

Towards a taxonomy of spatial scale-dependence

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Spatial scale-dependence is a ubiquitous feature of ecological systems. This presents a challenge for ecologists who seek to discern general principles. A solution is to search for generalities in patterns of scale-dependence – that is, what kinds of things are scale-dependent, in what ways, and why? I argue that this is likely to be a productive way forward for ecology, but that progress in this direction is currently hindered by the conflation of a set of distinct concepts under the category of ‘scale-dependence’. Here, I propose a taxonomy of spatial scale-dependence that categorizes its major types in hopes of moving towards a more formal and unambiguous vocabulary. I argue that three major distinctions are necessary and sufficient for this goal: that between grain size and extent (the scale component), between data and models (the subject), and between true and perceived scale-dependence (the class). I illustrate the need for these distinctions with a set of examples demonstrating causes of different types of scale-dependence. I then describe how this taxonomy relates to an array of scale-related concepts from other fields. Finally, I discuss the generalization that biotic interactions are most important at small scales in light of this taxonomy.

In an influential commentary, McGill (2010) began with an analogy to physics, noting that the explanatory power of Newton’s laws across a massive range of scales is unlikely to be replicated in ecology. Ecology, unfortunately, seems to be characterized by strong spatial scale-dependence, making general laws unlikely. I like the analogy, but take a somewhat different lesson from it. Newton’s laws were a revelation precisely because of their ability to explain seemingly distinct phenomena across a wide range of scales under one theory. This, I think, must be the challenge for ecologists. Our science is at the stage of identifying how patterns and processes change with scale. Ultimately, though, we also need to understand why these change with scale.

Reviewing the rise of the concept of scale in ecology, Schneider (2001) argued that scale had become a central concept in ecology, and may be poised to become a unifying concept, providing ‘theoretical unity’ for the field. Indeed, recognition of the central importance of spatial scale in ecology has increased dramatically in the last 25 yr (Wiens 1989, Levin 1992, Schneider 2001, Sandel and Smith 2009, Chave 2013). However, the potential for scale to become a unifying concept has gone relatively unrealized. In part, this is because scale-dependence is often discussed in a rather informal way. Though informal language is not necessarily a problem in itself, it becomes one when imprecise usage impedes generalization by confusing fundamentally different concepts. Previous papers (Scheiner et al. 2000) have worked towards clearing up ambiguity about the concept of

‘spatial scale’. Here, I will try to extend their efforts to work towards a more precise understanding about ‘spatial scale-dependence’.

Spatial scale-dependence, in one form or another, is ubiquitous in ecology. But it is this plurality of forms that is problematic when there is not a formal way to distinguish them. I propose a taxonomy of spatial scale-dependence, and seek to establish an associated formal vocabulary. It is my hope that this vocabulary will encourage more precise statements and thereby improved generalizations. Fundamentally, the vocabulary will seek to precisely describe the subject of scale-dependence (data, model parameters, model performance or model structure), and what component of scale it is sensitive to (grain, extent). I also make a distinction between two classes of scale-dependence: perceived scale-dependence (the appearance of scale-dependence as a result of imperfect data or models) and true scale-dependence (true changes with scale).

I begin by illustrating the need for these distinctions with a set of examples demonstrating the conditions under which certain kinds of scale-dependence can and cannot arise. I will then propose the taxonomy of scale-dependence, using a simple vocabulary that I believe is necessary and sufficient for clear communication of scale-dependence. Finally, I conclude with a brief examination of scale-dependence in biotic interactions, a topic that I think has suffered from unclear communication about what, exactly, is thought to be scale-dependent.

Examples

General methods

In these examples, I will use gridded surfaces that display spatial autocorrelation. Such a surface might represent soil nutrient concentrations, annual precipitation, a species' population density, or the pattern of a species' resource use intensity. Surfaces were created in R using the `gstat` package (Pebesma 2013) to generate random surfaces with known variogram properties. I used a nugget of 0 and three ranges (5, 15 and 45) to generate surfaces with different covariance structures. All variograms used an exponential model. Random realizations of these surfaces were obtained with the `predict.gstat()` function, on a regular 128×128 grid. Each realization was z-scaled (mean = 0, standard deviation = 1). Let λ_r indicate a random realization of such a surface where r indicates the range of the variogram. Throughout the manuscript, these surfaces will be referred to as 'spatially structured', with 'fine spatial structure' indicating a surface with a small variogram range (i.e. λ_5 has fine spatial structure [or small patch sizes] and λ_{45} has coarse spatial structure [or large patch sizes])

These gridded surfaces were then sampled with different sampling schemes using varying spatial grains and extents. Grain refers to the size of a sampling unit such as a pixel in a satellite image or a vegetation plot, while extent refers to the total area over which these units are distributed on the surface (Turner et al. 1989, Scheiner et al. 2000). Here, sampling units were always square and their sizes are specified by their side length as a fraction of the side length of the total surface. Extent was modified in two ways. In examples using a pair of sampling units, extent was increased by moving those units apart from one another along the surface, increasing the distance between them. In examples using more units, extent was modified by using various sizes of square subsets of the surface. In all examples, I used 100 replicate simulations, unless otherwise noted.

Example 1: measurements

Given a continuous spatial surface, we can make various measurements of that surface in plots of varying sizes, thereby altering spatial grain. What kind of measurements should change with grain size? The mean value within a plot will not change systematically, since the mean value of the entire surface is the expected value of a draw of any size from that surface. The within-plot variance, on the other hand, increases with increasing plot size (Fig. 1A), owing to spatial autocorrelation in the surface. The finer the spatial structure (i.e. the smaller the range of the variogram), the more rapidly within-plot variance increases. In the same way, as a pair of equal-sized sampling plots are moved apart on the surface (thereby increasing extent), the absolute difference in the mean values of the surface within those plots increases (Wiens 1989). This increase is rapid for surfaces with fine spatial structure (Fig. 1B, red lines) and gradual for those with coarse structure (Fig. 1B, blue lines). Grain size also influences this relationship, with larger grains producing smaller between-plot differences at a given distance (dashed compared to solid lines, Nekola and White 1999, Lennon et al. 2001, Keil et al. 2012). This distance-decay relationship is particularly pronounced for surfaces with fine spatial structure.

The difference in scaling between within-plot means and within-plot variance is a simple example of an important general phenomenon – the method that we use to aggregate a variable across different scales influences the scaling behavior we observe. Thus, it is not correct to ask whether a particular measurement is grain-dependent without also specifying how we intend to aggregate it across grain sizes (e.g. mean, variance, quantile, maximum, etc.).

The interaction between grain size and extent leads to an interesting property. As sampling plots are spread over a larger extent or become smaller-grained, the differences between them increase. The combined effect of changing grain size and spatial extent on between-plot differences can

