Scaling-up an autoregressive time-series model (of spruce budworm population dynamics) changes its qualitative behavior☆

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Abstract

The emergence of issues such as climate change has motivated the development of time-dependent models to forecast how plant and animal populations will react over large spatial extents. Usually the best data available for constructing such models comes from intensive, detailed field studies. Models, thus implicitly developed at the fine spatial resolution of experimental studies, are then scaled-up to coarser resolution for management decision-making. Typically, this process of scaling-up involves merely adapting the model’s computer code for data input so that it will accept the large scale spatial averages (often derived from relatively remote (e.g. aerial) sensing) that form the basis for management planning. Unfortunately, such scaling-up can inadvertently affect model predictions and dynamical behavior. Improper incorporation of data collected at multiple resolutions during model development and use, and misinterpretation of model output can result. The consequences of scaling-up a linear, second-order, autoregressive, time series model of spruce budworm population dynamics on the model’s predictions and on the interpretation of the model’s output are considered. Such time series models have been proposed as templates for incorporating outbreak dynamics in the decision systems supporting forest insect management that are currently being adapted to climatic change problems. Analysis of the underlying deterministic component of the time series model showed that: (1) parameter estimates changed with the spatial resolution-parameter values estimated from time series data consisting of large area averages were negatively correlated ($r = -0.931, P < 0.0005$) and as much as 40 or 50 times greater in absolute value than the parameters generating the fine resolution data from sampling sites 1600 times smaller in extent. (2) Even the qualitative nature of the dynamics appeared to change in response to scaling-up. The long cycle, converging oscillations generated at fine resolutions gave way to five additional types of qualitative
behavior at coarser resolutions including various types of divergent behavior and non-oscillating behavior. (3) The amount of distortion involved in scaling-up depends on the model’s degree of non-linearity and on the fine scale spatial variation in population densities. An approach to correcting for such distortion is outlined. The potential consequences of scaling-up deserve consideration whenever data measured at different spatial resolutions are integrated during model development, as often happens in climate change research. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

1.1. The scaling challenge

Most information in population biology has been generated at fine resolutions (i.e., over small areas) because it is generally simpler and cheaper to conduct field studies at fine resolutions, such as portions of forest stands, than over much coarser resolutions, such as entire forest landscapes. For similar reasons, field studies are generally run for 5 years or less. Management, however, is becoming increasingly concerned with population processes at very large temporal and spatial scales and with processes which cross (Holling, 1992; Peterson et al., 1998) scales. Examples of such processes are forest succession and the spread of disturbances where the respective concerns are primarily with temporal and spatial scales. Thus the challenge involved in scaling-up is to apply data generated at fine resolution to coarser resolution problems of concern to management (Walker and Steffen, 1997; Smith and Heath, 1998). Difficulties in scaling-up can arise for a number of reasons (Peterson, 2000), but the ubiquity of spatial heterogeneity and the prevalence of nonlinear ecological relationships make spatial transmutation perhaps the most universal of these difficulties.

1.2. Spatial transmutation

Changes in heterogeneity (Meentemeyer and Box, 1987) as well as changes in resolution (grain) and range (extent) are usually involved in shifting a study from one spatial or temporal scale to another. For instance, in scaling-up, heterogeneity inherent in variables observed at individual sites or stands often decreases when the values of these variables are averaged (or smoothed) to produce an aggregate value for the landscape unit as a whole (Gardner, 1998). In addition, the dynamics of the system under study sometimes appear to behave differently at different scales. This process, by which scaling-up can produce apparent changes in system dynamics has been termed spatial transmutation (and spatial aggregation error) in the theoretical modeling literature (e.g. O’Neill, 1979; King et al., 1991). Therefore, key aspects of the scaling challenge are understanding how scaling can affect measurements of spatial heterogeneity and recognizing the consequences of such effects on models of system dynamics.

Spatial transmutation has been successfully dealt with in some particular cases and special circumstances (e.g. Auger et al., 2000; Law and Dieckmann, 1998; O’Neill and King, 1998; Pascual and Levin, 1999; Wirtz, 2000 and references therein), but a general methodology for making accurate predictions across multiple spatial and temporal scales is still lacking (Levin, 1992; Pahl-Wostl, 1995; Schneider, 1994). Developing such a methodology may be particularly difficult for agents of large-scale disturbance regimes (Levin and Pacala, 1997) such as spruce budworm. As an initial step in this direction, this paper explores the extent of spatial transmutation involved in scaling-up a time series model of spruce budworm population dynamics (Royama, 1984) and suggests an approach to correcting for it.

1.3. The spruce budworm

Canada’s most destructive forest insect (Hall and Moody, 1994), the spruce budworm, Choristoneura fumiferana (Clem.) (Lepidoptera: Tortri-
cidae), attacks balsam fir, *Abies balsamea* (L.) Mill., and spruce, *Picea* spp. During uncontrolled outbreaks, millions of cubic metres of wood volume are often destroyed. Balsam fir is particularly vulnerable when growing in mature, single-species stands and typically dies after 5–8 consecutive years of heavy feeding. The economic impact of spruce budworm has motivated many modeling projects to improve our understanding of its population fluctuations (e.g. Hassell et al., 1999; Jones, 1979; Ludwig et al., 1978; Rinaldi and Muratori, 1992; Royama, 1992; Smith and You, 1990; Stedinger, 1984; Watt, 1964). All of these projects are at least partly based, either directly or indirectly, on observations from intensive field studies of spruce budworm population dynamics conducted in the Green River watershed of New Brunswick (Morris, 1963). These observations were collected from field plots of 0.1 km$^2$ (10 ha) area.

