Forecasting spatially structured populations: the role of dispersal and scale

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Abstract

We forecasted spatially structured population models with complex dynamics, focusing on the effect of dispersal and spatial scale on the predictive capability of nonlinear forecasting (NLF). Dispersal influences NLF ability by its influence on population dynamics. For simple 2-cell models, when dispersal is small, our ability to predict abundance in subpopulations decreased and then increased with increasing dispersal. Spatial heterogeneity, dispersal manner, and environmental noise did not qualitatively change this result. But results are not clear for complex spatial configurations because of complicated dispersal interactions across subpopulations. Populations undergoing periodic fluctuations could be forecasted perfectly for all deterministic cases that we studied, but less reliably when environmental noise was incorporated. More importantly, for all models that we have examined, NLF was much worse at larger spatial scales as a consequence of the asynchronous dynamics of subpopulations when the dispersal rate was below some critical value. The only difference among models was the critical value of dispersal rate, which varied with growth rate, carrying capacity, mode of dispersal, and spatial configuration. These results were robust even when environmental noise was incorporated. Intermittency, common in the dynamics of spatially structured populations, lowered the predictive capability of NLF. Forecasting population behaviour is of obvious value in resource exploitation and conservation. We suggest that forecasting at local scales holds promise, whereas forecasting abundance at regional scales may yield poor results. Improved understanding of dispersal can enhance the management and conservation of natural resources, and may help us to understand resource-exploitation strategies employed by local indigenous humans.

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1. Introduction

Spatially structured populations are common in natural ecosystems with spatial patterns having been documented in many taxa, including plants, beetles, fishes, birds, and mammals (Husband and Barrett, 1998; Cattadori et al., 2000; Epperson, 2000; Lennon et al., 2001; Roslin, 2001; Freckleton and Watkinson, 2002; Vinje et al., 2003). Developing an understanding of how the dynamics of spatially structured populations evolve and being able to predict their trajectories are of much interest to ecologists and resource managers. Applications of forecasting to resource management and conservation have been documented in recent years (Boyce and Miller, 1985; Noakes, 1989; Dennis et al., 1991; Chen and Shelton, 1996; Chen and Ware, 1999).

There are at least two ways that the dynamics of populations can be structured spatially. First, extinction and colonization are the key processes in metapopulation dynamics (Levins, 1969, 1970; Hanski and Gilpin, 2001; Roslin, 2001; Freckleton and Watkinson, 2002; Vinje et al., 2003). Developing an understanding of how the dynamics of spatially structured populations evolve and being able to predict their trajectories are of much interest to ecologists and resource managers. Applications of forecasting to resource management and conservation have been documented in recent years (Boyce and Miller, 1985; Noakes, 1989; Dennis et al., 1991; Chen and Shelton, 1996; Chen and Ware, 1999).
Yet, others have argued that the dynamics of regional populations need not be governed by extinction and colonization even though populations might show spatial pattern (Harrison, 1991; Hastings, 1993). Dispersal and habitat heterogeneity alone can structure the dynamics of regional populations. Spatial scale and dispersal have been shown to be important factors affecting population dynamics in spatial context (Wiens, 1989; Levin, 1992; Scheuring and Jánosi, 1996). For example, DeRoos et al. (1991) showed that population dynamics at different spatial scales depended on the characteristic scale imposed by the biology of the species with the dynamics at small spatial scales largely determined by interactions between individuals. Also, several studies have found that limited dispersal can increase the stability of population dynamics and reduce the risk of extinction (Taylor, 1990; González-Andújar and Perry, 1993; Hastings, 1993; Ruxton, 1994; Scheuring and Jánosi, 1996).

In the present paper, we investigate the role of dispersal and spatial scale in nonlinear forecasting (NLF) by projecting the dynamics of spatially structured population models. We envision model species that are relatively abundant, disperse among subpopulations, and are not subject to local extinctions. We focus on subpopulations that are unstable and show complex dynamics. This is reasonable for a variety of species typically exploited by humans, e.g. plants in the forest, fisheries, and wildlife, especially in tropical regions where biological interactions appear to have the greatest effect on the dynamics of populations and communities (Dobzhansky, 1950; Winemiller, 1990; Polis, 1991), thereby ensuring that nonlinear dynamics structure population fluctuations. Indeed, many populations in tropical regions show substantial fluctuations (Wolda, 1978; Gadagkar and Sundararaj, 1985) despite the expectation that the rigours of climate have less bearing on populations in the tropics than in more temperate regions (MacArthur, 1972). Also, May (1987) argued that exploited populations are among those most likely to exhibit chaotic dynamics. Although there is still debate about the relevance of chaos in biological populations (Hastings et al., 1993), there is no question that nonlinear structure is fundamental to any model of ecological interactions (Schaffer, 1988).

