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Species distribution models: Spatial autocorrelation and non-stationarity

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Abstract
The main goal of species distribution modeling is to identify important underlying factors related to broad-scale ecological patterns in order to make meaningful explanations or accurate predictions. When standard statistical methods such as regression are used to formulate these models, assumptions about the spatial structure of the data and the model parameters are often violated. Autocorrelation and non-stationarity are characteristics of spatial data and models, respectively, and if present and unaccounted for in model development, they can result in poorly specified models as well as inappropriate spatial inference and prediction. While these spatial issues are addressed here in an ecological context using species distribution models, they are broadly relevant to any statistical modeling applications using spatial data.

I Introduction

In their most basic incarnation, species distribution models (SDM) relate some measure of species importance to environmental factors. Although originally developed based on ecological concepts and vegetation theory such as gradient analysis and niche theory, the basic inductive modeling framework of SDM has been extended to study the spatial distribution of other biogeographic phenomena including biodiversity at the community level (Ferrier and Guisan, 2006), invasive potential (Richardson and Thuiller, 2007), disease susceptibility (Peterson, 2006), extinction risk (Araújo et al., 2005), wildfire risk (Syphard et al., 2008) and even 'crypto-zoological' species such as Sasquatch (Lozier et al., 2009).

Applications that have previously been labeled 'predictive vegetation mapping' (Franklin, 1995), 'predictive habitat distribution modeling' (Guisan and Zimmermann, 2000), 'habitat suitability modeling' (Hirzel and Le Lay, 2008), and 'niche modeling' (Stockwell, 2006), among other terms, are now more widely referred to as species distribution modeling, even if the biogeographical variable of interest is not an individual species. More recently, SDM has been the subject of a book (Franklin, 2009), several general reviews and overviews (Elith and Leathwick, 2009; Miller, 2010; Zimmermann et al., 2010), as well as studies that address specific conceptual or technical issues associated with data and methods used in SDM such as spatial autocorrelation (Beale et al.,

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2010; Bini et al., 2009), scale (Austin and Van Niel, 2011; De Knegt et al., 2010), data collection (Feeley and Silman, 2011; Lobo et al., 2010; Pyke and Ehrlich, 2010), model transferability (Duncan et al., 2009; Zanini et al., 2009), spatial accuracy (Hanspach et al., 2011; Smulders et al., 2010), as well as the development of a dedicated spatial analysis software package ('SAM': see Rangel et al., 2010).

Research activity in this area began to gain a foothold in the 1990s as computing capabilities and data availability increased along with the ability to perform more sophisticated analysis in a GIS. Many important developments in the field have been chronicled in this journal. In her seminal paper, Franklin (1995) provided one of the first reviews of the different types of applications from the previous decade that involved what she defined as 'geographic modeling of biospatial patterns in relation to environmental gradients' (Franklin, 1995: 474). In one of the first progress reports on geographical information science, Atkinson (1997) identified 'land use and habitat suitability' as one of four important research themes, and in a subsequent progress report Atkinson (2001) addressed non-stationary geostatistics. In a more recent review, Kent (2007) discussed the importance of 'macroecology', the analyses of broad-scale patterns in the diversity and distribution of species, as a focus of research in biogeography and physical geography, but noted that much of the previous research was done by ecologists instead of geographers. Finally, in a recent progress report on GIS that focused on biodiversity applications, Foody (2008) observed that spatial issues associated with analysis and modeling such as autocorrelation and non-stationarity warranted further attention.

This report extends the previous work described above by using species distribution models as an application framework that is of rapidly developing interest to researchers in biogeography and GIScience. I focus on conceptual and methodological issues associated with

spatial autocorrelation and non-stationarity in SDM; however, these spatial issues are relevant to many similar inductive and inferential modeling applications used in geography and other disciplines.

II SDM and spatial autocorrelation

Spatial autocorrelation (SAC), the observation that near things are more related than distant things, provides the basis for what has been codified as Tobler's First Law of Geography (Tobler, 1970), see also the 2004 special issue in the *Annals of the Association of American Geographers* (94(2)). A considerable portion of analytical research in geography and related disciplines such as econometrics has been devoted to quantifying the concepts of both 'near' and 'related' in order to measure the spatial characteristics of a pattern and subsequently infer the process(es) that generated it (see Getis, 2008, for review).

