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Transmutation and functional representation of heterogeneous landscapes

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Abstract

Models of local small-scale ecological processes can be used to describe related processes at larger spatial scales if the influences of increased scale and heterogeneity are carefully considered. In this paper we consider the changes in the functional representation of an ecological process that can occur as one moves from a local small-scale model to a model of the aggregate expression of that process for a larger spatial extent. We call these changes "spatial transmutation". We specifically examine landscape heterogeneity as a cause of transmutation. Spatial transmutation as a consequence of landscape heterogeneity is a source of error in the prediction of aggregate landscape behavior from smaller scale models. However, we also demonstrate a procedure for taking advantage of spatial transmutation to develop appropriately scaled landscape functions. First a mathematical function describing the process of interest as a local function of local variables is defined. The spatial heterogeneity of the local variables is described by their statistical distribution in the landscape. The aggregate landscape expression of the local process is then predicted by calculating the expected value of the local function, explicitly integrating landscape heterogeneity. Monte Carlo simulation is used to repeat the local-to-landscape extrapolation for a variety of landscape patterns. Finally, the extrapolated landscape results are regressed on landscape variables to define response functions that explain a useful fraction of the total variation in landscape behavior. The response functions are hypotheses about the functional representation of the local process at the larger spatial scale.

Introduction

The challenge of translating ecological information across spatial scales is a central issue in landscape ecology and in the investigation of global change (Dickinson 1986, Risser 1987, O'Neill 1988, Risser *et al.* 1988, Woodmansee 1988, Turner *et al.* 1989). Part of this challenge is the translation of models from descriptions of local small-scale (*i.e.*, fine-grained, small-extent) processes within homogeneous stands or patches to models of the larger-scale (*i.e.*, course-grained, large-extent) behaviors of heterogeneous landscapes as single aggregate wholes. Decades of ecological research have provided a wealth of models describing individual, population, community, and ecosystem processes. However, most of these models represent relatively small homogeneous areas, are not often spatially explicit, and they cannot be applied to landscapes (*i.e.*, spatially distributed ecological systems)

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without careful attention to scale and heterogeneity. Spatial scale and heterogeneity can influence the mathematical description of ecological processes, and failure to account for these influences can introduce error into model predictions of landscape behavior.

In this paper we address the phenomenon of 'spatial transmutation'. As defined by O'Neill (1979b), 'transmutation' occurs when the mathemtaical representation of a process changes as one moves from one level of hierarchical organization to the next. For example, a transmutation between individual and population levels occurs when the function describing the collective response of a population to a change in temperature is different from the function describing an individual's temperature response (O'Neill 1979b). We use spatial transmutation to refer to transmutation that occurs in moving from one spatial scale to the next. For example, a spatial transmutation occurs when the function describing the biomass dynamics of a single homogeneous patch of a few square meters is different from the function describing the aggregate biomass dynamics of the many-square-kilometer landscape that contains that patch along with many others.

The causes of spatial transmutation are varied. For example, changes in level of organization often accompany changes in spatial scale as the number and types of interactions among components of the system change with area (Allen and Starr 1982). In these circumstances a transmutation is expected as a consequence of the change in level of organization (O'Neill 1979b). Similarly, changes in spatial scale can alter the constraints, boundary conditions, or driving forces that control the expression of a process. For example, as one moves from the spatial scales of stomata to the spatial scales of canopies and regions the appropriate functional representation of transpiration changes and dominant control of transpiration shifts from stomata1 conductance to radiation receipt and temperature (Jarvis and McNaughton 1986). A spatial transmutation is also likely in moving from a small-scale model of water flow in a soil column to a model of water flow through a watershed. A new process, channel flow, is encountered in moving from the scale of the soil column to the scale of the watershed (Luxmoore et *al.* 1991). This larger scale process is probably not included in the smaller scale model, and thus the functions describing watershed flow will likely differ in form from the functions describing flow in a soil column. The functions are transmuted by the presence of a scale-dependent process or phenomenon.

Here we will limit our consideration to an important and prevalent cause of spatial transmutation, the change in spatial heterogeneity that accompanies changes in area1 extent (Meentemeyer and Box 1987). Specifically, we consider the increase in spatial heterogeneity encountered in changing from local models of homogeneous sites or patches to models of the aggregate behavior of larger heterogeneous landscapes. We assume that no new phenomena or processes are encountered in the increase in extent. The translation is limited to those spatial scales over which all relevant phenomena are included in the local small-scale model.

The purpose of this paper is to identify spatial transmutation as a characteristic phenomenon of heterogeneous landscapes. First, we present a theoretical background for the occurrence of spatial transmutation. We then illustrate the phenomenon with a simple example, and finally we discuss how spatial transmutation can be used to advantage in the functional representation of landscape behavior.

Our presentation is intentionally general. Our purpose is to illustrate the form or class of model that is subject to spatial transmutation as a consequence of landscape heterogeneity. To this end we use canonical models and functional forms as examples. We do indicate how these forms might be used in ecological applications, but we urge the reader to focus on the form (e.g., linear or nonlinear functions) and to not be distracted by the details of the indicated applications.

Theoretical development

Consider a heterogeneous landscape mosaic of homogeneous sites, stands, or patches (Forman and Godron 1986, Risser 1987). For any homogeneous patch in the landscape a process or dynamic of interest is described by the mathematical function

$$y = f(x, p, z)a \tag{1}$$

such that y, the local expression of the process at the scale of the patch, is a function of the vectors of local states, x, parameters, p, and driving variables, z, scaled by the area of the patch, a. For simplicity we will consider one-dimensional vectors (x, p, and z), but the approach can be easily generalized. The function f holds for all patches in the landscape, and for any patch, x, p, and z are constants with respect to space. However, the values of x, p, and z vary from patch to patch across the landscape as spatially distributed variables.

