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RESEARCH ARTICLE

Cross-scale contradictions in ecological relationships

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Abstract
Context Not accounting for spatial heterogeneity in ecological analyses can cause modeled relationships to vary across spatial scales, specifically different levels of spatial resolution. These varying results hinder both the utility of data collected at one spatial scale for analyses at others and the determination of underlying processes.
Objectives To briefly review existing methods for analyzing data collected at multiple scales, highlight the effects of spatial heterogeneity on the utility of these methods, and to illustrate a practical statistical method to account for the sources of spatial heterogeneity when they are unknown.
Methods Using simulated examples, we show how not accounting for the drivers of spatial heterogeneity in statistical models can cause contradictory findings regarding relationship direction across spatial scales. We then show how mixed effects models can remedy this multiscaling issue.
Results Ignoring sources of spatial heterogeneity in statistical models with coarse spatial scales produced contradictory results to the true underlying relationship. Treating drivers of spatial heterogeneity as random effects in a mixed effects model, however, allowed us to uncover this true relationship.
Conclusions Mixed effects models is advantageous as it is not always necessary to know the influential explanatory variables that cause spatial heterogeneity and no additional data are required. Furthermore, this approach is well documented, can be applied to data having various distribution types, and is easily executable using multiple statistical packages.

Keywords Ecological fallacy · MAUP · Missing variables · Multiscale · Mixed effects models · Spatial transmutation

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Introduction

Macrosystems ecology is the study of how biological, geophysical, and social components interact with one another across spatial and temporal scales to affect ecological patterns and processes at macroscales (Heffernan et al. 2014). The spatial heterogeneity nested within coarse (i.e. larger) spatial scales

(Heffernan et al. 2014; Soranno et al. 2014) often presents challenges to the investigation of macrosystems. Similarly, spatial heterogeneity has long been acknowledged as a research priority within the field of landscape ecology (Wu and Hobbs 2002). Given the vast amount of ecological heterogeneity occurring across large geographic areas (e.g. Cleland et al. 1997) and the fact that spatial heterogeneity in ecological processes can lead to the emergence of unpredictable patterns at coarse spatial scales (Peters et al. 2007), accounting for this heterogeneity is crucial to improving ecological understanding (Wu and Loucks 1995). It should be noted that spatial scale can refer to grain size/resolution, extent, cartographic ratio, among other things (Turner 1989; Wu 2004), but for the purposes of this paper, spatial scale will be used only to describe the level of resolution or grain size.

Spatial heterogeneity in the associations between variables is the uneven distribution of this association, whether in direction or magnitude, within a given area (Dutilleul and Legendre 1993). This can occur across nested geographic sub-regions and across varying spatial scales (Iannone et al. this issue). As this heterogeneity can emerge in multiple ways (Wu 2004), how to account for it within the context of macrosystem investigations is not clear. One way spatial heterogeneity can arise is due to the fact that a variable, which influences a response variable at one scale, may not at another (Hamer and Hill 2000; Wu 2004). For instance, avian species richness is affected most by forest edge density at the 10-m scale but more so by normalized difference vegetation index (NDVI) at the 30-m scale (Bar-Massada et al. 2012). Similar cross-scale differences determine whether or not the effects of habitat fragmentation are detected on avian nesting success (Stephens et al. 2003). This source of heterogeneity makes it difficult to ensure that all important variables are accounted for when analyzing data at spatial scales that differ from those of prior investigations or of data collection.

Spatial heterogeneity across coarse spatial scales also creates challenges when trying to make inferences about ecological phenomena or processes at one specific spatial scale, from data collected at other spatial scales (Wiens 1989; Gotway and Young 2002; Wakefield and Lyons 2010), as is often necessitated in macrosystem investigations due to data availability. This challenge has been discussed within the context of three inter-related issues. The first of which is "ecological fallacy". This sociological term describes when one falsely assumes that relationships revealed from aggregated data (e.g. proportion of a population in a given area) can be used to make predictions about the individuals used to devise these aggregated data, and vice versa (Robinson 1950; Selvin 1958). This false assumption can lead to errors in the estimation of relationship magnitude and direction, and in ecological research is termed "spatial transmutation" (O'Neill and Rust 1979; Kling et al. 1991). Changes in relationship magnitude and direction can also emerge by simply changing the size of the spatial unit used when analyzing data collected over large areas. This statistical anomaly is referred to as "modifiable areal unit problem (MAUP)" (Openshaw 1983; Jelinski and Wu 1996; Dark and Bram 2007) and is of particular concern given the increased use of remotely sensed data for applied ecological research (Wu et al. 1997; Pettorelli et al. 2014). Another aspect of MAUP is the placement of spatial units, i.e. the "zone effect", which can also affect the magnitude and directionality of relationships (Gotway and Young 2002).

Failure to account for the sources of spatial heterogeneity within statistical models and/or not analyzing data at appropriate scales may lead to cross-scale differences in both relationship direction and key drivers of ecological processes (O'Neill and Rust 1979; Kling et al. 1991; Levin 1992; McGill 2010; Azaele et al. 2012; Araújo and Rozenfeld 2014). These cross-scale contradictions make it difficult to discern true ecological relationships but nevertheless are commonplace across ecological investigations. For example, in the Northeastern United States of America (USA), the abundance of the bird the Least Flycatcher (*Empidonax minimus* Baird & Baird) is found to negatively influence the distribution of American Redstart (*Setophaga ruticilla* L.) territories when studied using four-hectare plots. However, this relationship becomes positive when examined at the regional scale (Sherry and Holmes 1988 in Wiens 1989). Similar cross-scale contradictions in correlation directions and magnitudes have also been found in the study of the relationship between the diversity of native and invasive species (Shea and Chesson 2002; Renne et al. 2003; Stohlgren et al. 2003; Taylor and Irwin 2004; Fridley et al. 2007; Powell et al. 2013, Iannone et al. this issue) and the relationship between the abundance of hydropsychid caddisfly larvae and blackfly larvae (Cooper et al. 1998).

