Landscape Ecol (2016) 31:1383–1394
DOI 10.1007/s10980-016-0380-z

RESEARCH ARTICLE

Estimating the spatial scales of landscape effects on abundance

Richard Chandler · Jeffrey Hepinstall-Cymerman

Received: 29 May 2015 / Accepted: 8 April 2016 / Published online: 20 April 2016

Abstract
Context Spatial variation in abundance is influenced by local- and landscape-level environmental variables, but modeling landscape effects is challenging because the spatial scales of the relationships are unknown. Current approaches involve buffering survey locations with polygons of various sizes and using model selection to identify the best scale. The buffering approach does not acknowledge that the influence of surrounding landscape features should diminish with distance, and it does not yield an estimate of the unknown scale parameters.
Objectives The purpose of this paper is to present an approach that allows for statistical inference about the scales at which landscape variables affect abundance.
Methods Our method uses smoothing kernels to average landscape variables around focal sites and uses maximum likelihood to estimate the scale parameters of the kernels and the effects of the smoothed variables on abundance. We assessed model performance using a simulation study and an avian point count dataset.
Results The simulation study demonstrated that estimators are unbiased and produce correct confidence interval coverage except in the rare case in which there is little spatial autocorrelation in the landscape variable. Canada warbler abundance was more highly correlated with site-level measures of NDVI than landscape-level NDVI, but the reverse was true for elevation. Canada warbler abundance was highest when elevation in the surrounding landscape, defined by an estimated Gaussian kernel, was between 1300 and 1400 m.
Conclusions Our method provides a rigorous way of formally estimating the scales at which landscape variables affect abundance, and it can be embedded within most classes of statistical models.

Keywords Appalachian Mountains · *Cardellina canadensis* · Habitat selection · Kernel smoothing · Moving window analysis · Characteristic scale

Electronic supplementary material The online version of this article (doi:10.1007/s10980-016-0380-z) contains supplementary material, which is available to authorized users.

R. Chandler (✉) · J. Hepinstall-Cymerman
Warnell School of Forestry and Natural Resources, University of Georgia, 180 E. Green Street, Athens, GA 30602-2152, USA
e-mail: rchandler@warnell.uga.edu

Introduction

There is widespread support for the hypothesis that ecological processes are affected by environmental variables at multiple spatial scales (Johnson 1980; Wiens 1989; Cushman and McGarigal 2004; Holland et al. 2004; Parrish and Hepinstall-Cymerman 2012). For example, numerous studies have demonstrated that habitat selection can depend on characteristics of the site as well as features of the surrounding landscape, and these multiscale habitat selection processes strongly influence spatial variation in abundance (Stouffer et al. 2006; Zeller et al. 2014). Studying multiscale processes therefore requires an understanding of what constitutes the "surrounding landscape", yet, in almost all settings, the scales at which organisms respond to the environment are unknown, and it is impossible to precisely define the surrounding landscape a priori.

Uncertainty regarding the scales of species-environment relationships poses two fundamental challenges when attempting to model the effects of landscape variables on ecological state variables such as abundance or occurrence. First, standard statistical models such as generalized linear mixed-effects models cannot accommodate uncertainty about covariate values, which is the case when the value of the landscape variable is unknown. Second, landscape variables are typically spatially autocorrelated, and ignoring or mischaracterizing the influence of landscape variables can violate the independence assumption of many statistical models (Fortin and Dale 2005; De Knegt et al. 2010).

The common approach for addressing the scale problem is to measure each landscape variable at multiple spatial scales, defined by polygons of various extents centered on a set of survey sites. For instance, in avian point count surveys, each point count location may be buffered by concentric circles with radii ranging from hundreds of meters to several kilometers, and landscape variables such as forest cover are averaged over each circle (e.g., Chandler et al. 2009; Parrish and Hepinstall-Cymerman 2012). Procedures such as this result in multiple highly correlated representations of each landscape variable. Model selection methods are then used to identify the "characteristic scale" or "scale of effect" (Jackson and Fahrig 2012), defined as the spatial extent at which each landscape covariate is most highly correlated with the response variable (Holland et al. 2004). This approach is commonly referred to as the "focal site multiscale study design" (Brennan et al. 2002).

A problem with this approach is that researchers must make arbitrary decisions about the number and range of extents to consider (Wheatley and Johnson 2009). Although theory suggests that the characteristic scale should be positively correlated with traits such as home range size and dispersal ability (Bowman et al. 2002; Thornton and Fletcher 2014), such general guidance is of little help when choosing specific scales. Perhaps for this reason, a recent meta-analysis revealed that most studies using this approach have identified the characteristic scale to be either the smallest or largest extent considered (Jackson and Fahrig 2015), indicating that the range of scales evaluated is usually too narrow. In addition to the problem of choosing among a small set of prescribed scales, the focal site multiscale approach does not acknowledge that the effect of landscape variables should decrease with distance from the focal site (Moilanen and Nieminen 2002). Instead, this approach involves averaging a landscape variable over a polygon and therefore implies that the environment within the polygon is uniformly influential while the environment immediately outside the polygon has no effect. As pointed out by Moilanen and Hanski (2001), this type of step function has no theoretical basis.

Another drawback of the focal site multiscale approach is that it does not result in a formal estimate of the characteristic scale, and consequently there are no associated confidence intervals or other measures of uncertainty that could be used for hypothesis testing or other forms of statistical inference. However, because the characteristic scale is an unknown parameter capable influencing spatial variation in abundance, it should be possible to estimate the scale parameter directly.

In this paper, we present a statistical model for understanding the scales at which landscape variables affect ecological processes. Our method improves upon the focal site multiscale study design by avoiding the need to prescribe sets of polygons around each site, by allowing the effect of landscape features to decay with distance, and by allowing for statistical inference about the scales at which landscape variables affect population parameters such as abundance or occurrence.

