

What kind of spatial and temporal details are required in models of heterogeneous systems?

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Spatial and temporal heterogeneity can make ecological systems hard to understand and model. We propose a simple classification of the types of spatial and temporal complexity contained in ecological systems, and describe the kinds of data and models needed to account for each. We classify ecological systems by the presence of heterogeneity at the scale of study, the nature of their dynamics (linear vs non-linear), attributes of the patches that constitute the heterogeneous system, and the presence and directionality of interactions among patches. Heterogeneity in space and time are nearly equivalent in our framework. Advanced modeling skills are necessary to create appropriate mathematical representations of highly complex systems (with non-linear dynamics, patches with more than one kind of important attribute, or interactive patches). Simple models can work well when the scale of heterogeneity is much finer than the scale of observation, when low precision is sufficient, when patches interact only weakly, or when empirical approaches are used to fit functions and constants. Having a way to classify complexity in space and time in ecological systems should help ecologists to select modeling approaches consistent with their abilities and goals.

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On a popular children's TV show, Bill Nye (The Science Guy) dumps a burger, fries, a coke, and a milkshake into a blender, hits the "puree" button, then drinks the resulting soup (ugh, gross). Although the soup that comes out of the blender is in some sense exactly the same as the food that went in, it is clear from the comments of children that they think the blending process produced fundamental, important changes in the food. Historically, ecologists have likewise used conceptual and mathematical blenders to reduce the spatial and temporal heterogeneity in ecological systems by averaging over various scales of time and space. There are several reasons why ecologists like to hit the "puree" button: (1) most ecologists probably find it easier to conceptualize relatively simple systems; (2) mathematical models of homogeneous systems generally

are much more tractable than those of heterogeneous systems; (3) it is simpler to relate a small-scale experiment to a homogeneous system than to a heterogeneous system; (4) our measuring instruments often cannot resolve heterogeneity, especially at time and space scales far from those of human perception; (5) ecologists have had some success with simple, averaged models.

In what circumstances are "pureed" ecological models that are averaged over space or time likely to adequately represent nature, which is heterogeneous over space and time? When are models that explicitly consider spatial and temporal patchiness likely to be needed? What kind of detail must these models incorporate? Here, we use a simple classification of spatial and temporal complexity in ecosystems to answer these questions.

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Spatial complexity in ecosystems

Ecosystems may possess several more or less distinct kinds of spatial complexity. We briefly discuss the kinds of data or models that might be needed to capture each kind of spatial complexity. Of course, spatial complexity possessed by a system depends on the question or process being considered – a system that is spatially complex with respect to one process may be homogeneous with respect to another. For example, the layers of a stratified lake may have different temperatures but not calcium concentrations. Further, real ecological systems usually contain a mixture of several kinds of spatial complexity rather than purely expressing of one kind of complexity. Therefore, we do not expect real ecological systems to map one-to-one onto the model systems we describe.

Homogeneous systems

In the simplest case, the system is spatially homogeneous (Fig. 1). Obviously, models of such systems need not include any spatial information; a measurement of variables at a single point in the system is an adequate description of the system. While it might seem that few ecological systems fall into this category, it is not necessary for a system to be literally homogeneous for it to be treated as homogeneous. All that is required is that controlling and response variables not vary at spatial scales at or coarser than the scale (grain size) of measurement or analysis. If the scale of variation is much finer than the scale of measurement, then the system is practically homogeneous. For example, if primary production is studied at a scale of 1 m², then a well fertilized, level lawn may be nearly homogeneous, and if production is studied at a scale of 1 ha, some forests may be nearly homogeneous over large areas. If

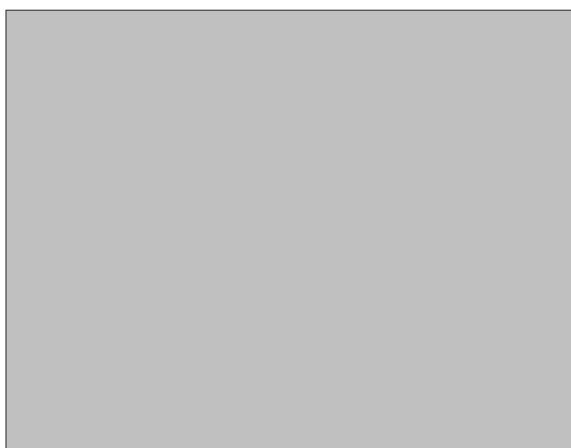


Fig. 1. A homogeneous system.

production is studied at fine scales, both systems are heterogeneous.

