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RESEARCH ARTICLE

Avian abundance thresholds, human-altered landscapes, and the challenge of assemblage-level conservation

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Abstract
Context Land-use change is a global phenomenon with potential to generate abrupt spatial changes in species' distributions.
Objectives We assessed whether theory about the internal structure of bird species' geographic ranges can be refined to reflect abrupt changes in distribution and abundance associated with human influences on landscapes, and whether the prevalence and diversity of bird–landscape threshold relationships may significantly complicate assemblage-level avian conservation.
Methods For three large regions in the United States, we used the North American Breeding Bird Survey, U.S. National Land Cover Data, and multivariate adaptive regression splines to assess whether land bird species' abundances were associated with landscape composition and configuration in a threshold fashion.
Results Threshold relationships between abundance and landscape characteristics were exhibited by 42–60 % of the species studied. The relationships were evident for five land types and five habitat guilds. We observed threshold relationships for more taxonomically diverse groups of bird species, a broader set of land types, and larger geographic extents than have been considered to date.
Conclusions Avian distribution and abundance theory can be refined by articulating that characteristics of human-altered landscapes have the potential to be widespread and biologically important contributors to abrupt spatial change in species' abundances. Our findings also expose bird–landscape threshold relationships as pervasive and diverse patterns that impose a much more complicated set of circumstances for assemblage-level conservation of birds than has been widely recognized. To cope with these complications, landscape planners and managers can use optimization analyses, multispecies frameworks, regulatory limits, and multivariate change-point analyses.

Keywords Abrupt spatial changes · Bird–landscape thresholds · Geographic ranges · Internal structure · Landscape planning and management · Threshold pervasiveness and diversity

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Introduction

The global phenomenon of human-induced land-use change is an important cause of the worldwide loss of biodiversity (Julliard et al. 2004) because, for many native species, land-use change often leads to the destruction or degradation of their habitat (Scharlemann et al. 2004; Johansson et al. 2005). Human alteration of habitat conditions across broad spatial extents may affect many individuals of a species and thus increase the potential for abrupt spatial changes in species' abundances. Spatial discontinuities in populations caused by habitat destruction can contribute to species declines by decreasing rates of inter-patch movements, decreasing densities of individuals, increasing demographic variability, increasing negative edge effects, and decreasing local genetic variation (Johansson et al. 2005). To combat such impacts, it is important to understand the degree to which characteristics of human-altered landscapes induce abrupt spatial changes in species' abundances.

A species' abundance, when viewed macroscopically, has been proposed to vary in a gradual Gaussian manner along spatial dimensions that span the central and peripheral portions of the species' geographic range (Brown 1984). Empirical expression of this general theory of distribution and abundance would be observed when abundance is limited by several variables that collectively define a species' niche, and when observed values of niche variables across space are autocorrelated (Brown 1984). Although departures from this general model are frequently acknowledged (Gaston 2003)—owing to resource patchiness, interspecific interactions, and abrupt environmental change caused by barriers (e.g., terrestrial-aquatic boundaries, cordillera) (Wiens 1989)—the pattern of gradual abundance decay with distance from local maxima remains a common expectation because discontinuities observed at small scales are thought to average out over sufficiently large spatial extents (Brown et al. 1995; Scheffer 2009).

Given this general model of variation in abundance within a species' geographic range, abrupt changes in abundance might be expected to be less common than gradual changes, and to be more likely at a species' range boundary (Rapoport 1982; Wiens 1989; Brown 1995). However, humans now appropriate substantial amounts of terrestrial net primary productivity through direct consumption or by converting indigenous habitats to intensive land uses, thus reducing ecosystem capacity to support native biodiversity (Vitousek et al. 1986; Rojstaczer et al. 2001) or the movement of species across landscapes (Lawler et al. 2013). Furthermore, because human use of ecosystem productivity is spatially heterogeneous, it can lead to "hot spots" of over-appropriation (Imhoff et al. 2004), causing local extinctions within a species' geographic range (Yackulic et al. 2011; Rybicki and Hanski 2013).

This pattern of natural capital consumption suggests that abrupt abundance changes could occur anywhere within species' geographic ranges, not just near range boundaries, and that such changes therefore may be more common than expected from the general theory of distribution and abundance. Moreover, growing empirical evidence indicates that human-impacted systems may be particularly susceptible to sudden shifts in ecosystem attributes—dynamics that are now discussed collectively under the rubric of critical thresholds (Barnosky et al. 2012; Scheffer et al. 2012; Bestelmeyer et al. 2013; Banks-Leite et al. 2014).

In the context of avian geographic distributions, a threshold is a value of an environmental variable (e.g., amount of forest cover) at which a species' abundance changes abruptly ("abrupt threshold" sensu Ficetola and Denoël 2009), and we refer to the change phenomenon itself as a threshold relationship or an abundance threshold. Much of the empirical evidence supporting the existence of landscape-level thresholds comes from birds, for which abrupt changes in species' occurrence, persistence, or abundance have been associated with small changes in landscape conditions (Swift and Hannon 2010). Such bird–landscape thresholds have been commonly detected for forest or woodland species over spatial extents that were relatively small compared to the size of most species' breeding or year-round ranges (e.g., Jansson and Angelstam 1999; Carlson 2000; Butler et al. 2004; Radford and Bennett 2004; Betts et al. 2010; Zuckerberg and Porter 2010).

What remains unknown is the prevalence of bird–landscape thresholds for a more taxonomically diverse set of species (Swift and Hannon 2010) in various land types (forest, grassland, shrubland, cropland, and development) and across broader geographic extents. It is important to clarify for these various conditions whether threshold relationships occur rarely (if at all) or commonly among species. Without this

information, it is difficult to know whether the general theory of distribution and abundance (Brown 1984) can be refined to explicitly recognize characteristics of human-altered landscapes as common sources of abrupt spatial change in bird species' abundances, and whether such effects are pervasive and diverse enough to complicate assemblage-level conservation. We addressed these uncertainties using data for more-diverse groups of bird species, a broader set of land types, and larger geographic extents than have been considered to date.

Our central questions were: (1) For three physiographic regions and five habitat guilds in the conterminous United States, what is the prevalence of abundance thresholds in bird–landscape relationships? (2) If such thresholds are common, does the diversity of the relationships among species significantly complicate conservation within a region? (3) If abundance thresholds add substantial difficulty to broad-scale conservation, how can landscape planners and managers use existing approaches to cope with the complications?

Methods

Study regions

To assess the prevalence of bird–landscape thresholds within and among major ecological systems in the conterminous United States, we studied bird–landscape relationships in three distinct geographic domains—eastern forests, central grasslands, and western shrublands and forests (Fig. 1a). Each of the three regions included two or more geographically adjacent Bird Conservation Regions (BCRs), which are defined on the basis of similar environmental conditions and bird assemblages (U.S. NABCI Committee 2000). The Eastern region included the Appalachian Mountains (BCR code = 28) and the Piedmont (29) BCRs; the Central region included the Prairie Potholes (11), Badlands and Prairies (17), Shortgrass Prairie (18), Central Mixed-grass Prairie (19), and Eastern Tallgrass Prairie (22) BCRs; and the Western region included the Great Basin (9), Northern Rockies (10), and Southern Rockies/Colorado Plateau (16) BCRs.

