Complex effects of scale on the relationships of landscape pattern versus avian species richness and community structure in a woodland savanna mosaic

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Landscape pattern metrics are widely used for predicting habitat and species diversity. However, the relationship between landscape pattern and species diversity is typically measured at a single spatial scale, even though both landscape pattern, and species occurrence and community composition are scale-dependent. While the effects of scale on landscape pattern are well documented, the effects of scale on the relationships between spatial pattern and species richness and composition are not well known. Here, our main goal was to quantify the effects of cartographic scale (spatial resolution and extent) on the relationships between spatial pattern and avian richness and community structure in a mosaic of grassland, woodland, and savanna in central Wisconsin. Our secondary goal was to evaluate the effectiveness of a newly developed tool for spatial pattern analysis, multiscale contextual spatial pattern analysis (MCSPA), compared to existing landscape metrics. Landscape metrics and avian species richness had quadratic, exponential, or logarithmic relationships, and these patterns were generally consistent across two spatial resolutions and six spatial extents. However, the magnitude of the relationships was affected by both resolution and extent. At the finer resolution (10-m), edge density was consistently the best predictor of species richness, followed by an MCSPA metric that measures the standard deviation of woody cover across extents. At the coarser resolution (30-m), NDVI was the best predictor of species richness by far, regardless of spatial extent. Another MCSPA metric that denotes the average woody cover across extents, together with percent of woody cover, were always the best predictors of variation in avian community structure. Spatial resolution and extent had varying effects on the relationships between spatial pattern and avian community structure. We therefore conclude that cartographic scale not only affects measures of landscape pattern per se, but also the relationships among spatial pattern, species richness, and community structure, often in complex ways, which reduces the efficacy of landscape metrics for predicting the richness and diversity of organisms.

Habitat attributes are widely used as predictive variables when describing the distribution and spatial patterns of species and communities (Guisan and Zimmermann 2000). More specifically, the type, structure, and cover of vegetation are frequently quantified and incorporated into models that predict species occurrence, abundance, richness, and diversity (Bergen et al. 2007). Descriptors of habitat can be divided into two general types: local and landscape. Local descriptors (e.g. field plots or individual pixels derived from remotely sensed data) quantify the habitat attributes at a plot level (i.e. within a very small spatial extent). Landscape descriptors, on the other hand, quantify the spatial pattern of habitat in a given area, at broader spatial extents than local descriptors (i.e. using groups of pixels that correspond to a larger area in the real world). When this information is based on remotely sensed data, the spatial resolution (i.e. the pixel size), the smallest unit of analysis within the extent, also has pronounced effects on the outcomes of the analysis (Wu 2004).

Several types of local habitat descriptors can be calculated from remotely sensed data. Most of these descriptors rely on multispectral satellite imagery, though active remote sensing tools such as LiDAR and SAR are emerging as useful alternatives when the vertical structure of the vegetation is an important aspect of habitat quality (Bergen et al. 2007, 2009, Müller et al. 2010). The normalized difference vegetation index (NDVI) (Tucker 1979), derived from multispectral imagery, is perhaps the most common metric for describing vegetation characteristics that are important as wildlife habitat (Kerr and Ostrovsky 2003, Gillespie et al. 2008). However, the usefulness of NDVI as a direct predictor of species richness and composition varies among ecosystems and taxonomic groups (Fairbanks and McGwire 2004, Seto et al. 2004, Foody 2005, Laurent et al. 2005, Ranganathan et al. 2007). Spectral mixture analysis, in which the relative cover of the main spectral components within pixels is derived, is often used to determine vegetation cover (Elmore et al. 2000, Asner et al. 2003), but also

has been used to predict avian species richness in urban parks (Bino et al. 2008).

Landscape based measures of habitat may use raw spectral values from remotely-sensed data directly, or be derived via a spatial analysis of classified remotely-sensed data. The best example of a direct measure is the quantification of structural heterogeneity of habitats with image texture measures applied to groups of neighboring pixels (Rey-Benayas and Pope 1995). Image texture from Landsat satellite data successfully explained the occurrence of seven bird species in Maine (Hepinstall and Sader 1997) and the group size (i.e. a proxy for habitat quality) of greater Rheas in Argentinean grasslands (Bellis et al. 2008). Image texture derived from both high-resolution aerial photography (St-Louis et al. 2006) and from Landsat imagery (St-Louis et al. 2009) also explained avian species richness in New Mexico desert.

Habitat description at the landscape scale, based on spatial analysis of land cover classifications, is a core component of the field of landscape ecology. There is a plethora of landscape metrics, which are mathematical and statistical indices that describe and quantify the spatial patterns of habitat maps (McGarigal and Marks 1995). During the past three decades, there were many attempts to elucidate the relationships between spatial pattern, as captured in landscape metrics, and species distributions, with varying levels of success. Recent examples include characterizing the occurrence of avian species (Cushman and McGarigal 2004, Zuckerberg and Porter 2010), avian species richness (Tavernia and Reed 2010), plant community composition (Goslee and Sanderson 2010), and the occurrence of large mammals (Gaucherel et al. 2010).

The majority of local and landscape measures that are derived from remotely sensed data operate at a single spatial scale (which consists of two components: resolution and extent). In addition, we distinguish between cartographic scale, which is a characteristic of the map depiction of the landscape, and ecological scale, which is a spatial level of organization in the real world. Hereafter, we will refer to scale in its cartographic context. Unfortunately, a single-scale approach may limit the effectiveness of the analysis of species–habitat relations for three reasons. First, the exact spatial resolution and extent most strongly associated with spatial patterns of species occurrence are usually unknown (Marceau 1999, Cushman and McGarigal 2004, Li and Wu 2004), since the human perception of the landscape may differ from the perception of other species (Johnson et al. 1992, Manning et al. 2004). Therefore, it is often unclear which scale should be used in the analysis of species–habitat relationships, and studies have typically defaulted to the scales of the available environmental data (e.g. the resolution of remotely sensed imagery), which may differ from the ecological scales at which species interact with their environment (Wiens 1981).

Second, species may interact with their environments at several spatial scales simultaneously (Wiens and Rotenberry 1981, Wiens and Milne 1989, Milne 1992, Lawler and Edwards 2006), thus variables that describe multi-scale habitat characteristics or how habitat changes with scale may prove to be more useful predictors of species–habitat relations than more static measures (Levin 1992), even when they are based on cartographic representations of

scale and not ecological ones. Finally, habitat descriptors (especially landscape metrics), are well known to be affected by scale in various ways, and often exhibit distinctive scaling laws that vary considerably among metrics and habitat types (Wu et al. 2002, Neel et al. 2004, Wu 2004, Bar Massada et al. 2008).

While the effects of spatial scale on landscape metrics are well known (Wu et al. 2002, Neel et al. 2004, Wu 2004, Bar Massada et al. 2008), and the relationships between species and landscape pattern are also well studied (Kumar et al. 2006, Torras et al. 2008, Caprio et al. 2009, Rossi and van Halder 2010), the effects of scale on the relationships between species and landscape structure have received relatively less research attention. These effects are complex, and likely differ among species and landscape types, since species perceive their environment in varying ways, and select their habitat hierarchically according to different requirements at multiple scales (Wiens and Rotenberry 1981, Lawler and Edwards 2006). However, most prior studies attempted to find the 'right' scale (or scales) at which species–habitat relationships are strongest (Saab 1999, Lawler et al. 2004, Lawler and Edwards 2006, Doherty et al. 2008). In contrast, the questions of how the type (e.g. linear, quadratic, exponential) and shape (e.g. intercept, slope, maxima) of species–habitat relationships are affected explicitly by scale have not been addressed before.

In an attempt to limit the effect of scale on the outcomes of spatial pattern analysis, we have previously developed multiscale contextual spatial pattern analysis (MCSPA), a pixel-scale approach to mapping spatial pattern at multiple scales simultaneously (Bar Massada and Radeloff 2010). MCSPA consists of two alternative approaches that quantify spatial context (i.e. the change in habitat cover at various spatial extents around every pixel in a landscape map) in a continuous manner, providing measures of habitat context for models of species occurrence, abundance, richness, and community structure. The two approaches are based on quantifying various characteristics of scalograms, which are functions that relate habitat cover to the size of the analysis window (i.e. $N \times N$ pixels or the corresponding areal extent) around a given focal pixel in a binary landscape map consisting of 'habitat' and 'non-habitat' pixels. MCSPA is conceptually related to previous methods where the properties of scalograms were used to quantify multiscale habitat structure. Earlier examples include fractal analysis (Milne 1992), lacunarity analysis (Plotnick et al. 1993, Elkie and Rempel 2001), conditional entropy profiles (Johnson et al. 2001), and cluster analysis of cover and connectivity at multiple scales (Riitters et al. 2000). The latter is the most closely related to MCSPA since it generates pixel-scale results, while all other approaches produce landscape-scale results (i.e. a single value for a given landscape).

In the first MCSPA approach (MCSPAp), a third order polynomial is fitted to the scalogram, and the four polynomial coefficients serve as descriptors of spatial context. In the second approach (MCSPAs), the mean, standard deviation, and the mean slope between the percent cover at the smallest analysis window and any other window serve as the descriptors of spatial context. However, MCSPA metrics have not yet been applied as predictive variables in models of species abundance, richness, or community structure, and it is

unclear if the theoretical advantages of MCSPA indeed result in higher predictive power.

Our objectives were: 1) to quantify the effect of spatial resolution and extent on the relationships between landscape and MCSPA metrics and, in turn, avian species richness and community structure in a mosaic landscape in central Wisconsin. Specifically, we were interested in the effects of scale on the type, shape, and predictive power of the model relating species richness, community structure, and landscape patterns; 2) to assess the usefulness of MCSPA metrics as predictive variables of avian species richness and community structure, compared to the three most commonly used single-scale landscape metrics, and the most commonly used satellite-based vegetation index.