Spatial autocorrelation in the species data (or in general modeling parlance, the response or dependent variable) can result from biotic processes such as competition and dispersal (resulting in what is termed 'endogenous' SAC) as well as from habitat preferences for spatially structured environmental gradients (predictor/independent variables; 'exogenous' SAC). While this report addresses positive SAC as it is more common and more problematic for statistical methods, negative SAC can occur as a function of processes such as competition and allelopathy, typically at finer scales than positive SAC. Despite the intuitive nature of the explicitly spatial aspect of many ecological processes such as competition, dispersal, and disturbance, the history of addressing spatial autocorrelation in early SDM research has been inconsistent (for reviews, see Dormann et al., 2007; Miller et al., 2007). While methods to measure and explicitly include spatial autocorrelation were being developed

and becoming more widely applied in quantitative geography, the relatively few SDM studies that acknowledged SAC focused largely on the problematic aspects associated with spatially autocorrelated data and strategies to remove it or neutralize its effects (Fortin and Dale, 2009; Legendre, 1993).

In spite of the increasing variety of parametric and non-parametric methods used to quantify the species-environment relationship on which SDM explanation and prediction is based, comparison studies have generally failed to identify a single method that consistently performs better in different situations with many types and scales of data (see Elith et al., 2006; Franklin, 2009). As a result, generalized regression is still the standard and most widely applied type of method in spite of its limitations, particularly those that are associated with its use with spatially autocorrelated data (Beale et al., 2010; Franklin and Miller, 2009). Recent reviews have addressed the effects of using spatially autocorrelated data in a regression context (Dormann et al., 2007; Miller et al., 2007) and empirical studies have examined the impact and type of effects using both simulated data (Beale et al., 2010; Dormann et al., 2007; Kissling and Carl, 2008) and real data (Bini et al., 2009).

The two main categories of effects important in SDM applications involve the coefficient estimates used to interpret the magnitude and direction of influence of each of the predictor variables. The only widely and consistently noted effect is that the precision of coefficient estimates is decreased, increasing the likelihood of committing type I errors (incorrectly rejecting null hypothesis of no effect). This spatial pseudoreplication results from the fact that the degrees of freedom used in significance testing are overestimated when the data are not independent. In order to reduce the risk of spurious inference resulting from incorrectly specified models, many SDM applications have moved away from traditional null hypothesis significance testing frameworks towards information criterion approaches (Diniz–Filho et al., 2008).

The second type of effect important in SDM applications involves how SAC affects the estimation of the coefficient value itself. Further investigation of this effect has been somewhat muddled by imprecise use of the term 'bias' when discussing the difference in coefficient values when comparing non-spatial (e.g. ordinary least squares (OLS)) to spatial methods (those that accommodate spatial structure, e.g. generalized least squares (GLS)). In a statistical context, an unbiased coefficient is one whose expected value coincides with its true value. While some studies have shown that coefficient estimates from non-spatial models are significantly different compared to those from spatial models (Dormann, 2007a; Kühn, 2007), using simulated data (for which true values were known), Beale et al. (2007) showed mathematically that coefficients estimated by standard non-spatial and spatial methods (OLS and GLS, respectively) are unbiased, although the precision for coefficients calculated using OLS rapidly decreased as SAC increased. Using simulated binary response data, Dormann (2007b) found that the coefficients estimated with autologistic regression (spatial model) were systematically different from the known true value compared to the coefficients estimated with (non-spatial) logistic regression. He also found that the autologistic model consistently underestimated the effects of an environmental predictor (Dormann, 2007b). Also using simulated data, and one of the only studies that tested more than one spatial model type, Kissling and Carl (2008) found that some spatial models generated coefficients that were as biased as those generated from the non-spatial model.