Heterogeneous systems with non-interacting patches and linear dynamics

Slightly more complex is a system containing multiple patches that do not interact with one another and which is governed by linear processes (Fig. 2). As long as all controlling functions are linear and (if multiple) do not interact with one another, the heterogeneity in this system can be dealt with satisfactorily by using a model based on the mean state of the variables, which gives the same numerical result as a spatially explicit model. Ecological systems probably aren't literally linear very often, but may be treated as linear in special cases. Even highly non-linear functions may be treated as linear over short ranges of the controlling variables. As long as controlling variables do not vary over wide ranges in the area of study, then the governing equations may be treated as linear, and mean values of the controlling variables will suffice to model the behavior of the system. If controlling variables vary over wider ranges or interact with one another, then non-linearities will come into play, and a model based on the mean values of variables will fail.

Heterogeneous systems with non-interacting patches and non-linear dynamics

Next, we may consider a system of multiple, non-interacting patches, but which is governed by non-linear dynamics (Fig. 3). A process with non-linear dynamics will produce different results in a heterogeneous system than in a homogeneous system with the same average characteristics. Consider a simple exam-

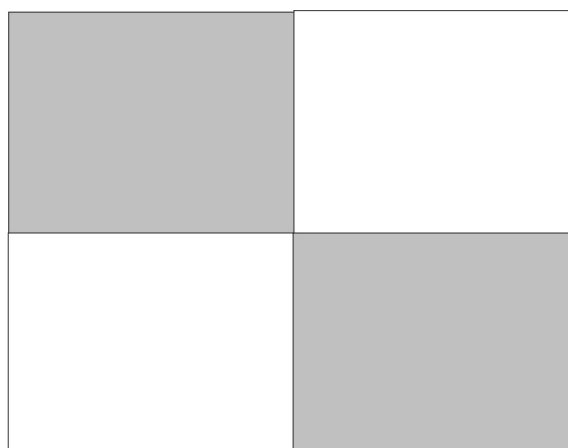


Fig. 2. A heterogeneous system with no interactions between patches, in which all governing functions are linear.

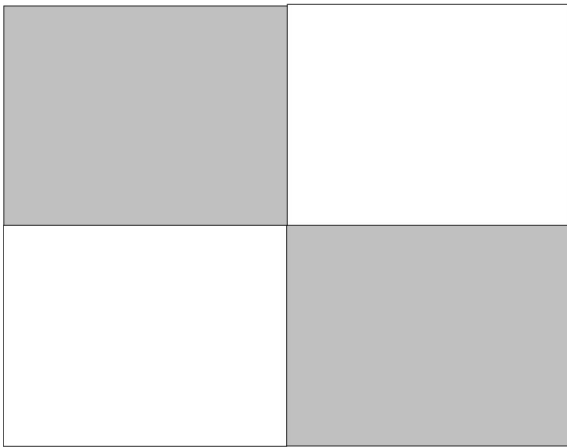


Fig. 3. A heterogeneous system with no interactions between patches, in which governing functions are non-linear.

ple in which the patches shown in Fig. 3 represent areas of shallow water (say 1 m deep) and deep water (say 15 m deep) in a lake. Light penetration through water is non-linear ($I_z = I_0 e^{-\eta z}$, where I_z and I_0 are the light levels at depth z and the water's surface, respectively, and η is the extinction coefficient; Wetzel 2001), so the average level of light reaching the sediments of this peculiar lake is not the same as the level of light that reaches the sediments at its average depth. (Suppose $I_0 = 100$ and $\eta = 0.5/\text{m}$. The average light level at the bottom of the lake is $0.5 \times 100e^{-0.5 \times 1} + 0.5 \times 100e^{-0.5 \times 15} = 30$, while the light level at the average depth is $100e^{-0.5(0.5 \times 1 + 0.5 \times 15)} = 1.8$). Likewise, the photosynthesis–irradiance curve for aquatic vegetation is non-linear (Harley and Findlay 1994), so that the average photosynthetic rate of plants in the lake is not the same as the photosynthetic rate at the average light intensity reaching the lake bottom. An estimate of the photosynthesis of submersed aquatic vegetation based on the light penetration at the average depth of the lake would be grossly incorrect (in fact, it would be zero). Instead, to adequately estimate photosynthesis of submersed aquatic plants, one needs to know the distribution of water depths (not just the average water depth), as well as the shapes of the light extinction and P-I curves. The heterogeneity of water depths is thus of central importance to the correct solution of the problem. There are many other ecological examples. In particular, non-linearities arise very commonly in ecological systems in cases where the response variable is controlled by two or more governing variables that interact.

