

MATTERS OF SCALE IN THE DYNAMICS OF POPULATIONS AND COMMUNITIES

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ABSTRACT

It is now well established theoretically that the stability of a population or community on a large spatial scale may depend on heterogeneities, fluctuations or instabilities on smaller scales. Asynchrony of local population fluctuations is often viewed as an alternative to density dependence in achieving long-term regional population stability. However, it is shown here that fluctuations achieve this effect only through their interaction with density-dependent processes. This observation relies on the fact that large spatial scales reflect the average of small scale variation. When local population dynamics are nonlinear (a reflection of density dependence), the variance on the small scale affects the average at the larger scale. This nonlinear averaging that links small and larger scales may have stabilising or diversity promoting effects in many systems. How nonlinear averaging leads to these effects can be understood by a simple graphical technique.

Key words: Density dependence, non-linear averaging, spatial scale, scale transition, model selection

Introduction

There is growing recognition of the need to consider spatial scale in ecological studies. On small spatial scales, populations are invariably *open*, i.e. there is appreciable immigration from outside the population. At larger spatial scales, the contribution from immigration declines in relation to dynamic processes within a population, until at some scale a population is effectively *closed*, i.e. eliminating immigration altogether would have a negligible effect on population dynamics. It may not be possible to understand an open population, or a community consisting of open populations, without an understanding of immigration and emigration. For example, Pulliam (1988) has suggested that many local populations may actually be *sinks*, i.e. insupportable without an excess of immigration over emigration. Thus, the persistence of such a population depends on factors beyond the boundary of the population itself.

Most ecological concepts and hypotheses, however, have been developed for closed populations. Applying them to local populations that are in fact open could be quite misleading. For example, it can be shown theoretically that a constant rate of immigration from outside a local population can be highly stabilising (Hughes 1990; Stone 1993), as it is equivalent mathematically to the 'constant number refuge' discussed in predator-prey models (Hassell 1978; Murdoch *et al.* 1995). Attempts to explain the stability of an open population based on the many stability concepts for closed populations may be pointless because the stability of such a population may depend entirely on stable immigration. Similarly, explaining species diversity of an open community suffers from the problem that a diverse local community can be sustained by immigration whether or not local conditions favour maintenance of high diversity (Sale 1977).

In both of the above examples, the question shifts from the characteristics of local population dynamics to the characteristics of immigration. We must ask respectively, why is immigration stable, and why is the immigrant pool diverse? These questions then shift to a larger spatial scale from the which the immigrants are derived. Only when the system is effectively closed can we be sure that explanations for the system's properties are to be found within the system. Moving to a large scale of an effectively closed system, however, does not mean lower scales can or should be profitably ignored. Lower scales derive importance from heterogeneity on those scales (Chesson 1991). Much ecological theory, however, has been developed assuming that populations are not only closed but also internally spatially homogeneous.

If a system is spatially homogeneous in terms of the physical environment and its fluctuations over time, and in terms of the biological species and their fluctuations over time, then an open subset of such a system could be studied as if it were closed as observations anywhere would be indicative of the workings of the system as a whole. Thus, the various concepts and hypotheses developed from models of closed systems would be perfectly applicable. In many field studies, the implicit assumption is not this extreme spatial homogeneity but unimportance of the spatial variation that is present. The variation is treated as noise – a nuisance that requires larger samples for statistical significance (Chesson 1986). But a growing body of theoretical and empirical evidence sees danger in putting spatial variation in the category of noise.

As an initial guide to whether the observed spatial variation is noise, one might first ask the question, Are the important ecological processes qualitatively similar in most localities? The answer, "no", to this question means that one ignores spatial variation to one's peril. If the answer is "yes" however, one asks, Are the important ecological processes quantitatively similar in space? Quantitative dissimilarity in the presence of qualitative similarity can often be important but need not be. One approach to answering this question is given below in the section on *The scale transition*.

Variation in space often has a temporal component, and so, to the questions above, one can add the question, Are temporal fluctuations spatially synchronous or asynchronous? It is generally unwise to ignore asynchronous fluctuations, but synchronous fluctuations that vary spatially in strength can be of major significance also (Chesson 1990).

The reasons for these answers have to do with the fact that on a large scale the appearance of processes is affected in major ways by variation on smaller scales. How this occurs depends on biological processes that cause various kinds of density dependence.

Density-dependence and the spreading of risk

Asynchronous local population fluctuations and density dependence are often seen as alternative means of achieving population stability. Indeed, some authors suggest that population asynchrony dominates over density dependence in nature (Den Boer 1981; Andrewartha and Birch 1984). Theoretical evidence, however, implies that fluctuations derive their importance through their interaction with density-dependent processes (Chesson 1991). To see that this is so, it is first necessary to develop a clear notion of the phenomenon of density dependence.