In a study predicting plant species richness as a function of environmental variables in Germany, Kühn (2007) observed that the coefficient for elevation was positive in a non-spatial regression, but changed to negative in a spatial

autoregressive model. He suggests that this inversion may be explained by the environmental situation in Germany, where higher elevations in the South and lowlands in the North may confound the broad-scale trend of species richness decreasing as latitude increases. Using bird species richness data for North and South America, Europe, Africa, and Australia ($\sim$110 km grid cell resolution), Hawkins et al. (2007) concluded that coefficients from non-spatial regression were statistically indistinguishable from spatial regression coefficients. The location-, data-, or scale-specific nature of these studies has impeded efforts to disentangle the effects of spatial structure in the data, sampling strategy, the scale of the study, and statistical methods used in order to generalize the results as applicable to other studies.

For studies primarily focusing on understanding the relative importance of environmental or ecological factors, a framework that does not rely on null hypothesis significance testing has evolved in which the standardized partial regression coefficients are ranked and translated as an indicator of relative importance/influence (Diniz-Filho et al., 2003; Hawkins et al., 2007). In a recent study using 97 multifactorial data sets from different regions and at a variety of spatial scales and sample sizes, Bini et al. (2009) demonstrated that the standardized coefficients did not maintain consistent rank when OLS results were compared to spatial model results, resulting in what has been termed 'coefficient shift'. They were unable to ascertain a consistent data- or method-related factor that was associated with the propensity for coefficient ranks to shift and concluded that 'changes in coefficients between spatial and non-spatial methods depend on the method used and are largely idiosyncratic, making it difficult to predict when or why shifts occur' (Bini et al., 2009: 193).

Results from these studies have enabled a number of general observations to be made when non-spatial models are compared to spatial models using the same data: when model fit is used as a comparison measure, spatial models often have improved fit over non-spatial models (Bahn et al., 2006; Beale et al., 2010; Dormann, 2007a; Ferrer–Castán and Vetaas, 2005; McPherson and Jetz, 2007; Piorecky and Prescott, 2006; Segurado et al., 2006; Tognelli and Kelt, 2004), coefficient estimates are often different (Dormann, 2007a; Kühn, 2007), and the relative importance of predictor variables shifts (Bini et al., 2009; Diniz–Filho and Bini, 2005; Diniz-Filho et al., 2003; Lennon, 2000; Tognelli and Kelt, 2004). In reviewing more than 20 studies that compared regression to autoregression models, Dormann (2007a) found that the average increase in adjusted model R^2 (autoregression – regression models) was 0.060 (minimum = –0.10, maximum = 0.20). He also found that where coefficients could be compared directly, the values were always different (he uses the word 'biased', Dormann, 2007a: 133), but he also cautions that the errors on the coefficient estimates could be large enough to render the differences statistically insignificant. Beale et al. (2010) caution against relying on SAC in the residuals as a robust metric of model stability (or instability); they found that even weak SAC could have notable effects on coefficient estimates and that correctly specified spatial models (based on simulated data) could still produce detectable SAC in residuals.

In spite of the inability to converge on specific suggestions for how exactly SAC should be treated in SDM, one consistent theme among all spatial/non-spatial comparison studies is that SAC should not be ignored, nor should non-spatial methods be used 'blindly'. Empirical evidence also suggests that spatial models are not uniformly superior to non-spatial models and the relative success of their use may be the result of a combination of complex factors related to scale, source(s) of SAC, sampling strategy, and non-stationarity. These incorrectly specified models could lead to faulty hypotheses about the effects of changing environmental conditions on species distributions.

III SDM and spatial non-stationarity

Spatial non-stationarity is a related concept but is less intuitive and less commonly considered compared to spatial autocorrelation and has only recently been addressed in SDM research. A general definition of the opposite condition, stationarity, refers to a model or process for which the parameters are fixed. A recent progress report discussed stationarity in the context of hydrological models, where stationary conditions apply to a natural system's fluctuations within a fixed window of variability (Peel and Blöschl, 2011). Biological population dynamics are considered to be stationary if their density and structure are consistent over time (Henden et al., 2009). In geostatistical prediction, stationarity is a prerequisite as part of the intrinsic hypothesis and refers to a covariance structure that is invariant with location (Atkinson, 2001). Spatial stationarity describes a model or process whose parameters are consistent throughout the region of interest (a 'global' model). If the parameters are not consistent and vary locally, a global model such as generalized regression may be inaccurate and any subsequent spatial inference may be inappropriate. Non-stationarity is a spatial variant of Simpson's paradox (Simpson, 1951), the observation that subsets of a data set can produce opposite results compared to results based on the entire data set.

