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RESEARCH ARTICLE

Using a species-centered approach to predict bird community responses to habitat fragmentation

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Abstract

Context The relative importance of habitat fragmentation versus loss on species richness has been much debated. However, recent findings that fragmentation effects are relatively weak may be an artifact of using human-classified vegetation rather than adopting a species-eye view to measure landscape structure.

Objectives We present the first example of a species-centered approach for examining fragmentation effects on ecological communities. We tested hypotheses relating to the relative influence of habitat amount, configuration, and focal patch size on southwest Oregon bird communities.

Methods We used boosted regression trees based on unclassified Landsat TM to create 'stacked' species distribution models (S-SDMs) for a large pool of avian species and nested subset of habitat specialists. We tested the relative importance of S-SDM-derived habitat amount, patch number, mean patch size, and focal patch size in explaining species richness. We compared this approach to metrics based on generic land-cover classifications.

Results Species-centered models had greater statistical support than land-cover models. In species-centered models, species richness increased as a function of focal patch size and decreased with patch number, supporting the hypothesis of negative effects of fragmentation per se. Land-cover based models indicated inconsistent support for habitat amount but a positive effect of fragmentation.

Conclusion The species-centered approach identified habitat configuration relationships obscured by land-cover based approaches. While positive land-cover based fragmentation effects were consistent with recent synthesis work, the species-centered approach consistently revealed strong negative effects of fragmentation matching traditional theoretical expectations. S-SDMs may offer promise for generalizing ecological theory to real species distributions.

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Introduction

In addition to the well known effects of local site characteristics on diversity (MacArthur and MacArthur 1961; Tews et al. 2004), the recent decades of research in landscape ecology and metacommunity ecology have made clear the additional importance of landscape and regional processes in determining local richness (Ricklefs 1987; Leibold et al. 2004; Harrison and Cornell 2008). As anthropogenic disturbance to natural ecosystems continues to alter both the extent and spatial pattern of habitats (Barnosky et al. 2012; Betts et al. 2017), disentangling the effects of landscape-level habitat composition and configuration on species richness has become a primary focus in ecology research and conservation planning (Whittaker et al. 2001; Ricklefs 2008; Tscharntke et al. 2012). The roles of habitat amount and fragmentation have been intensively studied, with the goal of informing on-the-ground biodiversity conservation (Fischer and Lindenmayer 2006; Newbold et al. 2016).

Despite extensive focus, consensus has not been reached on the relative importance of habitat amount versus fragmentation or the scales at which they are most influential to species richness (Prugh et al. 2008; Thornton et al. 2011; Fahrig 2013, 2017; Hanski 2015; Fletcher et al. 2018). Fahrig's (2013) 'habitat amount hypothesis' argues that community structure can be explained by a 'sample area effect' whereby local species richness increases with the amount of area sampled in a landscape regardless of its configuration. Thus, species responses often ascribed to configuration would in actuality be primarily driven by composition (Fahrig 2013). Additionally, the 'regional species pool' hypothesis posits that regional scale habitat availability determines which species can disperse to a site, influencing richness over and above filtering by local conditions (Tscharntke et al. 2012). According to these concepts, higher landscape-level habitat amount alone should indicate a larger potential species pool, and hence a greater potential for multiple colonization events and higher local diversity (Leibold et al. 2004).

Alternatively, theory and empirical evidence suggest the spatial configuration of habitat can influence species occurrence, abundance, and richness beyond the effects of habitat amount (Andren 1994; Haddad et al. 2015; Hanski 2015; Pfeifer et al. 2017). Size, pattern, and landscape context of individual habitat patches may further mediate local richness through independent and interactive effects on metapopulation and metacommunity dynamics (Moilanen and Hanski 1998; Leibold et al. 2004). For example, amount of available habitat surrounding a patch and its proximity to other patches may affect species diversity via the interactions between within-patch dispersal and extinction processes (Hanski et al. 2013) and interactions among patch-level communities (Leibold et al. 2004). This may be particularly true in landscapes with little remaining habitat and where configuration or species traits may contribute to low functional connectivity (Betts et al. 2015).

The established paradigm for defining 'habitat' in fragmentation research has included a strong dichotomy between habitat and matrix, following from conceptual roots in island biogeography theory (MacArthur and Wilson 1967; Fahrig 2013). Typically 'habitat' and 'matrix' (or non-habitat) are researcher-defined on the basis of classified vegetation or land-cover type, particularly when attempting to define 'habitat' for multiple species simultaneously (Driscoll et al. 2013; Fahrig 2013; Betts et al. 2014). However, classified land-cover may be an ineffective proxy for 'habitat' (Cushman et al. 2008), potentially leading to inconsistent results among studies and across taxa (Thornton et al. 2011). In reality, 'habitat' or 'matrix' can contain unique gradients of individual species responses to environmental conditions (Cushman et al. 2010), potentially producing error in simplified habitat amount and fragmentation metrics. While a patch/matrix simplification may be a necessary one for deriving fragmentation metrics, the method of delineating patches in a way that captures a species' true 'habitat' may be key to accurately predicting species or community responses.

The land-cover based approach to delineating 'habitat' has constrained investigation of habitat amount/fragmentation effects on richness to groups of species thought to share a strong affinity with a particular cover type (e.g., 'mature forest') (Fahrig 2013) or in systems where boundaries are clearly delineated (e.g., ocean-island mosaics; Leibold et al.

2004). However, this simplification likely limits the ability to test mechanisms that drive diversity (Belmaker and Jetz 2012). For instance, rare or more specialized species likely do not occupy all 'forest' surrounding a focal patch, so the total population available to serve as a pool of propagules is a small subset of that estimated using cover types. Similarly, it is unlikely that patch boundaries for all members of a community are congruent (even within a single taxon); it is well-known that bird species partition habitat at fine scales (Holmes and Sherry 1988; Valente and Betts 2018). Therefore, studies incorrectly defining habitat for multiple species in a community risk Type II error when it comes to uncovering primary drivers of community structure.