The manner by which dispersal occurs among subpopulations is likely to affect system dynamics, e.g. whether dispersal is density dependent (May, 1989; Hassell et al., 1991). Hassell et al. (1991) assumed rates of dispersal were density independent, although dispersal was proportional to population size. Even though rates of dispersal were not strictly density dependent, because more animals left high-density areas and fewer left low-density areas, the net effect was density dependent. This effect can be made even stronger by defining the rate of dispersal to be a direct function of density. Either form of dispersal has the potential to stabilize the dynamics of populations because emigration may be high when densities become large and/or immigration from surrounding population may bolster population size when it is small. We expect that density-dependent dispersal will occur as an adaptive response by individuals to local density conditions, whereas an innate propensity for dispersal amongst individuals in a population may be density independent. The distinctions and consequences for the evolution of dispersal are developed by Gadgil (1971) and Comins et al. (1980). We will examine both forms.

In addition, there are many modes of dispersal. Spatial scales, modes of locomotion, spatial heterogeneity, and behaviour can influence the manner and distance that organisms disperse into surrounding areas (Kot et al., 1996; Yamamura, 2002b). Also, dispersal may vary as a function of age or phenotype (Lomnicki, 1988; Skalski and Gilliam, 2000), or may be a complex function of distance among sites. To limit the scope of our analysis, we will consider only two modes of dispersal: one where dispersal occurs amongst n adjacent cells or subpopulations during each time interval, and the other where a dispersal pool of floaters develops that may settle in any of n subpopulations.

We begin by limiting spatial structure to simple homogeneous 2-cell populations, then examine the influences of spatial heterogeneity and different modes of dispersal, and subsequently expand the analysis to more complex spatial configurations. Also, we explore consequences of environmental noise and intermittency in population dynamics, which might lower the ability of NLF. Finally we discuss the implications of NLF ability for the exploitation and management of natural resources.

We examine the hypothesis that with low to moderate dispersal, populations on smaller spatial scales are better predicted implying that they can be managed more easily. We demonstrate that this hypothesis is true with critical levels of dispersal changing as a function of growth rate, carrying capacity, mode of dispersal, and spatial configuration.

2. Models and methods

We used the following Moran-Ricker nonlinear population model (Moran, 1950; Ricker, 1954), which is one of the most widely used models in ecology (Zheng and Kruse, 2003), to iterate the dynamics of each subpopulation:

\[ N_{i+1} = N_i \exp[r(1 - N_i/K)], \]  

(1)

where \( N_i \) is the density of a subpopulation at time \( t \), \( r \) is the potential growth rate, and \( K \) represents the carrying capacity. Except where specified otherwise, we assume a
homogeneous environment with \( r \) and \( K \) equivalent among subpopulations. The dynamics of this model, which has been studied extensively, are summarized in Fig. 1, illustrating the complicated dynamics for \( r > 2.6924 \). In the following simulations \( r \) is equal to 3.5 except when specified otherwise.

Use of this model is justified on the grounds that such a discrete-time model can capture the essential behaviour of more complex models (Schaffer, 1985; Murdoch et al., 2002; Geritz and Kisdi, 2004). Specifically, we assume that this model may approximate a 1-dimensional (1-D) map of a multi-species system in continuous time. And certainly it is the case that the spectrum of dynamical behaviours emanating from this model can be found in nature (Turchin and Taylor, 1992; Dennis and Taper, 1994; Cushing et al., 1996; Cushing et al., 2003). There are abundant applications of this model in fisheries and wildlife (Paulik and Bayliff, 1967; McCarthy, 1996; Elliott et al., 1997; Saitoh et al., 1999; Knutson et al., 2001; Rivet et al., 2001; Taper and Gogan, 2002; McCarthy et al., 2003; Travis, 2003; Zheng and Kruse, 2003).