When contradictory relationships between variables are observed across spatial scales due to spatial heterogeneity in the association between these variables, it is essential to be able to determine which relationships best represent reality. Cross-scale contradictions are particularly concerning when conducting analyses at scales that differ from those of data collection, as is often necessary for analyses of coarse spatial scales, such as those of macrosystem investigations. Yet, despite a large number of studies focusing on the effects of different scales on ecological phenomena and processes, and attempting to address cross-scale contradictions, practical solutions to this complication are still needed. That is, methods are needed to determine true relationships in the face of spatial heterogeneity. Here we review the existing approaches used to make inferences at scales that differ from those of data collection, discuss the effects of spatial heterogeneity on their utility, and then present how a common, and easily applicable, statistical approach can help to determine the underlying relationships by helping to account for the spatial heterogeneity inherent across coarse spatial scales.

Existing methods for cross-scale inference

In this section, we briefly describe some methods for utilizing data collected at one scale to derive inferences at another and how spatial heterogeneity can affect the utility of these methods. The methods described are not exhaustive but rather presented with the aim of illustrating the complications associated with trying to account for spatial heterogeneity when analyzing data from coarse spatial scales and the need for more widely applicable methods.

The scales at which analyses are performed are often based on the researchers' perceptions of nature (Wiens 1989) and/or driven by the resolution of available data (Jelinski and Wu 1996). Therefore, the choice of scale in many multi-scale studies is often arbitrary (Wheatley and Johnson 2009) and likely to be suboptimal (Jackson and Fahrig 2015). This is understandable due to the lack of information available prior to investigations on the scale at which factors of interest are most influential (Jackson and Fahrig 2015). One solution in dealing with this issue is to identify the characteristic scale of response by modeling the relationship between the response variable and explanatory variables of interest, to determine the scale at which the response variable is most strongly affected by the explanatory variables. This approach has been utilized in investigations into single species responses to habitat abundances (Holland et al. 2004). Many authors (Holland et al. 2004; Graf et al. 2005; Bradter et al. 2013) have developed methods to identify the "ideal" scale, but these approaches are only viable in situations where data are collected across multiple spatial scales. Furthermore, complications in statistical modeling will likely arise, as the scale of greatest effect is likely to vary among model terms (Wu et al. 1997; Wu 2004). This would necessitate the use of statistical models which contain multiple explanatory variables each potentially accounting for a distinct layer of spatial heterogeneity.

Up-scaling or downscaling of existing data is often of great utility in ecological studies due to data not being available across all potentially influential spatial scales (Wheatley and Johnson 2009). With regards to up-scaling (i.e., using data from finer scales to derive coarse-scale estimates), the avoidance of erroneous spatial transmutations is ensured only if there is no collinearity among explanatory variables, if relationships at finer scales are linear, and if relationships do not switch from linear to non-linear across scales (Kling et al. 1991). When these assumptions are not met and spatial heterogeneity is known to be the sole source of spatial transmutation, expected values from nested sub-sections can be used to derive coarse-scale estimates (Kling et al. 1991). Regardless, these approaches assume that all important variables are known, as is the manner in which the effects of these variables fluctuate spatially.

Downscaling involves making inferences at finer scales using data obtained from coarser scales. Such techniques which employ different functions (e.g. linear, logarithmic and exponential) have been developed and used to downscale landscape metrics using class-level metrics or fractional land cover abundance (Saura and Castro 2007; Argañaraz and Entraigas 2014; Frazier 2014). Occupancy curves have also been used to provide descriptions of a species at finer spatial scales given data at coarser scales (Azaele et al. 2012). Likewise, there are other techniques for downscaling that use statistical relationships, for example, between species occurrence and environmental factors, to derive predictions at finer spatial scales (Lloyd and

Palmer 1998; Araújo et al. 2005; McPherson et al. 2006; Bombi and D'Amen 2012). Although these methods have been shown to be effective in certain situations, they do not allow for the effects of factors to vary across different spatial scales nor are they able to account for the absence of information on, or knowledge of, explanatory variables that have strong influence on the response variable. Therefore, downscaling and up-scaling approaches cannot ensure the resolution of contradictory cross-scale results.

In more recent developments, hierarchical Bayesian models (HBM) have been used as an alternative to other downscaling techniques (Keil et al. 2013). This method is particularly useful if one needs to make use of data of different scales. It assumes that the scales of data are nested and defines the model through a hierarchy; that is, given the data of a coarser scale, data of a finer scale follow some statistical model. However, HBMs suffer similar limitations as other aforementioned methods in that they are unable to account for missing explanatory variables that have strong influence on the response variable.

A viable statistical approach

When analyses of data of different spatial scales lead to contradictory findings, it is problematic to interpret the results because of the risk of arriving at incorrect conclusions. From a statistical point of view, the contradiction means that the fitted models are an insufficient representation of the underlying ecological process or processes. This poor representation may be due to the model structure being inappropriate or inadequate. An example of this would be the inclusion of only linear terms in a model that should also contain higher orders, such as squared terms. It can also be due to the absence of explanatory variables that significantly impact the modeled response variable. It may also be due to both poor model structure and missing variables. Poor representation of an ecological process is generally remediable if the model structure is simply not specified correctly and data needed to resolve this problem are available. This problem, however, becomes difficult to resolve when important explanatory variables are not included in the model due to them being unknown, or due to the data for these variables being either not collected or unavailable.