We suggest that these problems may be addressed by using a 'species-centered approach', which reflects realities that (1) 'habitat' is a species-specific concept and (2) in terrestrial systems, habitat rarely occurs as islands, but is characterized by gradients in suitability (Comfort et al. 2016). Building on the 'continuum model' (Fischer and Lindenmayer 2006), a species-centered approach uses 'habitat' defined on a species-by-species basis (i.e., species distribution models) to address questions about the role of habitat loss and fragmentation on species distributions (Betts et al. 2007, 2014). Such an approach may be more realistic in that it is well-aligned with Gleasonian ecological theory of individualistic distribution of organisms in relationship to their environment (Gleason 1936; Cushman et al. 2010). This concept has been bolstered by studies showing better predictive accuracy of spatial patterns by continuum models in distributions of tree (Evans and Cushman 2009) and bird species (Shirley et al. 2013).

In a recent empirical test, individual bird species distributions were more consistently predicted by habitat amount metrics derived using a species-centered approach compared with classified vegetation-based metrics (Betts et al. 2014). If tractable, adopting a species-centered approach in studies of landscape pattern could aid in the mechanistic understanding of the drivers of species richness, to the benefit of conservation efforts. However, this approach remains unexplored—perhaps due to the technical and conceptual challenges associated with quantifying 'habitat' for multiple species with disparate habitat associations (Didham et al. 2012; Fahrig 2013).

Here, we demonstrate a novel methodology that attempts to overcome these challenges, and examines whether the method for defining 'habitat' may influence the outcome of a fragmentation study. We used a species-centered approach to test the relative importance of habitat composition and configuration on bird species richness using metrics derived from 'stacked' species distribution models (S-SDMs) based on unclassified Landsat TM land-cover data (Figs. 1, 2).

We considered the potential effects of landscape habitat amount, as well as mean size of patches in the landscape (hereafter 'mean patch size'), mean number of patches in the landscape (hereafter 'patch number'), and focal patch size on richness. Whether or not it is a primary driver of diversity in a particular landscape, habitat amount has a clear positive association with species occurrence (Fahrig 2013; Betts et al. 2017). Mean patch size has been hypothesized to influence local extinction dynamics, with small patches being more prone to stochastic vacancy (Hanski 1998). Patch number, another fragmentation metric, may influence species dispersal among patches; although patches are necessarily smaller for a given habitat amount, they may serve as stepping stones, thus positively influencing species richness (Saura et al. 2014; Fahrig 2017). This assumes that most species are capable of crossing non-habitat gaps, and if they cannot, we expect patch number to negatively influence richness. Finally, focal patch size reflects the hypotheses from metacommunity theory that large patches should have lower rates of local extinction (Leibold et al. 2004), have greater potential for conspecific and heterospecific information use (Fletcher 2009; Schmidt et al. 2015), and be less prone to stochastic disturbance effects (Elkin and Possingham 2008). Focal patch size therefore represents a core mechanism of metapopulation dynamics (i.e., the incidence function model [Hanski 1998])—particularly if patch size is considered in the context of its surrounding landscape (i.e., a "focal patch" approach [Hadley et al. 2014]).

We examined habitat amount and fragmentation effects for a pool of 48 locally common bird species in a heterogeneous temperate vegetation complex of oak- and mixed conifer/hardwood -dominated cover types in the Rogue Basin of southwest Oregon. To compare how relationships might differ for habitat specialists, we additionally examined a nested subset of 25 bird species that are highly associated with oak forest