Methods

Statistical model and data requirements

For simplicity, we will assume that the landscape can be characterized as a regular grid such that each pixel is a site with an associated value of abundance and an associated set of environmental covariates. In practice, the landscape-level covariate data will be available for the entire region, but the abundance data must be collected at a sample of sites. Although our approach could be generalized easily to landscapes defined by polygons or landscapes characterized by continuous variation in abundance or covariates, most spatial data are represented in this raster format, and most previous studies of landscape effects have operated under these conditions (De Knegt et al. 2010; Jackson and Fahrig 2015).

The coordinates of a site (i.e., pixel) will be denoted by $\boldsymbol{x}$, and the abundance at a site by $N(\boldsymbol{x})$. Our aim is to model the expected value of abundance $E(N(\boldsymbol{x})) = \lambda(\boldsymbol{x})$ as a function of the environmental covariates $\boldsymbol{z}(\boldsymbol{x})$. These covariates could be site-specific measurements that are collected in the field (e.g., stem density) or they could be landscape-level raster layers defined for the entire region of interest. To address the issues that (1) we do not know the scale at which the surrounding landscape affects $N(\boldsymbol{x})$ and (2) the effect should diminish with distance, we employ a spatial smoothing approach. This involves averaging each landscape covariate around each focal site using a spatial kernel to produce a distance-weighted representation of the original landscape variable. Numerous spatial smoothers could be considered, but here we focus on functions of the form:

$$s(z(\boldsymbol{x}_i), \sigma) = \sum_{(\boldsymbol{x}_j \neq \boldsymbol{x}_i) \in S} z(\boldsymbol{x}_j) w(\boldsymbol{x}_i, \boldsymbol{x}_j, \sigma) \tag{1}$$

which is a weighted average of the original landscape variable with weights, $w(\cdot)$, determined by a kernel such as the Gaussian, Epanechnikov, or exponential. In the Gaussian case, the weights are given by

$$w(\boldsymbol{x}_i, \boldsymbol{x}_j, \sigma) = \frac{\exp\left(-\|\boldsymbol{x}_i - \boldsymbol{x}_j\|^2 / (2\sigma^2)\right)}{\sum_{(\boldsymbol{x}_j \neq \boldsymbol{x}_i) \in S} \exp\left(-\|\boldsymbol{x}_i - \boldsymbol{x}_j\|^2 / (2\sigma^2)\right)} \tag{2}$$

where σ is the scale parameter that determines the shape of the kernel and $||\boldsymbol{x}_i - \boldsymbol{x}_j||$ is the Euclidean distance between sites i and j. If σ is high, then the kernel is relatively flat and landscape features far from the focal site are more influential than if σ is low. The smoothing takes place over the two-dimensional region S that encompasses the study area. In practice, S will be defined by the extent of the raster data, which should be large enough to ensure that landscape features near the boundaries of the region have no influence on abundance at the focal sites. It is also important to note that the summation in Eq. 1 is over all sites in S except the focal site $(\boldsymbol{x}_i)$. However, this need not be the case if one does not want to make the distinction between site-level and landscape-level covariates.

Estimating the spatial scale parameters is accomplished by embedding the smoothing, and the resulting smoothed landscape variables, in a statistical model. The focus of this paper is abundance, and thus a natural model for the expected value of abundance at location $\boldsymbol{x}_i$ is a log-linear model:

$$\log(\lambda(\boldsymbol{x}_i)) = \beta_0 + \beta_1 s_1(z_1(\boldsymbol{x}_i), \sigma_1) + \beta_2 s_2(z_2(\boldsymbol{x}_i), \sigma_2) + \cdots + s_p(z_p(\boldsymbol{x}_i), \sigma_p) \tag{3}$$

This equation includes a smoothing term for each of the p landscape covariate, but site-level covariates can be easily accommodated by removing the associated smoothing functions, i.e. the $s(\cdot)$ functions. Aside from the smoothing, Eq. (3) is identical to other log-linear models used widely in ecology in that the $\boldsymbol{\beta}$ parameters are the intercept and effects of each covariate. The addition of the smoothing terms makes the function resemble a generalized additive model, but here we are smoothing the covariate over space rather than smoothing the covariate's relationship with the expected value.

Equation 3 can be substituted into virtually any model of abundance, including mixed effects models, hierarchical models, and spatial point process models. As such, it is possible to account for processes such as overdispersion and imperfect detection that are associated with most ecological datasets. However, for clarity and ease of exposition, we focus on the Poisson model: $N(\boldsymbol{x}_i) \sim \text{Poisson}(\lambda(\boldsymbol{x}_i))$ whose likelihood is given by:

$$\mathcal{L}(\boldsymbol{\beta}, \sigma; \{N(\boldsymbol{x}_i)\}) = \prod_{i=1}^{R} \frac{\lambda(\boldsymbol{x}_i)^{N(\boldsymbol{x}_i)} e^{-\lambda(\boldsymbol{x}_i)}}{N(\boldsymbol{x}_i)!} \tag{4}$$

where R is the number of focal sites in the sample. This likelihood assumes that the site-specific abundances, $\{N(\boldsymbol{x}_i)\}$, are independent *after* accounting for spatial dependence attributable to the smoothed landscape variables. This is a much more relaxed assumption than the traditional independence assumption of generalized linear models, and it represents a tractable model of spatial dependence whose covariance function is non-stationary and anisotropic, meaning that it is not simply a function of distance and location. Maximizing Eq. 4 can be accomplished using numerical optimization routines available in most statistical software packages, and it can be easily modified to accommodate other discrete distributions such as the negative binomial or zero-inflated Poisson. Selecting among kernels (e.g. Gaussian vs exponential) can be accomplished using AIC or some other information criterion. **R** code for fitting the model is available in Online Appendix 1.

Simulation study

We assessed the general properties of the estimator using a simulation study in which we varied the spatial scale of the landscape effect (σ) and the amount of spatial correlation in the landscape itself. The reason for considering the degree of correlation in the landscape is that the landscape contexts of sites in either a highly correlated landscape or a highly uncorrelated landscape will be virtually identical, and hence it should be difficult to estimate σ in these extreme cases because there will be little variation among sites.