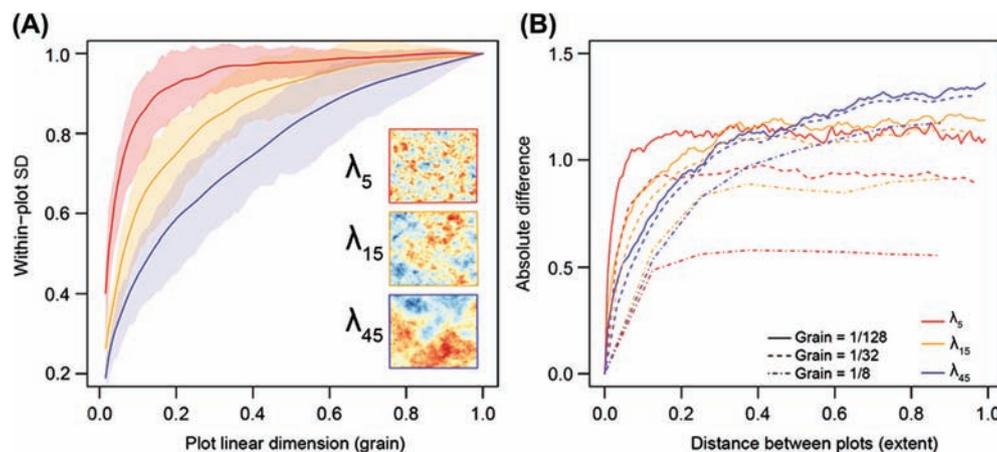


Figure 1. The relationships between grain size and within-plot variation (A) and extent and between-plot differences (B). Surfaces were simulated with fine, moderate or coarse spatial structure (λ_5 , λ_{15} , λ_{45} , examples in insets with colored boxes matching plotted curves). In (A), these surfaces were sampled with a series of nested square units ranging in grain size from 1/128 to 1 (relative to the side length of the entire surface). The lines show means of 1000 simulations, while the colored intervals show the interquartile range. In (B), pairs of plots with fixed size were moved apart from one another to generate increasing spatial extents. The lines show the mean absolute difference across 1000 simulations as a function of distance, surface spatial structure and grain size.

be visualized as a surface with isoclines of constant difference (Fig. 2). These isoclines describe a sort of equivalence between grain size and extent. On a λ_5 surface (Fig. 2A), grain size has a very large effect on between-plot difference, while extent is less important – thus a small increase in grain size requires a large increase in extent to offset it. Extent plays an increasingly important role as the spatial structure of the surface becomes coarser (λ_{45} , Fig. 2B). In this case, a relatively large increase in grain size is needed to offset a small increase in spatial extent.

Species richness represents an interesting special case of within-plot variation, measured as the number of classes (species) observed, rather than a continuous measure such as standard deviation (Connor and McCoy 1979, Palmer and White 1994). In general, as grain size increases, species richness increases for two major reasons (Scheiner et al. 2000). First, more individuals are sampled, which results in correspondingly more species being sampled. Second, a wider range of environmental conditions is sampled, so, assuming that species show varying environmental preferences, a wider range of species will be observed (Connor and McCoy 1979). The latter mechanism means that the rate of increase of species richness is related to the spatial structure of the environment – finer structure should contribute to more rapid increases in richness over small grain sizes (analogous to Fig. 1).

Example 2: relationships between pairs of variables

We can next ask how the relationship between spatially structured variables changes with grain and extent. When

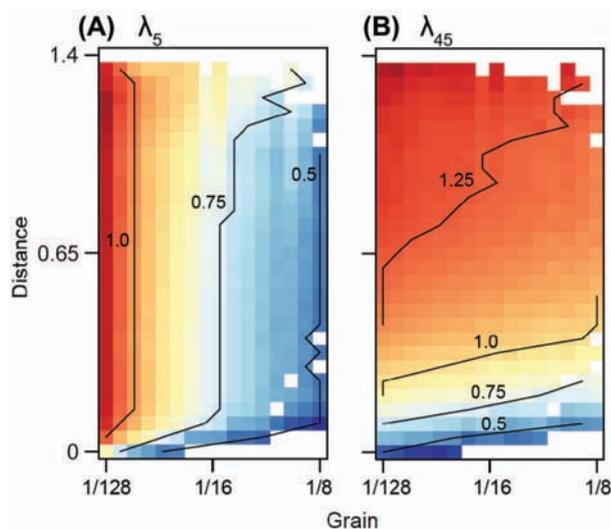


Figure 2. The relationship between grain size and spatial extent and between-plot differences. Given 100 λ_5 (A) or λ_{45} (B) surfaces, each was sampled at grain sizes ranging between 1/128 and 16/128 (1/8) in the linear dimension, across a wide range of extents (distance between a plot pair). The colors show the absolute difference between the plot mean values (red corresponds with large differences and blue with small). Note that the color scales differ between the two panels. Lines show isoclines of constant difference. With decreasing extent and increasing grain size, between-plot differences decrease. This increase is most rapid when increasing grain size when the surface shows fine spatial structure and most rapid for increasing extent when spatial structure is coarse.

arguing that the relationship between a pair of variables X and Y is scale-dependent, I suspect that most ecologists have in mind something like a regression relationship $Y = f(X) + \epsilon$, where something about the regression changes with grain size or extent. Three important changes that could occur are shifts in the coefficient estimates or their errors (model parameters), changes in the overall fit of the model (model performance), or changes in which variables are included in a model and the functional forms that are fit (model structure), though these alternatives are often not explicitly distinguished. Nevertheless, fundamentally different mechanisms can lead to these different types of scale-dependence. For example, limiting the extent of sampling an underlying linear relationship reduces the R^2 but does not bias the coefficient estimate (Fig. 3A).

For illustration, consider two scenarios. In the first, $X = \lambda_{45}$ and $Y = X + \epsilon$, where $\epsilon = \lambda_5$. In the second scenario, the spatial structures are reversed: $X = \lambda_5$ and $\epsilon = \lambda_{45}$. We can now ask how changing grain and extent affect the perceived relationship between X and Y (Fig. 4). Note that changes in the regression model are due only to changes in the spatial structure of X because in both cases $Y = \lambda_5 + \lambda_{45}$. I examined three grains, with linear dimensions of 1/128, 1/32 and 1/8, and three extents: 1/16, 1/4 and the entire surface, and ask whether changing the spatial structure of the predictor variable alters model parameters or performance.

The coefficient estimate is scale-independent. All coefficient estimates correctly center on 1 regardless of spatial structure, grain or extent. In general, and as expected, the best coefficient estimates (most tightly clustered around 1) are obtained with a large extent. Grain exerts relatively little influence on the distribution of coefficients, except as the grain size approaches the extent (Fig. 4).

On the other hand, model performance (here, R^2) is scale-dependent, increasing with grain size and extent in the first scenario and decreasing with grain size and extent in the second (Fig. 4). This occurs because the influence of the λ_5 noise in the first case declines as grain size increases, while increasing extent unveils more of the true linear relationship. Both contribute to higher R^2 . In the second case, R^2 declines with grain size because larger grains tend to smooth out the important fine structure in X , while larger extents introduce the full range of λ_{45} noise, increasing the influence of the noise over the signal.

The dependence of model performance on grain and extent has interesting consequences in applications involving multiple regression and model selection. Various model selection procedures such as stepwise or all-subsets selection eliminate variables from a model based on their contribution to a measure of model performance such as AIC (Symonds and Moussalli 2011). Thus, while the coefficient estimate for a particular variable might not change with scale, the probability that it will be included in the selected model can change. Thus, model structure can also be influenced by spatial scale.