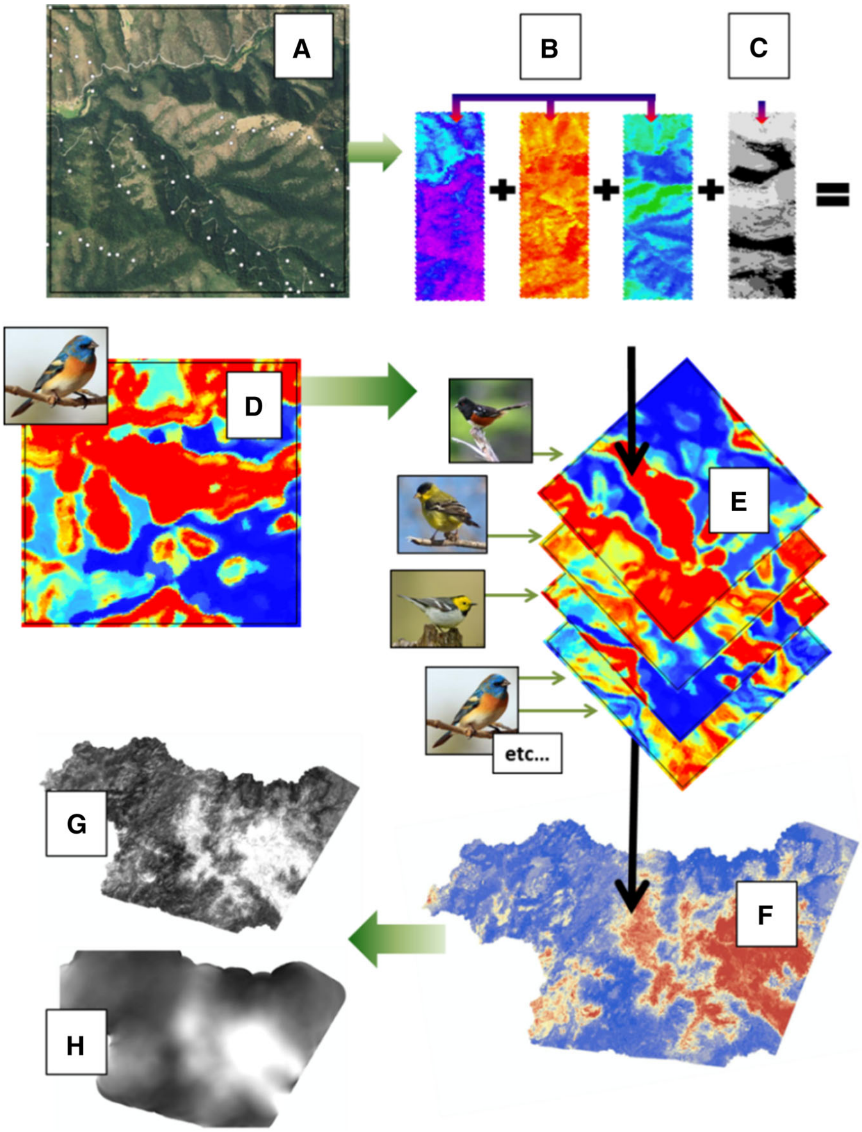

Fig. 1 Process for calculation of species-centered landscape habitat amount metric: (**a**) species occurrence data from an observational study was modeled as a function of predictors including (**b**) Landsat TM land-cover data and (**c**) elevation, as well as climate. The resulting SDMs were used to interpolate probability of species occurrence (which we interpreted as a measure of 'habitat amount') across all pixels in the landscape for each species; within this landscape subset (**d**), high probabilities of occurrence for lazuli bunting are red, and low probabilities are blue. Multiple SDMs for individual species were 'stacked', or summed (**e**), for a prediction of total habitat amount across the entire species pool at each pixel within a landscape (**f**). Finally, a moving window analysis was applied to calculate the mean of all pixels within a given radius as an index of community-level habitat amount at a given scale, e.g. a 150 m radius (**g**) or a 10,000 m radius (**h**). For **g** and **h**, highest summed mean values are white, and lowest values are black. Bird species pictured are included in the taxa examined in this study but are arbitrary with respect to this hypothetical illustration. (Color figure online)

during the breeding season (Altman and Stephens 2012).

We considered the following broad habitat amount versus fragmentation hypotheses: (1) the *landscape composition hypothesis* (Fahrig 2003), in which landscape-level habitat availability mediates environmental filtering via dispersal effects; (2) the *landscape fragmentation hypothesis* (Villard et al. 1999) whereby species richness declines linearly with increased fragmentation after controlling for

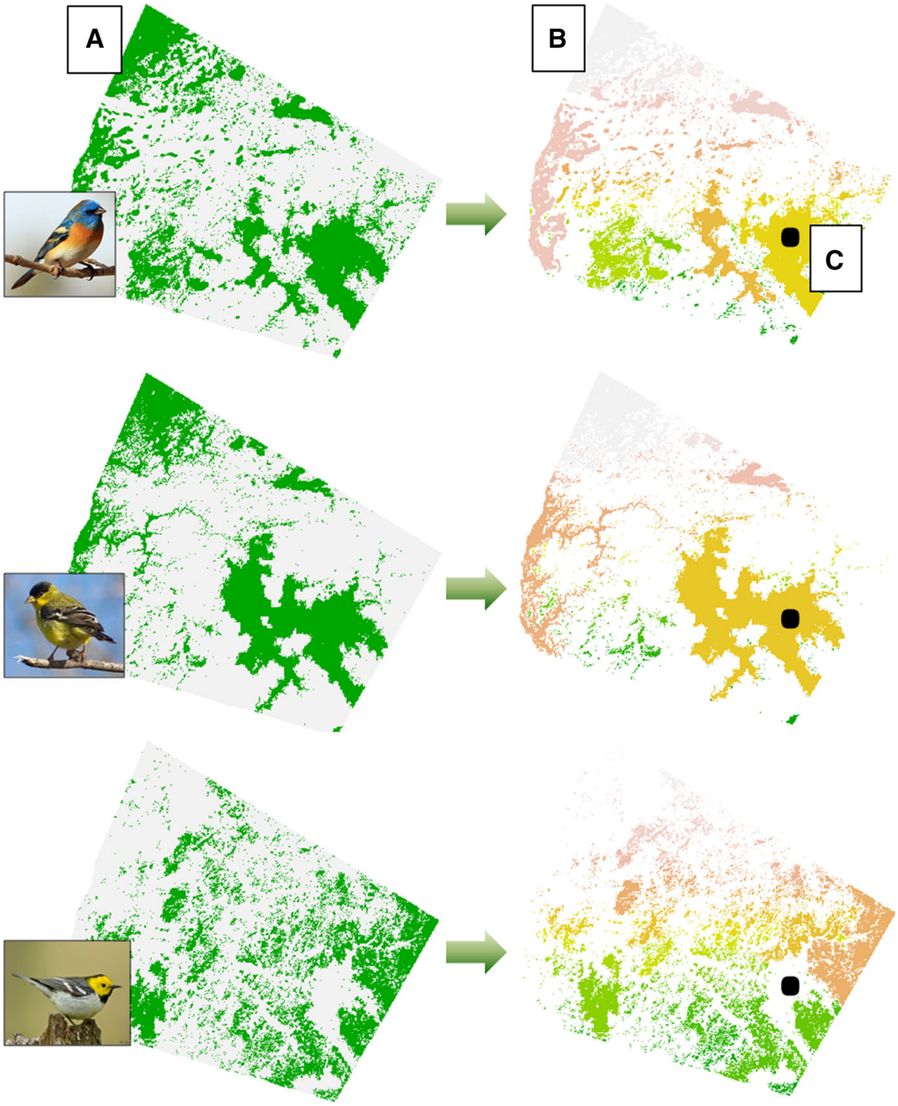

Fig. 2 Process for calculation of species-centered patch size metrics: **a** Continuous SDMs (see Fig. 1a–d) were converted to presence-absence maps for each of the study species. **b** For each species, contiguous pixels in the presence-absence maps were clumped to create distinct patches of 'habitat' and log size of each patch was calculated; various shades in these maps represent individual patches. **c** At each survey point (black dot) in the evaluation dataset, the focal patch size, mean patch size, and patch number were calculated across each of the two species groups. Bird species and respective maps pictured are from top to bottom: Lazuli Bunting, Lesser Goldfinch, Hermit Warbler. (Color figure online)

remaining habitat in the surrounding landscape; and lastly, (3) the *fragmentation threshold hypothesis* (Andren 1994; Fahrig 1998; Flather and Bevers 2002) where the effects of landscape habitat amount and fragmentation interact, leading to a loss of species richness under a certain threshold of patch size and isolation.

Finally, to test whether previously reported weak effects of patch size on species abundance and richness could be partly attributable to inaccurate delineation of 'habitat', we compared the performance of our species-centered approach to the commonly used method of using a generic land-cover based approach for habitat amount and patch metrics. We hypothesized that land-cover based metrics would not be effective in detecting these relationships.

