania range from 23.9 to 24.8 square kilometers. Atlas volunteers were provided with field cards, a list of potential breeding species within each block, 'safe dates' in which to document breeding observations, and a detailed list of behaviors used to determine an observed individual's breeding category (i.e., confirmed, probable, possible, or simply observed). For each block, Atlas organizers encouraged a minimum of 25 hours of effort and provided volunteers with a target species richness. Additional surveys were completed for marsh birds, nocturnal birds, and species of conservation concern. Over the five-year Atlas effort, volunteers achieved complete coverage of all 4937 blocks and submitted records for 854,773 birds of 218 species.

Among other notable innovations, the 2nd PBBA also included 33,763 roadside point counts collected by seasonal staff in parallel with the volunteer-based atlas effort, resulting in the observation of 176 species by this method alone. O'Connell et al. (2004) designed 8-stop 'mini-routes' for each block by randomly generating 16 potential points within each block that were then moved to the nearest road (excluding highways and interstates), while maintaining a minimum 400m distance between points. In the event that a point was deemed unsuitable (e.g. not occurring on an actual road, unsafe to stop, excessive noise), it was skipped in favor of subsequent points, until observers had surveyed 8 points per block.

Point counts were conducted by staff between May 25 and July 4 from approximately 0500 to 1000 in suitable weather (i.e., little to no wind and precipitation). Each year, these observers were trained in the point count protocol and tested for hearing ability and song identification. Staff surveyed each point one time between 2004 and 2009. At each point, a single observer counted all birds detected in two distance bands (within and beyond a 75 m radius) for a total of 6 minutes and 15 seconds (divided into five equal 75-second time intervals). Individual singing males were tracked through time intervals. Observers also recorded ancillary local weather and habitat data at each point, e.g., wind speed, cloud cover, road type, and dominant habitat type. An exploratory survey of nine observers indicated 90% agreement in basic habitat identification (O’Connell et al. 2004).

2.3. Landscape Selection

From the total number of point count locations in the 2nd PBBA, I selected those that have ≥50% forest cover within a 200m radius (16563 counts; Figs. 1-2). Landscapes were defined as circular areas centered on selected point count locations. Because it would be impossible to determine the appropriate scale of response *a priori* for each species and it has been shown that scale affects the relative importance of habitat amount, habitat configuration, and matrix quality (Smith et al. 2011), I investigated a range of landscape scales (Brennan et al. 2002). Most studies investigating the effects of landscape structure on forest birds use circular landscapes of 1km radii or smaller with the justification that most species' dispersal distance is less than 1km (e.g., Labbe and King 2014, MacKay et al. 2014). However, a recent meta-analysis provided evidence that scale of effect studies are frequently conducted at suboptimal scales, and recommended that landscape structure be measured at a wider range and greater density of scales (Jackson and Fahrig 2015). Jackson and Fahrig (2015) also determined that the observed scale of effect was a median of 2.6 times larger than a species' territory radius. Therefore, I have chosen ten landscape radii (0.2, 0.5, 1, 2, 4, 6, 8, 10, 12, and 16 km) in order to have scales with a wide range (1.9 orders of magnitude) and high density (0.6 scales per km radius) that are predicted to contain the scale of effect for the species in this study. Landscapes that would not have had complete data (i.e., the distance from the point to the state border was less than the landscape radius) were later omitted. For example, for a point 1.2 km from the state border, I created only 0.2, 0.5, and 1 km radii landscapes.

2.4. Habitat Amount, Habitat Configuration, and Urbanization Intensity

I quantified forest amount and configuration metrics as indicators of habitat amount and habitat configuration from the National Land Cover Database 2006 raster (Fry et al. 2011; Fig. 2). I quantified forest amount as the total area of all forest classes in landscapes.

I assessed forest configuration using patch density and the clumpiness index metrics in FRAGSTATS v3 (hereafter, Fragstats; McGarigal et al. 2002). The clumpiness index measures the proportional deviation of the proportion of like cell adjacencies involving the focal class (here, forest) from that expected under a spatially random distribution (McGarigal 2014). The index ranges from -1 to 1, where -1 indicates a maximally disaggregated distribution, 0 indicates a random distribution, and 1 indicates a maximally clumped distribution (McGarigal 2014). Patch density is one of the more common habitat configuration metrics in the literature, while the clumpiness index metric is widely supported in the literature as a measure of fragmentation with low correlation to habitat amount that retains differentiability among landscapes (Neel et al. 2004, Cushman et al. 2008, McGarigal 2014, Wang et al. 2014).

Due to certain programming software compatibility limitations, I calculated the clumpiness index for each landscape using a square raster file containing the circular landscape within a specified background, meaning that the background data was included with the landscape data in the clumpiness calculation. Because part of the clumpiness index formula involves calculating the proportions of patch types in the landscape, all of the clumpiness index values are disproportionate by the same factor and could not be adjusted later. Therefore, only the relative values of the clumpiness index for each landscape should be considered.

I quantified urbanization intensity as the first one or two components of a principal component analysis (PCA) of the areas of landscapes composed of the four developed land covers and the average population density and housing density in landscapes (Table 3, Fig. 3). PCA is a common variable reduction method when quantifying urbanization (e.g., du Toit and Cilliers 2011). I obtained developed land cover data from NLCD 2006, and block-level population and housing count data from the 2010 Census (U.S. Census Bureau 2015). There are 421,545 Census blocks in Pennsylvania, meaning that the mean block area is 0.283 km^2, or roughly double the size of my smallest landscape scale. I used the ‘isectpolypoly’ tool in the Geospatial

Modelling Environment GUI platform to calculate area-weighted average values of population density and housing density for each landscape (Beyer 2015).

At the 200m and 500m scales, two components had eigenvalues greater than one and explained 62 and 76 percent of the total variance (Fig. 3). At each scale ranging from 1km to 16km, one component had an eigenvalue greater than one and explained 67 to 90 percent of the total variance at each scale. Accordingly, the first component was included as a parameter in models at all scales, and the second component was only included in models for the 200m and 500m scales.

The first component of the urbanization intensity PCA (Table 1; hereafter referred to as urbanization intensity) was strongly negatively correlated (r>-0.90) with population and housing density at every scale (Fig. 3). Urbanization intensity was also strongly negatively correlated (r>-0.69) with the area of low developed intensity land cover at all scales, as well as with the other three developed land covers at scales 2km and greater (r>-0.70). The second component of the urbanization intensity PCA (Table 1; hereafter referred to as urbanization intensity 2) was strongly negatively correlated with the area of high intensity developed land cover (r>-0.74) at the 200m and 500m scales (Fig. 3). Because both variables describing urbanization intensity were negatively correlated to the original measures of urbanization intensity that were input into the PCA, I reverse the direction of their impacts when describing their effects for the sake of clarity.

Because agricultural intensity is also an aspect of matrix quality, I quantified agriculture amount as the area of cultivated crop and pasture/hay land covers in each landscape in order to separate the effects of urbanization intensity from agricultural intensity (Fry et al. 2011).

2.5. Other Predictor Variables

I included two indicators of local habitat quality in models from ancillary data collected by staff during point counts (Fig. 2). These two indicators were evidence of recent or active local land use change at the time of the count, and dominant habitat type within 75m of the point count at each point count location.

I included land cover heterogeneity as a variable that accounts for aspects of landscape structure not described above (Fig. 2). Land cover heterogeneity was quantified as the first one or two components of a PCA of elevation mean and range within each landscape, Shannon's diversity index of all the classes within each landscape, and contrast-weighted edge density for all forest-developed edges within each landscape. I obtained a 3.2ft Digital Elevation Model from the PAMAP Program (PA DCNR 2006), then resampled this raster to 30m resolution and used the 'ZonalStatsOverlappingPolys' geoprocessing tool to calculate the mean and range of elevation for each landscape (Clark 2012).

I used Fragstats to measure Shannon's diversity index (SHDI) to quantify the diversity of classes within each landscape (McGarigal et al. 2002). SHDI indicates the magnitude of 'information' in each landscape as the negative sum of the proportional abundance of each patch type multiplied by that proportion, across all patch types, for each landscape (McGarigal 2014). SHDI can range from 0 to infinity.

I also calculated the contrast-weighted edge density (CWED) of all forest-developed edges within each landscape using Fragstats. This index evaluates the functional significance of edge by incorporating both edge density and user-provided edge contrast to standardize edge contrast per unit area in a landscape (McGarigal 2014).

Edges between forest class patches and developed class patches were weighted to 1 (the maximum); all other edge combinations were weighted to 0. CWED is calculated by summing the lengths of each edge segment in the landscape multiplied by the appropriate contrast weight, divided by the total landscape area. This calculation results in a value with units of meters per hectare.

I included several variables as linear predictors in models to control for bird detectability. These four variables were derived from ancillary data collected by staff during point counts, and were the observer code for each point count and the start time, day of year, and year at which the point count occurred (Fig. 2).

2.6. Response Variables

From the 176 species observed at point counts, I excluded species that met the following criteria: 1) hybrid species; 2) irregular breeder in the state; 3) raptors; 4) waterfowl; 5) occurred at <30 forest point count locations. This resulted in a selection of 101 species that were observed at 16563 point counts (Table 2, Fig. 2). From that subset, I selected two species for occurrence analysis: American Robin (*Turdus migratorius*) as a representative of a generalist species, and Scarlet Tanager (*Piranga olivacea)* as a representative of a forest specialist species.

I measured five response variables: total bird abundance, species richness, species evenness, American Robin occurrence, and Scarlet Tanager occurrence at each point count. I estimated an index of total abundance across all species for each point by summing the number of individuals observed at each count. Occurrence of each species at each point is a binary indication of whether the species was present or absent at the time of a point count.

I also estimated species richness and evenness at each point. I generated the Chao1 estimation of species richness using the ‘fossil’ package in R. Chao1 is a non-parametric estimation of the true species richness based on the number of rare species observed (Chao 1984, Colwell and Coddington 1994). This estimator performs well when most observations are relatively rare species, as is commonly the case for point counts (Chao 1984). To determine species evenness, I used the R package ‘asbio’ to estimate Pielou’s evenness index at each point count.

2.7. Analyses

I used generalized linear modeling and a multi-model inference approach to test for the relative effects of forest amount, forest configuration, and matrix quality, controlling for local habitat attributes, landscape heterogeneity, observer, year, day of year, and start time, on total abundance, species richness, species evenness, American robin occurrence, and Scarlet tanager occurrence for multiple landscape scales. The inverse of species evenness was used in models to meet assumptions of homoscedasticity. All variables were standardized to a mean of 0 and a standard deviation of 1. Variables were apportioned for modeling by scale; i.e. variables measured at different scales did not appear in models together.

I used Akaike Information Criterion (AIC) to evaluate models that contained all explanatory variables singly and all possible combinations of two or more explanatory variables using marginal (Type III) sums of squares (Akaike 1973). I compared standardized partial effect sizes for the best models to elucidate the true relative effects of my landscape variables of interest (Smith et al. 2009). I checked a random subselection of two models from each set to ensure that assumptions of normality and homoscedasticity were met. For logistic regression models, I performed Hosmer-Lemeshow tests to assess goodness-of-fit for a random subselection of two models from each set. I performed analyses in R, version 3.2.1 (R Core Team 2015).

I calculated model-averaged standardized partial effect sizes for the explanatory variables present in the best models (Δ_i≤2), and used unconditional variances to calculate their standard errors (Burnham and Anderson 2002). I also calculated relative variable importance (RVI) for each explanatory variable by summing the Akaike weights of the best models in which a variable was included (Burnham and Anderson 2002). I interpreted RVI values as the relative strength of evidence of the explanatory importance of parameter estimates, whereby parameters with RVI values <0.50 have no evidence of explanatory importance, and parameters with RVI values 0.50-0.75, 0.75-0.99, and >0.99 have respectively weak, strong, and very strong evidence of explanatory importance (Gagné et al. 2016).