If we consider independent patches where y of one patch is not a function of y for another patch, then the larger-scale landscape expression of the local process is the sum of all local y:

$$Y = \sum_{i=1}^{n} f(x_i, p_i, z_i)a_i \tag{2}$$

where Y is the landscape expression of the process, i indexes individual patches, and n is the number of discrete patches. Many local ecological processes are independent of the concurrent process at other sites, at least over bounded time intervals, and the translation from patch to landscape described by (2) is appropriate. For example, the rate of CO, exchange between the atmosphere and given patch of vegetation is reasonably independent of the rate of atmospheric exchange in other patches. That is, the rate of exchange in one patch at time t is not dependent on, is not a function of, the rate for another patch at time t. Thus the translation of (2) can readily be applied to the problem of landscape-atmosphere gas exchange. Similarly the translation can be applied to the population biomass dynamics of sessile organisms during the non-dispersal stage of their life cycle, or to motile organisms over a time interval in which movement is negligible. Assumptions of independent forest gaps have been used in a similar translation from simulated forest gap dynamics to estimates of landscape biomass dynamics (Shugart 1984).

It is important to note that spatial correlation among the arguments x, p, and z does not prevent application of the translation described by (2). In principle, appropriate application of (2) is prevented only by dependencies of the forms where y at one site i is a function of y at another site m [i.e., $y_i = f(y_m)$] or where there are feedbacks within a patch such that arguments are functions of y [e.g., $x_i = f(y_i)$]. Thus, the translation of (2) is appropriate to a large number of ecological processes and the models describing them.

If landscape heterogeneity is defined not by individual patches but instead by the occurrence of discrete values of x, p, and z, then the landscape value, Y, of (2) is equivalently given by

$$Y = \sum_{j=1}^{q} \sum_{k=1}^{r} \sum_{l=1}^{s} f(x_j, p_k, z_l)a_{jkl}, \tag{3}$$

where a_{jkl} is the area of the landscape over which simultaneously x = x_j, $p = p_k$, and z = z_l, and q, r, and s are the numbers of discrete values of x, p, and z, respectively. The area a_{jkl} can be written as a fraction of the total landscape area, A, or

$$a_{jkl} = g(x_j, p_k, z_l)A, \tag{4}$$

where $g(x_j, p_k$, z,) is the joint probability that at any point in the landscape, x = x_j, $p = p_k$, and z = z_l. Substituting the right side of (4) in (3) yields

$$Y = A \sum_{j=1}^{q} \sum_{k=1}^{r} \sum_{l=1}^{s} f(x_j, p_k, z_l). \tag{5}$$

The triple summation in (5) is the definition of the expected value of the function f(x, p, z), denoted by $E[f(x, p, z)]$, where x, p, and z are discrete random variables with the joint probability function $g(x, p, z)$. In landscapes where x, p, and z are continuous random variables, the summations of (5) are replaced by integrations and

$$Y = A \int \int \int f(x, p, z)g(x, p, z)dx\, dp\, dz, \tag{6}$$

where g(x, p, z) is the joint density function for x, p, and z. Thus, in a landscape where the landscape expression of the local process is the summation of the local process for all patches in the landscape, the landscape expression of the process is the product of the area of the landscape and the expected value of the function describing the local small-scale process, or

$$Y = AE[f(x, p, z)]. \quad (7)$$

Spatial transmutation occurs, as a consequence of landscape heterogeneity, when the expected value of the local function f is not equal to that function evaluated at the expected value of the random variables x, p, and z, that is, when

$$E[f(x, p, z)] \neq f(E[x], E[p], E[z]), \quad (8a)$$

or for the landscape,

$$Y \neq Af(E[x], E[p], E[z]). \quad (8b)$$

In other words, spatial transmutation occurs when the aggregate landscape behavior is not described by the local or patch model evaluated at the means of the local-model arguments averaged over the landscape.

The inequality expressed by (8) is generally true whenever the local function, f, is a nonlinear function. The inequality is not true, and transmutation is not expected, when f is linear or f is simply the product of independent random variables. However, it is important to note that functions which are linear at the scale of the patch may be nonlinear when considered from the perspective of the heterogeneous landscape. Similarly, linear differential equations may yield transmutations since their solutions are often exponential (nonlinear) functions. The inequality of (8) holds for their solution, the variable of interest, and a transmutation is expected. Some simple examples will illustrate and clarify these points.

Consider first the simple function

$$f(x, p) = Y = px, \quad (9)$$

and a landscape where p is a constant across the landscape and x is a discrete random variable that varies among patches. An equation of this form might, for example, be used to describe the maximum potential growth rate of a monospecific population of trees where x is the number of trees and p is the maximum possible rate of growth (DeAngelis *et al.* 1986). This form might also be used to describe survivorship wherep is the probability of surviving to age k and x is the instantaneous birth rate at age k (DeAngelis *et al.* 1986).

For any patch i,

$$y_i = px_ia_i. \quad (10)$$

Assuming q discrete values of x with equal probability $\frac{1}{q}$ and applying (5) and (7),

$$Y = A\sum_{j=1}^{q} px_j\frac{1}{q} = AE[px], \quad (11a)$$

or

$$Y = A\sum_{j=1}^{q} px_j\frac{1}{q} = ApE[x] = Ap\bar{x}. \quad (11b)$$

Note that the local function (9) is linear with respect to the random variable x. The expected value of this linear function is equal to that function evaluated. at the expected value, the mean, $\bar{x}$, of x. Thus no spatial transmutation occurs in the translation from the patch to the landscape.

Now consider the same landscape, but the local process is now described by the function

$$f(x, p) = Y = pe^x. \quad (12)$$

An equation of this form might be used to describe seed dispersal (the number of seeds a unit distance from the mother plant) where p is the number of seeds produced by the plant and $x(= -k)$ describes the rate of decline in dispersal with distance (DeAngelis *et al.* 1985).