Two modes of dispersal—proportional dispersal and density-dependent dispersal—were examined. Proportional dispersal means dispersal is simply proportional to population size. We used the following dispersal model to describe this process:

\[
N_{0,t} = N_{t-1} + \sum_{j=1}^{n} (D_{ij}N_{j,t} - D_{ij}N_{i,t})(D_{ij}, D_{ij} < 1/n),
\]

in which \( N_{i,t} \) and \( N_{0,t} \) denote densities of subpopulation \( i \) at time \( t \) before and after dispersal, respectively; \( D_{ij} \) is the dispersal rate from subpopulation \( i \) to subpopulation \( j \), which can be expressed as a detailed form: \( D_{ij} = \delta_{ij}(1 - \mu_{ij}) \), where \( \delta_{ij} \) is an innate rate of dispersal and \( \mu_{ij} \) is dispersal mortality from subpopulation \( i \) to \( j \). For simplicity we used only the general form of \( D_{ij} \) to represent the rate of dispersal; \( n \) is defined as the number of cells that exchange dispersers with subpopulation \( i \). For different spatial configurations \( n \) has different values. For example, \( n = 2 \) in 2-cell models where the net effect of dispersal may involve either emigration or immigration, depending upon whether subpopulation \( i \) is smaller or larger than subpopulation \( j \).

The second mode is density-dependent dispersal. We assumed the rate of emigration from a subpopulation depends upon population size in a quadratic fashion, but otherwise the model is like model (2):

\[
N_{t+1} = N_{t} + \sum_{j=1}^{n} (D_{ij}N_{j,t} - D_{ij}N_{i,t})(D_{ij}, D_{ij} < 1/n),
\]

where all parameters are qualitatively the same as above.

For both dispersal modes, we assume that dispersal happens subsequent to recruitment within each subpopulation. And for convenience \( D_{ij} \) is set equal to \( D_{ij} \) for all cases, i.e., \( D_{ij} = D_{ij} = D \).

Based on the underlying dynamics and the dispersal mechanisms mentioned above, we explored one simple (2-cell model) and three more complex spatial configurations (dispersal pool model, linear chain model, and grid model) with each having 9 cells. For the dispersal pool model (DPM), we envision that dispersal involves a pool of individuals ready to colonize sites when they become available (Gadgil, 1971). This means that each of the 9 cells enjoys equal exchanges of dispersal with each of the other 8 cells. Dispersal pools of “floaters” appear to exist in many avian populations (Zink, 2002), as well as some mammal populations (Chepko-Sade and Halpin, 1987). Comparatively, dispersal occurs only between adjacent cells in a linear chain of cells for the linear chain model (LCM). Our motivation behind this spatial organization came from an interest in coastal marine fisheries where fish populations are distributed essentially in a linear fashion. Similarly, such organization is a reasonable way to consider populations of aquatic organisms occupying a stream or river where dispersal happens between adjacent subpopulations. For the grid model (GM), cells were arranged in a 3 \( \times \) 3 grid. In such a configuration, cells on the corners interact with two adjacent cells. Cells located in the middle on each of the four sides have three other cells with which they interact, and the central cell exchanges dispersers with each of these four cells. So, there exist three distinct types of cells depending upon the assignment on the grid.

There are many NLF methods (Casdagli, 1989; Noakes, 1989; Sugihara and May, 1990; Wolpert and Miall, 1990; Rice, 1993). In our study, the artificial
neural network back-propagation (BP) algorithm (Rumelhart and McClelland, 1986) was used to conduct NLF for population dynamics in various spatial configurations at different spatial scales. We used the optimal method of Levenberg-Marquardt (Lou and Shi, 1998) as the training rule, which is a technique for modifying the connection weights of the network through a momentum item and auto-adaptive regulation of learning rate. Lou and Shi (1998) showed that this type of training rule can increase the reliability of BP algorithm substantially and improve the speed of learning. By presenting a network with the first part of a time series and training it to output subsequent values, the network therefore could be trained to approximate the dynamics that underlie the series. The trained network was then used to predict forward from each point in the second part of the series (for details see Wolpert and Miall, 1990). To measure prediction success we used the correlation coefficient between predicted and observed values from the second part of the series (Sugihara and May, 1990).

To examine consequences of environmental noise we incorporated multiplicative noise (Kaitala et al., 1997) into Eq. (1) as \( N_{t+1} = N_t \exp[r(1 - N_t/K)(1 + \varepsilon_t)] \), and assumed \( \varepsilon_t \) to be uniformly distributed on the interval \((-H, +H)\), where \( H \) is the strength of environmental noise and \( H = 0 \) means that there is no noise. In all our simulations, initial population sizes were randomly and uniformly distributed between 0 and 1.