I re-calculated Δ_i and weights for all of the best models (Δ_i≤2) from all scales together for each response variable to determine the overall independent relative effects of forest amount, forest fragmentation, and urbanization intensity on abundance, species richness, species evenness, American robin occurrence, and Scarlet tanager occurrence.

CHAPTER 3: RESULTS

3.1. Abundance

When models from all scales were evaluated together, seven models containing variables measured within a 200m radius qualified as the top models explaining bird abundance at point counts (Table 3). There was very strong evidence that agriculture amount, forest clumpiness, and urbanization intensity were important predictors of bird abundance (Table 4). There was no evidence that forest amount, forest patch density, or either component of urbanization intensity were important predictors of abundance. Effect sizes from these models indicated that agriculture amount had the largest effect on bird abundance, followed by forest clumpiness and urbanization intensity (Fig. 4). Agriculture amount and urbanization intensity had positive effects, and forest clumpiness had a negative effect.

When models were considered for individual scales, there were between two and five top models explaining abundance at each scale. There was a general pattern that agriculture amount and forest clumpiness had the largest effects at the smaller scales, whereas agriculture amount and forest amount had the largest effects at larger scales (Fig. 5). For all scales at which there was evidence that a variable was an important predictor of abundance, agriculture amount, forest amount, and urbanization intensity had positive effects, and forest clumpiness and patch density had negative effects.

3.2. Richness

When models from all scales were evaluated together, ten models containing variables measured with a 1km radius qualified as the top models explaining bird species richness at point counts (Table 3). There was very strong evidence that agriculture amount and forest clumpiness were important predictors (Table 4). There was also weak evidence that forest amount was an important predictor. There was no evidence that forest patch density or urbanization intensity were important predictors of bird species richness. Effect sizes from these models indicated that agriculture amount had the largest effect on species richness, followed by forest clumpiness and forest amount (Fig. 4). Agriculture amount and forest amount had positive effects on richness, whereas forest clumpiness had negative effects.

When models were considered for individual scales, there were between six and twelve top models explaining species richness at each scale. There was a general pattern than agriculture amount and forest clumpiness had the largest effects on richness at the smaller scales, whereas forest clumpiness and patch density had the largest effects at larger scales (Fig. 6). For all scales at which there was evidence that a variable was an important predictor of species richness, agriculture amount had a positive effect and forest clumpiness and patch density had negative effects. Forest amount had positive effects at scales ≤8km and negative effects at scales ≥10km.

3.3. Evenness

When models from all scales were evaluated together, nineteen models containing variables measured within a 6km radius qualified as the top models to explain bird species evenness at point counts (Table 3). There was very strong evidence that forest amount was an important predictor (Table 4). There was strong evidence that agriculture amount and forest clumpiness were also important predictors. There was no evidence urbanization intensity or forest patch density were important predictors of evenness. Effect sizes from these models indicated that forest amount had the largest effect on species evenness, followed by agriculture amount, forest clumpiness, and urbanization intensity (Fig. 4). All four of these predictors had negative effects on species evenness.

When models were considered for individual scales, there were between seven and forty-four top models top models explaining species evenness at each scale. There was a general pattern that forest amount had the largest effect on species evenness at most scales (Fig. 7). For all scales for which there was evidence that a variable was an important predictor of evenness, urbanization intensity and forest amount, clumpiness, and patch density had negative effects. Agriculture amount had negative effects at all scales but 2km.

3.4. American Robin Occurrence

American robins occurred at 41.5% of point counts evaluated. When models from all scales were evaluated together, ten models containing variables measured within a 200m radius qualified as the top models to explain American robin occurrence at point counts (Table 3). There was very strong evidence that forest amount, agriculture amount, urbanization intensity 1 and 2, and forest clumpiness were important predictors (Table 4). There was no evidence that forest patch density was an important predictor of occurrence for this species. Effect sizes from these models indicated that urbanization intensity had the largest effect on American robin occurrence, followed by agriculture amount, forest amount, forest clumpiness, and urbanization intensity 2 (Fig. 4). Agriculture amount and urbanization intensity had positive effects on robin occurrence; urbanization intensity 2, forest amount, and forest clumpiness had negative effects.

When models were considered for individual scales, there were between two and nine top models explaining American robin occurrence at each scale. There was a general pattern that urbanization intensity had the largest effects at the smallest scales, and forest clumpiness had the largest effects at larger scales (Fig. 8). For all scales for which there was evidence that a variable was an important predictor of occurrence, agriculture amount and urbanization intensity had positive effects and urbanization intensity 2 and forest clumpiness had negative effects. Forest amount had positive effects at all scales but 200m, and patch density had negative effects at all scales but 1km.

3.5. Scarlet Tanager Occurrence

Scarlet tanagers occurred at 33.0% of all point counts evaluated. When models from all scales were evaluated together, ten models containing variables measured within a 500m radius qualified as the top models to explain Scarlet tanager occurrence at point counts (Table 3). There was very strong evidence that forest amount, agriculture amount, urbanization intensity, and forest patch density were important predictors (Table 4). There was also weak evidence that urbanization intensity 2 was an important predictor. There was no evidence that forest clumpiness was an important predictor of occurrence for this species. Effect sizes from these models indicated that urbanization intensity 1 had the largest effect on Scarlet tanager occurrence, followed by forest amount, forest patch density, agriculture amount, and urbanization intensity 2 (Fig. 4). Forest amount and urbanization intensity 2 had positive effects; forest patch density, agriculture amount, and urbanization intensity had negative effects.

When models were considered for individual scales, there were between four and thirteen top models explaining Scarlet tanager occurrence at each scale. There was a general pattern that urbanization intensity had the largest effect at smaller scales, and forest amount and agriculture amount had the largest effects at larger scales (Fig. 9). For all scales at which there was evidence that a variable was an important predictor, forest amount and urbanization intensity 2 had positive effects, and forest patch density had negative effects. Urbanization intensity had negative effects at scales ≤6km, and positive effects at scales ≥8km. Agriculture amount had positive effects at all scales but 2km, and forest clumpiness had positive effects at all scales but 200m.

3.6. Other Predictor Variables

Though only the variables of interest are discussed further, additional predictor variables describing dominant habitat type within 75m of each point count, the first two components of a PCA of landscape heterogeneity variables, and variables to control for detectability appeared in many top models. The following predictor variables had RVIs of 1 in the model-averaged regression formula from all scales combined for each response variable, but in all cases the effect sizes of these additional variables were relatively low compared to the variables of interest. Dominant habitat type appeared in models describing abundance, American robin occurrence, and Scarlet tanager occurrence. The first component of landscape heterogeneity appeared in models describing abundance and species richness. The second component of landscape heterogeneity appeared in models describing abundance, species evenness, species richness, and Scarlet tanager occurrence.

CHAPTER 4: DISCUSSION

I hypothesized that habitat amount would be the strongest determinant of biodiversity, followed by matrix quality and habitat configuration. However, this pattern occurred only for species evenness (Fig. 10). Instead, matrix quality in the form of agriculture amount had the largest effects on bird abundance and species richness, followed by forest configuration as indicated by forest clumpiness (Fig. 10). Occurrence of both the generalist species (American robin) and forest specialist species (Scarlet tanager) were best predicted by the same pattern, which was also not the pattern that was hypothesized. Instead, matrix quality in the form of urbanization intensity had the largest effect on occurrence for each species, followed by habitat amount and forest configuration (Fig. 10). Therefore, of the three elements of landscape structure that I investigated, matrix quality was the most influential predictor of diversity as well as occurrence for two species.

These results differ from other studies that have investigated the relative effects of habitat amount, habitat configuration, and matrix quality on passerine birds. Radford and Bennett (2007) and Smith et al. (2011) found that habitat amount was a stronger determinant of bird diversity than matrix quality. Some differences among our studies that may account for the disparate relative order of effects are the scales at which landscape structure were measured, the land use histories of the study areas, and the indicators of matrix quality analyzed. Scale is known to affect the relative order of variable importance, so the small range and density of scales measured in these studies relative to mine may have been inadequate for achieving the true scale of effect (Jackson and Fahrig 2015). Both of these studies also occurred in landscapes with significantly less remnant forest habitat than Pennsylvania, and there is evidence that there are thresholds of habitat amount at which the relative order of importance of landscape structure variables changes (Radford et al. 2005). Finally, the way each study defined and measured matrix quality obviously impacted its ranking in order of importance; this is discussed in more detail with respect to species richness below.

Several studies that investigated the relative effects of habitat amount and matrix quality for taxa other than passerines have reported that matrix quality is the most important predictor. In landscapes dominated by a matrix of rice fields, Guadagnin and Maltchik (2007) found that matrix quality was the strongest determinant of waterbird species richness in wetland habitat patches, followed by wetland patch amount. Brady et al. (2011) found that matrix attributes were the most important predictors of mammal species richness in landscapes with low levels of habitat amount. Similarly, Eigenbrod et al. (2008) found that matrix quality effects on anurans were larger than those of habitat amount.

I found that habitat configuration generally has the smallest effects on forest birds of the three elements of landscape structure investigated, which is consistent with the results of other studies comparing these relative effects on various groups of organisms (Radford and Bennett 2007, Guadagnin and Maltchick 2007, Quesnelle et al. 2013, Fahrig 2001).

Although the results from the top models from all scales combined were not in accord with my hypothesis, top models from some larger individual scales of each response variable were. For example, the hypothesized pattern of habitat amount > matrix quality > habitat configuration held true for abundance at scales ≥4km (Fig. 5), for species evenness at scales ≥4km (Fig. 7), and for Scarlet tanager occurrence at scales ≥8km (Fig. 9). This pattern is consistent with that found by Radford and Bennett (2007) for woodland birds in an agricultural matrix. The relative order of importance of predictor variables was also different among the top models from combined scales and larger individual scales for both species richness and American robin occurrence. For example, habitat configuration had the largest effect of all the predictor variables on species richness at scales ≥4km (Fig. 6) and on American robin occurrence at scales ≥6km (Fig. 8). No other empirical study has reported this result, but Cushman (2012) did find that habitat configuration was the strongest determinant of the ecological process of genetic differentiation via simulation modeling. There are several examples of multi-scale studies indicating that species-landscape relationships vary with the scale at which landscape structure is measured (Jackson and Fahrig 2015).

4.1. Abundance

Models containing predictor variables measured within 200m of point counts were the top models explaining bird abundance at point counts. At this scale, there was no evidence that forest amount was an important predictor of species richness. However, due to the selection process by which I chose forested point count locations, 200m landscapes contained a minimum of 50% forest cover. This suggests that the order of relative importance of predictor variables (matrix quality > habitat configuration > habitat amount) is only applicable to landscapes that already have ≥50% habitat cover. There was strong evidence in models at all scales >200m that forest amount was an important predictor of bird abundance, and it was the most influential predictor at the largest scales I investigated (10-16km). At all of these scales, forest amount had a positive effect on forest breeding bird abundance (Fig. 5).

At the 200m scale, agriculture amount had the largest impact on forest bird abundance (Fig. 5). This was true despite there being a relatively small proportion of agriculture cover on average in the landscapes at this scale (mean 6% with a range of 0-50%). Agriculture amount had a positive effect on forest breeding bird abundance at all scales. In contrast, the only study to date that has compared the effects of urbanization intensity and agricultural intensity in the matrix on forest breeding birds found that both low and high intensity agriculture at scales ranging from 200m to 5km had negative effects on abundance (Dunford and Freemark 2005). The 200m radius landscapes in their study were on average approximately 82% forest cover, which is very similar to the mean 78% forest cover in my 200m landscapes. However, their study area was a region with just 24% forest cover that was instead dominated by agricultural and urban land uses, unlike my study area with 64% forest cover. Though my analysis did not quantify any aspect of agricultural intensity, the differences between our results suggest that there may be a threshold of agriculture amount and intensity below which agriculture has positive effects on forest breeding bird abundance. It may also be possible that agriculture practices vary among the state of Pennsylvania and Ontario to the extent that agriculture has different impacts on forest breeding bird abundance in these regions.