Methods

Study area

The study was conducted at Fort McCoy Military Installation, which covers 24 281 ha in southwestern Wisconsin, USA (Fig. 1). Fort McCoy is an operational military installation and roughly 50% of the post is off-limits to non-military personal. In the remaining area, three dominant habitat types occur, and their distribution depends on edaphic features, elevation differences, and slope and aspect induced microclimates. These habitats are 1) forbs and grass dominated grasslands (< 5% tree cover and low shrub cover); 2) oak savannas (5–50% tree cover with variable shrub cover); and 3) oak woodlands (> 50% tree cover with variable shrub cover, Curtis 1959). Dominant tree species in these habitats include black oak *Quercus velutina*, northern pin oak *Q. ellipsoidalis*, bur oak *Q. macrocarpa*, jack pine *Pinus banksiana*, black cherry *Prunus serotina*, red oak *Q. rubra*, and white oak *Q. alba*. Dominant shrubs include American hazelnut *Corylus americana* and blueberry *Vaccinium angustifolium*, and dominant herbaceous species include big bluestem *Andropogon gerardii*, little bluestem *Schizachyrium scoparium*, and Pennsylvania sedge *Carex pensylvanica*.

Avian surveys

The avian surveys were conducted from 2007 to 2009 and included 243 sample plots. Sample points were allocated
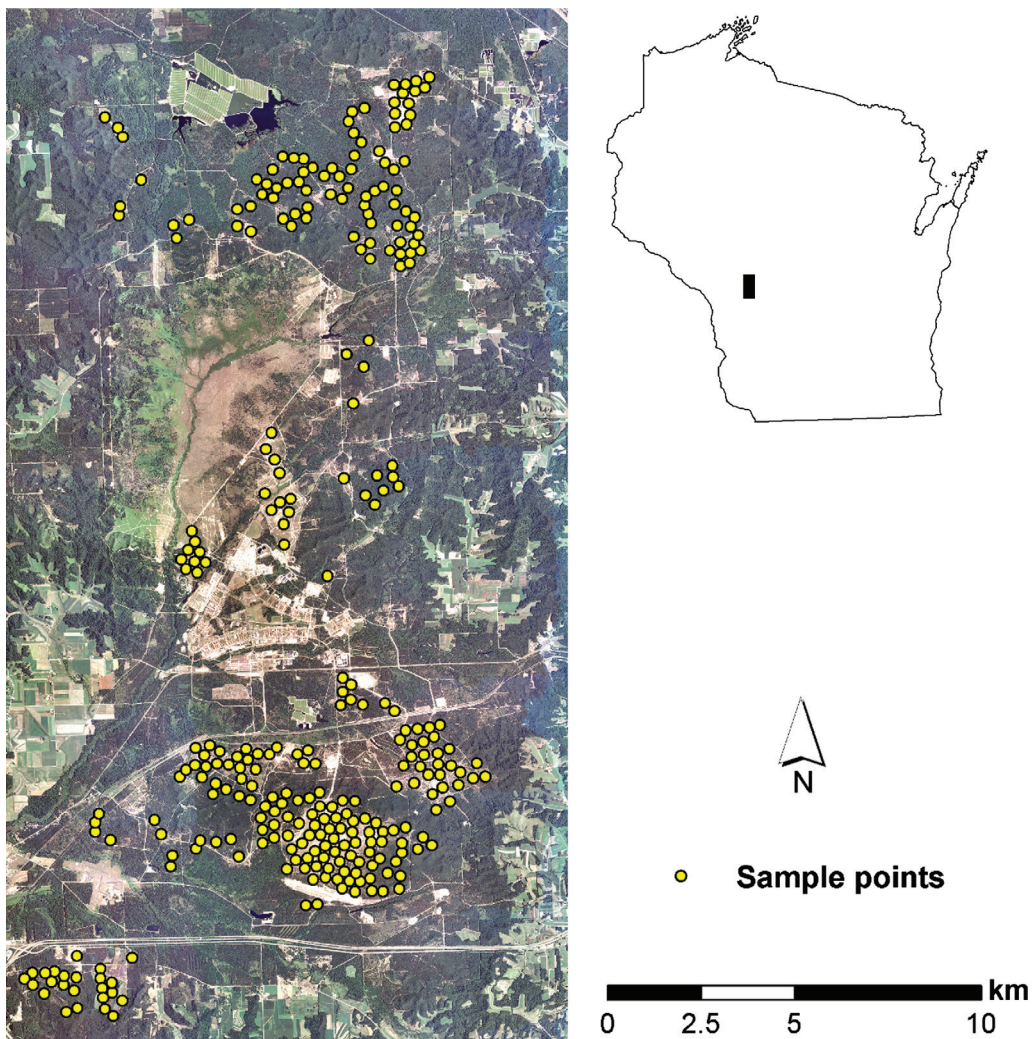

Figure 1. The study area in Fort McCoy (left) and its location in Wisconsin (right, marked by the black rectangle). The sample plots are depicted as yellow circles.

using a stratified random sampling design, stratified by habitat type. At each sample plot, a five-min point count was conducted, during which all bird species seen or heard were recorded by trained human observers (Hutto et al. 1986, Ralph et al. 1995). Distance to each detected bird was estimated using laser rangefinders, and detections were truncated at 100 m to allow comparability. Sample points were visited four times in 2007 and 2008 and three times in 2009. We quantified two measures of avian community structure: 1) species richness within each plot, averaged over three years of sampling to minimize the effects of interannual variation, and 2) average abundance of each species per plot (again in three year average).

Landscape map

Three landscape maps were used for the analysis. The first was a 10-m resolution binary image of woody vegetation. The map was generated by classifying and resampling a mosaic of 1-m resolution true color aerial photos obtained from the National Agricultural Imagery Program (NAIP, freely available from the WisconsinView database: <www.wisconsinview.org/imagery/>), acquired between 1 July and 15 August 2008. The second landscape map was a 30-m resolution binary image of woody vegetation, generated by resampling the 1-m mosaic. The third map was a 30-m resolution NDVI layer derived from a Landsat satellite image (path 25, row 29), acquired on 13 July 2009 (i.e. leaf on).

We classified the NAIP image mosaic using a supervised maximum likelihood classification, based on 300 randomly allocated training data points, which were manually classified as 'woody' or 'non-woody'. We assessed the accuracy of the classification using 250 different control points that were randomly located within 500-m of the bird sampling points, and were visually interpreted. We limited our accuracy sampling locations to these areas (rather than the entire image) since eventually we assessed the relationships between both richness and community structure versus the MCSPA metrics within a short distance from the bird sampling points. The overall accuracy of the classification was 95.2%. We then resampled the classified image using a majority rule to reduce the spatial resolution from 1 to 10 m, under the assumption that this level of resolution is most suitable for describing the habitat characteristics of the bird species in the study area (a pixel size smaller than 10 m would often be smaller than an individual tree, and we assumed that a tree and its immediate vicinity are the smallest potentially defended amount of space for many of the bird species in our study area). To test the effect of spatial resolution on our analysis, we also generated a 30-m resolution image by resampling the original 1-m classified image, again using a majority rule. We did not test a larger pixel size since preliminary analyses revealed that it led to an over-simplified description of the study area, which is characterized by significant fine-grained vegetation heterogeneity.

MCSPA metrics

We used three MCSPAs metrics developed by Bar Massada and Radeloff (2010). These metrics quantify the statistical properties of a scalogram, which is the function that depicts woody cover at monotonically increasing rectangular window sizes around a focal pixel in a binary raster habitat map. We used rectangular windows as they maintain their shape regardless of window size, in contrast to circular windows, where in particular the edge length of small circles is affected by the pixel size. We also tested the three MCSPAp metrics, but their results were unsatisfactory, and we therefore omitted them from the analysis.

The first MCSPAs metric, S0, denotes the average woody cover across extents, and serves as a rough measure of cross-scale habitat homogeneity:

$$S0 = \frac{1}{k}\sum_{i=1}^{k} P_{fi}(L)$$ (1)

where P_f is the percent cover in a given extent (window size) L_i, and k the number of extents analyzed. Low values reflect areas with little woody cover at all extents, while high values denote areas with abundant woody cover at most extents. The second metric, S1, is the standard deviation of woody cover across extents:

$$S1 = \sqrt{\frac{1}{k-1}\sum_{i=1}^{k}\left(P_{fi}(L)-S0\right)^2}$$ (2)

S1 is a measure of woody cover heterogeneity across extents; larger values imply that the proportion of woody cover varies greatly among different spatial extents. The third metric, S2, denotes the mean slope between the proportion of woody cover at the smallest spatial extent L_0 (here, a 3×3 window around the focal pixel) and the proportion of woody cover at any consecutive spatial extent:

$$S2 = \frac{1}{k}\sum_{i=1}^{k} \frac{P(L_i)-P(L_0)}{L_i-L_0}$$ (3)

Thus, S2 is a measure of directional consistency of the scalogram (e.g. a completely linear scalogram will have an S2 value of zero, as all slopes are identical).

Other landscape metrics

We compared the performance of the MCSPA metrics to a set of three commonly used single-scale landscape metrics, and to one remotely sensed vegetation index, NDVI. The landscape metrics were: proportion of woody habitat (Pf), woody patch density (PD), and edge density (ED, total length of all woody patch edges divided by landscape area). The proportion of woody habitat is strongly related to the average woody cover across extents (S0). Nevertheless, we tested both metrics since we wanted to assess whether spatial averaging (as in S0) improves the usefulness of woody cover in predicting species richness and composition.

Spatial scales and extents

The scale of an image consists of two components: spatial resolution (the minimal unit of description, i.e. a pixel, or grain), and extent (the size or area which is analyzed, consisting

of any number of pixels). To assess the effect of changing scale on the relationship between spatial pattern and species richness and composition, we conducted our analysis at two spatial resolutions (10 and 30-m pixels) and six spatial extents (from 210×210 to 510×510 m around each bird sample point, with 60-m intervals). The smallest spatial extent roughly overlapped the size of the bird sample plot, while the largest spatial extent was restricted to 510 m to minimize the overlap between adjacent plots to prevent spatial autocorrelation. The changing spatial extent was achieved by positioning rectangular analysis windows of varying sizes in each image, centered on each bird sample point. Therefore, for each bird sample point we generated a micro-landscape consisting of its surrounding pixels, which represents the habitat in its surrounding neighborhood. We used analysis windows of 21×21, 27×27, 33×33, 39×39, 45×45, and 51×51 pixels for the 10-m resolution image, and 7×7, 9×9, 11×11, 13×13, 15×15, and 17×17 pixels for the 30-m resolution image, to maintain identical spatial extents for both resolutions. We then calculated the landscape and MCSPA metrics in each resolution/extent combination. We calculated NDVI only for the 30-m resolution image, since we did not have 10-m NDVI data. Furthermore, since NDVI is a pixel based measure (i.e. it is calculated without considering neighboring pixels), we calculated its average value within each spatial extent.