3. Results

3.1. 2-cell model

3.1.1. Spatial homogeneity and proportional dispersal

We first examined the simple homogeneous 2-cell model with proportional dispersal. Initial population sizes were randomly chosen in the interval of \((0, 1)\) in all simulations. Because our ability to forecast population dynamics is closely related to the dynamical behaviour of populations, which is further influenced by dispersal, we first review the effects of dispersal on the model dynamics and corresponding 1-D maps which we will use to explain NLF precision. Details are shown in Fig. 2.

From this figure together with our numerical simulation results (not shown here), we note that there are five types of dynamics with increasing \( D \), summarized as zones in Table 1.

\[ D = 0, 1 \] representing no dispersal and free dispersal, are two extreme cases. If there is no dispersal, asynchronous chaotic populations occur in each of the two cells, but when there is free dispersal the entire population becomes a single chaotic superpopulation where the carrying capacity is the sum of those of the two cells. For both zone I and IV the two cells have chaotic asynchronous dynamics, but there is significant difference in their underlying 1-D maps. Examples for \( D = 0.005 \) in zone I and \( D = 0.2 \) in zone IV are illustrated in Figs. 3 and 4. When \( D = 0.005 \), 1-D maps of individual populations have good structures (Fig. 3A and B), while the summed population is not so well behaved because different initial population densities lead to very different chaotic dynamics of the two subpopulations, thereby the apparent randomness in the structure of 1-D map of the summed population (Fig. 3C). But when \( D = 0.2 \) the 1-D map of each subpopulation is almost as fuzzy as that of the summed population (Fig. 4). Obviously dispersal destroys the nonlinear structure of original dynamics of each single cell. In zone V the chaotic dynamics of two subpopulations become completely synchronous just as for free dispersal. The 1-D maps for each subpopulation regain the structure that existed when \( D = 0 \). In contrast with the case of no dispersal, the summed population also has a well-structured 1-D map because large dispersal rates cause the entire population to behave as a single superpopulation. Quasi-periodic oscillations (2-cycles) in zone

<table>
<thead>
<tr>
<th>Zone</th>
<th>( D )</th>
<th>Dynamical behaviour</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>[0, 0.021)</td>
<td>Chaotic asynchronous dynamics</td>
</tr>
<tr>
<td>II</td>
<td>[0.021, 0.035)</td>
<td>Quasi-periodic oscillations</td>
</tr>
<tr>
<td>III</td>
<td>[0.035, 0.165)</td>
<td>2-cycles</td>
</tr>
<tr>
<td>IV</td>
<td>[0.165, 0.260)</td>
<td>Chaotic asynchronous dynamics</td>
</tr>
<tr>
<td>V</td>
<td>[0.260, 1.0]</td>
<td>Chaotic synchronous dynamics</td>
</tr>
</tbody>
</table>

Fig. 2. Bifurcation diagram describing the dynamics of subpopulation 1 produced by the homogeneous 2-cell model with the dispersal manner as described in model (2). In the simulations, the first 500 values of population size were omitted to remove the initial transient and the next 500 values were printed for each \( D \).

Table 1: Five types of dynamical behaviour of the homogeneous 2-cell proportional dispersal model with increasing \( D \).
II (III) suggest that small to intermediate amount of dispersal can stabilize the 2-cell system as discussed by Yamamura (2002a). Fig. 5 illustrates the periodic structure of 1-D map for subpopulation for zone II.

For the five dynamical zones identified in Table 1, we forecasted the dynamics of subpopulation 1 and the summed total population, examining the relation between dynamics and the ability of NLF, and also the role of scale. When $D$ belongs to zone I, the prediction correlation of subpopulation 1 for $T_p$ (prediction step) = 1, 2 remains at 1.0 for all values of $D$ (Fig. 6A and B). For $T_p = 3$–6, the correlation coefficient generally decreases as $D$ increases, and this trend becomes more obvious when $T_p$ gets larger (Fig. 6C–F). From $T_p = 2$, the correlation coefficient for the summed population becomes smaller (the average value decreases from 0.7257 to about 0.2695 when $T_p$ increases to 2 from 1), and fluctuates around 0.0 with increasing $D$ for larger $T_p$ (Fig. 6). Another remarkable characteristic shown in Fig. 6 is that for any values of $T_p$, the correlation coefficient for subpopulation 1 is larger than for the summed total population because of the randomness in the structure of 1-D map of the summed population shown in Fig. 3. Our investigation of the dynamics for subpopulation 2 yields the same result. In other words, the ability of NLF for subpopulations generally decreases with increasing $D$, and the ability of NLF for the summed total population is always much weaker than for individual populations.

