INTERACTIONS BETWEEN DENSITY-DEPENDENCE AND DISPERSAL

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CANDIDATES DECLARATION

I declare that the work recorded in this thesis is entirely my own, except where otherwise stated, and that it is of my own composition. Much of the material included in this thesis has been produced in co-authorship with others and some has been presented for publication. My personal contribution to each chapter is as follows.

2. Published as: Fowler M.S. & Ruxton G.D. 2002. Population dynamic consequences of the Allee effect. Journal of theoretical biology 85: 481-486. The idea was jointly developed by MSF and GDR. MSF performed all model simulations and analysis, and was senior author of the manuscript.

3. The relationship between population density and individual fitness in the pea aphid, Acyrthosiphon pisum. The idea was jointly developed by MSF, GDR and Wolfgang W. Weisser. MSF performed all experimental work and analysis and wrote the manuscript.

4. Dispersal decisions and the Allee effect. The idea and model were developed by MSF, who also carried out the analysis and wrote the manuscript

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7. The effects of space and patch number on communities. The idea was suggested by Esa Ranta, Veijo Kaitala and Per Lundberg, and was developed by MSF, Peter Frodin, and Katja Enberg. MSF, PF and KE developed the model. MSF performed the analysis and was author of the manuscript.

8. Removal of differently ranked species in a community leads to surprising results. The idea was developed jointly by MSF, PF and KE. MSF and PF developed the model, carried out the analysis and wrote the manuscript.

I further declare that no part of this work has been submitted as part of any other degree.

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ABSTRACT

We take a well-known dynamic model of an isolated, unstructured population and modify this to include a factor that allows for a reduction in fitness due to declining population sizes, often termed an Allee effect. Analysis of the behaviour of this model is carried out on two fronts - determining the equilibrium values and examining the stability of these equilibria. Our results point to the stabilising effect on population dynamics of the Allee effect and an unexpected increase in stability with increased competition due to the interaction between competitive and Allee effects.

Density-dependence is an important regulating factor in population dynamics that is commonly considered to reduce individual fitness at high densities. Recently, interest in mechanisms that reduce fitness at low population densities, a phenomenon known as the Allee effect, has grown. Here we study the effect of a wide range of population densities on different measures of fitness in the pea aphid, Acyrthosiphon pisum. By subjecting aphids to predation pressure, we find that fitness at very low population densities can be reduced. Comparisons of the data to different non-linear models of density-dependence suggest that aphids may in fact be subject to an Allee effect. We discuss some of the implications of this and possible mechanisms driving it.

Lately, there has been a realisation that the assumption of density-independent dispersal is biologically unreasonable, due to the inherent complexity associated with

dispersal, and therefore more effort is being invested in creating models that incorporate a more realistic, density-dependant type of dispersal. Another aspect of migration that there is still considerable scope for exploration is in models that consider the cost of dispersal. This will affect an individual's propensity to disperse from the natal patch in the first place, as well as affecting overall fecundity of a parent. Here, I have included a cost of dispersal in a model with density-dependent dispersal, based on both an upper critical density dispersal rule (to escape competitive pressures), and a lower critical density rule (to escape fitness loss from an Allee effect). I ask whether varying the nature of this cost will have any effect on the dynamics of the system, or have potential implications for the evolution of dispersal.

Populations displaying cyclic fluctuations in their size over time have been of great interest to ecologists for the past three-quarters of a century. Here we present and examine a spatially structured model that simulates the population dynamics of Canada lynx (*Lynx canadensis*) and displays a time varying behaviour we term phase-shifting, where cycles in different population sub-units move in and out of phase with each other over time. We confirm that the phenomenon is more than different patches simply fluctuating at slightly different cycle period lengths; rather it is a new dynamical behaviour. We go on to demonstrate that this phenomenon can be found under a wide range of conditions, including some that were previously deemed unsuitable. The fundamental structure of the model is then altered in different ways, and we show that phase-shifting can still arise. Given the prevalence of this behaviour under a wide range of model conditions, it is perhaps surprising that little attention has been paid to it previously. The consequences of this type of dynamical behaviour are discussed, as well as discussing reasons why it may have been missed in previous time series analyses.

Disagreement exists between the results of theoretical and empirical exploration into the effect of increasing community complexity on the stability of multi-species ecosystems. A recent return to interest in this area suggests previous results should be re-assessed, from both experimental studies and models, to understand where this discrepancy arises from. Here we propose various simple extensions to a standard multi-species community model that each increase the complexity of the system in a different way. We find that increasing the number of species in a community leads to a decrease in community persistence after the system is perturbed, and go on to show that increasing the dynamical diversity of the community members leads to an increase in stability through a reduction in extinction events, relative to the less complex form of the model. Our results suggest that different forms of complexity lead to different outcomes in the stability properties of the community. While aspects of this work agree with previous empirical findings that more complex communities are more robust to perturbation, we stress that the type of complexity included and the measure of stability used in community models must be properly defined, to allow objective comparisons to be made with previous and future work.

Between-species interactions are well known to have important ecological implications. Removal of a single species from a community has been shown to have detrimental effects on community persistence, with cascading extinctions often resulting (Paine 1966, Borvall et al. 2000, Lundberg et al. 2000). Here we ask what effect introducing dispersal of individuals between different patches may have on the stability of communities in a perturbed environment, in terms of community assembly and species loss. This is studied in two different spatial contexts, firstly through allowing communities to develop over a number of linked patches in the environment and secondly studying the effects of habitat fragmentation (through division of a single patch, with associated reduction in carrying capacity of patch fragments). Results indicate differences between the distinct types of spatial frameworks tested. While there does not appear to be any difference in stability properties between a single unconnected patch and between 2 and 50 connected, randomly positioned patches after the removal of one community member, fragmenting the habitat can have seriously detrimental effects. The implications of these results are discussed in the context of the management of natural populations.

Different species in a community can be ranked according to the strength of their effect on the dynamics of the entire community. Despite a considerable research effort on community structure and the "keystone" species concept, there are still some unresolved issues in this area. We show here that removal of the most abundant species, i.e. that with the greatest relative density within the community, leads to the highest probability of community collapse, with the further loss of community members through cascading extinctions. Comparison of results based on ranking community members by either their abundance or competitive ability indicates that characterising species according to their relative density provides a more refined measure of each species importance within the community. We go on to analyze which ranked species are most likely to be involved with cascading extinction events, and stress the importance of these results in applications of such a model.

GENERAL INTRODUCTION

The essence of ecological study is knowledge based on understanding the nature of interactions between organisms and the environment they exist within. Therefore, a fundamental question that has always interested ecologists is exactly how the number of individuals of a certain species within a habitat will impact on the individual. In this respect, the number of conspecifics present will alter the evolutionary pressures acting on individuals within that population. This can be seen in a number of different ways. The current population size will impact upon (amongst other things) the ability of individuals to find mates, and consequently their ability to avoid inbreeding depression; the ability of individuals to utilise a common resource; their ability to avoid predation or find available prey; and their ability to find suitable new patches in the environment when necessary. Thus, the interaction of individuals within a population can in turn regulate the number of individuals present within that population. Exactly how these interactions influence the regulation of populations has been the subject of debate for some time now (Turchin 1995). Two major components of population regulation that have received considerable attention are density-dependent and density-independent regulatory mechanisms. This thesis adds to the body of work that addresses the impact of density-dependence in some of its different forms. Within this thesis, I follow the definition of density-dependence coined by Murdoch and Walde (1989); that "density dependence is a dependence of per-capita population growth rate on present and/or past population densities" (taken from Turchin 1995, p.27). This definition is chosen as it is concise and lacks a high degree of rigidity that otherwise precludes investigation of a wide range of different densities on population regulation.

There are various problems facing ecologists when studying large-scale ecological systems. Some of these may be so great as to prevent studies being able to address certain specific questions. Theoretical ecologists can often overcome these problems by carrying out numerical simulations using different mathematical functions that describe how populations can change in size over time. In many cases, parameter values can be derived from data sets taken from studying some aspects of natural systems.

Cohen (1995) lists eight commonly used non-linear, discrete-time population models, some of which have been used to model real biological populations. The major unifying aspect of all these models is their reliance on negative density dependence. In other words, all of the models studied were based on the assumption that as populations increase in size, competition between individuals will increase, and the number of offspring in the following generation will be less than the current population size. Here, I ask why functions describing populations in this way have traditionally focused on the competitive aspects of density-dependence, prevalent only at high densities? Evidence is accumulating that many different organisms are subject to different forms of density dependence, for example a fitness reduction at low population sizes (Fowler & Baker 1991). Also relevant are the effects of density-dependence on another important aspect of many organism's life histories, namely dispersal. The intention of this thesis is to investigate the important interactions that arise between density-dependence and dispersal.

Density dependence as an evolutionary force

Biologists have for some time now debated the importance of biotic and abiotic factors in regulating populations over time. In particular, the relative importance of density-independent (Andrewartha & Birch 1954) and density-dependent (Nicholson 1933, Elton 1949) factors in regulating population dynamics has been hotly debated over the last fifty years and more (reviewed by Turchin 1995). That external, (environmental) factors have an important effect on fitness is inarguable. For example, adverse weather conditions will often lead to a direct reduction in the number of offspring surviving to maturity (although this is only one measure of fitness).

For many years, the major problem facing ecologists interested in studying population dynamics has been the acquisition of suitable data sets for analysis. With a few of notable exceptions (Elton 1924, Nicholson 1933, Elton & Nicholson 1942*a* & *b*) very few time series existed of a suitable length, and with ecologists often guilty of concentrating on vertebrates with relatively long life-spans, it is only relatively recently that the most suitable data sets have been acquired. This situation has been helped by the further use of invertebrates (especially arthropods) in study systems, which can produce large amounts of high quality data in very short time periods (e.g. Cappuccino and Price 1995, Constantino *et al.* 1995, Begon *et al.* 1996, Benton *et al.* 2002).

The relative importance of abiotic and biotic factors has been compared over time in population regulation. Density-dependence (an important biotic factor) has traditionally focused on the effects of high densities on population dynamics, in particular on fitness, and has long been acknowledged as having important regulatory effects on populations (Nicholson 1933, Elton 1949). Simple within species "competition" has received by far the most attention, with recent advances accepting the importance of factors such as delayed density dependence, highlighted initially by Turchin (1990). Delayed effects are generally considered at the between-generation level, however, Bjørnstad *et al.* (1998) found negative density-dependence at a much finer scale in insect larvae, with significant lags at one week and also at two to three weeks. The idea of delayed density-dependence has recently been reformulated to some degree to highlight the importance of maternal (or parental) effects on population dynamics (Benton *et al.* 2001). Another aspect of density-dependence that has not (until recently) received the attention it deserves, is positive density dependence, often termed depensation but perhaps more commonly known as the Allee effect (Stephens *et al.* 1999). This describes the situation where there is a reduction in fitness at low population sizes. Again, this is a vital component to include in determining and interpreting the dynamics of many different populations. Further to this, inter-specific feedback has important implications in population regulation, over both horizontal and vertical interactions.

The importance of dispersal

Dispersal has rightly been recognised as being of great importance in ecology for a number of years (Nicholson 1954), and for number of reasons. However it was, until the 1990's, one of the most poorly studied mechanisms involved with population regulation (Taylor 1990). It has since been argued that dispersal is the most important mechanism regulating population dynamics (Denno & Peterson 1995). As one of the riskiest processes an organism can participate in, dispersal has become a challenging issue in contemporary evolutionary biology, as dispersal decisions are inexorably linked to matters of life and death and in some cases the more important matter of sex! Thus, one would expect strong selection pressures to mould the decision-making procedure. Dispersal behaviours lead to the avoidance of deleterious processes such as inbreeding and overcrowding, as well as providing an important link between local and spatial processes. It is closely related to extinction events, and therefore provides a highly significant link between advances in theoretical ecology and the practical applications of conservation biology. Of equal importance is the fact that it is quite likely that variation in habitat quality will somehow match the resource holding potential of the individuals competing for those habitats. Here again, dispersal can be seen to be at the heart of intraspecific competition and therefore under further selection pressure. Thus, the inclusion of dispersal into theoretical ecology studies can be seen to be of great importance on a number of levels.

One of the most important aspects of creating spatial models of dynamical behaviour in ecological situations, is the inclusion of the dispersal of individuals between the sub-populations in a spatially structured environment and the effects this will have on the dynamics of the population when taken as a whole and when compared at the level of the individual sub-populations. A significant amount of work has been carried out on the theory of dispersal, however up until now, most models have looked at the optimal *fixed-fraction* of dispersers. I intend to examine a more realistic situation where individual organisms have some control over the decision of whether to disperse or not, based on some factor such as environmental cues. Thus, the proportion of individuals leaving a patch will be determined by local patch conditions, rather than some fixed fraction of dispersers leaving the patch regardless of current conditions.

Aims and objectives of the current study

The first part of this thesis (**chapters II to IV**) presents work that addresses a form of density dependence that is currently feeling the benefits of a resurgence of interest, namely the Allee effect. **Chapters V to VIII** deal with different forms of density dependence, ranging from delayed density dependence (**chapters V & VI**) to interspecific community interactions (**chapter VI - VIII**). The interaction of dispersal with these diverse forms of density dependence is introduced in a variety of ways in **chapters III** to **V** and **chapter VII**.

The Allee effect (also known as depensation) can be simply defined as any reduction in fitness caused by low population density. In fact, there is still some uncertainty surrounding a precise definition of the Allee effect, with some distinction made between *component* and *demographic* Allee effects (Stephens *et al.* 1999). In **chapter II** I present a new dynamic model that allows for a reduction in fitness at low densities in a flexible way, and analyse the behaviour of this model, discussing the changes in stability that an Allee effect can bring about in population dynamics due to its interaction with competitive effects. This leads to an experimental study of colonies of the pea aphid, *Acyrthosiphon pisum*, and the effect of colony size on the production of offspring that develop wings upon reaching maturity (**chapter III**). I ask specifically if perceived predation pressure induces an increase in the proportion of alates, which are known to have a longer developmental time and produce fewer offspring than aphids without wings (Dixon 1985). I argue that production of alates can be equated to a reduction in fitness, due also to the high costs associated with dispersal.

The importance of dispersal in populations experiencing an Allee effect is studied further in **chapter IV**. Until recently, most models studying population dynamics had assumed a form of density-independent dispersal for migrants (e.g. Hassell *et al.*, 1991; Rohani *et al.*, 1996). The general consensus is that including this form of dispersal in a model will either lead to no change in the relative stability of population dynamics across an ensemble population, or an increase in the stability of the dynamics when compared to the dynamics of a single patch under the same initial conditions. One notable exception to this finding comes from Bascompte & Solé (1994), who found that simple, density-independent dispersal could lead to destabilisation of a steady equilibrium. When reviewing this paper, Hassell *et al.* (1995) pointed out that the model "fails to segregate the processes of survival and dispersal." and stress the importance "that assumptions about mortality and dispersal are properly ordered in the organisms' life cycle." In essence, Hassell *et al.* (1995) see the findings of Bascompte & Solé as biologically unreasonable due to the fact that "the same individual can fail to survive and yet disperse."

Lately, it has become clear that the assumption of fixed-rate dispersal is not always biologically reasonable, due to the inherent complexity of dispersal (Travis & French, 2000). This has led to more effort being invested in creating models that incorporate a more realistic type of dispersal, namely density-*dependant* dispersal (e.g. Ruxton, 1996; Ruxton & Rohani, 1998). This is done by increasing the fraction of individuals that leave a patch as the population size at the given patch changes in relation to some threshold value.

Another aspect of migration where there is considerable scope for exploration is the cost of dispersal. This will affect an individual's propensity to disperse from the natal patch in the first place, as well as affecting the overall fecundity of a parent. Hamilton & May (1977) provide a useful introduction to this topic. **Chapter IV** addresses a combination of biologically relevant factors that have not received particular attention previously. The effects of density dependent dispersal, based on a population trying to escape the fitness loss from an Allee effect are studied, incorporating differing costs to dispersers.

The importance of the interaction between simple and delayed density-dependence, and dispersal are considered in **chapter V**. Here I have taken a spatially structured population model that was developed to simulate the well-known cycles in the dynamics of Canada lynx (*Lynx canadensis*) populations (Ranta *et al.* 1997). Such cyclic population fluctuations have been of considerable interest to ecologists for well over seventy-five years (Elton 1924, Lindström *et al.* 2001). Ranta *et al.* (1997) highlighted the appearance of cycles in different lynx sub-populations that shift in phase relative to each other in their model, and this provided a stimulating subject area for further examination. Ranta *et al.* (1997) suggested these cycles could only arise under some strict assumptions of the model, in particular, if patches were not positioned uniformly around the environment (in a lattice formation). The parameter space of the model was studied carefully to assess the conditions under which this time varying behaviour, here termed "phase-shifting", would arise. This is a biologically significant phenomenon that has received little consideration in ecology so far. Given the prevalence of this behaviour, which we found under a wide range of model conditions, it is perhaps surprising that such little attention has been paid to it previously. The consequences of this type of dynamical behaviour are discussed, as are the reasons why it may have been missed in previous time series analyses.

A further form of density dependence is studied in **chapters VI** to **VIII**. Here we introduce inter- (as well as intra-) specific feedback on dynamics in the context of a multi-species competitive community. Lundberg *et al.* (2000) recently presented a paper that established the possibility for extinctions to cascade through a community when one species is forcibly removed from that assemblage. Furthermore, they highlighted the problems associated with subsequent reintroduction of the previously removed species. In some cases, the reintroduced species could not establish itself again in the community, a phenomenon termed community closure. Perhaps even more concerning was the fact further cascading extinctions also resulted from the attempted reintroduction event.

This work raised the topic of community complexity versus stability, a subject that has been hotly debated in community ecology for some time now (Pimm 1991, Putman 1994). Theory has tended to point to a decrease in stability with increasing community complexity (May 1972, Haydon 1994), while empirical studies have traditionally supported the view that increasingly complex communities tend to be more stable to perturbations. However a recent empirical study by Fox & McGrady-Steed (2002) suggests that some micro-organism communities may exhibit reduced stability with increasing complexity. **Chapter VI** adds to this discussion by asking if different forms of complexity in community dynamics are likely to increase or decrease community persistence following disturbance. This is done by increasing the dynamical diversity within the community in a number of ways; firstly by introducing variable species specific growth rates, then by allowing mutualistic as well as harmful species interactions, and finally by incorporating delayed density dependence into community feedback processes. We go on to stress that the type of complexity included, and the measure of stability used in community models must be properly defined to allow objective comparisons to be made with previous and future work.

The effect on community processes of allowing community members to disperse between different patches in the environment is explored in **chapter VII**. Using the same underlying framework as was employed in **chapter VI**, I studied the effects of linking different numbers of habitat patches in a community with a realistic dispersal kernel, and went on to compare communities that developed under those conditions with communities that were developed on one patch that was then divided into a number of patch fragments.

In **chapter VIII**, I investigate the differences that arise and the predictions that can be made when community members are characterised by either their relative abundance in the community, or their competitive ability within the community. This has direct implications for the "keystone" species concept (Gaston 1996), which is of considerable importance in conservation and management practices. I consider whether it is necessary to learn about the many interspecific interactions that are present within communities - often a discouragingly large task to have to undertake for natural ecosystems - or whether knowledge of the relative density of a species in a community is adequate. Given the fact that there are very few communities where the links between all different members are well understood (but see references within Williams & Martinez [2000] for details of the best examples of near complete multi-species assemblages and food-webs in the ecological literature), identifying the level of detail required to make useful predictions about multi-species assemblages remains an important challenge for ecologists studying such ecosystems (Ovadia & Schmitz 2002).

This thesis attempts to synthesise some of the most important mechanisms and processes in ecology; density-dependence in its different forms, dispersal (both density-independent and density-dependent) and their interactions. Finally, **chapter IX** provides an overall discussion of the work presented here.

POPULATION DYNAMIC CONSEQUENCES OF ALLEE EFFECTS

ABSTRACT

We take a well-known dynamic model of an isolated, unstructured population and modify this to include a factor that allows for a reduction in fitness due to declining population sizes, often termed an Allee effect. Analysis of the behaviour of this model is carried out on two fronts - determining the equilibrium values and examining the stability of these equilibria. Our results point to the stabilising effect of the Allee effect on population dynamics and an unexpected increase in stability with increased competition due to the interaction between competitive and Allee effects.

Introduction

An important strand of theoretical ecology over the last 25 years has been the study of simple difference equations representing closed populations that reproduce synchronously at discrete intervals. These equations have the generic form

$$N_{t+1} = N_t f(N_t), \qquad (1)$$

which allows the population size at the next generation N_{t+1} to be calculated given knowledge of its size at the present generation N_t. Since May (1973, 1974), many authors have shown that this simple formulation can give rise to a great diversity of behaviour, depending on the expression used for the function *f*() and the values given to the parameters of that function. Several different functions have been considered (see Cohen 1995 for a partial list), although these formulations tend to share one property, that of declining fitness with increasing population size. Specifically, they generally assume that

$$\frac{df(x)}{dx} \leq 0 \qquad (2)$$

for all values of x. In biological terms, this means that the reproductive output of an individual never increases as the population size increases. This can be motivated by considering that competition for a fixed resource will always increase as the number of competitors increases. Effectively this assumption means that individual fitness never increases as the population size increases. However, there has been recent interest in cataloguing ecological mechanisms that lead to an increase in some component of individual fitness with increasing population size (Dennis 1989, Fowler & Baker 1991, Stephens & Sutherland 1999). For example, theory predicts that the harmful effects of inbreeding depression reduce fitness as population size decreases. The above works consider many more mechanisms leading to such so-called Allee effects.

It seems likely that most natural populations will be simultaneously affected by a variety of mechanisms, some of which lead to a decrease in fitness with increasing population size (hereafter called competition effects), and some of which lead to a increase (Allee effects). The relative influence of each of these mechanisms will depend on the current population size. Previous studies (see Bellows 1981 for a list of examples) have explored the consequences of various descriptions of competition on the resultant dynamics of the population, but we feel insufficient consideration has been given to the consequences of adding an Allee effect on these dynamics (but see Dennis 1989 for an introduction and overview of previous work). Our aim in this study is to redress this imbalance. The small number of previous works that have considered the population dynamic consequences of Allee effects (see discussion) have confined themselves to consideration of what Stephens *et al.* (1999) termed demographic Allee effects. A demographic Allee effect causes such a decrease in individual fitness with decreasing population size that this effect dominates the effect of competition such that

$$\frac{df(x)}{dx} > 0 \tag{3}$$

for low values of population size x. That is, at low population sizes individual fitness increases with increasing population size. Stephens *et al.* (1999) distinguish this case from so-called component Allee effects, where, although individual fitness $f(x)$ is reduced at low population sizes, the effect of competition is still dominant, such that

$$\frac{df(x)}{dx} \leq 0 \tag{4}$$

for all values of x. Thus, for component Allee effects, fitness will still always decrease with increasing population size, but individual fitness is reduced compared to a situation where the Allee mechanism is not acting. Here we study a novel model that can represent the full continuum of both demographic and component Allee effects. We model density dependence after the Hassell (1975) model, in common with many previous studies and ecological textbooks (e.g. Begon *et al.* 1996). Other popular models, such as the Ricker (1954) function, were not considered due to objections raised in other studies (Doebeli 1995). In this work, we aim to demonstrate the various changes that introducing a factor representing an Allee effect (of variable magnitude) will have on population dynamics, through comparison with a population lacking such a constraint.

Model description

(a) the baseline Hassell model

One of the most popular formulations used for the function describing the effect of population size on individual reproductive output is that proposed by Hassell (1975),

$$f(N_t) = \frac{\lambda}{(1 + aN_t)^b}, \tag{5}$$

where λ, a and b are all strictly positive constants. We can consider λ to be the maximum reproductive potential of an individual in the absence of competition, a to scale the population size to the carrying capacity of the habitat and b to describe the strength and form of competition. The derivative

$$\frac{df(N_t)}{dN_t} = \frac{-ab\lambda}{(1 + aN_t)^{b+1}} \tag{6}$$

is always negative for all positive values of the population size N_t.

The behaviour of this model is well understood (Hassell 1975). Provided that $\lambda > 1$, then there is always one (and only one) non-zero equilibrium population size, given by

$$N^* = \frac{\lambda^{\frac{1}{b}} - 1}{a}. \tag{7}$$

This equilibrium will be globally stable providing

$$b\left(1 - \lambda^{\frac{-1}{b}}\right) < 2, \tag{8}$$

otherwise the population will exhibit some time-varying dynamics. For parameters close to the stable region, this will be a simple two-point cycle. However, if the system is moved in a direction away from stability, either by increasing b or λ, then the dynamics become progressively more complex. The system undergoes a series of bifurcations, leading to increasingly longer periodic cycles and finally deterministic chaos.

(b) the modified Allee model

Here we modify the Hassell equation, so as to add an Allee effect. We are required to introduce a component of fitness that increases with population size. Specifically, we assume that an individual's contribution to the next generation is that given by the Hassell function multiplied by an Allee effect $G(N_t)$, where

$$G(N_t) = \left(1 - A\exp\left(\frac{-aN_t}{\gamma}\right)\right), \tag{9}$$

where A and γ are positive constants, and A is restricted to $[0,1]$. This specific formulation was selected in the basis of its mathematical simplicity, rather than being driven by ecological theory or observation. However, we will demonstrate below that it is able to produce the effects that would be expected of both component and demographic Allee effects.

Parameter values can be chosen so that $G(N_t)$ can always be seen to increase with increasing population size N_t, as is required for an Allee effect, but does so at a decreasing rate (figure 1). The new reproductive fitness function including both the Allee effect and Hassell's competition effect is given by

$$f(N_t) = \frac{\left(1 - A\exp\left(\frac{-aN_t}{\gamma}\right)\right)\lambda}{(1 + aN_t)^b}. \tag{10}$$

Let us consider the effect of the values of the two new parameters (A and γ) on this function. The effect of varying the value of A is illustrated in figures 1*a* & *c*. In the limit $A \rightarrow 0$, the Allee effect is negligible, and eqn. (10) simplifies back to the Hassell function of eqn. (5). As we increase A, so the magnitude of the Allee effect increases. It is important here to note that having an Allee effect as described here does not automatically mean that the reproductive fitness function $f(N_t)$ will necessarily increase with N_t at low population sizes. When A has a low value, then although there is a non-trivial Allee effect that reduces individual fitness (especially at low population sizes) as population size increases, this increasing population size will always be affected more by competitive effects than by the Allee effect, and so individual reproductive fitness always decreases with population size. The maximum individual reproductive output in this case occurs when population size tends to zero. This was termed a *component* Allee effect by Stephens *et al.* (1999). In contrast, it is easy to show that if

$$A > \frac{\gamma b}{1 + \gamma b} \tag{11}$$

then, at the lowest population sizes, increasing population size has a stronger influence in overcoming the Allee effect than on competition, such that individual fitness increases with increasing population size. As population size increases further, the situation reverses, competition dominates, and individual fitness decreases with increasing population size. In such a situation, maximum individual reproduction occurs at a non-zero population size. This situation is called a *demographic* Allee effect by Stephens *et al.* (1999).

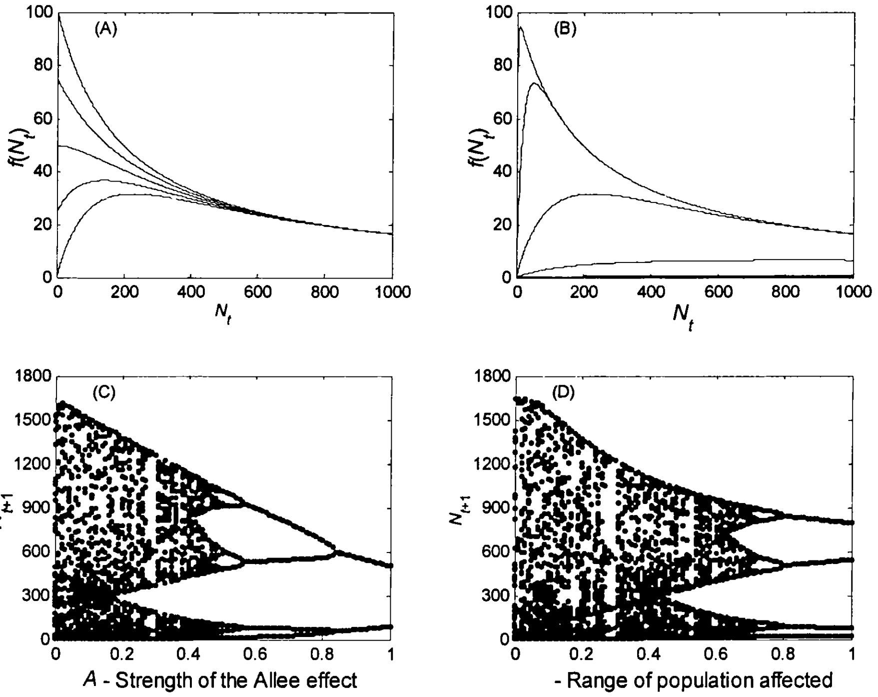


Figure 1. Numerical and bifurcation diagrams showing the behaviour of our novel model of the Allee effect (eqn. 10). Figures 1*a* & *b* look at the effect on fitness of a range of values for both of the new parameters describing the Allee effect, *A* (fig. 1*a*) and (fig. 1*b*). Other parameters are held at the following constant values: λ = 100, *a* = 0.005, *b* = 1.0, in figure 1*a*, = 1.0, while in fig. 1*b*, *A* = 1.0. In fig. 1*a*, we vary the value of *A* from 0 (the uppermost line, equivalent to the Hassell equation), to 1.0 (the lowest line). In fig. 1*b*, is varied between 0.01 (again, the uppermost line) and 1000 (the lowest line).

Figs. 1*c* & *d* are bifurcation plots of this new function (as in eqn. 1, including eqn. 10 as $f(N_t)$. For each value of *A* (Fig. 1*c*, = 1.0) or (Fig, 1*d*, *A* = 0.7), the starting population size is seeded with a random value between 0 and 200. The model was then iterated for 975 generations to remove any transient behaviour, and the size of the population for the next 25 iterations is plotted against that value of *A* or . By choosing parameter values that would produce chaotic dynamics in the equivalent Hassell model (λ= 100, b = 5.0, *a* = 0.005), we can clearly see that the gradual introduction of these components leads to stabilisation of the dynamics.

Figures 1*b* & *d* show the effect of varying the value of . We can see that as increases, so the range of population values over which the Allee effect has a significant influence also increases (fig. 1*c*). We see from (11) that a component Allee effect can always be translated into a demographic effect by sufficiently increasing (unless *A* is exactly equal to one). Similarly, in circumstances where a low value of *A* leads to a component Allee effect (i.e. when eqn. 11 is not satisfied), increasing *A* sufficiently will always eventually induce a demographic Allee effect. That is, there is always a set of *A* values that satisfy (11) regardless of the values of the other parameters.

Equilibrium values

Following convention, we are first of all interested in searching for equilibrium values, that is population sizes N^* such that $f(N^*) = 1$ in eqn. (10). Like the Hassell formulation, there is a so-called trivial equilibrium $N^* = 0$. Unlike the Hassell equation, we cannot solve for the non-trivial equilibria in closed form, however we can investigate these graphically. In the simple case of the Hassell equation, equilibrium population values occur where the two lines representing the numerator

[λ] and the denominator [$(1+aN_t)^b$] of eqn. 5 cross (fig. 2*a*). This can occur only once if $\lambda \geq 1$ and never if $\lambda < 1$. For the modified model (figs. 2*a* - *c*), the straight line (representing λ) seen in figure 2*a* is replaced by

$$G(N_t)\lambda = \left(1 - A\exp\left(\frac{-aN_t}{\gamma}\right)\right)\lambda. \qquad (12)$$

When N_t tends to zero, this has the value $(1-A)\lambda$. It then increases monotonically with increasing N_t, finally saturating at λ. If A is small, such that $(1-A)\lambda > 1$, then the situation is as shown in fig. 2*a*, and a single non-trivial equilibrium value is always obtained. Further, it can be seen from fig. 2*a* that this equilibrium population size is always lower than that of the equivalent Hassell model. This is an inevitable consequence of our formulation of $G(N_t)$, which reduces individual fitness at all population sizes, albeit by ever smaller amounts as population size increases. If $(1-A)\lambda \leq 1$ but $\lambda > 1$, then the situation is as shown in fig. 2b. We can now see that there will be some critical value of γ, for values above this there will be no non-trivial equilibria, for values below this critical value, there will be two non-trivial equilibria. Again, both these equilibria are smaller than the equilibrium of the equivalent Hassell model (obtained in the limits $A \rightarrow 0$ or $\gamma \rightarrow 0$). The effect of increasing γ is to increase the values of N_t for the lower non-trivial equilibrium point at the same time as decreasing the value of N_t for the higher equilibrium point. By increasing γ, we see the two equilibria become more and more similar until they coalesce and are finally lost. Figure 2*c* clearly illustrates that the population can never reach an equilibrium value when $\lambda < 1.0$.

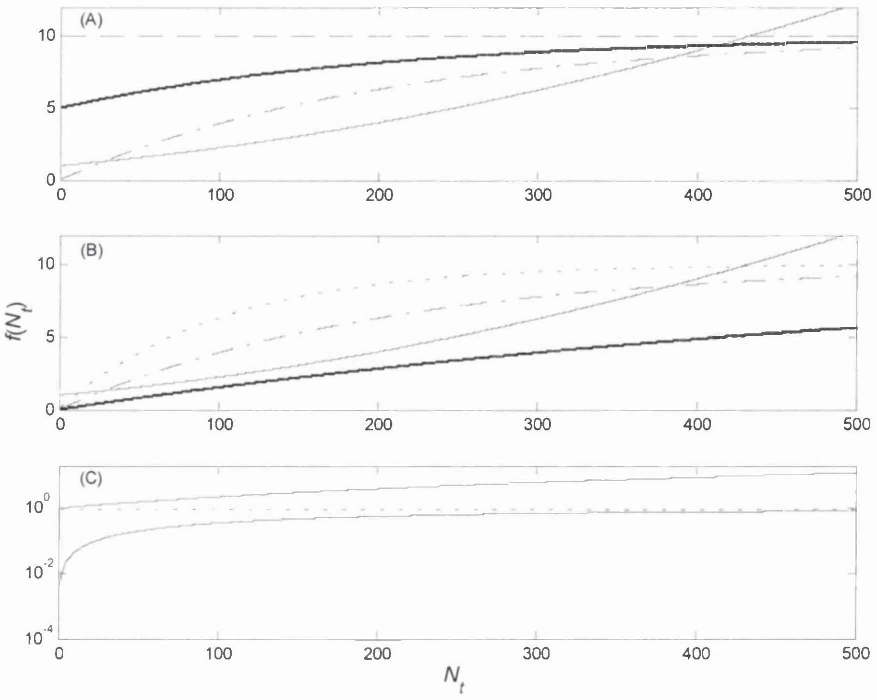


Figure 2. Determining the points of equilibria numerically. These can be found at the point where the different functions [i.e. the numerator and the denominator in equations (5) or (10)] cross each other (constant parameter values for figs. 2*a* to *c* are: *b* = 2.0 and *a* = 0.005). Fig. 2*a* (= 10) illustrates the equilibrium points (N^*) of both Hassell's (1975) function [eqn. (5)], where there is always and only one non-trivial point of equilibrium, and our new Allee effect function, where there can be up to two non-trivial equilibria. (Hassell's numerator: dashed line, the Allee numerator: dotted line (*A* = 1.0); dash-dot line (*A* = 0.5), with the solid line representing the denominator of both equations.) With these parameter values and a value of *A* greater than 0, we find two non-trivial points of equilibria will appear, the first of these equilibria being unstable, while the second will be at the point where the two lines representing $A(N_t)$ and $(1+aN_t)^b$ cross. Fig. 2*b* (= 10, *A* = 1.0) demonstrates the effect of varying γ, i.e. bringing the unstable and stable points of equilibrium closer together, where they will converge, meet, and ultimately disappear. Here, again, the solid line represents the denominator of equation 10, γ = 0.5: dotted line, γ = 1.0: dash-dot line, γ = 3.0: dashed line. Finally, Fig. 2c (= 0.9, *A* = 1.0, γ = 1.0) confirms that when < 1, then

there can be no points of equilibria for either the Hassell or our Allee function (Lines as in fig. 2*a*).

Hence, we conclude that adding an Allee effect never allows a stable point of equilibrium to form in circumstances where there would be no equilibrium without the Allee effect, i.e. where no points of equilibrium arise in the equivalent Hassell function using the same parameter values for λ, b and a. If the Allee effect is strong enough, and influences a wide enough range of population sizes, then no equilibrium is obtained in some circumstances where the equivalent simpler model would give an equilibrium point. For intermediate values of the Allee effect, two non-trivial equilibria can be obtained, reducing to one for weak Allee effects. When non-trivial equilibria are obtained, they are always lower than that of the equivalent simple competition-only model.

Stability of equilibria

For equations such as eqn. 1, May (1973) shows that an equilibrium N^* is locally stable providing

$$\left| 1 + N_t \frac{df(N_t)}{dN_t} \right|_{N_t = N^*} < 1 \quad . \tag{13}$$

When there are two non-trivial equilibria the lower one is always unstable. Any population initiated below this lower non-trivial (or non-zero) equilibrium population size, can never increase in size or even maintain its starting population size, so will therefore always go extinct. Any population initiated above this point may still become extinct should its size fall below the critical value. However, in contrast to the above, a population such as this does at least have the capacity to maintain its original starting size, or even increase in number.

For the case where there is only one non-trivial equilibrium, the rate of change in f with N_t at that point is always negative. In contrast, when there are two non-trivial equilibria, this rate of change is always positive for the lower point of equilibrium and negative for the higher one. This means that the smaller of two co-existing non-trivial equilibria is always locally unstable.

Thus, we find that when the upper and lower (non-zero) equilibrium points are relatively far apart, it will be possible for the population to experience large fluctuations in size around the upper attractor without risk of extinction. As we increase the size of , we also increase the probability of extinction, as the two equilibrium points come closer together. This occurs, as the potential for large fluctuations in population size becomes restricted, as any population falling below the lower equilibrium point will always decrease in size to extinction. Thus, increasing the range of population sizes that may be influenced by an Allee effect leads directly to a limitation in the magnitude of possible fluctuations of the population size.