Bird data

Our bird data originated from the North American Breeding Bird Survey (BBS, Sauer et al. 2008). Along each 39.4-km BBS route, detected individuals were recorded during 50 3-min stops that were spaced approximately 0.8 km apart along the route. Only BBS routes that were surveyed under standard sampling conditions (Sauer et al. 2008) each year during 2000–2002 were used; this period evenly encompassed the predominant year (2001) of the satellite imagery that underlied the landscape variables we used. Variation associated with interannual differences in observers was reduced by only using routes that were surveyed by the same person all 3 years. To avoid biases related to observer experience, none of the routes we used was run by a first-year observer. Only species that breed in a study region were included in analyses; we excluded observations for hybrid species and for which the species was uncertain (e.g., "unid. chickadee", as in Flather 1996). We also excluded waterfowl, shorebirds, waders, seabirds, raptors, colonial nesters, owls, and other crepuscular and nocturnal species because the BBS does not sample these groups well (O'Connor et al. 2000). Exotic species that do not belong to any of the groups listed above were included in all analyses.

Landscape data

To obtain data for landscape metrics, we used the 2001 USGS National Land Cover Data (Homer et al. 2007) for the following classes of land cover: developed (includes: 21-open space, 22-low intensity, 23-medium intensity, 24-high intensity); forest (includes: 41-deciduous, 42-evergreen, 43-mixed, 90-woody wetlands); shrubland (includes: 52-shrub/scrub); grassland (includes: 71-grassland/herbaceous, 81-pasture/hay); and cropland (includes: 82-cultivated crops). Land-cover classes that were defined in the National Land Cover Data, but not included in our assessment of bird–landscape thresholds, were lumped into an "other" category that included open water (11), barren land (31), and emergent herbaceous wetlands (95). Woody wetlands (90) were included with forest because we wanted to ensure that riparian forests were included in the forest class. This decision was especially important for the Central and Western

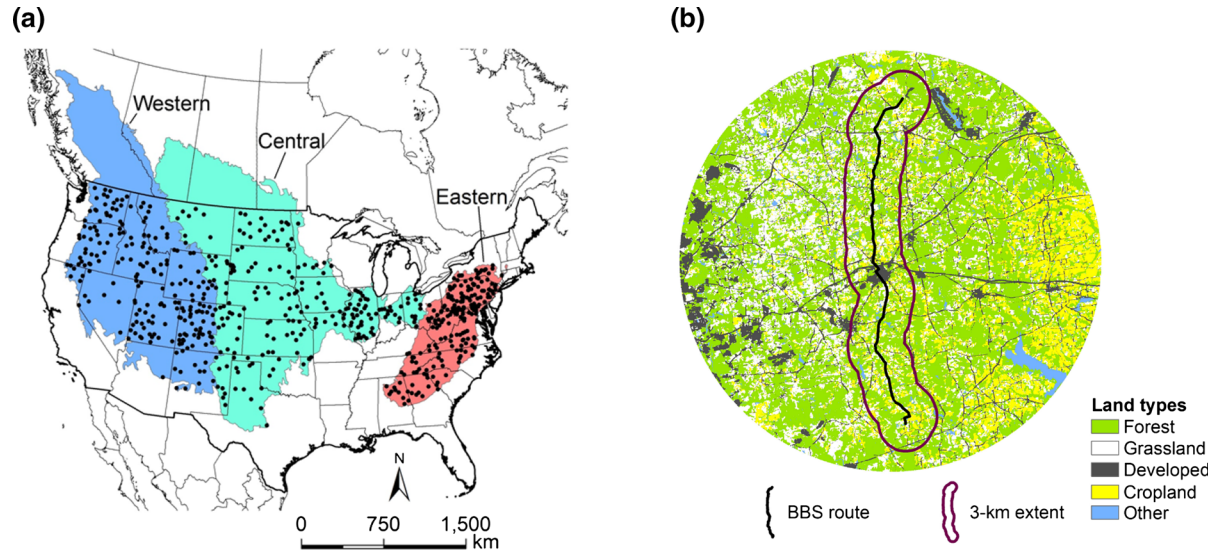

Fig. 1 Geographic origins of bird and landscape data. **a** Locations of study regions and Breeding Bird Survey routes used (*black dots* indicate route centroids). **b** Observation unit for measuring characteristics of landscapes around each route in an example landscape. A circular extent (radius = 23 or 25 km, depending on the study region) and a parallel extent (3 km along both sides of a route for all study regions) were based respectively on the mean of allometrically derived maximum natal dispersal and median natal dispersal distances for each regional pool of bird species that met the criteria for inclusion in the analyses

regions where there is considerable riparian forest that is important for supporting many bird species.

Birds often respond to environmental conditions at multiple spatial extents (e.g., Gutzwiller and Barrow 2002 and references therein). We measured such conditions within two spatial extents around each route (Fig. 1b). BBS route centroids (Fig. 1a) corresponded to the center of the minimum bounding rectangle that encompassed the route path. Path sinuosity varied among routes, and the center of the minimum bounding rectangle provided a standard location around which to position the circular landscape extent (Fig. 1b).

There is an emerging literature that suggests the observation grain for macroecological study of species' responses to landscape structure should be linked to some population process. It has been shown theoretically (Jackson and Fahrig 2012) and empirically (Tittler et al. 2009) that dispersal is an appropriate process for defining the spatial extent (or the scale of effect) within which individual species integrate the effects of landscape structure. Although dispersal distances will vary among individuals within a species and among species with different migratory and other life-history characteristics, and dispersal (or more generally species movement) is difficult to measure (Turchin 1998), it does scale with bird body size (Paradis et al. 1998). We used the allometric relationships derived by Sutherland et al. (2000) and data on bird body mass (Dunning 2008) and diet (Poole 2005) to estimate species' natal dispersal distances.

Because of uncertainty surrounding dispersal distance estimates, we used two definitions of the spatial extent within which we measured landscape structure variables. One was based on the median natal dispersal distance, and one was based on the maximum natal dispersal distance. Mean median and mean maximum dispersal distances for the species were computed for each of the three study regions separately. The smaller-extent (mean median dispersal distance) and larger-extent (mean maximum dispersal distance) distances for the Eastern, Central, and Western regions were 3 and 23 km, 3 and 25 km, and 3 and 23 km, respectively. For all three regions, the smaller extent followed the BBS route path and extended 3 km on both sides of the route path, and the larger extent was implemented as a 23-km (or 25-km) radius circle centered on each route centroid following the protocol of Flather and Sauer (1996) as modified by Pidgeon et al. (2007). We did not use routes whose landscape buffers intersected the U.S.-Canadian border, large water bodies (e.g., Great Lakes), or ocean coasts (e.g., Chesapeake Bay).