Statistical analysis

For each metric, we generated three types of univariate regression models: quadratic ($S = a + bM + cM^2$), logarithmic ($S = \log(a + bM)$), and exponential ($S = a + b \times (1 - \exp(-c \times M))$). In these models, S is species richness, M is the metric's value, and a–c are model coefficients. We fitted the models according to the nature of the relationship between the metric and avian species richness in the study plots, at the two spatial resolutions and the six spatial extents. We used Akaike's information criterion (AIC) to select the best model for each metric, and to compare the general goodness of fit among models of different metrics and the predictive power of metrics across the two spatial resolutions and six spatial extents.

To assess the effects of spatial resolution and extent on the metric/richness relationships, we quantified the change in model coefficients for the selected models. For the quadratic models, we quantified the change in the slope and intercept. For the exponential models, we quantified the change in the intercept, asymptote, and rate of change (a, b, and c, respectively). For the logarithmic model, we quantified the rate and intercept (a and b, respectively). In addition to the visual interpretation, we evaluated the significance of the effect of spatial extent in the following way for selected models that had near-linear relationships between model coefficient values and spatial extents (given that our preliminary results showed that for all metrics, model types were consistent across spatial extents). First, we combined the observations from all six spatial extents together, and added a new predictive variable that denoted the areal extent of each observation. We then fitted the following models using nonlinear least squares. For the quadratic model, the model was:

$$S = (a + dE) + (b + eE) \times M + (c + fE) \times M^2 \qquad (4)$$

For the exponential model, the model was:

$$S = (a + dE) + (b + eE) \times (1 - \exp(-(c + fE) \times M)) \qquad (5)$$

where S is avian species richness, E is spatial extent (in number of pixels), M is the corresponding landscape or MCSPA metric, and a–f are coefficients. The coefficients d, e, and f denote the effects of extent on the original coefficients a, b, and c, respectively, and therefore represent the effects of extent on the relationship between metrics and avian species richness.

Spatial autocorrelation is a recurring phenomenon in spatial analyses of ecological communities. Here, we minimized its effects by limiting the spatial overlap between adjacent analysis neighborhoods by limiting the largest neighborhood size to 510×510 m (i.e. a maximum distance of 250 m from the focal pixel). While the shortest distance between sample points was 237.5 m, the average distance was 314 m, and only nine points were closer than 250 m from another point. In addition, we computed and analyzed empirical variograms of the residuals of all of our models in all metric/resolution/extent combinations and found no significant spatial autocorrelation.

We also assessed the relative contribution of different metrics to the variation in avian community structure at each sample plot using non-metric multidimensional scaling (NMDS), (Kruskal 1964, Clarke 1993) as implemented in the package vegan (Oksanen et al. 2010) of the R statistical software (R development core team 2010). The species data table used for the NMDS analysis consisted of 243 rows (sample plots) and 70 columns (individual species abundances). We log-transformed the abundance data to limit the effect of extreme values. We then generated a dissimilarity matrix among sample plots using the Bray–Curtis distance measure. Finally, we ran a non-metric multidimensional scaling ordination (NMDS) using random starting coordinates, 10 runs with real data, two axes, and up to 20 iterations. For each combination of spatial resolution and extent we quantified the relative contribution of the landscape metrics to the variation in the avian community by fitting a generalized additive model (GAM) to the first two axes of the ordination simultaneously. We used a GAM instead of the common vector fitting approach since the relationships between the metrics and the first two NMDS axes were mostly nonlinear. The coefficient of determination of the GAM was used as a measure of the contribution of the metric to the variation in avian community structure.

Results

Metrics and species richness

Over three years, 68 bird species were detected in the study area. Avian species richness averaged 13.02 ($\pm$ 5.02 SD) species per plot per year and was highly variable depending on the habitat context of the sample plots. The annual average of species richness ranged from 1 to 23.5 species. Savanna plots had the highest richness, followed by woodland and

grassland plots. Brown-headed cowbird was the most broadly distributed species in the study area, occurring in 195 of the 243 plots (80.2%), followed by indigo bunting (77%), field sparrow (72.8%), eastern towhee (72.4%), chipping sparrow (69.5%), and vesper sparrow (66.3%) (Table 1).

We found clear relationships between avian species richness and the spatial pattern of woody vegetation. On areas of low edge density, low variation of woody cover across scales, little patchiness, and very low or very high woody cover (i.e. core areas of grasslands and woodlands), avian species richness was relatively low. In contrast, areas of high edge density, intermediate woody cover, high cover variation, and high patchiness (i.e. savannas) had high avian species richness. There were two general types of relationships between landscape metrics and species richness, and these relationships were consistent across spatial resolutions and extents (Fig. 2). Woody cover (Pf), average woody cover across extents (S0), and NDVI had a quadratic relationship with avian species richness, while standard deviation of cover across extents (S1), patch density (PD), and edge density (ED) had a nonlinear relationship with richness, best depicted by a saturation curve with either an exponential or a logarithmic form. The relationship between species richness and patch density was best explained by a logarithmic model at the finer resolution, and by an exponential model at the coarser resolution, while the relationship between species richness and the standard deviation of cover across extents behaved in the opposite manner (i.e. exponential at 10 m, logarithmic at 30 m).

The mean scalogram slope between the focal scale and all larger scales (S2) was difficult to relate to species richness, since it consisted of both positive and negative values. We therefore omitted it from the rest of the analysis.

The metrics that are strongly related to absolute forest cover (woody cover, average woody cover across extents, and NDVI at 30-m resolution) were highly and linearly correlated at all spatial scales and extents. The standard deviation of cover across extents was moderately but nonlinearly correlated with edge density and patch density, while the mean slope of the scalogram had weak nonlinear correlations with all other metrics.

Predictive power of metrics across different spatial scales

At 10-m resolution, and for all metrics except average woody cover across extents, the smallest spatial extent yielded the highest predictive power (Table 2a). Edge density was always the best predictor of avian species richness at 10-m resolution (Table 2b), followed by the standard deviation of woody cover across extents (S1) at all spatial extents. The third best predictor was patch density, but it was only superior to the average woody cover across extents and woody cover at the four smaller extents (21×21–39×39) and inferior to all other predictors at the two largest extents (45×45, 51×51). The average woody cover across extents was a better predictor than woody cover at the three larger spatial extents, and inferior to it at the three small spatial extents. For woody cover, larger spatial extents improved predictive power, and the strongest predictive power was obtained at the 45×45

extent (though the difference between the AIC of it and the next smaller and larger spatial extents was small).

At 30-m resolution, NDVI was consistently the best predictor of avian species richness (Table 2b). After NDVI, the order of predictive power was always patch density, edge density, standard deviation of woody cover across extents, woody cover, and average woody cover across extents. The effect of extent on the predictive power of metrics at the 30-m resolution was almost opposite to its effect at the 10-m resolution analysis. At 30-m resolution, all metrics except NDVI had stronger predictive power at larger spatial extents. Edge density and the standard deviation of woody cover across extents had the greatest predictive power at the 15×15 extent, while average woody cover across extents, woody cover, and patch density had the strongest predictive power at the largest extent, 17×17. NDVI did not exhibit a consistent effect of scale on predictive power of species richness.

In the vast majority of cases, metrics computed at 10-m resolution had a stronger predictive power of avian richness than metrics computed at 30-m resolution (Table 2c). The exception was patch density at the two largest extents, where the 30-m resolution yielded a better predictive power. Thus, in Ft McCoy, avian species richness was generally better predicted by metrics computed at finer spatial scales (both in terms of spatial resolution in almost all cases, and in terms of extent except for average woody cover across extents).

Effects of scale and extent on the relationships between metrics and richness

Interesting scale effects emerged when the best predictive models for each metric were compared across spatial extents based on the 10-m resolution image (Fig. 3). Four metrics (average woody cover across extents, standard deviation of woody cover across extents, woody cover, and patch density) exhibited consistent relationships with avian richness across spatial extents (i.e. for a given metric value, both the direction and magnitude of the predicted avian richness were consistent with the change in spatial extent). Average woody cover across extents was more robust than woody cover in predicting avian richness, since for a given value the range of richness predictions (across extents) was smaller than the range yielded by an equivalent woody cover value. In contrast to all other metrics, edge density exhibited a unique threshold effect in regards to spatial extent. For edge density values smaller than 0.4, smaller spatial extents predicted higher species richness than larger spatial extents, but the differences in richness predictions decreased as edge density approached 0.4. Once an edge density value of 0.4 was exceeded, the trend reversed, and smaller spatial extents led to lower predictions of avian richness compared to larger spatial extents.

Spatial resolution had varied effects on the relationships between richness and metrics at different spatial extents (Fig. 3). For the quadratic models (woody cover and average woody cover across extents), increasing the spatial resolution from 10 to 30 m slightly flattened the relationship, meaning that at extreme values (i.e. $< 20\%$ or $> 80\%$), the 30-m data tended to predict higher richness than the 10-m

Table 1. Avian species detected in the 243 sample plots during the three years study period. AOU column is American Ornithologists' Union four-letter code.