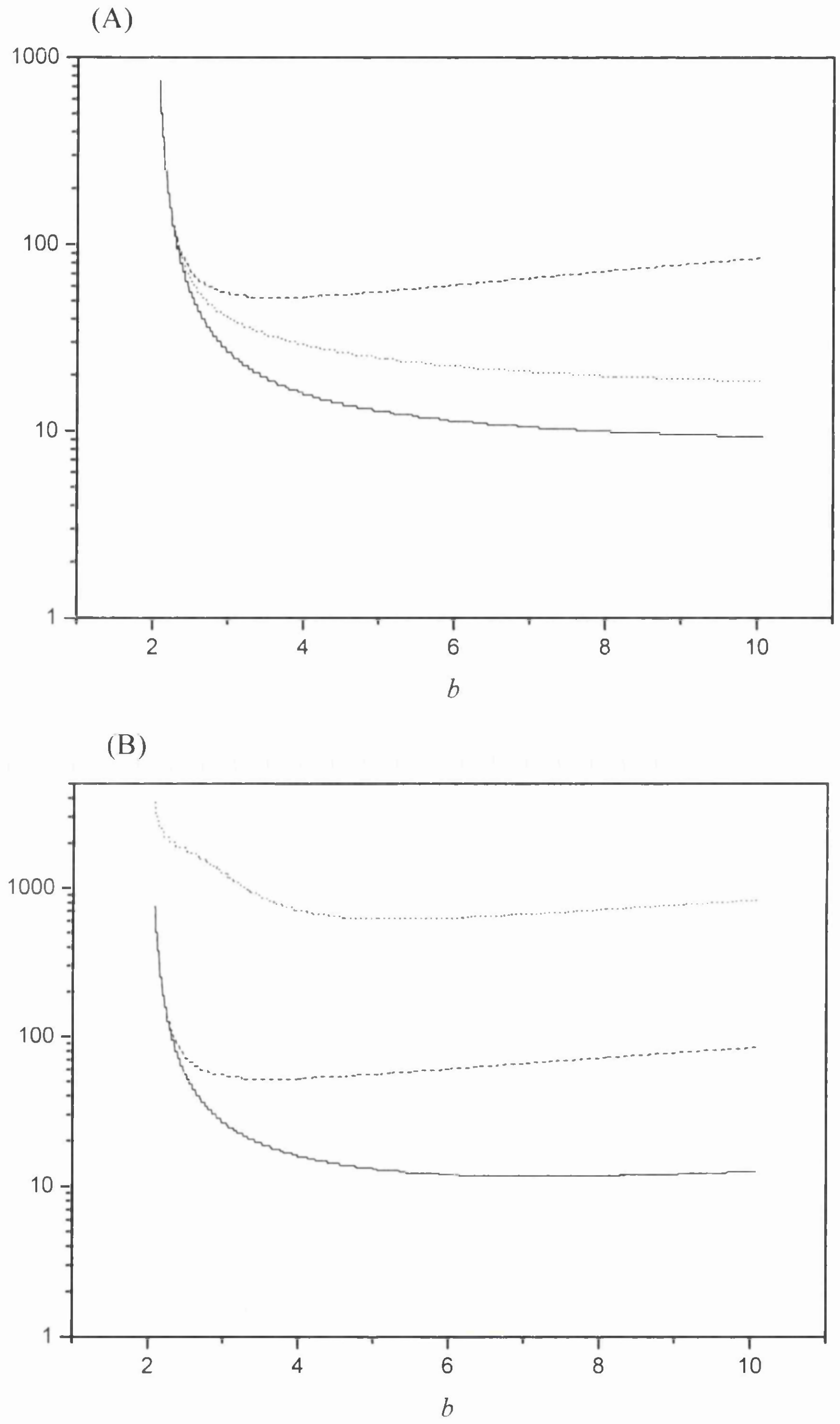


Figure 3. The regions of stability of the population dynamics, obtained from equation (8). The area below and to the left of any of the given lines indicates the region of stability for

that strength of the Allee effect. By varying the parameters A (Fig. 3*a*: $a = 0.005$, $\gamma = 1.0$, $A = 0$: solid line, $A = 0.5$: dotted line, $A = 1.0$: dashed line) and γ (Fig. 3*b*: $a = 0.005$, $A = 1.0$, $\gamma = 0.1$: solid line, $\gamma = 1.0$: dotted line, $\gamma = 10.0$: dashed line) we can see that increasing the strength of the Allee effect leads to an increase in the size of the stable region. It is also a significant finding that increasing the competition parameter (b) can lead to stabilisation of an unstable attractor. This is not possible under the Hassell model, but will occur under such conditions when the Allee effect is strong enough.

We now turn to the situation where the rate of change is negative. In figure 3, the value of λ that satisfies

$$\left|1 + N_t \frac{df(N_t)}{dN_t}\right|_{N_t = N^*} = 1 \qquad (14)$$

(where $f(N_t)$ = eqn. 10) is plotted for each of a range of b values. Parameter combinations to the left and beneath the line produce stable dynamics, whilst those above and to the right of the line produce unstable dynamics, starting with simple 2 point cycles in the region closest to this line. These dynamics gradually become more complex as parameter values shift further away from the line. When $A = 0$ we recover the Hassell model and find that increasing A (the strength of the Allee effect) has a stabilising effect on the dynamics, increasing the range of parameter values for which stability is obtained (fig. 3*a*). It is known that in the Hassell model, increasing b never changes the dynamics from unstable to stable, although it can simplify chaotic dynamics to a regular cycle because of the existence of periodic windows within the chaotic regime. However in our model, increasing b can stabilise an unstable attractor providing the Allee effect is strong enough. This can also be seen in figure 3*b*, where increasing γ is used to increase the strength of the Allee effect. This effect (where increasing the competition parameter b can convert what would otherwise be oscillatory population dynamics to a stable equilibrium) has, to our knowledge, never been shown in any previous works.

Discussion

Since the fitness benefits of aggregating with conspecifics were highlighted by Allee (1931), with the resultant loss of fitness with a reduction in population size consequently being termed an Allee effect, there has been relatively little consideration of what is surely an important ecological phenomenon. We have shown that introduction of an Allee effect into a model that simulates a population with density dependent competition leads to different outcomes depending on the interaction between these two effects.

It is no surprise that adding a mechanism that reduces the fitness of individuals at all population densities (albeit by a negligible amount at high densities) makes the conditions for a non-trivial equilibrium to exist more stringent. It follows that when a non-trivial equilibrium does exist, it will occur at a lower population size in a population under the influence of an Allee effect than the equivalent population modelled without such an effect. Furthermore, it has been recently been shown that Allee effects of intermediate strengths can lead to two co-existing non-trivial equilibria. (Gruntfest *et al.* 1997, Courchamp *et al.* 1999 and Avilés 1999). These studies report this phenomenon for models with different structures, but all are capable of representing only demographic Allee effects. In this report, we highlight the importance of both relatively weak component and stronger demographic Allee effects. While component Allee effects do not override the effects of competition (namely a reduction in fitness with increasing population size, even at low population sizes), they do still have some bearing on population dynamics compared to an equivalent population lacking such pressures. Under these circumstances, the rate of fitness decrease will be comparatively reduced in a population experiencing a component Allee effect.

Our analysis suggests that an Allee effect generally has a stabilising effect on population dynamics. Although this effect can be seen for small Allee effects (including component ones), the stronger the Allee effect, the more powerful the stabilisation. This is consistent with recent analytic results of Scheuring (1999). For a given value of , he calculates the equilibrium population size on the stability boundary for a wide general class of models, which includes the Hassell function. For the modified model, he then finds the value of that corresponds to the same equilibrium population size as the unmodified model somewhere on the stability boundary. The value of is always higher for the modified model than for the simple unmodified one. Hence, Scheuring (1999) concludes that if parameter values are modified so that the equilibrium value is held constant even though an Allee effect is introduced, then this will tend to move the system towards stability. We show (albeit only numerically) that the same is true more generally as stronger and stronger Allee effects are introduced, dropping the constraint of keeping the equilibrium population size a constant. Analogously, Scheuring (1999) demonstrated increasing stabilisation of a host-microparasite system, as an Allee effect was strengthened. Avilés (1999) performed limited numerical investigations of the stability properties of a model of demographic Allee effects. In every example shown, increasing the Allee effect is stabilising. In contrast, Wang *et al.* (1999) have shown that Allee effects reduce the likelihood of co-existence of competitors in predator-prey models. Our result, showing that if the Allee effect is strong enough then increasing the competition parameter b can have a stabilising effect (fig. 3), is quite unexpected, since increasing this parameter can only be destabilising in the equivalent model without an Allee effect (see Hassell 1975).

We show that, even when the Allee effect does not formally stabilise the population dynamics, it does act to restrict the amplitude of oscillations. This occurs because oscillations around the upper equilibrium that involve the population size falling as low as the intermediate equilibrium inevitably lead to the population crashing to extinction (the trivial equilibrium).

This paper adds to a small but growing body of work, suggesting that Allee effects can have important dynamical effects in very simple models of single unstructured populations. The next challenge will be to explore their effects in more complex systems.

THE RELATIONSHIP BETWEEN POPULATION DENSITY AND INDIVIDUAL FITNESS IN THE PEA APHID, *ACYRTHOSIPHON PISUM*

ABSTRACT

Density-dependence is an important regulating factor in population dynamics that is commonly considered to reduce individual fitness at high densities. Recently, interest in mechanisms that reduce fitness at low population densities, a phenomenon known as the Allee effect, has grown. Here we study the effect of a wide range of population densities on different measures of fitness in the pea aphid, *Acyrthosiphon pisum*. By subjecting aphids to predation pressure, we find that fitness at very low population densities can be reduced. Comparisons of the data to different non-linear models of density-dependence suggest that aphids may in fact be subject to an Allee effect. We discuss some of the implications of this and possible mechanisms driving it.

Introduction

It is well known that intraspecific competition reduces aphid fitness when the number of individuals feeding on the same plant is large (Dixon 1998). In many species, heavy infestation by aphids leads to plant death and a subsequent extinction of the aphid population. In contrast, the effects of density on fitness at low aphid colony sizes are less clear. In some studies, aphids within small clusters gained increased fecundity over isolated aphids (Way & Cammell 1970, Dixon & Wratten 1971, Lopez *et al.* 1989). Other studies have found no such synergistic effect (Messina 1993, Hodgson & Godfray 1999). In some aphid species, immigrants actively cluster on a plant (Ibbotson & Kennedy 1951, Michaud 1999), suggesting that aggregation is of benefit at low aphid densities. One possible reason is a reduced risk of predation with larger aphid densities (Turchin & Kareiva 1989): the larger an aphid colony, the more predators aggregate in the colony, but the per-capita-risk for the aphids may decrease. However, the precise relationship may depend on the type of predator attacking the colony. Syrphid flies (Diptera: Syrphidae) or predatory gallmidges (Diptera: Cecidomyiidae) are able to eradicate even large aphid colonies so that predator dilution may not be a successful strategy to reduce predation risk. Additionally, there are other potential benefits of aggregation. Aphids create a sink to which plants channel nutrients. At least at small colony sizes, aggregations may create a disproportionately large sink such that more nutrients are available for each individual aphid.

The morphological plasticity in many aphid species means they can be used as an ideal test organism when studying the effects of various treatments on their life history. Adult individuals may have wings (alates) or lack them (apterae), the presence of which is determined by the parent. A parent's decision over whether to produce alates or apterae has long been known to be affected by environmental conditions (Sutherland, 1969*a* & *b*), such as poor host plant quality, high levels of intraspecific competition (Bonnemaison 1951, Lees 1966) or the presence of predators (Weisser *et al.* 1999). Of particular interest are decisions relating to dispersal, which requires the development of wings. Alates have been shown to take a longer time to reach maturity, as well as having a reduced fecundity (Zera & Denno 1997, Dixon 1998). Thus, these costs of dispersal must be balanced by the benefits gained by moving to new areas by alates.

So far, no study has attempted to look at density-dependent aphid performance over a wide range of initial colony sizes, nor has anyone investigated the mechanisms that are responsible for any positive effect of density on fitness at low densities. Here we describe an experiment with two clones of the pea aphid, *Acyrthosiphon pisum*, designed to address these points. We focus on fecundity (the number of offspring surviving to maturity) and alate production as components of fitness.

Materials & Methods

General experimental approach: Aphid colonies were initiated with a varying number of first instar pea aphids (*Acyrthosiphon pisum*) on bean plants (*Vicia faba* var. 'The Sutton'). At most, two clones of the aphid were used in each experimental colony, differing only in colour. In each colony, the 'target individual' was of the red clone BP (Weisser *et al.* 1999) whereas all other individuals were of the green clone SG. This approach made it possible to measure the reproductive success of the target aphid without having to estimate reproductive success of all aphids on a plant. Colonies were reared for two generations in the laboratory (split into greenhouse and climate chamber experiments), where individual colonies were isolated by being caged in polypropylene bags.

Experimental design: Aphids of the clones BP and SG were propagated for two generations at low density to avoid alate formation. Plants used in the greenhouse experiment were at least two weeks old with a minimum of four leaves.

One day before the start of the experiment, adults of both clones were placed in low density groups of up to 10 individuals on plants and allowed to reproduce for 24 hours. The offspring were collected and used to initiate experimental colonies. To minimise maternal effects, care was taken to mix offspring of different mothers (of the same clone) from different plants before using them to initiate colonies. Plants were inoculated over several days. At least one full replicate (i.e. the full range of densities for each treatment) was completed on each day, so that 'day of set-up' could be used as a blocking variable in the analysis.

Ten replicates of each treatment were set up in the greenhouses, giving 20 experimental colonies, with a further 5 replicates being initiated in the constant climate chamber. Both sites were run by the Institute für Ökologie, Friedrich-Schiller Universität, Jena, Germany. Replicates (each colony caged with polypropylene bags) were placed in blocks of 10 colonies, of one full replicate per treatment.

Table 1: Treatment, for both greenhouse & climate chamber experiments:

Density	No. of 1st instar SG	No. of 1st instar BP	No. of replicates	Total number SG needed
1	0	1	25	0
2	1	1	25	25
3	2	1	25	50
5	4	1	25	100
10	9	1	25	225
20	19	1	25	475
30	29	1	25	725
50	49	1	25	1225
75	74	1	25	1850
100	99	1	25	2475
Totals			250	7150

No of plants used:	100 x 2 (control, predator treatements) + 50 (climate chamber) = **250**
No of SG aphids used:	**7150**
No of BP aphids used:	**250**

Observations and variables measure: Previous experiments (Weisser *et al.* 1999) have shown that survival of aphids in laboratory treatments should be high (close to 100%). From day six until the last individual matured, replicates were checked daily and the day of first reproduction (assumed to be the day of maturation) was noted for each colony in all replicates. In order to analyse the data describing the length of time taken for the aphids to mature in both experimental areas (greenhouse and climate chamber), maximum and minimum temperatures were recorded daily. This information was used to create a measure of time, "degree-days", which incorporated the midpoint temperature between the maximum and minimum daily temperatures and the length of time (in days) since that experimental colony was initiated. Degree-days were used to remove the effect of daily temperature variations as a confounding variable on the length of time taken for aphids to mature (taken as the day when the first offspring of the target aphid were produced). All data from the greenhouse experiment (control and predator treatments) have been grouped together to increase sample size in the following analyses of time taken to mature, as there was no difference in the treatments of these two groups before maturity.

The colony size of each replicate was recounted at maturity, and a single 2-spot ladybird larvae, *Adalia bipunctata*, was introduced to each of the Predator treatment colonies 24 hours after that colony's target aphid had matured. The predators were removed from the colonies after 24 hours (± hour1). Replicates were harvested 10 days after maturity of the target aphid and the total number of live offspring of the target aphid was determined (i.e. approximately 8-12 days of reproduction for each BP aphid). The proportion of winged individuals among the mature offspring of the target aphid was also determined at this point.

Analysis and Expectations: The effect of start date and density on the following variables were analysed (using non-parametric tests when the variance between groups was highly unequal, or data was non-normally distributed): Age of maturity; total fecundity; proportion of winged individuals among offspring; and impact of predators on colony (on the above factors). In the laboratory experiment we expected a negative effect of high density on aphid reproduction and maturity, and possibly a positive effect of density on reproduction at low densities (per capita fecundity of the aphids was expected to be between zero and 100 offspring). Statistical analyses were carried out using MINITAB for Windows Release 11.21 and SPSS for Windows Release 9.0.

Results

Time taken for Target Aphid to Mature.

The results of the analysis of the time taken for target aphids to mature are as follows. Figure 1 shows a comparison of the time taken for target aphids to mature (in degree-days) of colonies of different sizes and colonies initiated on different days. There was no significant effect of initial colony density (Kruskal-Wallis test; $H = 4.71$, *d.f.* $= 9$, $p = 0.859$), but while there was a significant effect of start date on the time taken for the target aphid to mature ($H = 71.91$, *d.f.* $= 6$, $p < 0.001$), there was no obvious trend in the result. This is supported by the result of a correlation between time (in days) after start of the experiment the colony was initiated, and time taken for the target aphid in that colony to mature in degree-days (Pearson's $r = -0.142$, $p = 0.085$).

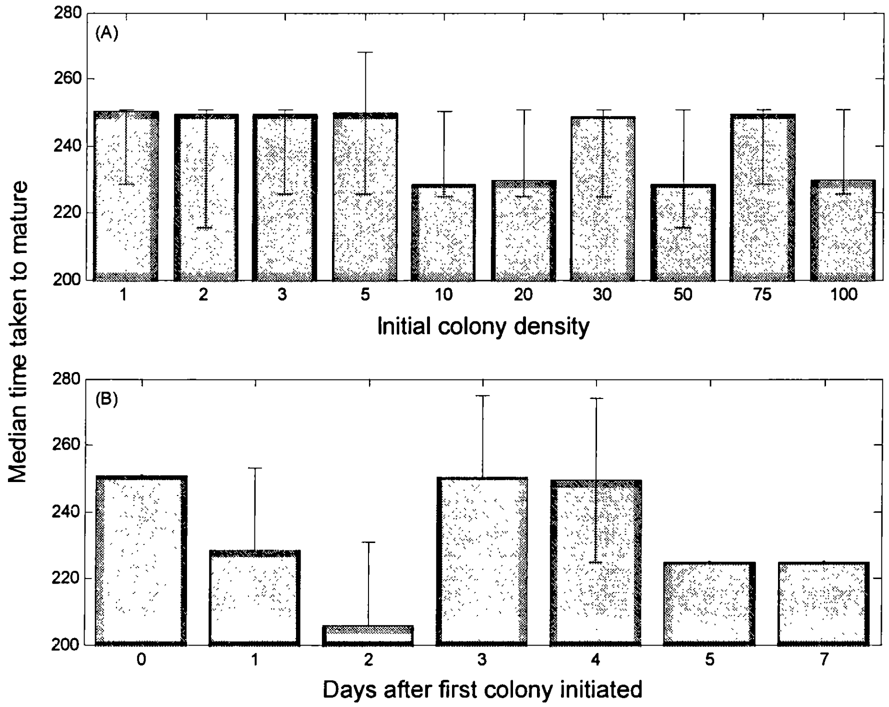


Figure 1: Time taken for target aphids in different colonies to mature. Here we compared the median time taken for the target aphid to mature in colonies of different initial density (1*a*), and found no significant effect of colony size on the time taken for the aphids to mature. However, there was a significant effect of start date of the experimental colonies (shown here as the days after the first experimental colony was initiated, 1*b*), although there was no obvious trend to this result. All times to maturation standardised to degree-days; error bars show first and third quartiles; data taken from greenhouse colonies.

For the experimental colonies from the Climate Chamber, Kruskal-Wallis tests show no significant effect of either start date or initial density on the number of degree-days taken for the target aphids to mature. Studying the effects of site (greenhouse or climate chamber) on the time taken to mature, we found a highly significant effect of the site on the time taken to mature ($H = 34.80$, 1*d.f.*, $p < 0.001$), with those colonies kept in the constant climate chamber developing at a faster rate than those kept in the greenhouse (median times to maturity: 220.0 degree-days and 247.0 degree-days respectively).

Introducing the Predator Treatments: Effect of Initial Density on Colony Size after Two Generations.

Colonies were harvested 10 days after the target aphid had matured, and the number of juveniles, adult apterae and adult alates remaining was recorded, and the proportion of winged adults (as a proportion of the total number of adults) was calculated.

As neither the Control, nor the Predator data on final colony sizes were normally distributed, the following parametric tests have been carried out with square root transformed data (Anderson-Darling test for normality indicates no significant difference from normality on the transformed data; $A^2 = 0.631$, $p = 0.09$). Figure 2 clearly demonstrates the negative density dependent effects on final population size that occur at high initial densities, due to increased competition.

Due to the introduction of a predator to half of the greenhouse colonies, a relative reduction in the final population size could be expected in colonies that underwent the predator treatment, due to the removal of reproducing adults by the beetle larvae. Here we use this treatment as a fixed factor to find if there is any effect on the final colony size, as well as any effect of initial colony density. A two-way ANOVA, with initial density and experimental treatment (Control vs. Predator treatment) as fixed factors shows a significant effect of both initial density ($p < 0.001$) and treatment ($p = 0.017$) as well as a significant interaction between these two factors ($p = 0.013$). Post-hoc comparisons (Tukey test) show that initial densities of up to 20 individuals can be grouped together as a homogeneous subset, as well as groups with 50 individuals or greater.

Correlation analysis shows a significant negative relationship between increasing density at maturity and final colony size in both the Control (Pearson's $r = -0.782$) & Predator ($r = -0.654$) treatments ($p < 0.001$ in both cases).

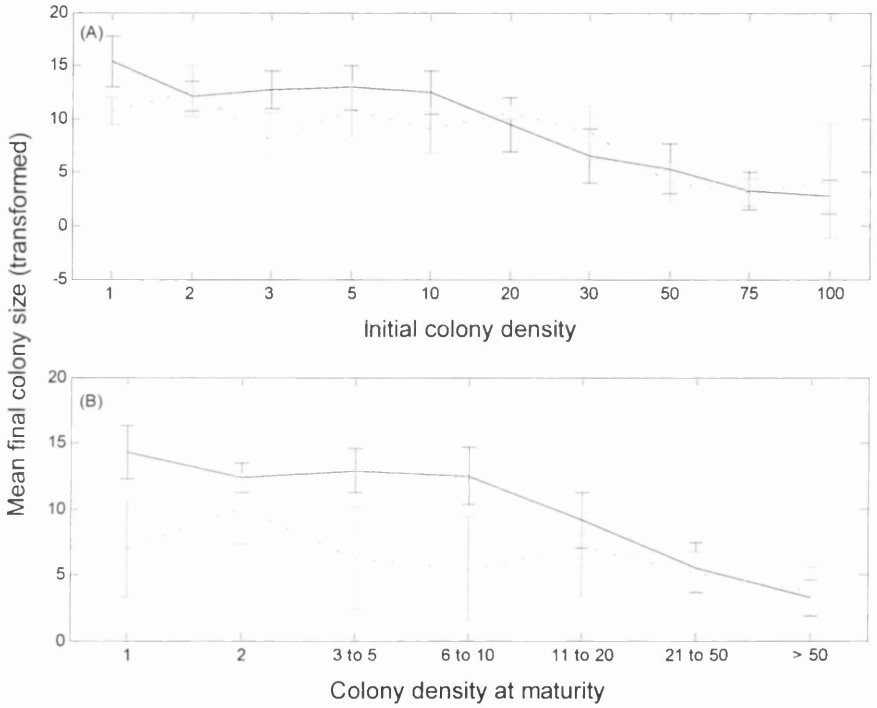


Figure 2: Mean final colony densities (square root transformed data). Colonies can be grouped by their experimental treatment (control [black lines]; predator [grey, dashed lines]) and either their initial density (2*a*), or the density of the colony when the target aphid matures (2*b*). Here we can clearly see that the mean final colony size is reduced at the highest densities in both treatment groups.

By looking at the density of colonies at maturity (rather than the initial density), we can gain a more accurate picture of the effect of competition on the colonies. The colonies were regrouped in new colony density at maturity classes as follows: colony size = 1, 2, 3 to 5, 6 to 10, 11 to 20, 21 to 50 and 51. Minimum sample size for the new groups was $n = 6$, maximum was $n = 15$. In this case, a two-way ANOVA of square root transformed data shows a highly significant effect of the density at maturity on the total colony size at the end of the experiment ($F_{6,13} = 27.204$, $p < 0.001$). There was also a significant effect of experimental treatment on the final colony sizes ($F_{1,13} = 7.246$, $p = 0.009$), as well as a significant interaction between these two fixed factors (density at maturity * treatment; $F_{6,13} = 2.263$, $p = 0.033$).

The effect of predation pressure on fecundity:

Adults present at the end of the experiment were counted as offspring of the target aphid that had survived to maturity. Data on the number of adults at the end of the experiment were not normally distributed, and could not be transformed to fit a normal distribution, therefore the following analyses were done using non-parametric tests. There was a tendency for the control treatment colonies to have a higher density of adults at the end of the experiment. The increase was found to be non-significant (Sign test, medians: control = 15.0; predator = 11.5 $p = 0.099$). A Kruskal-Wallis test of the medians reveals a highly significant effect of initial density on the adult population sizes at the end of the experiment (H = 53.85, 9*d.f.*, $p < 0.001$ for the Control treatment; H = 27.11, 9*d.f.*, p = 0.001 for the predator treatment). By looking only at the colonies with an initial density of 30 individuals or less, we can avoid incorporating the extreme effects of competition found at the highest initial densities. A sign test on this truncated data set reveals a significant effect of the introduction of predators into colonies (medians: control = 21.0; predator = 13.5; $p = 0.01$).

Using the colony density at maturity, rather than initial colony density, with the groupings outlined above, we find a highly significant effect of density on the number of adults present at the end of the experiment in both the control (H = 46.74, 6 *d.f.*, $p < 0.001$) and the predator treatment groups (H = 23.22, 6 *d.f.*, $p = 0.001$).

Figure 3 illustrates the different trends that appear in the number of adults present at the end of the experiment, between the control and predator treatments. In particular, it is apparent that colonies with a density of only one individual at maturity undergo an extreme reduction in final colony size when a predator is introduced.

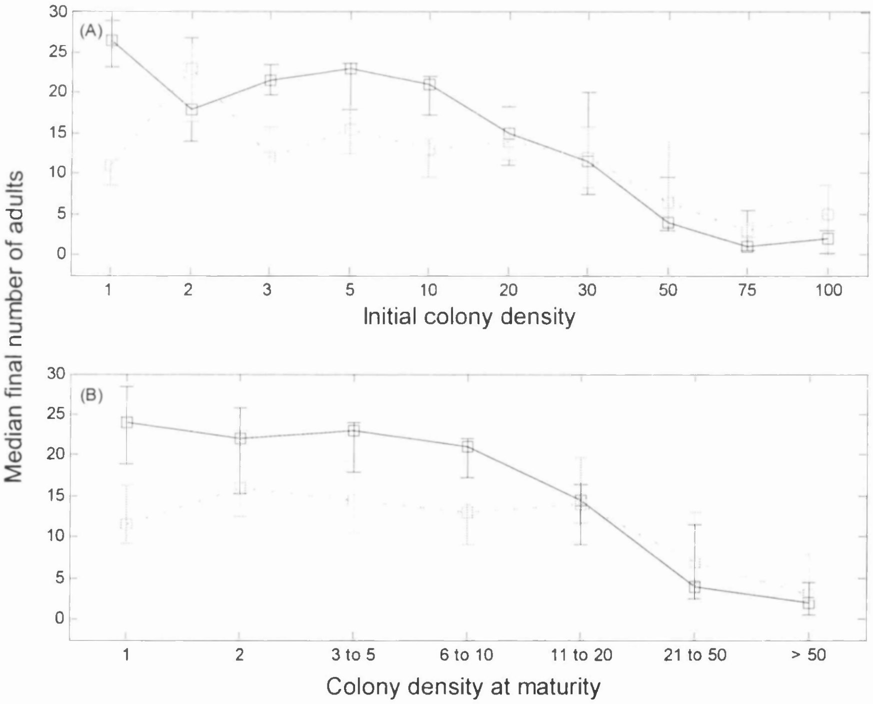


Figure 3: Median final number of adults in the colonies. Data were grouped according to treatment (control [black line] or predator [grey, dotted line]) and either according to the initial density of the colony (3*a*), or according to the density of the colony at maturity of the target

aphid (3b). We see the same pattern regardless of which way the data is grouped. At very high initial density or density at maturity, the final number of adults was relatively low, compared to lower densities (initial or at maturity). There is also a significant reduction in the final number of adults when predator colonies were initiated with only one individual, and when there is only one individual in the predator colony when the target aphid reaches maturity.

The presence of just one other aphid in the colony has been shown to increase the final colony size in the predator treatment group, with a relative decrease in control colonies upon the introduction of one more aphid. We found this reduction in the control group, possibly through increased competition. The increase in final colony density in predator treatment colonies with two aphids at maturity could be due to a predator dilution effect. A further increase in the density at maturity (between 3 and 10 individuals) seems to return to a case where there is a difference between final colony sizes of different treatment groups. A further increase (greater than 10 individuals present at maturity) shows the effects of competition decreasing both treatment groups final number of adults, bringing them more in line with each other.

Comparison of data to models:

Further analysis reveals a significant negative trend between population size at maturity and the colony size at the end of the experiment exists in both the control (linear regression: R^2 (adj.) = 0.553, $p < 0.001$) and the predator treatments (R^2 (adj.) = 0.251, $p < 0.001$). This is consistent with expectations of a density dependent form of competition. This type of analysis can be extended further, by comparing the data from these experiments to theoretical models of fitness in single species systems. Two well-known examples of such models are the often-used modification of

Maynard-Smith & Slatkin's (1973 [referred to as M-S & S]) model (e.g. Ruxton & Rohani, 1998 - eqn. 1)

$$f(N_t)=\frac{\lambda}{1+(aN_t)^b}, \tag{1}$$

and the Hassell (1975) model (eqn. 2), which both describe the effects of density dependence in single species populations.

$$f(N_t)=\frac{\lambda}{(1+aN_t)^b}, \tag{2}$$

In addition, a third function (eqn. 3), which includes a factor that allows for a reduction in fitness at low population sizes, termed the Allee effect (Fowler & Ruxton 2002, and chapter II of this thesis), is compared to the data set.

$$f(N_t)=\frac{\lambda\left(1-A\exp\left(\frac{-aN_t}{\gamma}\right)\right)}{(1+aN_t)^b}, \tag{3}$$

Some important assumptions of these models are met in this particular experimental set-up. These are that this is a single, parthenogenetically reproducing species, in a single patch system, with no dispersal into or out of the patches.

The parameters in these functions are defined as follows. Individual fitness $f(N_t)$ can be calculated according to the population size at a given time (N_t). λ describes the per capita growth rate in the absence of competition, a relates to the carrying capacity of the environment and b describes the form of competition. Specific discussion of these parameter values can be found in Maynard-Smith & Slatkin (1973) and Hassell (1975). The new parameters associated with eqn. (3) incorporate an Allee effect. These are A, the strength of the Allee effect; and γ, the range of population sizes under the influence of the Allee effect. Further discussion of these parameters and how they affect the model can be found in Ruxton & Fowler (2002, and chapter II of this thesis).

By considering the colony density at maturity, and the number of adults present at the end of the experiment, we can use linear and non-linear regressions to compare our results with the predictions from each of the above models (figure 4). Comparing the above functions to the data from the Control treatment data, we find the parameter values shown in table 2. Adjusted R^2 co-efficients are used, as they correct for the number of parameters incorporated into the models.

Table 2: Comparison of data (final number of adults present) from the control colonies to three models describing density dependence in a single species population in different ways. NA = Parameter not present in model. (Models were run with limits λ 1; $0.001 < a > 1$; $1 < b > 10$; $0.001 < A > 1.0$; $0.001 < \gamma > 1.0$.).

Function	Parameter Name					
Name	λ	a	b	A	γ	R^2 (adj.)
Hassell	24.577	0.004	10	*NA*	*NA*	0.634
M-S & S	23.499	0.048	1.552	*NA*	*NA*	0.635
Allee	59.283	0.048	2.049	0.6	0.823	0.635

The different functions used here provide relatively different predictions for parameter values, with extremely similar abilities to describe the data (see discussion for the biological relevance of these results). In other words, depending on the function used, the average reproductive output for each adult in the population (in the absence of competition) is estimated to be approximately either 24 or 59 offspring. The carrying capacity of the environment (each isolated plant) is estimated to be approximately either 21 or 250 individuals, with both scramble and contest types of competition being predicted. Linear regression of this data provides a reduced ability to describe the trends ($R^2 = 0.553$, $p < 0.001$). Carrying out the same procedure with data from the Predator treatment group yields the results shown in table 3. Once again, all non-linear functions produced return a slightly better description of the data than a simple linear regression ($R^2 = 0.251$, $p < 0.001$).

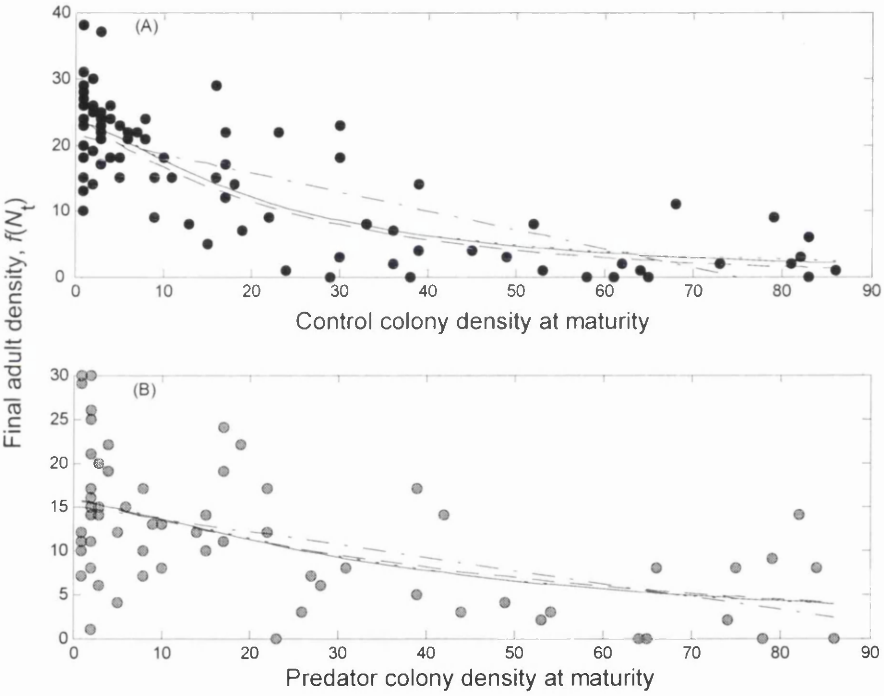


Figure 4: Regressions of the number of adults present at the end of the experiment against the colony density at maturity of the target aphid, using different models that describe density-dependence in single species populations (M-S & S: dotted line; Hassell: dashed line; Allee function: solid line), or a linear regression (dash-dot line). The data in the control treatment is described almost equally well by all the non-linear functions tested in the control treatment (4*a*). The predator data is described best by a function that includes an Allee effect (Fowler & Ruxton 2002; dashed grey line, 4*b*. See discussion for further comments).

In both treatments, non-linear functions described the data better than a simple linear equation.

Table 3: Comparison of data (final number of adults present) from the predator colonies to three models describing density dependence in a single species population in different ways. NA = *Parameter not present in model.* (Parameter limits as in *table 2*)

Function	Parameter Name					
Name	λ	a	b	A	γ	R^2 (adj.)
Hassell	16.049	0.004	4.647	NA	NA	0.280
M-S & S	15.533	0.025	1.437	NA	NA	0.281
Allee	23.270	0.027	1.480	0.329	0.402	0.281

The results from these analyses indicate that all three models are equally capable of describing the data for both treatments, particularly well in the case of the control colonies. In all cases, the non-linear functions produce significantly higher R^2 (adj.) values than those of a linear regression and thus are able to explain more of the variation in the data. Also relevant in the predator treatment case is the fact that the parameter values returned for the Allee function differ significantly from those returned for the Hassell function. This finding is interesting, as the function describing a population with an Allee effect is based on the Hassell equation (Fowler & Ruxton 2002, chapter II).

Effect of Density on Proportion of Winged Adults.

A Sign test of the medians using all available paired data shows that there is no significant difference in the proportion of winged individuals between the two treatments ($n = 58$, $p = 0.55$); the introduction of a predator does not appear to influence the proportion of winged offspring the target aphids are producing in one direction. There is, however, a relationship between density and the proportion of winged adults present (figure 5).

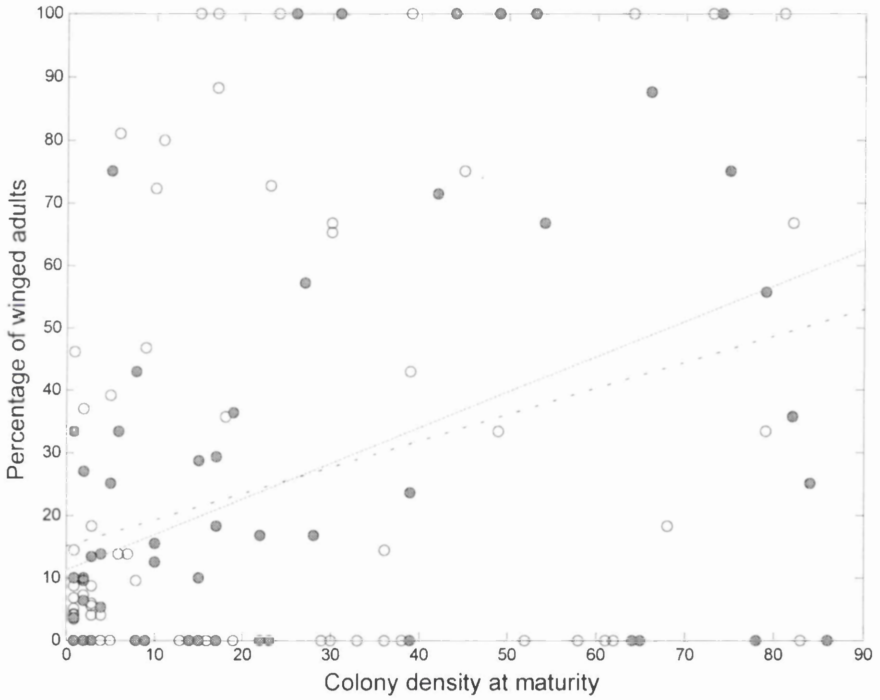


Figure 5: Percentage of winged adults at the end of the experiment. There is a significant positive relationship between the colony density at maturity of the target aphid, and the percentage of adults with wings at the end of the experiment, in both the control (open circles, dotted line) and the predator (grey circles, solid line) treatments.

These results are confirmed by carrying out Kruskal-Wallis tests (due to non-normality of data after appropriate transformation), which shows that while there is a significant effect of colony density at maturity on the percentage of winged adults present at the end of the experiment (H = 81.81, *d.f.* = 54, $p = 0.009$), there is no significant effect of the introduction of a predator (H = 0.12, *d.f.* = 1, $p = 0.725$). Linear regressions of density at maturity and proportion of winged adults show a significant positive relationship with increasing density in both treatments (control: $R^2 = 0.082$, $p = 0.006$; predator: $R^2 = 0.201$, $p < 0.001$), however this is a relatively poor explanation of the variance in the data.

Discussion

The work presented here represents the first study into the effect of density dependence on aphid fitness over such a wide range of densities. Here, we suggest that as well as the competitive effects that are known to occur at high densities, reproductive output may be affected at lower densities, due to a lack of conspecifics. We propose one possible mechanism for the occurrence of this, while ruling out another.

Three broad results can be taken from this work. Firstly, density was not found to influence the length of time taken for target aphids to mature. Secondly, density was found to have a direct influence on the fitness of the aphids, in two ways - on the number of offspring produced and on the proportion of offspring that developed wings. Finally, the presence of predators was found to affect the colony size at the end of the experiment, but not the proportion of alates produced. Thus, it is likely that predators had two separate effects in this experiment:

1) They killed individuals of the target clone and thereby drastically decreased their reproductive success. In particular, if they ate the initial target adult aphid, there could be no further reproduction until the first offspring of this individual matured.

2) Predators killed SG (non-target) aphids and therefore reduced competition for the target individuals. This could have increased the target aphid's reproductive success.

The relative strength of both effects determined whether predation is "beneficial" for the target aphid. As initial density increased, effect (1) will be reduced in importance (target aphids are less likely to be eaten due to the dilution effect), and effect (2) may also have been reduced, especially at higher initial densities when predation does not reduce total aphid population size as significantly.

While we tried to counter the effect of varying environmental conditions by incorporating temperature data into the measure of time taken for target aphids to mature, we still found a significant effect of start date of each experimental colony. It is possible that the temperature used to calculate degree-days was not fully representative of the variation in environmental conditions. Alternatively, some other environmental factor may have influenced the result in other ways. Other insect species are known to have adjusted their development to counteract adverse environmental effects, with some studies having been carried out on mechanisms and reasons for water conservation in Lepidopterans (e.g. Denno & Benrey 1997, Klok & Chown 1999 and Willmer 1980). It is known that high temperatures affect aphid developmental and growth rates (Dixon 1998), however the effects of humidity, or other environmental factors have not been studied in detail.