Clear definitions of density dependence are hard to come by in the literature. However, most commonly, density dependence means that the per capita growth rate is a decreasing function of population density (Murdoch and Walde 1989). For example, the logistic model is a simple expression of this idea. In the logistic model, the per capita rate of population growth has the maximum value r , at effectively zero population density, and declines linearly to 0 as population density approaches the carrying capacity K , as follows:

$$\frac{1}{N} \cdot \frac{dN}{dt} = r \left(1 - \frac{N}{K} \right) \quad (1)$$

The logistic model, however, represents a very special kind of density dependence, because it assumes that the per capita growth rate responds instantly to changes in population density – the per capita growth rate at time t is expressed directly as a function of population density at time t . Such a representation must invariably be an approximation only closely applicable when density dependence is caused by direct effects of a population on itself, for example by cannibalism or interference competition. When intraspecific competition is exploitative, Eq. 1 is best replaced by an equation of the form

$$\frac{1}{N} \cdot \frac{dN}{dt} = f(R), \quad (2)$$

where R is resource availability, and f is some increasing function relating resource availability to per capita population growth. A separate equation describes the dynamics of resources, for example

$$\frac{dR}{dt} = g(R) - h(R)N, \quad (3)$$

where $g(R)$ is the rate of resource renewal and $h(R)$ is rate of consumption of resource per individual in the population.

Eqs. 2 and 3 describe a feed back loop of a species on itself through the resource. Density dependence is not evident from Eq. 2 alone, but only from the pair of Eqs. 2 and 3 where the negative impact of the population on the resource is clear. However, the density-dependent feedback of the population on itself through the resource does not lead to instantaneous changes, but is often regarded as working with a time lag. The effect of an increase in the population is to decrease the

resource growth rate, lowering resource densities over time with a consequent gradual lowering of the population per capita growth rate Eq. 2.

From this discussion, it is evident that the rate of response of per capita population growth to changes in population density depends on the speed of resource dynamics. MacArthur (1970) pointed out that when resource dynamics are fast relative to population dynamics, the resource can be assumed to be at an equilibrium dependent on N . This equilibrium is the solution of the equation $g(R^*) - b(R^*)N = 0$ for R^* . This value R^* is a function of N describing the level of resource availability determined by a particular population density. It represents the balance between consumption and renewal of the resource for that particular population density. Substituting R^* for R in Eq. 2 leads to an equation for population per capita growth rate of the form

$$\frac{1}{N} \cdot \frac{dN}{dt} = q(N) \quad (4)$$

where $q(N)$ is some function of N expressing density dependence once again as an instantaneous change in per capita population growth with a change in the population density. Depending on the functions f , g and h , the function $q(N)$ can be linear in N , so that Eq. 4 is the logistic equation once more (MacArthur 1970). More importantly, but unsurprisingly is the result that fast adjustment of resource availability to population density leads to a fast adjustment of per capita population growth to population density.

Although Eqs. 1 and 4 are the standard way of expressing density dependence mathematically, they are best viewed as approximations or limiting cases of more complex equations such as the pair of Eqs. 2 and 3. Equation 2 alone, however, is not informative about density dependence. Indeed, population growth written in the form of Eq. 2 is sometimes thought of as density-independent simply because N does not appear explicitly on the right hand side of the equation. The results here show this perception to have limited utility.

In discrete time, rather than focus on the per capita rate of change, it is more natural to express dynamics in terms of the ratio of population sizes at successive points in time, $N(t+1)/N(t)$. The analogue of Eq. 4 in that case is

$$N(t+1)/N(t) = Q(N(t)), \quad (5)$$

where $Q(N(t))$ is some decreasing function of $N(t)$. For example, in the Ricker model (May and Oster 1976),

$$Q(N(t)) = R e^{-\alpha N(t)} \quad (6)$$

where R is a net reproductive rate without competition and α is an intraspecific competition coefficient. This model leads to the discrete time iteration

$$N(t+1) = RN(t)e^{-\alpha N(t)}. \quad (7)$$

Such discrete-time density dependence can represent exploitative competition with less stringent conditions than its continuous time counterpart Eq. 4. Resource dynamics must be on a shorter timescale than population dynamics, but Eq. 4 can hold simply if resources are renewed independently of population density in every unit of time, with no carryover of resources from one time to the next. Indeed, there are a number of important classes of populations where these conditions are applicable, for example, insects whose larvae develop in fruit, carrion or other ephemeral food sources (Shorrocks and Rosewell 1987; Ives 1991).

Density dependence through exploitative competition for resources is an indirect interaction between individuals in the same population. Resources are the medium of this indirect

interaction. A similar indirect interaction occurs through predators, pathogens and parasites. Holt (1977) has termed this indirect interaction 'apparent competition' in the situation where predators lead to indirect interactions between species. However, the idea that predators lead to density dependence within their prey populations, championed by Nicholson (1933), has a long history (see Kingsland this volume). Such density dependence can occur in a number of ways. Predators may modify their behaviour in response to prey density, and they may also increase in abundance or individual size and thus increase prey per capita mortality (Murdoch and Bence 1987). Some of these changes may be fast, so that an equation like Eq. 4 can summarise the impact on the prey, but those relying on changes in predator abundance will lead to a pair of equations analogous to Eqs. 2 and 3. In such cases, density dependence may not be apparent from the formula for the per capita growth rate of the prey population alone. Just as in the case of indirect interactions through resources, the density dependence only becomes apparent when the equation for the mediator of the indirect interaction is considered.