Within each spatial extent, we used FRAGSTATS software (McGarigal et al. 2002) to calculate landscape variables. Preliminary analyses to identify candidate predictors considered the number of routes at which a given land-cover class occurred, the range of values for a variable, correlations among landscape variables, existing knowledge about bird–landscape relationships, ease of understanding and measuring variables, and ease of application to conservation contexts. We used variables whose ranges for a given study region were close to the potential ranges for the variables (e.g., 0–100 % for percent cover) and whose values were distributed relatively evenly throughout this range. We selected composition (percent cover) variables that reflected the dominant land covers in each region. We chose configuration (nearest-neighbor distance, edge density, and patch density) variables that were least correlated with percent of landscape for the same cover class. The landscape variables used in the analyses are defined in Tables S1–S3 in Supplementary Material. These variables reflected conditions of composition and configuration that are commonly thought to be responsible for threshold relationships at the landscape level (see Swift and Hannon 2010 and references therein).

Although bird species with affinities to shrubland occurred in all study regions, shrubland variables were measured only for the Western region because this was the only study region in which shrubland was a major component of natural land cover. For edge variables, the point at which a cover type met the landscape buffer boundary was not included as edge. The 3-km spatial extents along each BBS route varied in size (area) because of variation in the sinuosity and length of route paths, and this variation could have generated area-related effects on landscape variables. We controlled for these effects by using landscape variables (% cover, density) that were either standardized for or independent of area. Because the size of the larger circular extent was fixed, area effects at this extent were not an issue for the landscape variables.

Response variable

The BBS sampling protocol and our use of the BBS data eliminated many factors (weather conditions, time of season, observer ability, types of species) that can bias BBS data. However, detectability bias from errors of omission can occur for species that are secretive, rare, or otherwise difficult to detect. Currently accepted methods to correct for detection bias require data from multiple visits (MacKenzie 2006). Because most BBS routes are surveyed just once each year, these methods cannot be implemented except in those limited special cases where routes were surveyed using a repeated-visit design (e.g., Royle 2006). The number and geographic distribution of routes with repeated visits was very limited and thus not appropriate for our macroecological analyses. Although we were not able to apply these methods to control for detection bias, the response variable we computed reduced the bias associated with omission errors.

Our response variable was an index of abundance over time ("abundance" hereafter) for a species on a route during the 2000–2002 breeding seasons. We computed this index as the average proportion of a route at which a species was observed. For a given route, we used the five 10-stop segment data to determine the proportion of segments at which the species was observed. This step was implemented for each year separately, and then an average of the three annual proportions for a route and species was calculated. This index of abundance was less subject to potential detection-related biases than estimates of abundance based on raw BBS counts would be. Compared to using 0/1 (presence/absence) data for a route as a whole, this approach reduced information loss. In addition, our index reduced the potential for bias associated with computing the proportion on the basis of presence/absence data for all 50 individual stops, which conceivably could have led to almost as much bias as using raw abundances [correlations between stop occurrence and raw counts have exceeded 0.98 for many (88 %) species; see Bart and Klosiewski 1989]. To avoid species that rarely breeded in a study region, species had to occur on at least 10 % of the routes in a region each year to be included in the analyses.

The maximum distance within which BBS observers can detect a species is approximately 400 m. Although the 50 stops along a route are designed to be spaced 0.8 km apart, route sinuosity may cause the straight-line distance between stops to be <0.8 km, which may lead to overlap in the 400-m-radius areas surveyed around stops. In addition, although all routes had the same number of stops, total route length differed among routes due to variation in actual road

distances between stops. Differences in route sinuosity and length may have influenced bird counts because straighter and longer routes had greater potential to sample a higher number of non-overlapping 400-m-radius areas in the landscape and hence additional individuals for a species. The area within 400 m of the route was linearly related to and highly correlated with route length ($r = 0.98$ for each region). To control analytically for possible area effects on abundance estimates, we included area400—the size of the area within 400 m of the route—as a candidate predictor during statistical analyses.

Statistical assessment of bird–landscape relationships

We used multivariate adaptive regression splines (MARS, Friedman 1991), which implements a form of piecewise linear regression, to study the shapes of bird–landscape relationships. Our focus was not on predictive models or specific estimates of threshold points but on whether there was any evidence of threshold relationships for species. For an assessment of the prevalence of threshold relationships, it is important to use a method that is capable of objectively fitting linear, abrupt nonlinear, and gradual nonlinear relationships (Fig. 2). MARS can fit these types of relationships and combinations thereof. During the model-fitting process, MARS seeks to minimize a "generalized cross-validation (GCV) measure of mean square error (MSE)" (Friedman 1991; Salford Systems 2001). Use of this GCV MSE criterion simultaneously optimizes both fit and parsimony; additional variables and splines will increase fit, and they will be retained in the model if the improvement in fit and the additional number of degrees of freedom (df) used result in a smaller GCV MSE than what has been computed for other models. Adding to the objectivity of the MARS algorithm, no inputs from the user such as starting values for numerical estimation of threshold points or visual identification of threshold points are involved. Instead, MARS directly estimates knots (breakpoints for adjoining splines) in basis functions (max [] functions of candidate predictor variables) based on least-squares fits of the observed data.

Considering the potential complexities of ecological thresholds (Huggett 2005; Groffman et al. 2006), MARS is well-suited for studying threshold relationships for several other reasons. It is a nonparametric machine-learning method that can detect and closely model changes in a response variable for single landscape variables, or for multiple landscape variables simultaneously. It can fit thresholds that occur in the form of interactions between landscape variables. MARS can fit local relationships, which means it can find important relationships that may be present in only parts of a landscape variable's range. The number of df that gets charged in the calculation of GCV MSE takes into account the entire model space (variables, basis functions, and knots) that MARS considers during the data-fitting process, which reduces the chance of finding spurious relationships. And MARS is a form of piecewise regression; Ficetola and Denoël (2009)