Generally, a model to predict the behavior of a system with noninteracting patches and non-linear dynamics must include information on the frequency distributions of variables, rather than just the mean value of variables (cf. King's 1991 "extrapolation by expected value"). If multiple independent variables jointly gov-

ern the process under study, the model will need information on the joint frequency distributions of these variables. Such data may be simple to collect (a bathymetric curve for a lake) or require great effort and expense (especially where the joint distribution of two or more variables is required). As non-linearities are very common in ecological relationships (e.g. light penetration, foraging behavior, nutrient uptake, interactive independent variables), many ecological problems will not be amenable to homogeneous models. Presumably, the more numerous the non-linearities involved in an ecological process and more non-linear they are, the more likely that a homogeneous model will fail.

Heterogeneous systems with non-interacting patches that have different attributes

Most often, patches are classified on the basis of a single attribute (e.g. vegetation type, soil type, water depth). However, a process under study may depend on attributes of a patch other than the one used for patch classification (Fig. 4). Probably the most obvious example is patch size. The suitability of a habitat for an organism may well depend on its size as well as its identity. For instance, if the gray patches in Fig. 4 are construed as oceanic islands, only the largest islands may be able to sustain viable populations of a species. Allan et al. (2003) provided an interesting example of size-dependence, in which the risk of contracting Lyme disease in a mixed suburban landscape was shown to be a strong function of woodlot size. Lyme disease risk could not be adequately predicted by knowing the amount of forest cover, but required knowledge of patch size distribution. Other attributes of a patch (e.g. shape, orientation) may likewise affect its ecological performance (Rodenhouse et al. 1997).

Although we define this category to contain only non-interactive patches, we note that apparent at-

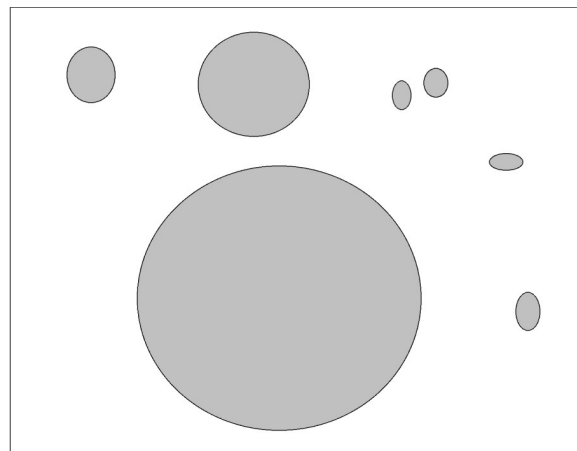


Fig. 4. A heterogeneous system with no interactions between patches, in which the function of patches is size-dependent.

tribute-dependence may in fact be caused by edge effects and other patch-matrix interactions. Nevertheless, such systems may successfully be modeled empirically as non-interactive, attribute-dependent systems.

Here, neither the mean value nor the frequency distribution of variables will be sufficient to predict the overall behavior of the system. Instead, the model will need to include information on the frequency of patches with different attributes (e.g. the frequency of patches of different sizes or shapes), as well as the frequency of different patch types in the system.

Attribute-dependence appears to be common in ecology. Although the solution for dealing with attribute-dependence is conceptually straightforward, it may be difficult to recognize the existence of attribute-dependence in the first place, and to collect enough data to parameterize a model that includes attribute-dependence.