All of the above are examples of density dependence, but can density dependence be given a clear definition? Fundamentally, density dependence concerns how an individual is affected by the density of other individuals. Per capita growth rates are about average effects on individuals, and are not fundamental, but derivative. A formal definition is as follows:

"...The dynamics of a population are density dependent if the lines of descent from individual members of the population are affected by population density..."

By focusing on lines of descent, this definition allows for arbitrary time lags. For example, if the number of great grandchildren of an individual is affected by the current density, then dynamics are density dependent. Normally, the term density dependence refers to negative effects of current density on future population numbers. The opposite case, which occurs when there is an Allee effect or a type II functional response (Hassell 1978), is commonly called inverse density dependence. The definition here includes both the usual and the inverse sort of density dependence.

The difficulty of defining density dependence in terms of per capita growth rates is apparent in stochastic models that incorporate demographic stochasticity (May 1973) or within-individual variability (Chesson 1978, 1990). In such models, the per capita rates of change can never be independent of density. When a population is not density-dependent according to the definition above, it is nevertheless true that the variance over time of the per capita growth rate is inversely proportional to population density (Nisbet and Gurney 1982). However, the idea that the per capita growth rate should depend on density provides a useful operational definition of density dependence, especially in large populations where fluctuations due to demographic stochasticity are small. In this regard, it is important to note that the definition above is an ideal definition for use theoretically. Indeed, it is exactly the general and precise definition of the concept that is needed for theoretical analysis, discussed below, of the possible sorts of population dynamics in highly structured but density-independent systems. However, the definition is difficult to apply to empirical data.

For empirical studies, operational definitions of density dependence must be constructed for particular systems, and indeed such operational definitions are implicit in many empirical tests of density dependence (e.g. Turchin 1990; Dennis and Taper 1994; see also Cappuccino and Harrison this volume). The role of the definition given above is to provide the ideal which is to be approximated operationally. The concept of density dependence is so general that we should expect its expression to vary greatly from system to system, and therefore particular circumstances need more restricted definitions of the idea, so that the idea becomes useful in practice for the system or data at hand. The ideal definition above then provides a point of reference for judging the adequacy of an operational definition given the assumptions applying for particular circumstances.

Many ecologists have felt that most populations in nature must have density-dependent dynamics (see Cappuccino and Harrison this volume). In spite of this, density dependence is often difficult to detect empirically (Murdoch and Walde 1989; Turchin 1990; Dennis and Taper 1994; Murdoch 1994; see also Fox and Ridsdill-Smith this volume). And if density dependence is weak, or occurs only some of the time, one may legitimately question the emphasis on density dependence in modern ecology (Andrewartha and Birch 1984; Strong 1986). To address this debate, the consequences of strict density independence of population dynamics are examined.

The simplest model of population dynamics without density dependence is the geometric growth equation,

$$N(t+1) = RN(t) \quad (8)$$

which can be obtained from Eq. 7 by setting $\alpha = 0$. The key feature is that population size at time $t + 1$ is simply proportional to population size at time t . It is well-known that Eq. 8 leads to exponential population growth, with unlimited increase if $R > 1$, decline to extinction if $R < 1$, and constancy if $R = 1$. The first two situations cannot describe persisting populations in nature if the idea of density independence is to be retained. Therefore, density-independent population persistence must be described by the last situation with $R = 1$. In this case, however, it is commonly argued that stochastic fluctuations will lead to a random walk, with extinction being the ultimate result. The idea of spreading of risk (den Boer 1968, 1981; Andrewartha and Birch 1984) is a response to this argument. According to this idea, it is very important to recognise that populations are structured in space into local populations (Andrewartha and Birch 1984) or interaction groups (den Boer 1981). The principal conclusion is that these local populations fluctuate asynchronously over time and lead to regional population fluctuations of a smaller order. Coupled with dispersal between local populations, such asynchrony and reduced regional variance is expected to lead to prolonged regional persistence.

To test this idea mathematically, we must generalise the density-independent model in Eqn 8 to a structured population (see Appendix). No matter how complex we make population structure, there is an inescapable conclusion: Eq. 8 remains a good summary of regional population dynamics in the long run. The actual value of R applying in complex settings is a complicated space-time average of the parameters of the system, which may fluctuate in various ways in space and time. However, the inescapable conclusion is that highly structured density-independent populations still grow exponentially in the long run. The only hope for long-term persistence of such a population is for R to equal 1 or very nearly. It does not seem likely that this could apply to many populations in nature. If it did apply, and there was any phenotypic variation leading to differences in average fitness, then natural selection would quickly ensure that R became greater than 1. Thus, stable regional populations with density-independent dynamics seem quite implausible, in agreement with previous arguments (Murdoch and Walde 1989; Murdoch 1994) and the stronger claim that density dependence is a logical necessity for persisting populations (Godfray and Hassell 1992).