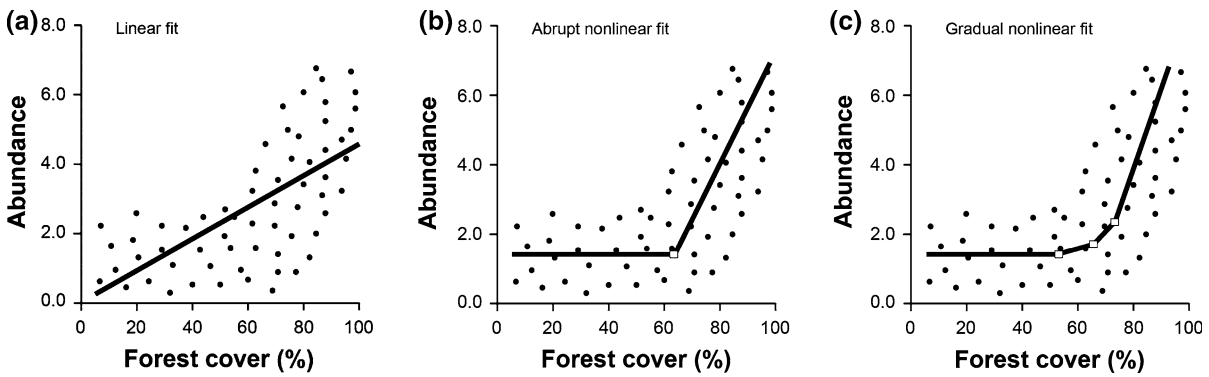

Fig. 2 A hypothetical scatterplot of a species' abundance versus percent of the landscape in forest cover. *Straight lines* represent linear splines, and *open squares* represent knots (breakpoints between adjoining splines). MARS will fit a linear (**a**), abrupt nonlinear (**b**), or a gradual nonlinear (**c**) relationship, depending on which type of fit minimizes a generalized cross-validated measure of mean square error

demonstrated that piecewise regression is an accurate and objective means for assessing the presence of abrupt changes in species–habitat relationships.

In implementing Friedman's (1991) method, we made the following changes to the default settings in MARS 2.0 (Salford Systems 2001). First, to reduce the chance of identifying spurious relationships, we used the 10-fold cross validation option to determine the number of df to be charged during the modeling process. This approach provided the most defensible results (see Friedman 1991; Salford Systems 2001) because it was based not on a rule of thumb but on the specific data and the building and pruning steps for a given model. Second, to improve the chance of detecting important complex relationships, we increased the maximum number of basis functions from the default of 15, which is considered to be much too small in most cases (Salford Systems 2001), to 75. Third, because we were interested in various main and interaction variables as a set, we included both main effects and our selected two-way interactions in the analysis from the beginning.

In least-squares regression involving our sample sizes (198–213 routes), we know from experience that a variable that is associated with less than 2 % of the variation in the response variable can be statistically significant. Our interest here was not whether explanatory variables were statistically significant, but whether they had potential to be biologically important. Toward that end, we used an effect-size criterion to define an important relationship. Studies like ours that have used regression to assess the effects of local- and broad-scale environmental conditions on bird response variables have considered individual predictors to be ecologically important if they were associated with at least 10 % ($r^2 \geq 0.10$, Pearson 1993) or 5 % (R^2 increment ≥ 0.05, Hawkins et al. 2003) of the variation in the response variable. Compared to using a smaller R^2 increment for a minimum effect size, a 10 % increment identified relationships that had greater potential to be biologically meaningful. We therefore defined an important relationship a priori as one in which a species' abundance exhibited a relationship with a basis function involving one or more landscape variables ("landscape basis function" hereafter), and that basis function increased GCV R^2 by $\geq$10 % (rounded to the nearest whole percent)—referred to as the "importance criterion" hereafter. GCV R^2 is a measure of strength of association that is penalized for the number of df that are used to fit the model (Salford Systems 2001) and is thus a collective gauge of model fit and parsimony. An important threshold relationship was defined a priori as one in which a landscape basis function increased GCV R^2 by $\geq$10 % and there was a change in slope (i.e., MARS identified a knot between adjoining splines) for the relationship between abundance and the landscape basis function.

We used a two-stage analysis to fit MARS models. The first stage involved relating a response variable to landscape variables. This step generated alternative MARS models. We used these results to determine whether there were any models with landscape basis functions that met our importance criterion. We selected the model that either contained all of the basis functions that met our criterion, or if there were no basis functions that met our importance criterion, the simplest model presented by MARS (an intercept-only model, or a 1-basis-function model). We checked whether the residuals for the model chosen in this first stage exhibited spatial autocorrelation. This step enabled us to confirm that spatial autocorrelation did not affect the MARS results we used to decide whether there were (or were not) important threshold effects. If the residuals did not exhibit spatial autocorrelation, this model was our final model and was interpreted for threshold effects, and the second stage of analysis was not needed for the species involved. If spatial autocorrelation was present in this model's residuals, the second stage of analysis was implemented.

The second stage involved relating a response variable to the same landscape variables as in the first stage, plus spatial eigenvector variables. This step generated a different set of alternative MARS models that could involve landscape basis functions, spatial basis functions (basis functions involving spatial eigenvector variables), both, or neither. Employing the same basic steps as in the stage-1 analyses, we used these results to determine whether there were any models with landscape basis functions that met our importance criterion. If spatial autocorrelation was present in a chosen model's residuals, models with sequentially more basis functions (chosen consecutively from the second set of alternative models generated by MARS) were examined until a model whose residuals were free of spatial autocorrelation was found. The model whose residuals did not exhibit spatial autocorrelation was our final model and was

interpreted for threshold effects. Additional information about MARS modeling and the autocorrelation and spatial eigenvector analyses is presented in Online Appendix S1.

Calculation of relative threshold abundance

In the MARS analyses of threshold relationships, we considered as candidate predictors more composition variables than we did configuration variables (Tables S1–S3). Consequently, more thresholds associated with composition could have been detected simply by chance. To prevent this difference in the number of candidate predictors from confounding the comparison between number of observed thresholds associated with landscape composition (land-type amounts) and landscape configuration (spatial structure of land types), we divided the number of detected thresholds in each category (composition or configuration) by the number of candidate predictors in the respective category that we considered in the MARS analyses. We compared the resulting ratios within study regions to gauge the relative abundance of comparatively simple threshold relationships (involving composition) and comparatively complex threshold relationships (involving configuration).

Illustration of bird–landscape thresholds

To depict a threshold between a species' abundance and a landscape variable, we plotted the partial response relationship—the fitted relationship that controlled for the other variables in the model. The calculations involved the MARS basis function, the regression coefficient for the basis function, and the values of the landscape variable at the threshold point and endpoints of the variable's range. Consistent with MARS plotting algorithms, our calculations for the plots did not involve addition or subtraction of the model intercept, and the regression coefficient for the landscape variable reflected the presence of the intercept and other predictors in the model.

Definition of basic threshold forms and conflicting threshold relationships

We recorded how many species exhibited basic threshold forms (Fig. 3) involving landscape composition (percent cover) or configuration (edge density, patch density, nearest-neighbor distance between patches). A species' abundance could increase (Fig. 3a) or decrease (Fig. 3b) above a certain magnitude of X (a landscape variable), or increase (Fig. 3c) or decrease (Fig. 3d) below a certain magnitude of X. Threshold relationships for two species in the same region were defined as conflicting if one exhibited increasing species abundance with a landscape variable and the other exhibited decreasing abundance with that variable.