At the 200m and 500m scales, forest clumpiness had a larger effect on bird abundance than forest amount; at scales ≥1km, the opposite relationship was found (Fig. 5). At all scales, forest clumpiness had a negative effect on bird abundance, indicating that more fragmented forest habitat contributes to higher forest breeding bird abundance. Though it seems counterintuitive, more than half of the published effects of fragmentation *per se* are positive (Fahrig 2003). There are several suggested mechanisms by which fragmentation may have a positive effect on bird abundance, but these mechanisms are overshadowed by the fact that that the effects of habitat amount are generally much larger than the effects of habitat configuration regardless (Fahrig 2003). This was the case for my landscapes with radii ≥1km.

Of our five predictor variables, urbanization intensity ranked third or fourth in magnitude of effect on forest breeding bird abundance, depending on scale (Fig. 5). The effects of urbanization intensity on abundance were positive at all scales. Though increases in bird abundance with urbanization are supported in the literature (Lepczyk et al. 2008, McKinney 2006), this relationship is typically explained by the process of replacement of native specialist species with native generalist and introduced species in urban areas (Gagne and Fahrig 2011). My analysis included non-native species, but there is some evidence that the positive relationship I found between urbanization intensity and forest breeding bird abundance is also driven by the replacement of forest specialist species with generalist species in Pennsylvania landscapes that have a low to intermediate degree of urbanization intensity (mean 13%, range 0-50%) . For example, when I determined the effects of urbanization intensity on species occurrence for a generalist (American robin) and a forest specialist (Scarlet tanager), urbanization intensity had a positive effect on the generalist's occurrence and a negative effect on the forest specialist's occurrence.

4.2. Richness

Agriculture amount had a positive effect on richness at all scales, which is a different result from that of another study that found the agricultural matrix within a 5km radius had no significant impacts on forest breeding bird species richness (Dunford and Freemark 2005). The best models from all scales combined indicated that models containing variables measured within 500m best explained species richness, and effect sizes indicated agriculture amount had the largest effect on richness, followed by forest configuration and forest amount (Fig. 6). Smith et al. (2011) investigated the relative effects of habitat amount, habitat configuration, and matrix quality on fragmentation-sensitive bird species richness, and found a different pattern than I did at the 500m scale; in their models, forest configuration had the largest effect, followed by forest amount and matrix quality. They also found that at larger scales (1-10km radii), forest amount had the largest effects on fragmentation-sensitive bird species richness, whereas effect sizes from my top models at these scales indicated that habitat configuration and matrix quality variables had larger effects on species richness (Fig. 6).

These differences in the patterns of order of relative importance of variables could be due to differences in predicting overall forest breeding bird species richness (herein, n=101 species) to fragmentation-sensitive species richness (Smith et al. 2011, n=13 species). However, Smith et al. (2011) explicitly discuss being unable to quantify agricultural intensity as an element of matrix quality, despite it being the dominant matrix type in their landscapes. Instead, they quantified road density as their representation of matrix quality, and concluded that matrix quality generally had weak effects that did not change with scale. Likewise, there was no evidence in any of my models at any scale that urbanization intensity as an element of matrix quality was an important predictor of species richness. Smith et al. (2011) suggest that their analysis may underestimate the absolute importance of matrix quality, and my results suggest that agriculture amount could be an important but overlooked element of matrix quality that can have large effects on species richness. Furthermore, my results concur with those of Smith et al. (2011) in that forest configuration, at least at some scales, has a larger effect on species richness than forest amount.

4.3. Evenness

Models containing predictor variables measured within 6km of point counts were the top models explaining forest breeding bird species evenness at point counts; at this scale, forest amount had the largest effects on species evenness, followed by agriculture amount, forest clumpiness, and urbanization intensity (Fig. 7). All of these predictor variables had negative effects at this scale, and the same relative order and direction of variables held true for the top models of all individual scales ≥4km. Urbanization decreases species evenness by differentially affecting the abundances of synanthropic and specialist species (Donnelly and Marzluff 2006), but it is surprising that forest amount also had a negative impact on species evenness, particularly given that it had the largest effect of all predictors (Fig. 7) . This suggests that the amount of forest cover affects the forest breeding bird species in this study differently, and that some species benefit more from forest than others. It is possible that this effect has to do with my simplistic designation of forest breeding bird species that does not take into account the spectrum of forest habitat preferences that bird species are typically categorized by (e.g., forest interior vs. forest edge; Kennedy et al. 2010). Radford and Bennett (2007) also found that individual species within their ‘woodland-dependent’ bird assemblage responded differently to landscape structure, by exhibiting different patterns of the relative order of importance of predictor variables. In response to this finding, Radford and Bennett (2007) called for the use of empirical data, rather than expectations or ecological characteristics, to formulate new species groups in future work. Implementing this approach would likely clarify the relative effects of forest amount, forest configuration, and matrix quality on forest bird evenness.

4.4. American Robin Occurrence

Models containing predictor variables measured within 200m of point counts were the top models explaining American robin occurrence at point counts. At this scale, matrix quality variables had the largest effect on occurrence, followed by habitat amount and habitat configuration (Fig. 8). Minor and Urban (2009) found that road density was a more important predictor than edge proximity for edge species in landscape scales ranging from a 150m to 3km radius, which is in accord with my finding that urbanization intensity had the largest effect on American robin occurrence at scales ≤2km.

At scales larger than 6km, habitat configuration in the form of forest clumpiness was the largest predictor of American robin occurrence. At all scales, forest clumpiness had a negative effect, indicating that American robins prefer less aggregated forest within a matrix of urban and/or agricultural land uses. These results are consistent with the American robin’s common classification as an edge species (Ehrlich et al. 1988) and the results of other studies conducted on the relative importance of landscape-scale variables on edge species. Minor and Urban (2009) suggested that many species classified as edge species may find edge more meaningful at larger scales; i.e., they prefer fragmented landscapes but do not always prefer to establish territories adjacent to edges. This explanation fits well with my finding that habitat configuration is more important to American robin occurrence at larger scales, while urbanization intensity is more important at smaller scales.

4.5. Scarlet Tanager Occurrence

My results did not entirely support the classification of Scarlet tanager as a fragmentation-sensitive species (Smith et al. 2011, Ehrlich et al. 1988); i.e., there was no evidence that forest clumpiness was an important predictor of occurrence. Forest amount had a relatively large positive effect on Scarlet tanager occurrence, and forest patch density did have a negative effect, potentially suggesting that Scarlet tanagers prefer fewer, larger patches of forest (Fig. 9). However, there was no evidence at most scales that forest clumpiness was an important predictor of Scarlet tanager occurrence (Fig. 9). Furthermore, Scarlet tanager occurrence was most strongly, and negatively, impacted by urbanization intensity. At scales ≥4km, agriculture amount also had a relatively large negative effect on Scarlet tanager occurrence. From these results, it is apparent that Scarlet tanager occurrence is most strongly influenced by matrix quality and habitat amount, and less so by forest configuration.

4.6. Scale of Effect

Despite providing an adequate range and density of scales as suggested in a recent review of scale of effect (Jackson and Fahrig 2015), abundance and American robin occurrence both had apparent scales of effect that were the smallest scale measured. This phenomenon indicates that the true scale of effect for these responses is likely even smaller (Jackson and Fahrig 2015). American robins have territory areas ranging from

0.04 to 0.84 ha (The Birds of North America Online 2015), suggesting the predicted scale of effect for their occurrence would be at most approximately 5.7 ha (Jackson and Fahrig 2015). This predicted area is far smaller than the smallest landscape scale I measured (200m radii, or 12.56 ha). Such small scales of effect for some species will preclude the use of commonly utilized remotely sensed datasets for landscape measurements because their resolution is too poor. For example, the NLCD raster has a resolution of 30m, meaning one pixel represents 0.09 ha. While it is possible to measure smaller landscape scales from this dataset, it is likely that this resolution is too coarse for some species in my assemblage that could have scales of effect equivalent to just a few pixels.

Furthermore, there is a strong rationale for not measuring landscapes smaller than the 200m scale measured here. Though a bird’s territory is often smaller than the 200m scale, it is not possible for a point count location and the territories of the birds present to overlap perfectly, e.g. for a point count within a 50m landscape, many bird detections would occur from beyond the 50m radius. In this case, attempts to capture the scale of effect by further reducing the landscape scale would thus result in false precision.

4.7. Conclusions and Future Work

My species selection, and thus the species assemblage results, are affected by sampling bias stemming from the roadside point count methodology. Roadside surveys can sample land cover types in different proportions than they occur in the surrounding region, resulting in sampling bias that differs among species (Harris and Haskell 2007). Furthermore, the detectability of the birds present may differ at roads versus in the same habitat away from the road, e.g., gregarious species associated with open landscapes are easier for observers to detect than forest birds, whose appearance and vocalizations can be stifled by forest cover (Ralph et al. 1995). Despite having chosen species on the basis of their occurrence at point counts in ≥50% forest cover during the breeding season, my bird species selection is clearly more varied than purely forest breeding birds: e.g., the admittance of Bobolink, a grassland breeding bird (Table 2). Unintentional inclusion of non-forest birds may be a partial explanation of the strong positive effects of agriculture amount and urbanization intensity on putative forest bird abundance and species richness. However, the degree to which roadside sampling biases the presence and detectability of species may be negligible, particularly when sample sizes are large (McCarthy et al. 2012, Ralph et al. 1995).

If the species assemblage herein is representative of forest birds, agriculture amount may be an important component of matrix quality contributing to forest breeding bird diversity, at least when landscapes are already majority forest. This result supports the landscape mosaic perspective, which recognizes the matrix as a gradient (rather than unequivocal non-habitat) with many potential roles (Kupfer et al. 2006). Some of these roles include providing resource supplementation or compensation, as well as altering functional connectivity, disturbance regimes, or microclimate (Kupfer et al. 2006). In particular, the matrix can serve as supplementary habitat and provide additional food sources (Brady et al. 2011, Kennedy et al. 2010). For example, Kennedy et al. (2010) found that bird species traits related to resource use best predicted species responses to the matrix in highly fragmented landscapes, e.g. omnivores and granivores were more abundant in habitats within an agricultural matrix. It will take more research to determine the mechanisms by which forest birds in Pennsylvania landscapes are benefiting from the agricultural component of the matrix, but resource supplementation appears to be a strong possibility.

Although the intermediate levels of urbanization intensity in Pennsylvania appear to be less important to forest bird diversity than other aspects of landscape structure investigated here, it is evident that urbanization is strongly impacting bird communities. It was particularly surprising that there was no evidence in any of the top models that urbanization intensity had an effect, positive or negative, on species richness. The same phenomenon was documented when urban and rural bird communities along an urban-rural gradient in North Carolina were examined (Minor and Urban 2009). Forest bird species richness was not different among the two communities, but each community rather contained a different set of native species; this may also be the case in Pennsylvania landscapes (Minor and Urban 2009).

This research marks the first time that the independent effects of urbanization intensity on forest breeding birds have been ranked in order of importance with two other well-supported predictors of bird diversity, habitat amount and habitat configuration. These effects are not yet fully understood and represent a significant knowledge gap in the literature.

From a pragmatic standpoint, the results of this research should be useful to inform decision-makers of the independent relative impacts of forest amount, forest configuration, and urbanization intensity on local biodiversity, as well as on the occurrence of individual species of interest. Decision-makers typically have limited knowledge and resources, so identifying and focusing on dominant processes is crucial so that efficient and effective biodiversity management action planning can be taken to mitigate further losses. This research suggests the relative prioritization of three somewhat manageable aspects of landscape structure towards biodiversity goals, which should lead to the formation and application of simple management frameworks (e.g., Gagné et al. 2015).