Common name	Scientific name	AOU	Relative frequency of occurrence (%)	Average abundance
American crow	Corvus brachyrhynchos	AMCR	63.4	0.57
American goldfinch	Spinus tristis	AMGO	37.9	0.3
American redstart	Setophaga ruticilla	AMRE	8.6	0.07
Baltimore oriole	Icterus galbula	BAOR	54.3	0.54
Barn swallow	Hirundo rustica	BARS	11.5	0.1
Black-and-white warbler	Mniotilta varia	BAWW	12.3	0.07
Black-billed cuckoo	Coccyzus erythropthalmus	BBCU	10.3	0.04
Black-capped chickadee	Poecile atricapillus	BCCH	40.3	0.3
Blue jay	Cyanocitta cristata	BLJA	51	0.35
Blue-gray gnatcatcher	Polioptila caerulea	BGGN	27.6	0.18
Blue-winged warbler	Vermivora pinus	BWWA	29.2	0.19
Brown thrasher	Toxostoma rufum	BRTH	35.8	0.28
Brown-headed cowbird	Molothrus ater	BHCO	80.2	1.28
Cedar waxwing	Bombycilla cedrorum	CEDW	26.7	0.42
Chestnut-sided warbler	Dendroica pensylvanica	CSWA	12.8	0.1
Chipping sparrow	Spizella passerina	CHSP	69.5	0.85
Clay-colored sparrow	Spizella pallida	CCSP	21	0.13
Cliff swallow	Petrochelidon pyrrhonota	CLSW	3.7	0.06
Common nighthawk	Chordeiles minor	CONI	8.6	0.05
Common yellowthroat	Geothlypis trichas	COYE	23.9	0.16
Dickcissel	Spiza americana	DICK	14	0.16
Downy woodpecker	Picoides pubescens	DOWO	11.9	0.05
Eastern bluebird	Sialia sialis	EABL	60.1	0.59
Eastern kingbird	Tyrannus tyrannus	EAKI	40.3	0.31
Eastern meadowlark	Sturnella magna	EAME	23.9	0.22
Eastern phoebe	Sayornis phoebe	EAPH	9.5	0.05
Eastern towhee	Pipilo erythrophthalmus	EATO	72.4	0.98
Eastern wood-pewee	Contopus virens	EAWP	58.4	0.5
Field sparrow	Spizella pusilla	FISP	72.8	1.47
Golden-winged warbler	Vermivora chrysoptera	GWWA	3.7	0.01
Grasshopper sparrow	Ammodramus savannarum	GRSP	51	1.31
Gray catbird	Dumetella carolinensis	GRCA	41.2	0.3
Great-crested flycatcher	Myiarchus crinitus	GCFL	37.4	0.22
Hairy woodpecker	Picoides villosus	HAWO	20.2	0.1
Hermit thrush	Catharus guttatus	HETH	5.3	0.04
Hooded warbler	Wilsonia citrina	HOWA	6.6	0.06
Horned lark	Eremophila alpestris	HOLA	14	0.22
House wren	Troglodytes aedon	HOWR	42.8	0.32
Indigo bunting	Passerina cyanea	INBU	77	0.99
Killdeer	Charadrius vociferus	KILL	2.9	0.02
Lark sparrow	Chondestes grammacus	LASP	22.6	0.14
Least flycatcher	Empidonax minimus	LEFL	6.6	0.08
Mourning dove	Zenaida macroura	MODO	59.3	0.54
Mourning warbler	Oporornis philadelphia	MOWA	7	0.05
Nashville warbler	Vermivora ruficapilla	NAWA	11.1	0.05
Northern flicker	Colaptes auratus	NOFL	20.6	0.1
Orchard oriole	Icterus spurius	OROR	26.3	0.2
Ovenbird	Seiurus aurocapillus	OVEN	32.9	0.52
Pileated woodpecker	Dryocopus pileatus	PIWO	5.3	0.02
Pine warbler	Dendroica pinus	PIWA	7.4	0.08
Red-bellied woodpecker	Melanerpes carolinus	RBWO	9.5	0.04
Red-breasted nuthatch	Sitta canadensis	RBNU	10.3	0.06
Red-eyed vireo	Vireo olivaceus	REVI	41.6	0.36
Red-headed woodpecker	Melanerpes erythrocephalus	RHWO	16	0.1
Red-winged blackbird	Agelaius phoeniceus	RWBL	5.3	0.04
Rose-breasted grosbeak	Pheucticus ludovicianus	RBGR	56.8	0.47
Ruby-throated hummingbird	Archilochus colubris	RTHU	10.7	0.05
Savannah sparrow	Passerculus sandwichensis	SAVS	3.7	0.02
Scarlet tanager	Piranga olivacea	SCTA	51	0.41
Song sparrow	Melospiza melodia	SOSP	29.6	0.23
Tree swallow	Tachycineta bicolor	TRES	8.2	0.06
Upland sandpiper	Bartramia longicauda	UPSA	16.5	0.13

(Continued)

Table 1. (Continued).

Common name	Scientific name	AOU	Relative frequency of occurrence (%)	Average abundance
Veery	*Catharus fuscescens*	VEER	7.8	0.08
Vesper sparrow	*Pooecetes gramineus*	VESP	66.3	1
White-breasted nuthatch	*Sitta carolinensis*	WBNU	42.4	0.27
Wood thrush	*Hylocichla mustelina*	WOTH	4.5	0.03
Yellow-billed cuckoo	*Coccyzus americanus*	YBCU	20.2	0.09
Yellow-throated vireo	*Vireo flavifrons*	YTVI	17.7	0.1

data. In intermediate metric values, the 10-m data tended to predict higher avian richness. For the standard deviation of woody cover across extents, the 30-m data predicted higher richness at high and very low metric values, while at low to intermediate values the 10-m data tended to predict more richness than the 30-m data. For patch density, once its value increased above ~0.1, the 30-m data predicted higher richness for all extents except 210×210 m, where the 10-m data consistently predicted higher richness. However, for both patch density and standard deviation of woody cover across extents the model type differed across spatial resolutions (from exponential to logarithmic or vice versa), thus the results are less conclusive. Finally, for edge density, the 10-m data consistently predicted higher richness (at comparable extents) for metric values above 0.4, but had mixed interactions between richness, spatial resolution, and extent at lower metric values.

When model coefficients were analyzed for resolution and extent effects (Fig. 4), we found that for the three quadratic models (woody cover, average woody cover across extents, and NDVI at the 30-m resolution) only the intercept (a) changed across extents, while all three coefficients were sensitive to spatial resolution (again, except for NDVI that had only one spatial resolution). This was confirmed by the regression analysis (Eq. 4), where d (the coefficient denoting the effect of extent on the intercept) was the only significant scaling coefficient (among d, e, and f. The original coefficients a, b, and c remained significant). For NDVI, d was almost significant, with p = 0.056. For the exponential and logarithmic fitted models, the relationships between coefficient values and extent were less consistent (Fig. 5). For edge density, the intercept (a) decreased nonlinearly with extent, the asymptote (b) increased with extent, and the rate (c) decreased with extent. All of these coefficients were significantly affected by extent (the coefficients d, e, and f in Eq. 5 were significant). For the exponential model of the standard deviation of woody cover across extents (at the 10 m resolution only), the intercept and the rate decreased while the asymptote increased across the first three extents, but remained fairly constant at higher extents. Finally, for the exponential model of patch density at the 30-m resolution, the intercept decreased with extent while the asymptote and rate generally increased with extent. Since both patch density and the standard deviation of woody cover across extents had different model types across pixel sizes, we could not compare the effect of spatial resolution on their model coefficients. In addition, since the relationships between coefficient values and extent were nonlinear, we could not assess the significance of the effects of extent using equations 4–5 as we did for the other metrics.

Metrics and community structure

The NMDS ordination of the sample plots had a stress value of 14.55 after 20 iterations, which is acceptable for the purpose of our analysis (McCune and Grace 2002). High values of the first axis of the NMDS (NMDS1 hereafter) corresponded to high abundance of woodland bird species (such as ovenbird, scarlet tanager, rose-breasted grosbeak, wood thrush, and red-eyed vireo) while low vales of NMDS1 corresponded to high abundance of grassland species (e.g. upland sandpiper, grasshopper sparrow, and eastern meadowlark) and intermediate values of NMDS1 corresponded to high abundance of savanna species (e.g. brown thrasher, eastern kingbird, baltimore oriole, and field sparrow). On the other hand, high values of NMDS2 corresponded to high abundance of savanna species, while intermediate values of NMDS2 corresponded to high abundance of either woodland or grassland species. There were two general types of relationships between landscape metrics and community structure. The metrics related to cover (woody cover, average woody cover across extents, and NDVI) peaked at the largest values of NMDS1, which corresponded with woodland species, and intermediate values of NMDS2. These metrics then decreased through intermediate values of NMDS1 and high values of NMDS2, and reached a minimum at low values of NMDS1 and intermediate values of NMDS2, which corresponded with grassland species (Fig. 6(S0), 6(Pf), 7(S0), 7(Pf), and 7(NDVI)). The heterogeneity related metrics (standard deviation of woody cover across extents, patch density, and edge density) peaked at intermediate NMDS1 values and high NMDS2 values, and decreased with both increasing and decreasing NMDS1 values, coupled with decreasing NMDS2 values (Fig. 6(S1), 6(PD), 6(ED), and 7(S1), 7(PD), 7(ED)). This gradient showed that areas of high spatial heterogeneity of woody cover (i.e. savannas) have a different avian community structure than areas either high or low heterogeneity (i.e. woodlands or grasslands), and the differences in community composition between savanna and woodland as well as between savanna and grassland communities were smaller than the compositional difference between woodland and grassland communities.