### 1.4. Spatial transmutation in spruce budworm models

It was during Fleming and Shoemaker (1992) validation study of Jones (1979) model that the potential for spatial transmutation in studies of spruce budworm population dynamics became evident. Fleming (1991) provides an extreme example of this. Population densities are predicted to increase everywhere within a large area when the model is applied at fine scales of spatial resolution to individual sampling sites, but when applied to the same data after they have been spatially averaged over the large area, the same model predicts declining average populations for the area as a whole. Thus the model produces contradictory predictions: increasing population densities at one scale of spatial resolution; decreasing densities at another scale.

In this paper, we address the vulnerability of Royama (1984, 1992) time-series approach to spatial transmutation. This approach is of particular interest because it has been adopted as the theoretical foundation for much of the work to describe insect disturbance regimes in Canada’s forests and disturbance regimes are recognized as key drivers of carbon dynamics in these forests (Kurz and Apps, 1999). Furthermore, time-series modeling has become a basis for a large effort to develop decision support systems for managing forest insects in Canada (MacLean and Porter, 1995). In addition, Royama’s work has spawned a variety of other approaches based on time series analysis (e.g. Berryman and Millstein, 1990; Turchin and Taylor, 1992) for modeling long-term population data. None of these approaches deals with spatial transmutation explicitly.

Fleming et al. (1999) showed that Royama (1984, 1992) time-series approach was vulnerable to the distortions produced by spatial transmutation. They found that the greater the ratio of spatial scales and the greater the spruce budworm densities in the region, generally the more prominent the spatial transmutation. This paper goes a step further by exploring the range of effects (i.e. qualitatively different dynamical behaviors) produced by spatial transmutation when Royama (1984, 1992) time-series approach is applied to the same data at two different scales of resolution: at the 1 km$^2$ scale at which the (survey) data used to parameterize the model was originally collected, and at a larger ‘landscape’ scale (1600 km$^2$) typical of the scales of interest to management. The analysis is purposefully simplified by isolating the deterministic and stochastic components of the time-series model under investigation. The interaction of these components on spatial transmutation of time-series models is beyond the scope of this paper but will be considered in future work.

### 2. Methods

#### 2.1. Survey sampling and data processing

For raw data we used the results of surveys of second-instar spruce budworm larvae from New Brunswick, Canada. These data were collected by the New Brunswick Department of Natural Resources and Energy (NB-DNRE) from 1985 to 1995. Sampling intensity in the province varied from a high of 2347 sample sites in 1985 to a low of 930 in 1995. At each sample site, one branch was collected from each of three trees, and the number of larvae on each 75-cm branch tip was...
recorded. The average number of larvae per 75-cm branch tip represented the larval density at each site.

Fleming et al. (1999) detail the data processing methods. Briefly, sample locations from years 1985 to 1992 were georeferenced using the Universal Transverse Mercator (UTM) co-ordinate system. Each sample site was located within a 1 × 1 km grid square by recording northing values to four digits and easting values to three digits. Sample locations from years 1993 to 1995 were georeferenced with 1 × 1 km resolution using a double stereographic projection for New Brunswick. UTM and NB Double Stereographic co-ordinates were then converted to a common azimuthal equidistant co-ordinate system which conserves true distances in all directions and expresses them as X and Y co-ordinate pairs in positive and negative metres.

Mean densities of second instar larvae were calculated at ‘landscape’ resolution by first overlaying an 11 × 11 grid of 40 × 40 km cells on the province of New Brunswick (Fig. 1). Each year, an average was calculated over all survey sites within each of these grid cells (landscape units) which overlapped the province’s infested area.

2.2. Applying the same model at different spatial resolutions

Royama (1984) used the simplest model possible that exhibited what he viewed as the main features of spruce budworm population dynamics in order to demonstrate his time-series approach. This was a linear second-order autoregressive model, which predicts the logarithm of population density in any year \( t + 1 \) as:

\[
N(t + 1) = (c + 1)N(t) + kN(t - 1) + z(t) \quad (1)
\]

Here \( N(t) \) represents the natural logarithm of \( n(t) \), the population density in year \( t \), and \( c \) and \( k \) are constants. Royama (1984) specified that at each location the \( z \)'s are temporally uncorrelated random numbers which are uniformly distributed in the interval \([-0.5, 0.5]\). These random numbers, \( z(t) \), are needed in Eq. (1) to maintain the persistent, long-term, oscillatory behavior which reflects the spruce budworm’s (35 year long) outbreak cycle. Taking the anti-logarithm of both sides of Eq. (1) results in an equivalent expression, but in terms of the untransformed population density directly:

\[
n(t + 1) = [n(t)]^{(c + 1)[n(t - 1)]^k} \exp\{z(t)\} \quad (2)
\]

The purely descriptive, phenomenological motivation for this equation is revealed by the lack of any mechanistic underpinning (sensu Jones, 1979; Ludwig et al., 1978) in its structure.

In what follows, we work with Eq. (2) rather than Eq. (1) because Eq. (2) represents the management situation of dealing with actual (spruce budworm) population sizes, while Eq. (1) deals only with a transformation of this variable of interest. A second advantage of Eq. (2) is that it provides potentially realistic (i.e. finite) values of \( n(t + 1) \) when the population is locally extinct (i.e. \( n = 0 \)) in either of the previous 2 years (depending on the values of parameters \( c \) and \( k \)); Eq. (1) does not.