Example 3: more complex relationships

In this example, I will consider relationships among an environmental variable (ENV) and interacting predator and

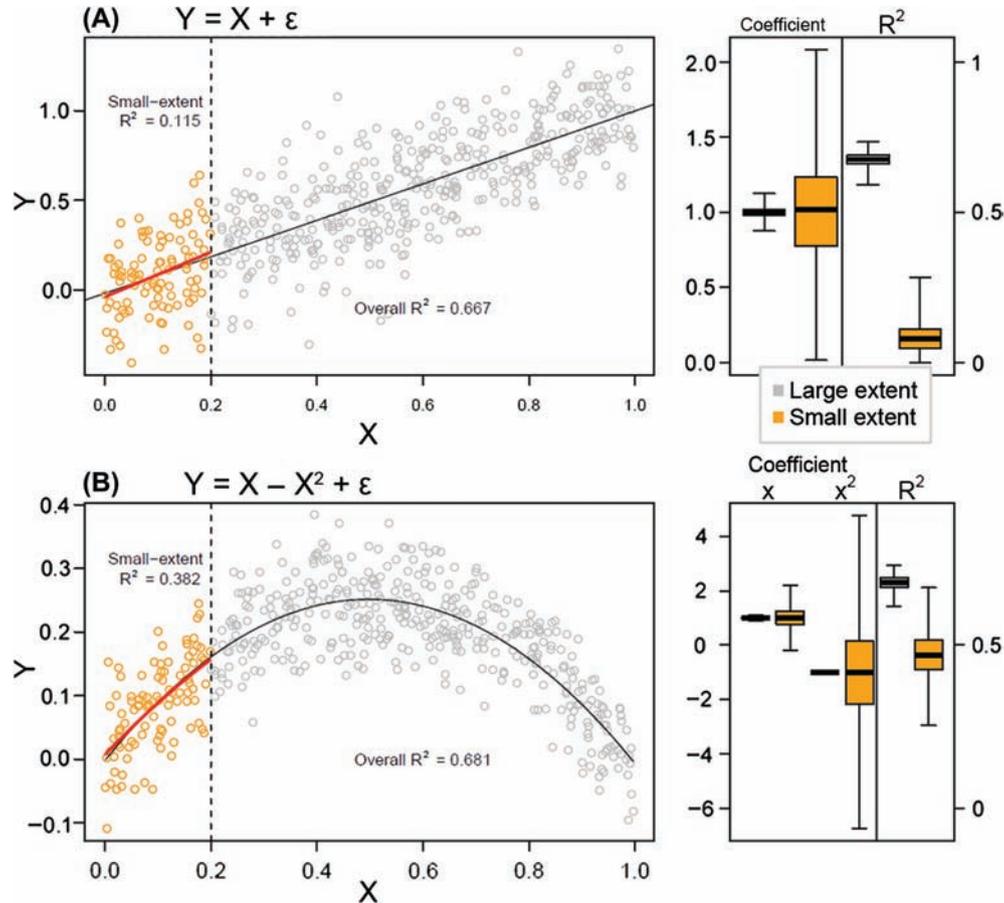


Figure 3. The effect of limiting the extent of sampling of the predictor variable on linear (A) and quadratic (B) regression. Given the full range of X (between 0 and 1), both linear and quadratic relationships are well detected, with coefficients correctly centered on 1 (A) and 1 and -1 (B), and high R^2 values. Limiting the extent of sampling of X to $(0, 0.2)$ (orange colors) does not bias parameter estimates, but does produce a large increase in uncertainty in the estimates and a reduction in R^2 . Thus, the coefficient estimate is not extent-dependent, while the explanatory power is. In the boxplots, the middle line indicates the median, the box shows the interquartile range and the whiskers show the full range of estimates. Grey boxes indicate the full extent and orange the limited extent across 1000 simulations.

prey species that respond to that variable. Predator abundance (PRED) was defined as $PRED = ENV + \epsilon_1$ and prey abundance (PREY) was $PREY = ENV - 0.5 \times PRED + \epsilon_2$ where ϵ_1 and ϵ_2 are spatially structured noise (λ_5, λ_{15} or λ_{45}). I then sampled ENV, PREY and PRED using grains with linear dimensions of $1/128$, $1/32$ and $1/8$ and asked if the relationship between PRED and PREY depends on grain size.

It is reasonable to think that it will. At large grain sizes, PRED and PREY might be positively associated, occupying areas with similar environmental conditions. However, at a fine grain containing limited environmental variation, more predators means fewer prey, leading to a negative correlation (Shea and Chesson 2002). Indeed, when $ENV = \lambda_{45}$ and ϵ_1 and $\epsilon_2 = \lambda_5$, this predicted dependence on grain size does appear (Fig. 5A). However, other variations are also possible. If all three surfaces are λ_{15} , there is no grain-dependence (Fig. 5B), while if $ENV = \lambda_5$ and ϵ_1 and $\epsilon_2 = \lambda_{45}$, the reverse pattern appears (Fig. 5C). Thus, depending on the spatial structure of the environment and noise, large or small grains can give the most accurate estimate of a biotic interaction.

Notably, though, all of these estimates are wrong! Large grains or small, none produced the correct estimate of the effect of predator on prey abundance (-0.5). All estimates were strongly biased towards zero. This problem arises because of the omission of a critical covarying variable from the model. When we supplement the $PREY = f(PRED) + \epsilon$ model with the environmental variable ($PREY = f(PRED, ENV) + \epsilon$), the coefficient estimate for the predator effect becomes correct. Further, it no longer depends on grain size, except that larger grains mean smaller sample sizes and therefore higher variance around the median estimate. Thus, we have to be very careful here to distinguish what an effect is from what we can detect. This is the distinction between true scale-dependence and perceived scale-dependence.

Another way to see this problem is that the simple linear regression of $PREY = f(PRED) + \epsilon$ violates an important assumption – the residuals are not spatially independent. Rather than correcting this problem by incorporating the environmental covariate (which is possible here, but probably not possible to do perfectly in most real applications), it could also be possible to remove the bias by using a spatial regression method, such as simultaneous

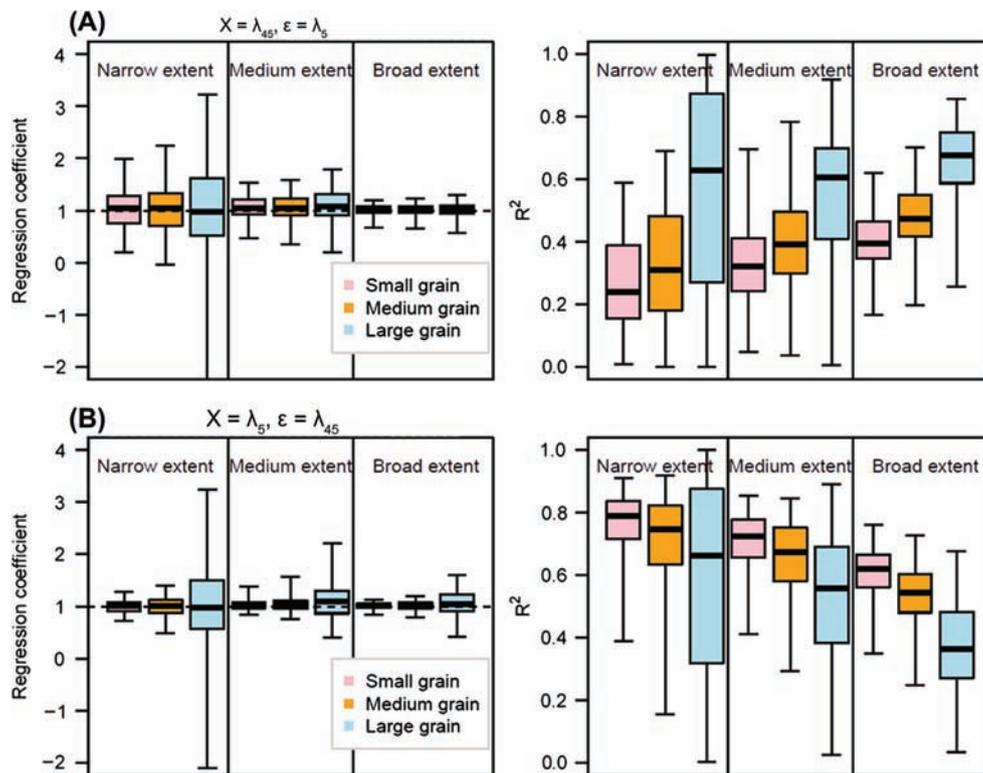


Figure 4. The effect of changing grain size and extent on the regression between spatially structured variables, where $Y = X + \epsilon$. In (A), X is λ_{45} and ϵ is λ_5 , while in (B) this is reversed. Each variable was sampled with narrow, medium and broad extents (using 1/16, 1/4 or the entire surface) and small, medium or large grains (linear dimensions of 1/128, 1/32 or 1/8 of the entire surface). In all cases, the estimated regression coefficients correctly centered on 1. However, the explanatory power of the model (R^2) was scale-dependent, increasing with grain size and extent in (A) and decreasing with grain size and extent in (B). This occurs because of the different spatial structures of X and ϵ in (A) and (B). The middle line in the boxplots shows the median, the boxes the interquartile range and the whiskers the full range across 100 simulations.