We considered a single landscape variable with five levels of spatial correlation. The autocorrelated variables were generated using a multivariate Gaussian process with exponential covariance determined by the parameter ρ. For ρ, we considered five values: 0.01, 0.25, 0.5, 0.75, and 1.0, which produce landscapes such as the examples depicted in Fig. 1.

For each of the five values of ρ, we considered eight values of σ: 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, and 1.0. The $\sigma = 0.3$ scenario represents a case in which local abundance is influenced by nearby landscape features whereas, in the $\sigma = 1.0$ case, local abundance is influenced by landscape features farther away. In other words, low values of σ result in low smoothing and high values of σ result in high smoothing.

For each of the 40 cases (5 values of ρ and 8 values of σ) we simulated 1000 datasets consisting of the landscape covariate as well as abundance data from the 100 sample locations shown in Fig. 1. The abundance data were generated from a model with one site-level covariate ($z_1(\boldsymbol{x})$) and one landscape-level covariate ($z_2(\boldsymbol{x})$):

$$\log(\lambda(\boldsymbol{x}_i)) = \beta_0 + \beta_1 z_1(\boldsymbol{x}_i) + \beta_2 s_2(z_2(\boldsymbol{x}_i), \sigma)$$

$$N(\boldsymbol{x}_i) \sim \text{Poisson}(\lambda(\boldsymbol{x}_i)) \quad (5)$$

The coefficients used in the simulations were $\beta_0 = 2, \beta_1 = 1$, and $\beta_2 = 0.5$, chosen to reflect a scenario in which abundance is strongly influenced by the site-level variable and moderately affected by the smoothed landscape variable. We assessed model performance by calculating bias, root mean squared error (RMSE), and confidence interval coverage of the estimators of the four parameters $(\beta_0, \beta_1, \beta_2, \sigma)$. **R** code to reproduce one of the simulation cases is found in Online Appendix 1.

Canada warbler example

We conducted avian point count surveys at 70 locations in and around the USDA Coweeta Hydrologic Laboratory in Macon County, NC, USA (35°3′35″N, 83°25′51″W) during June and July of 2014. These data were collected as part of a study designed to understand the factors limiting the distribution of species at low-latitude range margins. Point counts were positioned on a 500-m grid that covered a range of elevations from 850 to 1350 m. Each location was surveyed once for 10 min during which time all birds detected were recorded. To reduce heterogeneity in detection, the analysis was restricted to data on male Canada warblers (*Cardellina canadensis*) detected within 100 m. Ideas for formally accounting for imperfect detection are presented in the Discussion section.

We modeled Canada Warbler abundance as a function of elevation (30-m National Elevation Database) and evergreen vegetation cover as measured by leaf-off Normalized Difference Vegetation Index (NDVI) dervied from a Landsat 8 OLI image acquired 15 February 2014 (Soudani et al. 2006). Elevation was of interest because, like many other species in the region, Canada warblers appear to be restricted to higher elevations. Personal observations suggest that Canada Warblers are also closely associated with understory thickets of *Rhododendron* spp. and *Kalmia* spp., which in this region of minimal needle-leaf evergreen trees, are adequately measured

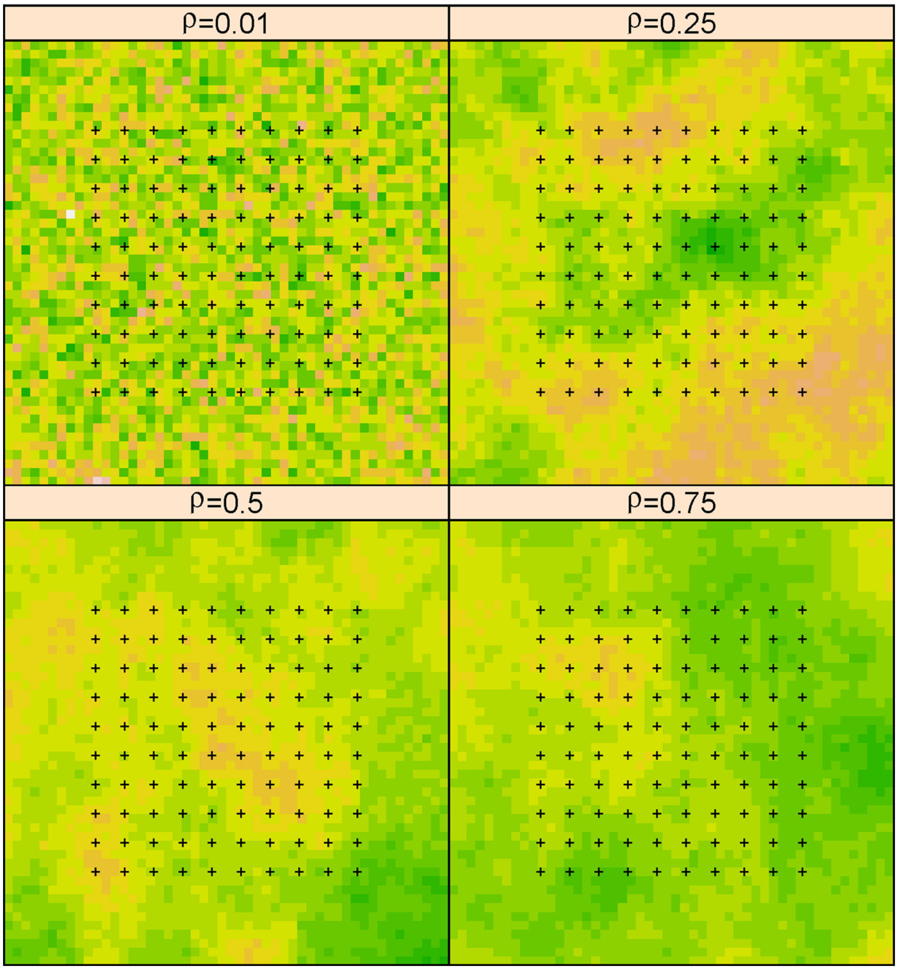


Fig. 1 Examples of the landscapes used in the simulation study. The parameter ρ determines the amount of spatial correlation in the landscape. For each of the four landscape types, we generated 1000 datasets and evaluated the model's ability to estimate the effect of the surrounding landscape on abundance at the 100 survey locations denoted by *crosses*

by NDVI recorded in the winter (see Laseter et al. 2012 and references contained therein for a complete site description). Elevation and NDVI rasters were aggregated from a 30-m to a 180-m resolution, making the area of a pixel similar to the area of 100-m radius point count plot. Images of the elevation and NDVI layers, along with the point count locations and count data, are shown in Fig. 2.