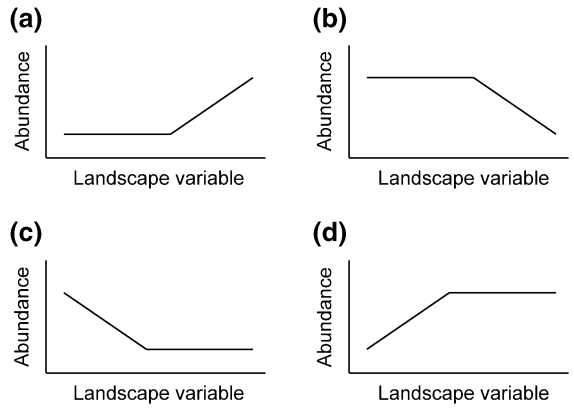

Fig. 3 Basic threshold forms that were possible for each threshold type. In each graph, a species' abundance is plotted against the increasing magnitude of a landscape variable

Results

The analyses involved varied levels of abundance for diverse assemblages of 95, 79, and 85 land bird species for the Eastern, Central, and Western regions, respectively (Table S4). Landscape variables involved in the analyses reflected wide variation in landscape composition (percent cover) and configuration (edge density, patch density, nearest-neighbor distance between patches) (Tables S1–S3). Threshold types considered for each region (Tables S5–S7) varied with the landscape variables used for each region.

For the Eastern, Central, and Western regions, respectively, 42, 52, and 60 % of species exhibited at least one abundance threshold (Tables S8–S10). The mean and range of effect sizes (percent of variation in abundance associated with a landscape variable that had a threshold influence; Tables S8–S10) were 23 [10–50] %, $n = 41$ (Eastern); 27 [10–70] %, $n = 48$ (Central); and 24 [10–55] %, $n = 56$ (Western).

Threshold effects associated with forest, grassland, shrubland, developed-land, or cropland variables were evident in the three regions (Fig. 4a). Five groups of species with different primary habitat associations (Online Appendix S1) within each assemblage showed threshold responses (Fig. 4b), and for each of the three regions these relationships involved landscape variables for land types that were similar to and different from the habitat types with which the species primarily associate (Fig. 4c–e).

A large majority of the threshold relationships involved only one univariate threshold and one landscape variable (Fig. 5a). In addition, for landscape composition (land-type amounts), the ratio of detected thresholds to the number of landscape variables considered in the analyses was 3.6–5.0 times larger than that for landscape configuration (spatial structure of land types) (Fig. 5b).

Among species that were associated with the same landscape variable in the same region, relationships exhibiting increasing abundance with a landscape variable and relationships exhibiting decreasing abundance with that variable—conflicting relationships (e.g., Figure 6a vs. 6b and 6b vs. 6c)—were often

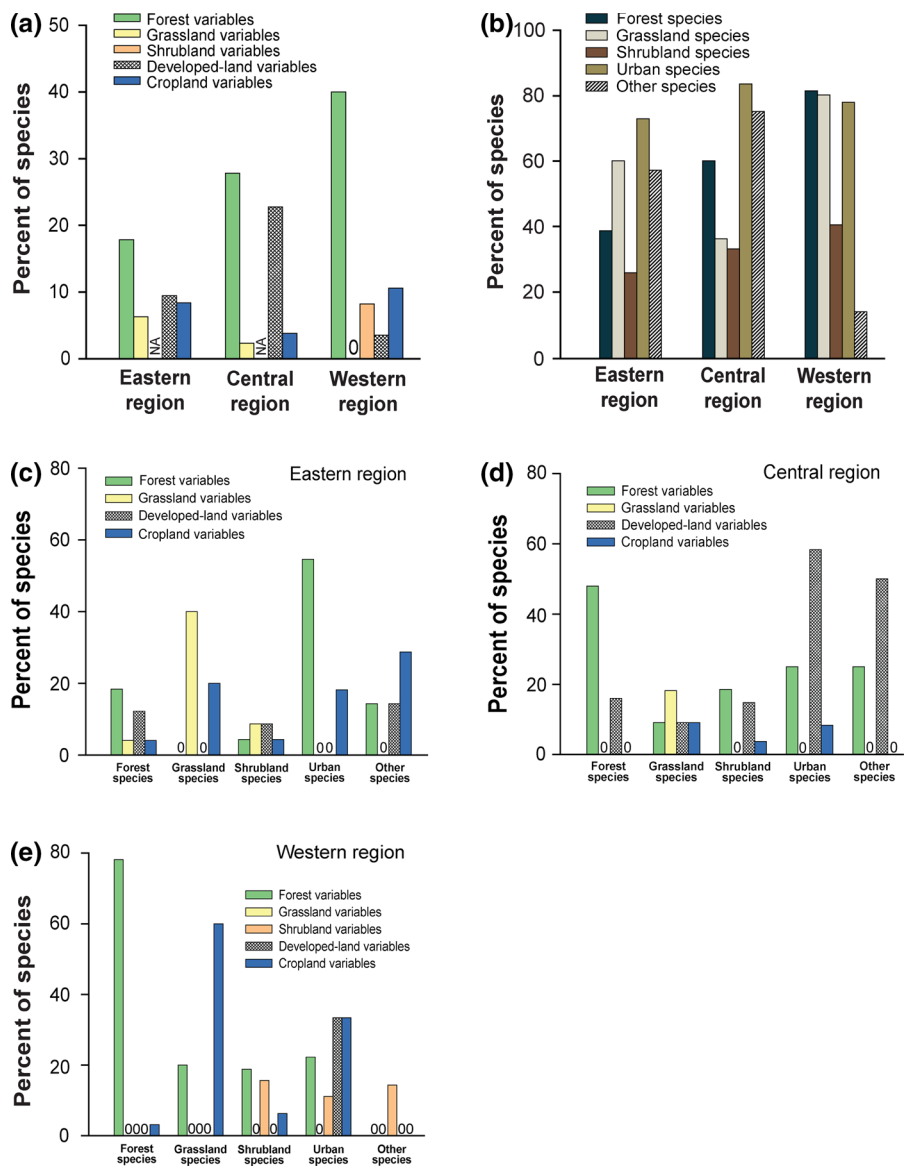

Fig. 4 Prevalence of threshold relationships. **a** Percent of species exhibiting threshold relationships with landscape variables for dominant land types by region; *NA* no landscape variables for shrubland were measured for the Eastern or Central regions, *0* no species exhibited thresholds in relation to grassland variables in the Western region. **b** Percent of species exhibiting threshold relationships by species' primary habitat associations (see Online Appendix S1) for each region. Percent of species exhibiting threshold relationships with landscape variables for dominant land types by species' primary habitat associations for the Eastern region (**c**), Central region (**d**), and Western region (**e**); *0* no species exhibited threshold relationships with landscape variables for a given land type