The deterministic and stochastic components of Eq. (2) were isolated to simplify the analysis. Initially we examined effects of the deterministic
by applying Eq. (3) to the appropriate population the subsequent year was made for each survey site years. Next, a prediction, i.e. each satisfactory pair of consecutively sampled

Next year, i.e. the spruce budworm population density in the regions. In each region, the parameter values dic-

therefore, cannot exhibit spatial transmutation). At each survey site, Eq. (3) was used to predict the spruce budworm population density in the next year, i.e. the \( n(t+1) \) value, from the data for each satisfactory pair of consecutively sampled years. Next, a prediction, i.e. \( n(t+2) \) value, for the subsequent year was made for each survey site by applying Eq. (3) to the appropriate population densities. This corresponded to replacing ‘t’ by ‘t + 1’ in all parentheses in Eq. (3). Overall, this process produced 3469 time series of population data, each 4 years long and at the 1 km\(^2\) scale of resolution of the survey sites. In each of these
time series, data for the first 2 years were originally collected by the survey and data for the latter 2 years were generated from Eq. (3). Thus, all data now remaining at the 1 km\(^2\) scale of resolution of the survey sites are strictly and exactly described by Eq. (3). This equation corresponds to Eq. (2) with \( z(t) = 0 \), and with parameters \( c \) and \( k \) set at Royama (1984) (figure 28) values of 0.8 and −0.89, respectively.

Average population densities were then separately calculated within each 1600 km\(^2\) landscape unit (Fig. 1) for each year of each 4 year sequence. These sequences included predictions from Eq. (3) in years \( t + 2 \) and \( t + 1 \) and survey data in years \( t \) and \( t − 1 \). Each resulting sequence of 4 consecutive years of landscape unit averages was then split into two strings of three consecutive years (\( t − 1 \) to \( t + 1 \), and \( t \) to \( t + 2 \)). Both strings of population density data were separately substituted into Eq. (2) with \( z(t) \) fixed at its mean, 0, for consistency with the generation of data at the scale of individual sampling sites using Eq. (3). This produced two simultaneous versions of Eq. (2) which were logarithmically transformed and algebraically solved to produce \( c \) and \( k \) values at the 1600 km\(^2\) scale of resolution of the landscape units.

2.3. Characterizing the extent and isolating the causes of spatial transmutation

To illustrate the patterns and extent of spatial transmutation, these values of parameters \( c \) and \( k \) determined at the landscape scale were plotted against each other. These plots were overlain with phase plane diagrams (e.g. Royama, 1992) which section the \( c \times k \) parameter space into six different regions. In each region, the parameter values dictate that Eq. (1), or equivalently Eq. (2), generates a time series of predicted population densities which is qualitatively different from the time series generated by parameter values from any other region. Minitab (Minitab Inc., 1999) software was used for much of the calculation and statistical analyses.

Different approaches were undertaken to examine possible mechanisms that might be contributing to spatial transmutation. Statistical analysis
was used to examine how landscape scale estimates of parameters $c$ and $k$ were influenced by where in time the regional population was located with respect to the decline portion of the spruce budworm’s outbreak cycle. For this, values of parameters $c$ and $k$ were regressed against the mean regional population density, $[n(t) + n(t + 1)]/2$, and against year, $t$.

Manipulative computer-based experiments were used to determine the roles of spatial and temporal autocorrelation among sites within landscape units. This involved first shuffling acceptable pairs of survey observations among landscape units and over time. In this process, all pairs of survey observations $[n(t), n(t − 1)]$ were kept together, but each pair, as a whole, was allowed to be randomly exchanged with the pair from any other acceptable survey site × time combination. Consequently, most acceptable survey observation pairs were exchanged with pairs from other landscape units and from different times, thus disrupting whatever spatial autocorrelation was originally inherent in the site data. The scaling-up process described above was then applied. We did this for three random shufflings of all 221 data pairs. To determine the role of temporal relationships between survey observations at each site, we performed a second series of three random shufflings of the survey observations, except this time observation pairs, $[n(t), n(t − 1)]$, were broken up and the data were shuffled individually.

3. Results

The results are presented as plots of the values of parameters $c$ and $k$ of Eq. (1) and Eq. (2). In interpreting these plots, recall that each $(c, k)$ pair of parameter values is the result of fitting these equations [after fixing $z(t)$ at its mean of 0] to a 4-year time series of landscape-resolution population density averages. Each of these landscape time series was generated by first applying Eq. (3) separately to the acceptable population density data at all 1 km$^2$ survey sites within each 1600 km$^2$ landscape unit (Fig. 1) and then calculating an average population density among these survey sites for each year of the 4-year sequence. Since the survey site data is exactly described by Eq. (3) in which $c = 0.8$ and $k = −0.89$, one can expect the same parameter values to apply at landscape resolution unless the parameter values depend on the scale of resolution. Thus, any departure of the parameter values fitted to the landscape resolution data from $(c, k) = (0.8, −0.89)$ indicates that the parameter values depend on the scale of resolution.