Metrics related to woody cover were much better predictors of variation in community structure than the heterogeneity metrics (Table 3). At both spatial resolutions, average woody cover across extents was the strongest predictor at the larger spatial extents, while woody cover was the strongest predictor at the smaller spatial extents. They were followed by (NDVI at the 30-m resolution) edge density, patch density, and standard deviation of woody cover across extents, in that order. The latter was consistently the weakest predictor
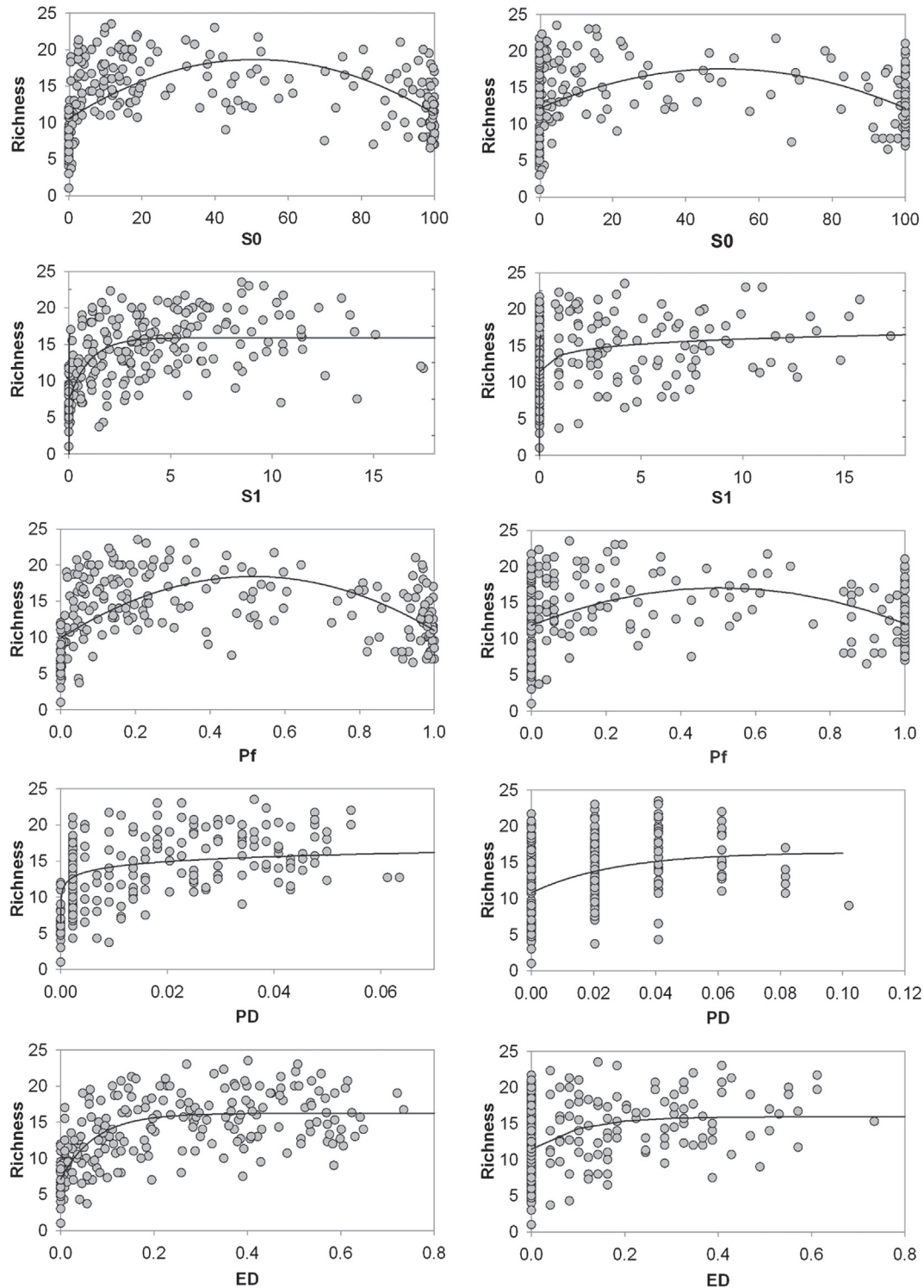
Figure 2. Relationships between landscape or MCSPA metrics and avian species richness. Plots depict the 210 × 210 m spatial extent, in two spatial resolutions (10 m, left column; 30 m, right column).

of community structure, with R^2 values only as high as 0.52. At the 30-m resolution, its performance was even worse (maximum $R^2 = 0.32$).

For individual metrics at a given resolution, the effect of spatial extent on their power to predict community structure was less pronounced than its effect on their power to predict avian species richness. At both resolutions, the

predictive power of average woody cover across extents increased with spatial extent, though the magnitude of the increase was small (Table 3). Woody cover exhibited an opposite pattern (i.e. decreasing predictive power with increasing extent), and its strongest predictive power was at the second smallest extent (270 × 270 m). Again, the difference in predictive power across scale was small. Patch

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Table 2. Goodness of fit of univariate models predicting avian species richness for different landscape and MCSPA metrics, across six spatial extents and two spatial resolutions (10 and 30 m). Differences in goodness of fit are represented by AIC differences (ΔAIC) from the best model (ΔAIC = 0), and are calculated between metrics (within rows in table a), spatial extent (within columns in table b), and spatial resolution (c). The left half of tables a–b represents the 10 m resolution, while the right side represents the 30 m resolution. The best models are highlighted in bold. Metric abbreviations are: average woody cover across extents (S0), standard deviation of woody cover across extents (S1), woody cover (Pf), patch density (PD), and edge density (ED).

(a) ΔAIC relative to the best model per metric across extents (row-wise).

	10 m						30 m					
	210×210	270×270	330×330	390×390	450×450	510×510	210×210	270×270	330×330	390×390	450×450	510×510
S0	12.16	6.18	2.40	1.15	**0.00**	0.46	9.32	6.64	4.15	2.37	1.05	**0.00**
S1	**0.00**	8.19	24.93	44.69	57.79	69.99	17.72	13.23	1.86	3.70	**0.00**	1.74
Pf	**0.00**	1.29	2.79	6.62	9.23	10.32	12.38	9.45	5.27	4.28	2.68	**0.00**
PD	**0.00**	20.55	43.48	54.34	68.87	76.91	57.94	44.02	17.27	19.89	12.73	**0.00**
ED	**0.00**	0.02	4.99	15.99	23.40	29.89	30.09	25.40	13.35	11.97	**0.00**	4.23
NDVI	–	–	–	–	–	–	3.11	**0.00**	3.95	5.20	2.32	1.86

(b) ΔAIC relative to the best model per extent across metrics (column-wise).

	10 m						30 m					
	210×210	270×270	330×330	390×390	450×450	510×510	210×210	270×270	330×330	390×390	450×450	510×510
S0	100.26	94.27	85.50	73.26	64.70	58.67	78.82	79.25	72.81	69.78	71.33	70.74
S1	22.35	30.52	42.29	51.04	56.74	62.45	69.77	68.38	53.07	53.65	52.83	55.04
Pf	86.62	87.90	84.42	77.25	72.45	67.05	75.43	75.60	67.47	65.23	66.51	64.29
PD	33.10	53.63	71.60	71.45	78.58	80.12	66.11	55.29	24.59	25.95	21.68	9.41
ED	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	66.17	64.59	48.59	45.96	36.87	41.56
NDVI	–	–	–	–	–	–	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**

(c) ΔAIC relative to the best model per metric/extent combination across spatial resolutions (extents are directly comparable). Negative values indicate that the 10 m model was stronger than the 30 m model.

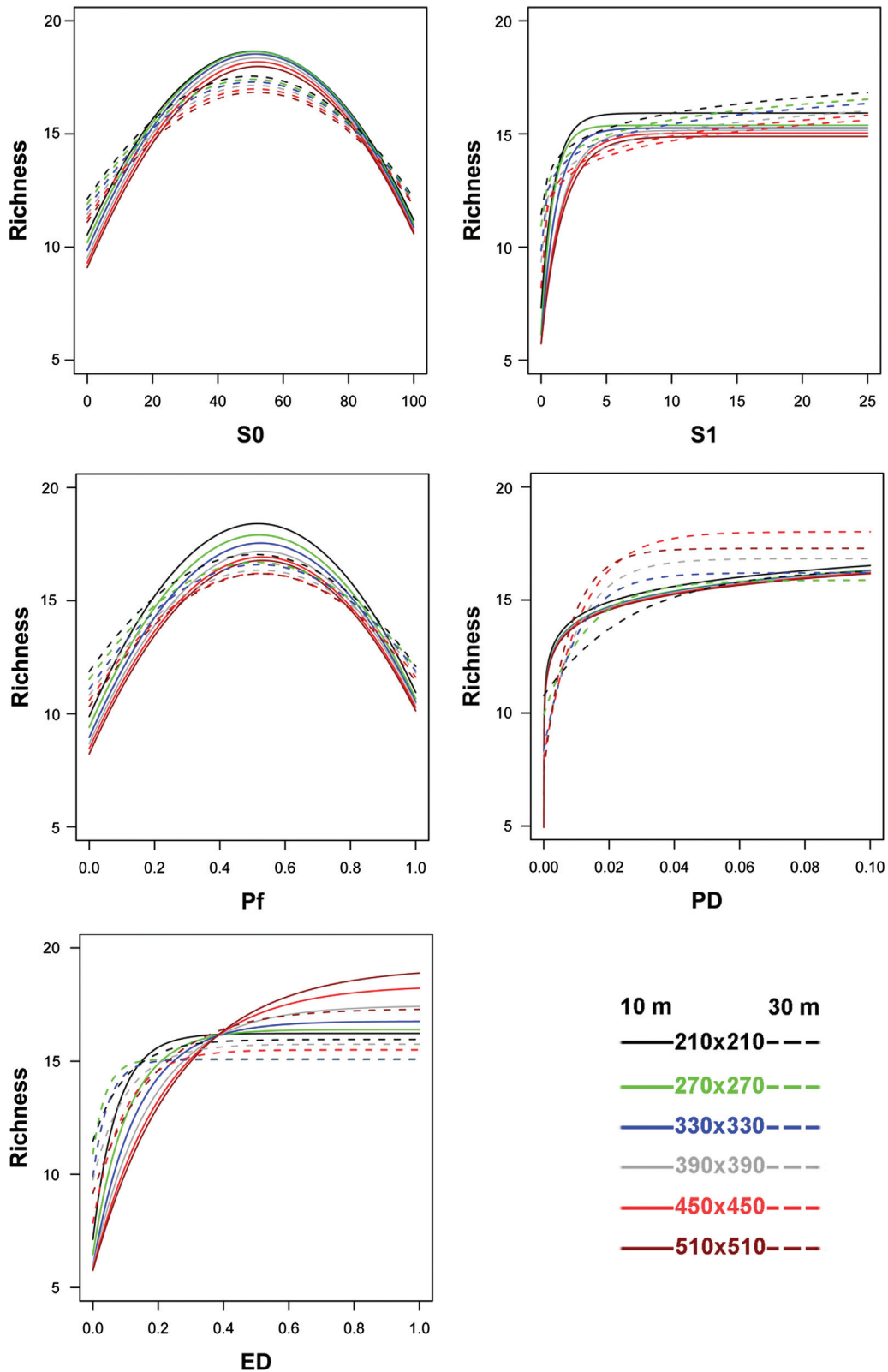|	ΔAIC (10–30 m)					
	210×210	270×270	330×330	390×390	450×450	510×510
S0	–49.95	–53.25	–54.55	–54.01	–53.84	–52.33
S1	–118.81	–106.13	–78.02	–60.10	–43.30	–32.84
Pf	–60.20	–55.97	–50.30	–45.47	–41.27	–37.50
PD	–104.40	–69.92	–20.24	–12.00	9.69	30.46
ED	–137.56	–132.86	–115.84	–103.45	–84.08	–81.81