Spatial non-stationarity is the statistical formalization of spatial heterogeneity, which refers generally to variation or differences across space. In an ecological context, spatial heterogeneity is functional, as it results from processes that operate at different scales (Legendre, 1993). While superficial observation may suggest that spatial autocorrelation and heterogeneity are somewhat incongruous ways of viewing the relationship between space and similarity, Fotheringham (2009) used the framework of local statistics as a way of linking the two concepts. Local statistics involve disaggregating a single mean or summary (global) value into a locally calculated value for each observation, the spatial variation of which can then be mapped. The applicability of local statistics is a function of the degree of spatial heterogeneity in the data, and the calculation of local statistics is based on a conceptualization of spatial relationships where 'near' values are more related than distant ones. Therefore spatial autocorrelation (as defined by a spatial weights matrix) is used to measure the pattern and intensity of spatial heterogeneity.

It is important to emphasize that stationarity/non-stationarity is not a property of data, but rather of a model or process, and that a non-stationary pattern can result from a stationary process, e.g. in the presence of a trend (Fortin and Dale, 2005). There are several factors that may result in spatial non-stationarity (Atkinson, 2001; Fotheringham et al., 2002): sampling variation; an intrinsically different process in different parts of the study area; and model mis-specification, such as a missing variable or incorrectly specified functional form. At macro-ecological scales typical of most SDM studies, an underlying ecological relationship that may be 'global' (e.g. water availability/precipitation and plant abundance) can be affected by local processes and conditions and result in a heterogeneous pattern that would be described more accurately by model parameter values that differ from the global values. Temperature can have an interaction effect with precipitation (as well as with aspect at an even more local scale) and this effect can be represented by an interaction term in a global regression model, as long as the interaction effect is somewhat consistent throughout the study area.

SDM applications have only recently begun to consider spatial non-stationarity and how it might affect model performance and inference. An early study modeling bird

distributions in Spain used models based on partitioned geographic subsets in order to detect spatial non-stationarity and concluded that 'some form of geographically-weighted regression' should be used for broad-scale modeling in the presence of non-stationarity (Osborne and Suárez-Seoane, 2002: 249). Geographically weighted regression (GWR), a local variant of traditional (global) regression, has since become the preeminent statistical method to deal with spatial non-stationarity explicitly (Fotheringham et al., 2002). GWR uses a spatial kernel-weighting scheme to define neighborhoods from which model parameters (coefficients, t values, R^2) are calculated for each observation. The size of the kernel is defined by its bandwidth, which can be a fixed distance or allowed to shrink and expand ('adaptive kernel') to include a fixed number of observations in order to accommodate variations in data density.

Of the relatively few previous GWR applications in SDM, most have focused on comparing GWR to a global model such as OLS, using some combination of model fit, prediction accuracy, or spatial autocorrelation in residuals as the metrics on which comparisons were based. The amount of explained variance (R^2) is the most widely reported model fit diagnostic in regression but is inappropriate for comparisons between GWR and OLS or between GWR models specified using different bandwidths (Jetz et al., 2005; Kupfer and Farris, 2007). The Akaike Information Criterion (AIC, or corrected AIC, AIC_c) and adjusted R^2 account for model complexity and provide a more meaningful comparison of model performance. Studies in which a comparison of model fit was a primary goal reported superior performance (i.e. lower AIC and/or higher adjusted R^2 values) by GWR compared to OLS when modeling species richness (Foody, 2004; Martín–Queller et al., 2011), tree basal area (Kupfer and Farris, 2007), tree crown area (Zhang et al., 2005), fire incidence (Sá et al., 2010), and landscape patterns (Gao and Li, 2011; Su et al., 2012). This is not surprising considering the increased flexibility associated with allowing coefficients to vary spatially, but this potential for 'over-fitting' can diminish the ability of GWR to generate predictions using independent data.