3.1. Parameter estimates dependent on spatial resolution

The 221 pairs of fitted landscape resolution parameter values are plotted in Fig. 2. That many of them differ substantially from the survey site values of $(c, k) = (0.8, −0.89)$ indicates some dependence on spatial resolution. Fig. 2 also suggests that the distributions of these fitted landscape resolution parameter values have some extreme outliers (statistical tests revealed that the distributions of $c$ and $k$ were both severely leptokurtic [kurtosis statistics (Sokal and Rohlf, 1981) = 27.0 and 52.0, respectively]). The position of the dense oblong cloud of points in the box in the center of the figure suggests that the distributions of $c$ and $k$ may be centered near their survey site values of $(c, k) = (0.8, −0.89)$. The means (and medians) of these distributions [$c = 0.24$ (0.36) and $k = −0.22$ (−0.32)] lend some support to this conjecture, but this support is limited: the 95% confidence intervals about each median, (0.19, 0.55) and (−0.45, −0.15) for $c$ and $k$ respectively, exclude the survey values.

Fig. 2 also reveals that the fitted landscape resolution parameter values do not vary independently of each other (correlation coefficient = −0.931, $P < 0.0005$). Linear regression of the data in Fig. 2 produced the relationship, $k = 0.0245 − 1.02c$. The intercept was not significantly different from 0 (S.E. = 0.124, $P = 0.843$) but the slope was highly significant (S.E. = 0.027, $P < 0.0005$). Apparently the $R^2$ (86.5%) was not affected much by the increasing variance at very high and very low values of parameter $c$. 

Fig. 2. Pairs of parameter values \((c, k)\) calculated by fitting Eq. (2) to time series of mean population densities of landscape units. In fitting Eq. (2), its stochastic factor, \(z(t)\), was fixed at its mean of 0.0. The cross locates \((c, k) = (0.8, -0.89)\), the values used to generate data at individual 1 km\(^2\) sites within the landscape units using Eq. (3). The fitted regression line is \(k = 0.0245 - 1.02c\). Fig. 3 shows detail within the central rectangle.

Fig. 3. Detail within the central rectangular area of Fig. 2. The lines constitute a super-imposed phase plane diagram which distinguishes four regions where the parameter values generate qualitatively different dynamics in Eq. (2) with \(z = 0\). These dynamics are illustrated for three regions by small, interior, schematic graphs of (log) population density, \(N\), against time, \(t\).
3.2. Overlaying a phase plane diagram

The sides of the rectangle drawn near the center of Fig. 2 corresponds to the borders of Fig. 3. The points illustrated in Fig. 3 correspond to those within Fig. 2 central rectangle. In Fig. 3, the three long lines which meet at \((c, k) = (-1, 1)\) and the small central triangle act to separate the \(c \times k\) parameter space into four regions in which Eq. (1) and Eq. (2) exhibit qualitatively different behaviors. This separation of parameter space into regions where these equations have qualitatively different behaviors amounts to the superposition of Royama (1992) (p. 58) phase plane diagram for a homogeneous second-order difference equation. This phase plane is symmetrical about \(c = -1\).

The qualitative behavior of Eq. (1) and Eq. (2) inside each of the three large outer regions is illustrated by the small interior graphs of (log) population density against time. In each of these outer regions of Fig. 3, the values of \(c\) and \(k\) dictate that Eq. (1) and Eq. (2) generate population densities which diverge from their initial levels over time. In the upper right, this divergence is monotonic; in the upper left and lower regions, the direction of divergence changes with time. In the upper left, the generated densities alternate every time unit (year) between new all-time high values and new all-time low values. In the lower region, the cycle length can be longer: 2 years at the left hand edge, 4 years when \(c = -1\), and infinitely long at the right hand edge of the region.

The detail inside the central triangle of Fig. 3 is shown in Fig. 4. Superposition of Royama (1992) (p. 58) phase plane diagram divides this area of parameter space into three regions in which the values of \(c\) and \(k\) dictate three more types of qualitative behavior from time series generated by Eq. (1) and Eq. (2). The small graphs of (log) population density against time inside each of these three interior regions of the large triangle in Fig. 4 illustrate the corresponding type of behavior. Everywhere within this large triangle, the values of \(c\) and \(k\) dictate that these equations generate population densities, which gradually converge from their initial levels to an equilibrium over time. Inside the upper right part of Fig. 4 large triangle, this convergence is monotonic; in the upper left and lower regions, the direction of convergence is

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**Fig. 4.** Detail within the central triangular area of Fig. 3. The phase plane inside the triangle is sectioned into three regions where the parameter values generate qualitatively different dynamics in Eq. (2) with \(z = 0\). Small, schematic graphs of (log) population density, \(N\), against time, \(t\), inside each region in the triangle’s interior illustrate the corresponding dynamics.
convergence changes with time. In the upper left, the generated densities alternate every year between ever decreasing high values and ever increasing low values. Under the parabola, the cycle length can be longer: 2 years at the left hand edge, 4 years when $e = -1$, and infinitely long at the right hand edge of the region.

3.3. Characterizing the extent and isolating the causes of spatial transmutation

Together, Fig. 3 and Fig. 4 distinguish six regions of $c \times k$ parameter space in which the values of these parameters generate qualitatively unique time series of population densities from Eq. (1) and Eq. (2). That data points are located in each of these regions shows that all six qualitatively different types of behavior can be generated from the fitted landscape scale parameter values. This demonstrates that the extent of the scale dependence in the values of parameters $e$ and $k$ is large enough to generate the entire range of qualitatively different behaviors of Eq. (1) and Eq. (2).