As there was no observable effect of increasing colony size on the length of time taken for the target aphid to mature under these experimental conditions, we suggest that the carrying capacity of these plants may be greater than 100 aphids. This would result in little competition between individuals for resources at this stage. Thus, when the colonies were initiated, all densities were likely to be at or below this critical level. However, as soon as individuals started to reproduce, this would have led to a rapid increase in the number of aphids feeding on the plant. In those colonies with higher initial densities, thus would result in the colony suddenly exceeding the carrying capacity of the environment. This may explain why there was no general trend with increasing density in the time taken (in days or degree-days) for target aphids to mature.

When looking at the effect of increasing initial colony density on final colony sizes, the results demonstrate that at high initial densities, competitive effects are strong enough to decimate entire populations. This result is not surprising, and as mentioned before, has been shown previously (Dixon 1998). However, this result should be taken in context, as the experimental set-up did not allow the aphids to disperse to other sites as competition for resources increased. The results from the predator treatment group clearly show that a predator that is only present for 24 hours can have a significant effect on aphid future reproductive success. The main mechanism here is likely to be the removal of reproducing adults, preventing further reproduction for several days. In some cases, it is possible that the predator removed the target aphid. At higher densities, the predator effect ceases to be as important; as the ladybird larvae ate a maximum of around twenty to fifty aphids per day. Thus, if the number of reproducing adults is high, maximum daily offspring production without competition will also be high (number of adults * approximately 8 offspring over a 24 hour period). In the replicates where more aphids were eaten, the remaining aphids may have had an increased rate of reproduction, offsetting the differences very quickly. While it has been shown that the adults of some coccinellid species do rely on visual cues, and show a preference for one colour morph over another in the pea aphid, this has not been found in studies of ladybird larvae (Harmon *et al.,* 1998, and references within).

The general results were in line with predictions of models for density dependent competition in single species systems (e.g. Maynard Smith & Slatkin 1973 and Hassell 1975). Bellows (1981) suggested the M-S & S model was one of the most flexible available at the time, in particular, more so than the Hassell model. If we compare the parameter values generated by the regression models for the control and predator treatments, there is some agreement about the per capita population growth rate across the different functions under different treatments. These regression models predict a λ-value of approximately 24 in "non-Allee" population functions when there is no predation pressure. Interestingly, the model describing the Allee effect actually predicts a very similar value for per-capita growth rate when there is predation pressure. We suggest that this convergence of results indicate that the aphid colonies do experience an Allee effect under predation pressure: the presence of a predator, even for a relatively short period of time, had an unexpectedly high impact on the reproductive output of target individuals at low densities. The results from this analysis indicate that the different functions performed similarly at describing the experimental data. However, the parameter values produced by the regression models must be taken in context, and we therefore suggest that in the experimental colonies that are suffering from an Allee effect, this is brought about by predation pressure.

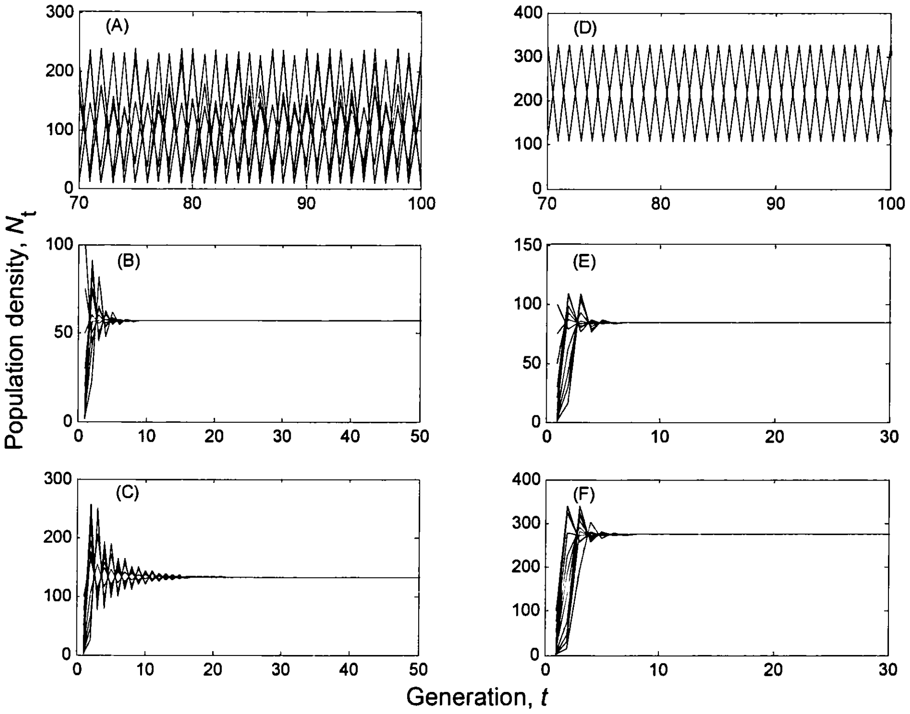


Figure 6: Simulated time-series using parameter estimates taken from the non-linear regressions [eqns. (1) - (3)]. Here we see the form of population dynamics over time that the parameter estimates for the different functions produce, for both the control (6*a* - *c*) and predator (6*d* - *f*) treatment groups. The Hassell function parameter estimates produce unstable fluctuations in the control treatment (6*a*), and a stable 2-point cycle in the predator treatment, even after a number of generations. All other parameter estimates, for both the M-S & S (6*b* & *e*) and the Allee function (6*c* & *f*) produce monotonic damping to a stable point equilibrium, regardless of what density the population was initiated at. Simulated populations were initiated with the same densities as experimental colonies.

Interestingly, when incorporated into a plot of the stability boundaries of the Hassell function (Hassell *et al.*, 1976), the combination of parameter values output by the regression model suggest dynamics that show unstable fluctuations (see figure 6), a relatively uncommon finding in real data sets. However, these models do not take any exogenous noise into account, an important ecological factor affecting population dynamics (Ranta *et al.* 2000). In a study that estimated parameter values for empirical data sets, Hassell *et al.* (1976) found only one population within the chaotic region of dynamics, a lab population of blowflies, *Lucilia cuprina* (Nicholson, 1954), with the majority of other populations falling in the region of monotonic damping. The estimated parameter values for the other functions (M-S & S and Allee functions) we find indicate monotonic damping of population dynamics; a common result according to Hassell *et al.* (1976).

As the results of matching the different models to the data differ between the two different treatments, we can suggest the following mechanisms leading to this outcome. The results from the control treatment group appear to be explained equally well by all three non-linear functions (compared to a linear regression). However, the parameter values the regressions generated allow us to assess their biological relevance. As an Allee effect is only present apparent in the populations under predation pressure, we suggest that the hypothesis that the plants used may be channelling disproportionate amounts of nutrients to regions where aphids have aggregated should be ruled out. Further to this, as the predator treatment group results are explained best by an equation specifically designed to model a reduction in fitness at low population sizes, we propose that the presence of conspecifics appears to benefit individuals at the lowest population densities, perhaps due to the predator dilution effect.

These results may have occurred for a number of reasons. Initially, and perhaps most obviously, an Allee effect may not have been seen in the control treatment group as this particular species of aphid does not gain any benefit from being in the presence of conspecifics at low population densities, when there is no predation pressure.

While there are reports studying aggregations in the pea aphid (e.g. Dixon 1998) none appear to have addressed this issue. Some authors have reported a reduction in fitness at lower densities occurring in other aphid species, (Lopez *et al.* 1989, Messina 1993), however, the methods used in these studies vary from the methods used here. The hypothesis that there would be negative density dependent effects at low population sizes (an Allee effect) was not found under the control treatment conditions. However, we have shown here that the introduction of a predator to the colonies has been shown here to have an important effect at the end of the experiment for the low initial density colonies.

Unfortunately, due to the enclosed nature of the colonies in this study, this work does not fully address the cost of dispersal in this species of aphid. Work by Plantegenest & Kindlmann (1999) does suggest that there should be a strong selection pressure for migration in parthenogenetically reproducing species such as aphids, even when there is a high cost associated with dispersal. Ward *et al.* (1998) estimated that less that one percent of autumn migrants of the cherry oat aphid (*R. padi*) found a suitable host, highlighting the extremely high mortality risk faced by dispersers. Sutherland (1969*a*) points out that aphids will increase production of alates with increased tactile stimulation, which can in turn be brought about through poor host plant quality, where aphids will be more unsettled than on a higher quality plant. Thus we would expect a higher proportion of winged aphids to be produced in colonies with a high initial density, as this leads directly to increased tactile stimulation via increased density, as well as indirectly through the faster degradation of host plant quality.

While Dixon & Agarwala's (1999) work suggests an increase in the proportion of alatae in the pea aphid due to the perceived presence of a predator, these results have not been replicated since (Weisser *et al.*, 1999 & Weisser, unpublished), nor was this borne out under these experimental conditions, which relied on actual rather than perceived predator presence. The fact that our results differed from other studies that have introduced predators into colonies may have been due to the fact that the predators were only left in each colony for 24 hours, while previous experiments have left predators in the colonies for a much longer period of time.

It must be noted that the results of this study should be taken in the context of the different colour morphs used. We may expect to see different results had the colour morphs been reversed (i.e. if the green morph, SG, had been used as the target aphid), or even if we had not employed a target aphid, and used only 1 colour morph for the experiment. Indeed, it has been reported that red and green clones produce different proportions of alates when placed under the same conditions (Sutherland 1969*a*, Weisser & Braendle 2001).

Further studies of this nature would be improved by excluding the highest density experimental groups. This was extremely time consuming, meaning that the experimental set up had to be spread over a number of days. Limiting the maximum density to (e.g.) 50 individuals would allow more replicates to be set up in a shorter time. Furthermore, this would reduce the confounding effect that the start date of each colony may have on the results. It can be shown that at the end of our experiment, there was no significant difference between any of the final population sizes of the three highest density groups (50, 75 and 100 individuals). In the control treatment, a one way ANOVA returned the following values: $F_{2,23} = 1.66$, $p = 0.212$, while the predator treatment produced $F_{2,17} = 1.08$, $p = 0.363$. As well as saving time as described here, a maximum density of 50 individuals per block would also allow more low density groups to be prepared, as the number of aphids available is likely to be a further limiting factor. This would allow a higher sample size at the lower densities, increasing the power of the results. As the competitive effects of aphids at high densities are already relatively well known, we advise that repetition of this experiment should take these factors into account when being designed. A further suggestion would be an earlier count of the colonies, perhaps 5 days after maturity, before colonies decline due to the die-off of plants. While this will lead to increased levels of disturbance to colonies, it will yield valuable results and is a valid consideration.

This study has highlighted the effects of both colony size and predation pressure on the fitness of the pea aphid, as well as the potential of environmental effects to influence developmental time. Comparison of the data with deterministic models of population dynamics suggests that the pea aphid may undergo an Allee effect when faced with predation pressures. Repetition of the experiment with the suggested improvements could produce valuable results concerning the propensity of aphids to produce winged offspring depending on different conditions.

DISPERSAL DECISIONS AND THE ALLEE EFFECT

ABSTRACT

The decision to move between patches in the environment is likely to be amongst the most important of life history choices an organism can make. Organisms are likely to base their decision to disperse away from a habitat patch on some cue, which may be either biotic or abiotic. Here we present a model where an individual's dispersal decision is based on some density dependent rule. Two different types of these density dependent rules are studied; with the organism either choosing to leave a patch to escape the fitness loss brought about by competitive effects, or to escape the fitness loss due to low densities of conspecifics, commonly referred to as the Allee effect. I go on to introduce a cost to dispersers, which is expressed in different ways. Results indicate that basing the decision to disperse on competitive pressures can strongly stabilise otherwise highly unstable (chaotic) population dynamics. If there is no cost, dispersing to avoid an Allee effect will not stabilise population dynamics, sometimes driving global populations to extinction. If a cost to dispersal is introduced, this can be shown to stabilise populations if dispersal is based on escaping the Allee effect, and in some cases will prevent populations from global extinction. I argue that this indicates that dispersal to avoid an Allee effect will only evolve under realistic conditions, i.e. where there is a cost to dispersal.

Introduction

Making the decision to remain in the natal patch or move away before breeding is one of the most important life history choices an organism may have to face. Dispersal away from a habitat close to its carrying capacity can alleviate the loss of fitness commonly associated with high levels of competition. However, this may have to be balanced against any costs involved with these relatively large-scale movements. The dispersal of individuals between discrete patches in the environment is, therefore, of great interest to both theoretical and empirical ecologists, with the implications of theoretical results applicable to management practices under the appropriate conditions (Kareiva & Wennergren 1995).

However, there remains some disagreement in the literature as to differences between theoretical models and empirical data series. Simple population models can be shown to display a wide range of behaviour, from stable equilibrium dynamics, through simple two- and four-point cycles, and on to more complex dynamics such as chaos (May 1974, May & Oster 1976). While there are good examples of populations that demonstrate regular (cyclic) fluctuations in their density over time (e.g. Elton 1927, Elton & Nicholson 1942*a* & *b*, Krebs & Myers 1974, Lindström *et al.* 2001) and even those with so-called quasi-cyclic behaviour (Nisbet & Gurney 1982, Potts *et al.* 1984), there is little evidence from real data sets for any of the most complex of these dynamic behaviours - i.e. deterministic chaos (Hassell *et al.* 1976, Berryman & Millstein 1989, Hastings 1993, Kareiva 1995; but see Constantino *et al.* 1995, Dennis *et al.* 1997 and Dennis *et al.* 2001 for elegant examples of complex behaviour arising from experimentally manipulated *Tribolium* populations). Dispersal has been shown to have a wide range of effects on population dynamics, from a situation where individuals moving between different populations do not alter dynamical properties when compared to a single, isolated population (Rohani *et al.* 1996); to dispersers either stabilising (e.g. Taylor 1990, Hastings 1993) or destabilising (Bascompte & Solé 1994 - but see Hassell *et al.* 1995 and Ruxton 1996) population dynamics. It should be noted that in this sense, stability refers to increasing or decreasing fluctuations in population dynamics, rather than any mathematical criterion of stability.

Ruxton & Rohani (1998) have previously studied dispersal where it is dependent on local competition without any explicit cost to dispersers. They called this a "fitness-dependent dispersal rule". However, as fitness in this context is not an entirely unambiguous term, and as our focus is on the population dynamical consequences of dispersal rather than on the evolution of dispersal, we refer to dispersal based on such a rule as density-dependent dispersal throughout this report. Ruxton *et al.* (1997) included dispersal mortality in a model where dispersal was density independent. Both of these works demonstrated a stabilising effect of dispersal. While the second of these studies may be a relatively simple, effective way to model a population, it may lead to misleading results due to the biologically unrealistic assumptions associated with a fixed fraction of individuals dispersing. In other words, a density dependent form of dispersal would seem to be more reasonable for many species from an evolutionary perspective, where more individuals will leave a population that has a higher density to escape competitive pressure. Here I introduce a cost to density dependent dispersal in single species population models in a number of novel ways to explore the dynamical behaviours of biologically realistic spatial models.

Initially, a simple mortality risk is applied to dispersers, where some fixed fraction of all emigrants are lost before arriving at a new patch. These simulations are contrasted under different boundary conditions. This is extended by including an accumulative mortality risk with each dispersal event between generations. I go on to consider a cost that is incurred by limiting the maximum possible number of dispersal events taken by individuals seeking to minimise the cost of competition within each generation.

Due to the current increase in interest, and realisation of the importance of the Allee effect (Amarasekare 1998*a* & *b*,, Courchamp *et al.* 1999*a* & *b*, Perrin & Mazalov 1999, Scheuring 1999, Stephens & Sutherland 1999, Stephens *et al.* 1999, Etienne *et al.* 2002, Fowler & Ruxton 2002), I then ask what happens if individuals choose to migrate when a population drops below some critical density? In this case, population dynamics are governed by a function that incorporates any reduction in fitness (in this case, reproductive output) due to low densities, known as the Allee effect (Allee 1931, Fowler & Ruxton 2002). An Allee effect can be brought about due to factors such as inbreeding avoidance (Perrin & Mazalov 1999), increased extinction risk from demographic stochasticity (Lande 1998), or the loss of co-operative benefits from conspecifics when there are low numbers in the population (Courchamp *et al.* 1999*a*). The latter of these may include such diverse interactions as co-operative breeding (Courchamp *et al.* 1999*b*); relief from predation pressure due to a dilution effect (Heubeck *et al.* 1997); or even decreased efficiency in social thermoregulation during hibernation (Stephens *et al.* 2002). If individuals within a patch experience a reduction in fitness (in terms of reproductive output) in any of these ways, they may be expected to leave the patch and search for another patch with a higher density of conspecifics, in order to increase their own reproductive output. This is contrasted with results from an Allee population with density-independent dispersal, including a cost to dispersal. Evidence from a study by

Kindvall *et al.* (1998) suggests that such directed movements away from areas of low density allow the bush cricket, *Metrioptera roeseli*, to escape an Allee effect. Another such examples is the six-spot burnet moth (*Zygaena filipendulae*), that has shown biased movements away from small populations (Menendez *et al.* 2002)

Finally, we examine what happens when dispersal decisions are based on both an upper and lower threshold density, and discuss how life history decisions based on these choices can affect individuals and populations.

The Model

1. The Hassell function with An Upper Critical Threshold

In this study, within-patch reproductive processes are governed by a commonly used function that models density dependence in single species populations (Hassell 1975, eqn. 1),

$$f(N_t) = \frac{\lambda}{(1 + aN_t)^b}, \qquad (1)$$

where N_t is population size in the current generation (t), λ is the maximum potential growth rate per individual, a scales the patch carrying capacity, and b describes the strength and type of competition, where $b = 1$ is scramble competition, tending towards contest competition as we increase the value of b (parameters λ, a and b were held constant across all patches within simulations, giving a homogenous spatial environment).

The population is positioned on an $L*L$ array of spatially separate patches, within each of which a single reproductive phase is followed by the dispersal phase in each discrete generation.

The number of individuals in each patch of the lattice (with co-ordinates *i,j*) can be calculated at the start of consecutive generations by multiplying the above function (eqn. 1) by the density of each patch at the end of each generation as follows:

$$N_{i,j,t+1} = \frac{\lambda N_{i,j,t}}{\left(1 + aN_{i,j,t}\right)^{b}}. \qquad (2)$$

Each patch's population was initiated with a density chosen at random from a uniform distribution with limits [0,1]. In order to determine the number of individuals that will emigrate from each patch after the reproductive phase, it is necessary to identify a critical (or threshold) population density, which can be calculated by defining some fraction (Δ) of the maximum growth rate (λ). An individual will only leave a patch if its expected per capita growth rate [$f(N_t)$] drops below this fraction (Δ). The critical population density, N_c, can be derived from equation (1), giving us

$$N_c = \frac{\left(\frac{1}{\Delta}\right)^{1/b} - 1}{a}. \qquad (3)$$

Thus, whenever any patch exceeds this critical population density dispersal will occur. The number of emigrants leaving a patch will be equal to the difference between the current patch density ($N_{i,j,t+1}$) and the threshold density (N_c). Following this initial round of dispersal, some patches may find that their density has again exceeded N_c. If this is the case, the dispersal phase is repeated, leading to a situation where individuals may end up at any patch in the lattice (effectively global dispersal). Individuals dispersing over the edge of the lattice are lost from the population (dissipating boundary conditions). Thus, dispersal phases are repeated until all patches in the lattice are at a density equal to or below N_c.

We go on to introduce an explicit cost to dispersers in two different ways, through dispersal mortality; either some fixed proportion of dispersers is lost with each dispersal attempt, or the mortality cost to dispersers increases with consecutive dispersal attempts, and through a limit to the maximum number of dispersal attempts allowed (analogous to limiting the "sampling time", or the maximum dispersal distance away from the natal patch). A mortality cost to dispersal ( ) can be included in the model by multiplying migrants during the dispersal phase by some proportion $(1-\varepsilon)$, representing those migrants that remain following dispersal mortality. An accumulative cost (ξ) can be introduced by multiplying all dispersers by a fraction that increases with consecutive within generation dispersal events (in this study ξ = 1-[number of dispersal events/100]).

2. *The Allee effect*

The underlying form of this second component of the study is based on a function describing population growth where reproductive output increases with increasing population size at low densities, termed the Allee effect (Fowler & Ruxton 2002). Therefore, the expected reproductive output (per capita growth rate) of each individual can be calculated according to equation 4.

$$g(N_t) = \frac{\left(1 - A\exp\left(\frac{-aN_t}{\gamma}\right)\right)\lambda}{(1 + aN_t)^b}. \tag{4}$$

Parameters A and γ are related to the strength of the Allee effect and the proportion of the population under it's influence, and their behaviour is outlined in detail in Fowler & Ruxton (2002 and Chapter II).

Again, considering an $L * L$ array of patches in the environment, we can calculate the number of individuals in any given patch in successive generations by multiplying the current population size by eqn. (4). This function is applied to the populations in each patch in the lattice (which are then linked through dispersal) as follows:

$$N_{i,j,t+1} = \frac{\left(1 - A\exp\left(\frac{-aN_{i,j,t}}{\gamma}\right)\right)\lambda N_{i,j,t}}{\left(1 + aN_{i,j,t}\right)^b} \tag{5}$$

giving us the population size, N, in the patch with co-ordinates (i,j), at generation t. The other parameters remain as described above.

(i) *The Allee effect: Density-Independent dispersal.*

Here we assume that some fixed fraction (μ) of the post-reproductive population in each patch ($N_{i,j}$) will disperse away from the natal patch, being distributed equally between the four nearest patches. We then assume that some fraction of the dispersers (ε) are subject to dispersal mortality, so that the size of the population at the start of the next generation can be given by

$$G_{i,j,t+1} = (1-\mu)G_{i,j,t} + \mu(1-\varepsilon)\left(\frac{G_{i-1,j,t} + G_{i+1,j,t} + G_{i,j-1,t} + G_{i,j+1,t}}{4}\right) \qquad (6)$$

(*sensu* Ruxton *et al.* 1997). We carry out analysis of this to allow comparison with the results from a density-dependent form of dispersal.

(ii) *The Allee effect: Density-Dependent dispersal, with a lower critical threshold*

Following the reproductive phase of the life cycle (eqn. 5), a dispersal stage may again take place. This time, decisions over whether to move may be based on one or both of two dispersal rules. Firstly, the decision may be based on the same rule as outlined before, where an upper density-dependent criterion (N_c) determines the density of individuals leaving each patch. Secondly, we introduce a new rule that is likely to affect populations under the influence of the Allee effect, where individuals will move from the current patch if their reproductive output falls below a certain level. In any population whose dynamics are governed by the Allee effect, there may be a lower threshold population density below which the loss of reproduction is severe enough to warrant dispersal away from that patch in search of a patch with sufficient numbers of conspecifics to overcome such reproductive loss. This can be cast as follows. The reproductive cost of the Allee effect (according to eqn. 2) is

$$g(N) = \left(1 - A\exp\left(\frac{-aN}{\gamma}\right)\right) \tag{7}$$

So we can say that an individual will leave a patch if the cost due to low population density is greater than δ, which has limits [$0 < \delta < 1$]. If we let

$$g(N_A) = \left(1 - A\exp\left(\frac{-aN_A}{\gamma}\right)\right) = \delta, \tag{8}$$

then the lower critical threshold population density (N_A) can be derived as

$$N_A = \frac{-\gamma \ln\left(\frac{1-\delta}{A}\right)}{a}. \tag{9}$$

Thus, if the current population size (N_t) is below this value in any patch, all individuals will leave that patch.

Increasing δ leads directly to an increase in the critical threshold density, the opposite effect to increasing Δ. Furthermore, if $\sum_{i,j=1}^{L^2} N_{i,j,t} < N_A$ then the species is assumed to be doomed to extinction across the whole environment, as even if all individuals were to arrive in the same patch, the density can never exceed the critical value, and the population will eventually dwindle to extinction through a combination of Allee and edge effects. Alternatively, if the sum of all migrants moving patches in any given dispersal events is $< 10^{-6}$, then these are considered insufficient to provide a density great enough to overcome any loss from the Allee effect, and these migrants are lost from the population. We then go on to introduce an explicit cost to dispersers as previously described.

The order in which the models examined within this work are presented in the results is summarised in table 1.

Table 1: Summary of the different models studied in this report.

Model No.	Population regulation	Regulation of dispersal	Dispersal costs included
1	No Allee effect (eqn. 2)	Density-dependent, Upper threshold: Δ	a) None b) Fixed mortality c) Increasing mortality risk d) Limit to dispersal events
2	Allee effect (eqn. 5)	Density-independent	a) None b) Fixed mortality
3	Allee effect (eqn. 5)	Density-dependent, Upper threshold: Δ	a) None b) Fixed mortality c) Increasing mortality risk d) Limit to dispersal events
4	Allee effect (eqn. 5)	Density-dependent, Lower threshold: δ	a) none b) Fixed mortality c) Increasing mortality risk d) Limit to dispersal events
5	Allee effect (eqn. 5)	Density-dependent, both upper and lower thresholds: Δ & δ	a) None b) Limit to dispersal events c) Limit & fixed mortality

Results

1. A population with no Allee effect (the Hassell Model):

The results of model simulation illustrate clearly that it is possible to simplify complex population dynamics through the introduction of some threshold population size above which individuals will leave a patch (figure 1). Parameter values were chosen that would yield unstable (chaotic) fluctuations in population density in a single unconnected patch, over a time period long enough to overcome the effect of transient dynamics (500 generations). We can see from fig. 1 that if dynamics exhibit chaotic fluctuations when there is no upper threshold population density ($\Delta = 0$), these dynamics can be simplified by gradually introducing a threshold population size above which individuals will disperse. Furthermore, originally chaotic dynamics can be simplified to a stable equilibrium if the threshold population size is reduced sufficiently (by increasing Δ).

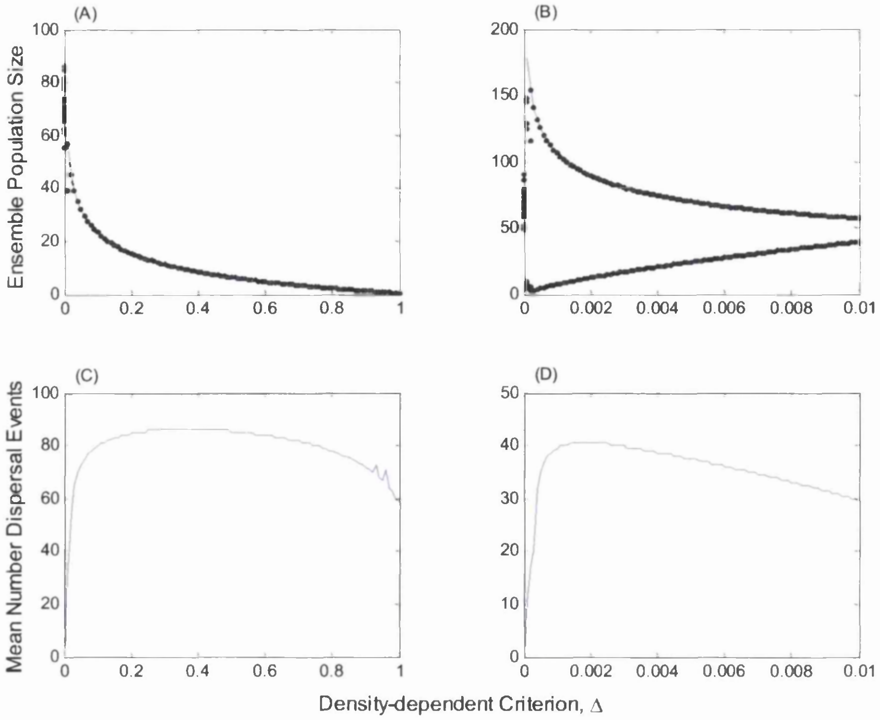


Figure 1: Introducing an upper threshold population size above which individuals choose to leave a population patch can simplify unstable dynamics. Increasing the density-dependent criterion leads to a direct reduction in the threshold population size N_c. In all figures above, the following parameter values are used: λ = 70; *a* = 1; *b* = 6. The bifurcation diagrams (1*a* & *b*) plot the population size for the final 20 generations (of a 500-generation simulation) summed across all patches in the lattice. Figures 1*c* & *d* illustrate the mean number of within generation dispersal events attempts required for the population to reach it's final dynamical state (averaged across 500 generations). Figures *b* & *d* show the left-hand side of figures *a* & *b*, extended. The blue line in figs. 1*a* & *b* shows the ensemble threshold population size (this is indicative only). When this is exceeded, the population is required to lose individuals (through edge effects) before each patch can settle with a density ≤ N_c. The variation in the mean number of dispersal events (fig. 1*d*) at very low values of Δ suggest a complexity that is not obvious when looking at low values of Δ in fig. 1*c*.

Thus, with no explicit cost to dispersal (other than boundary effects), introduction of a critical population size below which individuals will disperse can alter the stability properties of population dynamics. When the critical threshold population size is relatively high (low Δ values), we find that all patches will settle to their final densities within a small number of dispersal events.

INTRODUCING MORTALITY:

1b) Proportional mortality

Here we introduce a mortality cost to a fixed proportion of dispersers within each dispersal event. To do this we hold the density-dependent criterion (Δ) at a constant value, and ask if varying the proportion of dispersers that are lost when moving between patches will change the population dynamics compared to a situation where the only mortality is through edge effects. Figures 2*a* & *b* reveal that introducing this form of a cost to dispersers does not qualitatively alter the dynamics, i.e. the ensemble dynamics are highly insensitive to varying ε. Increasing the proportion of dispersers that are lost between patches simply reduces the number of dispersal events it takes for each patch density to fall to a level equal to or below the critical threshold patch density (fig. 2*b*). This result holds over different values of Δ, whether the global population dynamics are fluctuating or stable.

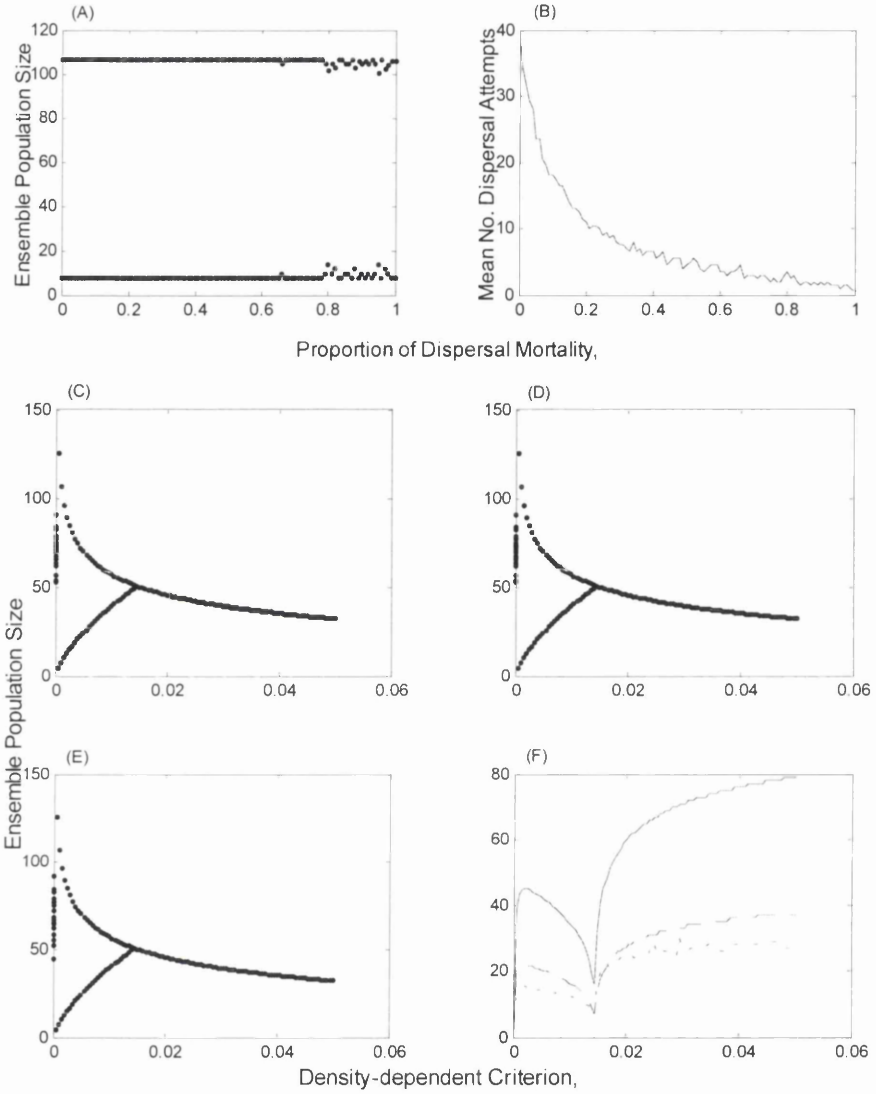


Figure 2: Introducing mortality cost to some proportion of dispersers does not change the dynamics qualitatively. (Parameter values as figure 1, with . held at a constant value while dispersal mortality is varied: = 0.001.) If a fixed proportion of all the dispersers experience mortality each time they move between patches, this will not change the dynamics (locally or globally) of the population - which are fluctuating over a two-point cycle in this case. Varying this mortality cost to dispersers does not qualitatively change the dynamics (2*a* - all values of ε produce a two-point cycle), but increasing the cost does decrease the number of dispersal attempts required before the population can settle to it's final state (2*b*). This result holds

even when all dispersers are lost when travelling between patches (= 1). A contrast of dissipative boundaries (2*c*) with periodic boundaries (2*d*), shows no difference in the final dynamical pattern. Although both models suffer the same overall proportion of dispersal mortality with each dispersal event (= 1/7 when boundary conditions are periodic), by losing a constant fraction from each patch in the lattice (rather than only those at the edge suffering), a lattice with periodic boundaries will arrive at the final dynamical outcome in fewer dispersal events (2*f*: Solid line = dissipative boundaries; Dashed line = periodic boundaries - Parameter values in *2c - f are* the same as those used in figure 1). By introducing an accumulative cost of dispersal, we do not qualitatively change the dynamics of the system (2*e*). Again, however, we arrive at this outcome with fewer dispersal events than when the model is run without any cost of dispersal (*2f*: Dotted line = increasing mortality to dispersers). In this case the model is run with absorptive boundaries only and then with a cost of dispersal that increases with each consecutive dispersal attempt in each generation.

Comparison of Boundary Conditions:

Here we run the model on a lattice where the boundary conditions are absorptive (i.e. migrants that disperse over the edge of that lattice are lost from the population), with no further explicit cost of dispersal (fig. 2*c*). We go on to compare the dynamics of this to a simulation run on a lattice with periodic boundaries, with a simple fixed cost of dispersal (fig. 2*d*), where some constant proportion of all dispersers experience mortality (ε). In this case $\varepsilon = (1/7)$, as this is approximately equal to the total proportion of emigrants that are lost to edge effects with each dispersal event in the absorptive boundaries case. We can see from figures 2*c, d* & *f* that once again, while there is no qualitative change in the final dynamical outcome for the population, this outcome is achieved in approximately half the number of dispersal events when there is a fixed cost to dispersers rather than dispersers only being lost through edge effects.

In a model where individuals can only be lost by dispersing over the edge of the lattice, it is not necessarily surprising that it takes more dispersal events (approximately twice as many) to arrive at the final dynamic outcome. As emigrants leave patches in four different directions, there will always be a constant source of migrants travelling towards the centre of the lattice (as well as those moving towards and over the edge). It will therefore take some time for central patches with a high density to finally drop to a sufficient level that will allow them to satisfy the density dependent criterion, and continue onto the next generation. In a lattice with periodic boundaries where all emigrants leaving each patch experience the same proportion of mortality, it will require fewer dispersal events for each patch in the lattice to drop to a density equal to, or below the critical value. The only effect changing this form of cost has on these results is to reduce the number of dispersal events required to arrive at the final global population density, as the cost is increased. This is true regardless of the boundary conditions applied.

1c) Introducing an accumulative dispersal cost

In this case, the number of dispersers is multiplied by a factor that increases with each consecutive dispersal event, within each generation (= 1-[number of dispersal attempts/100]), which can be motivated as follows. Dispersal can be an energetically expensive process. Therefore consecutive dispersal attempts may deplete reserves at an increasing rate, which can be expressed as an increasing mortality risk with increasing dispersal attempts. For a comparison of this form of dispersal cost on a lattice with periodic boundaries and the absorptive boundaries case (and no other dispersal cost), see figure 2. Once again, adding this type of cost to the model does not qualitatively affect the population dynamics, but it again reduces the mean number of dispersal events required to reach the final dynamical outcome.

In fact, there is no way in which introducing a cost to dispersal in this form (either a constant mortality or an accumulatively increasing proportion of mortality) will alter the population dynamics. This form of a dispersal cost simply serves to reduce the (global and local) population density until it is low enough that all patches can reduce their densities to a size equal to or below the local critical patch density (N_c). Therefore, introducing this form of dispersal cost can only reduce the number of dispersal attempts required to arrive at any predetermined dynamical outcome. Including dispersal costs of this form in a lattice with dissipating (absorptive) boundaries would simply reduce the number of dispersal events required even further.

1d) Limiting Dispersal Events

Dispersing individuals may have a finite amount of time to sample the environment before they decide to settle in a certain area. Therefore we limit the maximum number of dispersal events each individual can take within a generation. We find that doing this makes it possible to generate more complex dynamics compared to a simulation where dispersers are allowed to take as many dispersal events as they require to find a suitable patch (i.e. a patch at or below the threshold patch density). This is achieved particularly when the number of dispersal events permitted is relatively low (figure 3). An important assumption of the model here is that individuals will settle in the patch they find themselves in after the maximum number of dispersal events has taken place, and bear whatever reproductive loss arises from competitive effects in that patch. There is no mortality cost to dispersers under these conditions (other than edge effects).

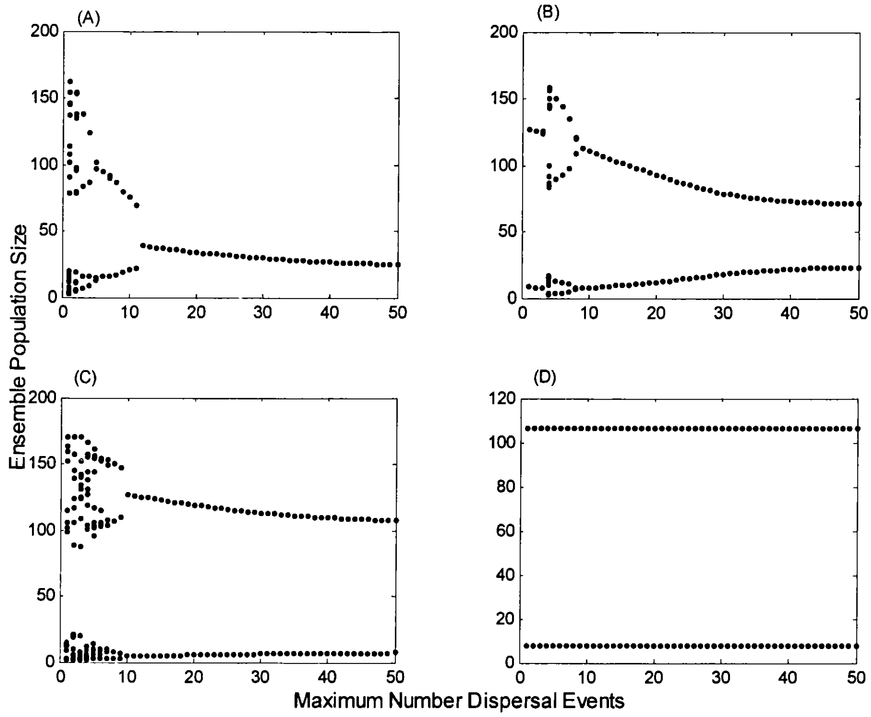


Figure 3: Limiting the maximum number of dispersal events can lead to more complex dynamics arising in the population, but allowing a high number of dispersal events will not simplify non-equilibrium dynamics. 3*a* - *c* exhibit the differences that arise when the population is in different dynamical states before the limit is introduced. All figures have the same parameter values as figure 1, differing only in the values of as follows: *a*) = 0.1, *b*) = 0.005, *c*) = 0.001. Figure 3*d* shows us that the unstable dynamics that arise when the number of within generation dispersal events are limited can be simplified upon the inclusion of the other costs to dispersal studied earlier. Here parameter values used are the same as those in figure 3*c*.