These conclusions, however, do not mean that the concept of spreading of risk is unimportant. It is most important when population dynamics are density-dependent. Indeed, there is an important interaction between density dependence and variation in space that helps reconcile their respective roles. This interaction is the topic of the next section.

The scale transition

I use the term *scale transition* for the changes that take place in population dynamics when the view shifts from one scale in space or time to another (Chesson 1991). Understanding this scale transition is crucial to understanding the effects of variation on population dynamics. The development here

has general lessons that apply in some form to most populations or communities. However, the analysis uses just a single-species, discrete-time, density-dependent model. To make the discussion concrete, it is worthwhile to have some examples in mind. Ideal examples are insects such as drosophilids (Shorrocks and Rosewell 1987) or carrion flies (Ives 1991) that colonise ephemeral patches of food in which they develop for just one generation before dispersal. Annual plants without a seed bank may also satisfy difference equations of these sorts (Warkinson 1980; Pacala and Silander 1985), although generally with milder density dependence, and with more local dispersal. The basic principles are the same. In both cases, organisms interact with each other locally in space but form part of a much larger population over which dispersal takes place. Although the specific development fits best in these cases, the lessons are general for populations in which density dependence occurs on the scale of a local population, which is open and therefore influenced significantly by dispersal.

In the above situation, What happens when we pass from the scale of a local population, where interactions occur within a generation, to the scale of a regional, effectively closed population? Total regional population size is simply the sum of all the local population sizes. Population density as number per unit area, is an average of the local population densities. This average is a simple arithmetic average if local populations all occupy the same area (e.g. by defining local populations in terms of equal sized areas), but otherwise it is a weighted average of local population densities, with weights equal to the areas occupied by the local populations. Thus, when we pass from the scale of the local population to the scale of the regional population we are taking an arithmetic average of the population densities.

Arithmetic averages may seem straightforward, but they can be rather surprising, especially when local population dynamics are density-dependent. Consider population dynamics in discrete time with discrete periods of dispersal, such that $N_j(t)$ is population density in patch j before dispersal, $N_j(t+h)$ is this local population density immediately after dispersal but before population growth (t to $t+h$ is the dispersal period), and $N_j(t+1)$ is local population density after local population growth and before dispersal ($N_j(t)$ one unit in time later). As remarked above, regional population density is the same as average population density (appropriately weighted), and can be denoted $\bar{N}(t)$. Although dispersal commonly involves mortality, for simplicity, we shall assume that dispersal merely leads to a rearrangement of the population without mortality. Thus, regional population density is the same after dispersal, i.e. $\bar{N}(t+h) = \bar{N}(t)$. This assumption has no effect on the conclusions below if dispersal is density-independent. Let us now assume that local population growth can be described by an equation of the form

$$N_j(t+1) = F(N_j(t+h)) \tag{9}$$

where F is some function of the local population density. If there were no variation in space, regional population dynamics would be described by this equation also. In other words

$$\bar{N}(t+1) = F(\bar{N}(t)) \tag{10}$$

For example, taking F from the Ricker model Eq. 7, Eq. 10 becomes

$$\bar{N}(t+1) = R\bar{N}(t)e^{-\alpha\bar{N}(t)} \tag{11}$$

With positive values of α , there is a point equilibrium which is stable provided $\ln R$ is ≤ 2 . For values of $\ln R > 2$, the equilibrium is unstable and a regional population satisfying Eq. 11 fluctuates over time (May and Oster 1976). These fluctuations can be in the form of regular cycles but for sufficiently large values of R , the population exhibits large chaotic fluctuations (Fig. 1a).