For any patch i,

$$y_i = pe^{x_i}a_i, \quad (13)$$

and for the landscape,

$$Y = A\sum_{j=1}^{q} pe^{x_j}\frac{1}{q} = AE[pe^x], \quad (14a)$$

$$Y = Ap \sum_{j=1}^{q} e^{x_j} \frac{1}{q} . \qquad (14b)$$

In this case, the local function (12) is nonlinear with respect to the random variable x. The expected value of the function is not equal to the function evaluated at the expected value, or mean, of the random variable x:

$$Ap \sum_{j=1}^{q} e^{x_j} \frac{1}{4} \neq Ape", \qquad (15)$$

and a transmutation is expected.

Consider next the local function (9) of the first example but a landscape which is heterogeneous in both p and x. For example, referring again to the survivorship application, both survivorship p and instantaneous birth rate x might vary from patch to patch.

For any patch i,

$$y_i = p_i x_i a_i \qquad (16)$$

where both p and x are discrete spatially-distributed random variables. For the landscape

$$Y = A \sum_{k=1}^{r} \sum_{j=1}^{q} p_k x_j g(p_k, x_j) = AE[px]. \quad (17)$$

In the previous use of this local function (9), only x was a spatially distributed variable and the function was linear with respect to the random variable (e.g., (11)). When viewed from the perspective of the heterogeneous landscape in this example, the function now involves the product of two random variables, is nonlinear, and a transmutation may occur.

If p and x are independent random variables, *i.e.,* $g(p_k, x_j) = g(p_k)g(x_j)$, then

$$Y = A \sum_{k=1}^{r} \sum_{j=1}^{4} p_k x_j g(p_k, x_j) =$$

$$Y = A \sum_{k=1}^{r} p_k g(p_k) \sum_{j=1}^{q} x_j g(x_j). \qquad (18)$$

Substituting $g(p_k) = \frac{1}{r}$ and $g(x_j) = \frac{1}{q}$ in (18) yields,

$$Y = A \sum_{k=1}^{r} \left(\frac{p_k}{r} \sum_{j=1}^{q} \frac{x_j}{q} \right) = A \sum_{k=1}^{r} \frac{p_k}{r} \bar{x}, \qquad (19a)$$

and

$$Y = A\bar{p}\bar{x}. \qquad (19b)$$

In this example, the random variables p and x are independent, and the expected value of the local function is equivalent to the local function evaluated at the expected values, means, of the random variables (*i.e.,* $E[px] = E[p]E[x]$). A transmutation is not expected. If, on the other hand, the random variables were not independent, it is not true in general that $E[px] = E[p]E[x]$, and a spatial transmutation would be possible. In ecological systems, correlations or interdependence among state variables, parameters, and driving variables are likely, and spatial transmutation of models involving functions like (16) are expected. For example, in the survivorship application the occurrence of transmutation depends upon whether probability of survivorship and birth rate are dependent or independent random variables. If they are correlated (dependent), perhaps as a consequence of common dependence on environmental conditions, a transmutation is expected.

Finally, consider a landscape in which the local functions of interest are the differential equation

$$f_1(x, p) = \frac{db}{dt} = cb, \qquad (20a)$$

and its solution

$$f_2(x, p) = \int_{t_0}^{t} cb\, dt = b = b_0 e^{ct}. \qquad (20b)$$

Functions of this form might, for example, be used to model the initial (exponential) increase in biomass of weedy species invading a disturbed patch.

At the local scale, within any patch, the differential equation is linear. For any patch i, if b and b_0

are spatially distributed variables, c is a constant across the landscape, and patch area does not change with time,

$$a_i \frac{db_i}{dt} = cb_i a_i, \tag{21a}$$

and

$$b_i = b_{0_i}\, a_i\, e^{ct}. \tag{21b}$$

For the landscape

$$A\frac{dB}{dt} = A\sum_{j=1}^{q} cb_j \frac{1}{q} = AE[cb], \tag{22a}$$

and

$$B = A\sum_{j=1}^{q} b_{0_j}\, e^{ct}\frac{1}{q} = AE[b_0\, e^{ct}]. \tag{22b}$$

Both the differential equation and its solution are linear with respect to the random varibles b and b_0, respectively, and thus there is no transmutation in moving from the local to the landscape.

On the other hand, if c of (20) is also a spatially distributed variable, for any patch i,

$$a_i \frac{db_i}{dt} = c_i b_i a_i, \tag{23a}$$

$$b_i = b_{0_i} a_i e^{c_i t}, \tag{23b}$$

and, for the landscape,

$$A\frac{dB}{dt} = A\sum_{k=1}^{r}\sum_{j=1}^{4} c_k b_j g(c_k, b_j) = AE[cb], \tag{24a}$$

$$B = A\sum_{k=1}^{r}\sum_{j=1}^{q} b_{0_j}\, e^{c_k t} g(c_k, b_j) = AE[b_0\, e^{ct}]. \tag{24b}$$

Now both the differential equation and its solution are nonlinear in the random variables c and b, and a transmutation is possible. If the random variables are independent, then the earlier discussion of the transmutation of the product of two random variables [(16)–(19)] applies to the differential equation (23a and 24a). A transmutation of the differential equation is not expected.

The independence of the random variables does not, however, prevent the transmutation of the differential equation's solution (23b and 24b). Even for independent b_0 and c, the expected value of (20b) is not equal to that function evaluated at the expected value of b_0 and c:

$$E[b_0\, e^{ct}] \neq E[b_0] e^{E[c]t}, \tag{25}$$

and transmutation is likely. Caution must be used in assessing the likelihood of transmutation solely from the structure of the differential equations used to model local processes.

In summary:

1. If a local process at the scale of the patch is described by a linear function, spatial transmutation is unlikely, although care must be taken that the function is not truly nonlinear when viewed from the perspective of the landscape;
2. If a local process is described by a nonlinear function, spatial transmutation is expected in the translation to the larger landscape; however,
3. The transmutation of nonlinear functions that are the simple products of random variables will in general depend upon correlation (covariance) among variables.