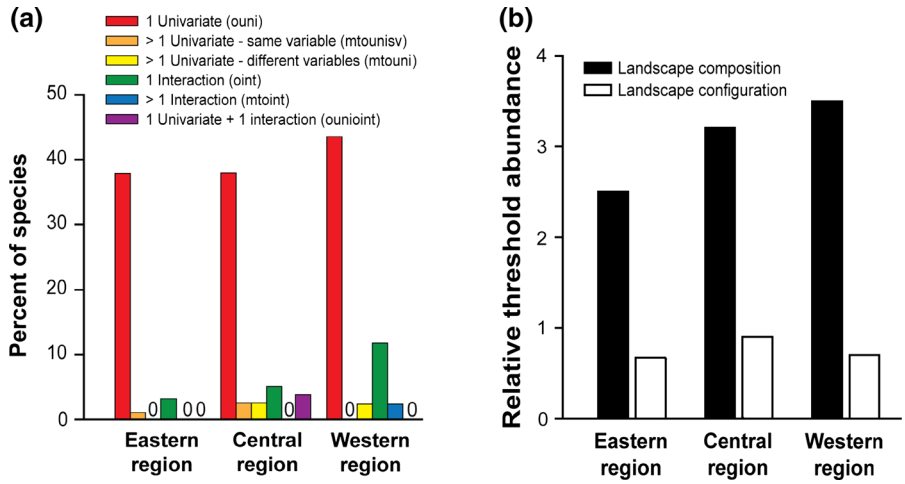

Fig. 5 Prevalence of threshold types, and the relative abundance of thresholds involving landscape composition and landscape configuration. **a** The percentage of species that exhibited threshold types of increasing complexity [*ouni* one univariate threshold involving one landscape variable, *mtounisv* more than one univariate threshold involving a total of only one landscape variable in an additive fashion, *mtouni* more than one univariate threshold involving a total of two or more landscape variables in an additive fashion, *oint* one threshold involving an interaction between two landscape variables (one 2-way interaction), *mtoint* more than one threshold involving a 2-way interaction (more than one 2-way interaction), *ounioint* one univariate threshold involving one landscape variable, plus one threshold involving a 2-way interaction between two other landscape variables], *0* no species exhibited a threshold type. **b** Relative threshold abundance was the number of observed threshold relationships involving landscape composition or configuration variables, divided respectively by the number of landscape composition or configuration variables that were considered in the analyses

observed (Fig. 7). Some species were associated with different landscape variables within the same land type (e.g., Figure 6d–f), whereas other species were associated similarly with the same landscape condition (e.g., Figure 6g–i).

Discussion

Threshold pervasiveness

The substantial prevalence of threshold relationships for the three regions suggests that landscape conditions at threshold points were a pervasive limiting influence in these assemblages. Because of the nature of threshold relationships, substantial threshold prevalence among species also implies that where current landscape conditions are near threshold points, even small and scattered changes in land-type composition or configuration that are typical of our study regions may cause abrupt changes in many species' abundances. The mean and range of effect sizes for landscape variables indicated that the threshold relationships had potential to be biologically meaningful. For birds, geographic variation in abundance across a species' range (the range's "internal structure") has been shown to be quite species-specific (Brown et al. 1996). This variation is consistent with the high variation we observed among species in the presence and nature of threshold relationships (Tables S8–S10), indicating that abrupt spatial changes in abundance arising from characteristics of human-altered landscapes may be an important source of internal structure of bird species' ranges. Threshold effects associated with the various land types in the three regions revealed threshold relationships involving more land types and much larger spatial extents than have been reported previously. Considering the number and broad spatial distributions of sampling units (BBS routes) within each region (Fig. 1a), and the extensive lengths (39.4 km) of the BBS routes themselves, the threshold relationships we observed likely reflect important population-level responses to landscape conditions (see Koenig and Knops 1998). Our results also demonstrated that threshold responses were prevalent across multiple habitat guilds (Fig. 4b), and that abundance thresholds associated with landscape conditions of non-habitat land types