autoregressive models (SAR, Kissling and Carl 2008, Beale et al. 2010). Thus, I asked whether an SAR model could produce more accurate estimates of the true species interaction. I used error SAR models with rook's-case neighborhoods and row-standardized weighting, though results were consistent under alternative model specifications (Supplementary material Appendix 1). Fitting SAR models in the scenario where $ENV = \lambda_{45}$, $\epsilon_1 = \lambda_5$ and $\epsilon_2 = \lambda_5$ produced less biased coefficient estimates. For the moderate grain, standard linear models produced a model median slope of -0.032 , while SAR models produced a median of -0.351 . For the large grain, standard models had a median of 0.182 , while SARs gave -0.037 . For the small grain, fitting SAR models was computationally infeasible. SAR models are an imperfect solution, but may provide less biased coefficient estimates when the environmental covariates cannot otherwise be controlled.

Cases where species interactions can be confounded with environmental variations are common. In his groundbreaking paper on scale in ecology, Wiens' (1989) first example of scale-dependence gives several cases where shared environmental preferences over large scales appear to swamp the local effects of competition. Veech (2006) also provides an example of this situation, showing that positive associations in the distributions of potentially competing birds are more common than negative associations. This may be because

of shared responses to environmental variation, though no environmental covariates were considered in the study.

Example 4: true scale-dependence

If the above example illustrates perceived scale-dependence, what can lead to true scale-dependence? Consider two plant species, A and B. A is indifferent to the presence or absence of B, while B is both competitively suppressed and facilitated by A, but over different distances. An individual of species A reduces the nearby population of B (perhaps because A shades out B), while increasing the population at greater distances (perhaps because A supports a population of pollinators that also benefit species B, for related empirical examples, see van de Koppel et al. [2006] and Hegland [2014]). The population density surface of A (P_A) thus produces two relevant interaction surfaces – one competition surface (C_A) that is tightly constrained around the population of A, and one facilitation surface (F_A) that is loosely constrained around A's population. These interaction surfaces can be obtained by applying a moving window filter to P_A , where the window is narrow for the negative interaction and wide for the positive interaction.

Under these circumstances, the effect size of P_A on the population density of B (P_B) can depend on the grain

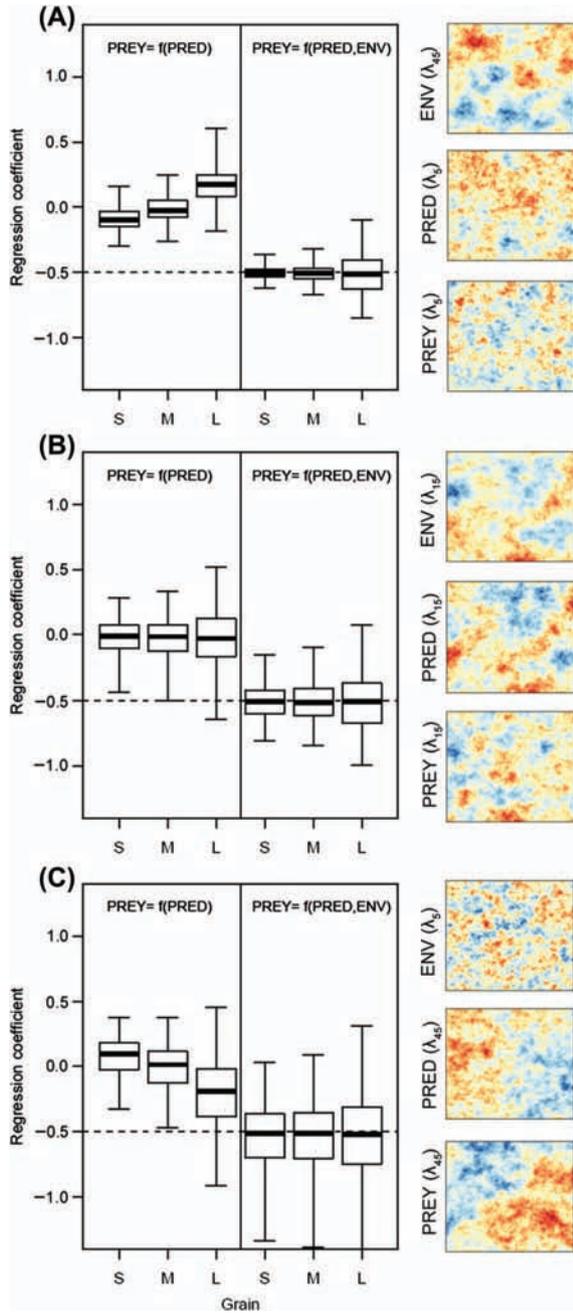


Figure 5. Relationships among simulated predator (PRED) and prey (PREY) densities in the presence of a shared environmental preference. Here, $PRED = ENV + \epsilon_1$ and $PREY = ENV - 0.5 \times PRED + \epsilon_2$. ENV and ϵ surfaces contained various degrees of spatial structure. In (A), ENV was λ_{45} , and ϵ_1 and ϵ_2 were λ_5 . Sampling this relationship with small (S, 1/128), medium (M, 1/32) or large (L, 1/8) grain sizes revealed a negative predator–prey relationship in small grains that graded into a positive relationship in large grains when the environment was not included in the regression relationship (left panels). However, when the environment was known and included, the correct regression slope of -0.5 (dotted line) was recovered (right panels). In (B), ENV, ϵ_1 and ϵ_2 were λ_{15} , and the coefficient estimates showed no grain-dependence. Finally, in (C), ENV was λ_5 and ϵ_1 and ϵ_2 were λ_{45} , leading to decreasing coefficient estimates with increasing grain size. Again, when the environment was known and incorporated in the models, there was no grain-dependence and coefficient estimates became unbiased. The middle line in the boxplots shows the median, the boxes the interquartile range and the whiskers the full range across 100 simulations.

size. Here, $P_A = \lambda_5$, C_A was averaged from P_A over 5×5 windows and F_A over 15×15 windows. Then, P_B was defined as $P_B = 5 \times F_A - 3.5 \times C_A + \epsilon$, where $\epsilon = \lambda_5$. I used three levels of grain size, with linear dimensions of 1/128 (small), 1/32 (medium) or 1/8 (large) of the surface edge length, and fit linear models according to $P_B = f(P_A)$, with each population variable averaged within plots of the appropriate size. Under these conditions, P_A is negatively related to P_B in small and medium grains, and positively related at large grains (Fig. 6). There is no environmental gradient – the scale-dependence in the relationship derives entirely from intrinsic characteristics of the species’ interactions. Hence, this is an example of true grain-dependence.

This example also illustrates the fine line between scale-dependence and scale-independence. Here, there was a true grain-dependent relationship between the population densities of species A and species B. However, if we had modeled the density of B as a function of the competitive intensity and facilitative intensity surfaces from A, there would be no grain-dependence.