We fit six models using several combinations of site- and landscape-level versions of elevation and NDVI. This allowed us to assess whether the landscape-level variables influenced abundance more than the site-level variables. For elevation, we considered a quadratic effect for both the site-level and the landscape-level variables because we hypothesized that abundance might peak at intermediate elevations. Models were fit using maximum likelihood and compared using AIC.

Results

Simulation study

The primary purpose of the simulation study was to evaluate the estimator of σ, the parameter determining the scale at which landscape features affect abundance. Our results indicate that the estimator is approximately unbiased and confidence interval coverage is nominal for all cases considered except when spatial correlation in the landscape is low ($\rho = 0.01$, Fig. 3). In this case, the landscape resembles white noise, and we found bias to be as high as 21 % and confidence interval coverage as low as 0.76 (Table 1). The poor performance associated with the uncorrelated landscape was not surprising because medium to high amounts of smoothing will result in similar

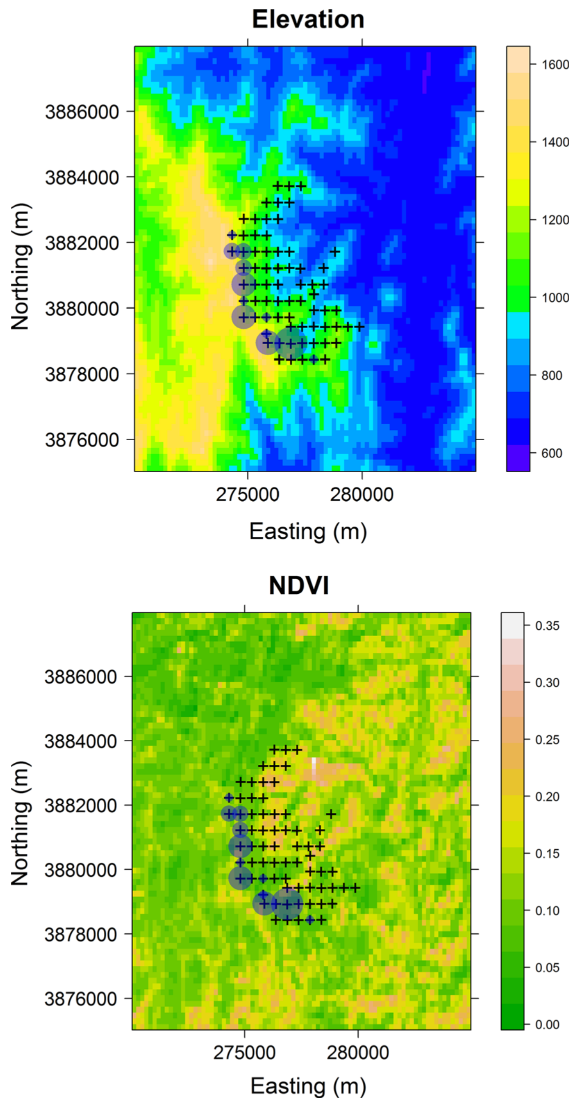


Fig. 2 Elevation and NDVI, the two spatial covariates used to model Canada warbler abundance. *Crosses* indicate point count locations and *circles* represent the number of male warblers detected at each site, which ranged from 0 to 4

averaged values of the landscape variable, and therefore the likelihood is flat with respect to σ.

Real landscapes rarely look like white noise, and our results indicate that the model performs well when there is moderate to high amounts of spatial autocorrelation (Fig. 3; Table 1). Bias of the σ estimator was <1.5 % in each of these cases and 95 % confidence interval coverage ranged from 0.90 to 0.96 (Table 1). Root mean squared error was lowest for intermediate values of σ indicating that bias and variance were highest when the surrounding landscape was either very small or very large. However, these differences were small indicating that the model performed well regardless of the magnitude of the scale parameter.

In addition to estimating the spatial scale at which the landscape affects abundance, we were also interested in the estimators of β_0, β_1, and β_2. Summaries of these parameter estimates are provided in Online Appendix 2. Bias was minimal and 95 % confidence interval coverage was correct for the intercept (β_0) and the coefficient of the site-level covariate (β_1). However, as with σ, the estimator of β_2—the effect of the smoothed landscape covariate—performed poorly in the unusual case of low spatial correlation in the landscape. Again, in this case, the surrounding landscape is effectively the same among sites and thus there is no variation to inform the model.

Our simulation results also indicate that σ cannot be estimated when β_2 is near zero. In other words, if there is no effect of the landscape variable, there is no characteristic scale to estimate (Online Appendix 2). Similarly, if σ is approximately zero, there is no effect of the landscape and β_2 cannot be estimated. The covariance between these two parameters results in convergence problems when the data suggest that either σ or β_2 is near zero. However, just as one would never consider a landscape scale defined by a circle with a radius of zero, it is not worth considering values of σ near zero, which can be achieved using constrained optimization as demonstrated in Online Appendix 1.

Canada warbler example

The most supported model of Canada warbler abundance included a linear effect of site-level NDVI and a quadratic effect of landscape-level elevation (Tables 2, 3). A model with site-level instead of landscape-level elevation received a similar amount of support, indicating that the landscape-level variable explained only slightly more variation in the data. Our estimate of the spatial scale parameter for elevation was $\hat{\sigma} = \exp(-1.86) = 0.156$ (Table 3), and the associated kernel, which defines the smoothing weights, is illustrated in Fig. 4. The estimated kernel weights decay quickly with distance such that the influence of elevation in the surrounding landscape was negligible beyond 400 m.