Figure 3. Effects of spatial resolution (10 m solid; 30 m dashed) and spatial extent (colors) on the relationships between metrics and avian species richness.

density and edge density exhibited opposite trends at different grain sizes. At the 10-m resolution, their power to predict avian community structure decreased with extent (and the highest R² from models using patch density occurred at the second smallest extent). At the 30-m resolution, their predictive power increased with extent, and the range of increase was larger than the range exhibited among models at different extents of any other metrics. The effect
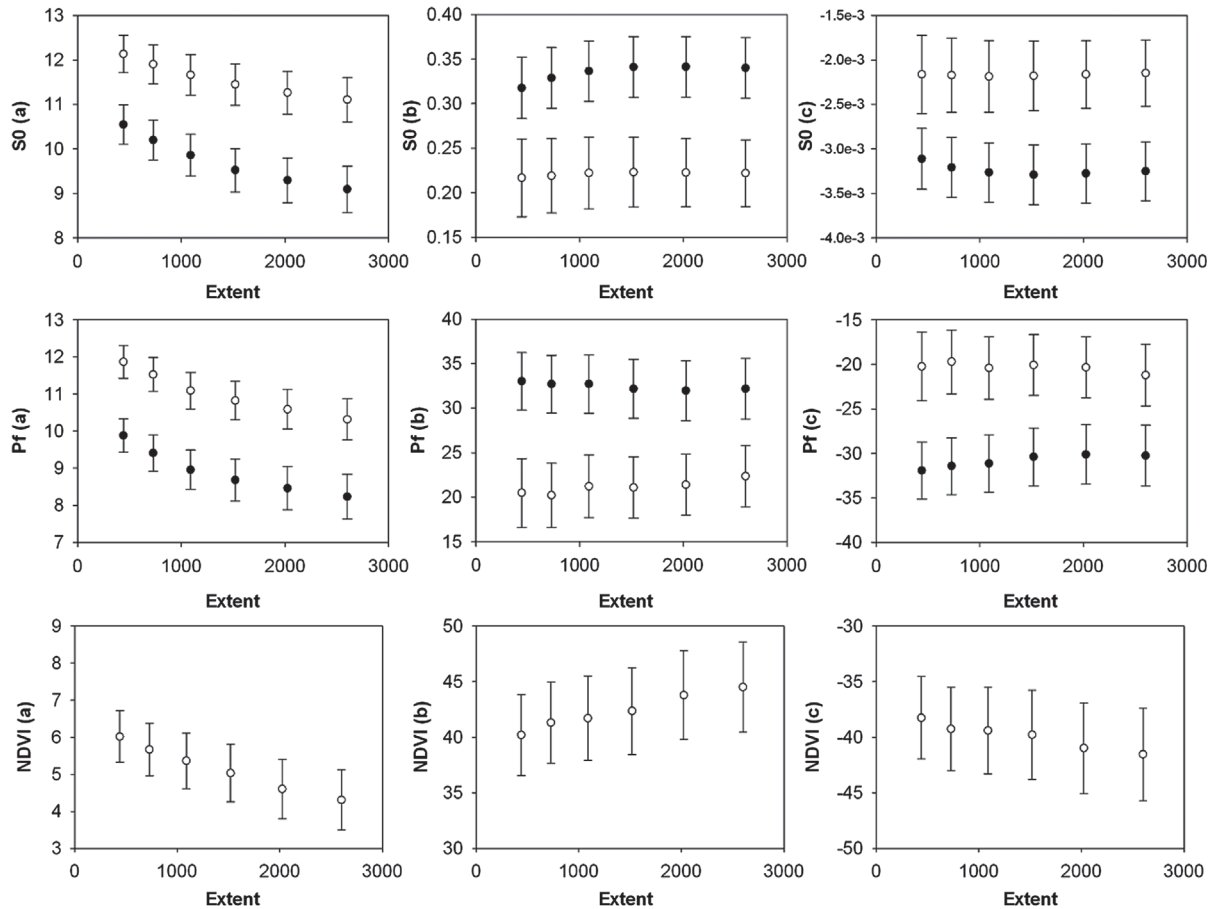
Figure 4. Effects of spatial extent on the coefficients of the quadratic models (average woody cover across extents (S0), woody cover (Pf), and NDVI). The 10-m resolution models are depicted by black circles, while the 30-m resolution models are depicted by white circles. NDVI was modeled only at the 30-m resolution; therefore there is no spatial resolution comparison. Error bars denote standard deviations.

of spatial extent on the predictive power of the standard deviation of woody cover across extents was also inconsistent across spatial resolutions, as it decreased with extent at the 10-m resolution, and peaked at a middle extent at the 30-m resolution.

Discussion

Models of species richness and community abundance distributions typically incorporate and benefit from spatial information about habitat and landscape characteristics. There are many ways to quantify habitat characteristics based on field and remotely sensed data. Yet the vast majority of these approaches analyze spatial information at a single cartographic or ecological scale (Li and Wu 2004). It is likely, however, that individual species perceive their environments at multiple spatial scales (Manning et al. 2004). Thus, using single scale information to describe habitat characteristics may not capture the relevant multi-scale landscape patterns species respond to (Wiens 1981, Lawler and Edwards 2006). Moreover, given the inherent scale dependence of spatial metrics (which are used to quantify species – landscape relationships), coupled with species – scale relationships per se, the relationships between species richness and

spatial patterns are scale dependent as well (Rahbek and Graves 2001). Here, by quantifying relationships between the avian community and the spatial pattern of habitat, we highlight the importance of explicitly considering scale in models of species habitat relationships, corroborating prior studies (Cushman and McGarigal 2002, 2004, Lawler and Edwards 2006). Landscape metrics (and NDVI) exhibited one of two general types of relationships with species richness, and these functional forms were mostly consistent across spatial grains and extents. We found quadratic relationships for metrics that quantify cover (woody cover, average woody cover across extents, and NDVI). For these metrics, intermediate cover values were associated with the highest levels of avian species richness. This made sense ecologically since intermediate cover values often represent the savannas in the study area. These savannas have considerably higher avian richness compared to less heterogeneous habitat types of woodland (high woody cover) and grassland (very low woody cover) (average species richness of 16.77 ± 0.33 in savanna, 12.78 ± 0.35 in woodland, and 7.36 ± 0.44 in grassland; Wood unpubl.). Areas of high vegetation and species richness and structural heterogeneity, such as the savannas at Fort McCoy, are typically associated with areas of higher bird diversity (Cody 1981, Rotenberry 1985). We found exponential or logarithmic relationships between
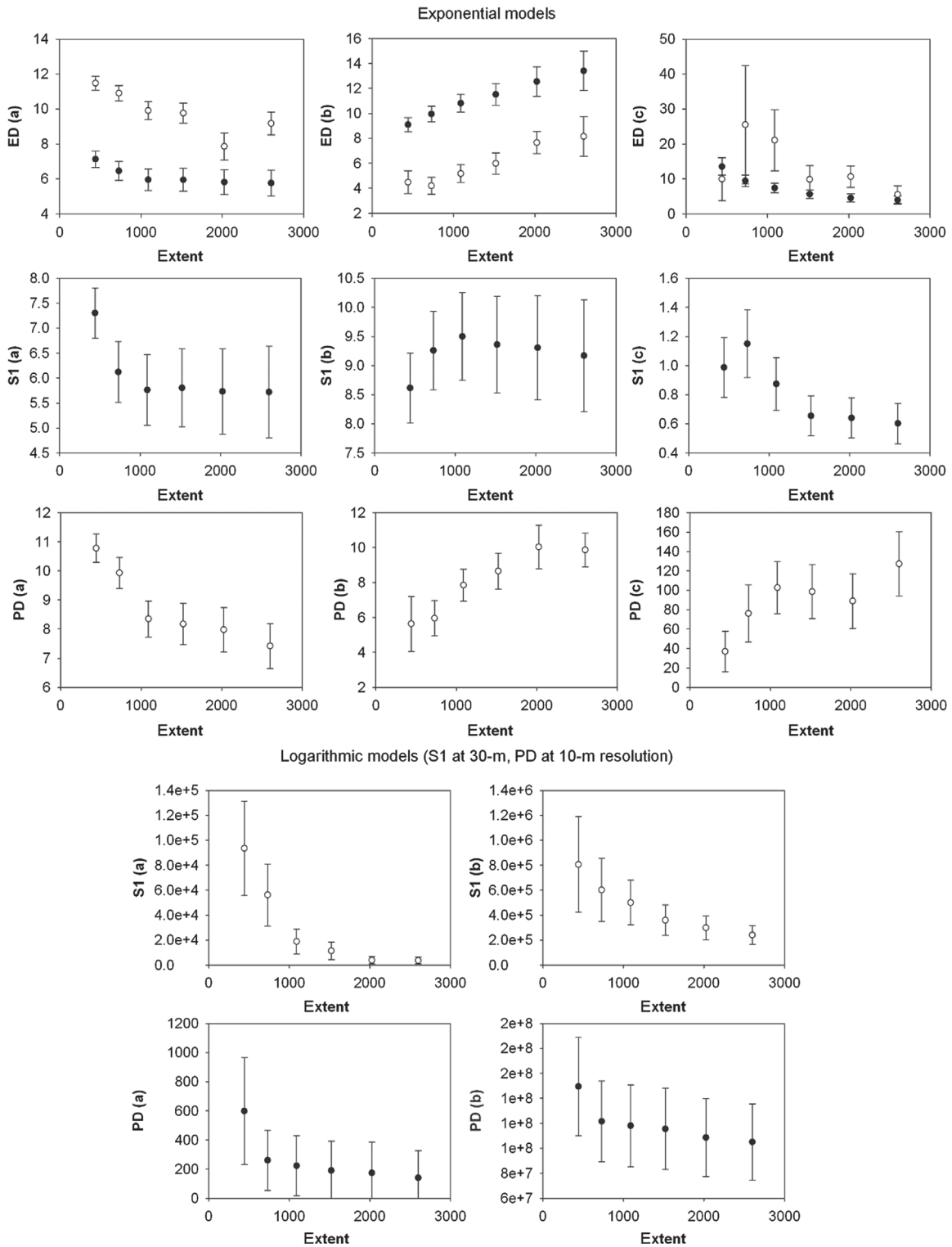
Figure 5. Effects of spatial extent on the coefficients of the nonlinear models. Edge density (ED) is fitted an exponential model at both spatial resolutions (10 m, black circles; 30 m, white circles), while the standard deviation of woody cover across extents (S1) and patch density (PD) were fitted with an exponential model at 10- and 30-m resolution, respectively, and a logarithmic model at the other spatial resolution. Error bars denote standard deviations.