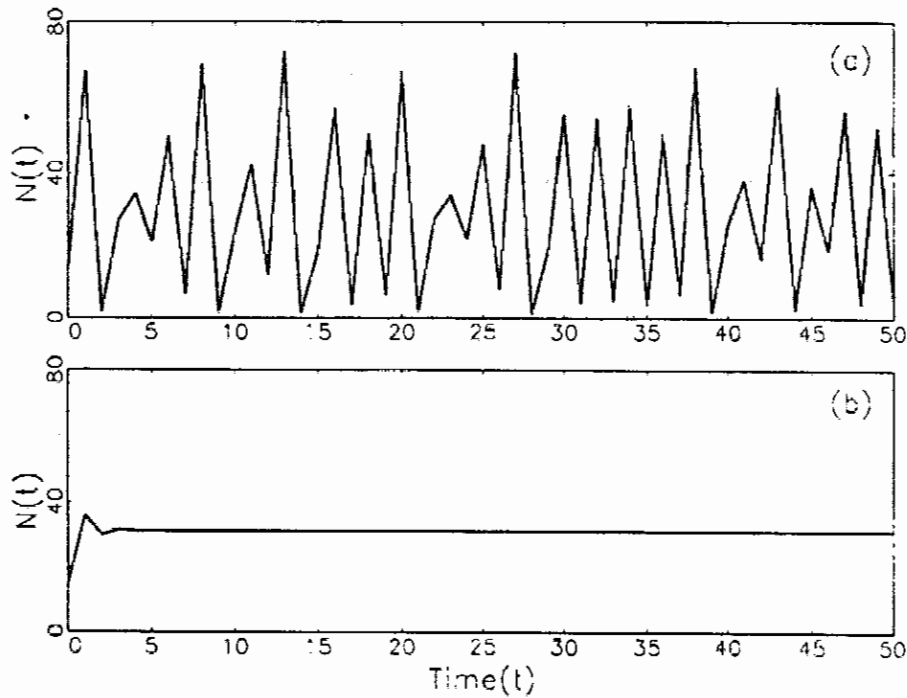


Fig. 1. (a) Simulation of the Ricker model, Eq. 11, with $\ln R = 3$ and $\alpha = 0.1$. (b) is a simulation of regional dynamics given by Eq. 13 with $k = 0.5$, and R and α as in (a).

Spatial variation can prevent this chaotic behaviour. That in itself is not surprising because if fluctuations in different patches are out of phase, the overall fluctuations are bound to be less. However, something more subtle and important is going on. With spatial variation, regional population dynamics are not described by Eq. 10 but by the equation

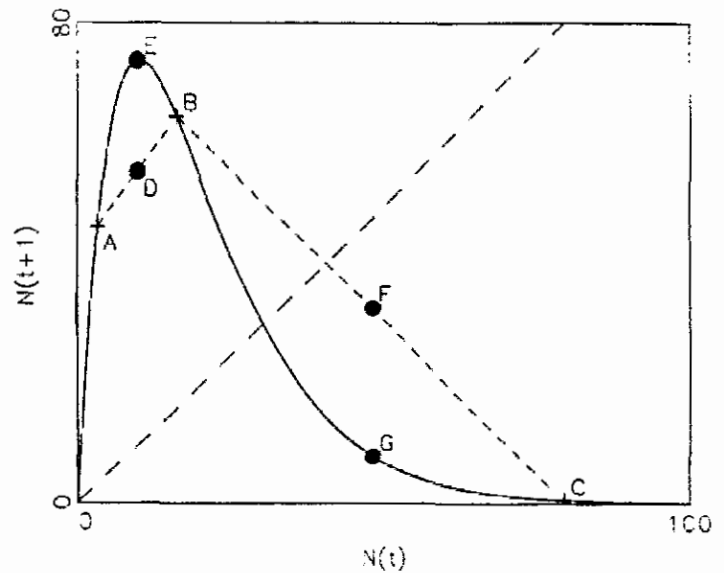
$$\bar{N}(t+1) = \frac{\sum_{j=1}^k F(N_j(t+h))}{k} = \overline{F(N(t+h))}. \tag{12}$$

The important point here is that the average $\overline{F(N(t+h))}$ differs from $F(\bar{N}(t))$ whenever there is variation in space. The reason for this difference is not a difference between $\bar{N}(t)$ and $\bar{N}(t+h)$ because we have assumed they are the same. The difference arises instead from the nonlinearity of the function F – the fact that F specifies a curved relationship between $N_j(t+1)$ and $N_j(t+h)$. Nonlinearity in turn arises from density dependence, as the density-independent relationship δ is not curved, but a straight line. The important interaction between nonlinearity and spatial variation is explained in Fig. 2.

The thick line in Fig. 2, gives the Ricker curve. The points A, B and C represent different spatial locations with different values of $N_j(t+h)$ and corresponding values of $F(N_j(t+h))$. Suppose for the moment that half the local populations are represented by point A and the other half by point B, then the average value of $F(N_j(t+h))$ ($= \bar{N}(t+1)$) corresponds to the y coordinate of the point D, the midpoint of the line joining A and B. The x coordinate of the point D is $\bar{N}(t) (= \bar{N}(t+h))$. These facts can be deduced from the geometry of the figure noting that $\bar{N}(t+1)$ ($= \overline{F(N(t+h))}$) lies half way between the two values of $F(N_j(t+h))$, and $\bar{N}(t)$ lies halfway between the two values of $N_j(t+h)$.

This diagram shows how spatial variation alters regional population dynamics. Note first of all that $F(\bar{N}(t))$ corresponds to the y coordinate of the point E, directly above $\bar{N}(t)$, showing that here, $F(\bar{N}(t+h)) > F(\bar{N}(t+h))$. Although this may initially be counter intuitive, the diagram makes it

Fig. 2. Averaging the Ricker curve in space as explained in the text. (Parameters as for Fig. 1)



clear that in this case there is no other possibility as $F(\bar{N}(t+h))$ is greater than both values of $F(N_i(t+h))$ and so certainly must be larger than their average.

The inequality $F(\bar{N}(t+h)) > \overline{F(N_i(t+h))}$ holds in all places where the curve is bending over (is concave), while the reverse inequality $F(\bar{N}(t+h)) < \overline{F(N_i(t+h))}$ applies whenever the curve is bending upwards (is convex). For example, if half the patches correspond to the point B and the other half to the point C, the new regional population density is the y coordinate of the point F midway between B and C. This point F has x and y coordinates $\bar{N}(t+h)$ and $F(\bar{N}(t+h))$ and lies above the point G with x and y coordinates $\bar{N}(t+h)$ and $F(\bar{N}(t+h))$. The important thing to note is that this spatial variation has led to a moderation of the density-dependent response on the larger spatial scale. The point D being less than the peak value E shows moderation by spatial variation of the maximum achievable density the next time period. Similarly, the point F being above G shows that the extent of the crash at high population densities is reduced also.