Example 5: averaging over nonlinear functions

A very important kind of scale-dependence can arise when nonlinear relationships are averaged at different grain sizes (Chesson et al. 2004, Chesson 2012). In general, the average of a function is not the function of the average. For example, the logarithm of the mean of a vector of numbers is not the same as the mean of the logarithms. To illustrate this, consider a surface X with some spatial structure, and a surface $Y = X - X^2 + \epsilon$, where ϵ has some spatial structure. Y is a nonlinear function of X, so the average value of Y at some large grain size will generally not be the same as the value of the function evaluated for X aggregated at that same large grain. In fact, because the function is concave down, the average of the function is less than or equal to the function of the average (according to Jensen’s inequality, Chesson et al. 2004). This is illustrated in Fig. 7. Without any aggregation (grain size = 1/128), the correct parabolic relationship is fit, and the model R^2 is high. Aggregating to a larger grain sizes (1/8), however, leads to biased parameter estimates and smaller R^2 values. This effect is particularly pronounced when $X = \lambda_5$ and $\epsilon = \lambda_5$, because a larger grain size in this case corresponds with a wider sampling of environmental heterogeneity within a cell, and therefore a stronger effect of nonlinear averaging.

Nonlinear relationships are probably rather ubiquitous in nature, suggesting that this is likely to be a common source of true grain-dependence (Chesson 2012).

Example 6: unveiling nonlinear relationships

In example 2, I showed a case where changing the spatial extent influenced the explanatory power of a regression relationship but not its shape (the estimated coefficients correctly centered on one for all extents). It is also possible for changing extent to change the perceived shape of a relationship. This can occur when the relationship between a pair of variables is nonlinear. A limited extent that captures only

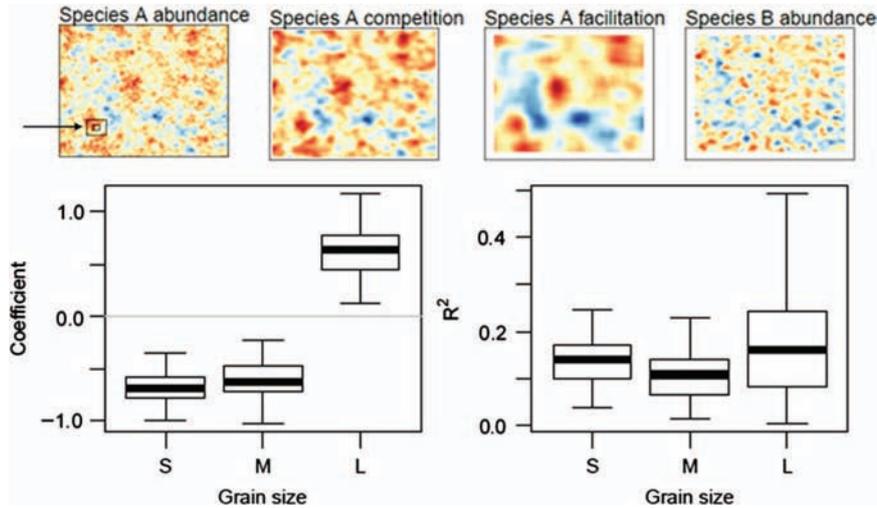


Figure 6. True scale-dependence in the relationship between abundances of two species. Species A both competes with and facilitates species B, but over different distances. Competition with A is limited to short distances (5 cell neighborhood, small square in first panel, indicated by arrow), while facilitation occurs over longer distances (15 cell neighborhood, larger square in first panel). In this case, a linear model of the population density of B (P_B) as a function of the density of A (P_A) shows a negative relationship at small and medium grain sizes (S, M, grain sizes of 1/128 and 1/32) and a positive relationship at large grain sizes (L, 1/8). The middle line in the boxplots shows the median, the boxes the interquartile range and the whiskers the full range across 100 simulations.

a small range in the predictor variable may only reveal part of the shape of a complex relationship. For example, species richness often shows a hump-shaped relationship with elevation (Rahbek 2005), yet incomplete sampling of the

elevational gradient (limited extent) can instead suggest a linear decrease with elevation. One can imagine that a limited extent obscures part of a relationship, while increasing the extent unveils it.

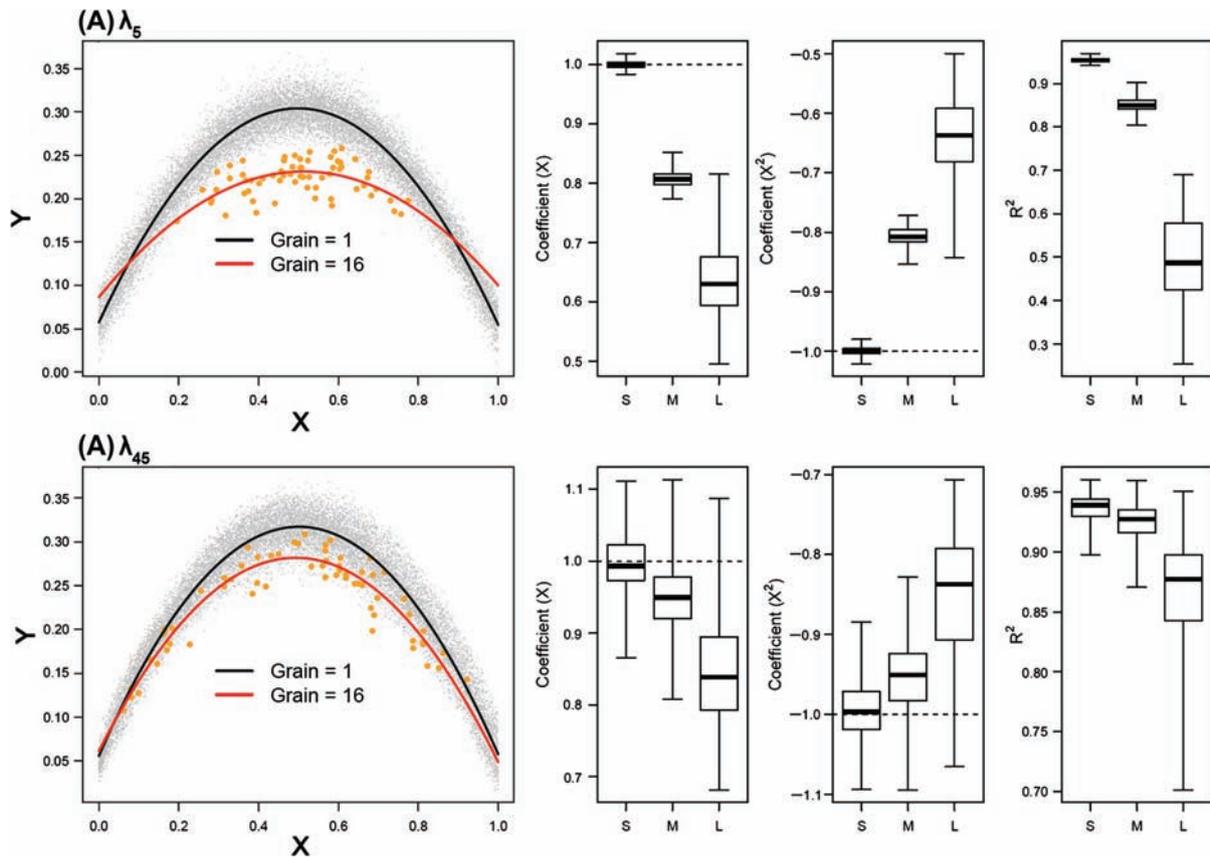


Figure 7. Illustration of scale-dependence through nonlinear averaging. In general for nonlinear functions, the average of a function is not the same as the function of an average. Here, a relationship of $Y = X - X^2$ flattens out as grain size increases, particularly for surfaces with fine spatial structure. The boxplots show the distribution of coefficients for X, X^2 and R^2 across 100 replicates. The middle line shows the median, the boxes the interquartile range and the whiskers the full range across 100 simulations.