Combining different types of costs

Figure 3*d* highlights the simplifying results when all the different methods of cost to dispersal are combined. This includes a minimum fixed mortality cost to all dispersers, an increasing cost to dispersers with consecutive dispersal attempts, as well as a limit to the number of dispersal events allowed within each generation. Thus, when there is a considerable cost to dispersal, population dynamics that would have been destabilised (by limiting the number of dispersal events) can be returned to their original dynamical state.

2. *Introducing the Allee effect, with density independent dispersal.*

Here we modelled population dynamics according to a function that describes a population experiencing an Allee effect (Fowler & Ruxton 2002). Again, the population is positioned in patches on an $L*L$ lattice (this time with periodic boundaries), which are linked through a fixed dispersal rate (μ). The dispersers are exposed to a cost of dispersal, where some constant fraction of those dispersing experience mortality (ε). The results of these simulations are shown in figure 4, and are presented mainly for comparison with the density-dependent dispersal results that appear later. We can see from figure 4 that the introduction of density-independent dispersal to a population under the influence of an Allee effect does not alter the dynamics qualitatively (fig. 4*b*) unless some cost to the dispersers is included (figs. 4*c* & *d*).

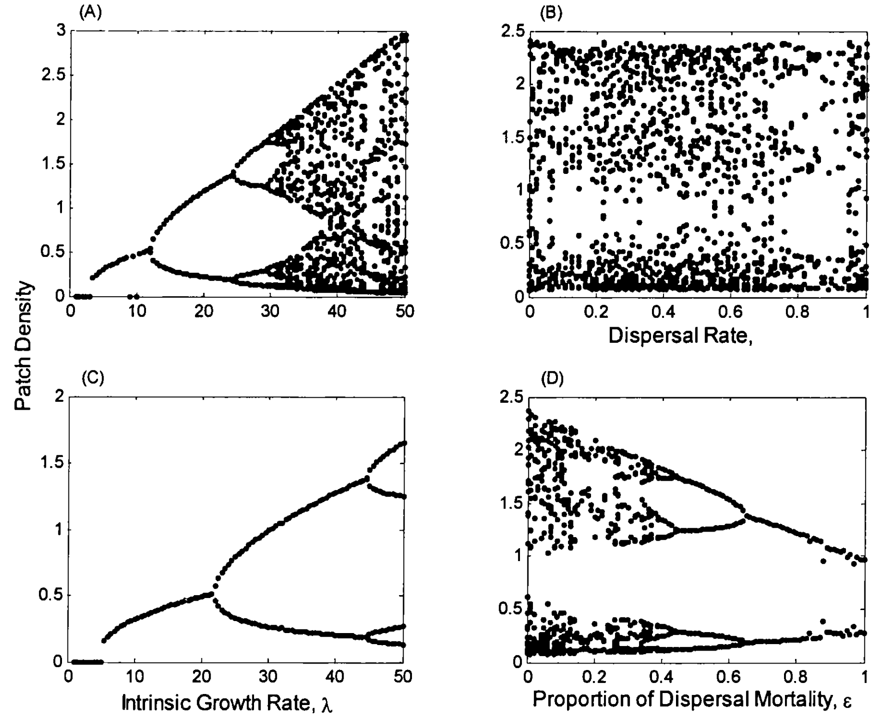


Figure 4: Introducing density independent dispersal to a population experiencing an Allee effect will only stabilise dynamics if there is a cost associated with dispersal. Here we plot the final 20 generations (from a single patch) of a 500-generation simulation of a population with an Allee effect under different conditions. In all cases, $A = 1$, $= 0.1$, $a = 1$ and $b = 6$. In 4*a* we vary the intrinsic population growth in a closed population. Fig. 4b shows that dispersal on it's own cannot simplify otherwise unstable population dynamics ($\lambda = 40$). Introducing a mortality risk to dispersal does stabilise dynamics (figs. 4c & *d*). Fig. 4*c* shows that introducing dispersal ($\mu = 0.6$) with a cost ($\varepsilon = 0.75$) can dramatically simplify otherwise unstable dynamics. The greater the dispersal cost, the more the dynamics are stabilised (Fig. 4*d* - $\lambda = 40$, $\mu = 0.6$)

As it is not possible to determine the equilibrium population size of the function we use to describe population growth here, it must be done numerically. The bifurcation diagrams shown in figure 4*a* & *c* indicate that at low population growth rates, the population can remain in a stable equilibrium state. Increasing λ gradually leads to increasing population fluctuations from two-point cyclic fluctuations, with periodic doubling leading eventually to chaotic dynamics appearing (fig. 4*a*). If we select a value of λ that produces such chaotic fluctuations, we can ask if introducing dispersal between patches changes the dynamics. Varying the (fixed) proportion of individuals that move between patches does not simplify complex dynamics (4*b*). However, by introducing a cost to dispersal, we can lead to a direct reduction in the rate at which simple dynamics become more complex (fig. 4*c*), indicating the stabilising effect of dispersal mortality on a population with an Allee effect. The higher the proportion of dispersers that experience mortality, the more complex dynamics become simplified (4*d*). It seems likely that the intrinsic rate of population growth (λ) can be reduced by a factor (approximately) equal to the rate of dispersal multiplied by the cost to dispersers ($\mu.\varepsilon$).

3. *Introducing the Allee effect, with density-dependent dispersal.*

3a) Upper critical threshold density, N_c

Again, we modelled population dynamics according to a function that describes a population experiencing an Allee effect (Fowler & Ruxton 2002). This time, we first introduced an upper critical population density for dispersal as previously described; whenever the population in any given patch exceeded an upper threshold value, individuals would emigrate from the patch to escape the reduction in reproductive output associated with density dependent competitive effects. The results, perhaps expectantly, do not differ qualitatively from the results of a population not influenced by an Allee effect (compare figs. 1 & 5). As the threshold density tends towards zero, we find the global population density is simplified (but reduced), before eventually being forced to extinction before the threshold population density actually becomes zero due to the inability of the population to establish itself at such low densities. [It should be noted that introducing an Allee effect of sufficient strength will increase the dynamical stability of a population, in the case of this model by simplifying otherwise chaotic dynamics (Scheuring 1999, Ruxton & Fowler 2002) and therefore although the parameter values used here are the same as those used previously where possible (λ, b & a), the dynamics produced when the upper threshold density is infinite (i.e. no dispersal occurs) may be less complex.] Patches that are initiated at a very low density may not become established due to the Allee effect, but these can be recolonised through dispersal from other patches.

Parameter values used for A and γ yield a 2-point cycle across the ensemble population. The results remain unchanged when parameter values yielding chaotic dynamics are used ($A = 1$; $\gamma = 0.4$ - Figs. 5*e* & *f*).

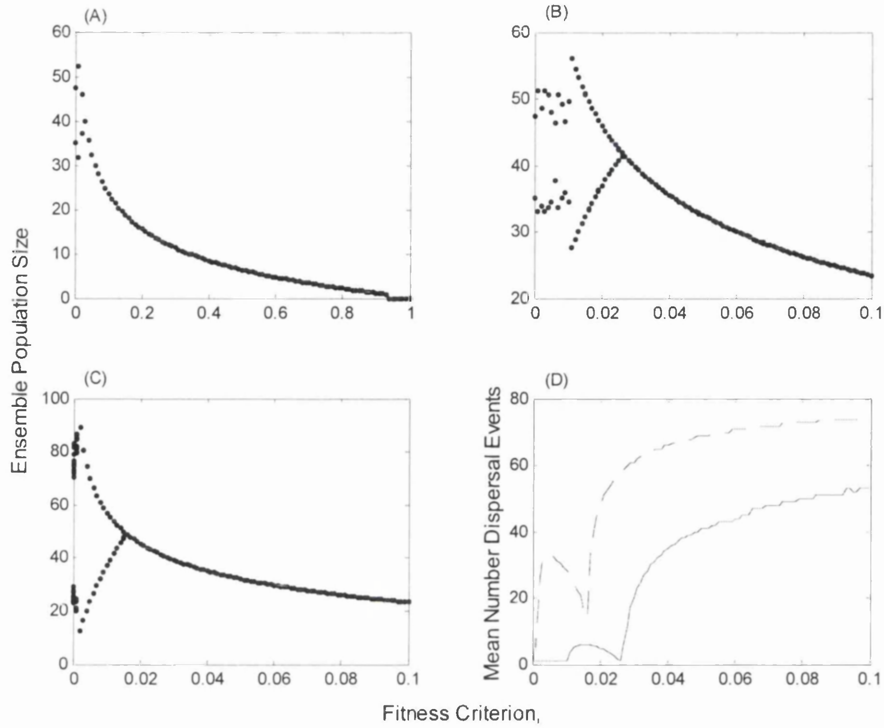


Figure 5: Introducing an upper threshold for density dependent migration into a population influenced by an Allee effect (parameter values used for , *b* & *a* as fig. 1; A = 1.0 in all figs.). Fig. 5*b* shows the left-hand side of 5*a* extended, $\gamma = 1$). Again, increasing the density-dependent criterion (decreasing the threshold population density) leads to non-stable dynamics becoming simplified to stable non-fluctuating dynamics. Populations can be forced to extinction when there is a very low threshold density due to an inability to overcome the Allee effect. Chaotic fluctuations (5*c*) can also be simplified by the introduction of a critical population size above which dispersal takes place, in a population under the influence of an Allee effect. Here, $A = 1$ and $\gamma = 0.4$. Increasing the range of the population influenced by the Allee effect (increasing γ) leads to a decrease in the number of dispersal attempts required to reach the final dynamic state (5*d* - solid line: $\gamma = 1$; dashed line: $\gamma = 0.4$).

3b) - d) An Allee population with upper threshold density and dispersal costs.

Here we ask whether introducing an explicit cost of dispersal to a population with an Allee effect will alter the dynamics in any way. We start by looking at the effect of introducing a mortality cost to some proportion of dispersers (ε) whose decision to move is made according to the upper density-dependent criterion (Δ).

When a cost of dispersal is introduced by having a fixed proportion of migrants facing mortality, there is no qualitative change in the population dynamics compared to simulations when there is no dispersal cost of this form (as is the case with the Hassell populations). Furthermore, introducing a mortality cost that increases with consecutive within generation dispersal events does not alter the dynamical outcome. Limiting the number of (density-dependent) dispersal events individuals can take will produce more complex dynamics (results not shown as they are the same as those from a Hassell population - figs. 2 & 3).

4. An Allee population with a lower critical threshold, N_A

4a) No cost to dispersal

If a new threshold population density is initiated, below which individuals will migrate away from a patch (due to the reduction in reproductive output caused by low patch densities), we do not find the same results as above. Two important assumptions of this form of the model are as follows. Any ensemble population density that does not exceed the critical population density for one patch will be considered globally extinct (This is due to the fact that even if all individuals were to reach the same patch through dispersal events, their density would be so low as to require dispersal away from the patch, the density eventually dwindling further due to Allee and edge effects.); and secondly, that if the sum of all migrants is less than 10^{-6}, then these migrants are considered insufficient to alter the outcome of the model and are thus lost from the population. This second assumption is required to prevent infinitesimally small numbers of migrants dispersing between patches over many dispersal attempts.

As we introduce this lower critical threshold (N_A) to the model, there are two possible outcomes for each patch (fig. 6). Firstly, the patch population may establish successfully, the density remaining above N_A (either in stable equilibrium, or with regular cycling fluctuations - fig. 6*a*). Secondly, a patch may become extinct due to the interaction between competitive and Allee effects (fig. 6*b*). This can occur if the amplitude of fluctuations increases, eventually falling below the threshold - leading to all individuals leaving the patch to escape the reproductive loss brought on by the low density. If a patch is initiated at a very low density, individuals will leave immediately in this manner.

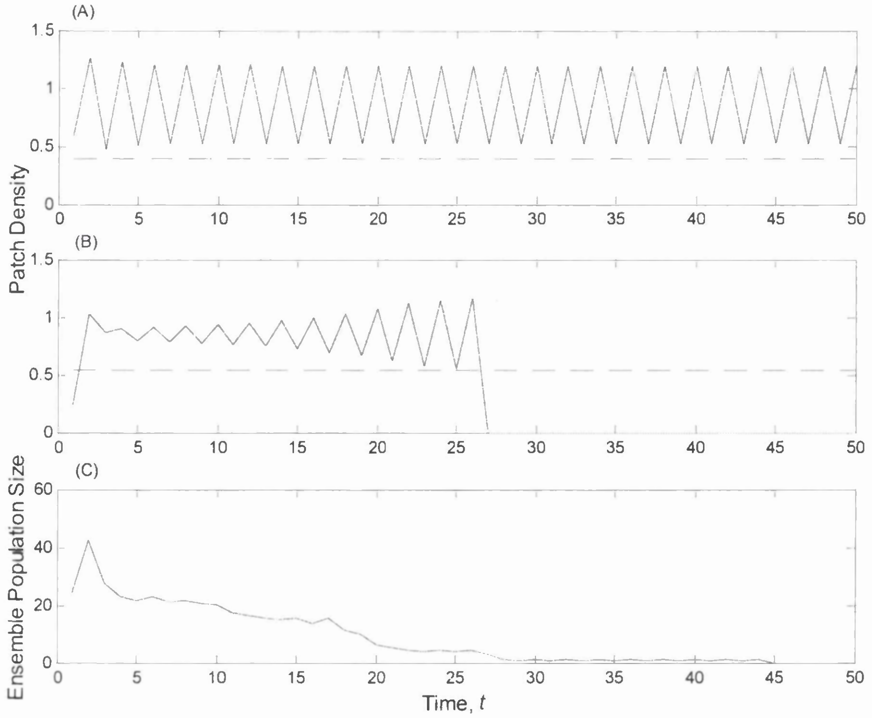


Figure 6: Individual patches of Allee populations may either establish or become extinct when populations fluctuate and there is a lower density-dependent criterion (parameter values used in figs. 6*a* - *c*: = 70, *a* = 1, *b* = 6, *A* = 1, γ = 1). With a relatively low value for the lower density-dependent criterion (indicated by the dashed line), individual patches may become successfully established (6*a* - δ = 0.32), remaining at a density above the lower threshold over time. Alternatively, fluctuations in population size may cause the local population to drop below the critical density, leading to patch extinction as individuals leave to escape reproductive loss caused by the Allee effect (6*b* & *c* - δ = 0.42).

Using parameter values yielding unstable dynamics (chaotic or even a 2-point periodic fluctuation), there is no stabilising effect of density-dependent dispersal (figs. 7*a* & *b*). We see that low values of δ do not lead to any dispersal, as the population densities remain fluctuating well above the critical density. However, global persistence is unlikely, if not impossible, as we increase δ, forcing individuals to leave patches with low densities in search of patches with higher densities to overcome reproductive losses from the Allee effect. As δ is increased (leading to an increase in N_A), we bring the critical lower threshold closer to the lower limit in the density of patch fluctuations, and dispersal is initiated. However, this leads directly to global extinction.

Figures 7*c* & *d* highlight the pattern of local patch extinction with an increasing density-dependent criterion, as the pressure leading to reduced reproductive output caused by the Allee effect leads to individuals leaving patches in search of a patch with a greater density of conspecifics. Local patch extinction is often determined by initial patch density. Examination of the time-series reveals that patches with low initial densities become extinct within the first few generations. This has very important implications for global population survival, as initiating all patches with the same density (perhaps a biologically unrealistic assumption) leads directly to global population extinction as soon as the patch densities fall below N_A. In contrast, patches initiated at different (random) densities can persist even when some patch densities in the lattice fall below the density-dependent criterion

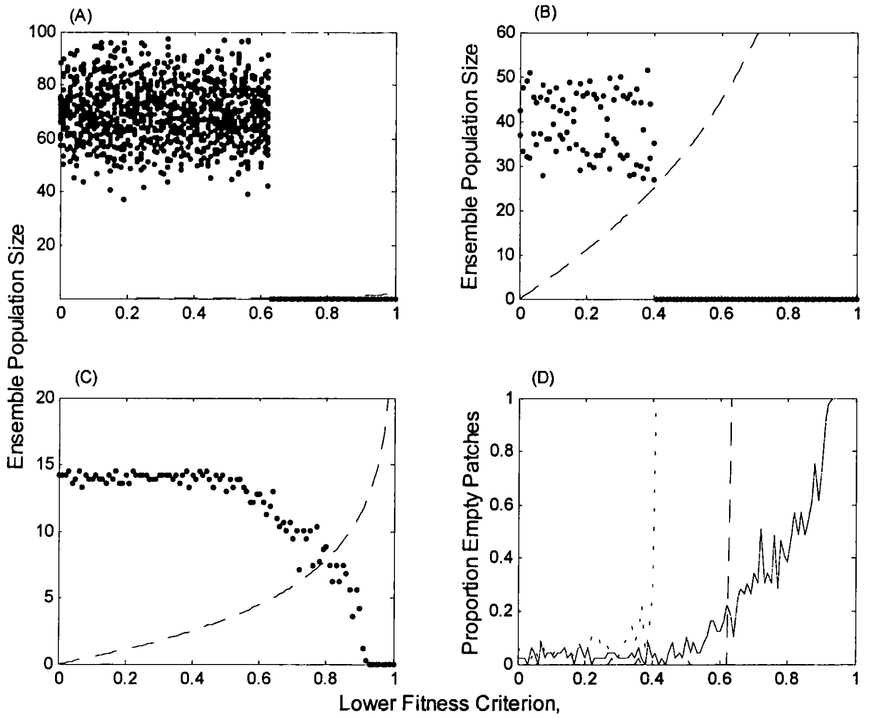


Figure 7: In a population under the influence of the Allee effect, as well as competitive effects, increasing the density-dependent criterion does not change the ensemble population dynamics, and will lead to global extinction (under certain parameter values) if the criterion is high enough (figs. 7*a* & *b*: = 70; *a* = 1; *b* = 6; *A* = 1. 7*a*: γ = 0.01; 7*b*: γ = 1). The dashed line in figs. 7*a* - *c* indicates the global value for N_A. Parameter values can be chosen that yield sustainable global population densities below the global threshold density, although the global population size does decrease as δ increases (figs. 7*c*: = 5; *a* = 1; *b* = 6; *A* = 1; γ = 0.1). Under these circumstances, some local patches become extinct, while others in the environment retain a stable local population. The proportion of empty patches in the environment is shown in figure 7*d*. Dashed line corresponds to parameter values used in 7*a*; dotted line corresponds to 7*b*; solid line corresponds to 7*c*.

We can see from figures 7*c* & *d* that choosing parameter values that produce non-trivial stable equilibrium dynamics allows dispersal to take place in the model based on a lower critical population density, without necessarily leading to global extinction. These parameter values remain biologically reasonable, although they do not lead to the population density fluctuating over time. In fact, dispersal only takes place over the first few generations while the population establishes itself in some of the patches in the lattice, leaving other patches empty. This occurs as patches that are initiated below the threshold population size (N_A) empty, with individuals seeking patches with a greater density. Low values of δ generate a relatively low critical density, increasing δ leads to a geometric (non-linear) increase in the critical population density. Patches that are initiated below this threshold (N_A) empty in the first generation, the individuals dispersing to surrounding patches in search of areas with a higher density, to alleviate the reproductive loss incurred by the Allee effect. As patches reach a density above the critical threshold, the parameter values used here mean that a stable equilibrium results, therefore once patches reach a density greater than N_A, they will stay at a density consistently above the critical density, and will not fluctuate (unless there is immigration, which leads to damped oscillations, returning to equilibrium). At higher levels of δ, more patches are initiated (at random) below N_A, and therefore fewer patches remain viable in the first generation. Patches that become extinct are unlikely to be recolonised.

4b) - d) A lower threshold density with a cost to dispersal

Once again, there are three different ways we can introduce a cost to dispersal. Initially, we can introduce a fixed mortality cost to every dispersal event. This does not change the population dynamics when they are unstable compared to simulations without any explicit cost to dispersal (Fig. 8*a*). This result holds if parameter values are chosen that lead to stable equilibrium dynamics.

Secondly, introduction of an accumulative mortality cost that increases with each within generation dispersal event will not qualitatively change dynamics (Fig. 8*b*).

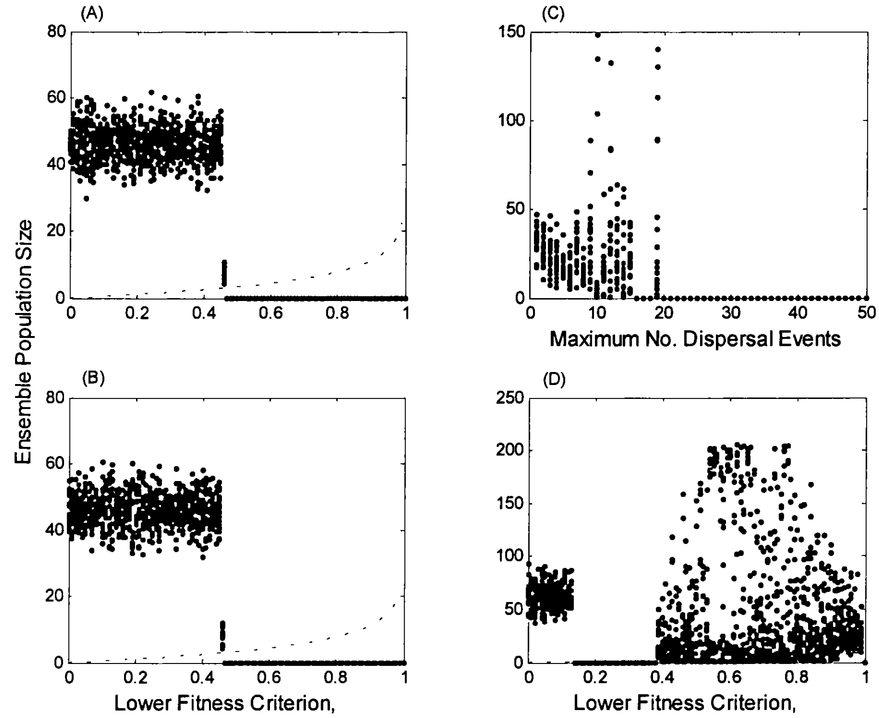


Figure 8: Introducing a cost to a population with a lower density-dependent criterion. By including either a fixed mortality cost to all dispersers (8*a*) or an increasing accumulative cost (8*b*), dynamics remain qualitatively unaltered. The only type of cost that will alter dynamics is a limit to the number of dispersal events that can take place within any generation (8*c* & *d*). Here we select parameter values that lead to global extinction (= 70, δ = 0.7), and find that limiting the number of dispersal events (to 5 in this case) can promote population persistence (8*c*).

Finally, introduction of a limit to the number of within-generation dispersal events can be shown to allow population persistence, without stabilising the population dynamics (Figure 8*c*). Choosing parameter values that would lead to global extinction if there were no limit to the number of dispersal events allowed, we can see that while limiting the number of within generation dispersal events does not simplify chaotic dynamics, it can lead to global population persistence. An underlying assumption with this form of cost is that the individuals migrating in the final permitted dispersal event will remain in the final patch they arrive in, and accept the fitness cost if the density is below the threshold. If we relax this assumption, and lose these dispersers from the population through mortality, global extinction occurs once again (fig. 8*d*).

5. Introducing both an upper and lower threshold to the population

5a) No cost to dispersal

Here we combine the different threshold densities that have been studied in this work, N_c and N_A. This obviously places greater constraints on the population, with a narrower range of population densities permitted before dispersal will occur (figure 9).

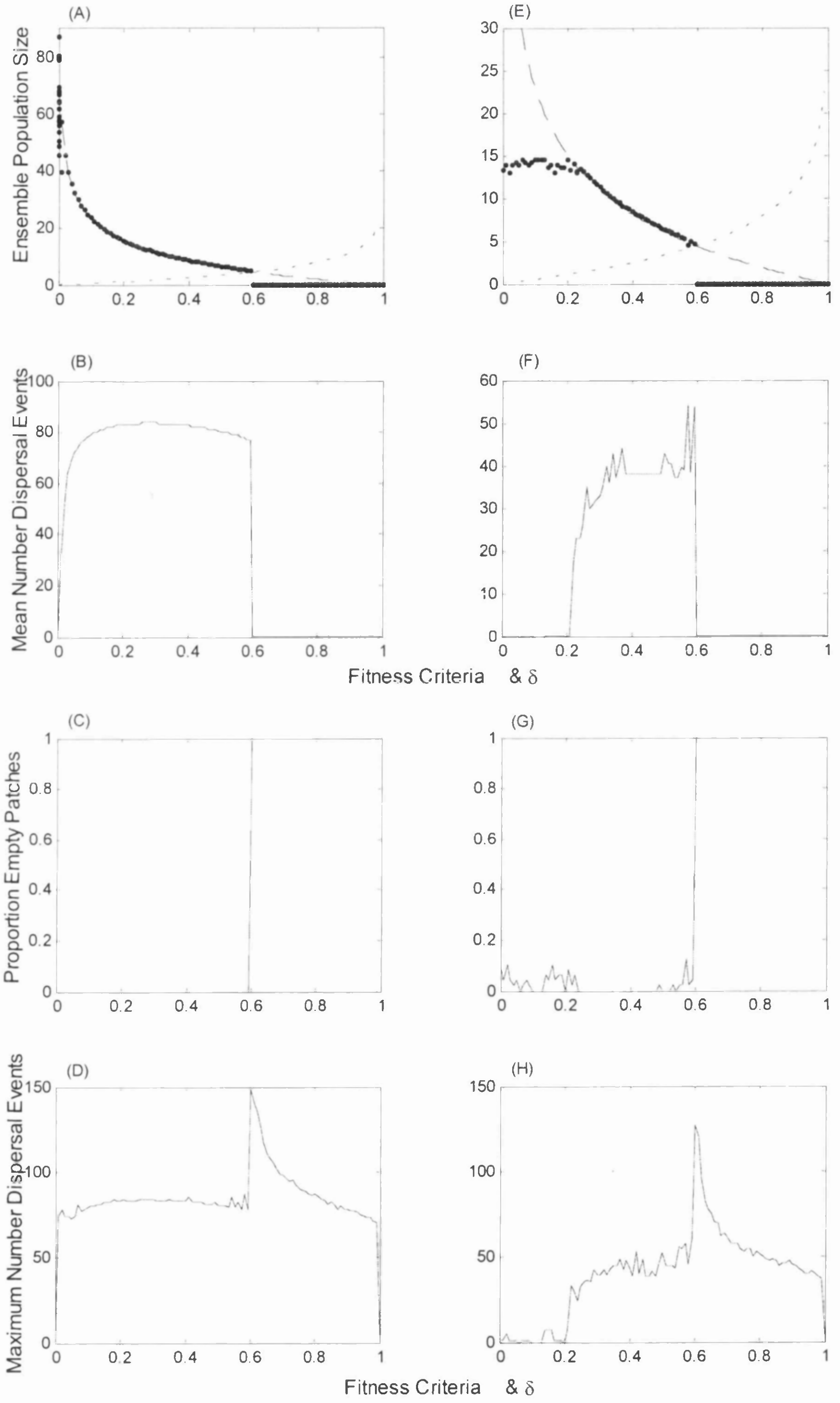


Figure 9: Introducing both an upper and a lower critical threshold density to each patch for dispersal. Figures 9*a* - *d* show the effect on unstable population dynamics (parameter values

as figure 8*a* - except = 0.1), while 9*e* - *h* show what happens with stable equilibrium dynamics (parameter values as 9*a* - *d*, except $\lambda = 5$).

At low values of Δ and δ, the dynamics (and dispersal decisions) are dominated by competitive effects (the upper threshold), as the unstable fluctuations are simplified to a non-fluctuating equilibrium (fig. 9*a*), which does not occur when only the lower threshold controls the dispersal rule (figs. 8*a* & *b*). As we increase the values of Δ and δ to the point where $N_c < N_A$, the dispersal rules become untenable, meaning that the population is always driven to global extinction. This occurs because the interaction between the upper and lower critical threshold densities always forces individuals to disperse, as the lower threshold density (N_A) is actually higher than the upper threshold density (N_c). Although the mean number of dispersal events is very small, high amounts of dispersal take place within the first generation, as individuals try to find a patch within which they can settle - which obviously cannot happen - they are therefore lost through edge effects, leading to global extinction (fig. 10). Here we can see the limits where N_c has a value above and then below the equilibrium population size (N^*). If N_c is greater than N^*, individuals will tend not to have to disperse. As we decrease N_c (by increasing Δ), each patch is forced below the equilibrium population size, and at the start of every generation all patch densities will tend to exceed N_c as their density tends towards the equilibrium attractor. Dispersal will continue until enough individuals have been lost through edge effects, and all patches have a density equal to or below N_c. It is in this manner that all patch densities are synchronised.

Decreasing the size of γ directly decreases the value of N_A, thus when the Allee effect has an influence over a relatively small population density, the global population can persist over a greater range of values for Δ and δ. This happens as the population fluctuates (chaotically or otherwise) within upper and lower bounds, the lower of which remains above the critical threshold density.

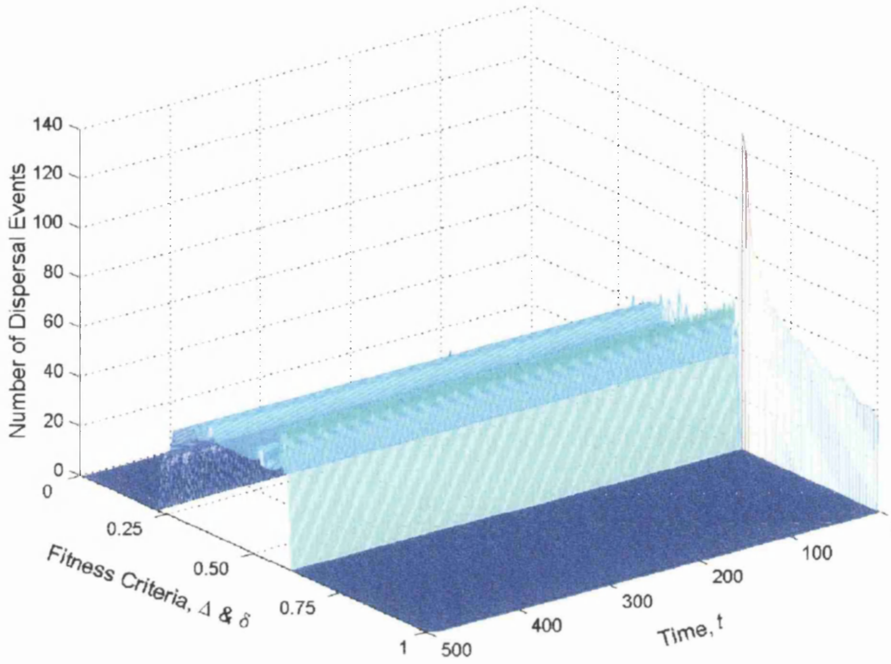


Figure 10: At low values of the density-dependent criteria there is little dispersal as each patch is in a stable equilibrium state. Gradually increasing the criteria forces individuals to seek a new patch to escape reproductive loss, mainly from competition. When the density-dependent criteria exceeds a critical value ($N_c < N_A$; Δ & δ approx. 0.6) global extinction occurs after the first generation. Individuals disperse many times, trying to find a patch where they can settle according to the density-dependent criteria - which is of course impossible!

5b) - c) Upper and Lower thresholds with costs

If we introduce a maximum number of dispersal events when there is both an upper and lower threshold density influencing dispersal, we can alter the dynamics of the population. If parameter values are selected that lead to non-fluctuating dynamics, limiting the number of dispersal events will lead directly to population fluctuations, becoming more complex with fewer dispersal events (fig. 11).

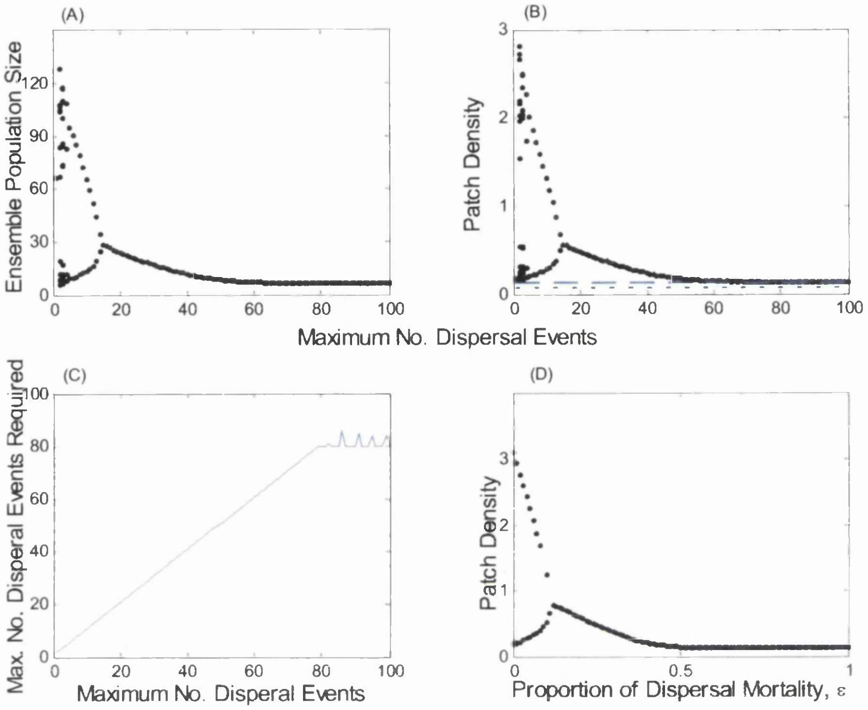


Figure 11: Limiting the maximum number of dispersal events migrants can take when trying to find a suitable patch to settle in leads to a loss of stability in population dynamics. In an Allee population, where dispersal decisions are based on both an upper and lower threshold density (Δ & δ = 0.5), a population that does not fluctuate in density over time can lose this stability, when the number of patches dispersers can visit before settling is limited (11*a* - *c* - other parameter values as fig. 10*c*. The dashed and dotted lines in 11*b* indicate the upper and lower threshold densities that govern dispersal respectively). Dispersing individuals must remain in the patch they find themselves in after the maximum number of within generation dispersal events has taken place. Fig. 11*c* indicates that with these parameter values, approximately 80 dispersal events are required for the population to reach global stability. Introducing a fixed proportion of dispersal mortality can simplify the dynamics again when the number of dispersal events is limited (11*d* - maximum number of dispersal events

permitted = 5), bringing them back to a non-fluctuating stable equilibrium again if dispersal mortality is high enough.

It is interesting that parameter values that produce chaotic dynamics without dispersal, but produce non-fluctuating dynamics when there is density-dependent dispersal (fig. 11*b* - Δ & $\delta = 0.5$) can lead to stable populations arising with densities above the upper density criterion. This means that it is possible to have a greater (global and local) density than would normally be possible if the dispersers were allowed as much time as they required to find patches that satisfy the density-dependent criteria. By limiting the number of dispersal events that can be taken, dynamics clearly become destabilised, which could perhaps lead to an increased risk of extinction if stochastic events were to influence the population in any way. However, introducing dispersal mortality will simplify dynamics, returning them to their original stable state with sufficient mortality even if the number of dispersal events is limited (fig. 11*d*).

Discussion

In this study, I have shown that density-dependent dispersal can indeed have a stabilising effect on population dynamics when dispersal is directly influenced by competitive pressures. This result is in agreement with previous findings (Ruxton & Rohani, 1998). The generality of these results is emphasised by the fact that the results from these different studies have been found using different functions to model population growth. Ruxton & Rohani (1998) employed the Maynard-Smith & Slatkin (1973) function to model population growth, while here we use the Hassell (1975) function for modelling density dependence in a population with no Allee effect, as well as the Fowler & Ruxton (2002) function for modelling competitive and Allee effects within a single species population. We go on to show that if individuals base dispersal decisions away from a population patch to avoid fitness loss from an Allee effect, this may lead directly to global population extinction, which is perhaps a surprising result, and is discussed further below.

Introducing a cost to dispersal in different forms produces different results. Ward *et al.* (1998) estimated that less than 1 per cent of autumn migrants of the bird cherry-oat aphid (*Rhapalosiphum padi*) found a suitable host, clearly indicating both the extreme costs involved with dispersal, but also the extremely strong selective pressure for dispersal ability. Of course, dispersal costs may be expressed in many forms, including dispersers having a reduced lifetime fecundity (Dixon 1985), including being unable to breed within a season (Danchin & Cam 2002), and here we only look at a few relatively simple costs that are easy to include within the model framework. A simple cost to dispersers, expressed as mortality to some (fixed) proportion of migrants was not found to alter the dynamics qualitatively, neither was a mortality cost that increased with subsequent dispersal events. These forms of cost simply reduced the number of dispersal events required for the dynamics to reach their final state. Introducing a limit to the number of dispersal attempts made within any generation was found to destabilise dynamics, although this type of dispersal cost did permit population persistence over a range of parameter values that would otherwise lead to global extinction in populations affected by Allee effects. Combining these different forms of costs lead the "limited dispersal" destabilised dynamics to return to a simpler dynamic form. This suggests that for dispersal to evolve, it will only arise under realistic conditions, i.e. when there is a cost associated with dispersing.

If dispersal decisions are based on a lower critical population density, and parameter values produce chaotic fluctuations, local patch extinctions occur readily, leading eventually to global extinction. Even when individuals move to find patches with a higher density (leading to local patch extinction), the chaotic dynamics could produce extremely low densities in the new patch in following generations, leading to further dispersal. As patches that have become extinct are extremely unlikely to be recolonised (due to the combination of small numbers of dispersers being distributed between surrounding patches and the lower threshold density leading to further dispersal unless it is exceeded) the risk of global extinction through edge effects is very high. This is supported by the fact that global persistence is permitted when parameter values that produce stable equilibrium dynamics are used (fig. 7*c*).

The fact that we do not use any individual variation, or spatial or temporal heterogeneity in habitat quality in this model, may have important implications for these results. By varying patch quality spatially or temporally, we may find global persistence with more complex dynamics. Although that is beyond the scope of this report, it is probably a useful extension. By looking at a "time-limited" cost to dispersal, we can show that limiting the number of within generation dispersal events (when dispersal is based on escaping the reproductive loss from the Allee effect) can lead to population persistence, without simplifying population dynamics when they are complex (fig. 11). This forces individuals to remain in a patch they wouldn't otherwise inhabit, but we feel that it is still a biologically reasonable scenario. This setting incorporates the ability of organisms to sense and assess their surrounding environment, as well as placing pressure on individuals to settle in a patch within a limited time period. Adding a mortality cost to this limited sampling time is perhaps the most biologically plausible scenario, and here we show that this can simplify the unstable fluctuations brought about by limiting the number of dispersal events within a generation.

Amarasekare (1998*b*) recently found that density-dependent dispersal mortality in a population suffering from an Allee effect was of little or no consequence. We find similar results, with the only difference comparing dispersal with or without mortality (other than edge effects) being the number of dispersal events required for the population to settle. However, the dispersal rule Amarasekare (1998*b*) uses is somewhat different to ours. Whereas we define some threshold value below (for Δ – or above for δ) which no dispersal will take place, there is always some dispersal away from patches in the Amarasekare (1998*b*) model, regardless of local patch density. A background level of emigration such as this may have clear benefits for individuals if patch quality changes over time. Sampling other patches in the environment would prevent all offspring being lost in local (natal) patch catastrophes. However, this only tends to hold if there is no cost to dispersal. If there is a mortality cost to dispersal (as there is in both our model and Amarasekare's) and no variation in patch quality over time, then forcing individuals to leave a patch regardless of the local conditions will lead to the unnecessary loss of dispersers when the local patch conditions are below the critical population density.