While it remains essential to focus first on retaining the extent of forest amount in Pennsylvania landscapes, my results suggest that modifications to the urban and agricultural matrix surrounding forest patches will have more influence on forest birds than attempts to alter forest amount or configuration. Some general suggestions for land managers to benefit forest birds include encouraging conversion to forest or agriculture over residential development or other more intensive uses, being cognizant of different effects at different scales occurring simultaneously, and aiming for vegetative complexity in the matrix. For example, there may be value in retaining or planting even seemingly small or poorly-configured patches of trees within agricultural and urban landscapes to improve matrix quality from the prospective of forest breeding bird species.

The results of this research are particularly pertinent to understanding how Pennsylvania’s forest birds might be affected by Marcellus shale natural gas mining, which has flourished in Pennsylvania since 2004 (Drohan et al. 2012). The Marcellus shale formation underlies approximately two-thirds of the state of Pennsylvania, and is believed to be one of the largest unconventional shale gas reserves in the world in terms of both area and potential gas volume (Johnson 2010). Shale gas development involves drilling wells that descend vertically 1.5km or more, then horizontally up to 1.5km, into the target shale stratum (Kiviat 2013, Johnson 2010). Water mixed with chemicals and physical proppants is forced into the shale at high pressure to fracture and then hold open spaces that allow natural gas to flow into the well for extraction (Kiviat 2013). One or more wells are drilled from a focal well pad, and each installation has associated access roads, pipelines, and storage areas for water, chemicals, sand, and wastewater (Kiviat 2013). It is projected that by 2030 there will be 60,000 wells across the state, resulting in the clearing of as many as 90,000 acres of forest (Drohan et al. 2012, Johnson 2010). Though any loss of forest cover will likely negatively impact forest birds, it seems unlikely that the independent effects of this degree of forest loss (<1% of current forest cover) due to shale gas development will drastically impact Pennsylvania birds.

In addition to forest loss, shale gas development is expected to result in significant forest fragmentation by well pads, pipelines, and roads (Kiviat 2013). As additional well pads are permitted, they occur further from pre-existing roads, meaning that hundreds of kilometers of new roads are also expected to be developed (Drohan et al. 2012). Though my results suggest that forest configuration is less important to forest birds than other factors, landscape fragmentation from shale gas development will almost certainly have negative impacts on birds.

The largest impacts of shale gas development on forest birds will likely occur via markedly reduced matrix quality in landscapes containing mining installations. One of the reputed benefits of horizontal drilling is that it theoretically offers more flexibility in the placement of new well pad and infrastructure development relative to important natural habitats, such as forest patches (Johnson 2010). Accordingly, as of 2011, more existing and permitted well pads in Pennsylvania occurred on agricultural cover (62% and 54% respectively) than forest cover (38% and 45% respectively; Drohan et al. 2012). Shale gas mining installations in the matrix also have the potential to cause tremendous disturbance in forest habitats through various forms of pollution: continuous loud noise and bright light, increased human presence and road traffic, and toxic synthetic chemicals, salt, and radionuclides (Kiviat 2013). Of the three elements of landscape structure that I investigated - habitat amount, habitat configuration, and matrix quality - matrix quality was the most influential predictor of diversity as well as occurrence for two species. Because shale gas mining and development reduce matrix quality in Pennsylvania landscapes, it seems highly probable that this growing industry will have significant negative impacts on Pennsylvania's forest birds.

Beyond investigating the specific impacts of Marcellus shale gas mining and development on Pennsylvania's birds, there are several potential avenues of future work suggested by the results herein. Because it is currently difficult to generalize the responses of functional groups of bird species to landscape change (Radford and Bennett 2007), it would be useful to conduct analyses of the relative effects of habitat amount, habitat configuration, and matrix quality on the occurrence of additional species in my forest bird assemblage to establish new species groups based on their pattern of variable effect order. It would then be possible to run the analyses discussed in this thesis for these groups across landscapes around all point counts, or across all landscapes within some minimum urban cover, to gain further understanding of how land use and land cover change will affect biodiversity.

In order to advance understanding of the mechanisms by which matrix quality affects avian biodiversity, a second goal for future work would be to determine the influence of certain species traits on the impacts of urbanization intensity for individual bird species. Matrix quality has been hypothesized to affect biodiversity in remnant habitat through four primary mechanisms, but the species traits upon which these potential mechanisms act to govern species-specific responses to matrix quality have not yet been determined (Kennedy et al. 2010).

A final line of future research should investigate the relative impacts of landscape structure for other taxa at relevant scales, as it has been demonstrated that the responses of birds to certain components of landscape structure may not be representative of all taxa (e.g., urbanization differentially affects birds and ground beetles, Gagné and Fahrig 2011). Large, spatially-explicit datasets from forthcoming ventures such as the Pennsylvania Amphibian and Reptile Survey (PARS) and the North American Bat Monitoring Program (NABat) have the potential to be invaluable in this regard.

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APPENDIX A: TABLES

Table 1: Descriptions of explanatory variables of interest used in predictive models.

Variable	Description
Forest amount	
Forest amount	The sum of deciduous, evergreen, and mixed forest cover
Forest configuration	
Forest clumpiness	Clumpiness index for summed forest cover
Forest patch density	Patch density of summed forest cover
Matrix quality	
Urbanization intensity	First component of urbanization intensity PCA
Urbanization intensity 2	Second component of urbanization intensity PCA
Agriculture amount	Sum of pasture/hay and cultivated crop cover

Table 2: 101 species observed at forested point counts, excluding hybrids, irregular breeders in the state, raptors, waterfowl, and species with <30 records.

Common Name	Scientific Name
Acadian Flycatcher	*Empidonax virescens*
Alder Flycatcher	*Empidonax alnorum*
American Crow	*Corvus brachyrhynchos*
American Goldfinch	*Spinus tristis*
American Redstart	*Setophaga ruticilla*
American Robin	*Turdus migratorius*
Baltimore Oriole	*Icterus galbula*
Barn Swallow	*Hirundo rustica*
Black-and-white Warbler	*Mniotilta varia*
Black-billed Cuckoo	*Coccyzus erythropthalmus*
Blue-gray Gnatcatcher	*Polioptila caerulea*
Brown-headed Cowbird	*Molothrus ater*
Blue-headed Vireo	*Vireo solitarius*
Blackburnian Warbler	*Setophaga fusca*
Blue Jay	*Cyanocitta cristata*
Bobolink	*Dolichonyx oryzivorus*
Brown Creeper	*Certhia americana*
Brown Thrasher	*Toxostoma rufum*
Black-throated Blue Warbler	*Setophaga caerulescens*
Black-throated Green Warbler	*Setophaga virens*
Blue-winged Warbler	*Vermivora cyanoptera*
Carolina Wren	*Thryothorus ludovicianus*
Canada Warbler	*Cardellina canadensis*
Cedar Waxwing	*Bombycilla cedrorum*
Cerulean Warbler	*Setophaga cerulea*
Black-capped Chickadee	*Poecile atricapillus*
Carolina Chickadee	*Poecile carolinensis*
Chipping Sparrow	*Spizella passerina*
Chimney Swift	*Chaetura pelagica*
Common Grackle	*Quiscalus quiscula*
Common Raven	*Corvus corax*
Common Yellowthroat	*Geothlypis trichas*
Chestnut-sided Warbler	*Setophaga pensylvanica*
Dark-eyed Junco	*Junco hyemalis*
Downy Woodpecker	*Picoides pubescens*
Eastern Bluebird	*Sialia sialis*
Eastern Kingbird	*Tyrannus tyrannus*
Eastern Meadowlark	*Sturnella magna*
Eastern Phoebe	*Sayornis phoebe*
Eastern Towhee	*Pipilo erythrophthalmus*
Eastern Wood-Pewee	*Contopus virens*
European Starling	*Sturnus vulgaris*

Table 2 (continued)

Field Sparrow	*Spizella pusilla*
Great Crested Flycatcher	*Myiarchus crinitus*
Golden-crowned Kinglet	*Regulus satrapa*
Gray Catbird	*Dumetella carolinensis*
Grasshopper Sparrow	*Ammodramus savannarum*
Golden-winged Warbler	*Vermivora chrysoptera*
Hairy Woodpecker	*Picoides villosus*
Henslow's Sparrow	*Ammodramus henslowii*
Hermit Thrush	*Catharus guttatus*
House Finch	*Haemorhous mexicanus*
House Sparrow	*Passer domesticus*
Hooded Warbler	*Setophaga citrina*
House Wren	*Troglodytes aedon*
Indigo Bunting	*Passerina cyanea*
Kentucky Warbler	*Geothlypis formosa*
Killdeer	*Charadrius vociferus*
Least Flycatcher	*Empidonax minimus*
Louisiana Waterthrush	*Parkesia motacilla*
Magnolia Warbler	*Setophaga magnolia*
Mourning Dove	*Zenaida macroura*
Mourning Warbler	*Geothlypis philadelphia*
Northern Cardinal	*Cardinalis cardinalis*
Northern Flicker	*Colaptes auratus*
Northern Mockingbird	*Mimus polyglottos*
Northern Parula	*Setophaga americana*
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*
Orchard Oriole	*Icterus spurius*
Ovenbird	*Seiurus aurocapilla*
Pine Warbler	*Setophaga pinus*
Pileated Woodpecker	*Dryocopus pileatus*
Prairie Warbler	*Setophaga discolor*
Purple Finch	*Haemorhous purpureus*
Rose-breasted Grosbeak	*Pheucticus ludovicianus*
Red-breasted Nuthatch	*Sitta canadensis*
Red-bellied Woodpecker	*Melanerpes carolinus*
Red-eyed Vireo	*Vireo olivaceus*
Rock Pigeon	*Columba livia*
Ruby-throated Hummingbird	*Archilochus colubris*
Red-winged Blackbird	*Agelaius phoeniceus*
Savannah Sparrow	*Passerculus sandwichensis*
Scarlet Tanager	*Piranga olivacea*
Song Sparrow	*Melospiza melodia*
Swamp Sparrow	*Melospiza georgiana*
Tree Swallow	*Tachycineta bicolor*
Tufted Titmouse	*Baeolophus bicolor*

Table 2 (continued)

Veery	*Catharus fuscescens*
Warbling Vireo	*Vireo gilvus*
White-breasted Nuthatch	*Sitta carolinensis*
White-eyed Vireo	*Vireo griseus*
Worm-eating Warbler	*Helmitheros vermivorum*
Willow Flycatcher	*Empidonax traillii*
Winter Wren	*Troglodytes hiemalis*
Wood Thrush	*Hylocichla mustelina*
Yellow-breasted Chat	*Icteria virens*
Yellow-billed Cuckoo	*Coccyzus americanus*
Yellow-bellied Sapsucker	*Sphyrapicus varius*
Yellow-rumped Warbler	*Setophaga coronata*
Yellow-throated Warbler	*Setophaga dominica*
Yellow Warbler	*Setophaga petechia*

Table 3: The top models (Δ_i ≤2) from all scales combined of forest breeding bird diversity and occurrence response variables at 13763 forested 2nd Pennsylvania Breeding Bird Atlas point counts. K = the number of estimated parameters; AIC = Akaike Information Criterion; Δ_i = AIC_i – minAIC for each model *i*; w_i = Akaike weight, or probability of being the best model given the observed data and the set of models evaluated.