This intuition, however, can be somewhat misleading. For example, if the true relationship is parabolic, this curvature can, in principle, be detected even with data from only part of one of the arms (Fig. 2B). The situation is actually quite similar to the linear variation described above (example 2), in that the coefficient estimates for the linear and quadratic portions of the model are unbiased even with a very limited extent (in this case correctly centering on 1 and -1 , respectively). However, the variation around these median values is large. Thus, there is no scale-dependence of the estimated model parameters, but there is an effect of the extent on the precision of the estimate, and on model R^2 .

Thus, if one has theoretical reasons to believe a relationship to be quadratic (or any other specific functional form), this relationship can be estimated without bias even given only a small portion of the full shape. It is, however, likely to be estimated with substantial error. Further, related to the discussion of model selection procedures above, if the non-linear form is not known in advance and one wishes to use an automatic method of determining whether a quadratic term is warranted, the extent matters a great deal. In this case, using the full extent where the hump-shaped relationship is clearly visible, the quadratic model yielded a lower AIC value than a linear model in 1000 out of 1000 instances, whereas the quadratic model was preferred for the limited extent in only 22% of cases.

Finally, if the non-linear pattern is more complicated, for example showing threshold changes (Toms and Lesperance 2003), then it will typically not be possible to use small extents to make inferences about the shape of relationships over larger extents.

Towards a taxonomy of scale-dependence

With these examples in place, I now seek to define the axes of spatial scale-dependence and work towards a formal vocabulary to describe them. One reason for presenting so many examples is that I hope to give a sense of the diversity of meanings currently encompassed by ‘scale-dependence’. It can mean that measurements of species richness increase with grain size, that a nonlinear relationship between elevation and species richness is obscured when the spatial extent is too small or that the R^2 of the relationship between the abundance of two species declines with increasing grain size, among other possibilities. These are all very different observations, so different in fact, that I think it does little good to call them all scale-dependence.

Thus, I propose a ‘taxonomy’ of scale-dependence, in analogy to standard systematic taxonomy. Ecologists have

long recognized that the phylogenetic scope of inference can be limited – this is a major reason that taxonomic names often appear in paper titles. I argue that we should give the same attention to different kinds of scale-dependence, to avoid the temptation to generalize from one kind to a fundamentally different kind. The examples above illustrate three major distinctions, specification of which will, I believe, lead to a clear and unambiguous description of spatial scale-dependence. These are the scale component, the subject of scale-dependence, and its class (Table 1).

Scale component

Many authors have emphasized the importance of understanding the influence of different scale components (Turner et al. 1989, Wiens 1989, Turner 1990, Scheiner et al. 2000). Still it bears repeating that some things vary with grain and not extent, some things vary with extent and not grain, and still others vary in opposite ways between the two. They are not interchangeable concepts. I therefore suggest that, whenever possible, we specify what we mean by saying ‘grain-dependent’ or ‘extent-dependent’ in place of the less informative ‘scale-dependent’.

Subject

By subject, I mean the kind of thing that is scale-dependent. I focus on the distinction between scale-dependence of data and scale-dependence of models. Data is scale-dependent when measured values or summary statistics change as a function of sampling scale (grain or extent). For example, species richness increases with increasing grain, while the dissimilarity between pairs of plots generally increases with extent.

Models are scale-dependent when estimated parameters, model performance or model structure varies with grain size or extent. Scale-dependent model parameters can appear in regression relationships where slope coefficients are sensitive to grain size (such as in example 4 above). They could also arise in mechanistic models, if, for instance, a population growth rate (r) depends on grain size. Scale-dependence of model performance could include R^2 , out-of-sample predictive performance or other related measures. There are numerous empirical examples of shifts in both model performance and model parameters with grain size (Hamer and Hill 2000, Scheiner et al. 2000, Rahbek and Graves 2001, Chase and Leibold 2002, Brown and Peet 2003, Belmaker and Jetz 2011, Sandel and Svenning 2013), though extent seems to have received rather less attention (Rahbek 2005,

Table 1. Summary of the categories in the taxonomy of scale-dependence.

Question	Category in taxonomy	Informal definition	Empirical examples
Data or model? Model parameter, performance or structure?	Subject	What changes with scale?	Palmer and White 1994, Chase and Leibold 2002, Davies et al. 2005
Grain or extent?	Component	What aspect of scale is it sensitive to?	Turner et al. 1989, Wu et al. 2002, Sandel and Corbin 2010
True or perceived?	Class	The result of a model or observability problem or a real effect?	van de Koppel et al. 2006, Aue et al. 2012, Hegland 2014

Sandel and Corbin 2010). Scale-dependence of model structure occurs when the variables included in a model, or the functional forms used to describe their relationships, vary with grain size or extent. For example, limiting extent can lead to incorrectly modeling a quadratic relationship as linear (example 6 above).

Class

Data can be scale-dependent because the measured property truly varies with scale, or because observability of the property depends on scale. I propose that the first be called true scale-dependence of data, and the second perceived scale-dependence. Measures of species richness across varying grains provides an example of both true and perceived classes. On one hand, species richness does show a true increase with grain size. On the other hand, at very large grain sizes (say, 10 km²), it is not typically possible to observe all species, such that the degree to which a survey underestimates true richness is a function of grain size. Similar problems occur when assessing species occupancy, where methods exist to correct for errors of non-detection (MacKenzie et al. 2002).

Similarly, models may be scale-dependent because of a fundamental change in the underlying relationship with scale (as has been proposed for the productivity–diversity relationship, for example [Chase and Leibold 2002]), or because imperfect models lead to confounding effects that appear as scale-dependence. Thus, the distinction between true and perceived classes can be applied to models as well. An example of perceived scale-dependence was shown in example 3 above, where the effect size of a relationship between a pair of species appeared to change with grain size, but this relationship reflected a problem with the statistical model, not a feature of the biotic interaction itself. On the other hand, a species pair showing competition over short distances and facilitation over longer distances can show true scale-dependence (example 4, van de Koppel et al. 2006). In the case of perceived scale-dependence, the disappearance of one species would have scale-invariant consequence for the population of the other, while in true scale-dependence, the consequences would be scale-dependent.

Unfortunately, in practice it is very difficult to distinguish perceived and true scale-dependence. In general, it will require some external information, such as a manipulative experiment or knowledge about possibly important missing covariates. In purely correlative studies, however, the possibility of perceived scale-dependence raises an important warning flag. The critical point is that scale-dependent behavior from a model might not tell us anything important about the system being modeled, only that our model is imperfect.

Relationships to scale taxonomies in other fields

Having proposed a system for describing scale-dependence in ecology, I now take a step back to consider the vocabulary of spatial scale and scale-dependence in other fields.

A useful review of the history and terminology of spatial scale across the social and natural sciences was provided by Marceau (1999). Of particular importance in this history is the modifiable areal unit problem (MAUP; Openshaw 1977, 1984, Fotheringham and Wong 1991). Building on earlier work showing changes in correlation coefficients under spatial aggregation of the variables of interest (Gehlke and Biehl 1934), the MAUP expresses the difficulty that results are often scale-dependent, yet our choices of scales is often purely operational (based, for example, on a the grain size of a satellite image). For example, a study of the MAUP in the grain-dependence of multiple regression concluded rather discouragingly that the MAUP results in ‘highly unreliable results in the multivariate analysis of data drawn from areal units’ (Fotheringham and Wong 1991, p. 1041).