As $D$ increases in zone II, the ability of NLF for the summed total population is still much weaker than for the individual subpopulations, which generally increases with increasing $D$ (Fig. 7). The periodic structure emerging from the 1-D map (Fig. 5A) makes NLF for subpopulation easier than in zone I. When $D$ continues to increase to zone III, this effect becomes much more evident and the ability of NLF is good for both individual and summed populations. The correlation coefficient remains at 1 for both cases even when the prediction step is infinite (Fig. 8).

Further increasing $D$ beyond 0.165 leads to chaotic asynchronous dynamics. NLF has similar ability for both individual and summed populations due to similar fuzzy 1-D maps shown in Fig. 4, and there is no obvious
tendency of increasing or decreasing NLF ability with increasing $D$ (Fig. 9). In the last zone V, the subpopulations and the summed population also have similar NLF results but precision of NLF is much better than in zone IV because both subpopulations and the summed population have well-structured 1-D maps.

In most biological populations, we suspect that $D$ is seldom larger than 0.5 because for $D > 0.5$ we observe inverse density dependence, i.e. subpopulations with relatively high densities get even more dispersers. Yet, perhaps such aggregation phenomena are more common than our intuition would suggest (Kareiva and Odell, 1986).

In terms of the relation between dynamics, NLF precision, and scale, for this homogeneous 2-cell model with proportional dispersal, we summarize the above results as follows (we use NLF(s) to denote the ability of NLF at smaller spatial scales and NLF(l) at larger spatial scales):

(i) In zone I & II—NLF(s) > NLF(l) and NLF(s) is better in zone II than in zone I.
(ii) In zone III—NLF(s) = NLF(l) is the best among the five zones.
(iii) In zone IV & V—NLF(s) is similar to NLF(l), both NLF(s) and NLF(l) are better in zone V than in zone IV.
(iv) Both NLF(s) and NLF(l) are better in zone V than in zone I because NLF(s) and NLF(l) in zone V are equal to those when there is no dispersal and in zone I NLF(s) decreases with increasing $D$.

Clearly, dynamics essentially determine NLF precision. Four main points also are suggested:

First, dispersal affects NLF precision because of its effects on the dynamics of populations.
Second, when $D$ is small (here for $D$ in zone I and II and the critical value is 0.035), the ability of NLF is closely related to spatial scale. NLF is much better at
smaller spatial scales. In other words, in the special dynamical zone (i.e. zone I and II) scale is another key factor determining the ability of NLF.

Third, NLF is perfect at any spatial scale when the dynamics are periodic.

Fourth, as D increases in zone I/II, the ability of NLF for subpopulations decreases/increases correspondingly.

In the following two sections, we will examine if these observations on forecasting are influenced by spatial heterogeneity or the mode of density-dependent dispersal.

3.1.2. Spatial heterogeneity and proportional dispersal

In the above, we assume the 2-cell model system is spatially homogeneous with r and K equivalent between the two subpopulations as would be observed in a homogeneous environment. In fact, heterogeneous environments are much more common in the natural world, and much of spatial variation can be attributed to spatial variation in habitats with the effect of altering r and K. Here, we investigate the case where the two subpopulations have different values of r or K. First, we check spatial variation in r. Because there are three types of behaviour relating to r in the dynamics of model (1), we choose r_2 = 3.0, 2.4, 1.5, respectively, denoting chaotic, periodic, and stable dynamics, with r_1 fixed to 3.5.

The bifurcation diagram of subpopulation 1 with D for r_2 = 3.0 is shown in Fig. 10, and the corresponding dynamical zones are listed in Table 2.

Our results of NLF for the dynamics of subpopulations and the summed population in all the zones are similar to the above. Especially, as D increases from zone I to zone II, the NLF ability for subpopulations generally decreases and then increases (Fig. 11). In both zones I and II, NLF is consistently better at smaller spatial scale (Fig. 11). From Fig. 11, we also can see that NLF is always better for subpopulation 2 than subpopulation 1. That is, the subpopulation with smaller growth rate yields better forecasting results. Although not shown here, our investigations suggest that NLF is quite good for periodic dynamics in zone III. An obvious difference between this case (r_2 = 3.0) and the above (r_2 = 3.5) is the critical value of D, which is 0.041 here.