Abundance models	K	AIC	Δ_i	w_i
Forest clumpiness + urbanization intensity + agriculture amount	10	37526.91	0.00	0.15
Forest clumpiness + urbanization intensity + urbanization intensity 2 + agriculture amount	11	37526.96	0.05	0.15
Forest clumpiness + urbanization intensity + urbanization intensity 2 + agriculture amount	12	37528.03	1.12	0.14
Forest clumpiness + urbanization intensity + agriculture amount	11	37528.06	1.15	0.14
Forest clumpiness + urbanization intensity + forest patch density + agriculture amount	11	37528.76	1.85	0.14
Forest clumpiness + urbanization intensity + urbanization intensity 2 + forest patch density + agriculture amount	12	37528.83	1.92	0.14
Forest clumpiness + urbanization intensity + forest amount + agriculture amount	11	37528.88	1.98	0.14

Richness models	K	AIC	Δ_i	w_i
Forest clumpiness + forest amount + agriculture amount	8	38323.68	0.00	0.11
Forest clumpiness + urbanization intensity + agriculture amount	8	38324.52	0.83	0.10
Forest clumpiness + agriculture amount	7	38324.91	1.22	0.10
Forest clumpiness + forest amount + agriculture amount	9	38324.94	1.25	0.10
Forest clumpiness + forest patch density + agriculture amount	8	38325.16	1.48	0.10
Forest clumpiness + forest patch density + forest amount + agriculture amount	9	38325.37	1.69	0.10
Forest clumpiness + urbanization intensity + forest amount + agriculture amount	9	38325.44	1.75	0.10
Forest clumpiness + forest amount + agriculture amount	7	38325.46	1.78	0.10
Forest clumpiness + forest amount + agriculture amount	9	38325.62	1.94	0.10
Forest clumpiness + forest amount + agriculture amount	9	38325.68	1.99	0.10

Table 3 (continued)

Evenness models	K	AIC	Δ_i	w_i
Forest clumpiness + urbanization intensity + forest amount + agriculture amount	8	38752.74	0.00	0.06
Forest clumpiness + forest amount + agriculture amount	7	38753.02	0.28	0.06
Urbanization intensity + forest amount + agriculture amount	7	38753.37	0.63	0.05
Forest clumpiness + urbanization intensity + forest amount + agriculture amount	7	38753.6	0.85	0.05
Urbanization intensity + forest amount	6	38753.79	1.05	0.05
Forest clumpiness + forest amount + agriculture amount	6	38753.8	1.06	0.05
Forest clumpiness + urbanization intensity + forest amount + agriculture amount	9	38753.85	1.11	0.05
Forest clumpiness + forest amount + agriculture amount	8	38754.11	1.37	0.05
Urbanization intensity + forest amount + agriculture amount	6	38754.23	1.49	0.05
Forest clumpiness + urbanization intensity + forest amount + agriculture amount	9	38754.32	1.57	0.05
Urbanization intensity + forest amount + agriculture amount	8	38754.32	1.58	0.05
Urbanization intensity + forest amount	5	38754.34	1.60	0.05
Forest clumpiness + urbanization intensity + forest amount + agriculture amount	9	38754.5	1.75	0.05
Forest clumpiness + forest amount + agriculture amount	8	38754.55	1.81	0.05
Urbanization intensity + forest amount + agriculture amount	8	38754.69	1.95	0.05
Forest clumpiness + urbanization intensity + forest amount + agriculture amount	9	38754.73	1.98	0.05
Forest clumpiness + forest amount + agriculture amount	8	38754.73	1.98	0.05
Forest clumpiness + urbanization intensity + forest patch density + forest amount + agriculture amount	9	38754.74	2.00	0.05
Urbanization intensity + forest amount	7	38754.74	2.00	0.05

American robin occurrence models	K	AIC	Δ_i	w_i
Forest clumpiness + urbanization intensity + urbanization intensity 2 + forest amount + agriculture amount	9	17108.7	0.00	0.10
Forest clumpiness + urbanization intensity + urbanization intensity 2 + forest amount + agriculture amount	10	17109.06	0.36	0.10

Table 3 (continued)

Forest clumpiness + urbanization intensity + urbanization intensity 2 + forest amount + agriculture amount	10	17109.25	0.55	0.10
Forest clumpiness + urbanization intensity + urbanization intensity 2 + forest amount + agriculture amount	10	17109.31	0.61	0.10
Forest clumpiness + urbanization intensity + urbanization intensity 2 + forest amount + agriculture amount	11	17109.5	0.80	0.10
Forest clumpiness + urbanization intensity + urbanization intensity 2 + forest amount + agriculture amount	11	17109.57	0.87	0.10
Forest clumpiness + urbanization intensity + urbanization intensity 2 + forest amount + agriculture amount	11	17109.8	1.09	0.10
Forest clumpiness + urbanization intensity + urbanization intensity 2 + forest amount + agriculture amount	12	17109.95	1.24	0.10
Forest clumpiness + urbanization intensity + urbanization intensity 2 + forest patch density + forest amount + agriculture amount	10	17110.35	1.65	0.10
Forest clumpiness + urbanization intensity + urbanization intensity 2 + forest patch density + forest amount + agriculture amount	11	17110.66	1.96	0.09

Scarlet tanager occurrence models	K	AIC	$d\Delta_i$	w_i
Urbanization intensity + urbanization intensity 2 + forest patch density + forest amount + agriculture amount	10	16883.14	0.00	0.11
Urbanization intensity + urbanization intensity 2 + forest patch density + forest amount + agriculture amount	9	16883.61	0.47	0.10
Urbanization intensity + urbanization intensity 2 + forest patch density + forest amount + agriculture amount	11	16883.93	0.79	0.10
Urbanization intensity + urbanization intensity 2 + forest patch density + forest amount + agriculture amount	10	16884.1	0.96	0.10
Urbanization intensity + forest patch density + forest amount + agriculture amount	8	16884.41	1.27	0.10
Forest clumpiness + urbanization intensity + urbanization intensity 2 + forest patch density + forest amount + agriculture amount	11	16884.52	1.38	0.10

Table 3 (continued)

Urbanization intensity + urbanization intensity 2 + forest patch density + forest amount + agriculture amount	11	16884.6	1.46	0.10
Urbanization intensity + forest patch density + forest amount + agriculture amount	9	16884.66	1.52	0.10
Urbanization intensity + forest patch density + forest amount + agriculture amount	9	16884.97	1.83	0.10
Urbanization intensity + urbanization intensity 2 + forest patch density + forest amount + agriculture amount	10	16885.02	1.88	0.10

Table 4: The relative importance of explanatory variables in the top models from all scales combined of forest breeding bird abundance, species richness, species evenness, and American robin and Scarlet tanager occurrence at 13763 forested 2nd Pennsylvania Breeding Bird Atlas point counts. The relative strength of evidence of the explanatory importance of each variable is denoted using conventional categories. Model-averaged standardized partial estimates and standard errors (SE) calculated using unconditional variances are also shown.

Abundance

Variable	RVI	Strength of evidence	Estimate	SE
Forest clumpiness	1.000	Very strong	-0.103	0.010
Urbanization intensity	1.000	Very strong	-0.044	0.009
Agriculture amount	1.000	Very strong	0.196	0.009
Urbanization intensity 2	0.431	Weak	0.005	0.004
Forest patch density	0.275	No evidence	0.001	0.003
Forest amount	0.137	No evidence	0.000	0.002

Richness

Variable	RVI	Strength of evidence	Estimate	SE
Forest clumpiness	1.000	Very strong	-0.051	0.014
Agriculture amount	1.000	Very strong	0.127	0.014
Forest amount	0.697	Weak	0.023	0.014
Urbanization intensity	0.201	No evidence	0.002	0.002
Forest patch density	0.198	No evidence	-0.002	0.003

Evenness

Variable	RVI	Strength of evidence	Estimate	SE
Forest amount	1.000	Very strong	-0.124	0.031
Agriculture amount	0.844	Strong	-0.043	0.020
Forest clumpiness	0.790	Strong	-0.027	0.014
Urbanization intensity	0.528	Weak	0.018	0.011
Forest patch density	0.051	No evidence	0.000	0.001

AMRO occurrence

Variable	RVI	Strength of evidence	Estimate	SE
Forest clumpiness	1.000	Very strong	-0.108	0.026
Urbanization intensity	1.000	Very strong	-0.518	0.032
Urbanization intensity 2	1.000	Very strong	0.105	0.020
Forest amount	1.000	Very strong	-0.133	0.035
Agriculture amount	1.000	Very strong	0.325	0.026
Forest patch density	0.095	No evidence	-0.003	0.004

SCTA occurrence

Variable	RVI	Strength of evidence	Estimate	SE
Urbanization intensity	1.000	Very strong	0.280	0.036
Forest patch density	1.000	Very strong	-0.099	0.027
Forest amount	1.000	Very strong	0.172	0.040
Agriculture amount	1.000	Very strong	-0.087	0.034
Urbanization intensity 2	0.706	Strong	-0.033	0.018
Forest clumpiness	0.086	No evidence	0.002	0.003

APPENDIX B: FIGURES

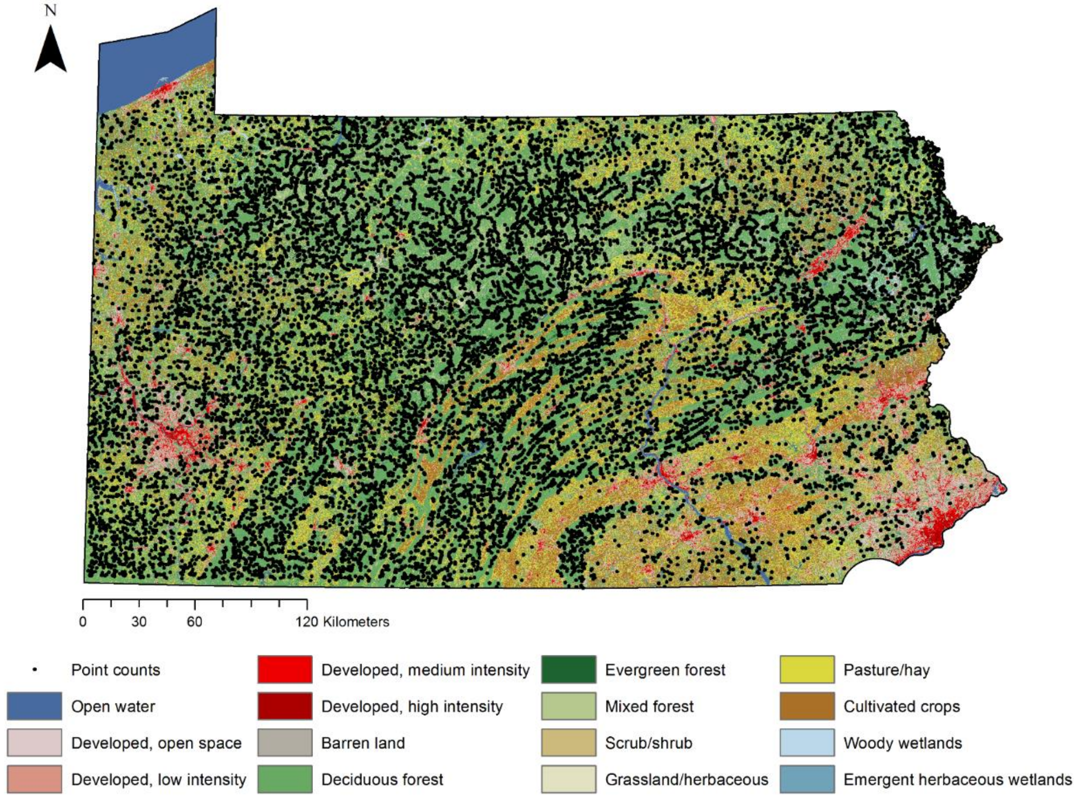
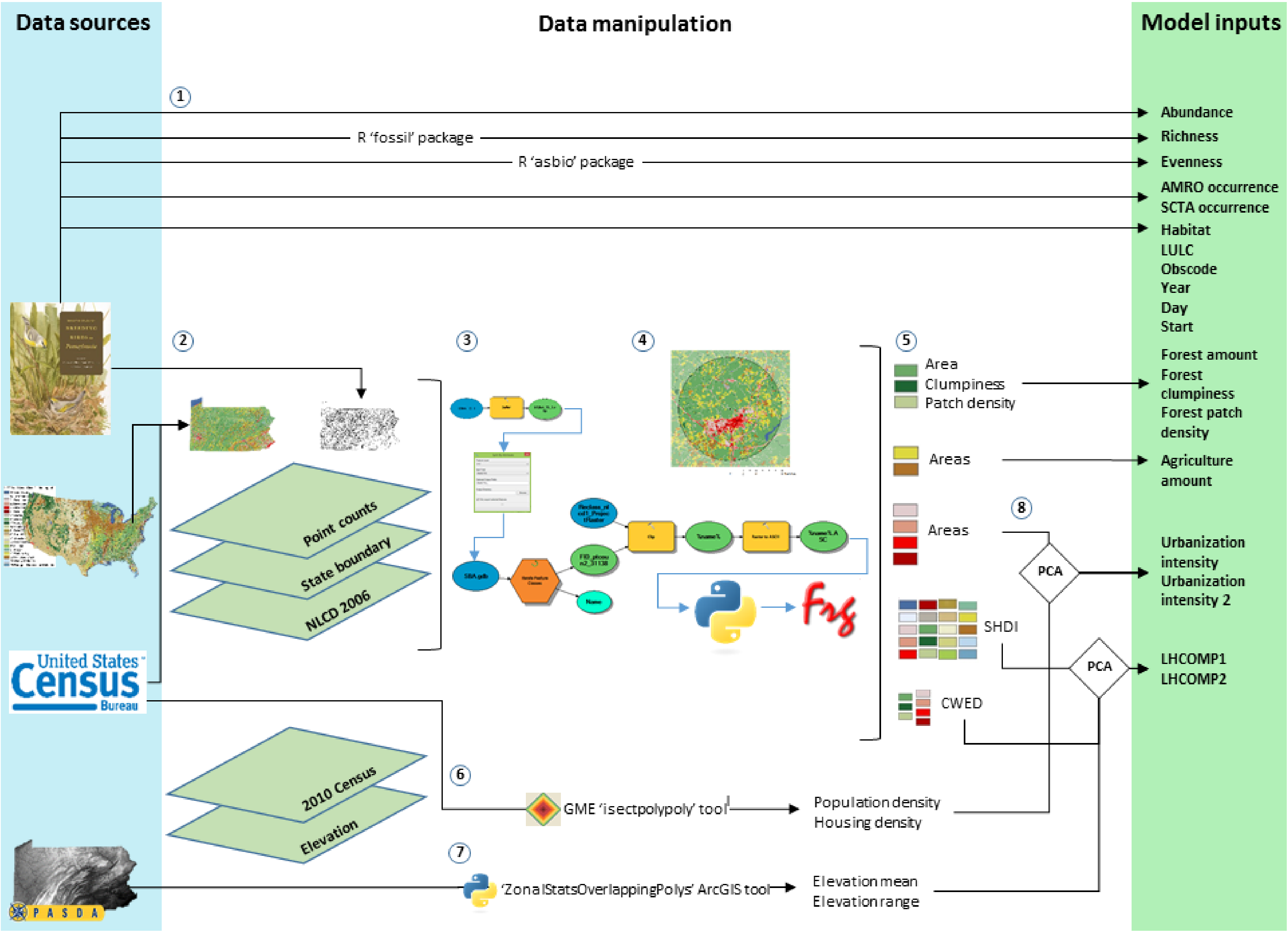