An important and novel aspect of the work presented here is the introduction of a lower critical threshold density, below which individuals will leave a patch. Heubeck *et al.* (1997) have suggested that Kittiwakes breeding on the island of Unst, in Shetland, abandoned low density breeding colonies due to the considerable predation pressure of Great Skuas. They reported that dispersing Kittiwakes move to other existing colonies and presumably benefit from a dilution effect on predation risk. This has occurred at the same time as an overall reduction in the number of breeding pairs of Kittiwakes around Shetland. While the structure of our model is not exactly analogous to the Kittiwake's life history, Heubeck *et al.*'s (1997) work does show that dispersal decisions based on a lower critical population density can arise under natural circumstances. Incorporating such decisions into our model also leads to global population persistence (as well as a decrease in global population size) with local patch extinctions (fig. 8) and we find our model results complement this study. Results from density-dependent dispersal with a mortality cost to some fixed proportion of dispersers (fig. 2) contrast with the findings from a similar model where such a cost was included in a population with density independent dispersal (Ruxton *et al.* 1997). We found no stabilising effect by including density-dependent dispersal mortality in this way while Ruxton *et al.* (1997) found that increasing the proportion of dispersers that suffered mortality before arriving at a new patch simplified dynamics considerably. This difference in results was also found when comparing results of density-independent and density-dependent dispersal rules with a population suffering from an Allee effect above (fig. 4). These differences arise because introducing a cost to density-independent dispersal in this way simply reduces the realised population growth rate by removing individuals from the population after reproduction has taken place. While it may be expected that the same process would occur with density-dependent dispersal, this was not found to be the case, i.e. population dynamics were generally insensitive to the proportion of disperses suffering mortality, which can be explained as follows. Running this model on a lattice with periodic boundaries, and no cost to dispersal, would mean endless rounds of dispersal taking place if the upper density-dependent criterion (Δ) lead to a threshold density below the maximum global density produced for any given set of parameter values (this could mean the stable equilibrium population size, or the upper bound for any form of fluctuating dynamics). Should the global population size ever exceed the global value for the threshold density, some individuals leaving patches due to competitive pressures may be able to find patches that are below the threshold density. By settling in a patch, they will have increased that patch density, which will eventually reach the threshold value, leading to all patch densities becoming synchronised. Once this has occurred, any individuals that are still seeking a patch below the threshold will continue to sample patches - unsuccessfully and infinitely. It is only by introducing some form of dispersal mortality that the population can settle to a suitable size. We do this implicitly by including absorptive (lethal) edge effects in the models (or a fixed proportion of dispersal mortality when we do use periodic boundaries). While the result from running the model on a lattice with absorptive boundaries compared to periodic boundaries with a fixed mortality cost to some proportion of dispersers is interesting, namely that the same qualitative dynamics can be reached in approximately half the number of dispersal events, it is not necessarily surprising. In an environment where individuals only experience mortality at the edge of their habitat range, those in the middle remain buffered from this mortality risk. However, eventually dispersers will move to an edge patch until the population density across each patch in the lattice is below the threshold density. Contrary to this, if all dispersers face a constant likelihood of mortality (regardless of which patch they are emigrating from) all patches in the lattice will reach the critical density at a faster rate.

Rohde & Rohde (2001) warn against the possible loss of dynamic information when averaging multiple population densities, however, results from individual patches in the models presented here lend confidence to the prediction our global dynamics are representative of the local patch dynamics. Recent work by Etienne *et al.* (2002) on a model simulating *Drosphila* population dynamics including dispersal, competitive and Allee effects, shows a variety of interesting results. They found that "reasonably smooth" global population dynamics had arisen even when local patch dynamics were deliberately set to be rather unstable. However, the method they employed to include competitive and Allee effects were somewhat different to the method used here. We use a non-linear function to determine future fitness (analogous to the density of offspring produced) based on the current population size, where reproductive output is reduced as a direct result of relatively high and low densities (there is some tentative evidence to suggest that this function can describe population processes in both aphids [chapter III] and *E. coli* [Gusev & Fowler, in preparation] with some accuracy). Etienne *et al.* (2002) used explicit (fixed) upper and lower larval population bounds, above and below which larvae could not survive due to extreme competitive pressure, or mechanisms arising from Allee effects. The assumption that populations are restricted in their population sizes in such a manner is likely to have an extreme effect on population dynamics that may not be biologically realistic. (Furthermore, the time periods used to determine establishment [2 generations] and persistence [20 generations] of populations may not remove the possibility of transients affecting their results.) By using explicit upper and lower population bounds to determine juvenile (offspring) dispersal rather than juvenile survival, we introduce the possibility for individuals to make a life history choice based on the trade-off between density-dependent reproductive loss and dispersal costs.

We tentatively suggest that the above results provide theoretical support for the lack of chaotic-type dynamics found in empirical data-series (excluding the difficulties associated with finding deterministic chaos in typically short and noisy time series [see Bjørnstad & Grenfell (2001) for a recent review]). If the adults of a species use some rule to decide what proportion of their offspring should disperse away from the natal patch, these findings support density-dependence (through competitive or Allee effects) as a cue for decision making. The fact that different costs influence the results in different ways highlights the importance of including biologically reasonable assumptions into models. A further extension to this work would be to find the optimum values for the upper and lower critical thresholds through selection simulations, or tests of invasions by individuals that base dispersal decisions on opposite density-dependent criteria (i.e. upper vs. lower critical densities). The results here add to the growing body of work that propose mechanisms that simplify the complex dynamics often produced by (perhaps overly-) simple non-linear models (e.g. McCallum 1992, Ruxton *et al.* 1997, Ruxton & Rohani 1998 and others). These mechanisms bring theoretical results into line with data from ecological and experimental time series. Adding even a relatively high density-dependent threshold to this model simplifies chaotic dynamics (brought about with biologically reasonably parameter values) to 2-point cycles and reducing the threshold density further leads quickly to stable single-point dynamics. These forms of dynamics have been found since the earliest examples of time series analysis of ecological data sets (e.g. Elton 1927, Elton & Nicholson 1942*a* & *b*) and our results point to mechanisms that can bring about such population fluctuations when including realistic life-history choices in a simulation model.

This study shows that including density-dependent dispersal rules (including a cost of dispersal) in relatively simple models of population growth clearly stabilises dynamics, in some cases from highly chaotic to stable equilibrium dynamics. These results highlight the importance of including such biologically relevant mechanisms in models that may be used in management or conservation practises, in order to avoid spurious results from over-simplified models adversely affecting species management decisions.

SPATIALLY STRUCTURED POPULATION DYNAMICS FEATURING CONTINUOUS RELATIVE PHASE-SHIFTING

ABSTRACT

Populations displaying cyclic fluctuations in their size over time have been of great interest to ecologists for the past three-quarters of a century. Here we present and examine a spatially structured model that simulates the population dynamics of Canada lynx (*Lynx canadesis*) and displays a time varying behaviour we term phase-shifting, where cycles in different population sub-units move in and out of phase with each other over time. We confirm that the phenomenon is more than different patches simply fluctuating at slightly different cycle period lengths; rather it is a new dynamical behaviour. We go on to demonstrate that this phenomenon can be found under a wide range of conditions, including some that were previously deemed unsuitable. The fundamental structure of the model is then altered in different ways, and we show that phase-shifting can still arise. Given the prevalence of this behaviour under a wide range of model conditions, it is perhaps surprising that little attention has been paid to it previously. The consequences of this type of dynamical behaviour are discussed, as well as discussing reasons why it may have been missed in previous time series analyses.

Introduction

Cyclic fluctuations in numbers have been known to occur for many populations under natural conditions, a phenomenon that has interested ecologists for the past 75 years (e.g. Elton 1924, 1927, Lindström *et al.* 2001). Long-term data sets for different species have been analysed to demonstrate the degree of synchrony between spatially separate populations of the same species (figure 1).

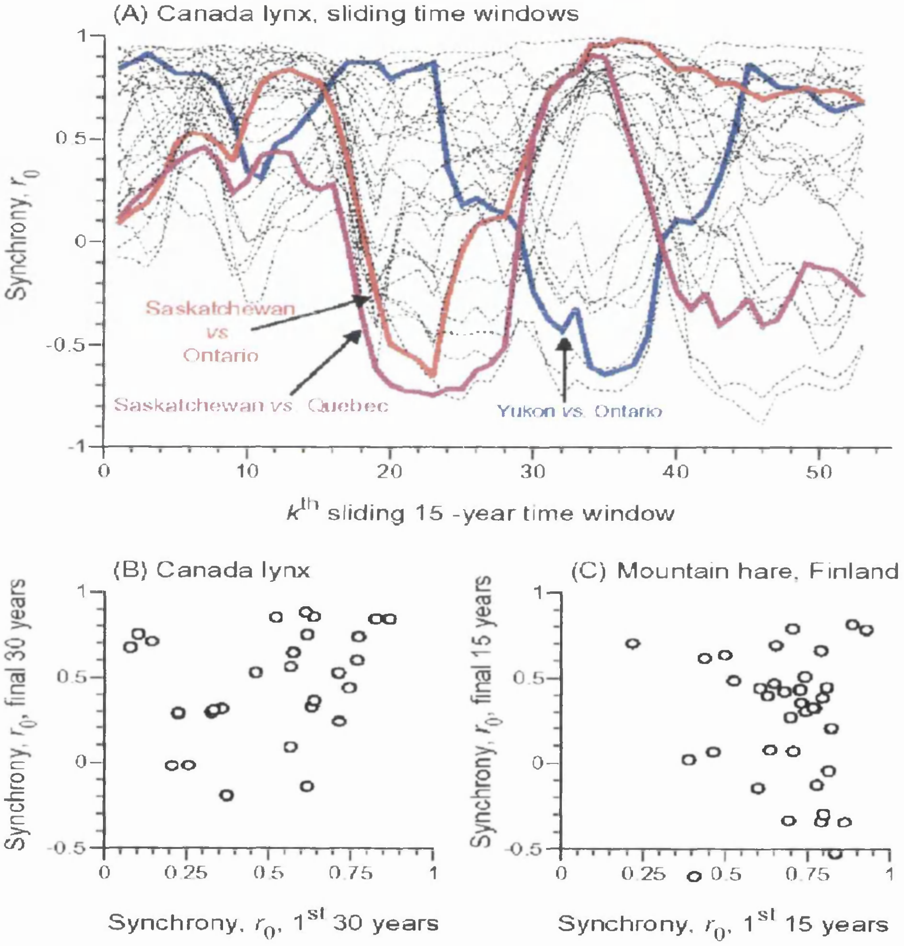


Figure 1: Examples of the degree of synchrony demonstrated by different populations changing over time. Fig. 1*a* shows how the degree of synchrony in Canada lynx populations in different Canadian provinces changes over time. Using a time window method, the degree of synchrony between lynx populations in different Canadian Provinces

can be plotted over time. There may be a considerable change in the relative amount of synchrony between different populations over time. Figs. 1*b* & *c* demonstrate the change in synchrony for populations of Canada lynx (between the first and last 30 years of time series; data for 1*a* & *b* from Ranta *et al.* 1997*a*) and mountain hare in Finland (first and last 15 years; data from Ranta *et al.* 1997*b*). The variation present here indicates a change in synchrony between patches over time.

In a report analysing data taken from the Hudson's Bay Company records of Canada Lynx populations (Elton & Nicholson 1942*a*), Ranta *et al.* (1997) present the output of a population model that displays a dynamical behaviour previously unreported in biological systems: that the degree of synchrony between the cyclic dynamics shown by different coupled populations changes over time. In other words, the relative phase of fluctuations in population size between any two local units in the spatially-structured population changes over time, shifting from being completely in phase to completely out of phase and back again (figure 2).

Recently, two probable causes have consistently been assigned as possible factors leading to synchrony arising in population dynamics, namely dispersal and spatially correlated environmental noise - the latter being termed the Moran effect (Moran 1953*a* & *b*, Royama 1992, Ranta *et al.* 1995, Koenig 1999, Bjørnstad & Bolker, 2000 and Ylikarjula *et al.* 2000). With each of these causes apparently dominating at a different spatial level (Paradis *et al.* 1999), these two factors have both been shown to lead directly to synchrony arising in different populations. Grenfell *et al.* (1998) have shown a link between weather patterns and synchronous fluctuations arising in the dynamics of two isolated sheep populations on small, geographically close islands, while Ranta *et al.* (1995, 1999) have reported that dispersal can maintain synchrony in various different species. It has been suggested that at a local scale dispersal will play an important part in promoting synchrony, while the Moran effect will dominate at a global level (Hudson & Cattadori 1999). Other possible causes have been suggested as causing synchrony in population cycles. For example, Ruxton & Rohani (1998) suggest that fitness dependant dispersal has a very strong synchronising effect, and Jansen (1999) claims that phase locking may act as a further cause of synchronicity arising in connected populations. However, phase locking actually appears to develop as an effect of dispersal between populations, rather than a being a cause of spatial synchronicity (Ranta *et al.,* 1999). Another important factor associated with cyclical fluctuations is the relationship between hosts and their pathogens (Grenfell *et al.* 2001, McVean *et al.* 2002). Given the considerable current interest in understanding patterns of synchrony in natural systems (Balmforth 2000, Holyoak 2000*a*, Kendall *et al.* 2000, Schwartz *et al.* 2002 and others), a greater understanding of the behaviour briefly reported by Ranta *et al.* (1997) would seem to be a useful starting point for further research.

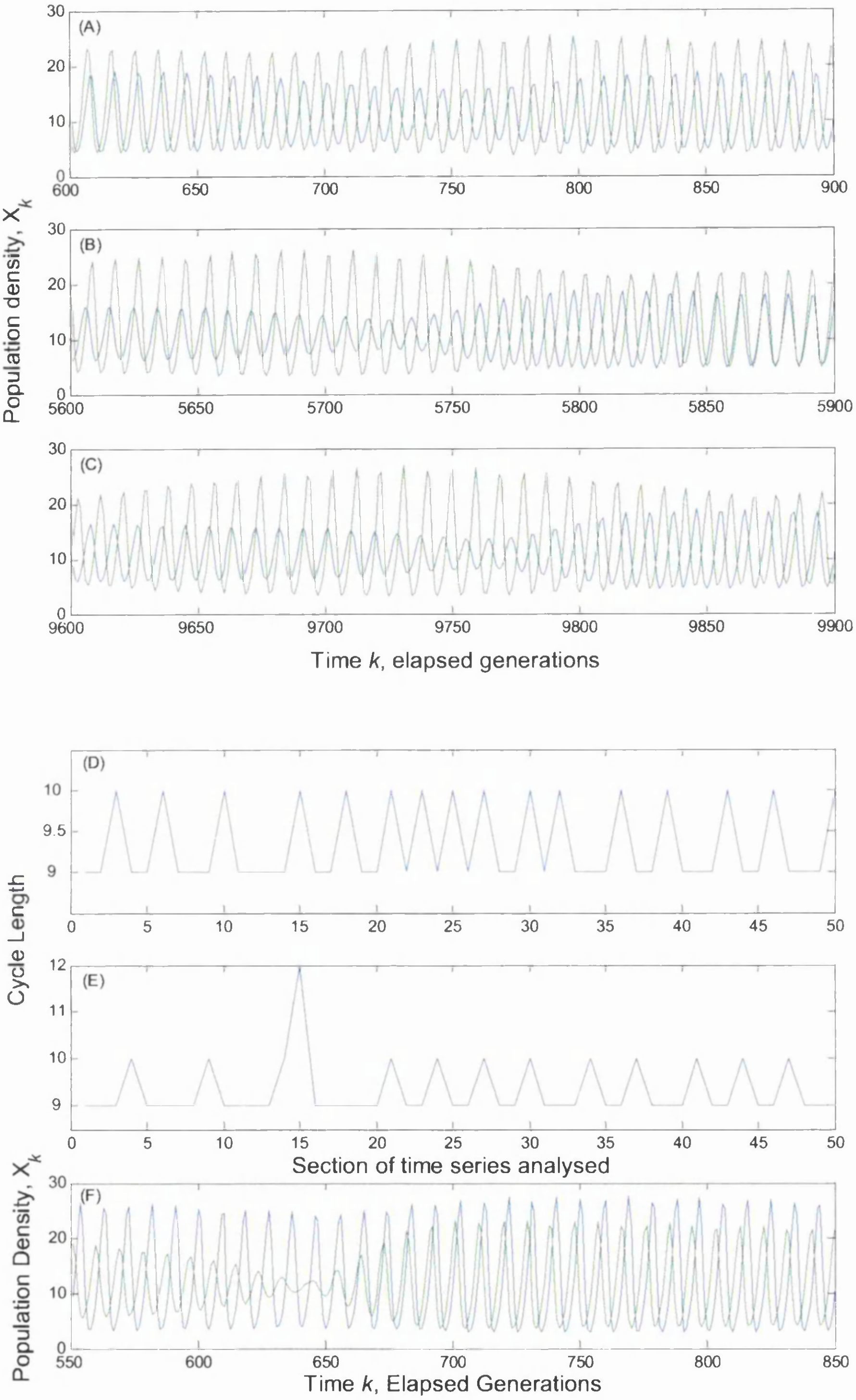


Figure 2: Results from time series of two randomly chosen patches in the model presented here. Figs. 2*a-c* exhibit the variation in relative synchrony between two patches that we term

phase-shifting, that is still present up to at least 9900 time steps. Figs. 2*d* & *e* describe the cycle lengths (in time steps) of 50 different cycles from two randomly chosen patches, with the time series of each displayed in fig. 2*f*.

In this study we seek to address the following questions. How robust is the phase-shifting behaviour against perturbations to the particular parameter values chosen by Ranta *et al.* (1997)? Studying this will allow us to form hypotheses as to the model characteristics that promote this behaviour and those that make it unlikely. This leads us on to the next section, where we perturb the fundamental structure of the model in a number of ways and across a wide range of parameter values, seeking to establish which aspects of the model are necessary for this behaviour to occur. Specifically, we will test the conjecture of Ranta *et al.* (1997) that such behaviour cannot occur if the populations in the environment are arranged in a spatially regular pattern.

In the following section, we describe the model used to simulate population changes over time. We demonstrate that the model can indeed produce the behaviour shown in figures 1 and 2, that this behaviour is persistent through time and that phase-shifting is potentially a biologically relevant dynamical behaviour.

The Model

This model is based on a long-term time series of Canada lynx describing a deterministic single-species model that accurately simulates a 10.8-year cyclical dynamic of population size that is found in the Canada lynx populations (Ranta *et al.* 1997). To give the model an increased level of biological realism, the authors choose a random method of patch positioning within an arena, rather than the more commonly used regular grid structure (coupled map lattice - CML). A fixed fraction

(10%) of individuals dispersed in an exponential distance-dependant manner between the 25 population patches, with the populations renewing after

$$X_{i(k+1)} = (1-m)F\left[X_{i(k)}, X_{i(k-1)}\right] + \sum_{s=1, s\neq i}^{n} M_{si(k)} \tag{1}$$

where $X_{i(k+1)}$ is the population size in patch (i) at generation number (k). Patches are numbered $i = 1, \ldots, n$, while $k = 1 \ldots T$, where

$$F\left[X_{i(k)} X_{i(k-1)}\right] = X_{i(k)} \exp\left[r + a_1 x_{i(k)} + a_2 x_{i(k-1)}\right], \tag{2}$$

r is the intrinsic rate of population growth (set at 0.47 in simulations, unless otherwise stated), and a_1 (0.056) and a_2 (-0.1) are parameters describing the strength of density dependent and delayed density dependent feedback respectively. $M_{si}(k)$ is the number of immigrants from patch s to patch i [*sensu* Hanski & Woiwod (1993)]

$$M_{si}(k) = mF\left[X_s(k), X_s(k-1)\right] \frac{\exp(-cd_{si})}{\sum_{i,i\neq s} \exp(-cd_{si})} \tag{3}$$

(d_{si} is the distance between patches s and i and $m = 0.1$ and $c = 0.75$ are parameters telling the proportion emigrating and distance emigrated, respectively). The populations were initiated in phase ($X_{i,1} = X_{i,2} = 10$) and left to renew for 1000 generations (again, unless stated otherwise) to remove the transient effect of the initial conditions, before sampling.

Testing the Time Series

To find out how relevant the phase shifting behaviour we report here actually is, the time series data for different patches were tested using an autocorrelation function (Chatfield 1996) to assess the period length of the cycling dynamics. Further analysis of the time series was carried out by measuring the length (in time steps) of one complete cycle of the dynamics within different patches. This process was repeated

50 times within a patch to assess whether the cycle length varied over time, or between patches. We suggest that variable cycle lengths within patches would indicate a biologically interesting event, namely phase-shifting.

Positioning Patches on a Coupled Map Lattice

We then go on to apply the above model to a situation where the patches are positioned regularly on a grid - also known as a CML - to explore whether the phase-shifting behaviour will not occur under such circumstances. The dispersal kernel is not changed initially - diffusion of individuals remains dependent on the distance between the focal patch and all other patches in the environment. We study the effect of varying different parameters to gauge whether phase-shifting will arise under these conditions.

The underlying structure of the model is then altered further by changing the dispersal rule to a simple nearest neighbour mode of migration. In this case, a fixed fraction of individuals are distributed equally from the focal patch to the four nearest patches in the lattice, that is, a quarter of the emigrants will travel to each patch above, below, left and right of their natal patch. Periodic boundaries are used here to avoid edge effects, which were not included in the other versions of the model due to the dispersal kernel used. This allows for a fair comparison of results between the different forms of the model described above. Here we relax the assumption that all population patch densities are initiated with the same value to see if it is possible to promote the phase-shifting behaviour in this type of model structure.

Results

As the phase-shifting phenomenon still appears after more than 9,000 generations (fig. 2), we can be sure that this is not a transient effect we are seeing, but a phenomenon that persists over time. This is an important point, as this shows that the phenomenon we are describing differs from the phase locking described by Jansen (1999) and exceeds the length of time associated with supertransient behaviours (Hastings & Higgins 1994, Crutchfield & Kaneko 1998).

Testing the time series generated with an autocorrelation function shows that $r_t = 9$. Thus, we have found that the conditions producing a cyclic dynamic here show a periodicity of 9 time steps (years), rather than the 10.8 (~11) year cycle displayed by the Canada lynx (Moran 1953*a* & *b*, Royama 1992, Ranta *et al.* 1997). We then tested whether each within patch time series actually varies in frequency over time. This allows us to rule out the possibility that the phase-shifting phenomenon found here is simply an artefact produced by different patches cycling at different frequencies to each other, while maintaining a constant within patch frequency. The results shown in figure 2*d-f* show there is a variable cycle length both within and between patches. Thus, we can say that although the dominant cycle length in the time series for the tested patches is 9 time steps, the actual frequency of cycling varies within patches over time, and also between patches. This confirms that the phase-shifting phenomenon we are describing here is in fact an event of considerable dynamical interest. Of particular note here is the loss of the cyclical dynamic, and it's subsequent re-appearance around $k = 640$, further demonstrating the variability between the time series both within and between patches.

Changing the fundamental structure of the model.

(i) CML retaining negative exponential dispersal kernel - varying dispersal parameters.

Here we position the patches regularly in the environment rather than in a random manner. Ranta *et al.* (1997) suggested that it was not possible to achieve phase shifting in this model by positioning patches regularly on a lattice grid. We show here (figure 3) that simply by changing the rate of diffusion (migration) it is possible to bring about phase-shifting when patches are positioned on a regular lattice framework. The relative shift in synchrony over time, viz., phase-shifting, is demonstrated in these figures through multiple synchrony values plotted for each single value of the parameter addressed. This is achieved using a sliding time window method for finding cross-correlation values for a 50-generation portion of the time series in 2 randomly chosen patches. This process is repeated for 15 consecutive 50-time step periods between 250 to1000 generations. Scoring cross-correlation (with lag zero) was begun at $k = 250$ to eliminate the potential effect of transients. If the two populations are cycling in phase over the 50-generation period, this returns a cross-correlation value of 1. Likewise, two populations cycling in opposite phase will have a cross correlation value of -1. As the cross-correlation time window moves along the time-series, two patches whose phase does not change relative to each other will always return the same cross-correlation value. However, if the relative phase of the two population patches changes over time, this will produce a wider range of cross correlation values for each parameter value tested, indicating the occurrence of phase-shifting.

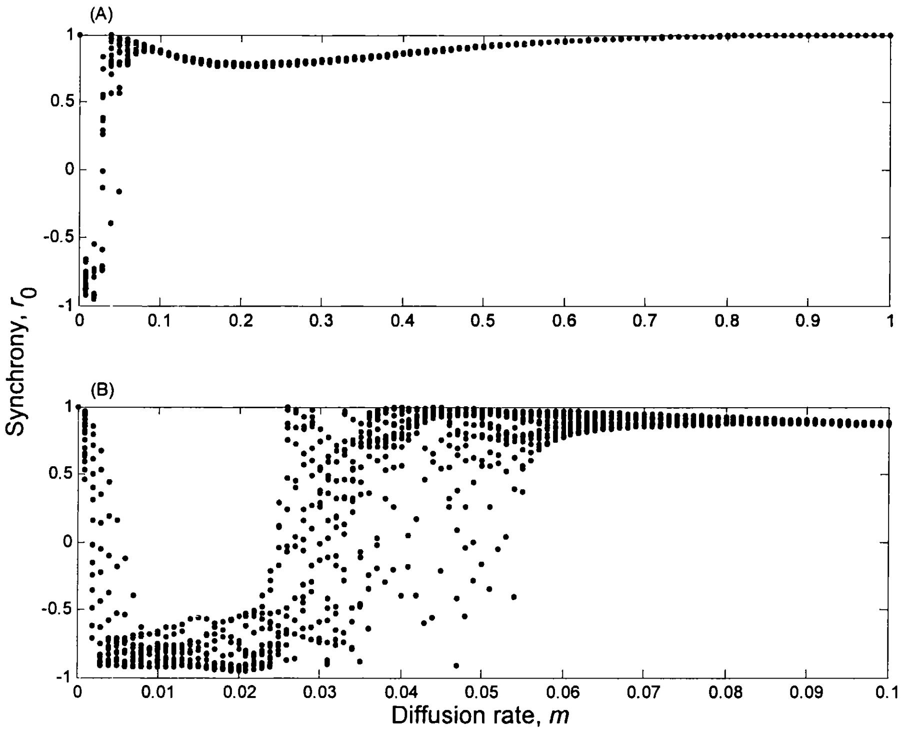


Figure 3: Synchrony can arise in a CML, through a reduction in diffusion rate. This is shown by plotting multiple cross-correlation values taken from a sliding time window in two randomly chosen patches. By varying *m*, the diffusion rate, we find that low levels of diffusion allow phase-shifting to occur (fig. 3*a*). Fig. 3*b* is the left-hand side of 3*a* expanded.

Therefore, we show here that at very low rates of diffusion (below 0.05) phase shifting will arise when patches are placed in a regular lattice structure (fig. 3). While this value is lower than that used by the Ranta *et al.* (1997), it is still of biological relevance (and seems a very important finding). It holds that phase-shifting will only arise at relatively low diffusion rates (less than 5% of individuals are dispersing) when patches are positioned on a regular lattice structure. By looking at the correlation between the distance between all patches in the arena, and their variation in the cross-correlation along the time series, we find that there is no significant relationship between the distance between any two patches, and their propensity to demonstrate phase-shifting relative to each other ($R^2 = 0.1, p = 0.567$ - $m = 0.02$, all other parameters as stated above).

According to the dispersal rule, the proportion of migrants leaving any patch and arriving at a new patch will depend on a negative exponential dispersal kernel. This function is comprised of both the distance of all patches from each other, and the value of *c*, a parameter describing the maximum distance emigrants will travel from their natal patch. Thus when $c = 0$, the model is spatially implicit, i.e., dispersal is independent of distances between the population sub-units, and phase-shifting does not arise (figure 4).

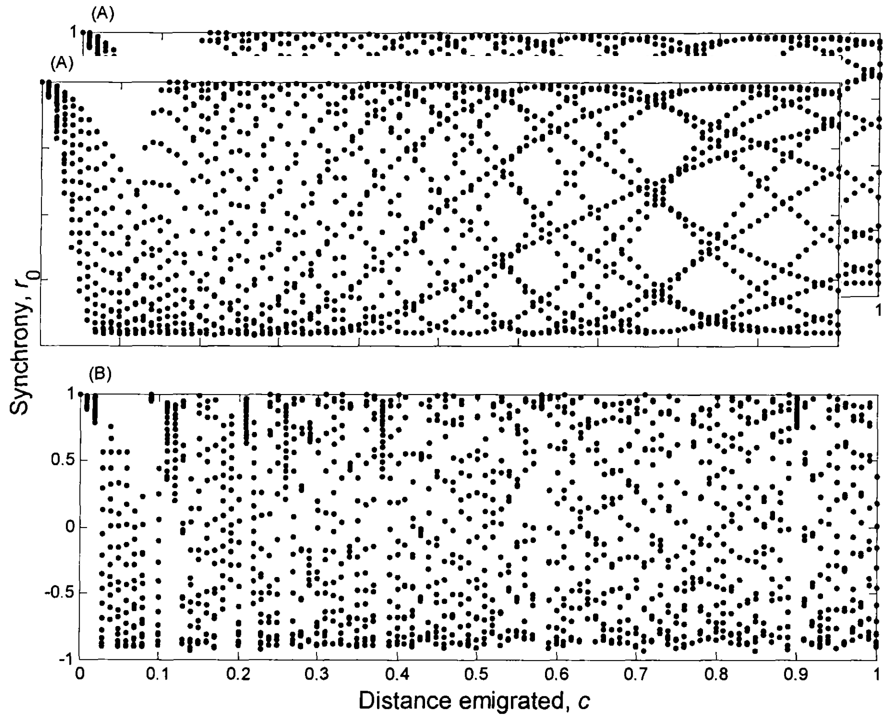


Figure 4: Varying the shape of the dispersal kernel. The parameter *c* determines the maximum distance emigrants can travel from their natal patch. When $c = 0$, dispersers are spread equally around all patches in the environment, and all patch dynamics remain

synchronised. Increase the value of *c* in the model means an increasing proportion of migrants will travel shorter distances, dispersing to patches closer to their own natal patch. The model was tested on patches positioned on a lattice (fig. 4*a*), and patches positioned randomly in the environment (fig. 4*b*).

Raising the value of parameter *c* above zero makes dispersal to other patches distance-related. Increasing *c* leads to a greater proportion of migrants travelling short distances, to patches closer to their natal patch. We can observe the onset of the phase shifting behaviour at very low values of *c*, reinforcing the generality of these results (figure 4).

Varying density dependent feedback mechanisms.

Three of the model parameters included here are directly associated with population regulation. These are the intrinsic rate of population growth (*r*), direct density dependent feedback (a_1) and delayed density dependent feedback (a_2). Varying the intrinsic rate of population growth, *r*, we find the following (fig. 5*a*): at low values of *r*, we do not see any phase-shifting as the populations are in a stable equilibrium state, which can be found analytically using the following formula (Kaitala *et al.* 1996*a*)

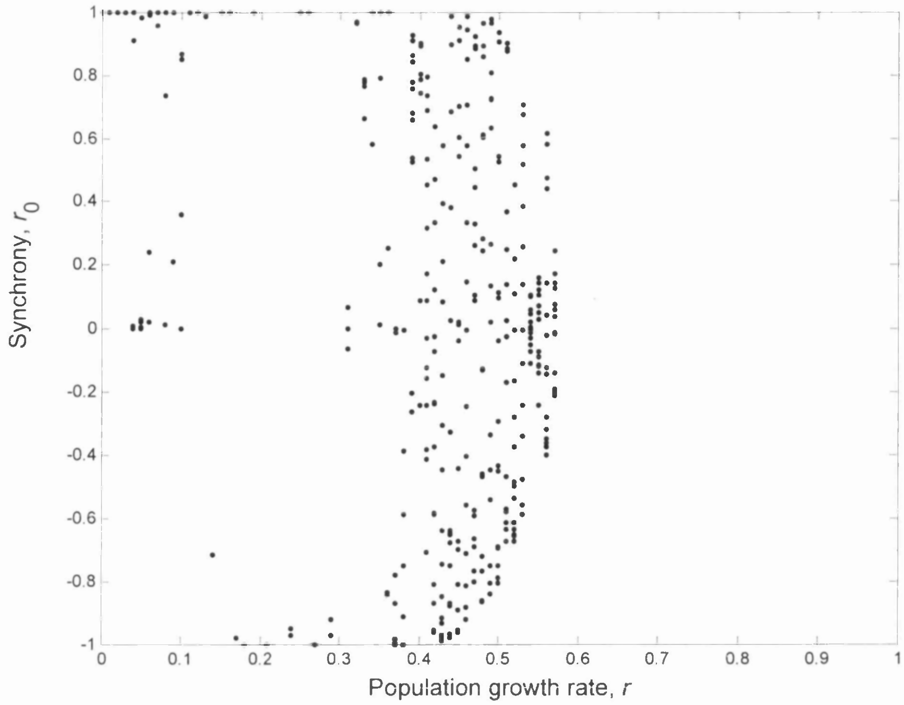
$$\bar{x} = -\frac{r}{a_1 + a_2} \qquad (4).$$

As we gradually increase the size of *r*, we see the phase-shifting behaviour arising. There is a window of phase-shifting for values of *r* of approximately $0.3 < r < 0.55$. Increasing *r* beyond this will lead to the population size increasing without bound, scaling exponentially or faster, and the subsequent loss of phase-shifting as the cyclical dynamic is lost. Thus, we can describe the limits of this behaviour numerically when varying the intrinsic rate of population growth and keeping other parameters constant.

A further condition for the positiveness of the equilibrium population size is

$$a_1 + a_2 < 0 \qquad (5)$$

[it should be noted that equation (5) does not provide the conditions for a stable equilibrium]. Thus, we are limited in the ranges we can vary the parameters a_1 and a_2 relative to each other. Figure 5*b* shows the different regions of dynamical behaviour that arise when varying a_1 and a_2 together, while keeping r at a constant value (0.47). We can see that there are no values for a_1 and a_2 where the dynamics are in a synchronous, cycling state where phase shifting will not occur. By varying parameters a_1 and a_2 in tandem for values similar to those used by Ranta *et al.* (1997), there is a narrow region under which phase shifting can arise. Parameter values below this region lead to the population reaching a stable (non-cycling) equilibrium, while the parameter space above the region of phase-shifting leads to exponential population growth. This leads us to deduce that phase-shifting is a relatively common occurrence under these model conditions - and will still be found when truly synchronous cycles are not.



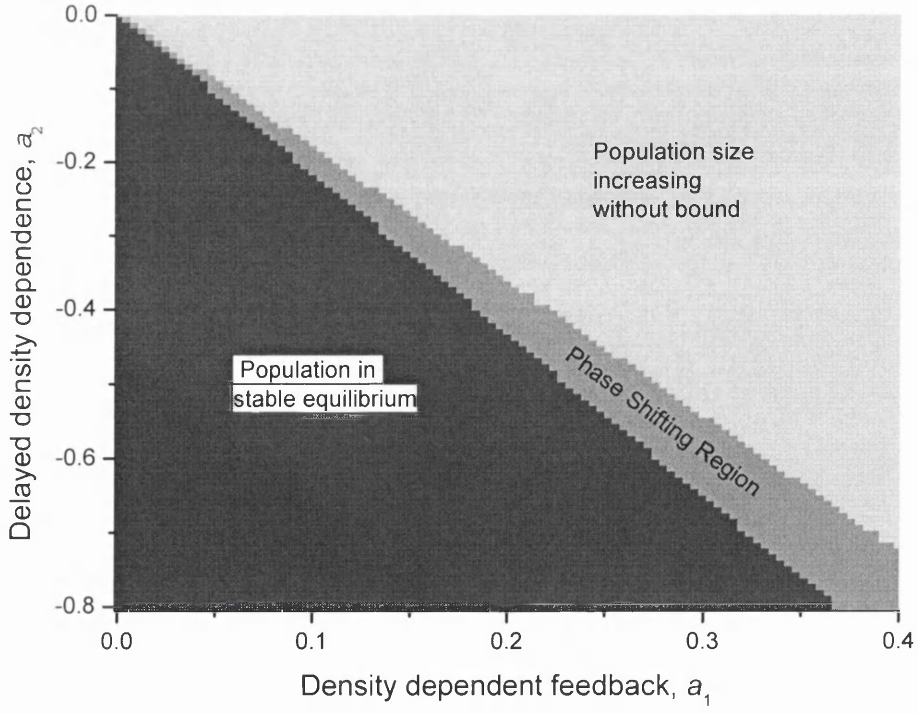


Figure 5: see caption on following page

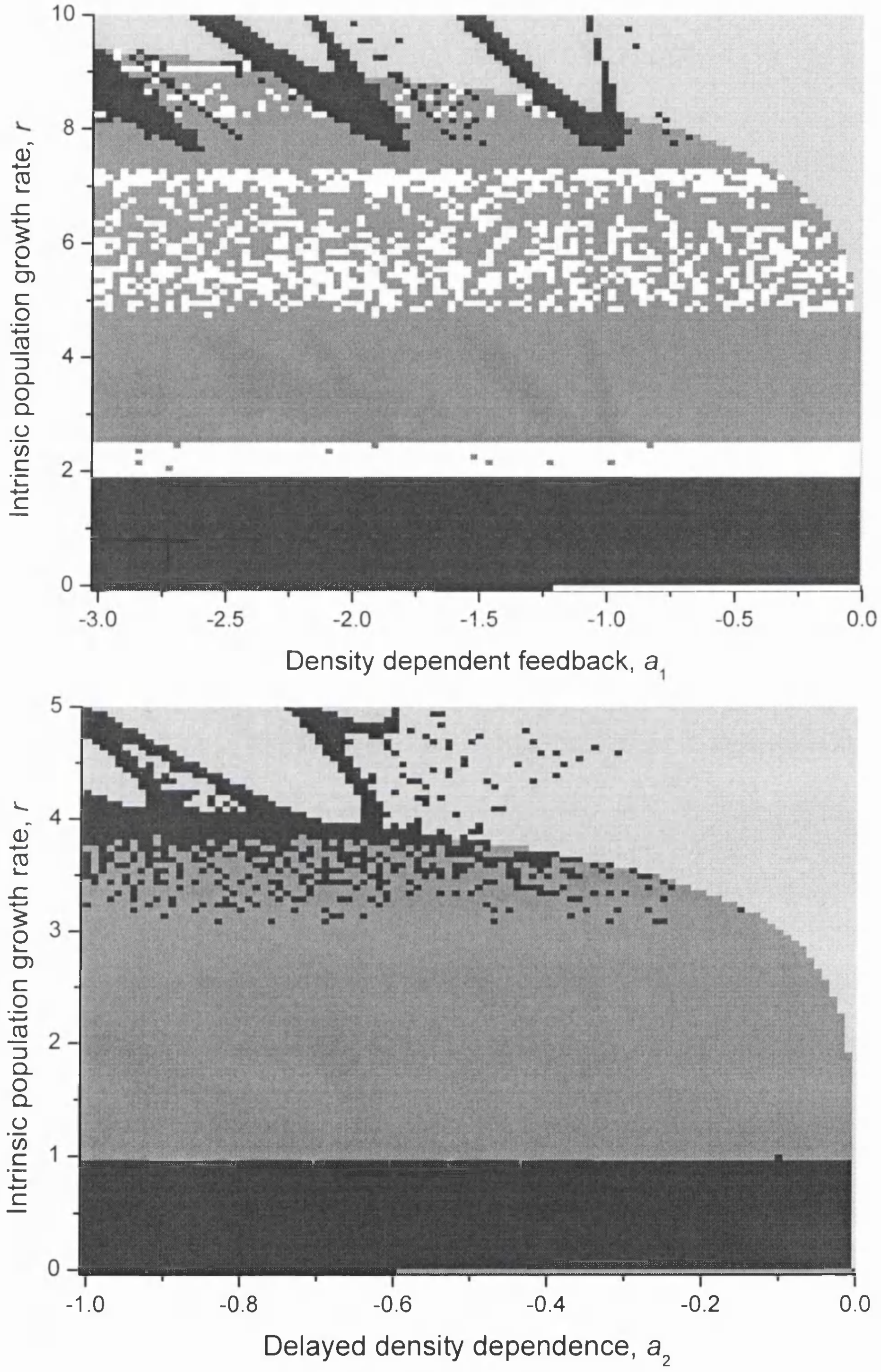


Figure 5: What is the effect of varying density-dependent regulation? By varying the population growth rate (fig. 5*a*), we find that at low values of *r*, all patches are in phase,

as they do not exhibit the cyclical dynamic. Increasing *r* allows a window to develop where phase-shifting can arise. As we increase *r* further, the population densities start to grow without bound, and phase-shifting is lost. Varying density-dependence and delayed density-dependence in tandem (fig. 5*b*) reveals a parameter space that increases in size as we increase the strength of positive density-dependence (shows a positive feedback on population density) and increase the effect of delayed density-dependence. Figures 5*c* & *d* show that phase-shifting can still arise as we remove either delayed density-dependence (5*c*) or rely only upon delayed density dependent feedback. (Key to shading figs. 5*b* - *d*: White = populations cycling synchronously, Light grey = population density increasing exponentially or faster, Grey = populations cycling with phase-shifting, Dark Grey = populations in stable equilibrium.)