Heterogeneous systems with non-directional interactions among patches

If the patches interact, whether governing processes are linear or non-linear, the spatial arrangement of patches will affect the behavior of the overall system and must generally be considered in a model (Fig. 5). Interactions among patches are very common in ecological systems, and can be highly varied. They may be thought of as falling into two indistinct classes (Fig. 6). First, a process may occur only at or near boundaries between two specific patch types (“boundary interactions”). Many processes occur only at interfaces. For instance, sulfide oxidation takes place where highly reduced habitats contact oxygenated habitats. The amount of sulfide oxidation that takes place in a landscape depends on the amount of such boundaries, not just on the average redox potential of the landscape, or even on the % of

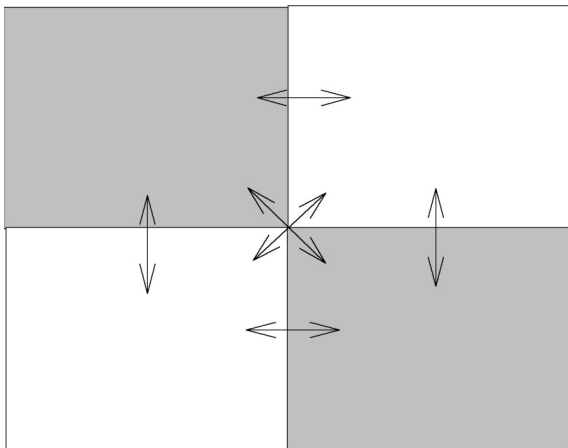


Fig. 5. A heterogeneous system with non-directional interactions between patches.

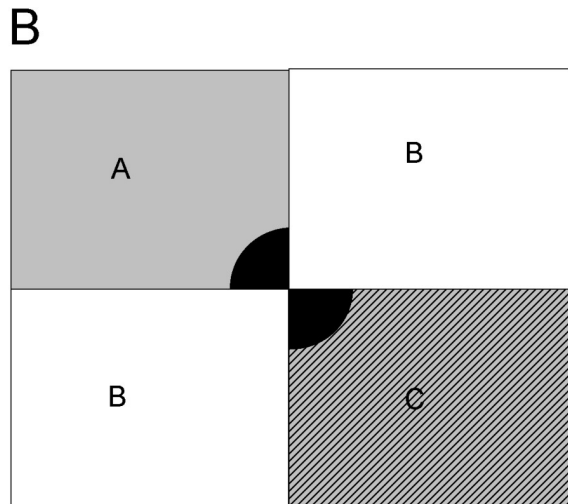
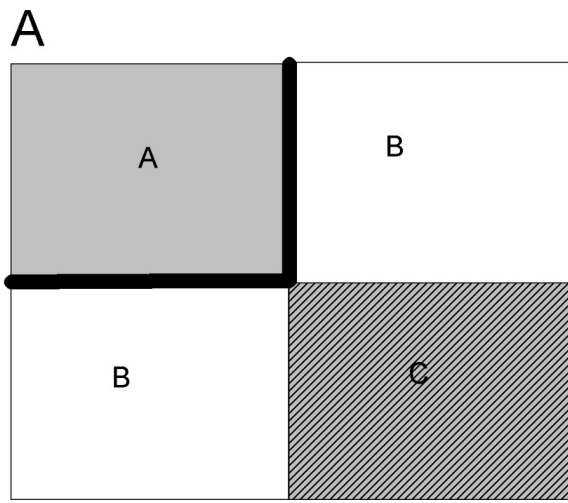


Fig. 6. Two kinds of interactions between patches. A. Boundary interactions: a process (shown in black) occurs only along boundaries between two specific patch types. B. Remote interactions: a process (shown in black) occurs where two specific patch types are within some distance of one another.

the landscape that is at various redox states. Instead, we need to know how often highly reduced patches are adjacent to oxygenated patches. Many other activities are concentrated along ecological boundaries (e.g. cloudwater deposition of nutrients and pollutants, Weathers et al. 1995; foraging activities of animals, Manson et al. 2001). Second, a process may occur only where two particular kinds of patches are within some given distance of one another. An animal species may require for its survival that two (or more) distinct habitats (e.g. for breeding and for feeding) be close to one another (e.g. within a home range or migration route). Air pollution from a smelter may affect biological communities and material cycling many km away (Winterhalder 1996). These “remote interactions” do

not require that interacting patches be contiguous, only that they are linked by some sort of ecologically important vector (e.g. movement of water, air, organisms, information).

If either boundary or remote interactions among patches are significant, then a simplified model that fails in some way to consider the spatial locations of patches will not correctly predict the behavior of the system of patches. Models of non-directionally interacting systems need not actually be spatially explicit, accounting for the location of all patches, but can contain much simpler information, such as the area of patch type B that is within 1 km of patch type A.