Figure 1: Land cover and locations of forested point counts (n=16563) in Pennsylvania.

Figure 2: Workflow of pre-modeling data management. 1) From point count dataset, used R to estimate response variables and local habitat and detectability variables. 2) Created point count ArcGIS layer from their xy coordinates, clipped NLCD 2006 to PA boundaries, and selected point counts with >50% forest cover. 3) Created and analyzed landscapes by buffering point counts at 10 different scales, separating them into independent files using USGS’s Split By Attribute tool, clipped NLCD to each buffer, converted landscape rasters to ASCII filetype, then used python script to batch process ASCII landscapes in Fragstats. 4) Example landscape shown as darkened circle. 5) Fragstats output for each landscape (see Methods). 6) Used Geospatial Modelling Environment ‘isectpolypoly’ tool to estimate area-weighted population and housing density for each landscape. 7) Resampled 1m DEM to 30m resolution; used ‘ZonalStatsOverlappingPolys’ script in ArcGIS to estimate elevation mean and range for overlapping landscapes. 8) Conducted two PCAs of sets of variables for variable reduction.


Data sources
Data manipulation
Model inputs
①
R 'fossil' package
R 'asbio' package
Abundance
Richness
Evenness
AMRO occurrence
SCTA occurrence
Habitat
LULC
Obscode
Year
Day
Start
②
③
④
⑤
Point counts
State boundary
NLCD 2006
United States Census Bureau
Area
Clumpiness
Patch density
Forest amount
Forest clumpiness
Forest patch density
Areas
Agriculture amount
⑧
Areas
PCA
Urbanization intensity
Urbanization intensity 2
SHDI
PCA
LHCOMP1
LHCOMP2
CWED
2010 Census
Elevation
⑥
GME 'isectpolypoly' tool
Population density
Housing density
⑦
'ZonalStatsOverlappingPolys' ArcGIS tool
Elevation mean
Elevation range
PASDA

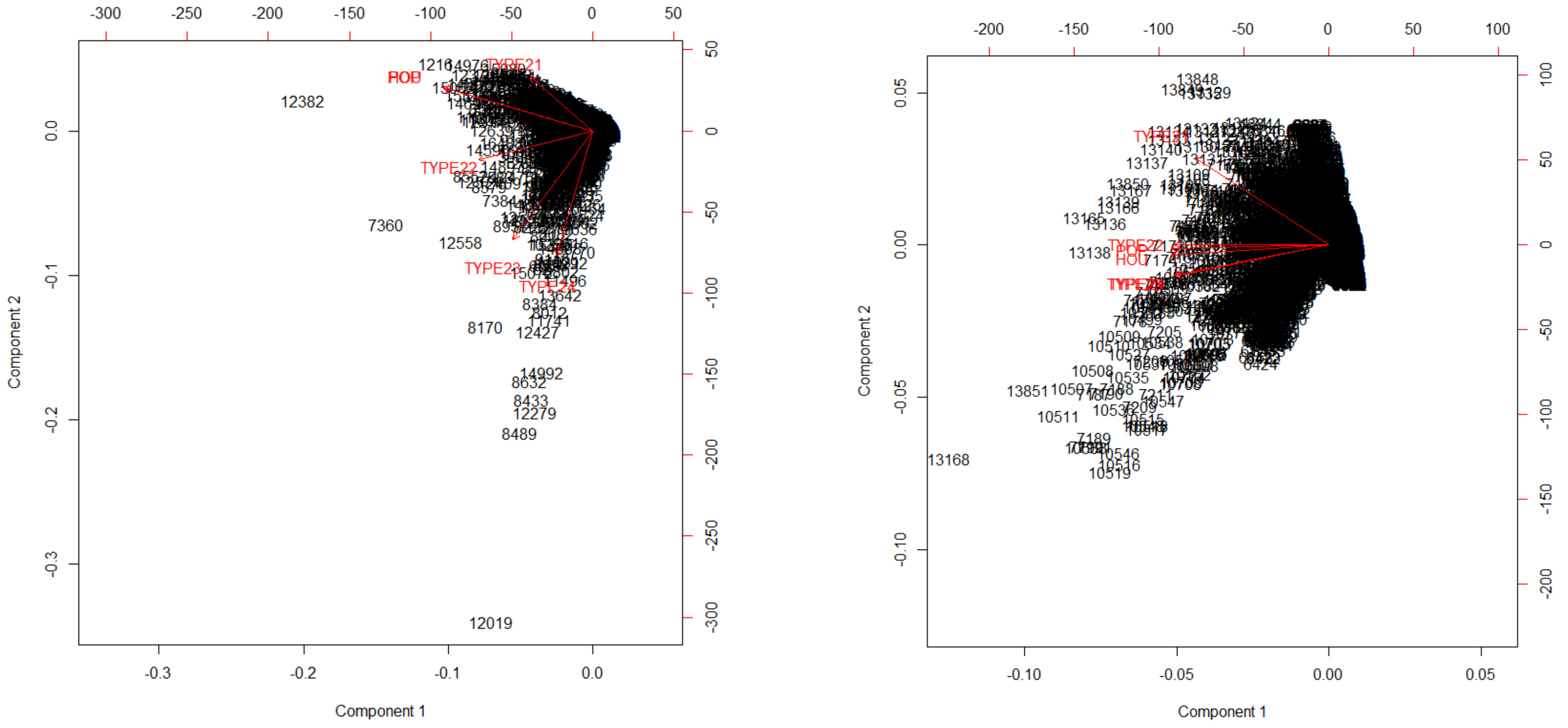


Figure 3: Biplots for urbanization intensity principal component analysis for the 200m scale (left) and 16km scale (right). At the 200m and 500m scales, the first two components were included in model parameters; at scales ≥1km only the first component was included in model parameters. POP = population density, HOU = housing density, TYPE21 = open space developed land cover, TYPE22 = low intensity developed land cover, TYPE23 = medium intensity developed land cover, and TYPE24= high intensity developed land cover.

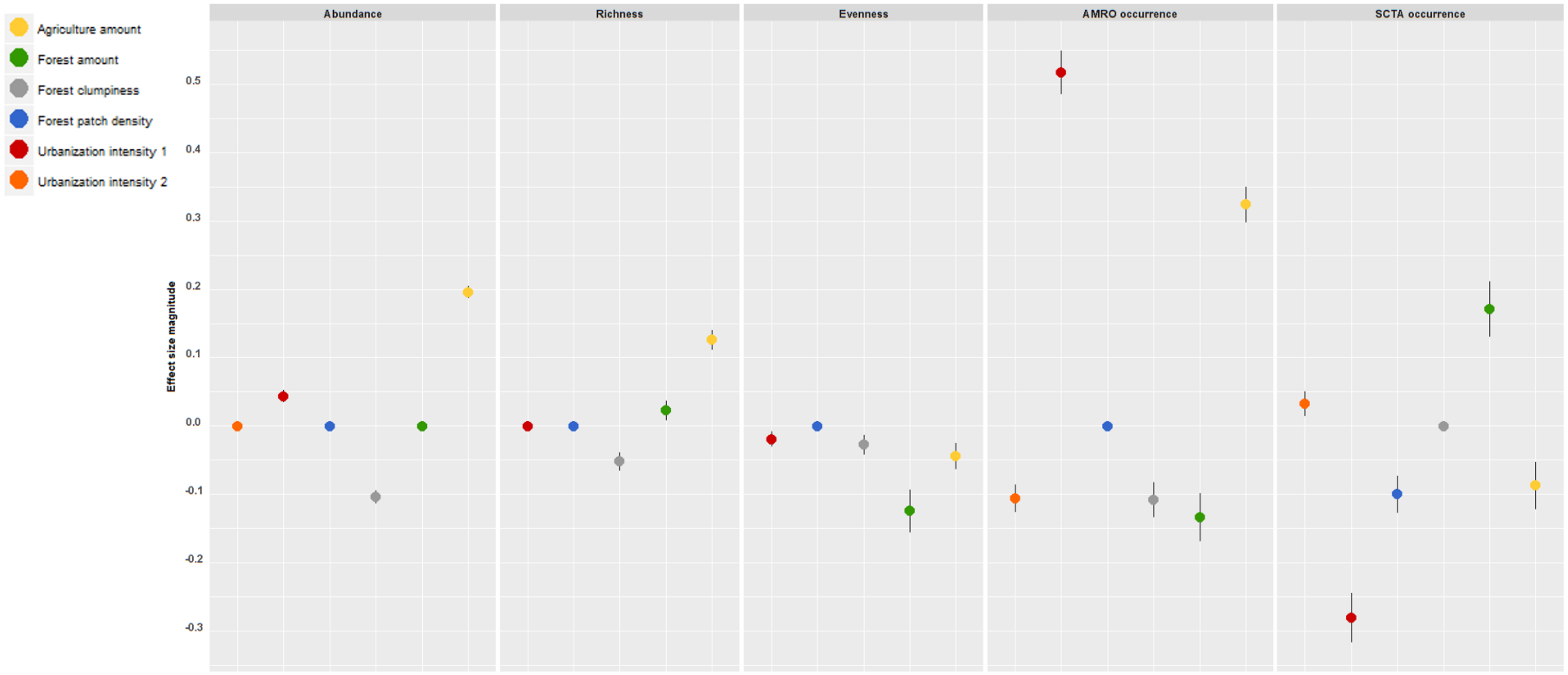


Figure 4: Model-averaged standardized partial estimates from top models ($\Delta_i \leq 2$) from all scales combined for each response variable (L to R panels): abundance, richness, evenness, American robin (AMRO) occurrence, and SCTA (Scarlet tanager) occurrence. Magnitudes of estimates represent relative order of importance of each predictor variable in explaining each response variable; estimates for which there was no evidence that the variable was an important predictor of that response are set to zero. Error bars represent ± 1 model-averaged standard error calculated using unconditional variances.