The location-specific model coefficients produced by GWR should only be applied within the spatial extent from which the data were collected; therefore prediction is less straightforward with GWR than with OLS. As a result, prediction accuracy using GWR has been the focus of SDM studies less frequently, owing also to the difficulty in measuring it. Prediction accuracy is typically measured using a subset of the data set (independent or 'test' data) that was not included in model fitting (see Franklin, 2009), and data partitioning can have important effects on the results of heavily data-dependent methods such as GWR. In their analysis of the relationship between basal area and fire history and topography, Kupfer and Farris (2007) used a 'leave-one-out' (jackknifing) methodology to compare residuals from GWR and OLS. They found that GWR often had more accurate predictions for sites that were difficult to predict (where both models had overall higher residuals). Using simulated data with different levels of spatial heterogeneity and autocorrelation, Harris et al. (2010) compared predictions from GWR to OLS and kriging methods with a root mean square error (RMSE) diagnostic and found that while universal kriging performed the best, GWR-kriging hybrid methods also showed promise. Finley (2011) used a 25% partition of two different 'real' data sets on bird richness and tree height and three simulated data sets to calculate mean squared error of prediction. He found that GWR performed better than the non-spatial method, but a more computationally intensive method that also addresses non-stationarity, spatially varying coefficients, performed the best (i.e. had the lowest mean squared error of prediction).

Many studies focused on SAC in model residuals as a metric for model performance,

in spite of the fact that GWR does not address SAC explicitly. Using both global (Gao and Li, 2011; Kupfer and Farris, 2007; Martín–Queller et al., 2011; Sá et al., 2010; Su et al., 2012) and local (Zhang et al., 2005) versions of Moran's I coefficient, GWR residuals were less spatially autocorrelated than OLS residuals. Griffith (2008) points out that allowing coefficients to vary spatially can absorb a lot of the spatial patterning in the variables used. The ability of GWR models to decrease spatial autocorrelation in residuals does not indicate the presence of spatial non-stationarity. It should be noted that few of the studies that compared OLS to GWR reported evidence of spatial non-stationarity as justification for using GWR (but see Kupfer and Farris, 2007), such as the Monte Carlo significance test for spatial variability of parameters described by Fotheringham et al. (2002).

Hothorn et al. (2011) provide one of the few studies that explored the effects of both spatial autocorrelation and non-stationarity (as well as non-linearity and multicollinearity) concurrently. They proposed a framework that decomposes a model into global (environmental) and local (spatiotemporal autocorrelation and non-stationarity) factors in a flexible and consistent way.

Outside of model performance/comparison, GWR has been used for mapping the spatial distribution of coefficient values in order to identify potential missing variables or to suggest other underlying factors associated with the observed non-stationarity. Martín–Queller et al. (2011) used GWR to explore ecological processes potentially related to spatial variation in the relationship between management decisions and biodiversity in Central Spain. In a study of lizard richness in Australia, Powney et al. (2010) used GWR to examine regional differences in the relationship between lizard richness and richness of each of three other classes (mammals, birds, and amphibians).

While many of the studies described above relied on the automatic selection of a single optimized bandwidth, GWR can be used to explore scale-dependent effects by testing how systematically increasing the bandwidth affects model parameters. A recent review of ecological journal abstracts that used the term 'spatial scale' over the past 20 years found that while only 56% of the studies looked at multiple scales, 90% of those observed scale-dependent relationships (Sandel and Smith, 2009). The scale-dependence of model predictive ability and species-environment relationships is an emerging issue in ecology (McAlpine et al., 2008; Rahbek and Graves, 2001; Sandel and Smith, 2009; Willis and Whittaker, 2002) and GWR provides a framework for evaluating how these parameters vary with the spatial extent of the analysis. Jetz et al. (2005) caution against using R^2 as a diagnostic for GWR models because smaller bandwidths will have inflated R^2 values and suggest using proportional deviations from a null expectation based on models fit to random variables.