To assess whether delayed density-dependence is a necessary and sufficient assumption of the model to promote phase shifting, the intrinsic growth rate and simple density-dependence parameters were varied in tandem. Figure 5*c* clearly shows that it is still possible to produce the phase-shifting behaviour even when there is no delayed density dependent feedback present in the model. In this case, a_1 is given negative values, as positive values for this parameter lead to population densities exploding exponentially or higher when they lack delayed density-dependence. We find four different dynamical behaviours depending on the combination of parameter values studied. These dynamical behaviours are; population density exploding; different populations cycling synchronously; different populations phase-shifting and populations in a stable equilibrium state (populations exhibiting the second and third dynamical behaviours listed here may cycling at different dominant periodicities for given parameter values). Figure 5*c* demonstrates that as the strength of density dependent feedback tends towards 0, increasing the population growth rate leads to populations increasing in size dramatically. There is a large region of phase-shifting across a wide range of parameter values, interspersed with populations cycling synchronously with each other. Finally there are windows of stable equilibria appearing at relatively high population growth rates, with a wide region of this behaviour with values of $r < 2$. These results verify that delayed density-dependence is not a prerequisite for phase-shifting to occur.

Removing simple density-dependence and replacing it with delayed density-dependence also allows phase-shifting to arise (figure 5*d*). Interestingly, by removing simple density dependent feedback, we again lose the synchronous cycling behaviour, finding only phase-shifting when populations exhibit a cycle in their dynamics.

(ii) CML with nearest neighbour dispersal

We can further change the underlying structure of this model by again positioning the patches regularly on a lattice, but this time patches are linked by a new function, the "nearest neighbour" dispersal rule, where each patch distributes one quarter of it's migrants to each of the 4 patches immediately above, below, and to the left and right of the focal patch. This method of diffusion has previously been studied extensively in models (e.g. Hassell *et al.* 1991, Kaneko 1998). Under the conditions described above, phase shifting will not arise. However, by relaxing one of the assumptions of the original model, namely that all population patches will be initiated at the same population density, we can easily produce the phase shifting behaviour.

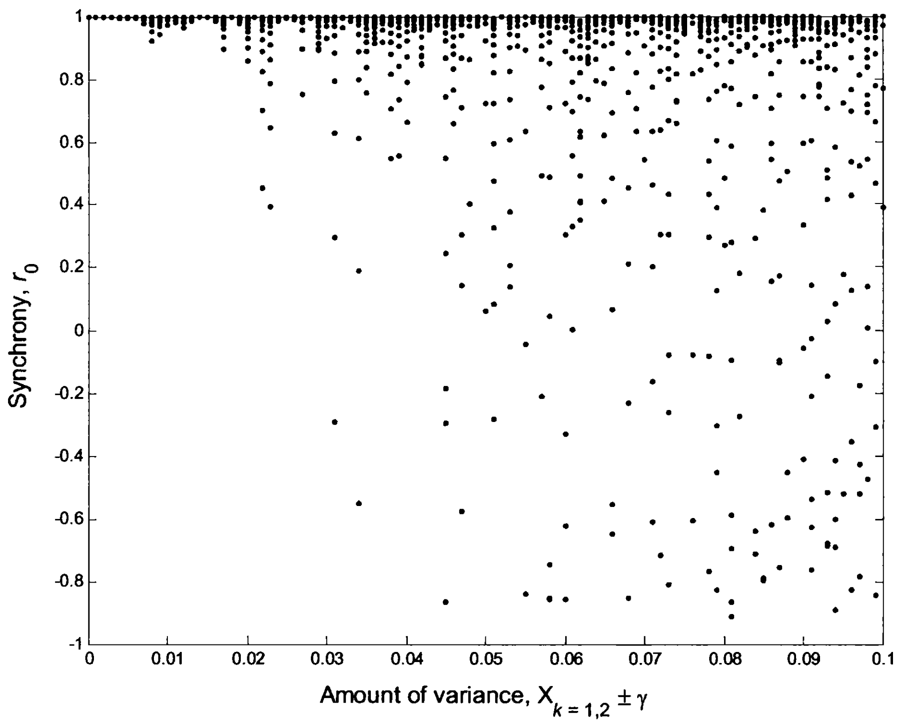


Figure 6: Phase-shifting can arise in CML with nearest neighbour dispersal. Altering the underlying structure of the model, we can still show that phase shifting will arise. With no, or little variation between the starting densities of different patches in the arena populations will remain cycling synchronously. As we increase the variation between the initial densities of different population patches (γ), we can promote phase-shifting.

By allowing populations to be initiated at some value chosen from a uniform random distribution, of 10 ± γ units, while still allowing $X_{i,1} = X_{i,2}$, we can study the effect of allowing some between patch variation in the initial population density. Figure 6 clearly shows that introducing even a very small amount of variation between patches can lead to phase-shifting appearing. When there is either no or only a very small amount of variation in the initial population densities between patches, all patches will cycle in complete synchrony with each other. Increasing γ leads directly to the onset of phase-shifting. Although it may be suggested that by dropping this assumption, the patches are not initiated in phase, we propose that by allowing the first and second generations to have the same population density within any given patch, in fact all patches are initiated in phase with each other. Allowing population patches to vary in their initial densities may also be a more biologically realistic permutation.

Discussion

Complementing the findings of Ranta *et al.* (1997), we show here that it is possible to find phase-shifting behaviour when patches are placed regularly in a lattice formation, simply by reducing the rate of diffusion while remaining within realistic parameter values. Furthermore, we have shown that it is relatively easy to produce this behaviour, both with a biologically realistic dispersal kernel and under a form of spatial model that has received considerable attention previously - the CML with nearest neighbour dispersal. Considering the amount of effort that has gone into studying such models, it is perhaps surprising that this interesting dynamical behaviour has not been investigated further. While the original study by Ranta *et al.* (1997) has highlighted and simulated a very interesting phenomenon in a biological context for the first time, they do so under a very strict range of parameter values. We have shown how phase-shifting differs to the phase locking phenomena that has been previously reported (e.g. Jansen, 1999), as well as "phase synchronized" and "full synchronization" behaviours highlighted by Blasius *et al.* (1999).

Many studies that have looked at synchrony in population data may possibly have missed phase shifting due to the relatively short time series' being considered. However, with data sets of suitable length (fig. 1), such results may become more apparent. Furthermore, in circumstances within the time series' where the cyclicity is lost and subsequently re-appears within a population (e.g., fig. 2*f*), when environmental stochasticity is included it is reasonable to expect that statistical tests would not find synchrony, or phase-shifting between populations, leading to an incorrect conclusion of a lack of synchrony between populations. It may also be reasonable to suggest that time-series data that we do have show unrepresentative dynamics. The apparent loss of cyclical dynamics from time series (Scandinavian microtines, Heikki Henttonen, pers. com; Finnish woodland grouse, Harto Lindén, pers. com.) has been described, and it is important to note that the presence of environmental noise can amplify cycles, as well as obscure them (Kaitala *et al.* 1996*a* & *b*).

We have extended the original work by Ranta *et al.* (1997) to show that the general result can occur over a much wider range of biologically relevant parameter values, and even under conditions that the original paper had deemed impossible.

While this model does not explicitly consider what occurs to patches positioned at the edge of the environment, future work could explore this, as well as how changing the patterns or type of dispersal further will influence the appearance of phase shifting in the population dynamics.

By looking at a relatively broad range of parameter values in this study, we have shown that it is not necessary to use extreme parameter values to produce phase shifting (i.e., it occurs across a biologically relevant parameter space). Varying the parameters that are associated with producing cyclic dynamics in the original model, we suggest that this model may be applicable to different data series. Unfortunately, there are as yet few other time series of sufficient length to be able to compare this model to any real data. As is often the case in theoretical ecology, the model is so far in advance of the majority of available data sets. This does not mean that the findings in this study are trivial. Similar results to those found here and by Ranta *et al.* (1997) have been found in the acorn production of individual oak trees in California (Koenig *et al.*, 1999). This work suggests that relative shifts in synchrony over time could be widespread even without dispersal of the organism. This viewpoint stresses the importance of correlated environmental events on the dynamics of spatially separated populations, and is supported by other studies (Stenseth *et al.* 1999). Since the model explored here does not incorporate any such environmental noise, it must therefore rely upon dispersal to induce synchrony, and the relative changes in synchrony, between different population patches. Indeed, recent microsatellite evidence strongly suggests that patterns of synchrony between spatially separate Canada lynx populations in North America is maintained through dispersal (Schwartz *et al.* 2002). The majority of organisms are likely to show a dispersive stage at some point in their life cycle, therefore this finding may be widely applicable across many different groups.

While other works (e.g. Adler 1994, Holyoak 2000*a*) have studied the effects of changing patch placement and the number of patches on populations, these have tended to look at the effect of these factors on population persistence rather than on a finer dynamical level, i.e., synchrony between patches may arise through rescue effects brought about as different patches act as either sources or sinks. For different individual population patches to reduce the risk of local extinction, they should avoid cycling completely in phase with all other patches in the environment, where possible emigrants may arrive from (Allen *et al.* 1993, Heino *et al.* 1997). It is conceivable that stochastic events may cause small populations to become extinct, and therefore if all populations in the environment were affected by such an event, the risk of extinction on a larger scale becomes magnified. By continuously changing the relative phase of a population cycle over time with other populations that are linked through dispersal, individual patches may be rescued through immigration from other patches if stochastic events occur at a point of low density during the cycle. If a number of patches are linked, such a beneficial effect is greatly enhanced, as it reduces the likelihood of many patches being at the same low point of the population density cycle.

As we have shown, it is relatively easy to find phase shifting in this simple model, indicating that complete synchrony may not be as prevalent in natural systems as previously thought, while phase-shifting may obscure attempts to find relationships in time series analyses. The findings of this report should therefore promote experimental work to find evidence of phase shifting in natural or laboratory systems, and encourage re-examination of much earlier work, of both a modelling and an empirical nature.

EXTINCTIONS IN SIMPLE AND COMPLEX COMMUNITIES

ABSTRACT

Disagreement exists between the results of theoretical and empirical exploration into the effect of increasing community complexity on the stability of multispecies ecosystems. A recent return to interest in this area suggests previous results should be re-assessed, from both experimental studies and models, to understand where this discrepancy arises from. Here we propose various simple extensions to a standard multispecies community model that each increase the complexity of the system in a different way. We find that increasing the number of species in a community leads to a decrease in community persistence after the system is perturbed, and go on to show that increasing the dynamical diversity of the community members leads to an increase in stability through a reduction in extinction events, relative to the less complex form of the model. Our results suggest that different forms of complexity lead to different outcomes in the stability properties of the community. While aspects of this work agree with previous empirical findings that more complex communities are more robust to perturbation, we stress that the type of complexity included and the measure of stability used in community models must be properly defined, to allow objective comparisons to be made with previous and future work.

Introduction

The question of community stability in relation to the complexity of an ecological system lies at the very heart of community ecology, as well as conservation biology (Pimm 1991, Putman 1994, Johnson *et al.* 1996). The view that increased structural complexity in food-web composition leads to increased stability (MacArthur 1955, Elton 1958, Hutchinson 1959) was taken as a fact in ecology for a long time. This view has also been supported by some recent empirical work (Frank & McNaughton 1991, de Grandpre & Bergeron 1997), although some studies failed to find any relationship (Rodriguez & Hawkins 2000), or even found a reduced resistance to community changes with increasing complexity (Rodriquez & Gomeszal 1994). However, theoretical analyses addressing the question of resilience (the tendency to return towards equilibrium after perturbance) in relation to food-web structure support the view that adding species into the community tends to result in a decrease in the stability of the system (May 1972, Haydon 1994). The question of the connection between temporal variability in population sizes and species richness in a community is even more open (recently reviewed by Cottingham *et al.* 2001). There is also a growing body of empirical evidence showing a connection between community processes and biodiversity (e.g. Naeem *et al.* 1994) but it is not a straightforward task to compare these results with theoretical studies, due to factors such as differences arising from the form of stability being studied.

A recent theoretical paper by Lundberg *et al.* (2000) highlighted the loss of further species from a multispecies community (cascading extinction events) following disturbance in model communities of different sizes. They found that single forced extinction events were often followed by cascading events, that is, one or more additional species were rapidly lost from the community besides the removed species. Additionally, their models showed that re-colonisation or re-introductions are not necessarily possible after a restabilisation period, because the altered community structure did not allow the coexistence of the impoverished community and the recolonising species. Failed re-colonisations also caused further extinctions in some cases, highlighting possibly detrimental implications for species management practises.

Here we build on their efforts and extend their model to address the following questions. First, how does the intra-community interaction diversity, i.e. the variety of possible interaction types between different species, affect the extinction tendency of the community? The way the model community of Lundberg *et al.* (2000) was structured only allowed species to be either neutral or harmful to each other (Lundberg *et al.* 2000: 466; all competition co-efficients [-values] were positive in the competition equations). As this is rarely the case in natural communities where, for instance, some species may benefit from the environment being altered in some way by another community member, this is a natural extension to the original model. In the following model, we have looked at a different range of possible interaction values comparable in magnitude with those used by Lundberg *et al.* (2000). Second, even a casual look at any published community dynamics (often restricted to a certain taxon) shows that all the species in the community are unlikely to follow the same population dynamics (see Schmitz *et al.* 1997 & Collins 2000). However, in the Lundberg *et al.* (2000) paper, all the species follow exactly the same dynamics, differing only in their competitive ability. Here, we elaborate upon this in two ways; by introducing delayed density-dependence into the system, and by altering the range of intrinsic growth rates experienced by different species. Both of these extensions are biologically relevant. Delayed density-dependence is commonly found in natural populations (e.g. Turchin 1990, Hansen et al. 1999), while the intrinsic growth rates of different species in any community are also likely to vary between species (Pimm 1991). We feel these three changes each increase the dynamical diversity of the studied communities. Thus, our aim is to look at the contribution of dynamical diversity as well as species number to the extinction likelihood in a simple model community following the removal and subsequent reintroduction of species from the system. Specifically, we define community stability via extinction probabilities: more stable communities are those with a lower probability of extinction events. Finally, we seek to assess the overall stability of the community to different types of disturbance, by looking at whether cascading extinctions after reintroductions are more likely to occur in communities which had cascading extinction events following the initial forced species removal event.

Model Description

Following Lundberg *et al.* (2000), we allow each species in our model community to renew themselves according to Ricker dynamics and interact according to Lotka-Volterra competitive interactions. Thus, in its basic form, the population renewal equation for species *i* in a community of *k* species is:

$$X_{i,t+1} = X_{i,t} e^{\left(r \left(1 - X_{i,t} \sum_{j=1}^{k} a_{ij} X_{j,t} \right) \right)}, \tag{1}$$

where X is the population size, t is the time step (generation number), r is the maximum population growth rate and α is the competition coefficient of species i in relation to species j. Initial community sizes (k) were between 2 and 10 species. A stable community was found by allowing the model to generate a k x k matrix of α-values each taken independently from a uniform distribution with limits [0,1]. The feedback control mechanism for within species competition was such that $_{ii} = 1$. Communities were initiated with each species having a starting size also independently drawn from a uniform random distribution with limits [0,1]. The community was considered stable if the number of species present after 1000 generations was equal to the initial community size. A species was considered extinct if its population size fell below a critical threshold value (in all cases presented here this critical value was $X_i < 1 \times 10^{-6}$). When a stable community was found, one randomly chosen species was removed at $t = 1000$. The community was then allowed to restabilize for 1000 generations, with any species loss recorded, according to the extinction criteria detailed above. At $t = 2000$, the originally removed species was then re-introduced to the community, and the model allowed to run for a further 1000 generations. Any further cascading extinctions were again recorded. This whole process was repeated 100 times for each of the model types described below, resulting in a probability of extinction following different types of perturbation.

Introducing Beneficial Interactions:

The first extension to this model that we carry out is changing the limits of to between [-0.5, +0.5]. This change means that species can have a range of competition co-efficients such that both harmful (positive -values) and beneficial (negative -values) interactions are possible. All competition co-efficients were drawn at random from a uniform distribution of range [-0.5, 0.5], rather than relying on an extension of the maximum value used previously, giving a possible range of [-1, 1]. This can be justified following the findings of Hughes & Roughgarden (1998), who show that the difference between interaction values in a two species community is more important in predicting the stability of the community than the magnitude of the interaction strengths.

Variable Population Growth Rates:

Secondly, we vary the population growth rates of individual species, assigning each a unique r value drawn from a Gaussian distribution with mean 1.75 and standard deviation of 0.5. In the original model, all species shared the same growth rate, with results presented using a value of r = 1.75. While the results of the original model were not found to change significantly after changing the value of r, we felt that applying different growth rates to different species within the community was a more rigorous test of the effect of population growth rate, rather than keeping this at a constant value across the community.

Delayed Density-dependence:

Finally, we introduce delayed density-dependence by updating the dynamics of half of the species in the community as follows:

$$X_{i,t+1} = X_{i,t} e^{\left(r \left(1 - X_{i,t} \sum_{j=1}^{k} a_{ij} X_{j,t} + \beta X_i (t-1) \right) \right)} \qquad (2)$$

where β corresponds to the strength of delayed density-dependence acting on the population, assigned a value of 0.1 in this study. We apply equation 2 to half of the species (chosen at random) present in a community with an even number of initial species (i.e. only communities with 2, 4, 6, 8 & 10 species) as this allows for maximum possible diversity of dynamics in the community.

Results

1) INCREASING DYNAMICAL DIVERSITY

Perturbing the system by random species removal:

In line with the results from Lundberg *et al.* (2000), we find that increasing the number of species initially present in a community, *k*, leads to an increase in the probability that the random removal of a species from the system will lead to further extinctions from that community (figure 1*a*).

We can also see from figure 1*a* (parameter values from the logistic equations are shown in table 1) that there is a clear reduction in the likelihood of communities with more complex dynamics to lose further species after the initial random species removal. The model type that shows the lowest probability of cascade extinctions relative to the baseline model is that which includes the opportunity for beneficial interactions to occur, rather than only harmful competitive interactions. The introduction of this sort of complexity can clearly be seen to stabilise the community to the described perturbation, relative to a community lacking this form of interaction. Introduction of other forms of dynamical diversity to the system, namely species specific growth rates and delayed density-dependence, also leads to a relative reduction in the probability of cascade extinctions occurring, although not to the same extent as the inclusion of beneficial interactions. It should be noted that each new version of the model addresses only a single dynamical change from the baseline model, and they do not represent an accumulation of factors of increasing dynamical complexity.

This result can be shown to be highly robust, by comparing the regression lines of the different model types (fig. 1*a*), and by looking at their Likelihood-Ratio statistics [analyses carried out using the SAS system (1997)]. While there was no significant interaction between community size and model type, we find that both do have a significant effect on the regression lines of different model types (community size: ^{2} = 904.36, 1*d.f.*, $p < 0.0001$; model type: ^{2} = 154.11, 3*d.f.*, $p < 0.0001$). Furthermore, introducing complexity to the model as described above can be shown to lead to a significant difference in the regression lines between all of the new model types compared to the less complex model (^{2} = 47.68, 1*d.f.*, $p < 0.0001$). This result remains statistically significant after correction for overdispersion (e.g. Crawley 1993).

Table 1a: Logistic equations for probability of cascading extinctions in communities following removal of species.

Model Type	*a* (± s.e.)	*b* (± s.e.)	x^2	*p*-value
Baseline	-4.142 (0.262)	0.588 (0.038)	329.964	< 0.001
Beneficial Interactions	-4.913 (0.337)	0.500 (0.042)	164.177	< 0.001
Variable Population Growth rate	-3.944 (0.255)	0.527 (0.036)	273.454	< 0.001
Delayed Density-dependence	-3.801 (0.333)	0.471 (0.045)	140.933	< 0.001

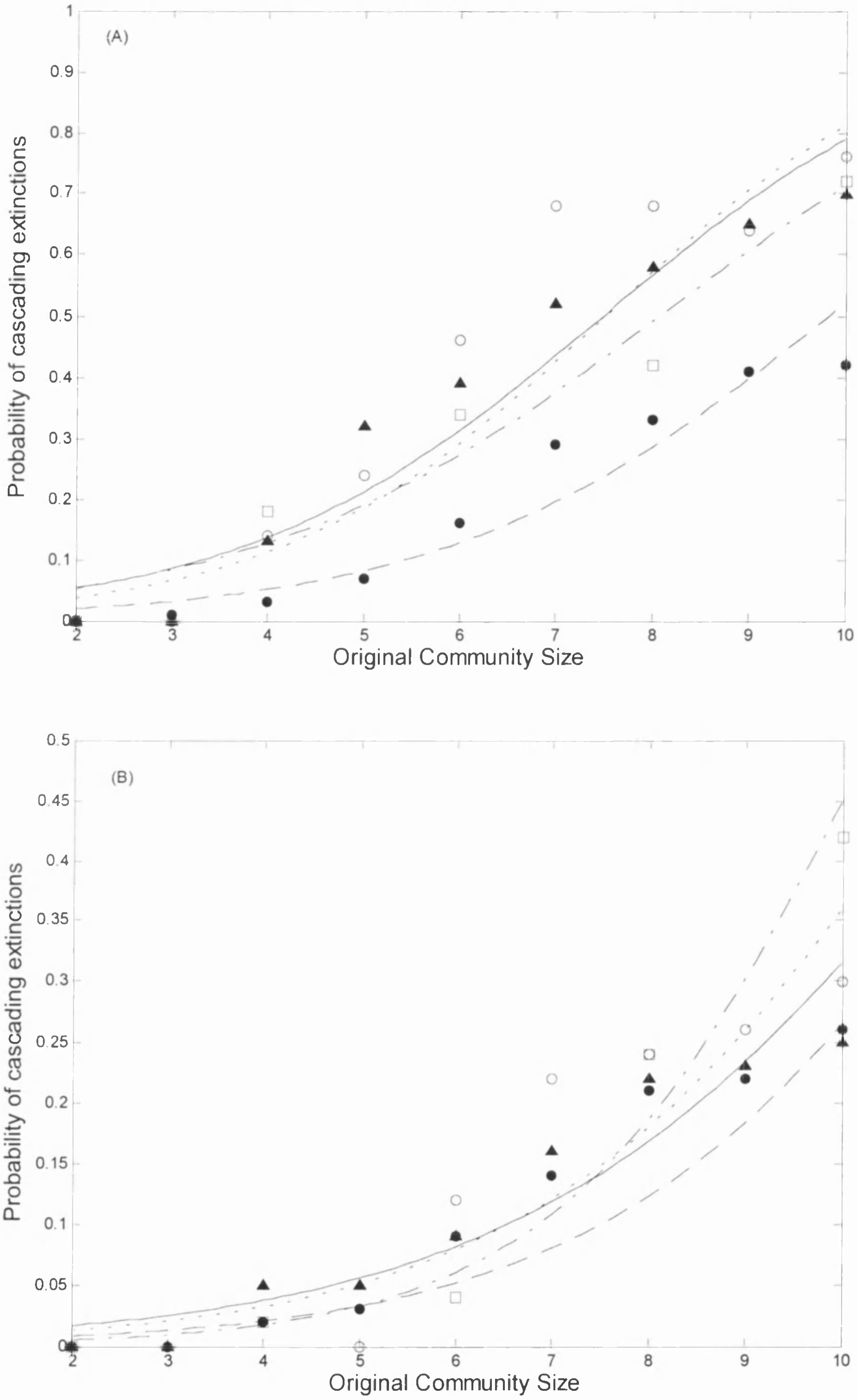


Figure 1: Probability of cascade extinction events occurring following the removal (1*a*) and reintroduction (1*b*) of one species from multispecies communities of different sizes. Models representing four different types of dynamical diversity, the simplest baseline model, a model

including beneficial and harmful interactions between species, one where each different species has a unique population growth rate and a model where the dynamics of half of the community are under the influence of delayed density-dependence, have had logistic regression lines fitted as follows: [Note the different y-axis scale in panels (*a*) and (*b*)]

$f(k) = \frac{e^{\alpha+bk}}{1+e^{\alpha+bk}}$. Baseline model: ○ (dotted line); Beneficial & Harmful interactions: ● (dashed line); Variable population growth rates: ▲ (solid line); Delayed density-dependence: □ (dash-dot line).

Reintroduction of the removed species:

Again, we find an increase in the probability of cascading extinctions occurring with an increase in the size of the community, upon reintroduction of the species that was previously removed (fig. 1*b*). Under these circumstances, however, there is no corresponding difference in the stability of the community with increased dynamical diversity in the model except in large original community sizes. Interestingly, with large *k*, including delayed density-dependence in the model appears to increase the propensity of cascading extinctions after the reintroduction of the originally removed species compared to the baseline model, although analysis of the regression lines of the different model types reveals that while there is still no significant interaction between community size and model type there is a significant effect of community size (χ^2 = 153.36, 1*d.f.*, p < 0.0001). Contrary to the findings after random species removal, regression lines of the probability of further extinctions after the reintroduction of the removed species are not significantly affected by model type (χ^2 = 1.73, 3*d.f.*, p = 0.6297).

Table 1b: Logistic equations for probability of cascading extinctions in communities following reintroduction of removed species.

Model Type	a (± s.e.)	b (± s.e.)	x^2	p-value
Baseline	-5.275 (0.390)	0.470 (0.048)	104.119	<0.001
Beneficial Interactions	-5.479 (0.428)	0.473 (0.052)	92.192	<0.001
Variable Population Growth rate	-4.893 (0.392)	0.412 (0.049)	80.437	<0.001
Delayed Density-dependence	-6.567 (0.625)	0.637 (0.071)	108.697	<0.001

2) OVERALL STABILITY

To study whether an unstable community (i.e. a community that has lost at least one further species after the random removal event) is more likely to lose additional community members after reintroduction than a community where no additional extinctions happened after the first species removal, we looked at the occurrence of four different scenarios: (a) No cascading extinctions occur upon removal or re-introduction of a species, (b) Cascading extinctions occur only after the reintroduction of a previously removed species, (c) Cascading extinctions occur only after the removal of a species and (d) Cascading extinctions occur after both the removal and reintroduction of a species from the community. These frequencies were then compared using Fisher's Exact test (significance levels shown in table 2).

Two and three species communities were not included in the analyses, as extinction events never occurred in these very small communities.

Table 2: Results of Fisher's Exact test testing for the connection between original community stability after a removal event and the probability of further cascading effects following reintroductions.

Initial community size	p-values for different models			
	Baseline	Beneficial interactions	Variable population growth rate	Delayed density-dependence
4	0.14	0.002449	0.14	0.18
5	1	0.001786	0.4	-
6	0.006353	<0.001	<0.001	0.002149
7	<0.001	<0.001	0.006353	-
8	0.005119	<0.001	<0.001	<0.001
9	0.001637	0.006385	0.008549	-
10	0.022168	0.00137	<0.001	<0.001

The results shown here (table 2) indicate a positive relationship between the probability of cascade extinctions occurring after one species has been removed from the system, and further extinctions occurring upon reintroduction of that species (all the statistically significant deviations from randomness in the contingency tables were in this direction). Where removal of a species from the community does not lead to further species loss, we have found that cascading extinction will never occur upon reintroduction of this previously removed species. Thus, we can say that the small communities tested here (4 and 5 species) do not appear to show any difference (with one exception, see below) to a random chance of cascading extinctions occurring following a reintroduction event if there were cascading extinctions after removal events. As we gradually increase community size, we find consistently stable, or unstable communities, when faced with different forms of perturbation. In other words, a community that has lost member species after it has been disturbed by the forced removal of a random species, is more likely (than random chance) to lose more members upon the reintroduction of the previously removed species. A community that remains stable (does not lose further species) after a forced removal event will never lose further species upon reintroduction of the removed species. This result holds true across all model types tested, with the exception of communities with beneficial interactions, where even small communities show a high likelihood of maintaining stability (or instability) following different types of disturbance.

Discussion

In this study, we present theoretical evidence that supports the long held empirical view that increasing complexity in a system leads to an increased robustness of the community to disturbance (MacArthur 1955, Elton 1958, Hutchinson 1959, Cottingham *et al.* 2001), which can be viewed as an increase in its stability, and contrasts with theoretical predictions that increasing community complexity leads to a reduction in stability (e.g. Haydon 1994, Lundberg *et al.* 2000). By introducing a wider range of possible interaction types between species, i.e. both beneficial and harmful, we show that a relative reduction in the probability of cascading extinctions results when one species is removed from a multispecies community model.

Introducing other aspects of dynamical diversity to the community, either by allowing different species to show different population growth rates, or by introducing delayed density-dependence into half of the species in the community, were also found to lower the probability of cascading extinction, in comparison to the less complex model, but not to the same degree as including beneficial interactions. Further, we show that re-introduction of the previously removed species does not necessarily produce the same outcome, with increasing dynamical differences between species not necessarily leading to a relative decrease in probability of cascading extinction events. Finally we demonstrate that communities are likely to retain underlying stability characteristics (either the maintenance of remaining community members, or the loss of members) when subjected to different types of disturbance.

One particular aspect of this result worthy of further discussion is the only difference that arises between the different model types in comparisons of overall community stability. Small communities (four and five species) with beneficial interactions tend to show consistency in their stability properties, whereas other model types tested do not show this at these small community sizes. This result may re-inforce our finding that introducing this type of complexity into the model has the most stabilising effect.

While the work by Lundberg *et al.* (2000) does highlight interesting phenomena, in particular that the loss of a single species from a community can lead to further degradation of species richness from the system, perhaps the most important finding in terms of conservation, is the fact that species re-introduction will often be unsuccessful, and even highly detrimental to the remaining community members. This occurs in a community that, when including the subsequently removed and reintroduced species, was previously stable. However, it is very important to consider these models in context. Lundberg *et al.* (2000) suggest that by increasing the number of species in their community, they are increasing the complexity of the system. However, the dynamics of individual species in the community are determined by exactly the same removal process, a situation that is extremely unlikely to occur in natural systems. Thus, it may be argued that increasing the number of species does not necessarily increase the complexity of the community, rather it merely increases the availability of species that can be lost from the system.

We would like to emphasise that our results do not contradict those found by Lundberg *et al.* (2000), rather they highlight the importance of clearly defining the measurement of community diversity and complexity. While some studies have noted the positive effects of diversity on stability in empirical work (see Schlapfer & Schmid 1999 for a comprehensive review), it has been suggested that this positive relationship is a statistical inevitability of the method used to measure stability (Doak *et al.* 1998). While our results do not seem to confirm this positive relationship at first glance, with the probability of extinction increasing with species number, we do not simply equate the community size in our model to complexity: In the less complex model there is very little actual difference between the dynamics governing the different species present in the community, changing only in their competitive ability (-values). Horizontal interactions in food webs (i.e. competition within a single trophic level) are thought in some cases to be as important a factor in determining community dynamics as vertical interactions (Fryxell & Lundberg 1998), and so should not be discounted as a source of diversity in a community.

To allow appropriate comparison both within and between empirical and theoretical studies, the concept of stability in both theoretical and empirical studies should be carefully defined (Grimm & Wissel 1997). The nature of stability in the present study can be viewed under two of Grimm & Wissel's (1997) proposed stability properties; namely resilience of the system to the disturbance of having a community member forcibly removed, and persistence of the resultant community upon reintroduction of this species. Thus, we are studying two different, but closely related phenomena. The question of temporal scale is fundamental to solving problems associated with defining stability in natural assemblages; what represents a stable community under natural conditions? Many natural populations are known to show temporal fluctuations, therefore, comparing the state of population dynamics after some disturbance event should only be done in full knowledge of the state of temporal population dynamics prior to the perturbation. In this study, we overcome these problems, and others such as transient growth following disturbance (e.g. Hastings & Higgins 1994, Neubert & Caswell 1997), by examining a long enough time period such that any transient behaviour has settled before we take our measure of stability, the loss of a species after the community has settled to either the original state, or a new equilibrium state with fewer species present.

In the present study, we start by looking at a highly simplified, theoretical representation of a multispecies community. This system is then perturbed by the "forced" removal of a single community member, and the response of the rest of the community to this perturbation is recorded. This method has been used in field trials, where selective removal of dominant and subordinate species produced differences in response over time (Viragh 1989). Further theoretical study of this sort may support this finding (chapter VIII). Finally, in the present model, re-introduction of the removed species causes a further perturbation, sometimes leading to further cascading extinctions. As mentioned above, this result should be kept in mind when developing re-introduction programmes for species that have been previously removed from an environment. This is especially true if further extinction events have occurred within the community since the loss of the species that is to be reintroduced. Our findings highlight the danger of attempting a reintroduction into this kind of unstable community, which is likely to lead to an unsuccessful recolonisation and/or the loss of further community members.

The introduction of beneficial interactions to the model does lead to a demonstrable relative reduction in the probability of extinctions, when compared to a model with only harmful interactions. However, the inclusion of such beneficial interactions still does not lead to an explicit expression of resource, a point that should be addressed in the future. Interaction co-efficients clearly play an important part in determining stability properties in this model, as in two cases this is the only parameter that varies between species. There are various studies that do directly examine interaction strength (e.g. May 1972, McCann *et al.* 1998), showing that weaker interactions tend to lead to stabilisation of communities. It is also worth emphasising that apart from interaction strengths, other qualities of the interactions, such as the differences between their strengths (Hughes & Roughgarden 1998), their trophic position in a food web (de Ruiter *et al.* 1998), and their response to environmental factors (Ives *et al.* 1999), can have an important role in determining the community stability.

While the model and results presented here may at first appear limited in their relation to natural systems, the fact that we find ourselves in agreement with many empirical studies (e.g. Death 1996, Schlapfer & Schmid 1999, but see Rodriquez & Gomeszal 1994 for opposing evidence) and some recent theoretical studies (Harding 1999, Lehman & Tilman 2000) indicates the value in the further study of such systems. The need for further empirical work to answer questions of how community complexity affects stability was highlighted some 30 years ago in an important introduction to theoretical analysis on this matter by May (1973). Since then, the advances in community models have not been matched by further evidence from empirical studies. Thus, controlled experiments are needed to directly address the question of stability in systems of varying complexity, as there are very few concrete examples of such work (but see Collins 2000, for one such example), with many previous arguments based on anecdotal evidence. Future studies of both natural and theoretical systems should carefully classify not only the type of stability being addressed, but also the nature of varying complexity or diversity that is present in the community.

THE EFFECTS OF SPACE AND PATCH NUMBER ON COMMUNITY PERSISTENCE

ABSTRACT

Between-species interactions are known to have important ecological implications. Removal of a single species from a community has been shown to have detrimental effects to community persistence, with cascading extinctions often resulting (Paine 1966, Borrvall et al. 2000, Lundberg et al. 2000). Here we asked what effect introducing dispersal of individuals between different patches would have on the stability of communities in a perturbed environment, in terms of community assembly and species loss. This was studied in two different spatial contexts. Firstly through allowing communities to develop over a number of linked patches in the environment and secondly studying the effects of habitat fragmentation (through division of a single patch, with associated reduction in carrying capacity of patch fragments). Results indicated differences between the distinct types of spatial frameworks tested. While there did not appear to be any difference in stability properties between a single unconnected patch and between 2 and 50 connected, randomly positioned patches after the removal of one community member, fragmenting the habitat had seriously detrimental effects. The implications of these results are discussed in the context of the management of natural populations.

Introduction

The question of whether dynamical or evolutionary differences will arise in populations due to their arrangement in the environment is one that has been considered by ecologists for some time (e.g. Skellam 1951, Andrewartha and Birch 1954, Huffaker 1958, MacArthur and Wilson 1967). Comparing the results of models that describe population dynamics in a single patch to populations that are spread over more than one patch (where these patches are linked through dispersal of individuals between the discrete patches) has been of considerable interest recently (Gilpin & Hanski 1991, Hastings 1993, Rohani *et al.* 1996, Ruxton 1996*a*, Lehman and Tilman 1997 and many others). The outcomes of such studies have shown a complete range of dynamical behaviours. Rohani *et al.* (1996) revealed that there may be no effect of individuals dispersing between patches on population dynamics, while other studies have found that population dynamics can be stabilised when there is a spatial component to such models, with a common finding being that the introduction of space leads to an increase in dynamical stability or persistence to some degree (Taylor 1990, Hastings 1993). It has also been demonstrated that there may be conditions under which the introduction of space to a simple dynamical model can be destabilizing (Bascompte & Solé 1994 - but see Hassell *et al.* 1995 and Ruxton 1996*b* for a critical discussion of these results). The results of these and similar studies have many important implications, such as in the management and designs of natural reserves (Bogaert *et al.* 2000, Collinge 2001), or in optimal harvest theories (Cohen 1987, McCullough 1996, Jonzén *et al.* 2001). The interactions of different species in a community are also of considerable interest to ecologists, and many attempts have been made to model such systems, with important early work carried out by May (1973) and Levin (1974). The focus of investigations on organisms competing on the same trophic level serves as a reminder that while horizontal interactions are of undoubted importance within such species assemblages, the significance of vertical interactions must still be emphasized (Fryxell & Lundberg 1998). Rohani & Ruxton (1998) have recently demonstrated destabilising effects of density independent dispersal on the dynamics of a 2-species system. The following study will look at community level stability in terms of assembly and extinction events, rather than explicitly dynamical processes, in this way.

Our study can be viewed as an extension of previous work by Levin (1974) and Lundberg *et al.* (2000), who have studied community interactions in different ways. Levin (1974) used a continuous time model to study co-existence of competitors subject to disturbance, while Lundberg *et al.* (2000) studied the effects of species removal and reintroduction on community persistence in a discrete time single patch model. Both works suggested that community stability would decrease with increasing community complexity. Our work differs in that we use a discrete rather than a continuous time model and, importantly, Levin's assumption that interspecific competition always outweighs intraspecific competition has been relaxed. Furthermore, we went on to study the effects of living in a patchy environment, with dispersal between different habitat patches. Some previous studies (Crawley 1990, Tilman 1994) utilised metapopulation type community models where co-existence of any number of species is facilitated in a spatial environment through an interspecific trade off between competitive and dispersal ability. An important difference between our work and such studies is the patch occupancy rule used. In the case of the family of metapopulation-like models (Lehman & Tilman 1997), within patch dynamics are not considered explicitly, whereas our model draws upon the outcome of such within-patch processes to produce the results. Thus, we present a model here in which species of different competitive ability can co-exist in local and global populations without different dispersal abilities being a prerequisite. Furthermore, we studied the effect of the number of patches present in the environment, using a realistic dispersal rule, asking whether differences in community stability arose when these communities are allowed to developed within a spatial environment compared to a non-spatial (single patch) model. Specifically, we wanted to address the influence of space in general and patch number in particular on the ability to form a stable community after many generations and to assess the persistence of such a community, in terms of extinction probabilities, following different forms of disturbance; namely habitat fragmentation and forced extinction events.