Applying the procedure illustrated in Fig. 2 to a continuous range of two-point spatial distributions allows the construction of a relationship between $\bar{N}(t+1)$ and $\bar{N}(t)$. Thus, in Fig. 3 each chord on the Ricker curve joins two different values of local population density; and the midpoints of these chords (large dots) then give the relation between $\bar{N}(t+1)$ and $\bar{N}(t)$ arising with spatial variation. As can be seen, the density-dependent response is much more moderate on the larger scale in the presence of spatial variation.

The simple two-point spatial distributions used in these figures illustrate well the phenomenon of nonlinear averaging, but they are not very realistic. Local density variation in nature, however, is often well-approximated by a negative binomial distribution (May 1978). For this spatial distribution, the exact value of $\bar{N}(t+1)$ is

$$\bar{N}(t+1) = \frac{R'\bar{N}(t)}{(1 + \alpha'\bar{N}(t)/k)^{k+1}}, \tag{13}$$

where $R' = Re^{-\alpha}$ and $\alpha' = 1 - e^{-\alpha}$ (de Jong 1979; Hassell and May 1985). These curves are plotted along with the Ricker curve in Fig. 4. Clearly shown is the strong flattening of the density-dependent relationship for small k corresponding to high spatial heterogeneity. The steep peak of the Ricker equation leads to a large build up of population density followed by a crash, and thus the highly oscillatory population dynamics shown in Fig. 1a. With spatial heterogeneity, the peak is

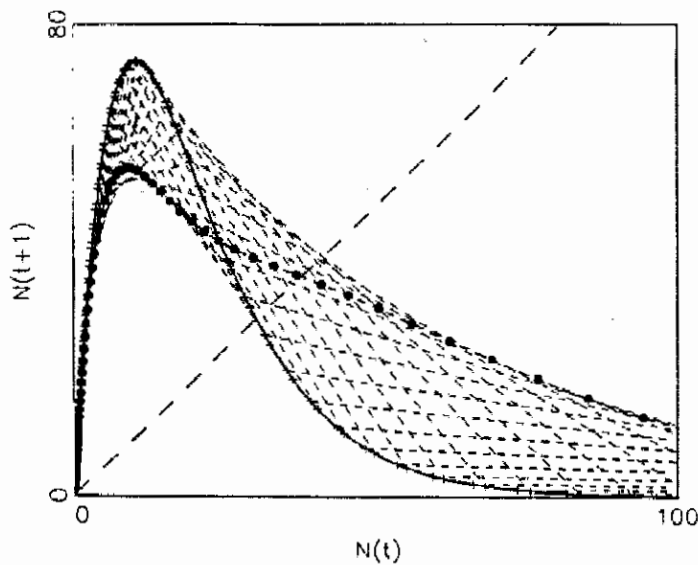


Fig. 3. Continuous averaging of the Ricker curve in space as explained in the text. (Parameters as for Fig. 1)

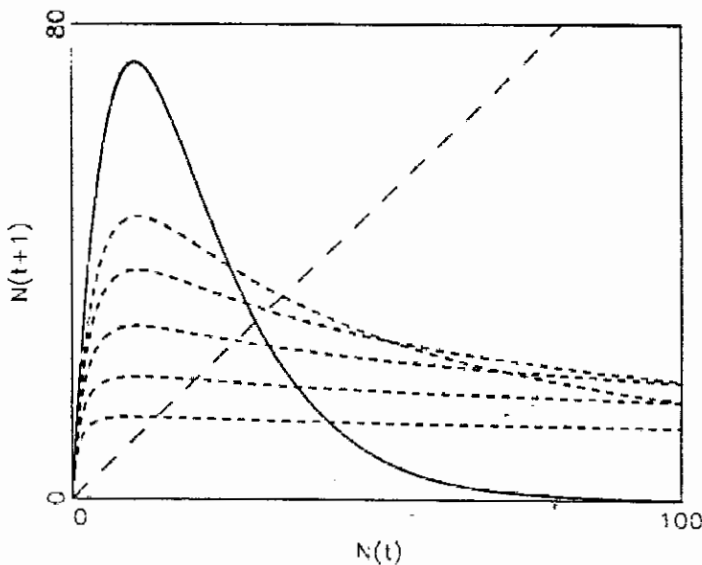


Fig. 4. The Ricker curve and Eq. 13 plotted for $k = 0.1$ to 1 in an ascending order. (Parameters as for Fig. 1)

reduced at the regional level (at the local level nothing has changed) and the decline after the peak is quite mild. Indeed, with high levels of heterogeneity, the response is nearly completely flat, which means that a regional equilibrium is achieved very rapidly and is very stable. This stability is a product of a high level of spatial variation (Hassell and May 1985).