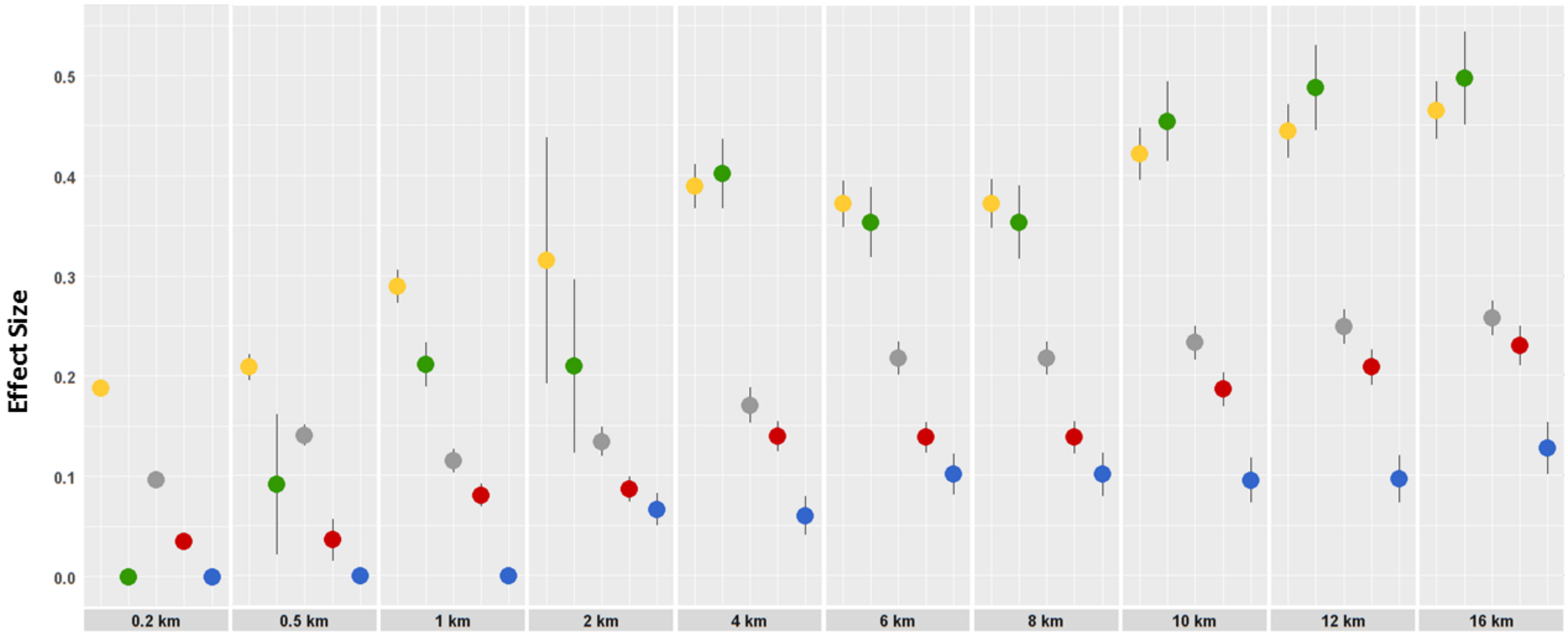


Figure 5: Model-averaged standardized partial estimates from top models ($\Delta_i \leq 2$) predicting total bird abundance at each scale. Effect sizes are absolute values of estimates and represent the relative order of importance of each predictor variable in explaining abundance; estimates for which there was no evidence that the variable was an important predictor of that response are set to zero. Error bars represent ± 1 model-averaged standard error calculated using unconditional variances. Yellow circles are agriculture amount, green circles are forest amount, grey circles are forest clumpiness, red circles are urbanization intensity, and blue circles are forest patch density.

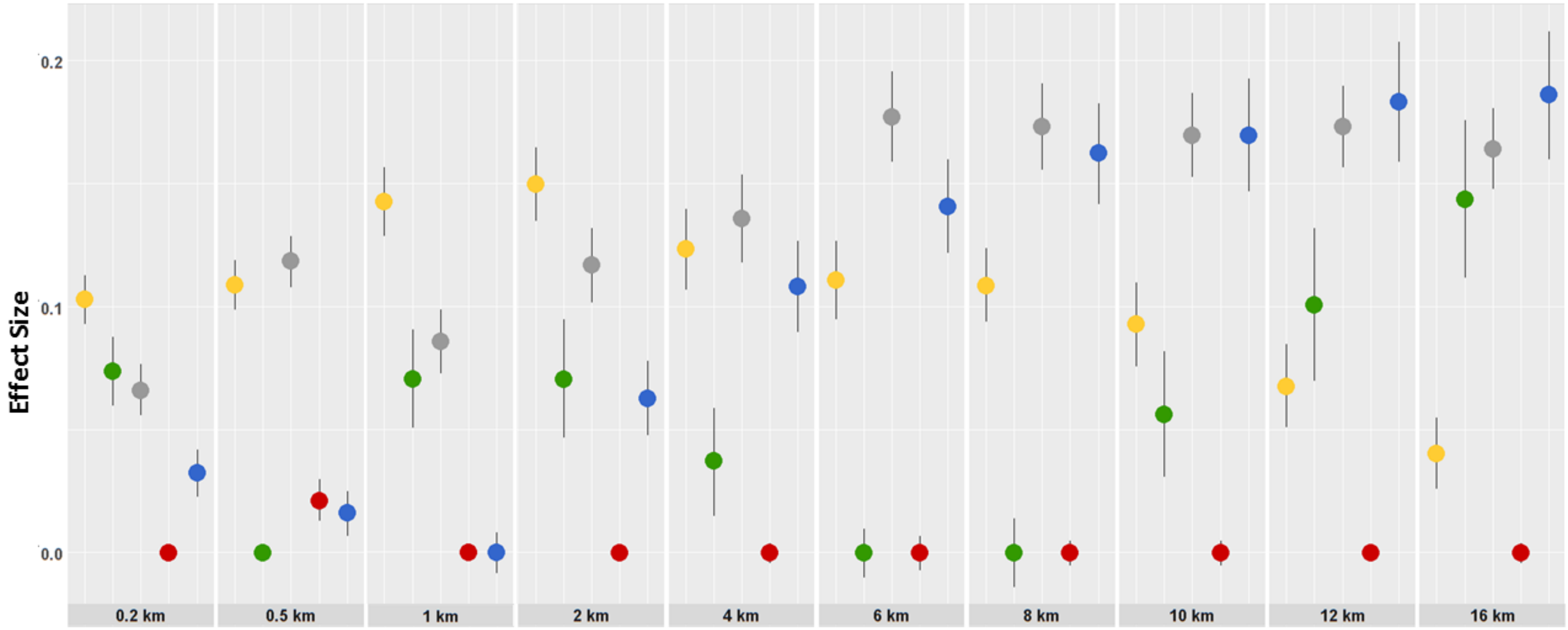


Figure 6: Model-averaged standardized partial estimates from top models ($\Delta_i \leq 2$) predicting species richness at each scale. Effect sizes are absolute values of estimates and represent the relative order of importance of each predictor variable in explaining species richness; estimates for which there was no evidence that the variable was an important predictor of that response are set to zero. Error bars represent ± 1 model-averaged standard error calculated using unconditional variances. Yellow circles are agriculture amount, green circles are forest amount, grey circles are forest clumpiness, red circles are urbanization intensity, and blue circles are forest patch density.

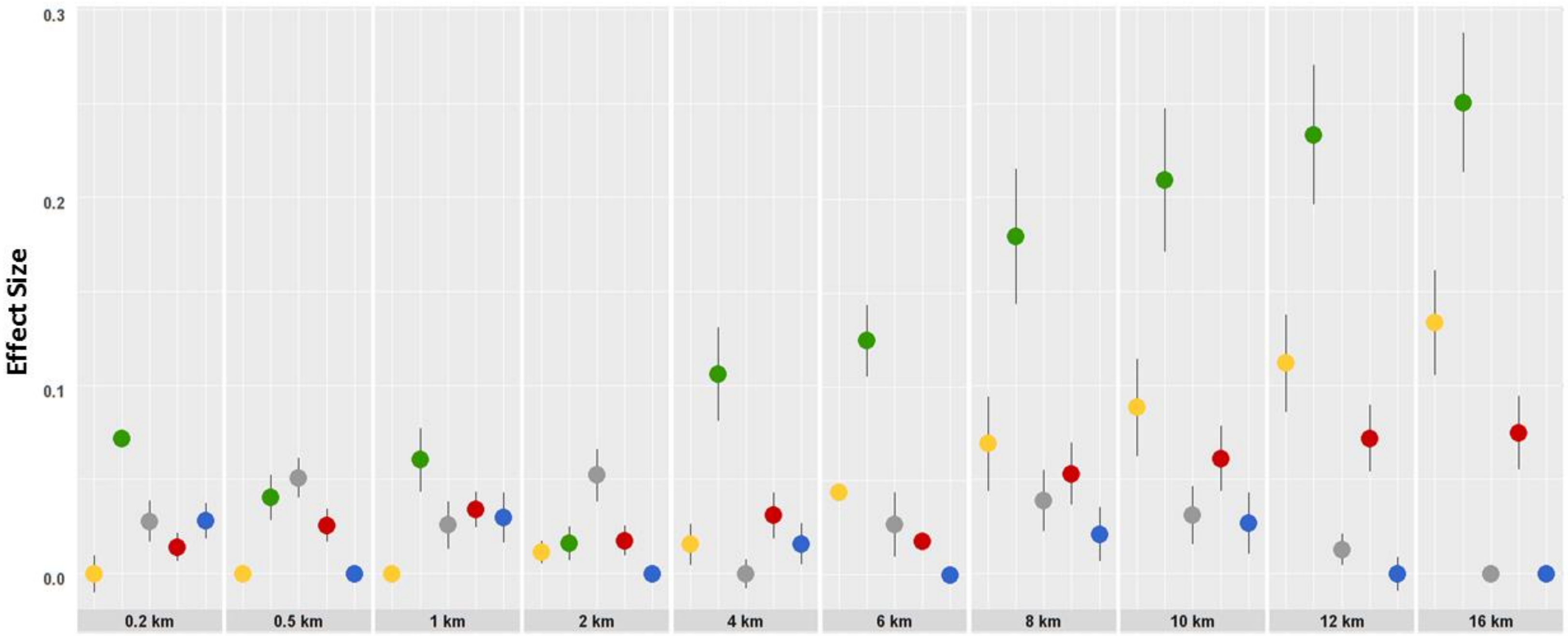


Figure 7: Model-averaged standardized partial estimates from top models ($\Delta_i \leq 2$) predicting species evenness at each scale. Effect sizes are absolute values of estimates and represent the relative order of importance of each predictor variable in explaining species evenness; estimates for which there was no evidence that the variable was an important predictor of that response are set to zero. Error bars represent ± 1 model-averaged standard error calculated using unconditional variances. Yellow circles are agriculture amount, green circles are forest amount, grey circles are forest clumpiness, red circles are urbanization intensity, and blue circles are forest patch density.