Methods

Study area

The Rogue Basin is part of the Klamath Mountains ecoregion and the California Floristic Province biodiversity hotspot (Myers et al. 2000), and contains the cities of Grants Pass (42.4389°N, 123.3283°W), Ashland (42.1914°N, 122.7008°W), and Cave Junction (42.1667°N, 123.6469°W) (Supplementary

Fig. A1). The Rogue Basin is composed of five watersheds that drain to the Pacific Ocean, and is characterized by complex topography, with elevation ranging from sea level to approximately 2300 m. Configuration of diverse vegetation types including prairies, riparian systems, shrub fields, and coniferous and deciduous forest results in spatial heterogeneity throughout the region (Franklin and Dyrness 1988; Sawyer 2006). Vegetation composition varies with elevation, aspect, soils, and disturbance history. Historically the primary disturbance in the Rogue Basin was fire, and then, more recently fire exclusion. At the stand scale, 8-year fire return intervals have been documented prior to disruption in those processes in the late 1800 s (Metlen et al. 2018). The Rogue Basin is composed of a diversity of land owners and associated land use and management practices, with logging the most notable disturbance type (Franklin and Dyrness 1988). The climate is Mediterranean with cool, wet winters, and hot, dry summers (Myers et al. 2000). Mean monthly precipitation ranges from 5.85 mm (July) to 849 mm (December), and mean monthly temperatures from − 4.41 °C (December) and 33.29 °C (July) (PRISM Climate Group).

Stacked species distribution model development

We developed a technique that uses a species-centered approach to quantify ‘habitat’ for an entire community (Fig. 1). We first developed species distribution models (SDMs) for each species using an independent training dataset (see “SDMs” below). The resulting SDMs were used to interpolate probability of occurrence across all pixels in the landscape for each species; for each species we interpreted this as a measure of ‘habitat amount’ at each pixel. Multiple SDMs for individual species were ‘stacked’, or summed, for a prediction of total species pool-level habitat amount each pixel within the landscape (see “Model ‘stacking’”; Fig. 1). Finally, we used S-SDMs to calculate metrics of habitat amount and configuration across all species (see “Species-centered landscape habitat amount” and “Species-centered patch metrics”; Fig. 2) and tested hypotheses using an independent evaluation dataset.

SDM training dataset

We trained SDMs using bird occurrence data from 2107 point count surveys collected from 2000 to 2011 in the Rogue Basin (“training dataset”; Alexander et al. 2004). We established survey points along gradients of elevation and vegetation and spaced points a minimum of 150 m apart along each transect to limit double-counting of individual birds (Ralph et al. 1993). We surveyed birds using 5-min counts that were conducted within 4 h of sunrise between mid May and early July to coincide with hours of peak forest bird activity during the breeding season (Stephens et al. 2010). Surveyors recorded all birds detected by sight or sound, and estimated the bird’s distance from the observer to the nearest meter. Flyover and individuals detected > 50 m from the point count location were excluded from the analysis. As number of visits per point count location varied both within and across years, we randomly selected data from a single visit to each point count location for use in SDM training.

SDM evaluation and hypothesis testing dataset

We collected an independent bird occurrence dataset in 2011 (“evaluation dataset”) to (1) assess the predictive ability of SDMs and (2) estimate observed species richness for hypothesis testing. We used aerial photography, landowner data, and land-cover data from the Gap Analysis Program (US Geological Survey 2011) across the study area to create polygons of oak or mixed oak/conifer/hardwood-dominated vegetation types that were both (1) publicly accessible and (2) large enough to contain up to twelve point count survey locations spaced 250 m apart. We placed 632 point count locations on the vertices of randomly placed 250 m grids in ESRI (2011) Spatial Analyst across each polygon (Supplementary Fig. A1). Surveyors visited each point count location once, using survey methods identical to the training dataset (Stephens et al. 2010).

SDM predictor variables

We included land-cover, elevation, and climate as SDM predictors to represent conditions important to forest bird distributions. We used unclassified Landsat Thematic Mapper (TM) imagery with a 30 m^2 pixel resolution to obtain continuous land-cover variables for each survey year and for each point within the model training dataset (USGS 1982; see Supplemental Material for details regarding Landsat TM image pre-processing). Following Shirley et al. (2013) we calculated the means and standard deviation of TM reflectance values at radii of 150, 500, 1000, and 2000 m at each pixel using a moving window analysis in ESRI Spatial Analyst (ESRI 2011) for all non-thermal infrared Landsat TM bands (i.e., 1, 2, 3, 4, 5, and 7), resulting in 48 land-cover variables.

Climate predictors consisted of monthly 30-year mean minimum and mean maximum precipitation (July and December, respectively); mean minimum and mean maximum temperature (December and July, respectively); mean precipitation, mean minimum and mean maximum temperature for June (corresponding to mid-avian breeding season for the Rogue Basin); and elevation. We obtained all climate variables from interpolated 800 m grids derived from years 1981 to 2010 (PRISM Climate Group 2004) which we resampled to 30 m to match the resolution of Landsat data. We obtained elevation from a 30-m digital elevation model (http://www.oregon.gov/DAS/CIO/GEO).

SDM training and evaluation

Using the model training dataset and environmental predictors, we developed SDMs for study species using boosted regression tree (BRT) models (Friedman et al. 2000; Friedman 2001). BRTs add a “boosting” method to a traditional regression tree methodology to improve model accuracy; beginning with a single regression tree, new trees are added iteratively in a forward, stepwise fashion that minimizes loss of predictive performance (Elith et al. 2008). BRTs model both non-linear relationships and interactions among predictors, and can be used with a variety of response distribution types. We developed BRTs for the 48 most commonly occurring bird species in the model training dataset (i.e., those species detected at $\geq$ 1% of survey locations), including 25 oak-associated species.

We fit BRTs in the package ‘dismo’ (Hijmans et al. 2017) in program R (R Development Core Team 2008), with additional source code from Elith et al. (2008). For initial runs, we used a ‘learning rate’ (*lr*) of 0.01, ‘tree complexity’ (*tc*) of 5, and ‘bag fraction’ of 0.5, as suggested in Elith et al. (2008) and validated for use in forest bird distribution models (Shirley et al. 2013). For each species, we adjusted *lr* adjusted to optimize the number of trees (*nt*) produced (with a goal of at least 1000 trees), and adjusted *tc* in tandem with *lr* for optimization of *nt* (Elith et al. 2008). We evaluated prediction success of each species’ SDM with (1) Area Under the Receiver Operating Characteristic Curve (AUC) scores and standard errors for within-model tenfold cross validation and (2) AUC scores for model prediction to the evaluation dataset, using the R package ‘pROC’ (Robin et al. 2011). All species’ models performed sufficiently well to be retained in further steps (see Supplemental Material for details, Table A2).