Heterogeneous systems with directional interactions among patches

If interactions (boundary or remote) between patches are directional, the specific arrangement of patches with respect to the direction of flow will affect the behavior of the system, and will often need to be taken into account by a model (Fig. 7). This might be called a spatial priority effect, by analogy with temporal priority effects in succession (Alford and Wilbur 1985, Stachowicz et al. 1999). Spatial priority effects are very common in ecology. As an example, suppose we are interested in the average concentration of nutrients in a stream as a function of land use. We have two identical watersheds, each of which has a sewage treatment plant and a nutrient-absorbing wetland (Fig. 8). In one watershed, the sewage treatment plant is just downstream of the wetland, so nutrient concentrations are high for a long distance below the sewage treatment plant, and average nutrient concentrations in the basin are high. In the other, the sewage treatment plant is just upstream of the wetland, so that nutrient concentrations are elevated for only a short reach of stream, and

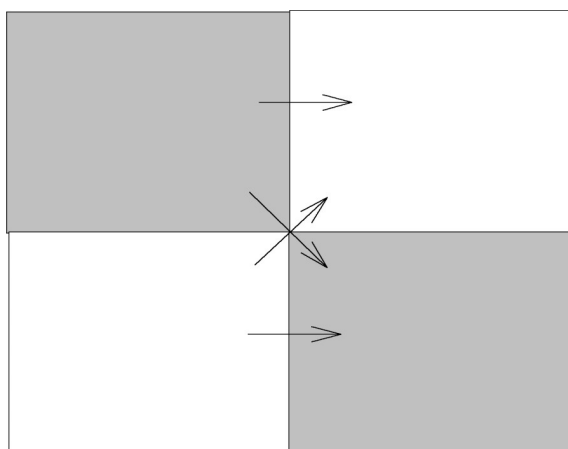


Fig. 7. A heterogeneous system with directional interactions between patches.

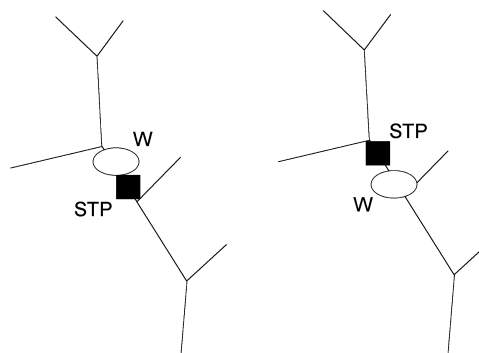


Fig. 8. An example of a spatial priority effect. Diagram shows two stream drainage networks in which a nutrient-absorbing wetland (W) and a sewage treatment plant (STP) occur in different configurations.

average nutrient concentrations in the basin are low. The only way to correctly estimate nutrient concentrations in these two systems is to explicitly consider the relative locations of these two important elements of the landscape. Spatial priority effects will often demand that spatial heterogeneity be incorporated into models. Specifically, the model will need to include information on the interaction between the flow field (direction, speed) and the patch structure of the landscape.

We note that the degree to which landscapes may be considered as interactive or non-interactive may depend

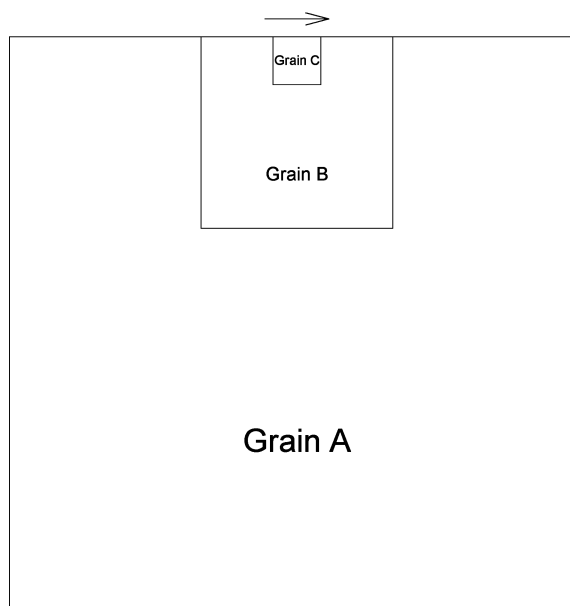


Fig. 9. The importance of interactions depends on the grain size of the patches. Consider three sizes of patches (A, B, and C) all subjected to the same interaction vector (arrow). Because the vector is large compared to the grain size of B and C, models of landscapes of this grain size probably need to be modeled as interactive. The same vector is small compared to Grain A, so a model of a landscape at this grain size may be modeled as non-interactive.