We were unable to relate the strong correlation developed between parameters $e$ and $k$ in the process of scaling-up (Figs. 2–4) to regionally declining densities of spruce budworm during the period of observation nor to patterns of spatial autocorrelation inherent in the site data. Plots of the values of parameters $e$ and $k$ against the mean regional population density and against year revealed no statistically significant ($z = 0.05$) relationships. Three random shufflings of acceptable pairs of survey observations among landscape units and over time produced the following relationships between the large scale parameter estimates: $k = 0.443 - 1.82c; R^2 = 92.5\%; k = 0.481 - 1.38c; R^2 = 87.3\%; k = 0.342 - 0.885c, R^2 = 92.7\%$. Indicator variable regression techniques (Draper and Smith, 1981) showed statistically significant ($z = 0.05$) differences among all three slopes and with the slope of the relationship derived from the unshuffled data. There were no statistically significant differences in intercepts among these three shuffled relationships although each differed from the intercept of the relationship derived from the unshuffled survey data (Fig. 2).

4. Discussion

4.1. The stochastic factor

The degree of spatial heterogeneity in the stochastic factor, $z(t)$, of Eq. (1) and Eq. (2) determines the potential contribution of this factor to spatial transmutation (Fleming et al., 1999). According to Royama (1984), this factor represents the effects of weather and moth dispersal. Since both of these processes can operate over large ranges [but see Martinat (1987)], $z(t)$ may be highly correlated in space and thus take on similar values over extensive areas. Our analysis deals with the extreme case in which $z(t)$ has the same value everywhere, namely 0.0, and hence can make no contribution to spatial transmutation. In addition, by assuming $z(t) = 0$ for all $t$, we also implicitly satisfy the condition that the $z(t)$s are temporally uncorrelated.

Thus the contribution of the deterministic factor to spatial transmutation in Eq. (1) and Eq. (2) was isolated and analyzed without necessarily violating conditions on temporal or spatial correla-
tion of the stochastic factor. This approach amounts to treating the landscape as a series of spatially disconnected sites in which each local population oscillates according to the same dynamic Eq. (3). In many ways, this approach concurs with Royama (1984, 1992) theory of independent local population fluctuations driven by a common density-dependent process (e.g. Eq. (3)) and brought into synchrony by spatial correlation among the density-independent perturbations, $z(t)$ (Royama suggests that synchrony in weather patterns may correlate reproductive rates over large areas).

In contrast to our approach, the stochastic factor varies over space and can contribute to spatial transmutation. Then, according to the central limit theorem (Hogg and Craig, 1970 pp. 182–5), the variance (among landscape units (Fig. 1)) of the mean value of $z(t)$ over the sampling sites within each landscape unit will be less than the variance (among landscape units) of the single value of $z(t)$ applied to each landscape unit as a whole. The consequence is simplest to envision when there is no spatial heterogeneity in population density in both years $t$ and $t−1$ among survey sites sampled within the landscape unit. In this case, expected values of population densities predicted for year $t+1$ at the two scales are equivalent, but fewer extreme (very high and very low) predicted population densities are likely in averages among the sample site means (within landscape units) than in averages among the single values of $z(t)$ for each landscape unit as a whole. Normally, of course, population densities and stochastic effects vary over space; then complex interactions between these quantities are possible in determining future population densities. We suspect that one consequence of such interactions would be ‘noisier’ patterns in the $k \times c$ parameter plane, perhaps enough to obscure the linear trend along $k = −c$ evident in Figs. 2–4. Investigation of such interactions is beyond the scope of this paper.

4.2. The deterministic factor

Following Fleming et al. (1999), we used non-parametric statistics to test for the widespread presence of resolution-dependence in the distributions of the landscape values of parameters $c$ and $k$. Since we eliminated all landscape units with a single acceptable survey site, and which were, therefore, incapable of demonstrating scale dependence anyway, we tested slightly more appropriate distributions than Fleming et al. (1999). Consequently, our numerical values were slightly lower in absolute value than those reported previously, but the conclusions are the same. The distributions of parameter values calculated from 221 landscape unit averages [our medians (95% confidence limits) were $c = 0.36 (0.19, 0.55); k = −0.32 (−0.45, −0.15)] tended to have lower absolute values than those of the parameters dictating population dynamics at the scale of individual survey sites ($c = 0.8; k = −0.89$). The net result of this resolution-dependence in parameter values is that many time series of population densities at the coarser resolution appear smoother, less non-linear than those at individual survey sites and this is symptomatic of spatial transmutation. For many 4-year sequences, the general dynamic behavior appears to be changed by scaling-up. For instance, Eq. (3) produces damped oscillations in population densities. Substituting $c = 0.36$ and $k = −0.32$ into Eq. (2), however, and fixing $z(t)$ at its mean, 0, as before in order to focus on the deterministic dynamics, results in a steady divergence of population densities over time from their initial value without oscillations (Fig. 4). Thus, using data collected at one scale of resolution (e.g. 1 km² survey sites) to parameterize or construct models operating on another scale of resolution (e.g. 1600 km² landscape units) can incorporate spatial transmutation severe enough to distort not just the quantitative aspects of predicted population trends, but even the qualitative behavior of these trends.