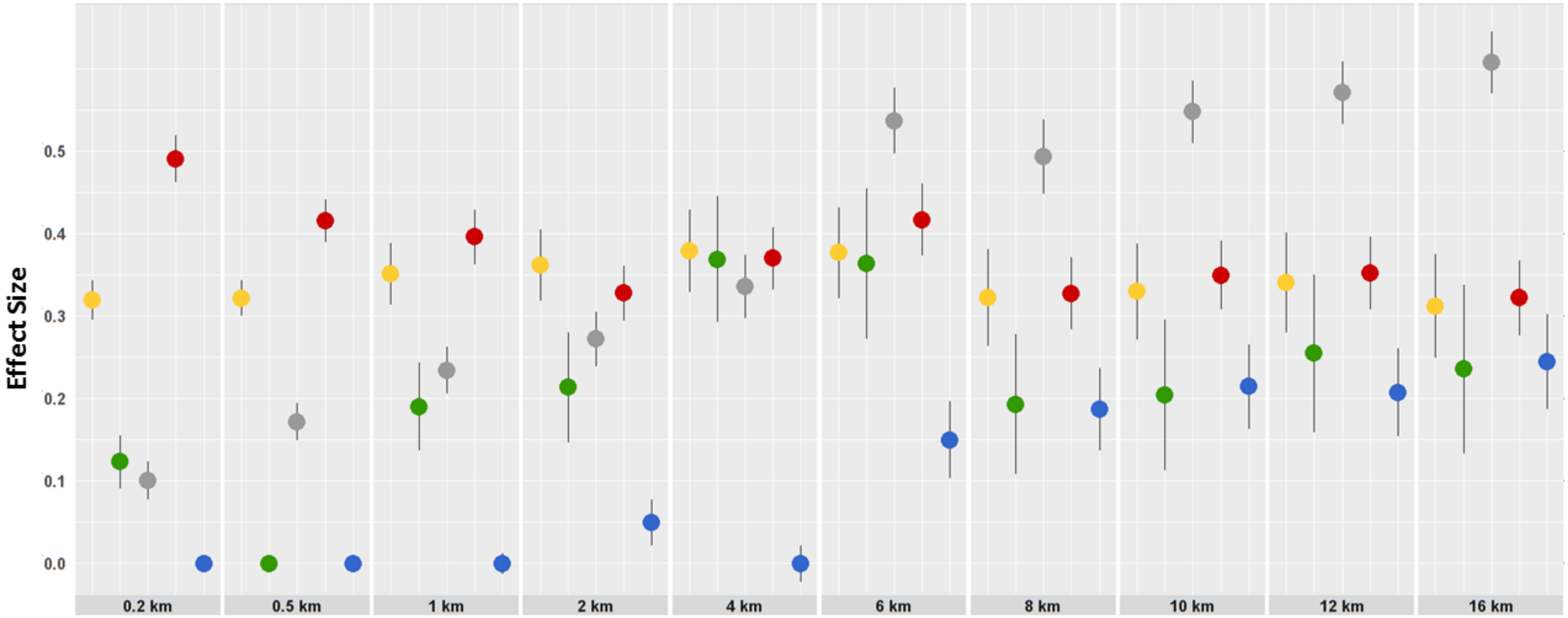


Figure 8: Model-averaged standardized partial estimates from top models ($\Delta_i \leq 2$) predicting American robin occurrence at each scale. Effect sizes are absolute values of estimates and represent the relative order of importance of each predictor variable in explaining American robin occurrence; estimates for which there was no evidence that the variable was an important predictor of that response are set to zero. Error bars represent ± 1 model-averaged standard error calculated using unconditional variances. Yellow circles are agriculture amount, green circles are forest amount, grey circles are forest clumpiness, red circles are urbanization intensity, and blue circles are forest patch density.

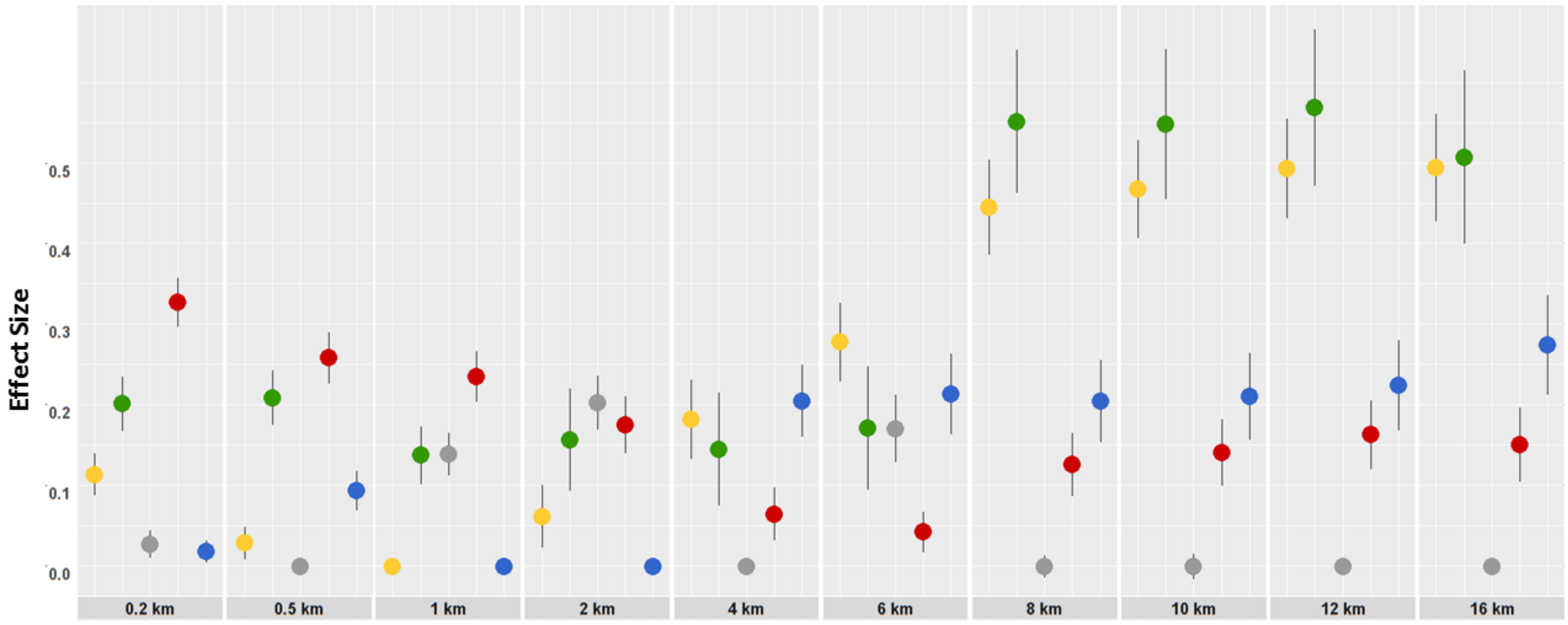


Figure 9: Model-averaged standardized partial estimates from top models ($\Delta_i \leq 2$) predicting Scarlet tanager occurrence at each scale. Effect sizes are absolute values of estimates and represent the represent relative order of importance of each predictor variable in explaining Scarlet tanager occurrence; estimates for which there was no evidence that the variable was an important predictor of that response are set to zero. Error bars represent ± 1 model-averaged standard error calculated using unconditional variances. Yellow circles are agriculture amount, green circles are forest amount, grey circles are forest clumpiness, red circles are urbanization intensity, and blue circles are forest patch density.

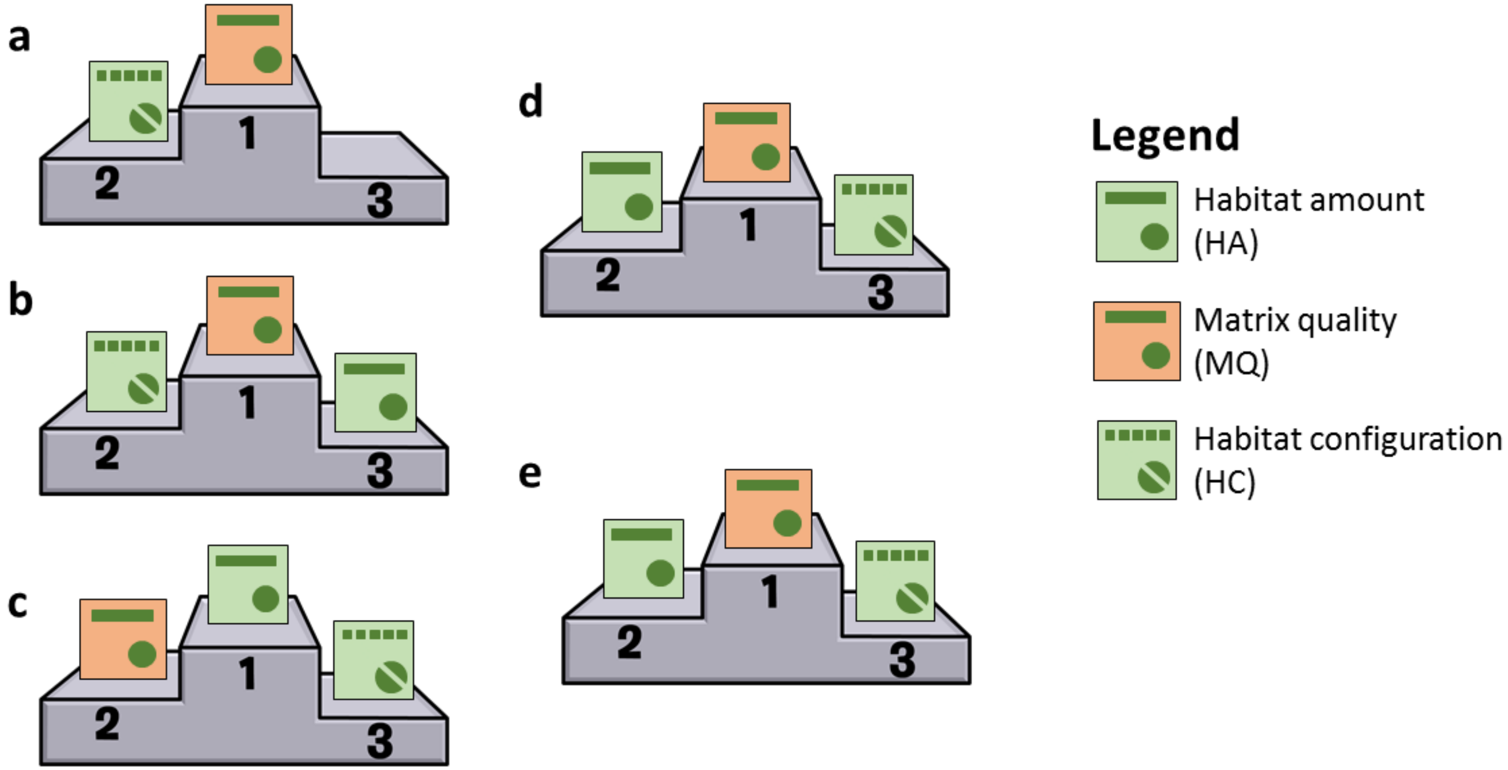


Figure 10: Ranking of predictor effect sizes for each response variable. For abundance (a), richness (b), and evenness (c), agriculture amount was the indicator of matrix quality. For American robin occurrence (d) and Scarlet tanager occurrence (e), urbanization intensity was the indicator of matrix quality. a) Abundance: MQ > HC. b) Richness: MQ > HC > HA. c) Evenness: HA > MQ > HC. d) American robin occurrence: MQ > HA > HC. e) Scarlet tanager occurrence: MQ > HA > HC.