avian richness and metrics that capture habitat heterogeneity (standard deviation of woody cover across extents, patch density, and edge density). In these cases, higher metric values were observed in the savanna areas, which again, had the highest avian diversity in the study area.

At the finer spatial resolution (10 m), measures of habitat heterogeneity (edge density, standard deviation of woody cover across extents, and patch density in that order) were the best predictors of avian species richness regardless of spatial extent. Interestingly, image variance, which is a first-order
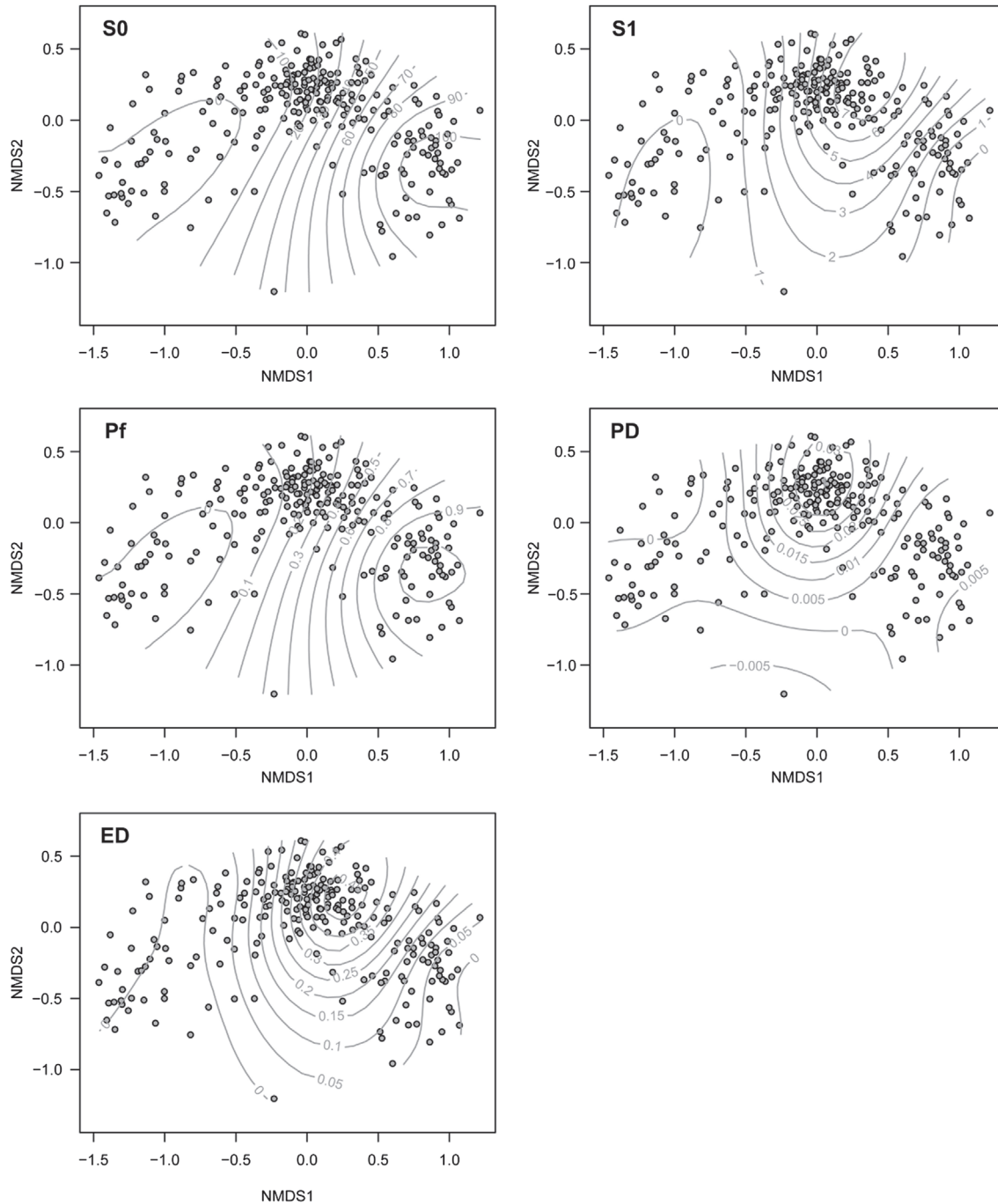
Figure 6. NMDS ordination biplot of avian community structure and its relationship with landscape or MCSPA metric. Metrics were calculated at a 10-m spatial resolution and a spatial extent of 210×210 m. Each circle represents a sample point, while contours depict the functional relationship between the ordination and a corresponding landscape/MCSPA metric.

image texture measure (Haralick 1979), and is conceptually similar to the standard deviation of woody cover across extents, was the strongest predictor of avian species richness in this study area (Wood unpubl.). In contrast to the finer spatial resolution, at the coarser spatial resolution (30 m), NDVI was the strongest predictor of avian richness at all spatial extents by far. We explain this superiority by the fact that in contrast to all other metrics that are based on a binary landscape representation, NDVI is based on a continuous representation of the landscape. As such, it is less prone to the loss of information about fine-scale habitat heterogeneity

that happens when a fine grained mosaic of woodlands and grasslands is depicted by a binary woody/non-woody map (McGarigal et al. 2009). In general, the contrasting effect of spatial resolution in terms of which variables better explain species richness may occur because bird species select their habitats in a spatially hierarchical manner (Wiens et al. 1987). At the coarse scale, habitat selection is driven by the presence of the dominant habitat type (e.g. woodlands), which is captured by cover-related metrics such as NDVI. At the fine scale, vegetation structure and species drive habitat selection by birds (Lawler and Edwards 2006).
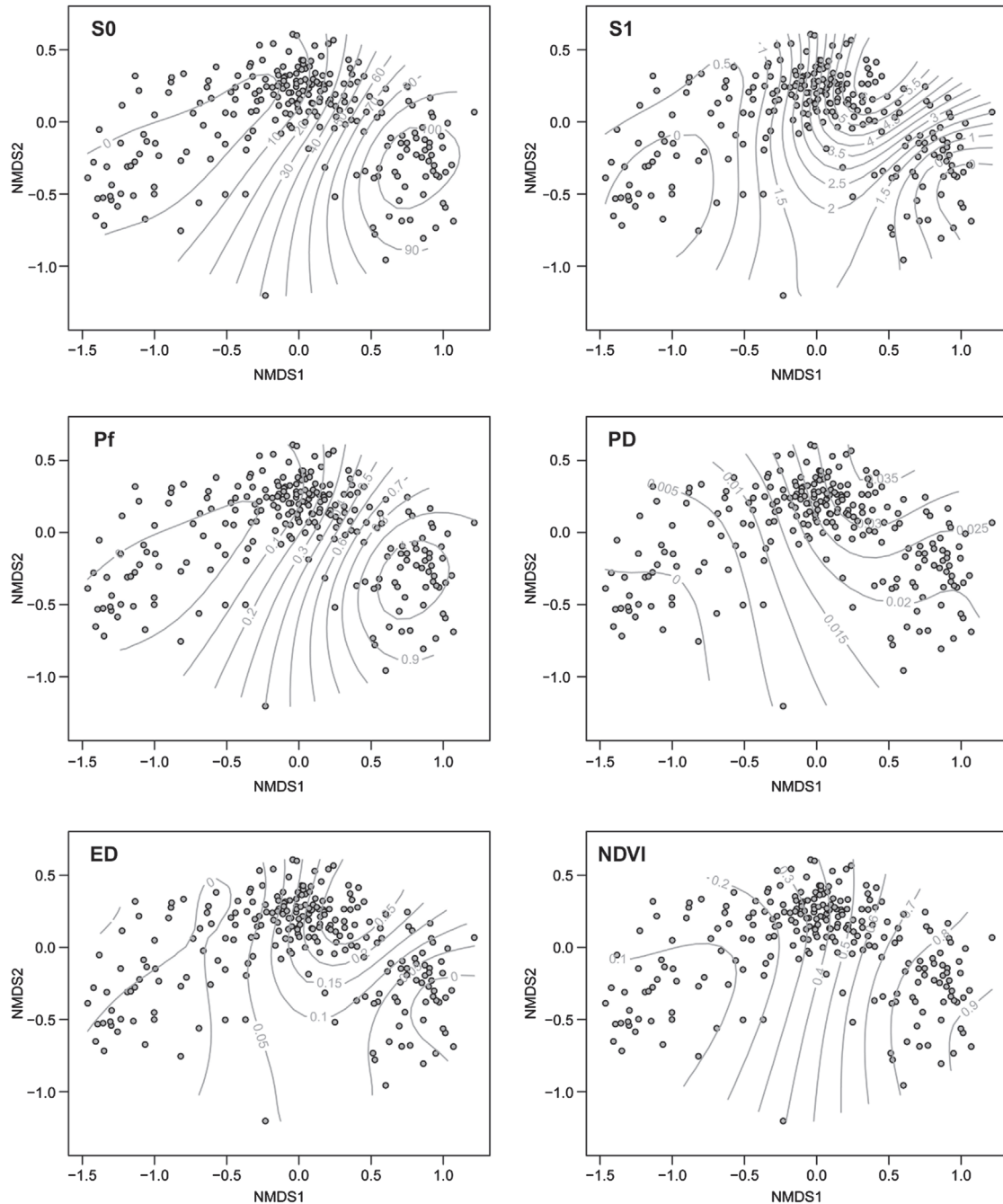
Figure 7. NMDS ordination biplot of avian community structure and its relationship with landscape or MCSPA metric. Metrics were calculated at a 30-m spatial resolution and a spatial extent of 210×210 m. Each circle represents a sample point, while contours depict the functional relationship between the ordination and a corresponding landscape/MCSPA metric.