on the grain size of the landscape (Fig. 9). The vectors that link patches in a landscape (whether by boundary or remote interactions) have both a speed (e.g. m/yr) and an amount (e.g. kg/m²-yr) at which material, organisms, or information is moved from one patch to another. Both the speed and the amount of a vector must be large in some sense if two patches are considered to interact. The speed of a vector scales with the grain size of the landscape, so that the same vector reaches all parts of small patches, but only a small part of large patches in a given time. Consequently, given an interaction vector (e.g. movement of water downslope), interactions are less likely to be important in landscapes with large patches than in landscapes with small patches. Consequently, it is likely that fine-grained landscapes will have to be considered as interactive more often than coarse-grained landscapes.

Spatially explicit response variables

Finally, an entirely different class of problems will cause averaged models to fail: if the response variable itself is spatially referenced, rather than being an average of conditions over some time or space. Thus, if the response variable varies spatially, and we are interested only in its value at one particular place, then an averaged model will not produce satisfactory predictions, even if it accurately predicts the average behavior of the entire system. Turner et al. (2001) refer to this as the ‘scaling-down’ problem, and note that it has no general solutions. There are many ecological examples. For instance, we may wish to predict the population density of an endangered species at the site where a shopping mall will be built. The fact that we have an averaged model that perfectly predicts the average density of this species in 100 km² blocks is of no use to us in predicting the impact of the shopping mall.

Temporal complexity in ecosystems

Most ecological systems are heterogeneous in time as well as space. Space and time are more or less substitutable in many ecological situations. For example, species may coexist if their resource use patterns are separated in time or space (Giller 1984), and a foraging model may stipulate that a foraging bird needs to find suitable food within a certain distance or flight time of a nest site. Chronosequences are sometimes substitutable for long-term studies as a tool for investigating succession and other ecological processes (Pickett 1989). Do our generalizations about spatial heterogeneity apply also to temporal heterogeneity?

First, it is worth considering how temporal variation relates to the patch structure commonly used to describe spatial variation. Although temporal variation is

most often conceptualized as continuous rather than discrete, it is possible to use a discrete patch structure to describe temporal variation. (We believe that the choice of a continuous vs a discrete view of nature does not affect any of the conclusions we reach about model requirements for heterogeneous systems). ‘Patches’ in time are periods of time during which ecological conditions differ from those in earlier or later times, a definition that closely parallels common definitions of spatial patches (Turner et al. 2001). The temporal equivalents of spatial patch interactions are lags (Pennington 1986, Crooks and Soulé 1999, Ernest et al. 2000) and legacies (Harding et al. 1998, Foster et al. 1998, Turner et al. 1998) – means by which events occurring at one time may have effects at later times. As is the case with spatial interactions, such interactions may occur between adjacent times (boundary effects) or between widely separated times (remote effects).

Several of the spatial situations described in Fig 1–8 have direct temporal analogues. The first two cases of linear systems without interactions (Fig. 1 and 2) apply equally to temporal variation. As is the case with space, few ecological systems are literally homogeneous temporally or are controlled by temporally varying factors with strictly linear effects. Nevertheless, systems may be treated as temporally homogeneous if the time-scale (period) of temporal variation is small compared to the temporal grain size of the study. Likewise, temporally varying controlling factors with non-linear effects may be treated as linear if the study is restricted to a sufficiently small range of variation in controlling factors.

If ecological processes are controlled by non-linear functions (Fig. 3), then models of temporally variable systems must be based on frequency distributions of variables rather than their mean values. Consider a plant that requires a threshold number of growing degree-days to flower. Knowing the mean temperature over a period of time does not predict whether flowering will occur. Instead, the frequency distribution of the temperatures over a period of time is required.

Attribute-dependence (Fig. 4) may occur in temporally variable systems as well as in spatially variable systems. A frost-sensitive plant requires an unbroken block of frost-free weather to complete its life cycle. We cannot think of any attributes of a temporal patch other than its length that might be of ecological importance.