Foody (2004) found that the relationship between environmental factors (climate and NDVI) and bird species richness in sub-Saharan Africa changed as bandwidth for the GWR models increased from 1° to 8° ($\sim$110 km to $\sim$880 km). Scale-dependence was also observed between pteridophyte species richness and climate variables in Australia at bandwidths ranging from 100 km to 800 km (Bickford and Laffan, 2006). In a study of bird distributions in Spain, Osborne et al. (2007) calculated a 'stationary index' that compared the variation in the local regression coefficient values fit using GWR to the standard error of the single global coefficient (Fotheringham et al., 2002). Using bandwidths ranging from 50 to 250 km, they found that relationships between different predictor variables became stationary and AIC indicated better model fit at the smallest bandwidth (Osborne et al., 2007). Miller and Hanham (2011) also showed scale-dependence in species-environment relationships for plants in the Mojave Desert. Testing bandwidths ranging

from 10 to 200 km, they found that climate predictors generally had stationary relationships at wider bandwidths, and that model accuracy (based on proportional deviations from the null expectation) was scale-dependent for all but the rarest of the species examined. Stationary indexes were also used to explore scale-dependent relationships between agricultural landscape patterns and indicators of urbanization (Su et al., 2012) and between landscape fragmentation and anthropogenic and topographic factors (Gao and Li, 2011).

Jetz et al. (2005) note that the ability to fit spatially varying coefficient values is ultimately one of the limitations associated with using GWR for testing hypotheses related to generalizations about species-environment relationships (but see Finley, 2011, for an alternative). While several of the above studies used GWR to analyze species richness patterns (see also Cassemiro et al., 2007), a recent novel application used GWR to test the water-energy theory on American palm (Arecaceae) species richness throughout their range in the Northern and Southern Hemispheres (Eiserhardt et al., 2011). Their results suggested that the shifting importance of water and energy on species richness was more related to gradual changes in available energy rather than abrupt transitions related to events such as frost occurrence (they note that this result may only apply to similar studies that focus on tropical and subtropical latitudes).

In a paper that summarizes many of the developments in spatial autocorrelation analysis over the past 40 years, Cliff and Ord (2009) noted that while new methods such as GWR add to our ability to describe spatial patterns, they question whether GWR enhances our understanding of these patterns. Several studies have observed that collinearity among explanatory variables can affect the accuracy of coefficients estimated by GWR (Wheeler and Calder, 2007). Spatial filtering (Griffith, 2008), ridge regression (Wheeler, 2007), and spatially varying coefficient (Finley, 2011) methods have been suggested as alternatives or modifications to GWR to produce more accurate and parsimonious model coefficients.

GWR has also been criticized as an alternative to global regression for inference and hypothesis testing (Griffith, 2008; Jetz et al., 2005) but, like many local versions of global statistics, it is particularly useful for exploratory data analysis and visualization. Spatial variation of model parameters, particularly the coefficient values, can be used to identify missing variables or to suggest the existence of local interactions or different processes that result in deviations from the global relationship. However, Austin (2007) has cautioned that spatially varying model coefficients can also result from a mis-specified GWR model – for example, a linear relationship is specified for what is really a curvilinear relationship.

IV Conclusions

Both spatial autocorrelation and non-stationarity affect the most important goal in SDM – to identify the underlying factors associated with broad-scale ecological patterns and to produce accurate maps of the biogeographical variable of interest. Valid model inference and mapped predictions from SDM are based on the ability to calculate accurate coefficient estimates and the assumption that the relationships described by the coefficients are constant throughout the study area. Both traditional SDM and more recent applications related to studying consequences of climate change are only as good as the model parameters used to quantify the relationships and only applicable where those relationships are stationary. While SAC is more widely addressed in SDM and spatial non-stationarity is starting to be addressed, it is rare that impacts associated with both are addressed in the same study (but see Hothorn et al., 2011).

Uncertainty is associated with each step, decision, and assumption in the modeling

process (for a review, see Heikkinen et al., 2006). Simulated data frameworks are particularly useful for assessing these issues (Beale et al., 2007; Dormann, 2007b; Finley, 2011; Harris et al., 2010; Wheeler and Calder, 2007). As increasingly sophisticated statistical methods become more accessible, it is important that model assumptions and consequences of violations are understood. Ultimately, these models must make ecological sense even when used in exploratory studies.

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