The Model

To investigate the difference between a spatially structured model and one that lacked any spatial structure we simulated different community sizes positioned over a different number of patches. In all structured community models here we applied a Ricker-type (Edelstein-Keshet 1988) growth model with Lotka-Volterra competitive interactions between *k* species as outlined below (eqn. 1). In our comparison of a spatially structured model with a non-spatially structured (or single patch model) we have chosen to use a Ricker-type equation as it allows for such flexibility without considerable re-working of the terms contained within the equation.

$$N_{t+1,i} = N_{t,i} e^{r\left(1-\sum_{j}^{k} \alpha_{i,j} N_{t,j}\right)} \tag{1}$$

Another reason for this choice is the comparison we intended to do with the Lundberg *et al.* (2000) study. To simplify this comparison we used the same growth-equation that they employed.

Therefore, population density, N was calculated for successive generations (t+1) given knowledge of the current population size (N_t). The intrinsic rate of population growth, r, was held constant for all species (i) (r = 1.75 under most circumstances or 2.25 when cyclic populations were being studied) and $\alpha_{i,j}$ was the species-specific competition co-efficient, a measure of relative competitive ability of species i in relation to species j.

All species in the community had a strict competition interaction free from predation; this competition was for a common implicit resource. The interaction strengths (α-values) between all species were constructed by randomly assigning positive values for each between-species interaction with all other species in the community, i.e. mutualistic relations could not arise. The α-values were drawn independently from a continuous uniform distribution with limits [0,1] and intraspecific interaction strength for all species = 1. Thus, the strongest possible influence was always due to within species interactions, while an α -value of zero indicated no interaction at all between two species. Between species interactions were asymmetric, therefore we made the assumption that species i might have a more negative influence on species j than species j has on species i. A new α-matrix was constructed for each new simulated community iteration (eqn. 2).

$$\alpha = \begin{pmatrix} a_{1,1} & a_{1,2} & \cdots & a_{1,k} \\ a_{2,1} & a_{2,2} & \cdots & a_{2,k} \\ \vdots & \vdots & \ddots & \vdots \\ a_{k,1} & a_{k,2} & \cdots & a_{k,k} \end{pmatrix} \qquad (2)$$

(i) Introducing Space: Random patch placement.

We introduced an explicit spatial structure to the model by positioning n population patches randomly around the environment. Population renewal was governed according to equation 3, which is of the same form as equation 1. However, we have now added an explicit spatial structure to the model. Thus the population densities of k species in each patch in the environment (p = 1,2...n) were calculated as follows:

$$N_{t+1,i,p} = N_{t,i,p} e^{r\left(1-\sum_{j=1}^{k} a_{i,j} N_{t,j,p}\right)}, \qquad (3)$$

where a fixed fraction (m) of the population migrated between patches p and q following reproductive bouts every generation (eqn. 4), according to an exponential dispersal kernel (eqn. 5).

$$N_{t+1,i,p} = (1-m)F\left[N_{t,i,p}\right] + \sum_{q=1,q\neq p}^{n} M_{p,q(t)}\ , \qquad (4)$$

where $F[N_{t,i,p}]$ = eqn. 3.

The proportion of migrants of each species moving between patches p and q is defined below (eqn. 5).

$$M_{p,q(t)} = mF\left[N_{t,i,p}\right] \frac{e^{\left(-cd_{p,q}\right)}}{\sum_{p,p\neq q} e^{\left(-cd_{p,q}\right)}}\ . \qquad (5)$$

The constants m and c describe the proportion and characteristic distance emigrated by migrants and $d_{p,q}$ is the distance between patches p and q. Community size (k) is varied between four and eight species, with patch number(s) varying from one to fifty patches.

We carried out a comparison between communities developed in a homogeneous environment (all patches are of the same quality over space and time) and those developed in a spatially heterogeneous environment. Here patch quality was determined by multiplying the density of each species in the patch by a factor drawn from a normal distribution μ,σ =? (1, 0.1). Patch quality affected the density of each species after immigration had taken place, during reproduction.

Stable k-species communities were assembled following random construction of the (k by k) α-matrix by allowing populations to renew for 1000 generations to reveal any instabilities, each species being initiated at a density of $1/k$. Simulating communities for this length of time overcomes the possibility of transients influencing results. After 1000 generations, the final community size was compared to the original community size (k) and the α-matrix was accepted as producing a stable community if they were equal. If the final community size was less than k, the process was repeated by assigning new random values to the α-matrix and following the procedure as above, until the desired stable community was found. An extinction threshold was set at a density of 10^{-6} of the carrying capacity (scaled to unity in this model - sensu Lundberg *et al.* 2000). Any species population density falling below this value was considered to be too low for successful species survival and reset to zero.

(ii) Forced Species Removal

Once a stable community had been found, one species was chosen at random and removed from the community by setting it's population size to zero in all patches at t = 1000. The community was then allowed to renew for a further 1000 generations. After this time the final community size (number of remaining species) was recorded with cascading extinction events noted. Species were considered extinct if their density fell below the extinction threshold in all patches in the environment, i.e. they were globally extinct. The whole process was repeated for 100 iterations, allowing the probability of extinction events to be calculated. As a further test for sensitivity of community persistence to disturbance, we repeated the process as described above, but decreased the density of the randomly chosen species to an artificially low level (2×10^{-6} in all cases) rather than removing it completely.

(iii) Fragmenting the environment

To assess the effects of fragmenting a single habitat patch into s habitat fragments, we took a k-species community that is stable after 1,000 generations in a single unconnected patch. At this point the community renewal process was updated to simulate the effects of habitat fragmentation (eqn. 6). To do this we divided the multi-species density feedback component of the population renewal process by a factor representing the number of habitat patches that resulted from the fragmentation process ($K = 1/n$).

$$N_{t+1,i,p} = N_{t,i,p} e^{r\left(1 - \frac{\sum_{j=1}^{k} a_{i,j} N_{t,j,p}}{K}\right)} \tag{6}$$

This method was chosen as it most closely resembles the original form of the Ricker model that the communities are based on.

Our aim in this study is to demonstrate the effect on both community assembly and persistence after perturbation of a previously stable community through habitat fragmentation, enforced species removal or rarity through harvesting. The number of attempts taken to find a stable community is likely to be influenced by the number of species in the community, and perhaps also by the number of patches in the environment. Finally, we asked how these different measures of stability would change when the community was spatially structured compared to a community existing on a single patch.

Statistical analysis on the following results was carried out with SPSS for Windows release 9.

Results

Cascading extinctions in Spatial vs. Non-Spatial models.

(i) Species removal.

We began by studying the effect of finding a k-species community that was stable after 1000 generations in a single patch, and removing a random species, then recording future extinction events. The same k-species community [with identical competition co-efficients (α-values)] was then positioned on a given number of randomly positioned patches that were linked through dispersal and allowed to regenerate for 1000 further generations before the same (randomly chosen) species was removed from the community. Extinction events were again noted and compared to the original single-patch version of the model to see if rescue events could take place. The results clearly showed no effect of allowing dispersal of individuals between different patches. If the species removal cause (no) extinction events in a single-patch community, removal of the same species when there are multiple patches in the environment produces an identical outcome (figure 1), regardless of the diffusion rate (m).

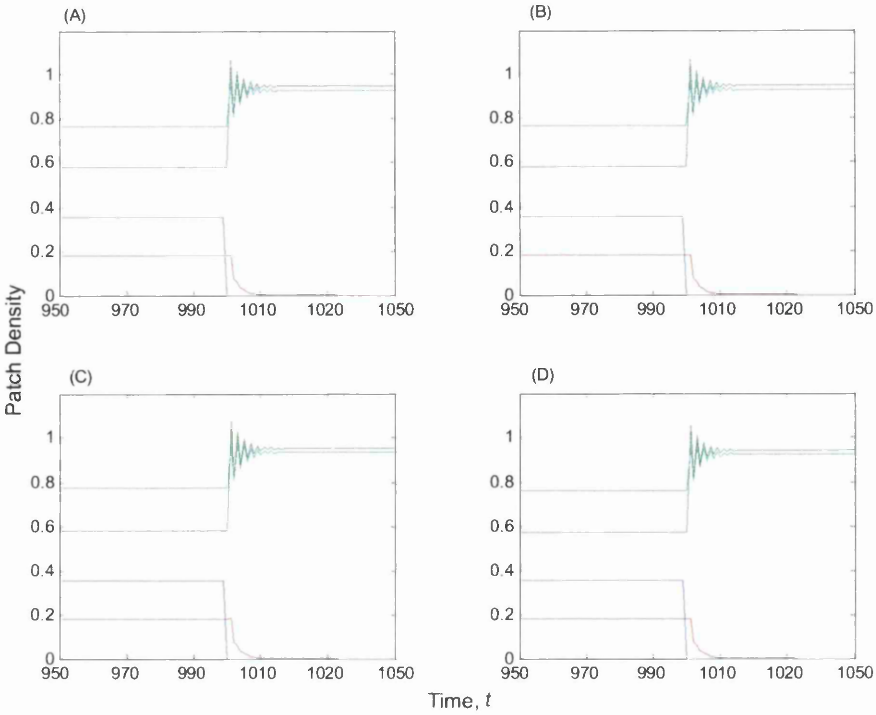


Figure 1: Placing a stable one-patch four-species community in space had no effect on extinction probability after a species was forcibly removed. If the removal of one species in a community based only on 1 patch led to further species loss (fig. 1*a*), positioning the same community over a number of patches linked through dispersal will not change the outcome (figs. 1*b* - *d*). In the case shown here, the community has been placed over 3 patches that are linked through diffusion (i.e. fig. 1*b* shows the population densities of the different species in patch one in the environment, 1*c* shows densities in patch 2 and 1*d* shows densities in patch 3; m = 0.01). We can see that the dynamics are almost identical in all cases and no rescue effect takes place if another species tends towards extinction after the disturbance event.

A direct comparison can be made with the results from the study by Lundberg *et al.* (2000), where we see the extinction probabilities in our single-patch model match closely the predictions made in their single-patch model. We used a global extinction criterion for simulations run in multi-patch environments to assess the probability of cascading extinctions occurring. Analysis of results shows that after 2000 generations, isolated extinctions of individual patches did not take place within a spatial environment - i.e. when cascading extinctions do take place they will always be global. In 100 iterations of the model, extinction events were recorded in 16 randomly formed communities regardless of the number of patches in the environment. The same result was found even when spatial variation in patch quality was introduced (figure 2). Once again, cascading extinctions that occurred in a one-patch community still always occurred when individuals were able to move between different patches in the environment, even if the different patches varied in their quality. Increasing the maximum variability in patch quality around the mean (σ = 0.25) still did not affect the outcome. Increasing the value of the S.D. above 0.25 made it rather likely that negative values could be selected for the patch quality - an unrealistic assumption that we did not investigate here. The same results were found for four-, six-, and eight-species communities (results not shown for six or eight species communities).

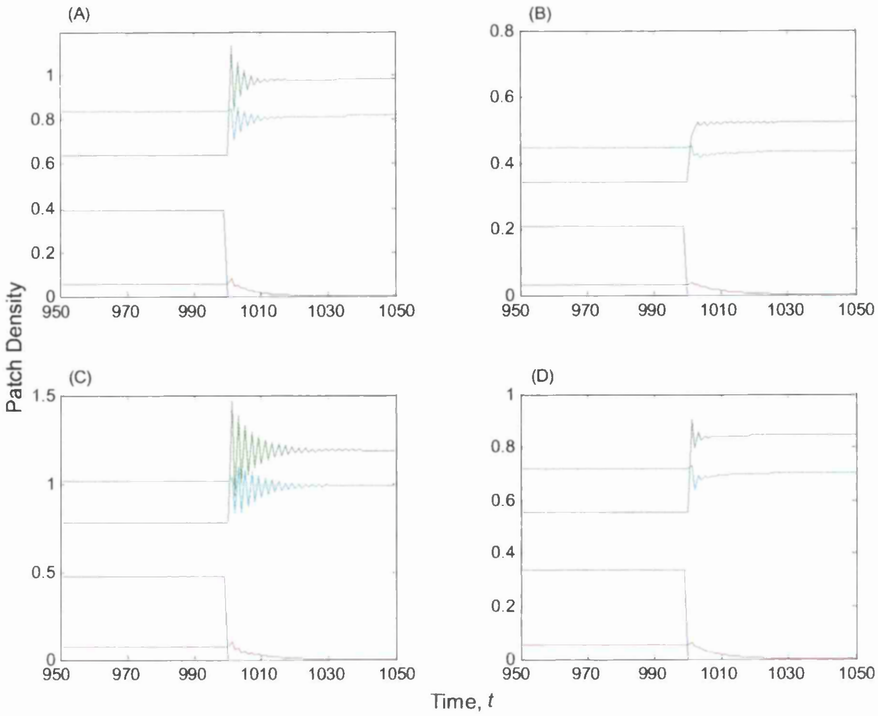


Figure 2: Cascading extinctions in communities based in a variable environment. When a stable one-patch four-species community (2*a*) was extended so that individuals can disperse between 3 patches of differing quality in the environment (2*b* - *d*: $c = 0.75$, $m = 0.1$; each individual patch's quality is based on random numbers chosen from a normal distribution: $\mu = 1$, $\sigma = 0.25$), cascading extinctions still occur after the forced removal of one species from the community. Likewise, if further extinctions did not occur after species removal in a single patch, the introduction of space will not influence the results. These results hold across all patch numbers tested (2 to 50 patches in the environment).

Varying the parameters associated with dispersal, namely c and m, can also be shown to have little or no effect on the probability of further cascading extinctions. By varying c, we can directly change the shape of the dispersal kernel. When $c = 0$, dispersing individuals are distributed equally around all patches in the environment, regardless of the distance from their natal patch. Increasing c gradually above 0 means more of dispersers will travel shorter distances, with fewer travelling to patches far away from their natal patch. When $c = 1$, the majority of dispersers will settle in the patches closest to the natal patch, with very few travelling longer distances. We selected a four species community based on ten patches in the environment that was stable after 1000 generations with parameter values $m = 0.1$ and $c = 0$ (all dispersers are distributed evenly amongst all patches). The probability of further extinctions after a forced species removal did not change when the same community was run (on the same patch positions) whilst varying c from 0 to 1 (values of further extinction probability = 0.16 for all values of c tested). Furthermore, varying the diffusion rate (m) had no effect on the probability of cascading extinction events occurring, with only very high diffusion rates showing a slight (though non-significant) increase in extinction probability ($c = 0.75$; while $m = 0$ to 0.8, extinction probability = 0.16; $m = 0.9$ or 1.0, extinction probability = 0.2; Kruskal-Wallis statistics: $\chi 2 = 0.845$, 1*d.f.*, $p = 0.358$).

We next asked what happened if different communities were allowed to develop according to the number of patches present in the environment. We see from figure 3 that again there was little effect on the relative probability of further extinctions occurring by allowing dispersal between patches positioned randomly in the environment. This is supported by the results of logistic regressions on the probability of further species loss after 100 iterations of the model, which show no significant effect of the number of patches on the probability of cascading extinction events in a community (*table 1*).

Table 1: Logistic regression analysis of probability of cascading extinctions in different sized communities (1 *d.f.*; R^2 values are Nagelkerke R^2; p values based on Wald statistic).

Community Size	Number of Patches in the Environment							Logistic Regression	
	1	2	4	9	16	25	50	R^2	p
Stable Dynamics ($r = 1.75$):									
4	0.18	0.16	0.13	0.14	0.22	0.15	0.21	0.002	0.250
6	0.49	0.38	0.50	0.53	0.48	0.46	0.47	0.000	0.961
8	0.63	0.66	0.68	0.62	0.66	0.58	0.67	0.000	0.991
Cycling Dynamics ($r = 2.25$):									
4	0.17	0.21	0.14	0.27	0.13	0.17	0.14	0.001	0.778
6	0.43	0.44	0.49	0.48	0.43	0.41	0.36	0.006	0.992
8	0.68	0.71	0.64	0.56	0.70	0.63	0.71	0.001	0.602
Harvesting (Population density forced to 2×10^{-6}):									
4	0.16	0.18	0.22	0.14	0.15	0.21	0.15	0.000	0.700
6	0.32	0.37	0.30	0.30	0.31	0.29	0.35	0.000	0.923
8	0.56	0.58	0.64	0.52	0.52	0.46	0.52	0.005	0.123

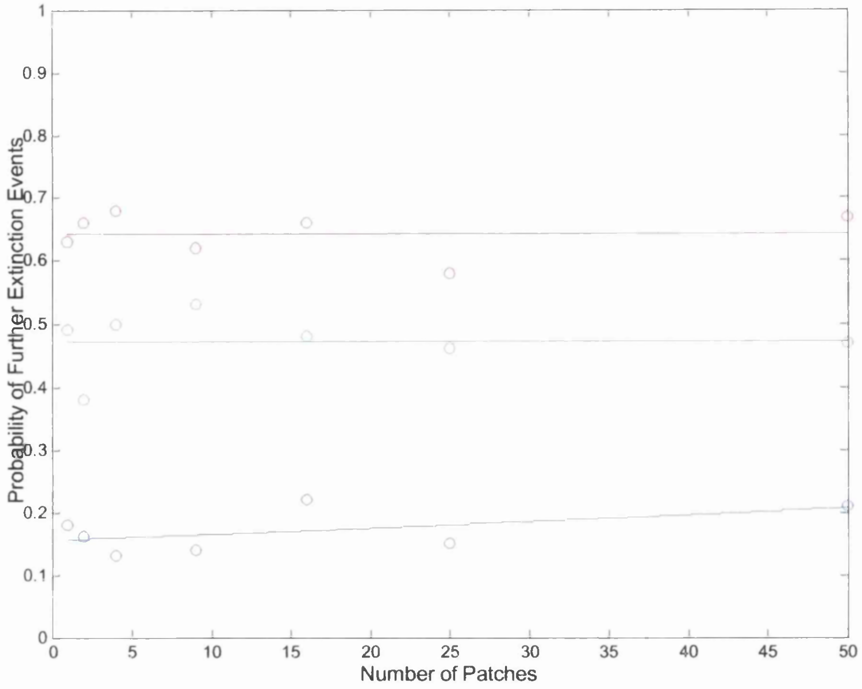


Figure 3: Extinction events in communities linked by dispersal (*m* = 0.01, *c* = 1). Simulations of competitive multispecies communities were run 100 times each for different sized communities on habitats composed of different numbers of patches, with the probability of further extinctions occurring after one species was completely removed plotted for each community size tested (blue = 4 species; green = 6 species; red = 8 species). Logistic regression lines are also plotted, revealing no significant trend with increasing the number of patches in the environment.

Similar non-significant results arose when the population dynamics of all species in the community fluctuated over a two-point cycle (Fig. 4, *table 1*). Two-way ANOVA's looking at the effect of the form of dynamics (stable vs. cycling) and the number of patches in the environment (within different community sizes) showed no significant effects of either factor on the frequency of species loss after species removal, and no significant interaction between these two factors.

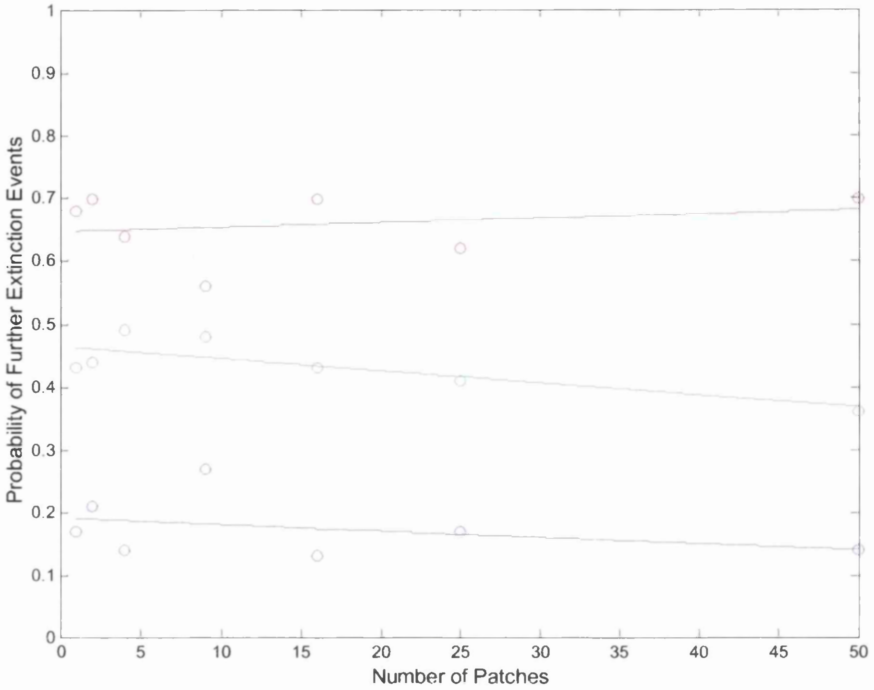


Figure 4: As figure 3, but this time parameter values were chosen to yield dynamics fluctuating over a 2-point cycle (*r* = 2.25). Again, there was no significant effect of the number of patches in the environment on the probability of further species loss after disturbance through forced removal of a community member.

The frequency of extinction events between communities with stable equilibrium dynamics and those with fluctuating dynamics was compared using χ^2 (6 *d.f.* in all cases). This showed that small communities may experience a slightly higher frequency of cascading extinction events after forced species removal when the dynamics of all species in the community fluctuate over a two-point cycle (4 species: $\chi^2 = 17.546$, $p = 0.007$ - although this result should be treated with caution - there is little obvious trend in either direction). However, there was no difference in the frequency of further extinctions after forced species removal in 6 (χ^2 = 6.749, p = 0.345) or 8 species communities (χ^2 = 2.463, p = 0.873).

(ii) Species Rarity.

We went on to manipulate the population densities without entirely removing the species. Therefore, we removed a species almost entirely, by saving only a fraction of the population, distributed equally over all patches (species densities were reset to $2\text{x}10^{-6}$ in each patch). The results from this analysis (figure 5) showed that once again there was no effect of space on the probability of further species loss from the community upon the introduction of space. We compared the frequency of species loss after this type of disturbance and species loss after a forced extinction event using a two-way ANOVA. This tested the effect of patch number and either complete or partial species removal. Here we found that while there was no significant difference between small communities (four species: effect of patch number - $F_{6,13}$ = 0.425, p = 0.863; effect of complete removal vs. harvest; $F_{1,13}$ = 0.372, p = 0.542), there was a significant difference in the frequency of extinction events following intensive harvesting in medium sized and larger communities (six species: effect of patch number - $F_{6,13}$ = 0.112, p = 0.995; effect of complete removal vs. harvest; $F_{1,13}$ = 748.776, $p < 0.001$; eight species: effect of patch number - $F_{6,13}$ = 0.776, p = 0.589; effect of complete removal vs. harvest; $F_{1,13}$ = 16.86, $p < 0.001$), tending towards a reduction in extinction events following harvesting rather than complete removal. There was no significant interaction between the number of patches in the environment or the effect of different types of disturbance (complete vs. partial removal) in any of these cases.

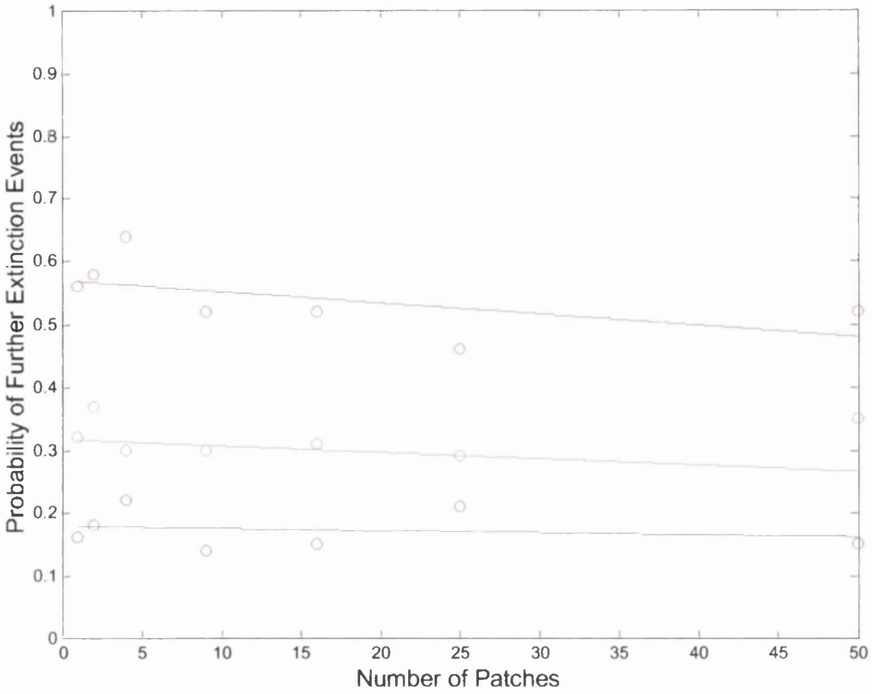


Figure 5: Intensive harvesting of species will also lead to cascading extinction events, and once again, connecting different patches in the environment will not significantly alter the probability of cascading extinctions. Figure details as figures 3 & 4.

(iii) Habitat Fragmentation

Fragmenting the environment in which a community has successfully established is found to be extremely destabilising, with more extinction events occurring the more the habitat is divided (figure 6), even when habitat fragments are linked by dispersal.

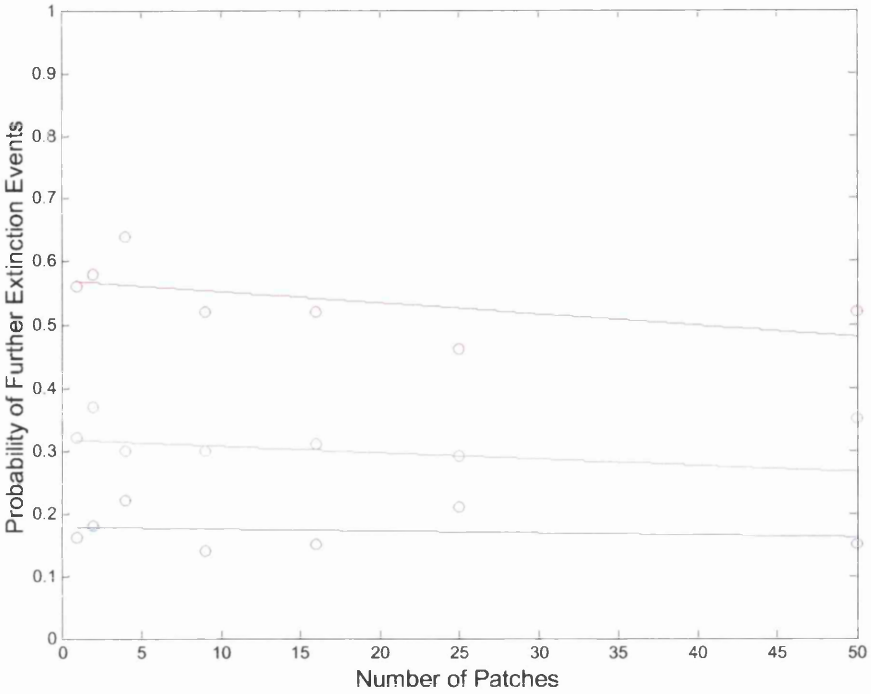


Figure 6: Fragmenting the habitat decreases the probability of a community becoming established, even when the habitat fragments are connected by dispersal (4 species community; Blue circle & line: c = 0.75, m = 0.01, Logistic regression: R^2 = 0.621, $p < 0.001$; Red star & line: c = 0.75, m = 0.1, Logistic regression: R^2 = 0.654, $p < 0.001$; 6 species community; Green triangle & line: c = 0.75, m = 0.01, Logistic regression: R^2 = 0.785, $p < 0.001$).

By finding a community that had successfully established after 1000 generations in a single patch, then running the same community for 1000 generations in a fragmented habitat (between 2 and 50 habitat patch fragments), we found that the probability of that same community successfully establishing in the new fragmented habitat decreased with increasing habitat fragmentation. Increasing the rate of migration between patches from 0.01 to 0.1 did not influence the results. Small amounts of fragmentation (up to four patches) did not seem to change community persistence in relatively small communities (four species); however, even minimal habitat fragmentation, i.e. dividing a single original patch into two patches, will reduce community persistence in slightly larger communities (six species). Larger community sizes were not tested due to time constraints

(iv) Community Assembly

Looking at the number of attempts required to create a stable community after 1000 generations tells us something about the community assembly process. We argue that the community assembly process was constrained purely by the random creation of the matrix containing the interspecific competition co-efficients, or by the relative positioning of patches in space. In this case (figure 7) we found that introducing an explicit spatial structure to the model does not change the assembly time taken to find a stable community. A two way ANOVA showed a significant effect of community size ($F_{2,12} = 497.527$, $p < 0.001$), but no significant effect of the number of patches in the environment ($F_{6,12} = 0.576$, $p = 0.75$), and no significant interaction between the two factors.

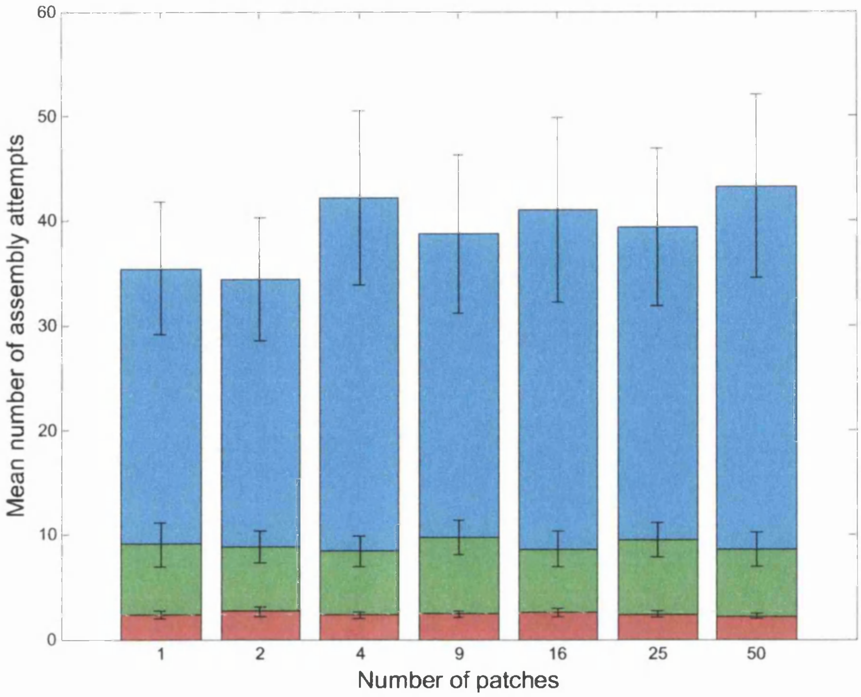


Figure 7: How long does it take to find a stable community? Larger communities took longer to assemble (red = 4 species; green = 6 species; blue = 8 species communities), but the effect of the number of patches that the community is based on was not significant. Error bars show mean ±95% confidence interval.

Furthermore, if the dynamics of individual species dynamics within the community fluctuate around a two-point cycle, there is no effect of space and dispersal on the number of attempts taken to find a stable community.

Discussion

The fact that further species can be lost from a community, as a direct result of the removal of another community member species, has been known in natural systems for some time (Paine 1966). We found the same results in the model presented here.

The relative reduction in competitive pressure did not necessarily translate to more stable communities. We have demonstrated here that no differences arose when a community was simulated under certain explicit spatial conditions; namely linking of patches in space that are either identical or variable. These results are demonstrated by disturbing communities through species suppression via either (forced) complete removal or rarity of one community member, two types of disturbance that are biologically reasonable. These results suggest that rescue effects may not always arise in competitive spatially structured communities. Furthermore, we have shown that there may be little chance of rescue effects arising when the habitat is fragmented or when patch quality varies spatially, even when species are capable of moving between different patches in the environment. This is in agreement with another study (Gonzalez *et al.* 1998) but contrary to some other findings (e.g. Holyoak 2000*b*). This finding is likely to be important in terms of conservation.

We only make a very basic attempt to analyze community assembly in this study, finding no significant effect of including space on the time taken to find stable communities. We tentatively suggest that under these circumstances it appears that patchiness does not necessarily lead to improved regional co-existence. This result supports the recent findings of Gutierrez *et al.* (2001), who studied a multispecies lepidopteran community that our model partially resembles. Varying the method of community assembly has been tested by Gilpin (1994), who found important differences arising between competing communities that form randomly compared to those that were allowed to self-organise, through a process of competitive exclusion. The invasion sequence of different community members has also been shown to have significant effects on dynamical patterns in multi-species communities (Sait *et al.* 2000).

Habitat fragmentation has been tested empirically by Davies *et al.* (2001), who hypothesised that this should lead to an increase in extinction rates within patches, although they did not find any such increase in the beetle community studied. Our results (fig. 6) also point to an increase in extinction probability when habitat fragmentation occurs, although the model presented here explicitly allows movement between habitat fragments (which is not possible in Davies *et al.*'s system). We suggest this is one reason why this finding conflicts with results of community persistence found in experimental studies by Gonzalez *et al.* (1998). An explanation why these results do not match those found in an experimental system by Holyoak (2000*b*) may be due to the fact that only horizontal (or competitive) interactions were studied here.

Asking whether the introduction of space can alleviate the pressure of competition in the environment may seem reasonable. Here we find little evidence for this, although we did not explicitly set out to address the question of space at the level of specific species. It may be possible to address this more directly by selecting stable competitive communities that have developed in a multi-patch environment and assessing whether or not the same stable community could develop when there is no dispersal between patches.

Huffaker's (1958) classic empirical work first showed the importance of spatial scale on species persistence when the species considered were interacting with another. More recently Ylikarjula *et al.* (2000) have found that when a population was linked over 25 patches by dispersal, the dynamics were qualitatively similar to a single patch system, but differed in a two-patch system. However, they found that results from a four-patch system closely resembled those of a 25-patch system, suggesting that the scale or number of patches over which a population is positioned is likely to have subtle, but important effects. When analyzing what effect the number of patches in the environment has on the probability of cascading extinctions occurring, it is important to take the dispersal kernel into account. Here we found no effect of varying the dispersal kernel on community persistence. We altered the distance travelled by dispersers by varying c between zero and one. This changed the dispersal kernel from a scenario where they were distributed equally across all patches in the environment, to one where the majority of dispersers were much more likely to travel to patches close to their natal patch than patches farther away.

Our attempt to investigate how different community structures (in terms of community size, and the number of patches in the environment) are sensitive to artificially reduced population densities, showed the risks associated with intensive harvesting pressure. This risk increases with larger communities as more severe competition occurs with a higher number of species. This may be due to the fact that the "implicit resource" within the model is sufficient for small communities (e.g. 4 species) irrespective of the number of patches, but when the number of community members increased, this resource was insufficient to sustain the community. While it has been shown that higher population densities may be possible in multi-patch communities (Wilson 1992), factors such as the Allee effect may play an important role as individuals may be dispersed among the patches at a rate independent of the population density in a given patch. Thus local extinction probabilities may increase.

It is also possible that stability characteristics of models are sensitive to initial patch conditions. In this study patches were initiated with the same starting population size for each species in each patch for each iteration of the simulation. However, varying the patch quality around the environment did not alter occurrence of extinction events. Although initial conditions seem an unlikely cause of variation, they should not be dismissed entirely as many different communities are still viable - each iteration differs in the competitive ability of the species in the community (defined by the interaction matrices). Nevertheless, Fagan (1999) finds only weak effect of initial conditions on metapopulation persistence times, placing a greater emphasis on the stronger influences of other factors such as the number of patches.

Further questions that may be addressed by this model include assessing if there is a pattern that allows us to predict which species are most likely to become extinct after disturbance events such as forced species removal, and whether the introduction of a spatial component is likely to influence this. This is looked at in a later chapter (Chapter VIII).

As mentioned in the introduction, results from theoretical studies such as the work we present here can provide important insights into management techniques for natural communities. The importance of the specific number of patches in an environment is supported by Garrabou *et al.* (1998), who note that patch number can be an important index in the description of spatial patterns in communities, and Ylikarjula *et al.* (2000) who caution against over generalising from simple population models. Other investigations such as Allen (1987) highlight the importance of the number of habitable patches in an environment, in terms of a minimum number required for a population to persist. As well as this, Jonzén *et al.* (2001) recently demonstrated the effects that harvesting species in one patch may have on other species in other patches. Our findings show that there may be an upper limit to sustainable habitat fragmentation. By dividing the environment into a large number of patches we may be consigning some species within a community to an unfavourable fate. Thus, the introduction and quantification of a spatial component to models, along with the type of disturbance experienced can be shown to have important and surprisingly variable consequences on community level processes.

PREDICTING COMMUNITY PERSISTENCE BASED ON DIFFERENT METHODS OF SPECIES RANKING

ABSTRACT

Different species in a community can be ranked according to the strength of their effect on the dynamics of the entire community. Despite a considerable research effort on community structure and the "keystone" species concept, there are still some unresolved issues in this area. We show here that removal of the most abundant species, i.e. that with the greatest relative density within the community, leads to the highest probability of community collapse, with the further loss of community members through cascading extinctions. Comparison of results based on ranking community members by either their abundance or competitive ability indicates that characterising species according to their relative density provides a more refined measure of each species importance within the community. We go on to analyze which ranked species are most likely to be involved with cascading extinction events, showing that the species with the lowest abundance is most likely to face extinction. We show that the asymmetry and non-linearity of community interactions mean that species' ranking can change unexpectedly following species loss, and stress the importance of these results in applications of such a model.

Introduction

Studies of community interactions have generated a variety of results. Interestingly, there has been a dichotomy between the findings of empirical and theoretical studies on the stability of multispecies systems (MacArthur 1955, Elton 1958, Hutchinson 1959, May 1972, Frank & McNaughton 1991, Pimm 1991, Haydon 1994, Putman 1994, Johnson *et al.* 1996, de Grandpre & Bergeron 1997). Theoretical findings have tended to point to a reduction in stability in increasingly complex systems, while empirical work has traditionally suggested the opposite. Recently, however, some models have predicted an increase in stability with increasing complexity (Harding 1999, Borrvall *et al.* 2000, Lehman & Tilman 2000, Rozdilsky and Stone 2001, Fussman & Heber 2002, Fowler and Lindström, *in press* and chapter VI of this thesis). Theory that addresses the effects of species number in interspecific assemblages at the population level has generally focused on the indirect effects across different trophic levels (Pimm 1991, Bender *et al.* 1984, Yodzis 1989). More recently, Abrams (1996) has reviewed the opportunity for evolutionary change to arise following alteration to food webs, predicting major differences in population level processes. What is of undoubted importance in studies such as these, and their practical implications, is the ability to assess the importance of each species in their respective assemblages.