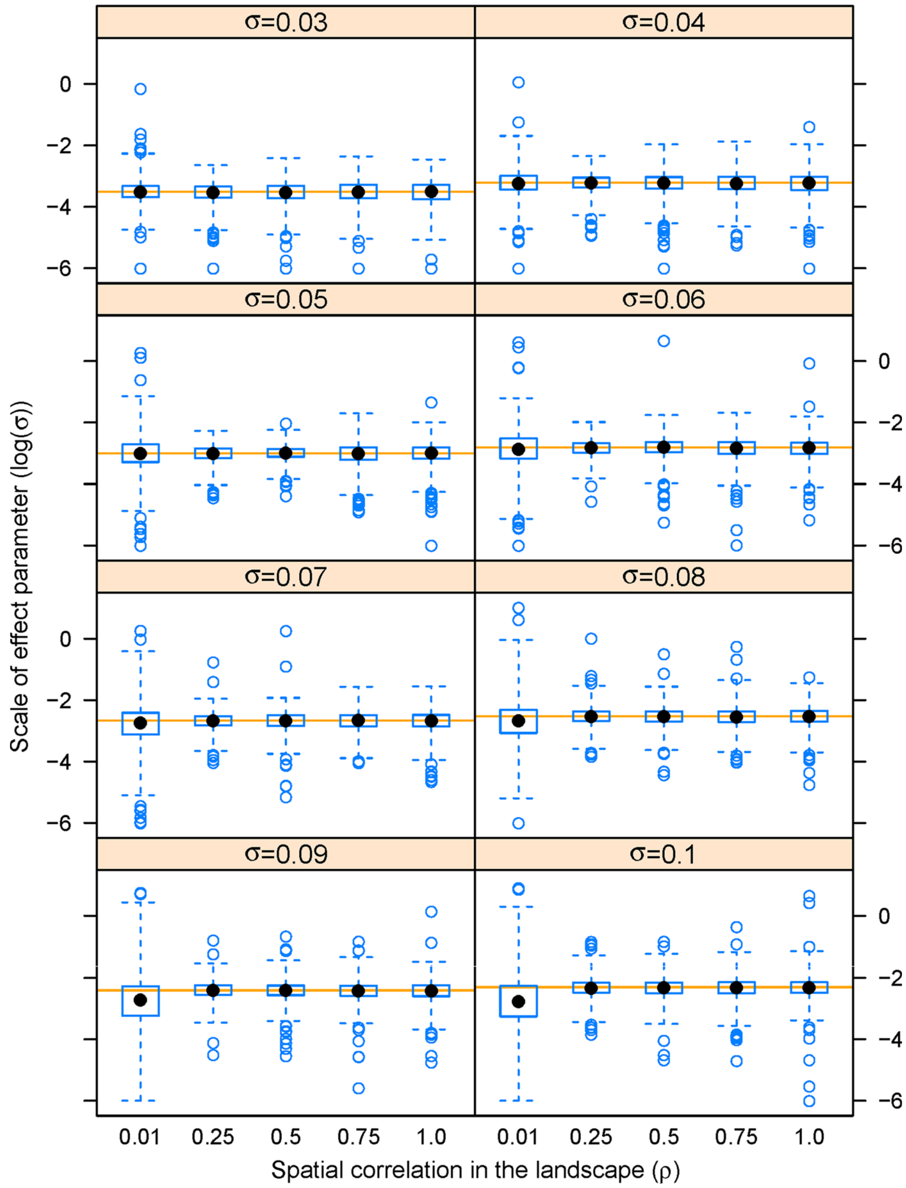


Fig. 3 *Boxplots* of simulation results. The *horizontal orange line* represents the actual value of the scale of effect parameter σ, which was estimated on the log scale. The *black dots* represent the median estimate from 1000 simulations of each case. The estimator exhibited little bias for any values of σ, except for the case in which the landscape did not exhibit spatial correlation (i.e., $\rho = 0.01$)

As with standard generalized linear models, our model can be used to predict abundance and generate distribution maps (Fig. 5). The most supported model predicts that Canada warbler abundance is highest at elevations between 1300 and 1400 m at sites with relatively high winter NDVI (understory evergreen vegetation). Even though the distinction between models with landscape-level and site-level elevation was slight, landscape-level elevation was a better predictor suggesting that abundance is more clustered than would be expected based on the site-level representation of elevation. Consequently, our model predicts that an isolated peak at a preferred elevation would have lower abundance than a site surrounded by similar elevations (Fig. 5).

Discussion

We developed a model that allows for statistical inference about the spatial scales at which landscape variables affect abundance. Unlike previous approaches,

Table 1 Percent bias, root mean squared error, and 95 % CI coverage for the estimator of σ (the spatial scale parameter) under each of the 40 cases considered

Case ρ	Case σ	% Bias	RMSE	Coverage
0.01	0.3	0.08	0.37	0.89
0.01	0.4	−0.18	0.44	0.90
0.01	0.5	−1.22	0.58	0.85
0.01	0.6	−2.45	0.65	0.85
0.01	0.7	−5.47	0.73	0.84
0.01	0.8	−7.80	0.72	0.82
0.01	0.9	−14.79	0.88	0.78
0.01	1	−21.70	0.96	0.76
0.25	0.3	−1.28	0.34	0.92
0.25	0.4	−0.57	0.30	0.94
0.25	0.5	−0.82	0.27	0.95
0.25	0.6	−0.77	0.26	0.95
0.25	0.7	−0.61	0.27	0.95
0.25	0.8	−0.28	0.28	0.93
0.25	0.9	−0.08	0.27	0.96
0.25	1	−1.09	0.31	0.94
0.5	0.3	−1.04	0.37	0.92
0.5	0.4	−1.03	0.37	0.92
0.5	0.5	0.11	0.23	0.95
0.5	0.6	−0.30	0.35	0.93
0.5	0.7	−0.73	0.32	0.95
0.5	0.8	−0.63	0.31	0.93
0.5	0.9	−0.34	0.30	0.94
0.5	1	−1.08	0.31	0.94
0.75	0.3	−0.89	0.40	0.90
0.75	0.4	−1.29	0.37	0.93
0.75	0.5	−1.37	0.38	0.93
0.75	0.6	−1.12	0.36	0.93
0.75	0.7	−0.89	0.31	0.94
0.75	0.8	−0.84	0.32	0.95
0.75	0.9	−1.22	0.33	0.95
0.75	1	−1.41	0.33	0.95
1.0	0.3	−1.54	0.43	0.90
1.0	0.4	−1.37	0.41	0.92
1.0	0.5	−1.02	0.38	0.92
1.0	0.6	−1.28	0.35	0.95
1.0	0.7	−1.21	0.35	0.93
1.0	0.8	−0.37	0.31	0.94
1.0	0.9	−1.04	0.36	0.93
1.0	1	−0.72	0.38	0.93