The above discussion of the dynamics of Eq. 13 assumes that k , the clumping parameter of the negative binomial distribution, remains constant over time. This is a reasonable proposition in some situations, for example, if local populations are ephemeral habitat patches that are colonised each time period based on their physical attributes without any density-dependent interactions between the organisms colonising a patch. In such cases, the negative binomial arises from heterogeneous Poisson sampling (a 'mixed' Poisson distribution; Johnson and Kotz 1969; Southwood 1978), and implies a constant value of k . Such heterogeneous Poisson sampling is potentially applicable to insects that colonise dead organisms or fruits (Ives 1991; Shorrocks and Rosewell 1987). With a constant value of k , Eq. 13 provides a sufficient description of the dynamics of regional density.

Other cases of colonisation of ephemeral habitats may involve some density dependence in the colonisation process. This is to be expected any time the number of individuals already present at a

site affects subsequent arrivals. In such instances, k should vary with density but not necessarily otherwise with time. Equation 13 is then modified by having a function of density substituted for k . There is no reason, however, to restrict application of these ideas to the case of ephemeral habitats (Hastings and Higgins 1994; Kareiva and Wennergren 1995), but in more general situations, patchiness will be affected by local population dynamic processes in addition to migration. Although the negative binomial distribution may remain a reasonable approximation, the value of k may vary over time in a manner that is not tied to population density. Even so, the graphical analysis above suggests that the stabilising tendency of variation should still be applicable provided variation in k is not too large. An example is instructive. From Fig. 3 we can see that provided k never varies 4 outside the range 0.1 to 1, no matter how k changes with time in this range, regional densities cannot fluctuate more than four fold, which contrasts with the more than eighty fold fluctuation of the corresponding Ricker model in a spatially homogeneous system. Such stability from spatial variation is amply illustrated by the Ricker model of Hastings and Higgins (1994) and Kareiva and Wennergren (1995), who consider continuous migration in one dimension. Although they make the point that their model may take a very long time to settle into its final pattern of fluctuation, the dampening effect of spatial variation is immediately evident.

The stabilising effect of spatial variation seen here does not depend on fluctuations being out of phase in the different localities, although such out of phase fluctuations appear to be a feature in Hastings and Higgins (1994) and Kareiva and Wennergren (1995). Indeed, the spatial pattern of densities could be fixed. Such a fixed pattern of variation might arise, for example, because some localities are more difficult for migrating organisms to find than others. Intuitively, spatial variation leads to stability by the fact that patches with high numbers are balanced by patches with low numbers such that the severe decline experienced in the high density localities is buffered by more moderate decline or even increases in other localities. There is no requirement for fluctuations to be out of phase in different localities for this to occur. There is also no requirement here for particular dispersal distances relative to the scale of local interactions so long as spatial heterogeneity is maintained within the regional population, as the results of Hastings and Higgins (1994) attest.

This paper has shown how this stabilising effect involves nonlinear averaging: the dynamics of regional density are given by $\overline{F(N(t+h))}$ which differs from $F(\overline{N(t+h)})$. This inequality is the key to the scale transition, or change in the dynamical behaviour when passing from local dynamics to regional dynamics because consideration of local population dynamics alone, without regard to spatial variation, predicts that regional dynamics should be given by $F(\overline{N(t+h)})$. Quantitative and qualitative differences between local and regional dynamics arise quite generally from nonlinear averaging in both single-species and multispecies settings (Chesson 1981; Durrett and Levin 1994), with both spatial and temporal variation (Chesson 1990). Moreover, such nonlinear averaging can occur on small scales as well as large scales (Chesson 1981; Durrett and Levin 1994), leading to large-scale dynamics that can be viewed as the outcome of an accumulation of scale transitions involving nonlinear averaging (Chesson and Huntly 1993). There is no necessity that nonlinear averaging should lead to stability as it has in the illustration given above. Instability from nonlinear average is possible also (Chesson 1990).

Discussion

Although variation in space may lead to lower temporal fluctuation at the regional scale than the local scale, in the density-independent case, population dynamics at the regional scale are not qualitatively different from dynamics at the local scale. In essence geometric growth occurs on both scales, discounting dispersal on the local scale. With density dependence, local and regional dynamics can be qualitatively different. For example, we have seen how chaos at the level of a local

population can change to very strong stability at the regional population scale as a consequence of the combined effects of variation and locally nonlinear dynamics. The reason for this qualitative change is the nonlinear nature of averaging occurring with the transition between scales.

In studies of metapopulation models (Gilpin and Hanski 1991), there is often such a strong emphasis on density-independent processes of colonisation and extinction (Caswell 1978) that there is a danger of assuming that they are examples of regional stabilisation with density-independent dynamics. However, the usual assumption in such models that local communities can be described adequately by the list of species present is an implicit assumption of strong density dependence locally in space. Although many kinds of density dependence will suffice, the simplest such assumption is that upon colonisation, a local population rises quickly to a carrying capacity, about which it fluctuates until extinction occurs. Hence strong density dependence is in fact assumed, and stabilisation of regional dynamics in such models can be viewed also as an outcome of nonlinear averaging (Chesson 1981).