Analogies between time and space are not exact for interactive patches. Time is always directional – materials, organisms, and information can move in only one direction. Thus, the situation shown in Fig. 5 has no temporal analogue. Directional spatial models (Fig. 7) have clear temporal analogues; in fact, phenomena such as pre-emption, inhibition, facilitation, and priority effects are well known in studies of succession and other

temporal phenomena (Alford and Wilbur 1985, Glenn-Lewin et al. 1992, Stachowicz et al. 1999). For instance, in primary succession on a sand dune, if seeds sensitive to desiccation arrive before there has been adequate accumulation of soil organic matter to retain water, they will not germinate successfully. If the sequence of events is reversed, with organic matter accumulating before the seeds arrive, germination may be successful.

As is the case with spatially referenced response variables, a temporally averaged model cannot accurately predict the value of a particular point in time (the "scaling-down" problem. For example, suppose we have a model that perfectly predicts the long-term average fish biomass in a lake as a function of averaged land cover in the watershed. Such a model would not necessarily be good at predicting fish biomass at any particular time, because of the considerable temporal variability in fish populations and land cover.

In general, temporally explicit models may be easier to handle than their spatially equivalent counterparts because temporal sequences can be ordered in only one way. Thus, temporal effects can be modeled with simple recursive equations. The situation in space can be more difficult because there are three dimensions in space, each with two possible directions.

Joint spatial and temporal heterogeneity in ecosystems

Up to this point, we have assumed that the ecological systems being studied vary over either space or time, but not both. Of course, many ecological systems are heterogeneous in both space and time. Wildfires and other disturbances typically affect only parts of the landscape (Christensen et al. 1989, Foster et al. 1998), and invasive species spread unevenly across heterogeneous landscapes (Buchan and Padilla 1999, Kraft and Johnson 2000). Conceptually, treatment of joint spatial-temporal variation is similar to treatment of spatial or temporal heterogeneity, although models that incorporate joint spatial-temporal variation may be very cumbersome and demanding in practice.

If the system is homogeneous in both space and time, then it is trivially true that a successful model can be based on measurements taken at a single point in space and time. If the system varies over space and time, but the patches do not interact and governing functions are all linear, then a model based on the average values of variables will suffice. In cases where the patches are non-interactive over space and time, but governing functions are non-linear, then the model must include the joint space-time distribution of all variables involved in significantly nonlinear functions. This requirement may greatly complicate attempts to evaluate models of systems that are heterogeneous in both space and time.

As in the case of spatial or temporal variation, models of systems in which patches interact significantly over space or time may also be complicated to evaluate. If patches interact across space but not time, then the model must be spatially explicit at every time for which the model must be evaluated. If patches are interactive across time (i.e. the system has legacies) but not space, then the model must be temporally explicit for all points in space where the model must be evaluated. Finally, if patches interact across both space and time, a spatially explicit model that includes information at all times up to the present time is required. Unfortunately, this last situation (a system where the patches interact significantly across both space and time) is often the best literal description of ecological systems.

Why do simple models work at all?

Given that most ecological systems, processes, and questions are subject to one or more of these problems, we might conclude that complex, spatially and temporally explicit models are needed for nearly all ecological phenomena. In light of this conclusion, the widespread success of simple models in ecology (Peters 1986, Pace 2003) presents an apparent paradox. Why do simple models work at all? We can think of three reasons why simple models might be adequate to describe a complex world.

Using coarse-grained studies

First, although all ecological systems are heterogeneous at some scale, this heterogeneity may occur at much smaller scales of time and space than the grain size of the study. The choice of a coarse grain for the study can improve the performance of simple, averaged models in several ways. Most obviously, it can make a heterogeneous system practically homogeneous with respect to the process under study. Even classically homogeneous systems like the pelagic zone and sandy beaches have measurable heterogeneity that is important at some scale (Lehman and Scavia 1982, McLachlan and Erasmus 1983). However, if the temporal and spatial scale of the patches is fine compared to the spatial and temporal grain size of the process being studied, it may be permissible to ignore this patchiness and treat the system as homogeneous, especially if functions and constants are empirically fitted, rather than being scaled-up from fine-grained studies of controlling functions (see below). A good example is models of nutrient export from watersheds (Caraco and Cole 1999), which ignore the fine-grained heterogeneity of watershed soils that is undoubtedly important in nutrient processing (Jacinthe et al. 1998).