Spatial heterogeneity is known to be a potential contributing factor to the scaling issue (McGill 2010). Strictly speaking, there must be spatial variables that cause the spatial heterogeneity. In reality, however, we just do not know all the possible variables contributing to the spatial heterogeneity in an ecological process occurring within course geographic areas. Consequently, spatial heterogeneity is frequently only partially accounted for in statistical models. Therefore, an important and interesting problem is how to account for the factors which drive spatial heterogeneity in a given ecological process without explicitly knowing all the contributing factors. This issue is particularly pertinent to macrosystems research given that the factors affecting a specific ecological process may vary spatially within a given study region. We believe that the solution relies on either novel statistical approaches or on the novel application of existing approaches.

To account for the spatial heterogeneity that our observed variables do not represent, it is sensible to treat the spatial heterogeneity as driven by latent random variables. Latent variables are variables that are not directly observed but can be assessed indirectly using proxy variables. Spatial heterogeneity, for example, cannot always be measured explicitly and in such cases, sub-divisions of the larger geographical area which are known to contain fairly homogenous ecological conditions can be used as a proxy for the direct measurement of spatial heterogeneity. Therefore, to account for the factors which drive spatial heterogeneity that our observed models do not represent, it is sensible to treat the factors as driven by latent random variables. There are various statistical models developed to handle latent random variables of which mixed effects models and random fields are the two most popular (Laird and Ware 1982; Cressie 1993).

Next, we construct two examples to illustrate the points we made in the previous paragraphs. Specifically, the objective of these examples is to show (i) that failing to account for the key variables which drive the spatial heterogeneity in the association between two variables can result in contradictory findings, and (ii) a remedy to reconcile the contradictory results.

The method presented may be applied to any missing variable. If this missing variable could be measured (such as latitude), then a simple remedy exists—that is, we need only to add that variable to the model. However, as is often the case, the missing variables cannot be measured or identified. In such instances, it is impossible to include these variables, and surrogates have to be sought to offset the effects of the missing variables. We treat these variables as random and apply statistical approaches to analyze them.

A misspecified model

In what follows we will assume that the size of the sampling unit is relatively small compared to the total sampling area, or study region, and hence can be treated as a single point. Suppose our response variable, the abundance of a given plant species (Y) comes from the following statistical model

$$Y = \beta_0 - \beta_1 Tmp - \beta_2 Z + \varepsilon_Y \quad (1)$$

where $\beta_0, \ \beta_1, \ \beta_2 > 0$, temperature ($Tmp$) is an explanatory variable that is negatively correlated with Z, an unknown variable with linear latitudinal gradient, and ε_y captures the unexplained variability in the dataset and is assumed to be normally distributed, i.e. $\varepsilon_Y \sim N(0, \sigma_Y^2)$. More specifically, we assume temperature relates to Z as stated in Eq (2):

$$Tmp = \alpha_0 - \alpha_1 Z + \varepsilon_{Tmp} \quad (2)$$

where $\alpha_0, \alpha_1 > 0$ and $\varepsilon_{Tmp} \sim N(0, \ \sigma_{Tmp}^2)$.

Suppose the following model is fitted to the data at both coarser and finer scales, where temperature is the only explanatory variable and Z is missing from the model, either because a researcher does not know of its importance or because of data unavailability:

$$Y = b_0 + b_1 Tmp + e \quad (3)$$

where e is again an error term with mean 0. This fitted model is a misspecified model because the important variable Z is missing. When this model is fit to a dataset for the entire study region, the coarsest possible scale, the relationship between temperature and Y (i.e. b_1) is determined to be positive, a contradictory result. This occurs because Z can be written in terms of temperature to give

$$Z = \frac{1}{\alpha_1}(\alpha_0 - Tmp + \varepsilon_{Tmp}). \quad (4)$$

Substituting Eq. (4) for Z in Eq. (1) results in the slope coefficient b_1 being equal to $\beta_2/\alpha_1 - \beta_1$. The contradiction will occur once $\beta_2/\alpha_1 > \beta_1$. However, if the model is fitted at a finer scale where the Z is approximately constant, the slope of the relationship between temperature and Y will be negative. This is because, with Z being constant, Model (3) is now a better approximation of the ecological processes being modeled.

Contradictory results of analysis of data of different scales

To further illustrate how contradictory relationships between two variables can emerge across spatial scales due to the absence of an important, but potentially unknown, explanatory variable, and how to remedy this scaling issue, we simulated a data set from Model (1) with the pre-chosen set of parameter values: $\alpha_0 = 325, \ \alpha_1 = 0.4, \ \beta_0 = 300, \ \beta_1 = 0.35, \ \beta_2 = 0.85$ and $\sigma_{Tmp}^2 = 0.5, \ \sigma_Y^2 = 0.01$. We generated independent observations at 2000 sampling locations uniformly distributed in a rectangular area having a latitudinal range of 35°–41° and a longitudinal range of 70°–80° as displayed in Fig. 1. The region was divided into six latitude bands as it is believed that the association between temperature and Y is fairly homogeneous within each band and the divisions are ecologically meaningful.

If we use this simulated data to fit the misspecified Model (3) across the entire study region, i.e. the square in Fig. 1, we get a positive estimate of the slope for the relationship between temperature and Y ($b_1 = 0.66 \pm 0.02$; estimate $\pm$ se) as shown in Fig. 2. This is a contradiction because the relationship between temperature and Y is negative (see Model (1)). However, if we fit Model (3) within each of the six latitude bands (i.e., at the finer scale), we get negative slope estimates within each of the six bands. Again, this contradiction (illustrated in Fig. 2) is because at the finer scale, Z is close to a constant and has little effect on Y, whereas at the larger spatial scale it has a greater effect, but is unaccounted for; thus the model is misspecified at the coarser spatial scale.