When r_2 is equal to 2.4, the critical value of D is 0.005, under which NLF for subpopulations is again better than for the summed population, and subpopulation 2 has better NLF results than subpopulation 1, similar to results above. There is a large range of D values (both [0.005, 0.06] and (0.61, 1]), where the model system has stable, periodic, or quasi-periodic dynamics, making NLF essentially perfect for both subpopulations and the summed one. And for r_2 = 1.5, there are only several, separate, very small intervals where the model has complex dynamics. In other remaining intervals the dynamics are stable, periodic, or quasi-periodic, so that
NLF for both subpopulations and the summed one is perfect for most of $D$ values. Our investigations of other $r_2$ values in stable, periodic, or chaotic range have similar results.

To check the consequences of disparity in $K$ between cells, we chose $K_1 = 1.0$ and $K_2 = 0.6$. The simulation results suggest that in the $D$ interval of $[0, 0.021)$ the ability of NLF for subpopulations is larger than the summed population, forecasting ability generally decreases with increasing $D$, and NLF for subpopulation 1 is better than subpopulation 2. Our investigations of other $K$ values would not qualitatively change these results.

In general, the main points we obtained from our analysis of “Spatial homogeneity and proportional dispersal” remain in spatially heterogeneous environments. But the critical value of $D$ varies with growth rate, $r$, and carrying capacity, $K$. Also, we found NLF is better for subpopulations with smaller $r$ or larger $K$ when $D$ is below its critical value.

3.1.3. Spatial homogeneity and density-dependent dispersal

The bifurcation diagram of subpopulation 1 with $D$ (Fig. 12) is structurally similar to Fig. 2, and we found similar results here as for proportional dispersal. The critical value of $D$ under which the four summary points mentioned above hold, is 0.0146, smaller than for proportional dispersal.

3.2. Other spatial configurations

3.2.1. Dispersal pool model

As in Fig. 13A, the bifurcation diagram here is like that for the homogeneous 2-cell model. But periodic dynamics and convergence of subpopulations emerge at lower values of $D$ (about 0.0065 and 0.05, respectively) because of the strong averaging effect imposed by the dispersal pool (Fig. 13A and simulation results not shown here). The dynamics of the DPM have much more complex structure when $D$ varies from 0 to 0.0065 (Fig. 13B). Again, we observe the pattern that NLF is better at smaller spatial scales in two small continuous intervals of $D$, that is, $(0, 0.0003)$ and $(0.0025, 0.0047)$. As before, NLF is a reliable predictor for either subpopulations or the summed population when the system has periodic dynamics.

3.2.2. Linear chain model and grid model

For these two models, when $D$ increases to 0.013 and 0.008, respectively, the dynamics become simple abruptly. We found the same pattern as for DPM when $D$ belongs to $[0, 0.013)$ and $[0, 0.008)$, respectively. NLF for periodic population fluctuations is still perfect at any spatial scale although it is not shown here.

Fig. 12. Bifurcation diagram describing the dynamics of subpopulation 1 produced by the homogeneous 2-cell model with the dispersal manner as described in model (3). In the simulations, the first 500 values of population size were omitted to remove the initial transient and the next 500 values were printed for each $D$.

Fig. 13. Bifurcation diagram describing the dynamics of subpopulation 1 produced by DPM with the dispersal manner as described in model (2). In the simulations, the first 500 values of population size were omitted to remove the initial transient and the next 500 values were printed for each $D$. Panel B is a detailed part of panel A.
3.3. Consequences of environmental noise

In the above, we project the dynamics of deterministic models. Because natural populations are subject to stochastic perturbations, in this section we explore how environmental noise affects the forecasting patterns obtained above. Our simulation results incorporating noise into the homogeneous 2-cell proportional dispersal model suggest that randomness does not change the forecasting patterns qualitatively, but quantitatively, observed from zones I and II listed in Table 1 (Fig. 14A and B). As $H$ increases from 0 through 0.25 to 0.5, the forecasting ability of NLF for subpopulations is gradually corrupted. But we note that this simply reduces the forecasting correlation, with our observed patterns of “the ability of NLF for subpopulations decreases/increases with $D$ increasing in zone I/II,” and “NLF is better at smaller spatial scales” remaining for both $H = 0.25$ and 0.5. Investigations of other values of $H$ yield similar results except for $H$ large (e.g. $= 1$) when NLF performs poorly at any spatial scale with prediction correlation around 0 for any $D$ value, and there is no trend of increasing or decreasing in NLF for subpopulations with increasing $D$ (simulation results are not shown here).