Cases were defined by unique combinations of σ and ρ (the degree of spatial correlation in the landscape). Results are based on models fit to each of 1000 simulated dataset generated for each case

Table 2 Top five models and the intercept only model of Canada Warbler abundance ranked by AIC

Model	Parameters	AIC
NDVI + s(Elevation) + s(Elevation)^2	5	77.6
NDVI + s(Elevation)	4	79.7
NDVI + Elevation + Elevation^2	3	80.2
NDVI + Elevation	3	81.0
s(NDVI) + Elevation	4	83.2
Intercept only	1	122.6

The s() notation indicates that the variable was a smoothed landscape-level variable rather than a site-level variable. The most supported model included a quadratic effect of the smoothed version of elevation and a linear effect of site-level NDVI

our method does not involve specifying a set of landscape scales a priori and thereby eliminates the possibility that the characteristic scale is outside the range of scales considered (Jackson and Fahrig 2015). In addition, rather than choosing among a set of prescribed polygons using model selection procedures, our approach results in an estimate of the scale parameter for each of the landscape-level covariates of interest.

The scale parameter considered here is not defined in terms of the extent of a polygon, but instead it is a parameter that determines the shape of a kernel used to compute a distance-weighted average of a landscape feature. This averaging is superficially similar to the moving window approach (Betts et al. 2014) and the focal site multiscale study design (Brennan et al. 2002), however both of these approaches involve averaging landscape variables using nested polygons of predefined size, thereby implying that the surrounding landscape is influential within the polygon but not outside it. Our approach differs in that it

Table 3 Parameter estimates from the most supported model of Canada Warbler abundance

Parameter	Description	Estimate	SE
β_0	Intercept	−6.06	1.89
β_1	Effect of site-level NDVI	0.56	0.51
β_2	First term of quadratic effect of landscape-level elevation	8.70	3.60
β_3	Second term of quadratic effect of landscape-level elevation	−2.80	1.59
log(σ)	Scale of the landscape effect	−1.86	0.79

The scale of effect parameter σ determines the shape of the kernel used to smooth elevation in the surrounding landscape

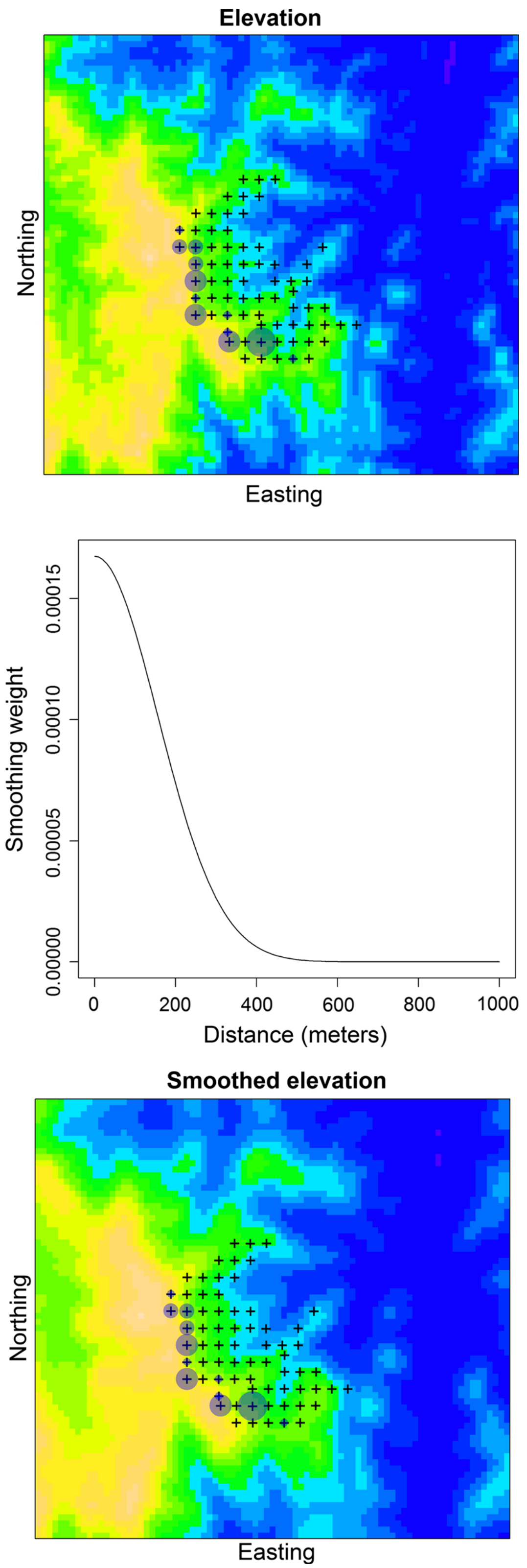
recognizes that the influence of the surrounding landscape should diminish with distance. Nonetheless, one could use our approach to estimate the radius of a circle or the dimensions of a rectangle by replacing our smoothing kernel with a step function that produces equal weights within the polygon and zero weights outside it. As argued previously, however, we can find no theoretical basis for averaging landscape variables over a polygon, and we believe that such an approach could lead to poor conservation decisions. For example, if a conservation organization is interested in protecting habitat around a focal site, financial resources might be used inefficiently if potential sites are given equal weights within some radius instead of being weighted based on distance and the estimated scale parameter σ.