A remedy through a mixed effects model

Mixed effects models are made up of two main parts—fixed and random effects. The explanatory variables which are associated with the entire population can be

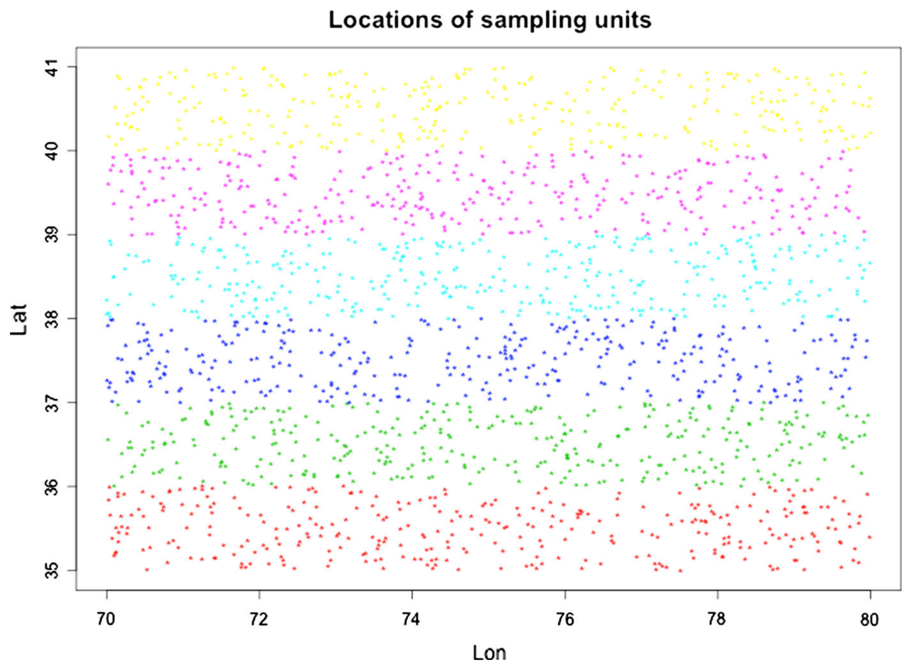

Fig. 1 Simulated sampling locations: 2000 sampling units within in a rectangular area (latitude 35°–41° and longitude 70°–80°). The area is divided into six latitude bands represented by different *colors*. (Color figure online)

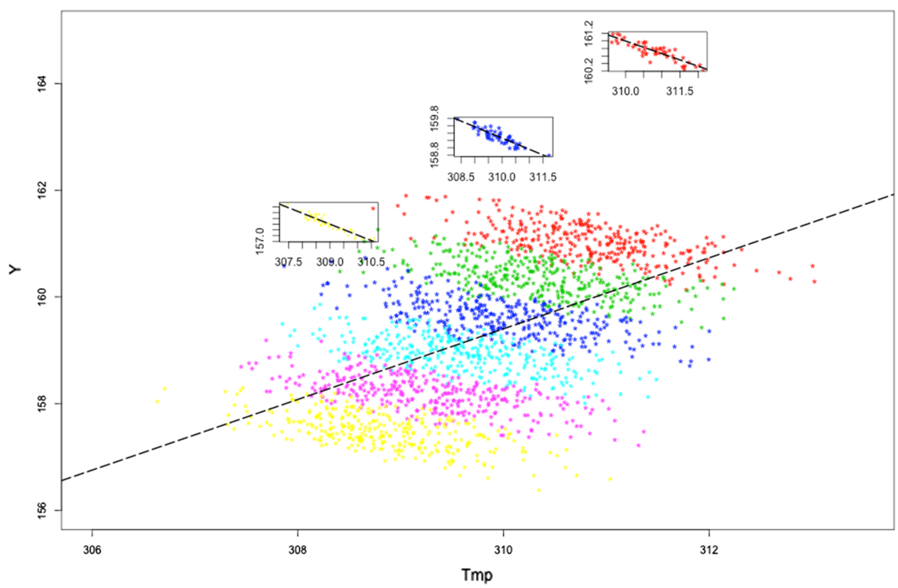

Fig. 2 Scatter-plot of Y versus temperature (*Tmp*) indicates a positive relationship at the coarser scale and a negative relationship at the finer scale. Subplots display the scatter-plot of a smaller region (approximately 0.15° latitude band). Each *color* represents a single latitude band with the same *color* scheme as Fig. 1. (Color figure online)

considered fixed effects. The random effects part of the model allows us to account for the important, but perhaps unknown, factors that drive spatial heterogeneity in the ecological processes being modeled (Laird and Ware 1982). We can achieve this by dividing larger study regions into smaller sub-regions each with independent random slope and intercept estimates for the modeled ecological process (Buckley et al. 2003).

In this particular example, we know that such a discrepancy is caused by the fact that *Z*, which has a significant relationship with the response variable, is not accounted for in the fitted model of the larger geographic area (Model (3)). In reality, however, we may not know which significant variable is ignored in the fitted model. Statistically we may treat the effects of the missing explanatory variable or variables as random. This will result in a mixed effects model which has, to some degree, the advantage of accounting for the effects of the missing, yet important, explanatory variables. Another advantage is that no additional data are needed to fit the model.

To illustrate these benefits, we re-fit our simulated dataset using a mixed effects model that subdivides our geographic region into six sub-divisions, each having independent intercept and slope estimates for the relationship between temperature and Y. Furthermore, the model ignores data on Z. This model allows us to account for the heterogeneity in the 'unknown' effect that Z has on Y, resulting in a more consistent relationship across spatial scales. This is modeled as follows:

$$Y_{ij} = (\beta_0 + B_{0i}) + (\beta_1 + B_{1i})Tmp_{ij} + \varepsilon_{ij} \qquad 1 \le i \le I,\ 1 \le j \le J \tag{5}$$

where I is the number of sub-regions that the larger geographic area is divided into, and $\mathrm{Y_{ij}}$ denotes the jth observation of the response variable in sub-region i, and X_{ij} the jth value of the explanatory variable in sub-region i. Furthermore, B_{0i} and B_{1i} are the intercept and slope estimates, respectively, for sub-regions 1 through I, both of which are assumed to be identically and independently (i.i.d) normally distributed and with mean zero and variance equal to σ_0^2 for the intercepts and σ_1^2 for the slopes. Model (5) therefore assumes that slopes and intercepts vary from one region to another, hence accounting for the possible unknown variables that may drive spatial heterogeneity.