Locating the median of the distributions of landscape resolution parameter values provides little information about the broad patterns and extent of resolution-dependence and spatial transmutation. Scatter plots of the $c \times k$ parameter values calculated for each landscape unit (e.g. Fig. 2) showed some extreme resolution-dependence: in the most extreme a landscape unit with 35 acceptable survey sites had $c = 35.0$ and $k = −
These values are over 40 and 50 times, respectively, the corresponding values used to generate the data initially at the survey site scale: $(c, k) = (0.8, -0.89)$. The scatter plots also revealed a pattern in the resolution-dependence: a strong negative correlation ($-0.931$) between the landscape units’ parameter values.

Placing phase plane diagrams over the $k \times c$ scatter plots (Figs. 3 and 4) showed that scaling-up produced considerable spatial transmutation: the entire range of qualitatively different behaviors of Eq. (1) and Eq. (2) was generated. Since the same scaling-up process was applied to all data, it is clear that knowing this process alone does not necessarily make the emergent qualitative behavior at the new scale predictable. Information about the temporal and spatial heterogeneity of the survey site data within each landscape unit may be crucial to forecasting changes in mean population densities for the unit as a whole when time series models are involved. For instance, an approach to correcting for spatial transmutation in time series population growth models is explored in the Appendix A. This scheme, which extends that of Allen (1988), requires estimates of the variances and covariance in the survey site data for years $t$ and $t - 1$ (in this scheme, non-linearity in the model, as measured by its second-order partial derivatives, also affects the degree of spatial transmutation).

Figs. 2–4 reveal a pattern whereby many of the landscape scale $(c, k)$ points are located close to the line, $c + k = 0$. The medians, $(c, k) = (0.36, -0.32)$, and Royama’s (Royama, 1984 figure 28) values that were used in Eq. (3) to generate the survey scale data, $(c, k) = (0.8, -0.89)$, are both close to this line. For $c > -1$, parameter values along this line (which is drawn running from the peak of the triangle, down its right side, and out the lower right of Fig. 3), generate time series of population densities from Eq. (3) which neither converge nor diverge. In effect, Eq. (3) has a neutral equilibrium point when $c + k = 0$ for $c > -1$. Such parameter values would allow the density-independent stochastic factor, $z(t)$, to dominate and impose a random walk on the time series of generated population densities.

The tendency for landscape unit estimates of $c$ and $k$ to lie near the line $c + k = 0$ may result from the preservation of long-period oscillations rather than the adoption of neutrally stable dynamics at landscape scales. The parameter values $(c, k) = (0.8, -0.89)$ used to generate the survey site data, lie just inside the right side of the parabola in Fig. 4, slightly below the line $c + k = 0$. In this region of Fig. 4, Eq. (3) generates converging time series which have long-period oscillations. Generally, long-period oscillations in the population densities of individual survey sites within landscape units were at least slightly out of phase. Consequently, the corresponding changes in landscape unit averages often followed a somewhat ‘confused’ pattern. In essence, ‘noise’ was introduced into the landscape scale dynamics by the lack of synchrony in the survey site dynamics. Consequently, the process of fitting Fig. (1) or Eq. (2), $z(t) = 0$, to the landscape unit averages amounted to ‘overfitting’ in the sense that the parameters $c$ and $k$ were calculated to fit exactly the basic oscillation (dictated by $c = 0.8$ and $k = -0.89$) plus the ‘noise’ introduced by the asynchrony between survey site dynamics. The pattern of data points in Figs. 3 and Fig. 4 suggests that often the ‘overfitted’ parameters correctly reflect the general (first-order) temporal trends in the average population densities of the landscape units, but that the introduced ‘noise’ disguised the more subtle (second-order) feedback effect. This may explain why 51% of the landscape scale pairs of parameter values occur in the upper right region of Fig. 3 where time series diverge monotonically, and only 16% of them occur in the lower region inside Fig. 4 triangle where time series undergo long-cycle oscillations and where the parameters dictating survey site dynamics lie. This may also explain the relative absence of points in the lower left in these figures because that is the region of very short period oscillations where feedback effects are particularly evident (conducting the same scaling-up experiment as illustrated in Figs. 2–4, but with fine scale $c \times k$ parameter values chosen from the lower left of Fig. 4, e.g. $(c, k) = (-2.8, -0.89)$, produced much noisier and weaker relationships [correlation coefficient $= -0.192$] than those described above.
for \((c, k) = (0.8, -0.89)\) and almost all landscape unit estimates fell in Fig. 3’s upper left region.

An alternative possible explanation for the pattern of points in Figs. 2–4 is based on the fact that the spruce budworm population was declining regionally during the data collection period: from 8.85 second instars per 75 cm branch tip in 1985 to 0.011 in 1995. Hence, at the majority of acceptable survey sites one could expect \(n(t) < n(t - 1)\). Since the parameter values used to generate data at the survey sites, \((c, k) = (0.8, -0.89)\), produce long-period oscillations, the generation of a pattern of continuing decline, i.e. \(n(t + 2) < n(t + 1) < n(t) < n(t - 1)\), at most survey sites within any landscape unit is not unexpected. However, this possible explanation was ruled out when random shuffling of the site data did little to disrupt the patterns evident in Figs. 2–4.

One biologically misleading feature of Eqs. (1)–(3) is their implicit use of an annual (logarithmic) rate of increase which can rise linearly with population density. Typically, competition for resources, disease, or other density-dependent factors constrain population growth at very high densities. Using more realistic rate of increase functions which level off at an upper limit at high population densities has been shown to dampen divergent dynamics (Royama, 1992 pp. 60–68). This damping of divergent dynamics is likely to reduce the potential asynchrony among survey sites in our ‘thought’ experiments and thus ultimately moderate any ensuing spatial transmutation.