However, incorporating randomness obviously changes the pattern observed from the 2-cycles zone of III in Table 1 (Fig. 14C and D). Even very small values of $H$ (e.g. = 0.05) can dramatically erode the ability of NLF for the summed population, reducing the correlation coefficient to below 0.5 for small $D$ values, reduced from 1 when there was no environmental noise (Fig. 14C). In other words, when randomness was incorporated into a system that has periodic dynamics, NLF was no longer a reliable predictor for the summed population. As before, we also can understand these results by examining the underlying 1-D maps. Because of space constraints we do not present these maps here. But for subpopulations NLF is still perfect when $H$ is relatively small (e.g. = 0.1), and forecasting predictions have flat signatures with correlation coefficient close to 1 (Fig. 14D). Only when $H$ is large (e.g. = 0.8) does forecasting ability decay with increasing forecast interval (Fig. 14D).

In general, forecasting patterns are qualitatively the same when environmental noise is added except that NLF becomes much worse for the summed population when the system has periodic dynamics.

![Fig. 14](image-url)

Fig. 14. Correlation coefficient between predicted and observed values for the second half of the time series of subpopulation 1 (panel A) or the summed total population (panel B) as a function of dispersal rate, $D$ in zone I and II of the 2-cell homogeneous proportional dispersal model when environmental noise is incorporated. Notation: +, $H = 0$; o, $H = 0.25$; and *, $H = 0.5$, respectively, and prediction step, $T_p = 3$. Panel C, correlation coefficient for the summed population in zone III of the same model. Notation: o, $H = 0$; and *, $H = 0.05$, respectively, and prediction step, $T_p = 1$. Panel D, correlation coefficient for subpopulation 1 of the same model as a function of prediction step, $T_p$. Notation: o, $H = 0.1$; and *, $H = 0.8$, respectively, and dispersal rate, $D = 0.15$. 
3.4. Intermittency in population dynamics

Intermittency means population moving in and out of one type of behaviour, e.g. chaos, through time. Intermittency is a common phenomenon in spatially structured population models, particularly those with greater complexity in spatial structure (Doebeli, 1994). As one might expect, intermittency is most common for values of $D$ that cause transition from one type of dynamics into another, i.e. where we see transitions occurring between chaotic and periodic or equilibrium behaviour.

For the homogeneous 2-cell proportional dispersal model, the interval of $D$ values where intermittency occurs is [0.1646, 0.169], in which we see transition occurring between 2-cycles and chaotic dynamics. As an illustration, in Fig. 15A we present a time series of subpopulation 1 with $D = 0.165$. Note that periods of diverging oscillations towards chaos appearing around time 660, 790 and 975.

Intermittency in population dynamics has a negative consequence for NLF, as illustrated in Fig. 15B. We see that NLF is much worse for values of $D$ in the interval where intermittency occurs than at other values.

4. Summary and discussion

We have projected the dynamics of spatially structured population models using a NLF method (ANN-optimal BP algorithm), and have investigated the way in which dispersal and spatial scale affect the ability of NLF. Several conclusions were obtained:

First, dispersal affects population dynamics and consequently NLF ability. When the dispersal rate, $D$, is below some critical value, the ability of NLF for subpopulations decreases and then increases with increasing $D$. This result is obvious for 2-cell models but does not change qualitatively with spatial heterogeneity, mode of dispersal, or even environmental noise. But for complex spatial configurations, this result is not so clear due to complicated dispersal interactions across subpopulations. One point that deserves mention here is that subpopulations with different values of $r$ and $K$ have different NLF results. NLF is more reliable for the subpopulations with smaller $r$ or larger $K$.

Second, NLF is perfect for periodic dynamics at any spatial scale. The correlation coefficient remains at 1 even when the prediction step increases towards infinity. This conclusion holds for all deterministic cases of periodic dynamics that we have examined, but when environmental noise is incorporated NLF is a reliable predictor only at smaller spatial scales for low to moderate levels of noise.

Third, when the dispersal rate, $D$, is small (i.e. zone I, II in Tables 1 and 2), the ability of NLF is closely related to spatial scale. NLF is much worse at larger spatial scales as a result of the asynchronous dynamics of subpopulations. Even though asynchronous fluctuations in spatially structured populations may dampen total population fluctuations (DeRoos et al., 1991), the nonlinear structure that permits local forecasting is lost at larger spatial scales. As $D$ increases beyond the critical value, the asynchrony tends to disappear. Especially, when $D$ increases to the value for which the convergence of subpopulation dynamics occurs, we have similar NLF results at any spatial scale. This important conclusion holds for all cases that we have examined, and the conclusion is robust to variation in spatial heterogeneity, mode of dispersal, spatial configurations, and randomness. The difference among all the deterministic cases is tied to the critical value of $D$, which varies with growth rate, $r$, carrying capacity $K$, mode of dispersal, and spatial configuration.
Finally, intermittency, a common phenomenon in the dynamics of spatially structured populations, works against the ability of NLF.