Further, because the speed of a vector scales with the grain size of the landscape (Fig. 9), cross-boundary fluxes may dominate the structure of a fine-grained model but be safely ignored in a coarse-grained model of the same landscape. Thus, coarse-grained models may be fundamentally simpler in structure than fine-grained models in cases where cross-boundary fluxes occur.

Finally, if the grain size of the study is chosen to correspond to the scale of some higher-level constraint, then the internal dynamics of the heterogeneous system may be irrelevant to its broad-scale behavior. Suppose we are interested in primary production in a stratified lake. If we take very fine-scale measurements (e.g. minutes to hours), we probably would conclude that primary production is controlled by light. Nevertheless, at longer time-scales, we would find that primary production over the summer stratified period (i.e. months) is controlled by the amount of nutrients in the epilimnion at the onset of stratification. Stratification imposes a strong constraint on primary production at a characteristic scale of several months. Including the fine-scale heterogeneity in light could actually result in a poorer model than basing a model on a coarse temporal grain size that corresponds to the strong constraint of stratification. In cases such as these, including the fine-scale details of heterogeneity can actually degrade the performance of the model, as well as making the model substantially more complicated.

Accepting approximate answers

Second, ecologists rarely require exact answers and may achieve considerable insight from even approximate answers. Even if factors such as non-linearities, attribute dependence, or patch interactivity produce a modest amount of imprecision or bias in model results, a simple homogeneous model may be acceptable to ecologists. Ecological models with modest r^2 (e.g. ~ 0.5) often provide useful insights and are regarded as successful, so considerable model imprecision may be acceptable, particularly if bias is small. Thus, a simple model may provide an acceptable answer at much lower cost than a complex, spatially and temporally explicit model.

Empirical fitting

Third, ecologists often use empirical or semi-empirical approaches that allow for the introduction of empirically determined constants or functions. Empirical fitting of models is an important way in which bias between averaged models and spatially explicit models can be eliminated. Suppose that two variables are actually related to one another as follows

$$Y = f(X)$$

But instead of measuring X and Y at the fine spatial and temporal scales at which X and Y really interact, an ecologist measures coarse-scale averages X' and Y' . If $f(X)$ is non-linear, then

$$Y' = g(X') \neq f(X')$$

The practical consequence of this inequality is that even if you knew the “true” relationship $f(X)$ from controlled laboratory measurements or from theory, you would not be able generally to predict the behavior of the system from coarse-scale averaged measurements. However, if the internal structures (e.g. distribution of patch sizes, governing functional relationships, patch geometry) are similar across systems being compared, it is possible to derive $g(X')$ empirically, and to proceed without explicitly considering heterogeneity. Of course, if these internal structure differ across systems or over time, an empirically derived $g(X')$ will not apply perfectly to all systems under study.

As an example, suppose we are trying to predict denitrification rates in 1 m² plots from coarse-scale measurements of redox potential. Further suppose that we know from careful lab measurements that denitrification actually takes place only at redox potentials between a and b mV. Soils are very heterogeneous, and the redox potential measured by a large electrode does not adequately reflect, say, the redox potential inside soil aggregates. It is quite possible that none of our coarse-scale measurements of redox potential are between a and b mV, leading to the potentially erroneous conclusion that denitrification does not occur in the plots. In fact, denitrification occurs inside some of the soil aggregates. An empirical relationship might be established between coarse-scale redox potential and measured denitrification rates, which could hold over sites with a similar particle size distribution, moisture content, and organic matter content as the plots, and which could predict that denitrification occurs at redox potentials between c and d mV, where c and d are much higher than a and b . The widespread use of empirical or semi-empirical models in ecology probably has been an important reason why models that ignore heterogeneity have achieved some success.

Conclusions

Ecological systems are spatially and temporally complex. This complexity may arise from several more or less distinct causes (Fig. 1–5, 7). Despite the ubiquity and importance of spatial and temporal heterogeneity in ecological systems, it is not always necessary to include such heterogeneity in models of these systems.

The adequacy of simple models to represent spatially and temporally complex ecological systems depends on:

- The mathematical form of key dynamic relationships in the system
- The degree to which the function of patches depends on the size or other attributes of the patches
- The strength of interaction among patches
- The directionality of interaction among patches
- The spatial and temporal scale of the question being asked, relative to the scales of spatial and temporal heterogeneity and controlling processes
- The level of accuracy required of the model
- The use of empirically fitted functions or constants in the model

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