Our method performed well in most of the settings considered in our simulation study, and it explained more variation in the Canada warbler data than did a model using only site-level variables. The method performed poorly when the landscape variable exhibited little spatial autocorrelation. In such cases, the landscape variable resembles white noise, and therefore, the surrounding landscapes are effectively the same among sites, leaving little variation to model. The same type of problem would occur if the landscape exhibited perfect autocorrelation because each site would have exactly the same surroundings. The method should also not be expected to work well when a species responds to the landscape at a scale much greater than that covered by the focal sites. Once again, each site would effectively have the same landscape context, and there would be no variation to model. Such issues would affect any method designed to estimate landscape scales, including the standard buffering approach, not just ours. However, these issues are either unlikely to be encountered in most studies, because environmental variables rarely resemble white noise, or can be addressed by sampling a region with an extent large enough to ensure variation in the landscape context of the focal sites.

The kernel smoothing we employed incidentally provides a means of modeling spatial correlation beyond that arising from spatial correlation in the landscape itself. Specifically, it allows for the possibility of excess clustering because high quality sites surrounded by other high quality sites will be predicted to have higher abundance than high quality sites that are isolated. Other models of clustering and spatial dependence involve smoothing latent random variables (Wolpert and Ickstadt 1998; Higdon 2002), which is much more computationally challenging and possibly less mechanistic than smoothing a set of landscape covariates as we have done here.

While we focused on models of abundance, our model could be used for other ecological state variables such as occupancy, and it could be extended to allow for observation error, including imperfect detection (Royle and Dorazio 2008). For example, if $N(\boldsymbol{x})$ cannot be observed directly because some individuals are hard to detect, replicate observations could be recorded and the observed data could be modeled using a binomial distribution with parameters $N(\boldsymbol{x})$ and p. This amounts to a simple extension of an N-mixture model (Royle 2004). Similar approaches could be used if distance sampling data, capture-recapture data, or data from other ecological sampling methods are available.

We developed our model for situations in which sites can be equated with pixels in a rasterized representation of a landscape, and the data are site-specific measures of abundance. Strictly speaking, if density varies continuously in space, an analysis of site-level abundance data represents a form of



◀**Fig. 4** The original elevation covariate (*top*), a cross-section of the estimated smoothing kernel (*middle*), and the smoothed version of elevation (*bottom*). The smoothing kernel determines the weight given to features in the surrounding landscape. In this case, site-level abundance was associated with elevation out to approximately 400 m. *Crosses* indicate survey locations. *Circles* are proportional to the number of Canada warblers detected at each location

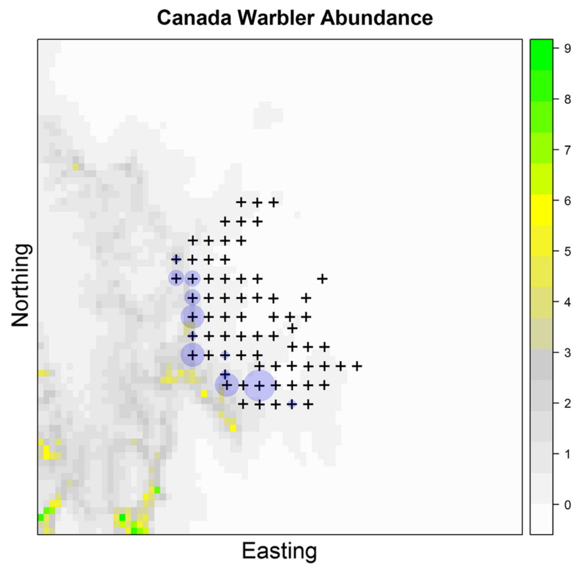


Fig. 5 Expected values of Canada Warbler abundance based on the most supported model, which included a quadratic effect of landscape-level elevation and a linear effect of site-level NDVI. *Crosses* indicate survey locations. *Circles* are proportional to the number of Canada warblers detected at each location

aggregation that can result in inaccurate inferences about spatial variation in density (Robinson 1950; Lechner et al. 2012; Banerjee et al. 2014). This has been called the modifiable areal unit problem (Best et al. 2000; Gotway and Young 2002; Wakefield 2004) and is an issue common to virtually all models of count data. However, when sites are small relative to the rate at which density varies in space, density can be assumed to be locally constant, and the issue can be ignored (Sillett et al. 2012). If this assumption is not justified, the notion of a site could be done away with altogether, for example by recording the actual locations of individuals and fitting spatial point process models to estimate the underlying density surface (Best et al. 2000; Diggle 2013; Royle et al. 2014). Our method could be embedded in a spatial point process model by defining $\boldsymbol{x}$ as a point in space, rather than a site. One issue that might arise when there is no clearly defined site is the need to estimate multiple scale parameters for each landscape variable as a way of describing the hierarchial habitat selection process envisioned by Johnson (1980). For instance, one scale parameter might be used to average the environment at the home range level while another scale parameter could define the surrounding landscape (Mashintonio et al. 2014). While conceptually appealing, it may be difficult to estimate multiple scale parameters for each covariate, and this complication can, and should, be avoided if a biologically meaningful definition of a site exists, as in studies of metapopulations (Hanski 1998).

Although we believe that the model presented here represents an important development in efforts to understand the scales at which landscape variables affect ecological state variables such as abundance, all static models of abundance are essentially phenomenological because, ultimately, patterns of abundance are determined by spatial variation in survival, recruitment and movement. From a mechanistic perspective, efforts to model landscape effects on abundance can be viewed as proxies for understanding site-level connectivity, which results from a species' movement behavior in response to landscape structure. It is therefore preferable to use process-based spatio-temporal models (Chandler and Clark 2014; Chandler et al. 2015), rather than models that ignore temporal dynamics, and we suggest that additional research is needed to understand the scales at which landscape variables affect the underlying ecological processes governing spatial variation in abundance.