Effects of dispersal on population dynamics have been well documented. For example, Stone (1993) reported that with the addition of a small immigration term the process of period-doubling route to chaos in a range of simple, nonlinear difference equations may break down and suddenly reverse, giving rise to distinctive period-halving bifurcations. Ruxton (1996) suggested similar avoidance of chaos could occur in continuous-time three-species models, and the stabilizing effect of dispersal in other contexts (McCallum, 1992; González-Andújar and Perry, 1993; Ruxton, 1994; Yamamura, 2002a). Consistent with previous work, here we show that small to intermediate dispersal can stabilize chaotic dynamics to quasi-periodic oscillations or 2-cycles dynamics. We also found that NLF precision is closely related to population dynamics, as discussed by Sugihara and May (1990) and Wolpert and Miall (1990).

Forecasting of future population trajectories would have obvious value to fisheries, wildlife management, and conservation. For resource management agencies attempting to regulate resource exploitation, we would expect greatest success for policies and regulations focused at a local level. Regulations applied at a regional level, say state or provincial, are less likely to be successful. Likewise, detailed harvest models are likely to be highly unreliable if generalized over too large an area. For example, in India there are many recognized native tribes each occupying a specific locality and exploiting natural resources from a small geographic locality (Gadgil and Berkes, 1991; Gadgil et al., 1993). Consistent with previous work, here we show that local resource exploitation strategies would develop that may not be very efficient if applied over larger geographic areas (Gadgil and Berkes, 1991).

Our results also point to the importance of securing data on dispersal across the scales at which populations are being managed. For each spatially structured population there may be a specific critical value of dispersal rate. Only when dispersal rates are below this critical value will we expect resource exploitation and management on a local area to be more successful than regionally. Regrettably dispersal data can be challenging to estimate for natural populations and often are lacking (Clobert et al., 2001).

Intermittency in population dynamics is another factor influencing whether forecasting can be a useful tool for conservation and management. Clearly this dynamical behaviour would cause resource managers much difficulty, e.g. if a pattern could be observed and strategic management programs implemented, only to have these programs become superannuated upon the emergence of a new sort of dynamics. Intermittency has been reported in the dynamics of populations of Daphnia magna (Mitchell et al., 1998), desert locusts (Showler and Potter, 1991; Showler, 1995), and breeding birds (Bradley et al., 2000).

Our second conclusion shows that in deterministic models NLF is a reliable method for predicting periodic populations. This is true simply because it only requires a small number of mappings of future population to capture the system’s dynamics in the local forecasting library. In nature, however, such periodicity is unlikely to be mapped so perfectly, being eroded by noise in various components of the system, as illustrated by our analysis of “consequences of environmental noise”. Consequences of environmental noise depend upon the range of parameter space in which the deterministic system has periodic behaviour. If phase locking (Schaffer, 1988) or other mechanisms sustain periodicity at a particular frequency over a wide range of parameter values, perturbations may not push the system out of the periodic range (Crutchfield et al., 1982; Schaffer et al., 1986), and NLF for population dynamics will be nearly perfect for any prediction step. Yet, it is often the case that periodicity appears in a relatively small region of parameter space (Ellner and Turchin, 1995; Kaitala et al., 1997; Sun and Yang, 1999). When this happens, stochasticity has a propensity to launch the time series into forays of chaos or other complex dynamics. And the resulting forecast interval signatures are just like Sugihara and May (1990) characterized for chaos with noise, i.e. the correlation between predicted values and observed values decreases with the prediction step.

In our investigations thus far, we assume reflecting boundaries, i.e. when dispersing individuals encounter a boundary, which is not contiguous with another subpopulation, individuals will not disperse. Yet such an assumption is species and/or habitat dependent (Matthysen, 2002; Schtickzelle and Baguette, 2003), and the extreme alternative assumption is that non-contiguous boundaries are absorbing, and that dispersers are simply lost to the population. Examining alternative assumptions about boundary effects is beyond the scope of the present study, but remains an interesting and important area for future work.

Although our focus has been on forecasting applications for natural resource management, forecasting ability or “tracking ability” might have implications for other species (Boyce and Daley, 1980). The ability of a predator to anticipate the spatial distribution of prey has obvious selective advantage, and conversely, spatial heterogeneity can permit persistence under predation (Ellner et al., 2001; Xu and Li, 2002).

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References