The inequality expressed by (8) and the problems associated with using averages in nonlinear functions are well known. O'Neill (1979b) introduced the concept of transmutation in reference to modeling across hierarchical levels, and he discussed error in model predictions as a result of ignoring natural variability. Welsh *et al.* (1988) discussed what they referred to as the 'fallacy of averages', and Leduc and Holt (1987) described the problem of using means in models of regional plant yield. The extensive literature on aggregation error in ecological models (e.g., Cale and Ode11 1979, 1980; O'Neill and Rust 1979; Gardner *et al.* *1982;* Cale *et al.* 1983; Luckyanov *et al.* 1983; Luckyanov 1984; Hirata and Ulanowicz 1986; Iwasa *et al.* 1987, 1989; Rastetter *et al.* 1991) also discusses the error that may result from the imprudent use of mean

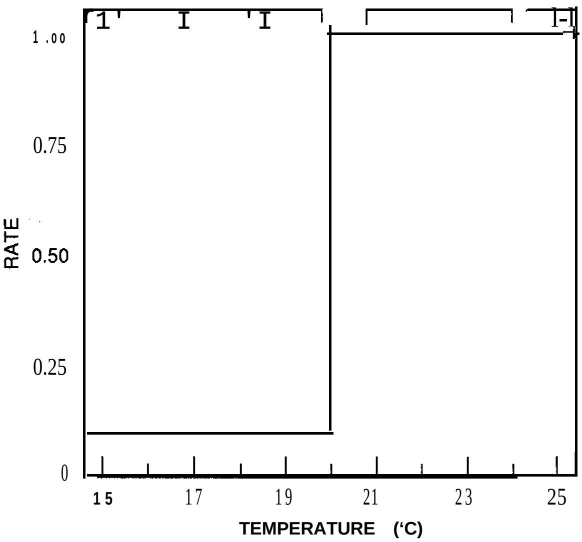

Fig. 1. Rate as a function of temperature (°C) at the scale of the individual site or stand with a critical temperature, t_c, of 20°C (see Equation 26). Units for r are arbitrary.

values in ecological models. The discussions which deal explicitly with spatial aggregation are especially useful (e.g., O'Neill *et al.* 1979; Gardner *et al.* 1981; Iwasa *et al.* 1987). Given: (a) the current interest in translating models and other information from smaller to larger spatial scales (b) the common use of non-linear functions in models of local small-scale ecological processes, and (c) the probability that variables in models of ecological systems will be dependent random variables, it is important to point out how and when spatial transmutation can occur. Similarly, it is important to note how this transmutation affects model predictions of landscape behavior.

Spatial transmutation as a consequence of spatial heterogeneity can express itself in one of two ways. In the more extreme cases, the mathematical form of the function $f(x, p, z)$ will change (O'Neill 1979b). The form of the mathematical function describing the dependency of the local process on local small-scale variables is different from that of the function describing the process as it is expressed at the scale of the landscape. In some cases, the form of the function does not change, but the variables in the larger-scale landscape function are not the mean values of the small-scale variables averaged over the landscape (Rastetter *et al.* 1991). In the following example we illustrate the first and more extreme case.

An example of spatial transmutation

For this demonstration we use a simple step function to represent a hypothetical local process at the scale of the patch or stand. Consider a homogeneous stand of vegetation for which some arbitrary rate, r, is dependent upon the local temperature, t, of the stand (Fig. 1). At or above a critical threshold temperature, t_e, the rate is 1 .O. Below t_c the rate is 0.1. Thus,

$$f(x, p, z) = f(t_c, t) = r = \begin{cases} 1.0. & \text{if } t \geq t_c \\ 0.1, & \text{if } t < t_c. \end{cases} \quad (26)$$

This function was used by O'Neill (1979) to illustrate transmutation associated with changes in hierarchical levels of organization.

Consider a collection of landscapes. Equation (26) describes the local stand rate r for any stand in any of the landscapes, but the value of t_c varies among stands, perhaps due to differences in stand composition. Stand temperature, t, can also vary among stands within each landscape. In the example which follows we consider several combinations of within-landscape and among-landscape variability in t and t_c.

We calculated the landscape rate, R, for a collection of landscapes using the extrapolation of (7) and a nested Monte Carlo simulation (Fig. 2). We assumed that t and t_c were independent random variables and, for simplicity, that the area of'each landscape was 1.0 (units are arbitrary). First, we selected parameters (e.g., means and variances) describing the within-landscape distributions of t and t_c for a single landscape. We made the selections from distributions describing the among-landscape variability of these parameters. For example, we selected a mean value of t for the landscape from a distribution of mean values of t. We used the Monte Carlo and Latin hypercube sampling (McKay *et al.* 1979) algorithms of PRISM to select the parameters. PRISM is a computer pro-

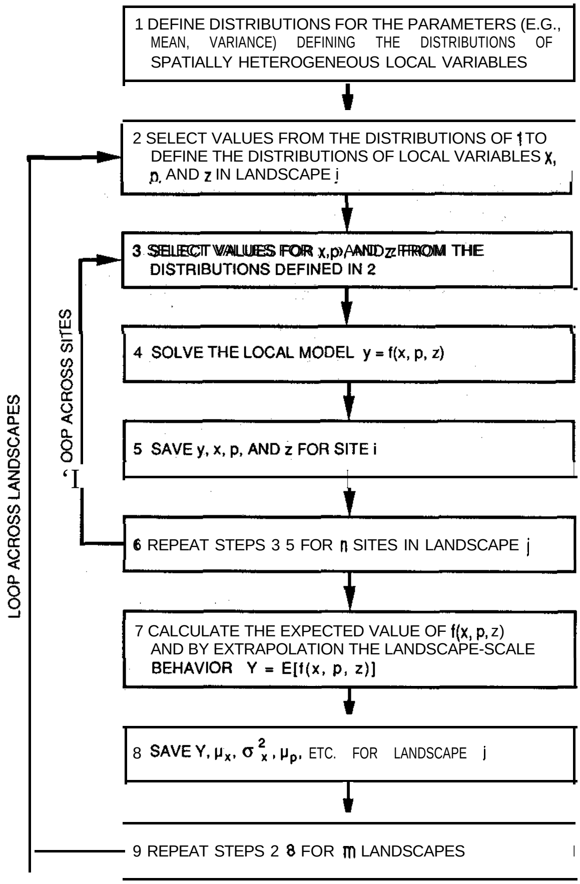

Fig. 2. A nested Monte Carlo approach to modeling heterogeneous landscapes.