We refit our simulated data using a mixed effects model using the lmer function in the package lme4 in R (Bates et al. 2014; R Core Team 2014). The estimate obtained from this model for the relationship between temperature and Y is now negative ($\beta_{1,}$ is -0.28494) and therefore in agreement with our actual data (see Model (1)). In addition, this model can be utilized to produce sub-regional estimates for the ecological process being modeled. For example, for our simulated dataset, the random slope estimates for each of the six geographic sub-regions are 0.00418, -0.00250, -0.00082, 0.00081, 0.00250 and 0.00419. Adding these random effects values to the estimate of the fixed effect ($\beta_{1,}$) will give sub-region level slope estimates, which are -0.28902, -0.28734, -0.28566, -0.28403, -0.28234 and -0.28065. At the finer scale, a negative correlation between temperature and Y is also correctly revealed.

Although the estimated values for the association now have the same direction as the true value (β_1) and the magnitude of the relationship is close to the true value, the confidence interval of the estimate does not include β_1, as shown by the standard error bands in Fig. 3. It should be noted, however, that as number of sub-divisions increase, the closer the estimate gets to the true value and the confidence intervals are not only smaller, indicating greater precision, but also they include β_1. There also seems to be some optimal point, where an increase in the number of bands does not increase the precision of the estimate or change the value of the estimate significantly. This is evidenced by the estimates for 25 and 49 sub-divisions not differing much from each other and the size of the error bands being similar (Fig. 3).

To demonstrate that this remedy may also work in more complex situations, let us now extend our illustration and suppose that our response Y comes from the following model

$$Y = \beta_0 - \beta_1 Tmp + \beta_2 Precip - \beta_3 Precip^2 + \beta_4 Z + \varepsilon_Y \tag{6}$$

where $\beta_0 = 300$, $\beta_1 = 0.35$, $\beta_2 = 0.25$, $\beta_3 = 0.01$, $\beta_4 = 0.85$, Z is, as before, an unobserved variable with

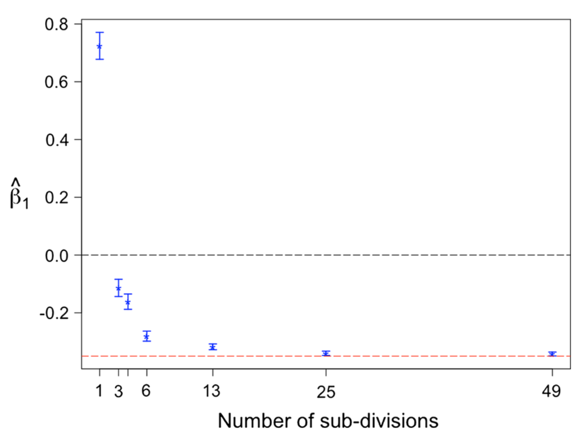

Fig. 3 Plot of estimates for β_1 (and their respective standard error bars) for different numbers of sub-divisions of the study region. The *red dotted line* represents the true value of β_1. (Color figure online)

a linear latitudinal gradient and $\varepsilon_Y \sim N(0, \sigma_Y^2)$. Temperature (*Tmp*) is related to Z in the same way as before (Eq. 2) and *Precip*, a variable with values that mimic the monthly precipitation of the given region, has a quadratic relationship with *Z* as stated in Eq. (7):

$$Precip = \gamma_0 - \gamma_1 Z + \gamma_2 Z^2 + \varepsilon_{Precip} \quad (7)$$

where $\gamma_0 = 1570$, $\gamma_1 = 77$, $\gamma_2 = 1$ and ε_{Precip} is an error term centered at 0 with variance $\sigma_{Precip}^2 = 1$. In this case, both temperature and *Precip* are dependent, as they are both functions of the latent variable *Z*.

As with our previous illustration, suppose that the following model is fitted to the entire study region at the coarsest possible scale:

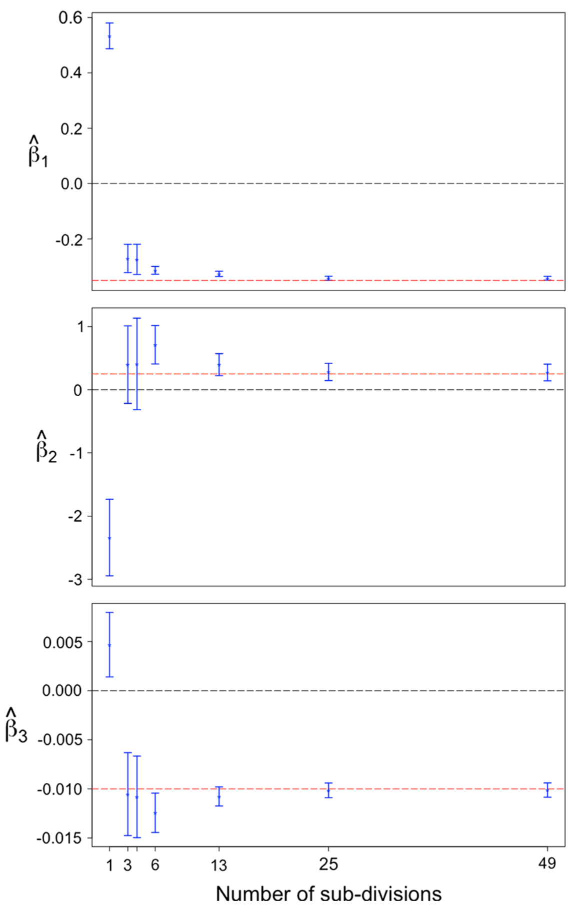

Fig. 4 Plot of estimates for β_1, β_2 and β_3 (with their respective standard *error bars*) for different numbers of sub-divisions of the study region. The *red dotted line* in each panel represents the true value of β_1, β_2 and β_3 respectively. (Color figure online)