SDM ‘stacking’

Using the packages ‘raster’ (Hijmans 2016) and ‘dismo’ in R, we used final BRTs to create 30 m^2 pixel resolution maps of predicted probability of occurrence (POC) for the entire study area for each of the 48 species (Fig. 1A–D). For both the full pool of 48 species and the subset of 25 oak-associated species (Supplementary Table A2), we stacked POC maps for all species in each group to create a summary map in which each pixel’s value was the sum of POCs for all species at that pixel (Fig. 1E), resulting in two separate S-SDMs for the study area. Thus, the value of each pixel represents an estimate of total ‘habitat amount’ across the entire species pool, and the final map represents an estimate of community-level habitat amount across the study area. Although use of summed POCs versus summed threshold values (i.e., presence/absence) in S-SDMs is a matter of some debate (Wilson et al. 2005; Dubuis et al. 2011; Pellissier et al. 2013), we chose the more conservative approach of using summed POCs to avoid overestimation of species richness (Calabrese et al. 2014).

Species-centered landscape habitat amount

We calculated landscape habitat amount from S-SDMs as the mean habitat amount at a 10,000 m radius around each point count location in the evaluation dataset for each species group (Fig. 1G). We chose this distance as an outside range for habitat use and breeding/natal dispersal distances for passerine birds (Paradis et al. 1998; Bowman 2003; Betts et al. 2007), and as it was least correlated with an estimate of local-scale habitat amount (see Supplemental Material for details).

Our approach required that we split habitat gradients into dichotomous categories for our patch metrics (see "Species-centered patch metrics" below), whereas our habitat amount metric is continuous. Unfortunately, to date, we know of no methods to quantify patches that do not require strict definitions of boundaries. To ensure that use of a continuous habitat amount metric did not give spurious results, we conducted a sensitivity analysis in which we transformed our continuous species-centered measure of habitat amount into a dichotomous one. We reclassified the SDMs for each species to 'habitat' or 'non-habitat' based on the same unique cutpoints that were calculated to derive patch metrics (see "Species-centered patch metrics" below). We then summed all reclassified SDMs to generate a prediction of the total 'habitat amount' at each pixel across the study area, and calculated the mean value at 10,000 m as the dichotomous landscape habitat amount metric. The relative influence of patch and landscape variables did not differ substantively in this sensitivity analysis (Supplementary Table A8).

Species-centered patch metrics

We calculated species-centered patch metrics for both species groups as follows. First, we converted all species' probabilistic SDM maps to presence/absence maps, using an objective a posteriori probability cutpoint to determine the presence threshold uniquely for each species (Fig. 2A). We calculated cutpoints using the "coords" function with the "youden" method (or Youden's J statistic) in the R package 'pROC'. The Youden method maximizes the sum of the sensitivity (the ability of the model to detect true presences) and the specificity (the ability of the model to detect true absences) of the Receiver Operator Characteristic Curve. This is a preferable threshold method for SDMs compared to use of a pre-selected fixed cutpoint (e.g., 0.5) in terms of reducing both the false positive rate and the false negative rate of species presence and absence predictions (Liu et al. 2005).

For each species, we clustered contiguous 'presence' pixels into discrete patches using the "clump" function in the R package 'raster', where all adjacent "habitat" pixels within all eight directions were considered part of the same patch (Fig. 2B). The minimum gap size between patches for all species was a single pixel's distance of 30 m. Given that the gap-crossing tolerance is not known for all study species in our focal habitats, it was not possible to apply a species-specific minimum gap size to each species' patch delineation. We then calculated the mean log focal patch size, mean log landscape patch size, and mean number of patches in the landscape at every survey point (Fig. 2C).

Generic land-cover based habitat amount and patch metrics

We reclassed all classified vegetation types from Gap Analysis Program (GAP; USGS 2011) land-cover data layers as (1) 'forest' and 'non-forest' cover and (2) 'oak' and 'non-oak' cover. We then used these two new classifications to calculate 'forest habitat amount' and 'oak habitat amount', corresponding to the full pool and oak-associated subset of species respectively, at the local (150 m) and landscape (10,000 m) scales.

For generic land-cover-based patch metrics, we used our clumping method to identify all patches within 'forest/non-forest' and 'oak/non-oak' layers, and from this calculated our fragmentation metrics. Due to the high connectivity of forest cover, the resulting landscape structure was dominated by several large patches; this issue is likely to be common in forest-dominated landscapes.

Species richness as a function of habitat amount and patch metrics

To test the relative effects of habitat amount and patch metrics on bird species richness, we applied the following model-selection strategy for each species group and for both the species-centered and land-cover based method. First, to test whether habitat amount may be the sole driver of richness, we modeled species richness as a function of landscape habitat amount for each species group and habitat metric method (Model 1; Supplementary Tables A6, A7). We then tested for the independent effects of each configuration metric in a separate model (focal patch size [Model 2], mean patch size [Model 3], patch number [Model 4]; Supplementary Tables A6, A7); each metric's model also contained habitat amount and the interaction between them (e.g., richness $\sim$ habitat amount * focal patch size). This approach allowed us to control for the effect of habitat amount and test for non-linear effects of each metric. If 95% confidence intervals for either the configuration variable or its interaction did not bound zero, we retained these for inclusion in the top global models.

We examined the AIC (Akaike's Information Criterion) of each of the preliminary models versus the top models, and between species-centered and land-cover based models, to test which was more parsimonious (Burnham and Anderson 2002). We calculated the ΔAIC (difference between the model with the lowest AIC and all other models), and considered models within 2 ΔAIC from the top model to be equally well supported, models within 6 ΔAIC to have potential merit, and models approximately $\geq$ 10 ΔAIC to be poorly supported (Symonds and Moussalli 2011).

We used simultaneous autoregressive (SAR) spatial error models in the package 'spdep' (Bivand et al. 2011; Bivand and Piras 2015) in R to account for variation in species richness resulting from the influence of spatial autocorrelation which may result from both biotic and abiotic processes (Legendre 1993). SAR models account for spatial structure using an additional term based on a user-defined 'spatial weights' matrix. Spatial error models are most appropriate when predictor variables do not fully explain spatial autocorrelation, and have been recommended for species distribution data over other SAR types (Kissling and Carl 2008). We used correlograms and Moran's I in the package 'ncf' (Bjornstad 2016) in R to test for spatial autocorrelation and found significant effects up to 10,000 m. We ran final SAR models with a spatial weights matrix based on a 10,000 m neighborhood to remove these effects.