Spatial heterogeneity of the population (or population processes) and the dependence of population processes on population size affect spatial transmutation. An example of heterogeneity and density dependence affecting calculated parameter values was given by Barclay (1992) in a somewhat different context from our computer experiments. He showed that the required rate of sterile releases, or of pheromone trapping, in a program for pest control was higher for an aggregated pest population than for a spatially uniform pest population, and that this discrepancy increased with the degree of aggregation. The mechanism in that context was clear since the efficiency of either control technique increases as population density decreases and the models being used were more mechanistic than Eq. (1) and Eq. (2).

The approximation methodology developed in the appendix is particular illustrative. It shows that the correction factor (Eq. (A.5)), which can be considered one measure of the degree of spatial transmutation, increases with the degree of fine resolution spatial heterogeneity (as measured by the variances and covariance among site data) and with the non-linearity of the population growth rate (as measured by the partial derivatives). It is generally true for non-linear functions that the mean of the functions of individual values is not the same as the function of the mean of the individual values so that if a population response occurs locally as a function of some condition, then the means of the individual responses will not be the same as the response to the mean value of the condition taken over the space in question (Eq. (A.5)). Allen (1988) and Ruel and Ayres (1999) have explored this in terms of Jensen’s inequality.

5. Summary and conclusions

The importance of issues like global change and ecological disturbance have increased the need to extend the dynamic models of forest research to larger spatial scales. But there are hazards to moving between scales and these hazards permeate most aspects of forest science, from modeling to field work.

Spatial transmutation, a mechanism by which the behavior of a process’s dynamics can appear to change with the scale of investigation, is one such hazard. Spatial transmutation is a property of system dynamics and can be a problem when it is ignored in developing models and in applying them for purposes such as prediction and decision support. Spatial transmutation can arise when accurate models developed at one spatial resolution are applied to another. In this case, spatial transmutation is a problem of application, it is not an inherent fault of the model. On the other hand, when models using one scale of resolution incorporate data, mathematics, or the results of analyses, which represent relationships among
variables at another resolution, then spatial transmutation can become an intrinsic problem of the model.

This paper focused on how the same information, even when measured with complete accuracy, can produce apparent distortions when used to make predictions at different scales. Specifically, we analyzed some characteristics and consequences of spatial transmutation in applying a second-order autoregressive time-series model of spruce budworm population dynamics (Royama, 1984) at different spatial resolutions. In these models, parameter estimation proved to be resolution-dependent: parameter values estimated from time-series data consisting of large area averages were as much as 40 or 50 times greater in absolute value than the parameters generating the raw data at the much finer resolution of survey sampling sites. Examination of phase plane diagrams showed that the distribution of landscape unit parameter values called for a wide variety of qualitatively different types of dynamic behavior. Thus Royama (1984) autoregressive time-series models are capable of producing difficulties when some form of spatial aggregation is used to scale them up. Spatial transmutation should be a concern when there is both variability in fine scale population densities and non-linearity in population growth rates.

In many situations, the intensity of spatial transmutation may be milder than that shown here. For instance, more realistic ‘rate of increase’ functions which are constrained at high population densities can be expected to dampen (incompletely) tendencies toward spatial transmutation. It would also seem that longer time series are more capable of ‘smoothing out’ the ‘noise’ introduced by fine scale spatial heterogeneities and asynchronies than shorter time series. Due to this, we suspect that generating longer (than 4-year) time series at fine spatial resolutions would be less prone to produce as much spatial transmutation as seen in our results.

Our results also highlight a difficulty with using only remotely sensed data (e.g. landscape unit averages of population densities) to make predictions at landscape scales when the intrinsic dynamics of the system occur at finer scales. In the absence of fine scale observations, it is impossible to calculate their variability. Consequently, as the appendix shows, this impedes the estimation of the error involved in using the population growth rate calculated at the average densities within the landscape unit to approximate the average of the growth rates at all sites within the unit. Augmenting the remotely sensed data with a few fine scale measurements each year would seem to be the most practical approach to estimating this error. A related concern is that the observed scale dependence in parameter values was sufficient to generate the entire range of qualitatively different possible behaviors of the underlying dynamic model. Since the same scaling-up process was applied to all data, it is clear that knowing this process alone does not necessarily make the emergent qualitative behavior of the system or model at the new scale predictable. Information about the fine resolution spatial heterogeneity within landscape units is needed to correct for the effects of spatial transmutation.

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Appendix A

Consider a landscape unit which is composed of $s$ sites. Suppose that at each site $i$ within the landscape unit the discrete-time, population growth model:

$$n_{i,t+1} = r(n_{i,t}, n_{i,t-1}, \ldots)n_{i,t},$$

(A.1)
applies where \( n_t \) is the population density at time \( t \), and the per capita population growth rate, \( r(n_t, n_{t-1}, \ldots) \), can be related to previous population densities at the site. This model is purely deterministic; it excludes any net effects of exogenous, density-independent factors operating in \( t \), \( t + 1 \). Eq. (3) is a specific example of such a growth model.