$$Y = b_0 + b_1 Tmp + b_2 Precip + b_3 Precip^2 + e \quad (8)$$

where e is an error term with mean 0. The slope estimates for β_1 and β_3 are both positive, while the slope estimate for β_2 is negative (Fig. 4—number of sub-divisions = 1). These results are contrary to the true values of each parameter, that is, temperature and the squared *Precip* terms should have negative values, while the linear *Precip* term should be positive (Model (6)). The following mixed effects model was used to model the data, again using latitude bands as a proxy for the missing latent variable *Z*:

$$\begin{aligned} Y_{ij} = {} & (\beta_0 + B_{0i}) + (\beta_1 + B_{1i})Tmp_{ij} + (\beta_2 \\ & + B_{2i})Precip_{ij} + (\beta_3 + B_{3i})Precip_{ij}^2 \\ & + \varepsilon_{ij} \quad 1 \le i \le I, \ \ 1 \le j \le J \end{aligned} \quad (9)$$

where B_{0i} is the random intercept estimates and B_{1i}, B_{2i} and B_{3i} are random slope estimates for sub-divisions 1 to *I*. As before, these are all assumed to be normally distributed and centered at zero with their respective variances. This mixed effects model is also able to recover the 'true' relationship and magnitude from our data. Additionally, the behavior of the parameter estimates in this illustration are similar to those for the univariate example; they become more precise and closer to the true direction and magnitude as the number of sub-divisions increase (Fig. 4).

Discussion

When the variables which drive spatial heterogeneity are unaccounted for, analysis conducted at different spatial scales can lead to contradictions between the results. This is of particular concern for macrosystems investigations, as the amount of spatial heterogeneity inherent to large geographic areas is considerable and the factors contributing to this heterogeneity in a given ecological process are likely to vary spatially. It is therefore vital to be able to decide which result best represents reality or better yet to be able to reconcile the resulting contradiction. It has been highlighted in numerous investigations (e.g. Levin 1992; McGill 2010; Azaele et al. 2012; Araújo and Rozenfeld 2014) that spatial heterogeneity can contribute to the scaling issue and failing to account for the key sources of heterogeneity found across large study areas, or doing so inappropriately, may result in cross-scale contradictions in findings (Kling et al. 1991; Jelinski and Wu

1996). The simulated examples in this paper corroborates this point.

Our simulations further showed how accounting for the unknown sources of spatial heterogeneity, by treating sub-regions as random effects via the use of mixed effects models, can help to alleviate this concern by uncovering the relationship directions that are most likely correct regardless of scale of inference. The effectiveness of this method is due to the fact that the spatially heterogeneous effect of the latent random variable is absorbed into the random effect terms within the model. This outcome has some important practical implications for investigations of ecological process across large spatial scales. First, it reveals an approach that is not only effective, but also easily understandable and accessible. Mixed effects models are well documented and frequently utilized in ecological research (e.g. Faraway 2006; Zuur et al. 2009). These statistical models are also easily executable in leading statistical software packages [e.g. the R statistical language has two separate packages for constructing mixed effects models (Pinheiro et al. 2013; Bates et al. 2014)]. Finally, this easily assessable method can facilitate the analysis of remotely sensed data on which ecologists increasingly rely to derive broad scale understanding of applied importance (Wu et al. 1997; Pettorelli et al. 2014); but see comments below regarding MAUP.

Although mixed effects models have been employed in many applications to account for spatial heterogeneity, the extent to which a mixed effect model is effective is very hard to define. Therefore, it remains to be seen how broadly applicable the mixed effects model is in macrosystems ecology. The key objective of this paper is to show that it can be a very effective approach to account for spatial heterogeneity due to unknown sources.

Although the model presented assumes normality which is not valid for many types of ecological data, current statistical advancements are increasing the utility of mixed effects models even further. These models are now being extended to data having non-normal distributions via generalized linear mixed effects models (GLMMs) (Faraway 2006; Zuur et al. 2009), which are again increasingly available in popular statistical packages (e.g. Bates et al. 2014). Mixed effects models can also be used to model the variables that drive spatial heterogeneity that exhibit more complex spatial patterns than that described via the differentiation of discrete random spatial units. These patterns can be described by a covariance function in geostatistics and statisticians have employed geostatistical methods to analyze data of different scales, also called data of different support (e.g., Gotway and Young 2007). Unfortunately, at this time not all statistical software can address this level of complexity [e.g. the R library lme4 does not handle spatial correlation (Bates et al. 2014)]. Another extension is to consider non-normal distributions for the random effects in the mixed effects model. Currently, in most mixed effects models, the random effects are assumed to have a normal distribution. Non-normal and skewed distributions of random effects could be considered when needed, including a skew-normal distribution (Zhang and El-Shaarawi 2010). Like complex spatial patterns, the expansion of mixed effects models to include non-normal and skewed distributions of random effects is currently not easy to achieve in most statistical packages.