We standardized all model predictor terms to a mean of 0 and a standard deviation of 1, allowing us to directly compare the regression coefficients as 'effect sizes' of all terms. Use of standardized coefficients to compare effect sizes has been identified as a least-biased option for comparing the relative importance of predictors in regression analysis when using collinear habitat variables (Smith et al. 2009).

To assess the level of multicollinearity in our top models (i.e., the amount of extra variance likely in model regression estimates due to correlation among predictors), we calculated Pearson r correlations, as well as variance inflation factor (VIF) scores in the R package 'fmsb' (Nakazawa 2017). A VIF score indicates the multiplicative factor by which the estimated variance of a model term is likely inflated given the other terms in the model. VIF < 10 for a term is generally taken to be an acceptable threshold for model inclusion; however, it may not always be appropriate to reject variables that are collinear, depending on the goals of the analysis and the other relationships between covariates such as suppressor effects (O'brien 2007; Smith et al. 2009). We found low to moderate correlation (Supplementary Table A4) and multicollinearity (Supplementary Table A5) in the species-centered metrics for top models. A number of the land-cover based metrics were highly correlated (Supplementary Table A4) and multicollinearity within the top land-cover models was high (Supplementary Table A5).

Many studies of landscape-scale habitat amount use a local habitat amount term to control for the effects of local site characteristics on the response of interest (e.g. Betts et al. 2007). To ensure that important effects of local habitat amount were not unaccounted for, we conducted an additional sensitivity analysis in which we added a term for local habitat amount (150 m) to the top models for each species group and for both the species-centered and land-cover based models. Local habitat amount was calculated using the same methods employed for landscape habitat amount (Fig. 1G). The relative influence of patch and landscape variables did not differ substantively in this sensitivity analysis (Supplementary Table A9).

Results

Species-centered models versus generic land-cover-based models

Species-centered models appeared to be better supported overall than land-cover models, according to AIC ranks (Table 1). For the full species pool, the species-centered top model had marginally more support than the land-cover model (ΔAIC = 3). The oak-associated species-centered model had substantially more support than the land-cover model (ΔAIC = 35).

Table 1 Top SAR models of species richness for two bird species groups (full pool of species, oak-associated specialists) as a function of landscape composition and configuration metrics using both a species-centered approach and a land-cover based approach

Method	Species group	Metric	Standardized coefficient (SE)	CI	AIC
Species-centered	Full pool	Landscape habitat amount	0.082 (0.28)	− 0.471, 0.634	2753.4
		Focal patch size	**0.372 (0.13)**	**0.126, 0.618**	
		Patch number	**− 0.472 (0.18)**	**− 0.822, − 0.122**	
		Patch number × landscape habitat amount	0.261 (0.14)	− 0.018, 0.541	
	Oak-associated	Landscape habitat amount	0.008 (0.18)	− 0.348, 0.365	2494.3
		Focal patch size	**0.671 (0.10)**	**0.474, 0.868**	
		Patch number	− 0.208 (0.14)	− 0.484, 0.067	
Land-cover based	Full pool	Landscape habitat amount	**1.175 (0.50)**	**0.186, 2.165**	2756.4
		Patch number	**1.847 (0.50)**	**0.862, 2.831**	
		Patch number × landscape habitat amount	**0.255 (0.10)**	**0.059, 0.451**	
	Oak-associated	Landscape habitat amount	**− 0.880 (0.32)**	**− 1.502, − 0.257**	2529.7
		Mean patch size	**1.529 (0.58)**	**0.387, 2.671**	
		Patch number	0.350 (0.40)	− 0.427, 1.127	
		Patch number × landscape habitat amount	− 0.165 (0.11)	− 0.379, 0.050	

Bold font for model results indicates that the 95% CI did not contain zero

Species-centered models

We found consistent support for the landscape fragmentation hypothesis as an explanation for bird community richness when using species-centered models. Top models for both species groups contained focal patch size and mean patch number; the model for the richness of the full species group also contained the statistical interaction between mean patch number and habitat amount (Table 1), however the CI included zero and thus did not fully support the fragmentation threshold hypothesis (Table 1). Additionally, the top model for the full species pool was $<$ ΔAIC 2 from the best preliminary model, indicating that these model sets were essentially tied (Supplementary Table A6).

Focal patch size was an important positive predictor for both oak and full species groups, and was the only predictor in the top model for oak species with a confidence interval that did not include zero (Table 1). The effect of focal patch size tended to be stronger for oak species richness than for the full species group (Table 1). The top model for the full species group also contained a negative coefficient for patch number (Table 1), indicating that the effects of focal patch size scaled up to the whole surrounding landscapes. For oak species however, the CI for patch number bounded zero when it was included with focal patch size in the top model (Table 1). The direction of effects was consistent with our hypotheses that species richness would be positively associated with habitat amount and focal patch size.

Habitat amount had a weakly positive relationship with richness in top models for both groups (Table 1), although CIs bounded zero. According to preliminary models, there was more support for habitat amount as a predictor of oak species richness than for the full species pool (Supplementary Table A6). However, using the species-centered method, standardized effect sizes for configuration metrics tended to be greater overall than for landscape composition (Supplementary Table A6). Mean patch size did not emerge as an important predictor for either species group, but this may have been due to a relatively high correlation with landscape habitat amount (Supplementary Table A4).

Generic land-cover-based models

In land-cover based models, we found support for both the fragmentation threshold hypothesis (full species group) and landscape fragmentation hypothesis (oak species). Both top models contained habitat amount and patch number as well as their interaction, and the oak species model also included mean patch size. The top model for the full species group was $>$ 6 ΔAIC from the next best preliminary model (Table 1; Supplementary Table A7). The top oak species model was < 2 ΔAIC from the next best model, indicating that these model sets were essentially tied (Table 1; Supplementary Table A7).

In contrast to species-centered models, CIs for habitat amount (i.e., forest/oak amount) did not include zero for both species groups, and effect sizes were considerably larger, albeit with high SEs of the coefficients (Table 1); this indicated relatively greater importance of habitat amount when we used land-cover based metrics. However, the direction of habitat amount effects was opposite between the two species groups (positive for full species, negative for oak species; Table 1).