Acknowledgments We thank Samuel Merker and Anna Joy Lehmicke for collecting the point count data. Paige Howell provided useful suggestions and comments on a previous version of the manuscript. Two anonymous reviewers provided insightful comments that improved the manuscript. Permission to conduct research within and around the Coweeta Basin Hydrologic Laboratory was granted by the Coweeta Hydrologic Laboratory, the USDA Forest Service, and the North Carolina Wildlife Resources Commission. JHC was supported by the Coweeta LTER, NSF Grant DEB-0823293.

References

Banerjee S, Carlin BP, Gelfand AE (2014) Hierarchical modeling and analysis for spatial data. CRC Press, Boca Raton

Best NG, Ickstadt K, Wolpert RL (2000) Spatial Poisson regression for health and exposure data measured at disparate resolutions. J Am Stat Assoc 95(452):1076–1088

Betts MG, Fahrig L, Hadley AS, Halstead KE, Bowman J, Robinson WD, Weins J, Lindenmayer DB (2014) A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. Ecography 37(6):517–527

Bowman J, Jaeger JAG, Fahrig L (2002) Dispersal distance of mammals is proportional to home range size. Ecology 83(7):2049–2055

Brennan JM, Bender DJ, Contreras TA, Fahrig L (2002) Focal patch landscape studies for wildlife management: optimizing sampling effort across scales. In: Liu J, Taylor WW (eds) Integrating landscape ecology into natural resource management, Cambridge University Press, Cambridge, pp 68–91

Chandler RB, Clark JD (2014) Spatially explicit integrated population models. Methods Ecol Evol 5(12):1351–1360

Chandler RB, King DI, DeStefano S (2009) Scrub-shrub bird habitat associations at multiple spatial scales in beaver meadows in Massachusetts. Auk 126(1):186–197

Chandler RB, Muths E, Sigafus BH, Schwalbe CR, Jarchow CJ (2015) Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. J Appl Ecol 52(5):1325–1333

Cushman SA, McGarigal K (2004) Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. Ecol Appl 14(4):1090–1105

de Knegt HJ, van Langevelde F, Coughenour MB, Skidmore AK, De Boer WF, Heitkönig IMA, Knox NM, Slotow R, Van der Waal C, Prins HHT (2010) Spatial autocorrelation and the scaling of species–environment relationships. Ecology 91(8):2455–2465

Diggle PJ (2013) Statistical analysis of spatial and spatio-temporal point patterns. CRC Press, Boca Raton

Fortin MJ, Dale MRT (2005) Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge

Gotway CA, Young LJ (2002) Combining incompatible spatial data. J Am Stat Assoc 97(458):632–648

Hanski I (1998) Metapopulation dynamics. Nature 396(6706):41–49

Higdon D (2002) Space and space-time modeling using process convolutions. In: Anderson CW, Barnett V, Chatwin PC, El-Shaarawi AH (eds) Quantitative methods for current environmental issues. Springer, New York, pp 37–56

Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. BioScience 54(3):227–233

Jackson HB, Fahrig L (2012) What size is a biologically relevant landscape? Landscape Ecol 27(7):929–941

Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? Glob Ecol Biogeogr 24(1):52–63

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 6(1):65–71

Laseter SH, Ford CR, Vose JM, Swift LW (2012) Long-term temperature and precipitation trends at the Coweeta Hydrologic Laboratory, Otto, North Carolina, USA. Hydrol Res 43(6):890

Lechner AM, Langford WT, Jones SD, Bekessy SA, Gordon A (2012) Investigating species-environment relationships at multiple scales: differentiating between intrinsic scale and the modifiable areal unit problem. Ecol Complex 11:91–102
Mashintonio AF, Pimm SL, Harris GM, van Aarde RJ, Russell GJ (2014) Data-driven discovery of the spatial scales of habitat choice by elephants. PeerJ 2:e504. doi:10.7717/peerj.504
Moilanen A, Hanski I (2001) On the use of connectivity measures in spatial ecology. Oikos 95(1):147–151
Moilanen A, Nieminen M (2002) Simple connectivity measures in spatial ecology. Ecology 83(4):1131–1145
Parrish MC, Hepinstall-Cymerman J (2012) Associations between multiscale landscape characteristics and breeding bird abundance and diversity across urban-rural gradients in Northeastern Georgia, USA. Urban Ecosyst 15:559–580
Robinson WS (1950) Ecological correlations and the behavior of individuals. Am Sociol Rev 15:351–357
Royle JA (2004) N-Mixture models for estimating population size from spatially replicated counts. Biometrics 60(1):108–115
Royle JA, Dorazio RM (2008) Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press, New York
Royle JA, Chandler RB, Sollmann R, Gardner B (2014) Spatial capture-recapture. Academic Press, New York
Sillett TS, Chandler RB, Royle JA, Kéry M, Morrison SA (2012) Hierarchical distance-sampling models to estimate population size and habitat-specific abundance of an island endemic. Ecol Appl 22(7):1997–2006
Soudani K, François C, Le Maire G, Le Dantec V, Dufrêne E (2006) Comparative analysis of IKONOS, SPOT, and ETM+ data for leaf area index estimation in temperate coniferous and deciduous forest stands. Remote Sens Environ 102(1):161–175
Stouffer PC, Bierregaard RO Jr, Strong C, Lovejoy TE (2006) Long-term landscape change and bird abundance in Amazonian rainforest fragments. Conserv Biol 20(4):1212–1223
Thornton DH, Fletcher RJ Jr (2014) Body size and spatial scales in avian response to landscapes: a meta-analysis. Ecography 37(5):454–463
Wakefield J (2004) A critique of statistical aspects of ecological studies in spatial epidemiology. Environ Ecol Stat 11(1):31–54
Wheatley M, Johnson C (2009) Factors limiting our understanding of ecological scale. Ecol Complex 6(2):150–159
Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3(4):385–397
Wolpert RL, Ickstadt K (1998) Poisson/gamma random field models for spatial statistics. Biometrika 85(2):251–267
Zeller KA, McGarigal K, Beier P, Cushman SA, Vickers TW, Boyce WM (2014) Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioral state: pumas as a case study. Landscape Ecol 29(3):541–557