One challenge not addressed by our investigation is how to determine the scale that best captures spatial heterogeneity in a given ecological process across large geographic areas. After all, the magnitude and direction of relationships can vary greatly with the size of spatial units used in analyses (Jelinski and Wu 1996; Dark and Bram 2007). Subsumed within this challenge is the determination of the optimal number of subdivisions required to recover the true magnitude and direction of the association being investigated. The results of the two illustrations presented in this paper show that after a point there is very little increase in the precision and the accuracy of the estimated associations. The existence of this issue of MAUP reveals the need for careful consideration when selecting the size of areas being treated as random effects (i.e., proxies for the units of spatial heterogeneity). One straightforward approach is to utilize ecologically meaningful spatial units (Fotheringham 1989). The use of these units may not only assist in guarding against the scale effect but also the zone effect associated with the MAUP. The ecological sub-regions of the USA (Cleland et al. 1997, 2007) currently used by Iannone et al. (this issue) to account for spatial heterogeneity within the contexts of macroscale forest plant invasions is an example of such units. When such units are unknown, one can attempt to find the scale at which inter-regional variation in explanatory variables is minimized (Openshaw 1977) or conduct sensitivity analyses to determine the extent to which MAUP affects results (Jelinski and Wu 1996). When multiple variables are being investigated, however, the optimization of inter-regional variability may not be possible (Fotheringham and Wong 1991) and sensitivity analyses may become overly complex to properly interpret (Jelinski and Wu 1996). Although model selection for linear mixed effects models is not straightforward (Vaida and Blanchard 2005; Greven and Kneib 2010; Müller et al. 2013), one advantage of the mixed effects model is that an increase in the number of sub-divisions does not lead to a loss in the degrees of freedom available to estimate the parameters in the model because the sub-divisions are modeled as random effects and not fixed effects.

We note that no statistical approach is universally applicable. The mixed effects model may provide improvement of statistical analysis in many applications, but it should not be expected to always resolve multiscale issues. Therefore, one must be sure that the random effects that they utilize are in fact those that best capture influential spatial heterogeneity. Notwithstanding, the work presented here is a good starting point and will have implications for modeling ecological processes at macroscales given the absence of understanding of the factors that lead to spatial heterogeneity in that process. By helping to identify the actual directionality and magnitude of ecological relationships, mixed effects models have the potential to contribute greatly to the understanding of how nested spatial variability in a given ecological processes contributes to the same process at large spatial scales, and in doing so offer a practical and reliable tool for macrosystems ecology.

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References

Araújo MB, Rozenfeld A (2014) The geographic scaling of biotic interactions. Ecography (Cop) 37:406–415

Araújo MB, Thuiller W, Williams PH, Reginster I (2005) Downscaling European species atlas distributions to a finer resolution : implications for conservation planning. Glob Ecol Biogeogr 14:17–30

Argañaraz JP, Entraigas I (2014) Scaling functions evaluation for estimation of landscape metrics at higher resolutions. Ecol Inform 22:1–12

Azaele S, Cornell SJ, Kunin WE (2012) Downscaling species occupancy from coarse spatial scales. Ecol Appl 22: 1004–1014

Bar-Massada A, Wood EM, Pidgeon AM, Radeloff VC (2012) Complex effects of scale on the relationships of landscape pattern versus avian species richness and community structure in a woodland savanna mosaic. Ecography (Cop) 35:393–411

Bates D, Maechler M, Bolker B, Walker S (2014) lme4: linear mixed-effects models using Eigen and S4

Bombi P, D'Amen M (2012) Scaling down distribution maps from atlas data: a test of different approaches with virtual species. J Biogeogr 39:640–651

Bradter U, Kunin WE, Altringham JD, Thom TJ, Benton TG (2013) Identifying appropriate spatial scales of predictors in species distribution models with the random forest algorithm. Methods Ecol Evol 4:167–174

Buckley YM, Briese DT, Rees M (2003) Demography and management of the invasive plant species Hypericum perforatum. I. Using multi-level mixed-effects models for characterizing growth, survival and fecundity in a long-term data set. J Appl Ecol 40:481–493

Cleland DT, Avers PE, McNab WH, Jensen ME, Bailey RG, King T, Russell WE (1997) National Hierarchical Framework of Ecological Units. In: Boyce M, Haney A (eds) Ecosyst manag appl sustain for wildl resour. Yale University Press, New Haven, pp 181–200

Cleland DT, Freeouf JA, Keys JE, Nowacki GJ, Carpenter CA, McNab WH (2007) Ecological subregions: sections and subsections for the conterminous United States. General Technical. Report WO-76. U.S. Department of Agriculture, Forest Service, Washington, D.C. Map, presentation scale 1:3,500,000; Albers equal area projection; colored

Cooper SD, Diehl S, Kratz K, Sarnelle O (1998) Implications of scale for patterns and processes in stream ecology. Aust J Ecol 23:27–40

Cressie NA (1993) Statistics for spatial data, revised. Wiley, New York

Dark S, Bram D (2007) The modifiable areal unit problem (MAUP) in physical geography. Prog Phys Geogr 31: 471–479

Dutilleul P, Legendre P (1993) Spatial heterogeneity against heteroscedasticity: an ecological paradigm versus a statistical concept. Oikos 66:152–171

Faraway J (2006) Extending the linear model with r: generalized linear, mixed effects and nonparametric regression models. Chapman & Hall/CRC Taylor & Francis Group, Boca Raton

Fotheringham A (1989) Scale-independent spatial analysis. In: Goodchild M, Gopal S (eds) Accuracy spat databases. Taylor and Francis, London, pp 221–228

Fotheringham A, Wong D (1991) The modifiable areal unit problem in statistical analysis. Environ Plan 23:1025–1044

Frazier AE (2014) A new data aggregation technique to improve landscape metric downscaling. Landscape Ecol 29: 1261–1276

Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Von Holle B (2007) The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17