Similar to species-centered models, CIs for patch number excluded zero for the full species group and included zero for oak species; in contrast, the direction of effects was positive for both groups (Table 1). The model for the full species group contained a positive interaction between patch number and habitat (Table 1). However, CIs for the land-cover based patch number *x* habitat amount interaction did not include zero; this indicated greater support for the landscape threshold hypothesis than in the species-centered approach. The land-cover based model for oak-associated species was the only top model to include a term for mean patch size (Table 1); although the SE was high, CIs did not include zero and effects were positive.

Discussion

To our knowledge, this is the first study to apply a species-centered approach to quantifying the relative effects of habitat loss and fragmentation on species richness. Using this approach, we did not find evidence for the landscape composition hypothesis (Fahrig 2003), suggesting that community-level landscape scale dispersal or “mass effects” may not be the dominant drivers of community structure in the avian community we examined. Rather, the species-centered approach indicated that bird richness was primarily influenced by habitat configuration (i.e., a positive effect of focal patch size and a negative effect of number of patches in the landscape), even after statistically controlling for habitat amount. Hence, our results are inconsistent with the habitat amount hypothesis (Fahrig 2013), but consistent with the landscape fragmentation hypothesis (Villard et al. 1999). Evidence from preliminary models also indicated potential support for the fragmentation threshold hypothesis (Andren 1994; Fahrig 1998; Flather and Bevers 2002), specifically that the negative effect of number of patches might be mitigated by increasing habitat in the landscape.

Species-centered models supported the idea that while habitat loss is of clear importance to biodiversity (Pimm and Raven 2000; Betts et al. 2017), the configuration of remaining habitat may have the potential to exacerbate the negative impacts of that loss and thus should not be ignored (Villard and Metzger 2014). This approach consistently revealed strong negative effects of fragmentation matching traditional theoretical expectations (Hanski 2015). A number of other studies have found positive or no effects of fragmentation per se on species richness and occupancy (Prugh et al. 2008; Fahrig 2017; De Camargo et al. 2018), and a relatively high importance of habitat amount compared to fragmentation (Smith et al. 2009). However to our knowledge, previous efforts have relied solely on human-derived land-cover classifications (e.g., forest/non-forest), similar to our land-cover models which found relatively more positive fragmentation effects and a greater relative importance of habitat amount.

Indeed, our land-cover models led to different conclusions, in which landscape habitat amount (i.e., forest/oak amount) was more explanatory of species richness, and fragmentation had primarily positive but variable effects. Increasing number of patches in the landscape (*increased* fragmentation) had a positive relationship with species richness; in contrast, increasing mean patch size (*reduced* fragmentation) had a positive effect. These models performed better than expected at detecting fragmentation relationships, although the multicollinearity with habitat amount, also an important predictor, made the relationships difficult to discern. This was particularly true for the oak species group, for which the top model contained a negative effect of landscape habitat amount. This may indicate that mean patch size as defined by land-cover was not truly reflective of a unique ecological process, but was simply another measure of habitat amount in our landscapes.

In our system, the positive effect of fragmentation (i.e., increasing number of patches) observed with the land-cover approach would likely be driven by the fact that despite 'forest cover' being subdivided into more patches, suitable habitat for many species was not actually more fragmented. The 'cross-habitat spillover hypothesis' predicts that the richer species pool in more heterogeneous landscapes may contribute to higher potential local richness, beyond that which may be supported based solely on focal patch size or quality (Tscharntke et al. 2012). This may result in the amount and connectivity of habitat actually increasing for edge-associated species, non-forest species, or species that benefit from habitat complexity. Conversely, the negative association of patch number with richness in the species-centered models may reflect that after controlling for habitat amount, reduced functional connectivity among increasingly subdivided habitat patches may have a detrimental affect on local colonization and extinction balance.

We found evidence for greater sensitivity to focal patch size in oak-associated birds than for the bird community as a whole in species-centered models, supporting previous findings that specialists may be particularly sensitive to habitat fragmentation (Devictor et al. 2008; Valente and Betts 2018). This finding has potential conservation importance given the declining status of oak habitats and their associated bird populations in the region (Altman and Stephens 2012). This variation in the fragmentation-richness relationship highlights the potential for landscape sensitivity to depend on the life history or ecological traits of the species being examined (Valente and Betts 2018).

Criticisms have been leveled at the use of focal patch in fragmentation studies (Fahrig et al. 2019) stemming from the notion that patch size can be an ambiguous configuration metric unless the amount of habitat within the landscape is taken into account (Fahrig 2003). Importantly, we found focal patch effects even after statistically controlling for habitat amount and number of patches in the landscape in both of the species-centered top models. We argue that focal patch size captures biologically relevant habitat configuration attributes perhaps not effectively quantified through landscape-scale variables.

We expect that a focal-patch approach most closely reflects the processes which are thought to influence individual species and subsequently species pool-level responses to habitat fragmentation (Leibold et al. 2004; Hanski 2015). Metapopulation theory (Hanski 1998) posits that patch occupancy is driven by colonization and extinction dynamics at the scale of individual patches, where the risk of stochastic local extinctions is lower in large patches due to greater local population sizes. In addition, locations that are well connected to other populations are more likely to be colonized following local extinctions. Sites within large focal patches are inherently better connected than sites in small focal patches. If birds show reluctance to cross gaps (Hadley et al. 2014) or utilize social information (Fletcher 2009; Schmidt et al. 2015), vacant territories within well-connected single patches should be more likely to be colonized than vacant territories contained within more isolated patches. Area of connected habitat surrounding the sampling site (as quantified by the focal patch approach) is unlikely to be adequately captured by mean patch size, as this metric can be identical in landscapes with very different configurations; this is a well-known problem for any metric based on averages.

The frequency with which species persist as metapopulations in extinction/colonization balance, as opposed to persisting as a result of stable large populations, is still debated among ecologists (Hanski 1998, 2015). However, it is important to note that many species are highly specific in their habitat requirements, and are rare (Preston 1948) and thus patchily distributed. It is therefore reasonable to expect that the spatial dynamics described above, which are driven by patch size and landscape context, should be of critical importance to driving population dynamics of species, playing a key role in structuring communities. In other words, due to the naturally patchy distribution of most species, the necessity for a species-centered approach should be the rule rather than the exception in terms of understanding drivers of community structure and assembly.