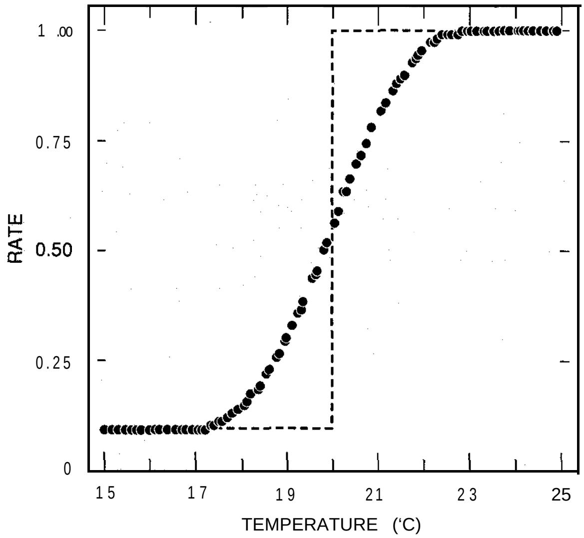

Fig. 3. The transmuted relationship between rate and temperature. The dashed line shows the local small-scale relationship for individual stands. The points represent landscape-scale rates for individual landscapes of constant temperature, t, and normally distributed t_c with a mean of 20°C and variance of 1.0°C.

gram designed for the Monte Carlo analysis of model sensitivity and uncertainty (Gardner 1984, Gardner and Trabalka 1985, Dale *et* al. 1988, Gardner *et al.* 1990). For each landscape, we ran 100 Monte Carlo iterations of the local stand function with stand values oft and t_c chosen from the distributions specified in the first round of Monte Carlo sampling. We again used PRISM and Latin Hypercube sampling in these simulations. We saved the stand rate, r, from each iteration for calculation of the expected value of r. We repeated this process for 100 landscapes. Thus we calculated the expected value of the local stand function (26) and consequently the larger-scale expression of that function for 100 landscapes, each described by the probability distribution of t and t_c in that landscape.

Consider first the case where the variability in t_c for each of the landscapes is described by a normal distribution with a mean value of 20°C and a variance of 1.0°C. The distribution of t_c is the same for every landscape. The parameter t is constant across each landscape, but t is different for each landscape with values of t uniformly distributed between 15°C and 25°C.

The transmuted function is shown in Fig. 3; the original stand function is superimposed as a broken line. While the temperature dependency of the stand rate is described by a sharp discontinuous step function, the temperature dependency of the landscape rate is described by a smoothed sigmoidal curve. The spatial heterogeneity of t_c on the landscape has transmuted the form of the original stand function. The temperature dependency of the landscape rate, ***R,*** is better described by an arctangent function than the original step function. The difference between the two curves is the error involved in predicting the landscape rate using the stand function without carefully considering the spatial transmutation induced by landscape heterogeneity.

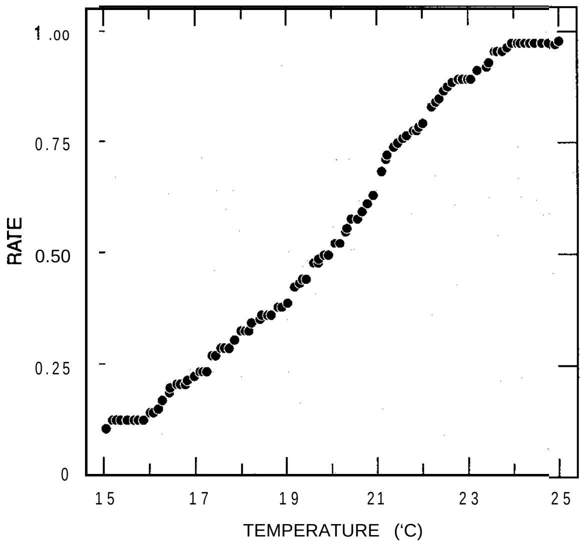

Fig. 4. The transmuted relationship between rate and temperature for landscapes with normally distributed t_c (means of 20°C and variances of 1.0°C for each landscape) and normally distributed t. The means for t are uniformly distributed among landscapes from 15°C to 25°C; the variance of t is 6.25°C for each landscape.

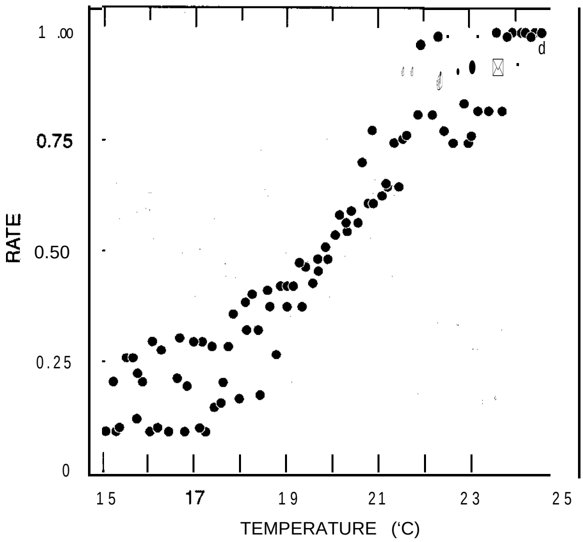

Fig. 5. The transmuted relationship between rate and temperature for landscapes with normally distributed t_c (means of 20°C and variances of 1.0°C for each landscape) and normally distributed t. The means for t are uniformly distributed among landscapes from 15°C to 25°C; the variance of t is uniformly distributed among landscapes from 0.0001°C to 25°C.