Gotway CA, Young LJ (2002) Combining incompatible spatial data. J Am Stat Assoc 97:632–648
Gotway CA, Young LJ (2007) A geostatistical approach to linking geographically aggregated data from different sources. J Comput Graph Stat 16:115–135
Graf RF, Bollmann K, Suter W, Bugmann H (2005) The importance of spatial scale in habitat models: Capercaillie in the Swiss Alps. Landsc Ecol 20:703–717
Greven S, Kneib T (2010) On the behaviour of marginal and conditional AIC in linear mixed models. Biometrika 97(4):773–789
Hamer KC, Hill JK (2000) Scale-dependent effects of habitat disturbance on species richness in tropical forests. Conserv Biol 14:1435–1440
Heffernan JB, Soranno PA, Angilletta MJ, Buckley LB, Gruner DS, Keitt TH, Kellner JR, Kominoski JS, Rocha AV, Xiao J, Harms TK, Goring SJ, Koenig LE, McDowell WH, Powell H, Richardson AD, Stow C, Vargas R, Weathers KC (2014) Macrosystems ecology: Understanding ecological patterns and processes at continental scales. Front Ecol Environ 12:5–14
Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. Bioscience 54:227–233
Iannone BI, Potter KM, Dixon Hamil K, Huang W, Zhang H, Guo Q, Oswalt CM, Woodall CW, Fei S. Understanding biotic resistance to invasions across forests of the Eastern USA. Landscape Ecol current is. (this issue)
Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? Glob Ecol Biogeogr 24:52–63
Jelinski D, Wu J (1996) The modifiable areal unit problem and implications for landscape ecology. Landscape Ecol 11:129–140
Keil P, Belmaker J, Wilson AM, Unitt P, Jetz W (2013) Downscaling of species distribution models: a hierarchical approach. Methods Ecol Evol 4:82–94
Kling A, Johnson A, O'Neill R (1991) Transmitation and functional representation of heterogeneous landscapes. Landscape Ecol 5:239–253
Laird NM, Ware JH (1982) Random-effects models for longitudinal data. Biometr Int Biometr Soc 38:963–974
Levin SA (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. Ecology 73:1943–1967
Lloyd P, Palmer AR (1998) Abiotic factors as predictors of distribution in Southern African Bulbuls. Auk 115: 404–411
McGill BJ (2010) Matters of scale. Science (80-) 328:575–576
McPherson JM, Jetz W, Rogers DJ (2006) Using coarse-grained occurrence data to predict species distributions at finer spatial resolutions - possibilities and limitations. Ecol Modell 192:499–522
Müller S, Scealy JL, Welsh AH (2013) Model selection in linear mixed models. Stat Sci 28:135–167
O'Neill R, Rust B (1979) Aggregation error in ecological models. Ecol Modell 7:91–105
Openshaw S (1977) Optimal zoning systems for spatial interaction models. Environ Plan 9:169–184
Openshaw S (1983) The modifiable areal unit problem. Geo Books, Norwick, Norfolk
Peters D, Bestelmeyer B, Turner M (2007) Cross-scale interactions and changing pattern-process relationships: consequences for system dynamics. Ecosystems 10: 790–796
Pettorelli N, Laurance W, O'Brien T, Wegmann M, Nagendra H, Turner W (2014) Satellite remote sensing for applied ecologists: opportunities and challenges. J Appl Ecol 51:839–848
Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2013) nlme: linear and nonlinear mixed effects models, R package version 3, p 57
Powell KI, Chase JM, Knight TM (2013) Invasive plants have scale-dependent species-area relationships. Science 339(80):317–319
R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Renne IJ, Tracy BF, Rejmánek M (2003) The rich get richer: responses. Front Ecol Environ 1:122–123
Robinson WS (1950) Ecological correlations and the behavior of individuals. Am Sociol Rev 15:351–357
Saura S, Castro S (2007) Scaling functions for landscape pattern metrics derived from remotely sensed data: Are their subpixel estimates really accurate? ISPRS J Photogramm Remote Sens 62:201–216
Selvin HC (1958) Durkheim's suicide and problems of empirical research. Am J Sociol 63:607–619
Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17:170–176
Soranno PA, Cheruvelil KS, Bissell EG, Bremigan MT, Downing JA, Fergus CE, Filstrup CT, Henry EN, Lottig NR, Stanley EH, Stow CA, Tan P, Wagner T, Webster KE (2014) Cross-scale interactions: quantifying multi-scaled cause-effect relationships in macrosystems. Front Ecol Environ 12:65–73
Stephens S, Koons D, Rotella J, Willey D (2003) Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biol Conserv 115:101–110
Stohlgren TJ, Barnett DT, Kartesz JT (2003) The rich get richer: patterns of plant invasions in the United States. Front Ecol Environ 1:11–14
Taylor BW, Irwin RE (2004) Linking economic activities to the distribution of exotic plants. Proc Natl Acad Sci U S A 51:17725–17730
Turner MG (1989) Landscape ecology: the effect of pattern on process. Annu Rev Ecol Syst 20:171–197
Vaida F, Blanchard S (2005) Conditional Akaike information for mixed-effects models. Biometrika 92:351–370
Wakefield J, Lyons H (2010) Spatial aggregation and the ecological fallacy. In: Gelfand AE, Diggle P, Guttorp P, Fuentes M (eds) Handb spat stat. CRC Press, Stat, pp 541–558
Wheatley M, Johnson C (2009) Factors limiting our understanding of ecological scale. Ecol Complex 6:150–159
Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397
Wu J (2004) Effects of changing scale on landscape pattern analysis. Landscape Ecol 19:125–138

Wu J, Hobbs R (2002) Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. Landscape Ecol 17:355–365

Wu J, Loucks O (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Q Rev Biol 70:439–466

Wu J, Gao W, Tueller P (1997) Effects of changing spatial scale on the results of statistical analysis with landscape data: a case study. Geogr Inf Sci 3:30–41

Zhang H, El-Shaarawi A (2010) On spatial skew-Gaussian processes and applications. Environmetrics 21:33–47

Zuur AF, Ieno EN, Walker NJ, Savekiev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer Science and Business Media, New York