Much of the work on the MAUP derives from remote sensing research (Marceau and Hay 1999). In that field, terminology is quite close to that proposed here, except that grain size is sometimes called ‘resolution’ or ‘support’, and extent may simply be referred to as ‘area’ (Cressie 1993, Nekola and White 1999). A different kind of vocabulary related to spatial scale comes from signal processing and the decomposition of complex patterns into combinations of simpler patterns with different wavelengths (or frequencies) and amplitudes. The classic version of this is Fourier analysis, which decomposes a pattern into a combination of sine waves. Related methods include principal coordinates of neighborhood matrices (PCNM, Borcard et al. 2004) and wavelet analysis (Keitt and Urban 2005). The mathematics of geometry also has its own language of scale, based heavily on research on fractals beginning with Mandelbrot (Mandelbrot 1967). Fractal dimensions describe a sort of scale-dependence of measurements, in which the measured length of a complex curve (for example, a coastline) depends on the length (i.e. grain size) of the measuring stick. Self-similarity describes a kind of scale-independence, in which one can continuously zoom in to a geometric object (such as the famous Koch snowflake, Sugihara and May 1990) without changing the perceived structure of the object. Both concepts have seen some adoption in ecology (Sugihara and May 1990, Harte et al. 1999).

Scale-related terms from other fields have infiltrated ecology through various subfields, yielding a somewhat larger-than-necessary, though still largely consistent vocabulary. A noteworthy difference, however, is in the use of ‘scale-dependence’. Some reserve the term for cases where ‘the functioning of a system varies over scales to the point where scales of observation divorced by an order of magnitude in resolution or extent can be treated as essentially independent’ (Manson 2008, p. 779). This is a stronger version of scale-dependence than is generally used by ecologists, who often simply wish to say that something changes across scales. An example of this kind of strong scale-dependence can be found in statistical mechanics, which scales from the microscopic behavior of particles to the macroscopic behavior of large collections of particles (Gould and Tobochnik 2010). The behavior of individual molecules is so far divorced from the aggregate properties of a volume of gas that they are described, not only by different models, but by wholly different state variables (position and velocity versus pressure, temperature and volume in the case of the ideal gas law).

Across the social and natural sciences, there seems to be an emerging consensus that analyzing patterns across multiple spatial scales may be the best solution to the MAUP (Marceau 1999). This viewpoint appears to be becoming widespread in ecology, with the recognition of the ubiquity of scale-dependence and an increasing number of studies focused on changes in patterns across spatial scales (Sandel and Smith 2009). Jelinski and Wu (1996) provide a perspective on the MAUP similar to that advocated here, that it is not strictly speaking a 'problem', but rather a real feature of systems with complex hierarchical structure, carrying 'critical information needed to understand the structure, function and dynamics' of these systems (140).

Scale-dependence of biotic interactions

I am particularly interested in ecologist's ideas about the scale at which biotic interactions matter. The claim that biotic interactions primarily matter at small scales has almost become axiomatic (Huston 1999, Pearson and Dawson 2003, Willig et al. 2003, McGill 2010). This generalization is at best incomplete. It could mean that 1) the explanatory power of biotic interactions decreases as extent increases, 2) the perceived effect size of the interaction declines with increasing grain size because the relationship becomes swamped by unmeasured environmental covariates or 3) the true effect size declines towards zero as grain increases, among numerous other possible meanings. These are very different statements, and as the examples above show, can arise for different reasons. Finally, we have not specified what biotic interactions are supposed to matter for. Do we mean that biotic interactions matter little for the abundance of particular species, for the distribution of a species, for species richness, or for net primary productivity? For example, California has been invaded by more than 1000 species of plants, and has lost only 14 native species (Seabloom et al. 2006). Thus, competition with invasive species has caused at most a rather modest reduction in native species richness at the grain size of the state. However, many native species have experienced marked population declines at the state level because of competition with invasive species (D'Antonio et al. 2007). In this case, the effect of competition at large grain is clear for population sizes, but minor for species richness.

Somehow, the ecological culture has put the onus of proof on demonstrating that biotic interactions do matter at large scales, a task that is now being taken up (Wisz et al. 2013). How did we get there? Why is the common wisdom that they do not matter at large scales? One common argument is that interactions are pairwise things (between a wolf and an elk, for example), and that these pairwise things are inherently local. For example, McGill (2010) notes that 'it is difficult to imagine how the interaction between two birds can be influential at large scales' (p. 576). More specifically, if species A and B compete via resource depletion, an individual of species A can only deplete resources within some patch, therefore having no effect on individuals of B that are further away. Of course that is true, but it is not what matters.

Rather, we need to consider the entire surface of resource depletion generated by all individuals of species A. This surface is a joint function of the patch size of resource depletion by an individual and the spatial distribution of individuals of species A. Some species are relatively uniformly distributed (tending to produce rather smooth resource use surfaces), while others are extremely patchy (tending to produce very heterogeneous resource use surfaces) (Seidler and Plotkin 2006). These different patterns have very different consequences for the grain sizes and extents where biotic interactions will have most explanatory power (e.g. Fig. 5). For interactions to matter at large scales, it is not required that individuals interact over large scales, but only that the surface describing total interactions is variable over large scales, in the same way that the influence of any one raindrop is spatially restricted but the total effect of precipitation variation has large-scale ecological consequences.

Besides the 'pairwise interactions are local' argument, others might have in mind something like the situation illustrated in example 3 (Fig. 5A). In this case, the overwhelming effect of the environment in large plots swamped the effect of interaction between two species. Thus, the smaller a plot, the more accurate was the estimate of the biotic interaction. There are two major problems with this generalization revealed by this simple example. First, the perceived scale-dependence was a result of our model being incomplete rather than a true scale-dependent effect of predators on prey. Completing the model by adding the environment led to unbiased, scale-independent estimates of the effect of predators on prey. Of course, in real applications, we typically have not measured all of the environmental variables that matter, so this kind of correction will not usually be possible. That does not change the fact that a scale-dependent relationship between two species does not necessarily tell us anything about the nature of the interaction between the two; it may simply indicate that there is an important environmental variable missing from the model. Second, the generalization that small plots give better estimates of biological interactions only holds when the spatial structure of the missing environmental variable is coarser than noise in the species distributions.

Thus, I argue that 1) generalizations about the scales at which biotic interactions matter have suffered so far from a lack of specification about what they should matter for and how, ambiguities that should be resolved by following a more formal approach to discussing scale-dependence, and 2) the theoretical basis for the claim is weak. Finally, in a recent review on the topic, Wisz et al. (2013) provided numerous examples of cases where biotic interactions matter for the distribution of species at large extents and grain sizes. It is time to stop assuming that biotic interactions only matter at small scales.

Conclusion

Spatial scale-dependence is in fact a cluster of loosely related concepts, arising through a variety of effects. While it is a ubiquitous feature of many natural and social systems, it is not magic – some mechanism must be responsible for

data or models changing across scales. To move ecology forward in the face of scale-dependence, identifying and focusing on these mechanisms is likely to be productive and promises to provide more fundamental understanding and improved generalizations about ecological systems. This can only be realized with clear communication and distinctions between fundamentally different kinds of scale-dependence. The taxonomy proposed here provides such a way forward, by specifying the component, subject and class of scale-dependence.