Let us now assume that temperature is no longer constant across each landscape but is instead normally distributed. The mean t for each landscape is different and varies among landscapes according to a uniform distribution with a minimum of 15°C and a maximum of 25°C. The within-landscape variance in t is the same for each landscape; we use a value of 6.25°C. Within and among landscape heterogeneity in t_c is not different from the preceding case.

Figure 4 shows the landscape rates, ***R***, plotted against the mean landscape temperatures, $\bar{t}$ = ***T***. The introduction of within-landscape variance in t results in a flattening of the earlier sigmoidal curve (Fig. 3), and the transmuted function describing the temperature dependency of the landscape rate approaches a straight line.

If the within-landscape variance in t is not constant among landscapes (but is instead uniformly distributed between 0.0001°C and 25.0°C), the transmutation is more complex (Fig. 5). The landscape rates are dispersed, although a sigmoidal dependency on temperature is still discernable. At this point, landscape heterogeneity induces a transmutation from a simple mathematical function for the stand to a more complex representation for the landscape.

In the next case the stand variables, t and t_c, are normally distributed on any given landscape, and the means and variances of each differ among landscapes. The means for t_c are uniformly distributed between 17°C and 23°C, and the variances are uniformly distributed between 0.0001°C and 4.0°C. The means for t are uniformly distributed between 15.0°C and 25.0°C, and the variances are uniformly distributed between 0.0001°C and 25.0°C. The result is a mixed collection of 100 landscapes with different spatial heterogeneity in both t and t_c.

The spatial transmutation for this latter case is shown in Fig. 6. The step function dependency on temperature of the stand rate is virtually obliterated, and the sigmoidal dependency seen in the first transmutation is barely discernable. Landscape rate is dependent upon mean landscape temperature, but the transmuted relationship is complex. Any functional representation of the temperature de-

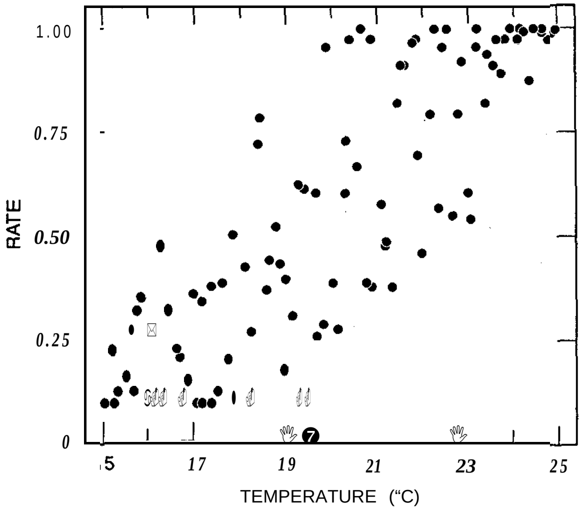

Fig. 6. The transmuted relationship between rate and temperature for landscapes with normally distributed t_c and t. The means for t_c are uniformly distributed among landscapes from 17°C to 23°C, and the variances are uniformly distributed among landscapes from 0.0001 °C and 4.0°C. The means and variances for t are as in Fig. 5.

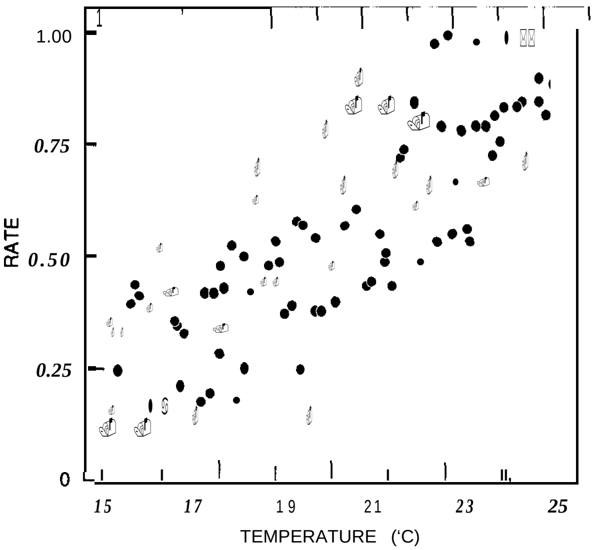

Fig. 7. The transmuted relationship between rate and temperature for landscapes with normally distributed t_c and t in which the means for t_c and t are distributed among landscapes as in Fig. 6, but the upper bounds on the variances are doubled.

pendency of the landscape rate is necessarily statistical or probabilistic.

The final case we consider is a simple extension of the previous case. The ranges of within-landscape variance for t and t_c are widened (the maxima are doubled); otherwise the two cases are identical. We are increasing among-landscape heterogeneity, a situation which might arise if the geographical distribution of real landscapes was extensive. The transmuted relationship is shown in Fig. 7. Increasing the range of within-landscape heterogeneity increases the scatter of the landscape rate. The spatial transmutation of the original stand function is otherwise very similar.

As illustrated by Figs. 5-7, spatial transmutation may not yield a well defined mathematical function (according to the strict definition of function [Swokowski 19791). Finding a useful functional representation may require further derivation. The results from the cases illustrated in Figs. 5 and 6 can be used to demonstrate the statistical derivation of a transmuted function. The transmuted temperature dependency of the landscape rate, R, shown in Fig. 5 is a complex one. No simple mathematical function will explain all of the observed pattern. A statistical approach can, however, generate a simple functional representation which approximates the observations and explains much of the pattern. For example, using the data in Fig. 5, a linear least-squares regression of R on $T = \bar{t}$ (the mean landscape temperature) explains 92% of the variation in the landscape rate (r^2 = 0.92; Fig. 8a), and a cubic least-squares fit explains slightly more of the variation with an r_2 of 0.94 (Fig. 8b). Similarly, a linear least-squares regression of R on T for the data of Fig. 6 explains 69% of the variation in the landscape rate (r_2 = 0.69, Fig. 9). A cubic least-squares regression only explains an additional 1% of the variation (r_2 = 0.70). The increased variability in the landscapes of Fig. 6 reduces the predictability of the landscape rate, R, as a simple function of landscape temperature, T.