Spatial resolution and extent had complex effects on the relationships between spatial metrics and avian species richness. While spatial extent had overall consistent effects on the relationships between metric (except for edge density), its interaction with spatial resolution had more complex effects on metric–richness relationships, especially for the metrics that are best described by exponential (and logarithmic) models.

Our results reveal that univariate models that explain avian species richness using landscape metrics tend to be better at smaller spatial extents when the pixel size is small (10 m), but better at larger extents when the pixel size is large

(30 m), for all metrics except average woody cover across extents. We suggest that this contrasting effect of spatial resolution is caused by the relationship between fine-scale landscape heterogeneity and avian richness in our study area. Generally, our fine-resolution models are always better than the coarse-resolution models in predicting avian richness. The 10-m resolution is sufficient to describe the fine scale heterogeneity that is known to successfully explain avian richness (St-Louis et al. 2006). At the 30-m resolution, much information about the fine scale heterogeneity is lost, thus larger scale variations in habitat (here, distinctions between three major habitat types of grassland, savanna, and

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Table 3. Goodness-of-fit (denoted as R²) of the generalized additive models that relate landscape or MCSPA metrics to the NMDS ordination of avian community structure. The left side of the table denotes the 10-m resolution metrics, while the right side denotes the 30-m resolution metrics.

	10 m						30 m					
	210×210	270×270	330×330	390×390	450×450	510×510	210×210	270×270	330×330	390×390	450×450	510×510
S0	0.89	0.90	0.91	0.91	0.92	0.92	0.89	0.90	0.91	0.91	0.91	0.91
S1	0.53	0.49	0.43	0.40	0.34	0.31	0.28	0.32	0.33	0.31	0.29	0.27
Pf	0.91	0.92	0.91	0.89	0.87	0.85	0.90	0.90	0.89	0.87	0.85	0.83
PD	0.68	0.74	0.71	0.69	0.68	0.66	0.28	0.29	0.37	0.42	0.45	0.49
ED	0.71	0.75	0.77	0.77	0.77	0.76	0.40	0.46	0.49	0.51	0.49	0.52
NDVI	–	–	–	–	–	–	0.89	0.89	0.88	0.86	0.85	0.83

woodland, which require larger spatial extents to be captured) explain better the variation in avian species richness. Therefore, even within the relatively few scale combinations studied here (compared to a much larger number of ecological scales relevant to all species in the avian community in our study area) it is obvious that varying factors affect species richness at different scales, and the choice of sampling design (resolution and extent) and modeling framework may thus strongly affect the results (Wiens 1981, Wiens et al. 1987, Rahbek and Graves 2001).

In the quadratic models of richness versus metrics (woody cover, average woody cover across extents, and NDVI), the only significant effect of spatial extent was the decrease of the intercept. On the other hand, spatial resolution had a more complex effect on the model, where extreme metric values (very low or very high) tended to predict higher richness at a coarser spatial resolution, and intermediate metric values predicted lower richness at a coarser (Fig. 3). We explain this result by the way the coarser resolution (30 m) image was generated. We followed the path of the vast majority of scale studies and used a majority filter to resample the fine resolution image to a coarser resolution. However, resampling with a majority filter means that areas that are characterized by very fine scale heterogeneity (at a 3×3 focal window of 10 m pixels, which is used to resample the image to 30 m resolution) tend to be converted to either grasslands or woodlands. Thus, the overall abundance of these areas is expected to decrease (while their higher richness values are retained). This can shift higher richness values towards the extremes (i.e. low or high metric values) of the richness–metric relationship, and explain the effect of spatial resolution that was evident in our results (Fig. 3). Ultimately, this is an outcome of the reliance on a binary landscape for spatial analysis, coupled with the choice of a majority filter to rescaling to coarser resolutions (which is known to affect the pattern of the coarser-scale maps, and as a consequence the species–pattern relationships; Parody and Milne 2004). We expect that NDVI, which is a continuous measure, will be less susceptible to this phenomenon (McGarigal et al. 2009). Unfortunately, we did not have 10-m NDVI data to test this assumption.

The most striking effect of spatial extent on the richness–metrics relationship was exhibited by edge density. At the finer resolution, the exponential models of richness versus edge density intersected approximately when edge density was 0.4. Mathematically, this was caused because the intercept (a) and the rate (b) coefficients of the model decreased significantly with extent, while the asymptote coefficient (c) increased significantly with extent. We do not have a plausible ecological explanation for this phenomenon.

The avian community in the study area consisted of three main assemblages, which roughly corresponded to the three major habitat types, grasslands, savannas, and woodlands. The variation in avian community structure corresponded strongly to gradients of landscape and MCSPA metrics. In general, there were two types of metrics–community structure relationships. Woody cover based metrics (woody cover, average woody cover across extents, and NDVI) were mostly related to variation in the first axis of the NMDS ordination surfaces. Sample plots with high metrics values (right side of the x-axis of the biplots in Fig. 6, 7) corresponded to forested areas, and were characterized by woodland bird species.

On the other extreme, plots with low metric values (left side of the biplots) were characterized by low woody cover, and were associated with grassland bird species. Plots with intermediate metric values represented intermediate woody cover areas, or savannas, and were represented by savanna species and other species that are less habitat obligatory. Overall, the metrics' predictive power of community structure was not substantially affected by changes in extent except for the standard deviation of woody cover at the finer resolution and patch density at the coarser resolution. The heterogeneity-based metrics (standard deviation of woody cover across extents, patch density, and edge density) were stronger at the finer resolution, while the cover-based metrics (woody cover and average woody cover across extents) were mostly insensitive to spatial resolution. This makes sense, since in our study area considerable fine-grained heterogeneity is lost when pixel size is increased, while the overall woody cover is less affected by changes in spatial resolution.

MCSPA metrics were generally similar to single scale metrics in their explanatory power of both avian species richness and community structure. Among the MCSPA metrics, the standard deviation of woody cover across extents (S1) was the best predictor, and this made sense given that it is a good representative of habitat heterogeneity. Habitat heterogeneity in turn is generally positively associated with species richness (McArthur and McArthur 1961, Cody 1981, 1985) since complex landscapes often contain a larger variety of resources than simple habitats, and a larger variety of resources can support more species. On the other hand average woody cover across extents (S0) was highly correlated with the basic woody cover metric (Pf), and did not result in models that were substantially different from it, so we conclude that at least in our study area, it is less useful.

While MCSPA is a multiscale approach, it is still expected to be sensitive to scale. In other words, MCSPA quantifies the change across scales, but is still affected by the pixel size, number and size of analysis windows, and the maximal window size. Bar Massada and Radeloff (2010) tested the effects of extent on MCSPA metrics, and found that average woody cover across extents decreases nonlinearly with increasing extent when woody cover is low, but is less sensitive to extent under intermediate to high woody cover conditions. The other MCSPA metrics increase nonlinearly with extent, but as the extent increases, their increase tapers off. All MCSPA metrics are mostly affected by extent when overall woody cover is low, and are less sensitive to extent when woody cover is high.

The efficiency of MCSPA and landscape metrics in predicting avian species richness and community structure is also affected by the definition of habitat type (here, woody versus non-woody). Both types of metrics are based on a binary landscape (though MCSPA can be used with continuous landscape maps, when the continuous variables' reaction to scale is known and can be accounted for), which captures only a limited amount of information about the variation in the landscape (McGarigal et al. 2009). Here, we classified the landscape into woody and non-woody pixels, regardless of plant species and structure. Since this choice of habitat classification is broad (though it is the most commonly used in similar studies), it may have affected the overall results because different species have different habitat requirements

in terms of woody vegetation. In Ft McCoy, there are three major types of habitat, which differ substantially in the amount of woody cover: grasslands (little or no woody cover), savannas (intermediate woody cover), and woodlands (high woody cover). Grassland areas had low tree cover and low species richness, while woodland areas had high tree canopy cover and moderate species richness, and savanna areas had intermediate tree canopy cover and high species richness. By being successfully able to distinguish among these general habitat types, we expected that all landscape and MCSPA would perform moderately well.

The main conclusion that emerges from our results is that cartographic scale (both spatial resolution and extent) has profound and complex influences on the relationships between avian species and spatial measures of their habitat (here, described using landscape and MCSPA metrics, and NDVI). The effects of scale are manifested in two ways. First, the ability of habitat pattern to predict species richness varies by the scale at which habitat pattern is measured in a complex way, through the interaction with both spatial resolution and extent. Thus, the choice of the resolution/extent combination (which in many studies is driven by data availability) influences the strength of the relationship between species richness and habitat. Second, and equally important, the form of the relationship itself will vary with spatial resolution and extent. We conclude that since both components of scale profoundly affect the relationships between habitat pattern and species richness and community structure, the efficacy of using landscape metrics to predict the diversity of organisms is limited, unless their sensitivity to scale effects is accounted for.

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