In many situations, Eq. (A.1) or its stochastic counterparts (e.g. Eqs. (1) and (2)) can be estimated through detailed experiment at particular sites. But to forecast future population densities for the landscape unit in the next time period, i.e.: 
\[
\bar{n}_{t+1} = \bar{r}\bar{n}_t, \\
\text{(A.2)}
\]
where \( \bar{n}_t \) is the average population density in the landscape unit at time \( t \), we need to determine the mean population growth rate at time \( t \) in the unit as a whole:
\[
\bar{r}_t = \int \ldots \int \left( r(n_s, n_{s-1}, \ldots) f(n_s, n_{s-1}, \ldots) \right) dn_s dn_{s-1} \ldots \\
\text{(A.3)}
\]

In Eq. (A.3), the integrations are over the ranges of the population densities, \( n_s, n_{s-1}, \ldots \), encountered among the \( s \) sites within the landscape unit, and \( f(n_s, n_{s-1}, \ldots) \) is the probability density function which describes the frequency with which each particular time series of population densities occurs at sites within the landscape unit. Since \( f(n_s, n_{s-1}, \ldots) \) is almost never known explicitly, one can not rely on solving Eq. (A.3) in closed form. However, an approximation can be generated when it is possible to expand \( r(n_s, n_{s-1}, \ldots) \) in Taylor series about the landscape unit’s mean population densities, \( \bar{n}_s, \bar{n}_{s-1}, \ldots \).

For instance, if \( r(n_s, n_{s-1}, \ldots) \) corresponds to a second order population dynamics model such as Eqs. (1)–(3), above, then its Taylor series expansion can be written as (Thomas, 1968):
\[
r(n_s, n_{s-1}, \ldots) \\
= r(\bar{n}_s, \bar{n}_{s-1}, \ldots) + (n_s - \bar{n}_s)\bar{c}r/\bar{n}_s \\
+ (n_{s-1} - \bar{n}_{s-1})\bar{c}r/\bar{n}_{s-1} \\
+ (n_t - \bar{n}_t)^2\bar{c}^2r/\bar{n}_t^2 \\
+ 2(n_s - \bar{n}_s)(n_{s-1} - \bar{n}_{s-1})(\bar{c}r/\bar{n}_t) \\
+ (n_{t-1} - \bar{n}_{t-1})^2\bar{c}^2 r/\bar{n}_{t-1}^3/2! + \text{hot}, \\
\text{(A.4)}
\]

where all partial derivatives are evaluated at \( \bar{n}_s, \bar{n}_{s-1}, \ldots \) and ‘hot’ indicates higher order terms which we assume are negligible as part of the approximation process.

Substituting Eq. (A.4) into Eq. (A.3):
\[
\bar{r}_t \approx r(\bar{n}_s, \bar{n}_{s-1}, \ldots) + (\bar{c}r/\bar{n}_s) \int \left( (n_s - \bar{n}_s) f(n_s, n_{s-1}, \ldots) \right) dn_s dn_{s-1} \\
+ \left( (\bar{c}^2 r/\bar{n}_s^2) \int \left( (n_s - \bar{n}_s)^2 f(n_s, n_{s-1}, \ldots) \right) dn_s dn_{s-1} \\
+ 2(\bar{c}r/\bar{n}_s)(\bar{c}r/\bar{n}_{s-1}) \int \left( (n_s - \bar{n}_s)(n_{s-1} - \bar{n}_{s-1}) f(n_s, n_{s-1}, \ldots) \right) dn_s dn_{s-1} \\
+ (\bar{c}^2 r/\bar{n}_{s-1}^2) \int \left( (n_{s-1} - \bar{n}_{s-1})^2 f(n_{s-1}, n_{s-1}, \ldots) \right) dn_s dn_{s-1} \\
+ (\bar{c}^2 r/\bar{n}_{s-1}^3) \int \left( (n_{t-1} - \bar{n}_{t-1})^3 f(n_{t-1}, n_{t-1}, \ldots) \right) dn_s dn_{s-1} \\
\right) /2!
\]

This equation for the mean population growth rate in the landscape unit can be simplified by noting that the second and third terms vanish during integration, and that the expressions under the last three double integrals correspond to variances and covariances [specifically \( \sigma^2(n_s), \text{COV}(n_s, n_{s-1}), \text{ and } \sigma^2(n_{s-1}) \), respectively]. Consequently, the mean population growth rate in the landscape unit can be approximated by:
\[
\bar{r}_t \approx r(\bar{n}_s, \bar{n}_{s-1}, \ldots) + \text{cf} \\
\text{(A.5)}
\]
where
\[
\text{cf} = (\bar{c}^2 r/\bar{n}_s^2)\sigma^2(n_s) \\
+ 2(\bar{c}r/\bar{n}_s)(\bar{c}r/\bar{n}_{s-1})\text{COV}(n_s, n_{s-1}) \\
+ (\bar{c}^2 r/\bar{n}_{s-1}^2)\sigma^2(n_{s-1})/2
\]
is a correction factor which approximates the error involved in estimating the mean population growth rate in the landscape unit by the growth rate corresponding to the mean population densities. For example, for Eq. (2) above with \( z(t) = 0 \),
\[
\text{cf} \approx \{c(c-1)\bar{n}_s^{-2}\sigma^2(n_s) \\
+ 2c\bar{n}_s^{-1}\bar{n}_{s-1}^{-1}\text{COV}(n_s, n_{s-1}) \\
+ k(k-1)\bar{n}_{s-1}^{-2}\sigma^2(n_{s-1})\bar{n}_s^{-k}/2
\]
References