However, a larger fraction of the among landscape variability in R, 88%, can be explained by the multivariate linear model

$$R = 0.33 + 0.09T - 0.08T_c, \tag{27}$$

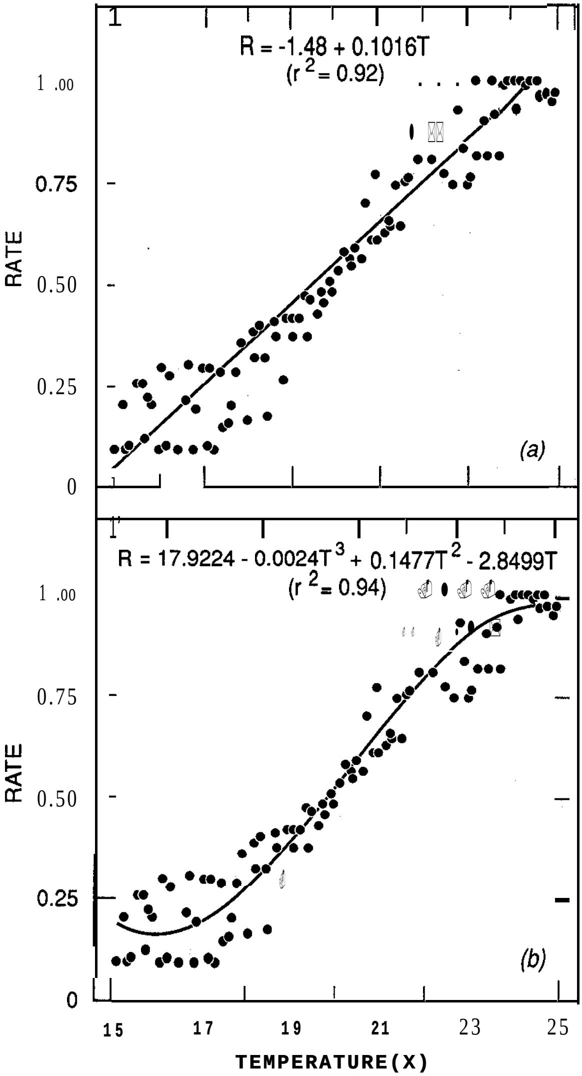

Fig. 8. A linear regression (a) and a cubic regression (b) of landscape rate, *R*, on landscape temperature, T (the mean of the stand temperatures in that landscape), for the landscape data of Fig. 5.

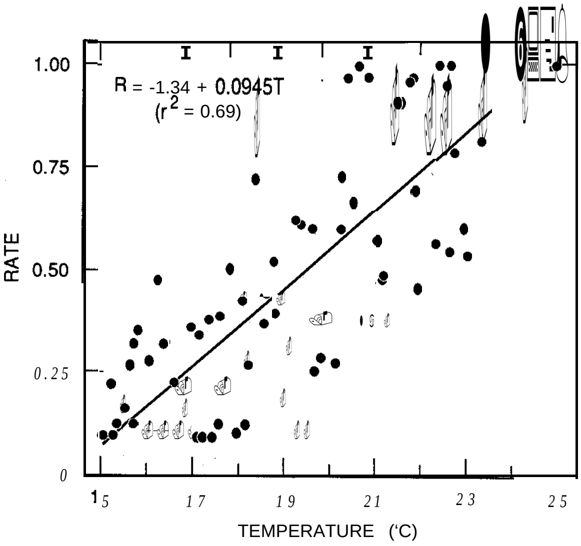

Fig. 9. A linear regression of landscape rate, *R*, on landscape temperature, T (the mean of the stand temperatures in that landscape), for the landscape data of Fig. 6.

where R is the landscape rate, Tis the mean temperature $\bar{t}$, of the landscape, and T_c is the mean critical temperature, $\bar{t}_c$, of the landscape (Fig. 10). The linear landscape function of (27) is a transmutation of the original step function (26). King *et al.* (1990) further discuss response-surface modeling as an approach to translating models across temporal scales. Here, we want to emphasize that our cautions against modeling the landscape with mean values pertain to the use of mean values for the landscape in the local or small-scale functions. It is appropriate to use the means of local variables as larger-scale landscape variables in the transmuted functions describing the integrated behavior of the entire landscape.

Discussion

Our example illustrates the potential dangers of ignoring spatial transmutation in the translation from local small-scale models to models of the heterogeneous landscape. We chose the discontinuous step function because it is simple and the transmutation is dramatic; however, transmutations can occur with other classes of functions (see O’Neill 1979b). It is unwise to assume that an accurate description of the larger-scale landscape expression of a local small-scale process can be made with the assumption that the landscape responds like the average site or patch. Landscape heterogeneity can introduce error in model predictions if the landscape is modeled with the small-scale model evaluated at the mean values of the small-scale arguments averaged over the landscape.