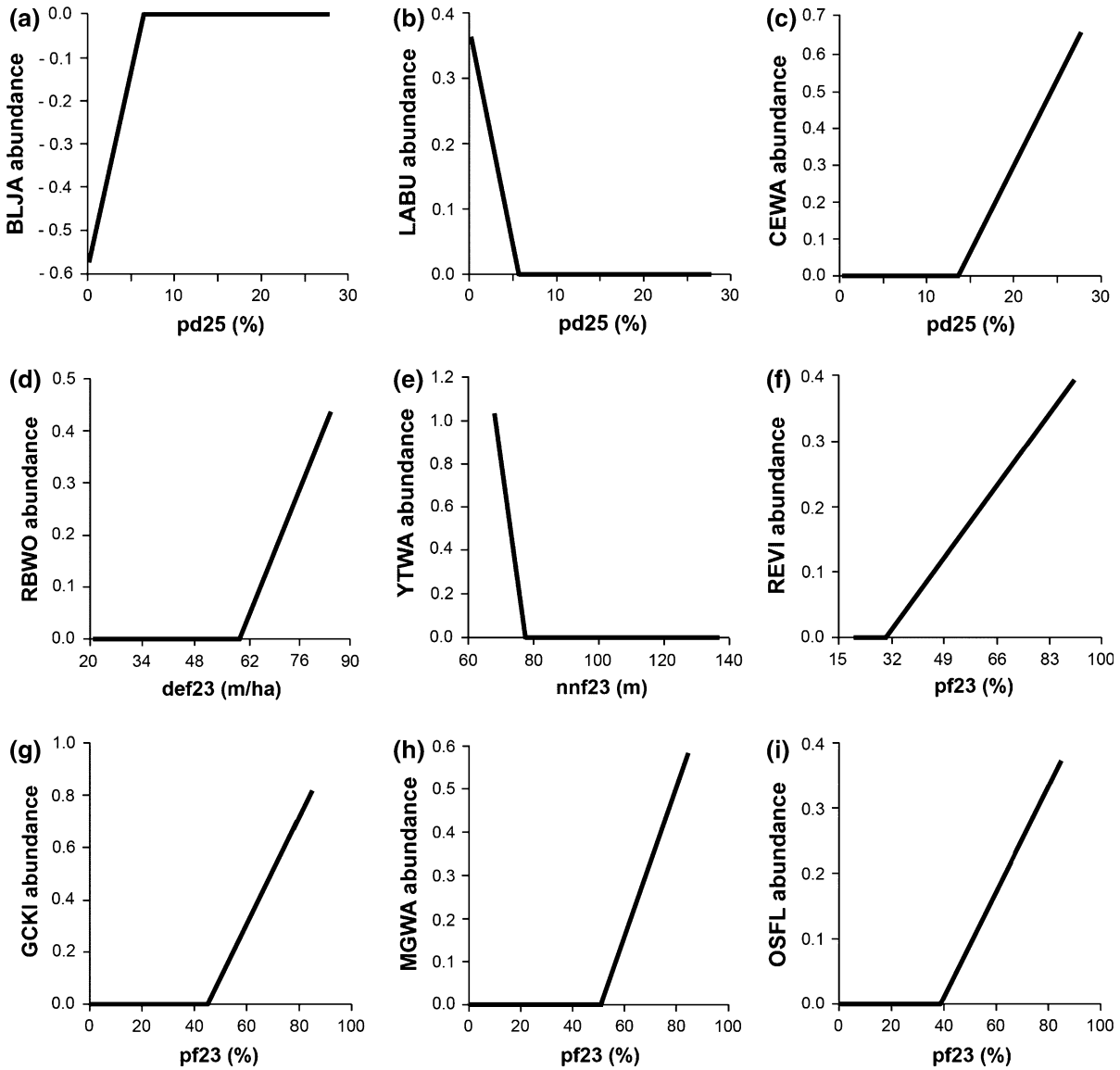

Fig. 6 Partial response relationships (fitted relationships after controlling for other variables in the model) between a species' abundance and landscape variables. For the Central region, abundance in relation to development cover within 25 km (pd25) for **a** blue jay (BLJA), **b** lark bunting (LABU), and **c** cedar waxwing (CEWA). For the Eastern region, **d** red-bellied woodpecker (RBWO) abundance in relation to the density of forest edge within 23 km (def23), **e** yellow-throated warbler (YTWA) abundance in relation to mean nearest-neighbor distance between patches of forest within 23 km (nnf23), and **f** red-eyed vireo (REVI) abundance in relation to forest cover within 23 km (pf23). For the Western region, abundance in relation to forest cover within 23 km (pf23) for **g** golden-crowned kinglet (GCKI), **h** MacGillivray's warbler (MGWA), and **i** olive-sided flycatcher (OSFL). Species' scientific names are in Table S4; landscape variables are defined in Tables S1–S3

were common (Fig. 4c–e). Taken together, these various sets of results suggest that the general theory of distribution and abundance can be refined to articulate that characteristics of human-altered landscapes have the potential to be geographically widespread and biologically important drivers of abrupt spatial changes in bird species' abundances.

One might argue that the prevalence of abrupt nonlinear relationships we observed arose because MARS penalized for model complexity and, as a

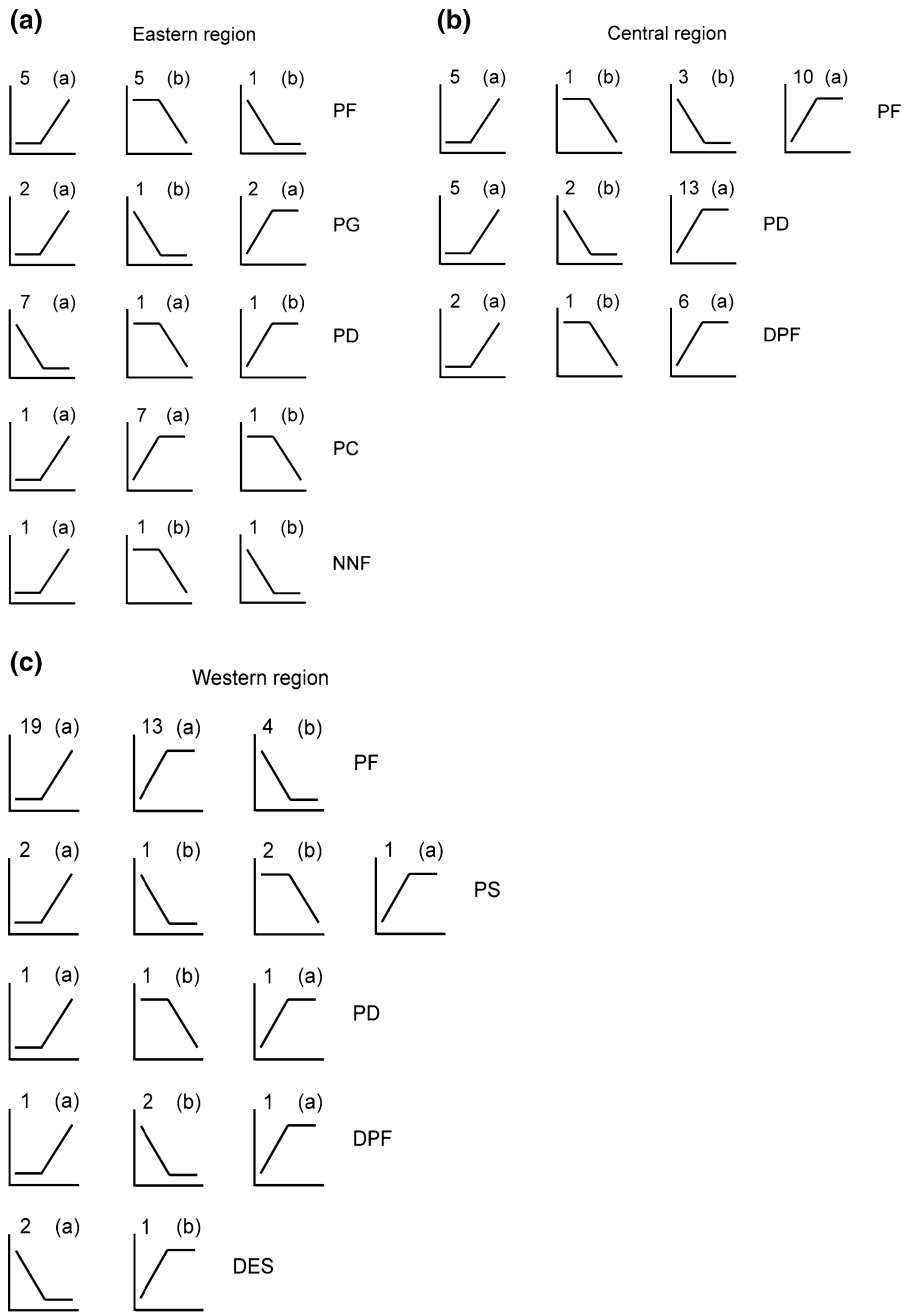

Fig. 7 Conflicting threshold relationships within regions. Basic forms of threshold relationships (see Fig. 3) between species abundance and landscape variables observed for the Eastern region (**a**), Central region (**b**), and Western region (**c**). *Numbers above plots* indicate the number of species that exhibited a threshold form. Threshold relationships for two species in the same region were defined as conflicting if one exhibited increasing species abundance with a landscape variable and the other exhibited decreasing abundance with that variable. Relationships in the same row marked with different *lower-case letters* are conflicting relationships. *Upper-case letters* indicate the landscape variable (defined in Tables S1–S3) for a given row of relationships: *PF* percent forest, *PG* percent grassland, *PD* percent development, *PC* percent cropland, *PS* percent shrubland, *NNF* nearest-neighbor distance for forest patches, *DPF* density of patches of forest, *DES* density of edge for shrubland

consequence, some relationships that were truly gradual nonlinear relationships (three or more splines) were fit as abrupt nonlinear relationships (two splines). But MARS chooses which variables, basis functions, and knots to include based on the combination of these elements that best minimizes GCV MSE (Friedman 1991; Salford Systems 2001). In this process, complexity is not the only factor that is examined; rather, MARS considers both fit and complexity simultaneously. Compared to an abrupt nonlinear fit (Fig. 2b), a gradual nonlinear fit (Fig. 2c) could be achieved with as few as one or two additional basis functions, so the additional df to be charged was small relative to our sample sizes. Had the data for a given species supported a lower GCV MSE for a gradual nonlinear model (e.g., through an improved fit) than it did for an abrupt nonlinear model, a gradual nonlinear fit would have emerged as better.