Poorer fit, in terms of AIC, higher covariance between model terms, and larger effect size SEs within land-cover based models relative to species-centered models appear to be the result of the noise associated with attempting to create a single classification of 'habitat' for a large, diverse species pool. Particularly for oak-associated species, poorer relative performance and a negative effect of forest amount may indicate that the land-cover data were not sensitive enough to accurately delineate the region's heterogeneous oak vegetation at a scale relevant to breeding

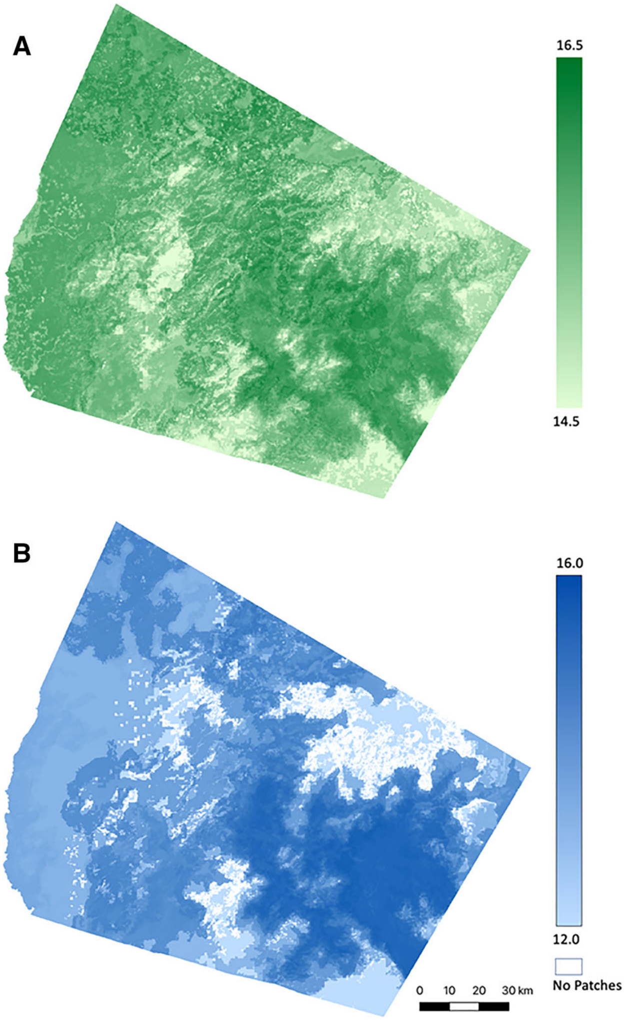

Fig. 3 Patch size across the study area for all species combined (**a**) and oak-associated species (**b**). For both species groups, we stacked all individual species' patch size maps (Fig. 2b) and calculated the log (sum + 1) of patch sizes across the community at each pixel. For both species groups, darkest areas are those where patch sizes tend to be highest across the greatest number of species in the bird community; lightest areas are where the fewest and smallest size of patches occurred across the community. For the oak-associated species (**b**), areas in white are where no patches occurred for any of these species. (Color figure online)

birds. One additional drawback of land-cover metrics was the high correlation between them, a perennial issue in fragmentation research (Smith et al. 2009). We retained collinear variables in our top models, as we could not fully reject the possibility of suppressor or additive effects, and because each of our metrics represented unique ecological processes (Smith et al. 2009). Although CIs for the parameter estimates in the full species model did not include zero, large SEs indicated a high amount of variance in the relationships between richness and both habitat amount and patch number. In contrast, species-centered metrics were much less correlated and thus easier to interpret when included in the same model. This may highlight a potential problem with creating 'one-size-fits-all' generic land-cover classifications for such large and diverse species pools, and a possible benefit of a species-centered approach.

A potential weakness of using our S-SDM based method over a traditional generic approach is the perceived complexity of the results; it is challenging to visualize the sum of individual species-centered patches versus a map of 'habitat' patches based on land-cover classifications. However, to determine which locations might warrant conservation prioritization it is possible to map species richness "hotspots" that constitute locations where large patches exist across multiple bird species, by simply mapping the sum of patch sizes for all individual species of interest at each pixel in a landscape (Fig. 3).

Overall, this study may be viewed as a consilience between the polarized views in the fragmentation versus habitat loss debate (Fletcher et al. 2018). In our system, quantifying 'fragmentation' for large biotic communities in forest mosaics led to very different conclusions depending on the method for defining those metrics; this observation may be reflected in some of the lack of consensus on the importance of fragmentation and direction of its effects across studies. The current reliance on land-cover 'habitat' classification does not preclude metapopulation-style processes exerting strong influences on biological communities, but could obscure them. We suggest the discrepancies between our species-centered and land-cover models are important. If the observed relationships were indeed a function of the way 'habitat' is defined, we argue that our carefully validated species-centered models may have provided insight into fragmentation relationships that could be present in other taxa and systems, but have previously gone undetected.

Implications for future research

Current difficulties in uncovering generalities in responses of biodiversity to landscape changes, and the resulting uncertainty, may be at least partially a result of challenges in quantifying 'habitat' simultaneously across pools of species. Our novel technique, which reflects metacommunity processes without ignoring the complexity inherent in natural systems, could be used for any group of species where sufficient data exists for species distribution modeling. As SDM techniques using remote sensing data continue to improve (Kennedy et al. 2007) and global-scale empirical datasets become more common (Pfeifer et al. 2014), the opportunities for testing landscape sensitivity of species and communities will only increase. Given high variability in life history traits and differential responses to habitat perturbation, the use of more sensitive tools that account for species-specific complexity may allow currently obscured relationships to be clarified, to the benefit of conservation efforts.

As this is the first application, to our knowledge, of a species-centered approach for assessing the relative importance of habitat amount and configuration metrics for biological communities, replication across other taxa and systems will be required to refine the technique and compare against previous research using land-cover based metrics. It is possible that in other landscapes, with very different land use histories and subsequently different grain size of species' habitat distributions, relationships between landscape pattern and richness will not be consistent with our findings; however only additional research will determine to what extent generalities may exist. With time, further development, and broader application, we suggest that the species-centered approach has the potential to reveal more accurate predictions about species and community sensitivity to alterations in landscape structure.

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