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References

- Aue, B. et al. 2012. Distance weighting avoids erroneous scale effects in species-habitat models. – *Methods Ecol. Evol.* 3: 102–111.
- Beale, C. M. et al. 2010. Regression analysis of spatial data. – *Ecol. Lett.* 13: 246–264.
- Belmaker, J. and Jetz, W. 2011. Cross-scale variation in species richness–environment associations. – *Global Ecol. Biogeogr.* 20: 464–474.
- Borcard, D. et al. 2004. Dissecting the spatial structure of ecological data at multiple scales. – *Ecology* 85: 1826–1832.
- Brown, R. L. and Peet, R. K. 2003. Diversity and invisibility of southern Appalachian plant communities. – *Ecology* 84: 32–39.
- Chase, J. M. and Leibold, M. A. 2002. Spatial scale dictates the productivity–biodiversity relationship. – *Nature* 416: 427–430.
- Chave, J. 2013. The problem of pattern and scale in ecology: what have we learned in 20 years? – *Ecol. Lett.* 16: 4–16.
- Chesson, P. 2012. Scale transition theory: its aims, motivations and predictions. – *Ecol. Complex.* 10: 52–68.
- Chesson, P. et al. 2004. Scale transition theory for understanding mechanisms in metacommunities. – In: Holyoak, M. et al. (eds), *Metacommunities: spatial dynamics and ecological communities*. Univ. of Chicago Press, pp. 279–306.
- Connor, E. F. and McCoy, E. D. 1979. The statistics and biology of the species–area relationship. – *Am. Nat.* 113: 791–833.
- Cressie, N. A. 1993. *Statistics for spatial data*. – Wiley.
- D’Antonio, C. M. et al. 2007. Ecology of invasive non-native species in California grassland. – In: Stromberg, M. et al. (eds), *California grasslands*. Univ. of California Press, pp. 67–83.
- Davies, K. F. et al. 2005. Spatial heterogeneity explains the scale-dependence of the native–exotic richness relationship. – *Ecology* 86: 1602–1610.
- Fotheringham, A. S. and Wong, D. W. S. 1991. The modifiable areal unit problem in multivariate statistical analysis. – *Environ. Plann. A* 23: 1025–1044.
- Gehlke, C. E. and Biehl, K. 1934. Certain effects of grouping upon the size of the correlation coefficient in census tract material. – *J. Am. Stat. Assoc. Suppl.* 29: 169–170.
- Gould, H. and Tobochnik, J. 2010. *Statistical and thermal physics with computer applications*. – Princeton Univ. Press.
- Hamer, K. C. and Hill, J. K. 2000. Scale-dependent effects of habitat disturbance on species richness in tropical forests. – *Conserv. Biol.* 14: 1435–1440.
- Harte, J. et al. 1999. Self-similarity in the distribution and abundance of species. – *Science* 284: 334–336.
- Hegland, S. J. 2014. Floral neighborhood effects on pollination success in red clover are scale-dependent. – *Funct. Ecol.* 28: 561–568.
- Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. – *Oikos* 86: 393–401.
- Jelinski, D. E. and Wu, J. 1996. The modifiable areal unit problem and implications for landscape ecology. – *Landscape Ecol.* 11: 129–140.
- Keil, P. et al. 2012. Patterns of beta diversity in Europe: the role of climate, land cover and distance across scales. – *J. Biogeogr.* 39: 1473–1486.
- Keitt, T. H. and Urban, D. L. 2005. Scale-specific inference using wavelets. – *Ecology* 86: 2497–2504.
- Kissling, W. D. and Carl, G. 2008. Spatial autocorrelation and the selection of simultaneous autoregressive models. – *Global Ecol. Biogeogr.* 17: 59–71.
- Lennon, J. J. et al. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. – *J. Anim. Ecol.* 70: 966–979.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. – *Ecology* 73: 1943–1967.
- MacKenzie, D. I. et al. 2002. Estimating site occupancy rates when detection probabilities are less than one. – *Ecology* 83: 2248–2255.
- Mandelbrot, B. 1967. How long is the coast of Britain? Statistical self-similarity and fractional dimension. – *Science* 156: 636–638.
- Manson, S. M. 2008. Does scale exist? An epistemological scale continuum for complex human–environment systems. – *Geoforum* 39: 776–788.
- Marceau, D. J. 1999. The scale issue in social and natural sciences. – *Can. J. Remote Sens.* 25: 347–356.
- Marceau, D. J. and Hay, G. J. 1999. Remote sensing contributions to the scale issue. – *Can. J. Remote Sens.* 25: 357–366.
- McGill, B. J. 2010. Matters of scale. – *Science* 328: 575–576.
- Nekola, J. C. and White, P. S. 1999. The distance decay of similarity in biogeography and ecology. – *J. Biogeogr.* 26: 867–878.
- Openshaw, S. 1977. A geographical solution to the scale and aggregation problems in region-building, partitioning and spatial modelling. – *Inst. Br. Geogr. Trans. New Ser.* 2: 459–472.
- Openshaw, S. 1984. *The modifiable areal unit problem*. – CATMOG 38, GeoBooks, Norwich, England.
- Palmer, M. W. and White, P. S. 1994. Scale dependence and the species–area relationship. – *Am. Nat.* 144: 717–740.
- Pearson, R. G. and Dawson, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? – *Global Ecol. Biogeogr.* 12: 361–371.
- Pebesma, E. 2013. *gstat 1.0*. – <<http://cran.r-project.org/web/packages/gstat/index.html>>.
- Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. – *Ecol. Lett.* 8: 224–239.
- Rahbek, C. and Graves, G. R. 2001. Multiscale assessment of patterns of avian species richness. – *Proc. Natl Acad. Sci. USA* 98: 4534–4539.
- Sandel, B. and Smith, A. B. 2009. Scale as a lurking factor: incorporating scale-dependence in experimental ecology. – *Oikos* 118: 1284–1291.
- Sandel, B. and Corbin, J. D. 2010. Scale, disturbance and productivity control the native–exotic richness relationship. – *Oikos* 119: 1281–1290.

- Sandel, B. and Svenning, J.-C. 2013. Human impacts drive a global topographic signature in tree cover. – *Nat. Communications* 4: 2474.
- Scheiner, S. M. et al. 2000. Species richness, species–area curves and Simpson’s paradox. – *Evol. Ecol. Res.* 2: 791–802.
- Schneider, D. C. 2001. The rise of the concept of scale in ecology. – *BioScience* 51: 545–553.
- Seabloom, E. W. et al. 2006. Human impacts, plant invasion and imperiled plant species in California. – *Ecol. Appl.* 16: 1338–1350.
- Seidler, T. G. and Plotkin, J. B. 2006. Seed dispersal and spatial pattern in tropical trees. – *PLoS Biol.* 4: e344.
- Shea, K. and Chesson, P. 2002. Community ecology theory as a framework for biological invasions. – *Trends Ecol. Evol.* 17: 170–176.
- Sugihara, M. and May, R. M. 1990. Applications of fractals in ecology. – *Trends Ecol. Evol.* 5: 79–86.
- Symonds, M. R. E. and Moussalli, A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion. – *Behav. Ecol. Sociobiol.* 65: 13–21.
- Toms, J. D. and Lesperance, M. L. 2003. Piecewise regression: a tool for identifying ecological thresholds. – *Ecology* 84: 2034–2041.
- Turner, M. G. 1990. Spatial and temporal analysis of landscape pattern. – *Landscape Ecol.* 4: 21–30.
- Turner, M. G. et al. 1989. Effects of changing scale on the analysis of landscape pattern. – *Landscape Ecol.* 3: 153–163.
- van de Koppel, J. et al. 2006. Scale-dependent interactions and community structure on cobble beaches. – *Ecol. Lett.* 9: 45–50.
- Veech, J. A. 2006. A probability-based analysis of temporal and spatial co-occurrence in grassland birds. – *J. Biogeogr.* 33: 2145–2153.
- Wiens, J. A. 1989. Spatial scaling in ecology. – *Funct. Ecol.* 3: 385–397.
- Willig, M. R. et al. 2003. Latitudinal gradients in biodiversity: pattern, process, scale and synthesis. – *Annu. Rev. Ecol. Evol. Syst.* 34: 273–309.
- Wisz, M. S. et al. 2013. The role of biotic interactions in shaping distributions and realized assemblages of species: Implications for species distribution modelling. – *Biol. Rev.* 88: 15–30.
- Wu, J. et al. 2002. Empirical patterns of the effects of changing scale on landscape metrics. – *Landscape Ecol.* 17: 761–782.

Supplementary material (Appendix ECOG-01034 at <www.ecography.org/readers/appendix>). Appendix 1.