Stabilisation of population fluctuations, however, is just one possible effect of nonlinear averaging in the scale transition. In models of competing species, nonlinear averaging can enable coexistence in spatially variable environments (Chesson 1985; Comins and Noble 1985; Shmida and Ellner 1985; Pacala 1987; Durrett and Levin 1994) and in temporally variable environments (Abrams 1984; Ellner 1984; Chesson 1986, 1990; Loreau 1992). Nonlinear averaging can also lead to persistence of predator-prey, and host-parasitoid associations (Comins and Hassell 1987; Hassell *et al.* 1991). The variation on which these effects depend can arise from fixed patterns of spatial (Chesson 1985) or temporal environmental variation (Loreau 1992; Chesson and Huntly 1993) or randomly varying patterns (Comins and Noble 1985), or it may be generated largely by intrinsic population fluctuations (Armstrong and McGehee 1980; Hastings and Higgins 1994).

In some cases, nonlinear averaging can create a stable equilibrium at the regional scale (Hassell and May 1985; Chesson 1985; Gilpin and Hanski 1991; Murdoch 1994) or on a large temporal scale (Chesson 1984; Chesson and Huntly 1993), where no equilibrium exists on smaller scales. This is most apparent in competition models where in the absence of spatial and temporal variation, only one species could persist in the long run and therefore stable equilibria have just a single species at positive density, with other species at zero density. Spatial and temporal variation may have the effect of creating stable equilibria with many species at positive densities. Murdoch (1994) has posed the question of whether long-term persistence must always involve an equilibrium of some form. The answer to this question is "yes" in all essentials. Indeed, it is essentially tautological that long-term persistence on particular spatial and temporal scales involves an equilibrium on the relevant spatial and temporal scales.

This fact is commonly used in the standard invasibility analysis for species coexistence (Turelli 1978; Levins 1979; Chesson 1994), which involves an argument of the following sort. Ruling out the possibility of indefinite increases in density, and assuming that persistence means that the population does not converge to zero or show ever stronger population crashes, the long-term average change in log population size must be approximately zero. This near zero average change can be regarded as implying that the system is in equilibrium or approximately so. In this sense, equilibrium is inevitable on a sufficiently long timescale, and is almost a rephrasing of persistence as the idea that on a long timescale population density does not change much relative to the time involved. Thus, it makes no sense to expect long-term population persistence without an equilibrium on a long timescale. Such an equilibrium may not involve precise densities (a point equilibrium), however, but a probability distribution of densities, being the stochastic analogue of an equilibrium point (Turelli 1981; Ellner 1989).

Density-independent systems are no exception to the equilibrium requirement for long-term persistence. As remarked above, they must have R close to one (on a log scale, $\ln R$ close to 0). However, such an equilibrium cannot be stable in the sense that perturbations of density will lead to a return to some range or distribution of densities. Indeed, systems with density-independent dynamics are neutral to perturbations of density. To suggest otherwise is to contradict the assumed density independence. In density-dependent systems, however, the long-term equilibrium can be stable, which is observed as a long-term trend to increase or decrease when a population is perturbed from its normal range or distribution of fluctuations (Ellner 1984; Chesson and Huntly 1993; Chesson 1994). But, it is important to keep in mind that a stable equilibrium on a long timescale may be an emergent property of heterogeneity and nonlinear dynamics on smaller scales. Small scale heterogeneity may stabilise the equilibrium on a larger spatial scale, even though an equilibrium need not be present on the smaller scale for it to emerge on the larger scale. It can be created on the larger scale by nonlinear averaging in the transition between scales.

Appendix

The population projection matrix approach (Caswell 1989), commonly used for stage or age structured populations can also be generalised to model density-independent population growth for a population with any spatial structure or stage structure, or combinations of both stage and spatial structure: elements of the matrix can represent density-independent migration rates between localities in addition to transition rates between stages. The elements of this matrix can also vary stochastically in time, and thus represent environmental variability of great complexity. Population dynamics are then given by the equation

$$N(t+1) = M(t)N(t) \quad (14)$$

where the components of N correspond to the numbers of individuals in each stage, age and place combination, and the elements of $M(t)$ express the rates of change between these possible states of an individual organism. This iteration was studied mathematically many years ago (Furstenberg and Kesten 1960), and generalised more recently (Heyde 1985) with the conclusion that the elements of $N(t)$ exhibit a common exponential rate of growth with stochastic fluctuations about this rate. More specifically, there is a constant R such that total population size $N(t)$ satisfies the following equation:

$$N(t) = N(0)R^{t(1 + Z(t))} \quad (15)$$

where $Z(t)$ is a random variable that converges to 0 as t becomes large. The individual elements of $N(t)$ all satisfy similar equations.

This analysis does not include demographic stochasticity, but branching process theory (Jagers 1975) shows that the addition of demographic stochasticity does not alter the essence of these conclusions.

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