For a given species, a gradual nonlinear fit would have involved two or more basis functions (three or more splines) for the same landscape variable. We observed three instances in which a species' abundance was associated with a univariate threshold involving two basis functions of the same landscape variable (Tables S8, S9), and two instances in which a species' abundance was associated with an interaction threshold involving two basis functions of the same variable (Table S10). All five of these relationships were abrupt nonlinear relationships, not gradual nonlinear relationships. The criterion that a landscape basis function had to increase GCV R^2 by $\geq$10 % to be considered further in the analyses was applied to all landscape basis functions irrespective of the type of fit (linear or nonlinear) in which they were involved, so this aspect of the analysis would not have biased the results toward finding any particular type of fit.

Our use of a single modeling approach that was capable of fitting different forms of relationships (linear, abrupt nonlinear, gradual nonlinear) avoided problems of comparing results from methods with different fitting algorithms (least-squares versus maximum likelihood; model building and pruning versus stepwise or backward elimination methods) and possibly different statistical power. In addition, some methods that are commonly used to study species-habitat relationships are unable to accurately or objectively identify abrupt relationships (see comparisons in Ficetola and Denoël 2009). Overall, our results indicated that when nonlinear relationships were present, fits that reflected abrupt relationships were better supported by the data than were fits that reflected gradual relationships.

Threshold complexity and the challenge of assemblage-level conservation

Although the prevalence of species that exhibited threshold relationships was substantial, most of the relationships involved simple threshold types and relatively simple landscape conditions. Sample sizes for each species (n = 198–213 routes) and the ability of MARS to fit complex nonlinear relationships made it unlikely that the preponderance of relatively simple thresholds (Fig. 5a) was due to low statistical power of our analytical method. Our finding that landscape composition (percent cover) variables were involved in many more threshold relationships than were landscape configuration variables (nearest-neighbor distance, edge density, patch density) (Fig. 5b) supports the idea that in a conservation context it may generally be more important to maintain habitat amount than to manage habitat configuration (Fahrig 1997, 2002). However, there will likely be situations in which it will be valuable to carefully consider both habitat amount and configuration (Villard et al. 1999; Fahrig 2002; Flather and Bevers 2002; Betts et al. 2006) depending, for example, on the scale of the observation unit (landscape versus patch versus site), the scale of the conservation or land-management problem, species-specific sensitivities to habitat configuration, and the proximity of the landscape state to threshold conditions (Rhodes et al. 2008; Rueda et al. 2013; Villard and Metzger 2014). Our results imply that management of landscapes for birds in the study regions may be relatively straightforward because the number of landscape-level limiting factors on a given species' abundance was typically low, and because the focus could be on relatively simple thresholds (involving one main effect and land-type amount variables) rather than on relatively complex thresholds (involving multiple main effects, one or more interactions, and land-type configuration variables).

But broad-scale species-level management is often not feasible, and the relatively simple nature of most of the threshold relationships belies the difficulty of assemblage-level conservation. Even among species that were associated with the same landscape variable in the same region (Fig. 6a–c), conflicting relationships

were often observed (Fig. 7). Although these conflicts likely reflect differences in ecological requirements (e.g., an increase in percent forest would be expected to increase the abundance of a forest obligate breeder and decrease the abundance of a grassland breeder), ensuring that management actions directed at improving the threshold situation for some species does not degrade it for others is a complex prospect for land management focused on conserving the full assemblage of species. Simultaneous consideration of species that respond to different variables within the same land type (e.g., Figure 6d–f) would further complicate assemblage-wide conservation. Although some species may respond to landscape conditions similarly (e.g., Figure 6g–i), the considerable variety of threshold relationships we observed in each assemblage (Tables S8–S10) indicates that such similarities may not be common enough within a large assemblage to adequately reduce the aforementioned management complications.

Our findings from three distinct geographic domains expose threshold relationships as pervasive, diverse, and often-conflicting patterns that impose a much more complicated set of circumstances for assemblage-level conservation of birds than has been widely recognized. To cope with these circumstances, it may be possible to adapt approaches that have been used in related contexts. For example, researchers can assess whether there are species traits (see Rueda et al. 2013) that predict threshold responses so that the most vulnerable species can be identified. Conservationists can identify species whose thresholds reflect limiting cases so that conservation of these species has the potential to extend to other species in the assemblage. To inform conservation planning and management, investigators can consider using optimization analyses (Lampert and Hastings 2014), multispecies frameworks (Schwenk and Donovan 2011), regulatory limits (Johnson 2013), and multivariate change-point analyses for whole communities (Becker et al. 2015). And, through efforts to model bird–landscape relationships using actual habitat variables rather than land-use and land-cover variables (Betts et al. 2014), researchers may be able to reduce the number of conflicting threshold relationships they find among species.

Our results provide starting points for research that was beyond the scope of the present analysis. We used a 3-year time interval for bird data that was centered on the time that the landscape data were collected. This strategy reduced the chance for artifacts in the results stemming from temporal mismatches between bird and landscape data. Examination of our results along with those from analyses of additional non-overlapping time intervals from the multi-decadal BBS data could be used to improve understanding of the temporal variation in threshold prevalence—knowledge that would be valuable in planning and management contexts. Before we conducted this research, little was known about threshold relationships for the species and regions we studied, and we asked what evidence (if any) existed for threshold relationships. The results we report for individual species can be used to develop a priori hypotheses for future confirmatory analyses that would refine knowledge about threshold variables for the assemblages we considered. Ultimately, use of thresholds to guide conservation will require assessment of how different levels of threshold variables (e.g., various intervals of percent forest cover) are spatially distributed across actual landscapes. Mapping various levels of the threshold variable for a species would enable identification of where in the landscape, and in how much of the landscape, different levels of the variable occur. This information coupled with knowledge of threshold points for many species may help to identify where to implement on-the-ground management for an assemblage of species. One of the more challenging aspects of dealing with global change impacts is the limited ability to foresee and hence plan for threshold responses (André et al. 2010). For the regions and bird species we studied, our results and those from the future analyses outlined here will improve the ability to predict threshold relationships and incorporate such predictions into conservation planning.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

Research involving human subjects The authors declare that they are in full compliance with all of the ethical standards for publishing in *Landscape Ecology*. Data retrieved from the North American Breeding Bird Survey Web site involved birds, but the authors' research did not involve actual interaction with birds, other animals, or human subjects.

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ERRATUM

Erratum to: Avian abundance thresholds, human-altered landscapes, and the challenge of assemblage-level conservation

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The original publication of the article includes incorrect common and scientific names for a bird species listed in Tables S4 and S10 in the online Supplementary Material.

Instead of Bell's Sparrow (*Artemisiaspiza belli*), the correct names for the species we studied are Sagebrush Sparrow (*Artemisiospiza nevadensis*).

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