How then can we avoid the error introduced by

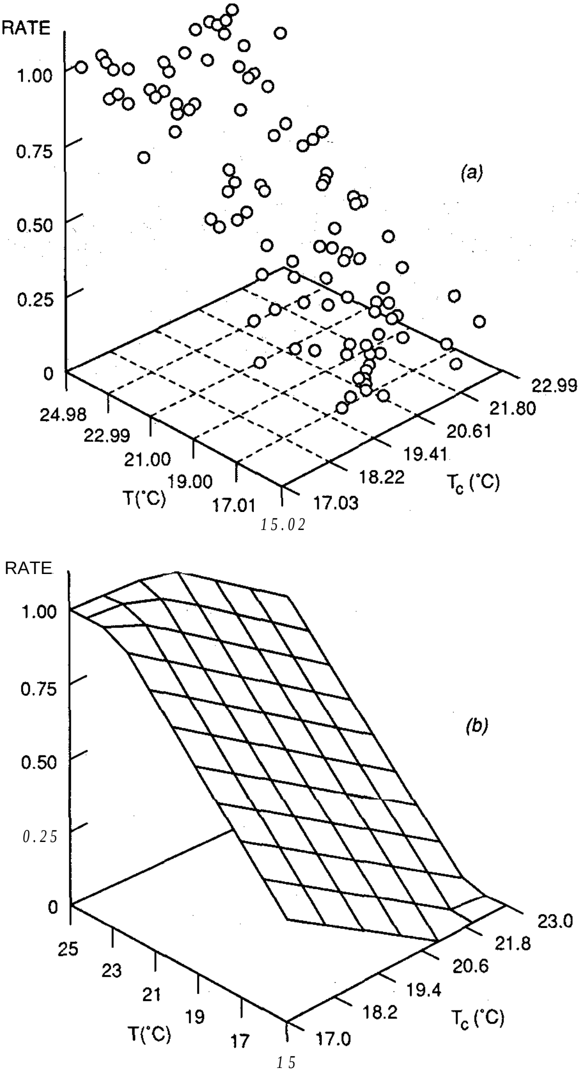

Fig. 10. The transmuted dependency of landscape rate, *R*, on landscape temperature, T, and critical temperature, T_c, for the landscapes of Fig. 6. The landscape variables T and T_c are the landscape means, of the respective stand variables. (a) simulation results; (b) a larger-scale landscape model for *R* as a function of T and T_c derived by multivariate linear regression of the simulations in 10a. See Equation 27 in text.

spatial transmutation, or better yet, how can we use spatial transmutation to our advantage in the functional representation of landscape behavior? On the one hand, translation from local models to landscape models can be avoided altogether by directly analyzing the integrated holistic behavior of the landscape at the scale of the landscape. Models of landscape behavior can, in principal, be derived at the scale of the landscape by a combination of observation and theory, induction and deduction, without first invoking local small-scale processes. However, we frequently do not have direct access to observations on large landscapes (e.g., large-scale trace-gas fluxes between the landscape and the atmosphere), or we may lack both the experience and insight to deduce functional relationships at large scales (e.g., what factors control the population growth of pests over very large areas). In other situations we may need or want to explicitly link local small-scale processes with their expression at larger spatial extents, perhaps to gain understanding of the mechanisms underlying larger-scale dynamics. In these cases we can avoid the errors introduced by spatial transmutation by explicitly incorporating the sources of transmutation into the translation from site to landscape. For example, Jarvis and McNaughton (1986) explicitly incorporate both spatial heterogeneity and scale-dependent changes in constraint in their analytical translation from stomatal conductance to landscape transpiration. In some cases observed scale-dependencies in measured phenomena can be used to translate from smaller to larger scales (O'Neill *et* al. 1989, Turner *et al.* 1989). When spatial heterogeneity is the sole source of transmutation, the method of extrapolation by expected value we have used here and that King *et al. (1987,* 1989) used to simulate regional CO_2 fluxes can be used to explicitly account for spatial heterogeneity. King (1991) discusses several general approaches to scaling up across landscape heterogeneity. Any of these methods are preferable to the assumption that spatial heterogeneity can be ignored.

If we can avoid the error of spatial transmutation, can we also use spatial transmutation of local functions to our advantage? In some cases, the transmuted function is simpler than the original smaller-scale local function. The second case we present here, where the transmuted function approximates a straight line (Fig. 4), is an example, and O'Neill (1979b) presents others. Statistical response-surface methods can be used to derive functional representations for the landscape when the transmutation does not yield a simple mathematical function. Certainly, using the transmuted function to predict or model landscape behavior can be easier than explicitly rescaling or translating from site to landscape each time we wish to predict landscape behavior. This is especially true for large, complex, and computer intensive models. Therefore, provided we can determine landscape behavior over the appropriate range of independent variables, either by the translation of site models or direct observation, we need only develop adequate mathematical representations of landscape behavior as a function of larger-scale landscape variables that can easily be quantified. We can use these functions as models of landscape behavior. These models might be used to predict the behavior of different landscapes, or they might be used to analyze the behavior of the same landscapes under changing conditions. The models might also be part of regional or global models that incorporate the landscapes as smaller-scale components.

Summary and conclusions

We have shown how spatial heterogeneity, a definitive characteristic of landscapes, can affect the larger-scale landscape representation of a local small-scale process by inducing a transmutation in the function used to describe or model that process. A spatial transmutation is expected whenever the function describing the local process is nonlinear with respect to the spatially distributed random variable or variables of the heterogeneous landscape. The exact nature of the transmutation is dependent upon the form of the nonlinear function, the degree of spatial variability in the arguments of the function, and dependencies among arguments that are random variables.

We have used simple models and landscapes to illustrate spatial transmution. More complex models and landscapes (e.g., those including spatial autocorrelations and correlations among parameters and driving variables) should be examined in a search for general patterns. However, the implications of spatial transmutation for modeling landscapes are obvious. Spatial transmutation must be considered in any attempt to model aggregate landscape behavior with small-scale models or functions describing local processes. Incorporation of spatial heterogeneity in an explicit translation from small-scale to large-scale model accounts for a major cause of transmutation and reduces the error associated with using functions developed at small-scales to model the expression of local processes at the larger scales of the landscape. Calculation of the expected value of the local model can accomplish this translation for a large class of ecological phenomena and the models that describe them, and Monte Carlo methods provide generality in calculating the expected value (King *et* al. 1989, King 1991). Furthermore, the results of these translations can be used to define simple and appropriately scaled models for the landscape. These methods enhance our ability to deal with the conceptual and operational problems of extrapolation from current understanding of local small-scale processes to an improved understanding of larger-scale landscape, regional, and global phenomena.

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