A keystone species is a species with a disproportionately large influence on the abundance or growth rate of other members of the community (Paine 1966, Menge 1995, Gaston 1996). The idea of keystone species is also related to the notion of ecosystem or community engineers, i.e. species that influence, for example, either habitat structure or nutrient flow such that other species are greatly affected (Lawton 1994, Coleman & Williams 2002, Reichman & Seablom 2002). Generally the keystone concept hinges on the assumption (and at times observation) that interspecific interactions in the community are reasonably strong, at least between the keystone species and other community members. That is why, for example, model communities where interaction strength can be specifically modified, may produce strong cascading effects. Such cascades can be either trophic cascades (indirect effects across trophic levels) or extinction cascades; the removal of one species is accompanied by additional extinctions from the community (e.g. Borrvall *et al.* 2000, Lundberg *et al.* 2000, Fowler & Lindström *in press*). Cascading extinctions are difficult to detect in natural systems. It either requires large-scale and long-term experimental manipulations, or, when such manipulations are not possible, control for other changes than solely the loss of a particular species. Therefore, extinction cascades have largely remained a theoretical construct, with some notable exceptions (Paine 1966, Fritts & Rodda, 1998, Berger *et al.*2001, Carr *et al.* 2002, Pauly *et al.* 2002). Previous works on extinction cascades have generally only paid attention to the identity of the species responsible for cascades. One exception is Borrvall *et al.* (2000), who looked at properties in food webs that decreased the risk of cascading extinctions.

In the present study, I address the question of cascading extinction events in a competitive community by systematically removing species from a community, and compare the effects of defining those community members by either their relative density (abundance), or their competitive ability within the community. I ask whether predictions about community persistence following disturbance (in terms of cascading extinction events and species removal respectively) should be based on the rather complicated methods required to establish interspecific competitive relationships (both mathematically and under natural conditions), or a more simple measure of interspecific relationships, in this case, relative abundance within the community.

The Model

To simulate a multi-species community we applied a Ricker-type growth model with Lotka-Volterra competitive interactions between k species. This is a commonly used function in ecological models (e.g. Levin 1974, Lundberg *et al.*, 2000) allowing a wide range of biologically relevant deterministic dynamical behaviours to arise. Thus the population size N of any species i was calculated for successive generations (t+1), given knowledge of the present population size ($N_{t,i}$) as follows:

$$N_{t+1,i} = N_{t,i}e^{\left(r\left(1-\sum_{j=1}^{k}\alpha_{i,j}N_{t,j}\right)\right)} . \qquad (1)$$

The intrinsic growth rate for each species is represented by r, which was held constant at 1.75 in all simulations. All species in the community competed with each other over some implicit resource, while intraspecific competition was set to unity for all species. Fryxell and Lundberg (1998) have highlighted the importance of such horizontal species interactions. In this model, interspecific interaction strengths (α-values) were asymmetric, being drawn from a uniform random distribution with limits [0,1], while intraspecific α-values had a value of 1. The nature of these asymmetric interactions means that species A might have a more negative influence on species B than species B has on species A. For each new model iteration, a new α-matrix was constructed.

Community size was varied from four to eight species. Each separate community with its assigned α-matrix was then run for 1000 generations to reveal instabilities.

The purpose of this was to remove transients and allow the community dynamics some time to settle to a steady state. The community was considered stable if the number of species present after 1000 generations was equal to the initial community size. A species was considered extinct if its population size fell below a critical threshold value (in all cases presented here this critical value was $N_{t,i} < 1 \times 10^{-6}$, a conservative limit for a species density). With the α-values generated in this way, it was possible to calculate the eigen-values of the system (see section on "*Ranking community members*" below).

It is also possible to derive the equilibrium stable state for such communities analytically (Ranta *et al. accepted for publication*), using vectors to represent the population density of each species in the community, at time t. This allowed us to derive the steady state (equilibrium) population size of each species in the community (N^*), and a vector of length k containing the carrying capacity of the environment for each species (K - set to unity for all species here).

$$\overrightarrow{N^*} = \alpha^{-1}\overrightarrow{K} \qquad (2)$$

Following derivation of the community steady state, any communities where any elements of the vector N^* are lower than the extinction threshold (10^{-6}) were discarded. If this was the case, a new α-matrix was again randomly generated, and the process was repeated until a suitable community was found. At this point, one species was selected and removed from the community. This was done by renewing the interaction matrix by simply removing the row and column that related to the removed species. This gave a new k-1 by k-1 interaction (α-) matrix. Once again, the community steady state was derived from this (eqn. 2). This time, however, any species with a corresponding element in the new N^* vector below the extinction threshold (10^{-6}) was considered to have become a victim of a cascading extinction event, and these were noted. This model was carried out 500 times, to allow the probabilities of cascading extinctions to be calculated after the removal of each community member.

Ranking Community Members

The relative influence of each species on the community dynamics was found when calculating the eigen-values and eigen-vectors of the -matrix, as follows:

$$det(\alpha - \lambda I) = 0 \tag{3}$$

where we set equation (3) equal to 0 to solve for λ. I is the identity matrix, and solving this gives a k:th order polynom, the characteristic equation (4), as below

$$\lambda^{k} + b_{1}\lambda^{k-1} \dots b_{k}\lambda^{1} = 0 \tag{4}$$

where each λ is an eigenvalue.

This information was used for ranking the species in the community, and when analyzing the outcome of the sequential removal of each species. Thus, every one of the species in the community is removed, and the new community (with one species less) is allowed to renew for a further 1000 generations. Again, as described above the structure is controlled for further extinctions according to the densities of the remaining species. The lower density limit of any species to be considered extant was again set to 10^{-6}, all species with densities below that were treated as extinct.

The following results are based on 500 iterations of the community model, unless otherwise stated.

Results

We compared the predictive power of different measures of species' characteristics in the community using linear regressions. Doing this we found that by ranking species according to their abundance (linear regression: $R^2 = 0.839$, $p < 0.001$), we can explain extremely accurately (and unsurprisingly) their actual density compared to the ability of a ranking system based on competitive ability explaining density ($R^2 = 0.03$, $p < 0.001$). This should be treated with some caution, however, as abundance rank and density are clearly not independent of each other. This simply serves to illustrate the comparatively poor predictive power of competitive ability in relating to species density. Abundance rank was then compared with the competitive rank (e.g. in an eight species community, figure 1). This showed us that there is only a relatively weak relationship between the abundance rank of a species and it's competitive rank. In fact, the relationship between these two species characteristics can be shown to differ significantly from a 1:1 relationship. Regressing abundance against competitive rank shows a highly significant difference from an expected 1:1 relationship (i.e. slope 1 [Sokal & Rohlf 1995]; $t = 59.79$, $p < 0.001$). Thus, I concluded that competitive rank used in the following analyses does not successfully predict the abundance rank within the community.

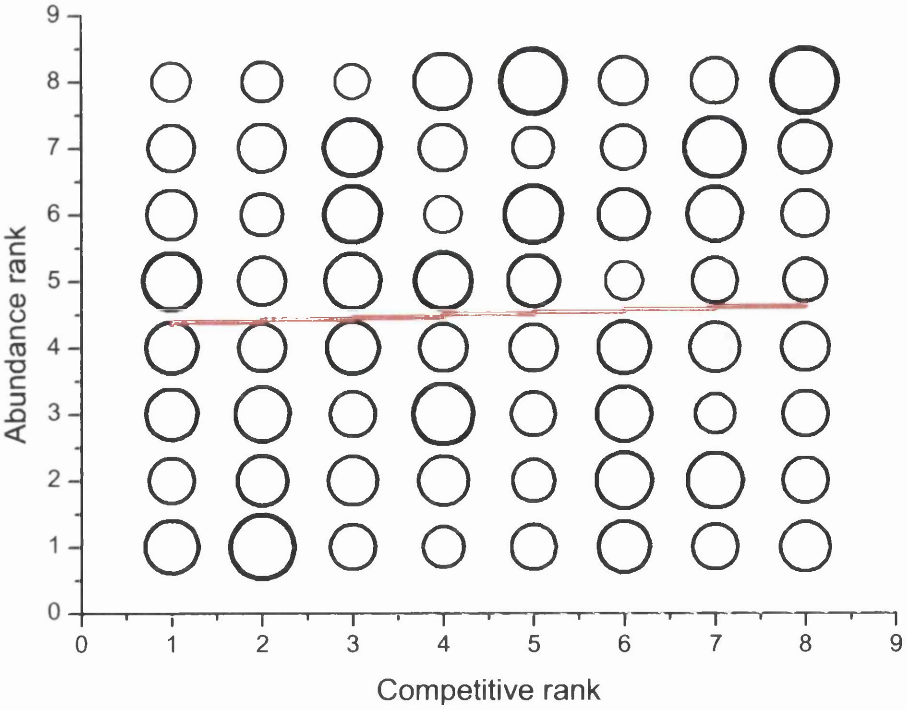


Figure 1: The relationship between ranking species according to their abundance and ranking them according to competitive ability. The size of the circles represents the frequency that each species abundance rank was equal to a given competitive rank, larger circles indicate a more common occurrence (after 500 community iterations). The red line is a linear regression between these two variables ($R^2 = 0.002$, $p = 0.006$). Although there is a significant positive relationship between these two measures of community presence, the explanatory power is very poor. Comparing this regression line to an expected 1:1 ratio reveals a highly significant difference ($t = 59.79$, $p < 0.001$).

Furthermore, differences between the probability of cascading extinction events occurred when species of different competitive ranks are removed, compared to when those of different abundance were removed (figure 2).

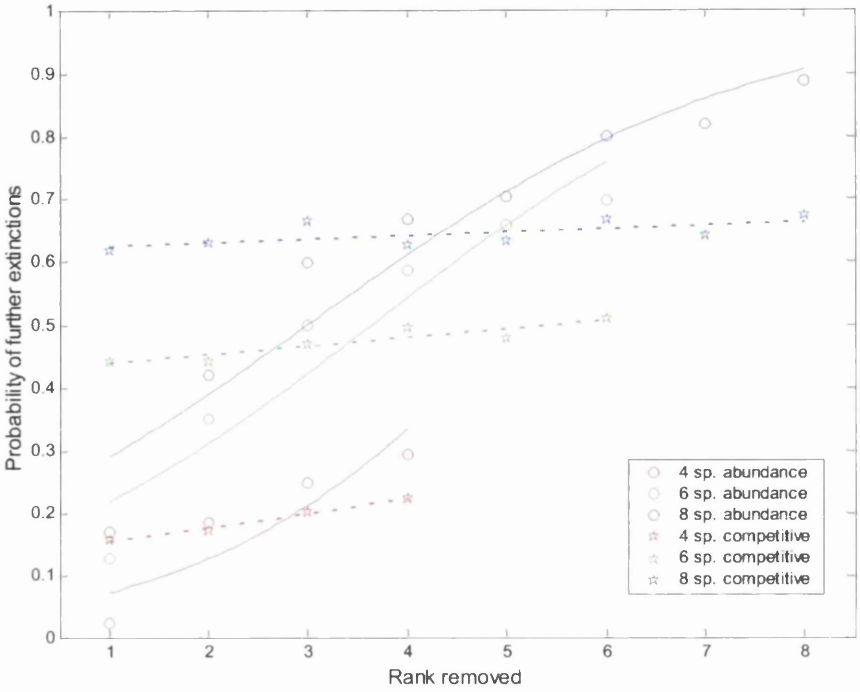


Figure 2: Removing species of different rank from a community leads to different probabilities of further extinction events after this form of disturbance. Species were ranked according to the relative influence they exerted over the other members of the community (competitive ability; stars), or ranked according to their relative abundance in the community (circles). Species with low ranks (1 being the lowest) had relatively little influence on the community and higher (8 being the highest) ranks had a greater influence on community dynamics. In all cases there was a trend towards increasing probability of further extinctions as we increase the rank of the species removed. However, logistic regressions (statistics shown in *table 1*) indicated that ranking species according to abundance (solid lines) gives a more refined measure of community extinction processes than ranking species according to competitive ability (dashed lines). Probabilities based on 500 community iterations.

Table 1: Logistic regression statistics for removing species by competitive or abundance rank. In all cases, the variation is explained better by ranking species according to their relative abundance (density) in the community.

Original Community Size	Competitive Rank		Abundance Rank	
	R^2	p	R^2	p
4 species	0.007	0.058	0.102	<0.001
6 species	0.003	0.012	0.148	<0.001
8 species	0.001	0.021	0.247	<0.001

The results shown in figure 2 and table 1 demonstrate that assessing the species importance in the community can be done in a more refined way through consideration of each species' abundance rather than their competitive ability within the community.

It is possible to assess which species are likely to be lost from the community when extinction events do occur. If species are ranked according to their relative abundance in the community, we can clearly see that the least abundant species in the community is (unsurprisingly) the most likely to be involved in extinction events, regardless of which species is removed from the community (fig. 3).

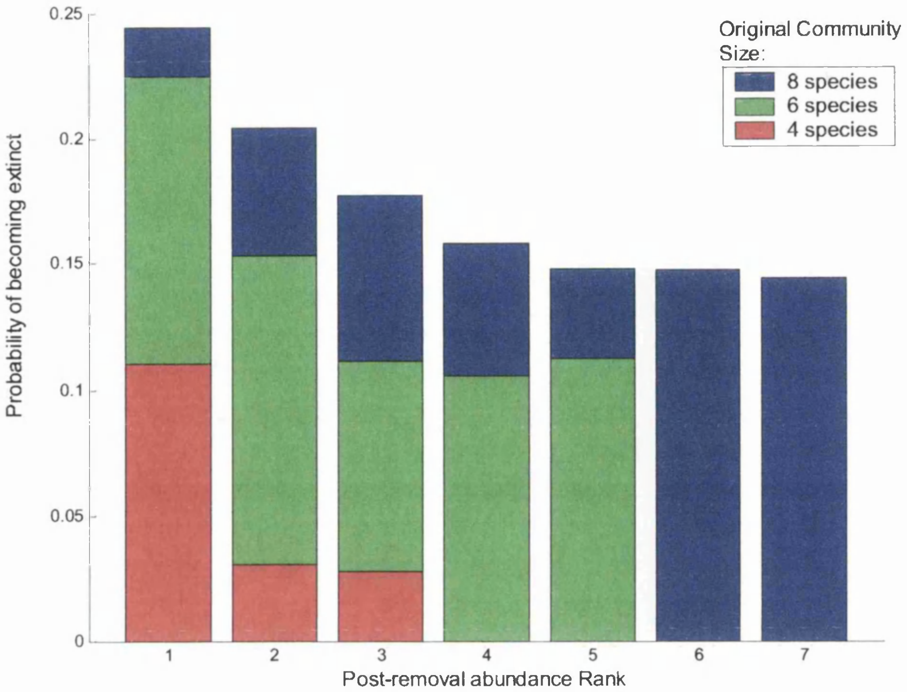


Figure 3: Which species are likely to be lost if cascading extinctions do occur? The same pattern arose in all community sizes tested, namely that the less abundant a species is the more likely it is to be involved in an extinction event following the removal of a species from the community. This pattern is consistent regardless of the abundance of the removed species (results shown here are averaged across all removed species ranks). The fact that some species of higher ranks were also lost is due to cascading extinction events involving more than one species at a time.

A further interesting result was the relative movement of species along a rank following removal of a community member of known rank. It may be expected that species will simply move up a rank position if a species with a higher competitive rank is removed. In fact, this was shown not to be the case (fig. 4*a*), due to a more complex interspecific interaction system (assymmetric) in operation than such a simple linear ranking system. For example, by removing the highest competitively ranked species (ranked 1 in a 6 species community), we may expect other species to increase their rank position due to the removal of this highest ranked competitor. While this does occur in many cases, it is clearly not the only outcome. Frequently, species may drop down the competitive ranking, even following removal of the highest ranked species. Figure 4*b* clearly demonstrates the similarly variable effect of removing the species with the lowest abundance.

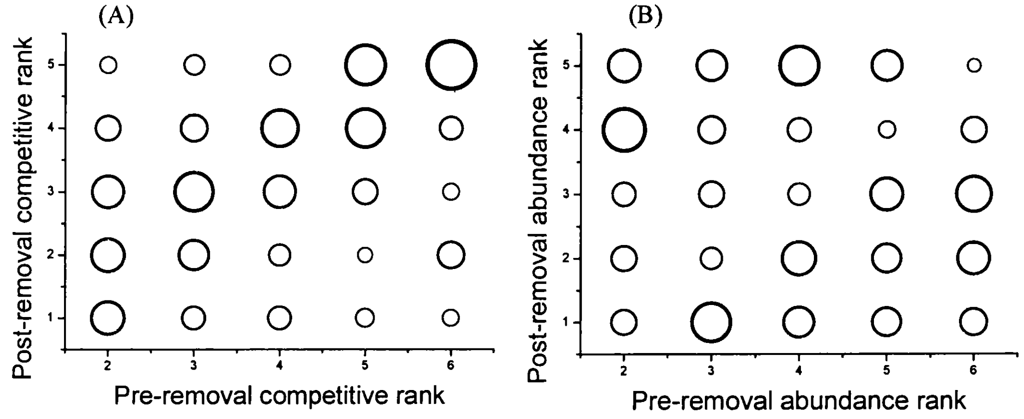


Figure 4: Removal of the species originally ranked 1 either competitively (fig. 4*a* - the species with most influence on community dynamics) or by abundance (fig. 4*b* - the species with the lowest abundance) showed a non-linear effect on community changes that took place following removal (results taken from 100 model iterations). The size of the "bubbles" is directly related to the number of times a given outcome occurred - i.e. larger bubbles signal a more frequent event. By plotting the pre-removal rank against the new species rank following removal of the species in a 6 species community there is definite deviation from an expected linear movement along the competitive ranking (4*a*), while removing the least abundant species can lead to both increases and reductions in the abundance of other species in the community (4*b*).

After the least abundant species was removed, the remaining species in the community again showed highly variable responses. Here, it might be expected that the remaining community members would simply shift up a place in the rank order. However, in many cases it was actually less likely that the new abundance rank would follow the expected trend than arriving at a lower rank. It could be argued that cascading extinction events involving more than one species might explain this result. However this is unlikely to be the main source of variation for at least one reason. If further cascading extinctions do occur following a removal event, the remaining species would only be expected to shift even further along the abundance ranking. In many cases, the opposite is true. After removing the least abundant species, the remaining community members often rose in the abundance rank. In other words, removing the least abundant species often had a disproportionately beneficial effect on other community members. A specific example of this can be seen with those species' originally ranked 2 in abundance (the second least abundant community member). The most common outcome following removal of the least abundant species is for rank 2 to take on a new abundance rank of 4. This means that instead of becoming the "new" least abundant community member, it actually increased its relative density to such a degree that it now becomes the second *most* abundant community member. This result is due to the non-linear (asymmetric) competitive effects found in the α–matrices, and holds true for all cases of removing differently ranked species both in terms of competitive ability and abundance, across different community sizes. This result is of considerable interest, as it points to a significant restructuring of a community following the removal of one member.

Discussion

The results presented here suggest that when studying competitive communities (i.e. those on the same trophic level), species abundance is often a more suitable approach for defining different community members' status. This includes when assessing effects that may have some bearing on community level processes, e.g. the probability of extinction events occurring following different types of disturbance. However, it has also been shown here that the complex nature of interspecific interactions can lead to somewhat surprising effects arising when communities are disturbed. It seems that some species seem to have a disproportionately large suppressant effect on others, so when such a "bully" is removed, the victim can actually become a better competitor in the remaining community than it's original rank would suggest. This analogy can apply to all members of the community and their effect on other members, regardless of their relative rank (competitive or abundance). These subtle but important processes are not obvious when a community is not viewed in the correct context, and provide a clearer insight to changes in community dynamics that can have important consequences to species persistence that may not be clear due to averaging of species performance (e.g. chapter VI). This appears to be an encouraging finding in terms of conservation practises, as it is almost certainly easier to establish relative abundance of community members than it would be to try and establish overall community interaction between all members. The indirect consequences of disturbing communities must still be kept in mind, however, during conservation management schemes. The results here (figure 4 in particular) clearly indicate that competitive communities can dramatically alter their structure following a disturbance event, in this case species removal.

The keystone species concept has been debated repeatedly in the ecological literature (Gaston 1996, Coleman & Williams 2002). It is not only of interest for a more general understanding of community dynamics, but has also been used in conservation biology as a means of understanding the consequences of loss of biodiversity. Should we be able to predict the relative importance of species in ecological communities, then limited conservation effort could in principal be largely targeted towards those species with such important effects. Here, we have explored the effects of a possible candidate for the definition of a keystone species in simple competitive communities. Our results unambiguously indicate that density is a good predictor of the direct and indirect effects a species will have on the rest of the community. Perhaps surprisingly, removing those species with the highest density leads to a higher probability of further (cascading) extinction events. While it may be expected that removing a competitor with a high density from a system would reduce competition between the remaining community members, the above results show that in fact, such a removal is much more likely to lead directly to the loss of other competitors from the community.

It would be interesting to test the generality of these results by introducing a different community structure such as a multi-trophic system e.g. food webs (Goldwasser & Roughgarden 1993). It remains to be seen, however, exactly how and why differently structured communities respond differently to extinction events. Also, it is possible that less rigid and deterministically structured communities than our model may respond differently simply because of changes in the species properties as deletions occur (Abrams 1996). Williams *et al.* (2002) have recently emphasised that species dynamics within ecosystems may be more highly coupled than previously suggested, and underline the potentially catastrophic effects of biodiversity loss.

A number of properties can potentially make a keystone species. We have shown here that equilibrium density is a strong candidate in competitive communities such as those studied here. Although community closure and re-introduction cascades were not specifically addressed here, they have been shown to potentially have far reaching consequences for conservation and community and ecosystem restoration (Lundberg *et al.* 2000). More detailed knowledge about species-specific effects on those processes is, therefore, required for successful management and protection of natural systems. More rigorous definitions of keystone species and similar concepts are therefore critical.

Another potentially important aspect of community ecology that has not been addressed here is the effect that space has on systems such as this. It has previously been shown that linking discrete community patches in the environment through dispersal may either have little effect on the probability of further extinctions after some form of disturbance (chapter VII) or even that harvesting in one patch can have detrimental effects on species in other patches in the environment (Jonzén *et al.* 2001). However, as I have shown here, knowledge gained from removing species from the community on the basis of their abundance can help to predict population or community level processes to a higher degree than basing predictions about differences on the competitive structure of such communities. Future studies could assess whether differently ranked species react differently in a spatially explicit model. It is possible to ask whether some species suffer increased or decreased extinction risks due to the effects of dispersal between different habitat patches. Furthermore, if this is the case, is it necessary to have knowledge of individual species reactions to help manage and protect these species effectively?

GENERAL DISCUSSION

Over the last ten or so years, there has been an upsurge in interest in the outcome of interactions between dispersal and population regulation. We can see from figure 1 that following a sudden increase in the number of papers focusing on such an interaction between dispersal and dynamics (circa 1991), there has been a relatively constant increase in the number of published studies on this topic since then. While it is possible that this reflects a change in semantic usage, it is much more likely to indicate an increase in both the interest in this subject area, and the increase in personal computing power that has allowed more complex theoretical approaches to be taken in this field.

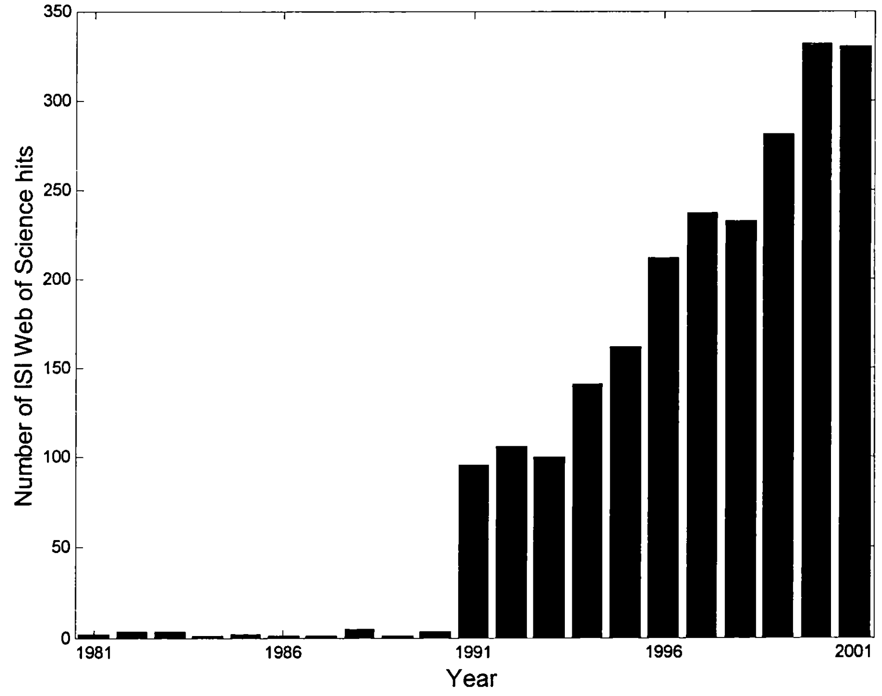


Figure 1: The number of papers containing the words "dispersal" and "dynamics" in their title, abstract or keywords.

While organisms are not solely influenced by density-dependent factors in their environment, density-dependence is a highly relevant mechanism for population regulation (Turchin 1995). It is therefore important to address the interactions between the different forms of density-dependence (e.g. competitive effects, Allee effects and between-species interactions) and dispersal, to be able to understand the reactions of organisms in a changing environment. Here, I discuss the work within this thesis and consider the need to regard these results over a range of interaction levels.

Summary

Aggregation is an important life history component of a number of species (Allee 1931). In some cases, it is likely that organisms aggregate in order to avoid a reduction in fitness brought about by low population densities. In **chapter II**, I show that Allee effects can stabilise population dynamics, a result that agrees with Scheuring (1999). For some cases, I can show that by increasing the strength of an Allee effect in populations whose density fluctuates chaotically over time, unstable dynamics can be simplified and brought to a stable point equilibrium. I go on to demonstrate that in populations that do experience an Allee effect, increasing the strength of competition can stabilise population dynamics compared to a population without an Allee effect. Previous models (Ricker, 1954, Hassell 1975, Maynard-Smith & Slatkin 1973) predicted that increasing the strength of within-species competition would lead directly to more unstable dynamics. This leads me to suggest that if Allee effects do arise in natural populations, they could be of great importance dynamically. Fowler & Baker (1991, p.545) go as far as suggesting that "many, if not all, animal populations experience a depression of their capacity for increase at very low population levels". While it remains to be seen exactly how many populations are constrained by an Allee effect, one relatively well-studied example is the African wild dog (Courchamp *et al.* 1999*a* & *b*, Courchamp *et al.* 2000). Here, the presence of non-breeding helpers within packs is suggested to be a mechanism to overcome fitness loss from low population sizes. Unfortunately, this is one of only a very few species that has been studied specifically with an Allee effect in mind. Further examples must be studied to understand the mechanisms involved with avoiding an Allee effect, whether through finding conspecifics by leaving the current habitat and searching elsewhere, or by attracting conspecifics. Therefore, I asked what other populations or species would be expected to be under the influence of an Allee effect.

Previous studies have shown that some aphid species do show a reduced growth rate at low population densities (Way & Cammel 1970, Dixon & Wratten 1971, Lopez *et al.* 1989). In **chapter III** I attempted to assess whether the pea aphid (*Acyrthosiphon pisum*) would also suffer from an Allee effect. By initiating colonies over a wide range of densities, I attempted to establish whether density-dependence operates at low as well as high population densities to reduce individual fitness. Aphid colonies either faced predation pressure following the introduction of ladybird larvae (predator groups), or were left undisturbed (control groups). Testing the data against different non-linear models, I contend that these aphids do indeed benefit from the presence of conspecifics at low colony densities. One of the models the data was tested against was that developed in **chapter II**, i.e. a model describing the Allee effect. I suggest that by taking the parameter values predicted by non-linear regression in a biological context, the model describing a population with an Allee effect explains the data from aphid colonies facing predation pressure.

Furthermore, by setting up aphid colonies under two different experimental treatments (predator or control), I was able to rule out one possible mechanism leading to an Allee effect, while proposing another mechanism that could potentially lead to an Allee effect. The control treatment colonies did not appear to suffer from an Allee effect, while those colonies where a predator was introduced did suffer reduced fecundity at low (as well as high) population densities. Thus, it appears that the mechanism aphids employ to avoid fitness loss from an Allee effect was due to predator dilution. This also allowed me to rule out another mechanism that aphids could employ to avoid the Allee effect; aggregating around an area where the plant channels disproportionate amounts of nutrients (plant sinks).

It should be pointed out that the parameter estimation used in the non-linear regression analysis was a post-hoc procedure. It would be very useful to carry out further small-scale experiments to estimate parameter values more accurately. Recently, work has been focused on setting up experimental systems that can specifically address theoretical predictions (e.g. Constantino *et al.* 1995, Dennis *et al.* 1997, 2002, Benton *et al.* 2000, 2002). These methods provide an invaluable link between theoretical and empirical studies that has been required for some time, and must be pursued further.

While data concerning another aspect of fitness, the production of alates, confirmed fitness loss due to density-dependence at high colony sizes, the data were not considered for further analysis. Further study of this aspect of aphid fitness could elucidate other mechanisms behind the prevalence and influence of Allee effects.

Another interesting aspect of pea aphid ecology is the presence of a colour polymorphism in different clonal lineages. Losey *et al.* (1997) described one possible method through which this colour polymorphism in *Athyrosyphon pisum* may be maintained. They suggested that differing rates of parasitism and predation lead to the different colour morphs co-existing in an evolutionary stable state. This hypothesis is backed up with a mathematical model that demonstrates that if parasitism and/or predation are biased in a density dependent manner on different morphs, this would be sufficient to maintain the colour polymorphism in the population. Further works by Weisser *et al.* (1999), Weisser & Braendle (2001), and Sloggett & Weisser (2002), indicate a differing propensity of the different colour morphs to produce winged offspring, as well as the effects of parasitism on the production of winged offspring. Sait *et al.* (1996) highlighted the potentially severe costs to parasites if they select a host that is already infected by another pathogen, while Vasconcelos *et al.* (1996) have shown that moth larvae infected with a Baculovirus will vary their dispersal behaviour, depending on the stage of infection. These studies demonstrate the range of factors that are likely to impact on dispersal behaviour in insects. To fully answer the question of how maintenance of the colour polymorphism in the pea aphid is achieved, it is important to ask what has led to these colour differences arising in the first place? Is the red coloration a by-product of some immunological defence against parasitism or disease, which has the unfortunate effect of rendering the aphids more obvious to predators? The logical continuation of this line of thinking would be that this it is for this reason that red aphids have had to evolve a higher rate of alate production to allow dispersal away from sites after a predator has arrived. However, ladybird larvae are major predators of aphids, and as different coccinellid species vary in their ability to use visual cues (Harmon *et al.* 1998), we must ask if there are other (possibly chemical) cues associated with the hypothesised immune response to the parasites.

It has been shown that within the green clones, apterae have a lower probability of being parasitised than alates (Sloggett & Weisser 2002). This result may seem surprising, as it can be hypothesised that it is more beneficial for the parasitoid to attack a wingless individual. The aggregative behaviour of aphids would allow further generations of the parasitoid many easy targets, while dispersing aphids may lead to the extinction of the parasitoid in the following generation due to a lack of available hosts. However, dispersal by aphids would also allow transmission of the parasite to potentially new hosts when the dispersers reproduces, or if it arrives at a new site already populated by other hosts. Thus, while we can say that there appears to be a hierarchy of potential host choice for the parasitoids, with red wingless morphs being the least likely to be parasitised and green alates the most popular, we cannot yet be absolutely sure why the parasitoids make this choice. The high dispersal costs associated with some aphid species (Ward *et al.* 1998) make this an intriguing subject for future study.

Given that dispersal, and space more generally, has attracted a great deal of interest from ecologists, it is perhaps surprising that very little attention has been focused on the Allee effect acting as a pressure leading to dispersal. For this reason, I developed a model that simulated a population with individuals that would leave a patch to escape density-dependent fitness loss at either high and/or low population sizes (**chapter IV**). Ruxton & Rohani (1998) had previously shown that density-dependent dispersal simplifies highly unstable population dynamics very easily, when individuals base their choice to disperse away from a patch on competitive pressures. Using the model of the Allee effect developed in **chapter II**, I derived both an upper and a lower threshold population density based on expected fitness in a given patch. Individuals left a patch if their expected fitness was either above or below the relevant threshold, and search for a new patch where fitness could be maximised. The results when individuals left a patch to avoid competitive pressures agreed with those of Ruxton & Rohani (1998), i.e. unstable population fluctuations quickly stabilised under these conditions. However, if individuals left a patch to escape the fitness loss from an Allee effect, there was no simplification of unstable dynamics. In some cases, a global population could be driven to extinction if the critical threshold density was sufficiently high. If both an upper and lower critical threshold are introduced, competitive effects dominate dispersal decisions, until the combination of the two critical thresholds forces the global population to become extinct.

Dispersal costs are likely to have an enormous impact on an individual's decision over whether to move or not. These costs can be manifested in a number of different ways, from physiological differences to mortality (Dixon *et al* 1993). The benefits required for dispersal to have evolved and persisted must therefore be considerable. For this reason, I went on to study the effects of different types of cost to dispersers in the same model; mortality risk and limited sampling time. I showed that the combination of these costs can be promote global persistence of the population when it would otherwise go extinct in trying to avoid fitness loss from an Allee effect. Furthermore, inclusion of these factors can stabilise otherwise unstable population dynamics, something that did not happen without any cost to dispersal. These results led me to ask if dispersal to avoid an Allee effect can only arise under specific conditions. In order to study the evolution of dispersal to avoid an Allee effect further, it will be necessary to study an invasion model.

With the exception of the classic metapopulation approach, developed by Ilkka Hanski and colleagues (Hanski 1989, Gilpin & Hanski 1991, Hanski & Gilpin 1991, Gyllenberg & Hanski 1992, Hanski & Thomas 1994 and others), the majority of spatial models have relied upon the coupled map lattice (CML) approach to patch positioning (Allen 1975). Here, discrete population patches are positioned on a grid that divides the environment evenly. Following internal (within-patch) interactions, individuals can then disperse between these different patches according to some specific dispersal kernel. While the metapopulation approach does not take internal patch dynamics into account explicitly, in some circumstances it is vital to take this sort of information into account.

Ranta *et al.* (1997) highlighted an interesting dynamical behaviour that arose in a model they developed to simulate the well-known regular cycles that appear in Canada lynx (*Lynx canadensis*) population dynamics (Elton & Nicholson 1942*b*). Using time-series data generated by the model, the authors noticed that fluctuations in different lynx population patches could change in their phase relative to each other. In some cases, two populations could have their dynamics completely in phase with each other over time, before drifting out of phase and returning to being in phase again some time later. The authors suggested that one component of their model that was necessary for this behaviour to arise was the random method of patch placement in the habitat they employed. They claimed that this phase-shifting could not arise if patches were positioned regularly in space. In **chapter V** I studied this model further. As well as studying this interesting dynamical behaviour, which has received little attention from ecologists, I asked exactly how does changing the way space is included in models affect model predictions? Is the coupled map lattice an oversimplification that leads to misleading results? Do population models that explicitly deal with space and within patch processes need to include space in a more realistic manner, *sensu* Hanski and colleagues? In fact, my results showed that random patch positioning was not a necessary requirement for phase-shifting to occur in this model. However, I was able to show that dispersal between different patches is required for this interesting phenomenon to arise. I went on to demonstrate how easily phase-shifting could arise, under a wide range of different parameter values for different regulatory mechanisms, including both direct and delayed density-dependence. However, neither of these were sufficient or necessary conditions for phase-shifting to arise, whereas dispersal was. Furthermore, I showed phase-shifting could even arise when patches were regularly positioned on a lattice. In other words, modelling populations can probably be done satisfactorily using the CML, without necessarily missing biologically relevant dynamical behaviours. However, my work has highlighted a relatively poorly known, but very interesting dynamic behaviour: phase-shifting. It is rather surprising, given the ease with which I showed phase-shifting could arise, that it has not been focused upon in real ecological systems. It is likely that this dynamical behaviour has been noted in relation to coupled systems of oscillating units in the mathematical and/or physics literature (Rolf Ims *pers. comm.*). Important work on phase differences in epidemiology (Grenfell *et al.* 2001) and work on grouse dynamics (Cattadori & Hudson 1999) addressing quasi-periodicity and "phase-forgetting" have been valuable contributions, pointing to the existence of this interesting family of dynamical behaviours in real systems, and encouraging further work in this field.

Another key point to remember in the analysis of population dynamics is that species seldom exist in isolation. The interaction between different species should be taken into account where possible. This has of course received considerable attention, from the earliest theoretical ecologists (Volterra 1926, Lotka 1932), to more recent attempts to establish more complex interactions in large-scale food-webs (see

Williams *et al.* 2002 for a list of the best examples). Begon *et al.* (1996*b*) have shown that period shifts can arise in predator-prey cycles due to changes in the size of the community studied. However, these (and other) studies of trophic interactions have tended to focus on the vertical interactions that occur within such assemblages. Fryxell & Lundberg (1998) recently reinforced the importance of horizontal interactions in multi-species communities, and the final part of this thesis (**chapters VI to VIII**) attempts to assess how important intraspecific competition of this form is and what predictions can be made from studying models that incorporate this form of density-dependence.

The question of complexity and stability in multispecies assemblages is one that is of considerable interest to ecologists. The view originally held by empiricists, that more structural complexity would yield more stable communities (MacArthur 1955, Elton 1958, Hutchison 1959), was challenged by theoreticians, who predicted a loss of stability with increasing community complexity (May 1971, 1972). More recently, however, both camps have reassessed their standpoints. Experimental work has shown that complex communities can be less stable than simpler groups (Rodriquez & Gomeszal 1994, Tilman 1996, McGrady-Steed & Morin 2000), while theoretical work has pointed to increasing stability with complexity (Harding 1999, Lehman & Tilman 2000, Rozdilsky and Stone 2001, Fussman & Heber 2002). These changes in long-held attitudes have certainly enlivened the debate. Haydon (1994) notes that stability can both increase and decrease according to different measures of complexity in a class of commonly used model ecological communities. Grimm & Wissell (1997) and Lehman & Tilman (2000) have both stressed the importance of clearly defining the specific aspects of stability and complexity that are being addressed, to avoid conceptual confusion. **Chapter VI** shows that increasing the dynamical diversity within a community can increase the stability of that community following the removal of one member species. However, this is only true under specific circumstances, namely if community members can have beneficial as well as harmful interactions, and the increased stability is in terms of cascading extinction responses to species removal events. It is therefore vital to understand the nature of the interspecific interactions within a community to be able to make useful predictions about that system.

The effect of dispersal between communities is studied under different circumstances in **chapter VII.** I have shown that connecting separate population patches in the environment through dispersal may not promote improved community persistence following disturbance, even after the inclusion of patches that vary in their quality. This may be worrying in terms of conservation practices. Habitat corridors have been suggested to be of great importance in conserving populations in habitats that have become divided (Saunders & Hobbs 1989). My study suggests that this may not always be the case. Furthermore, I have shown that fragmenting the habitat can be shown to have detrimental effects on community persistence. This has already been known for some time under natural circumstances (Gilpin 1987). One aspect of this chapter that is particularly surprising is the fact that introducing spatial heterogeneity does not appear to influence results. It has been shown that introducing variability in patch quality over space or time can alter population dynamics (Hastings 1993). For the communities studied here, the only form of spatial variation found to make a difference was habitat fragmentation. As mentioned previously, conservation practices must also take this sort of information into account.

An interesting extension to this work would be to try incorporating the different types of dynamical and spatial diversity addressed in **chapters VI** and **VII.** In addition, it would be of great interest to study the effects of introducing vertical as well as horizontal interactions into these models. A further aspect of these models that is of considerable importance is understanding the specific roles that different species play in a community. In **chapter VIII**, I show that knowledge of the relative abundance of a species within a community allows good predictions to be made about community level processes following perturbation. Abundance is compared to the competitive ability (determined by interspecific interaction strengths) of each community member and found to be considerably better at predicting such processes than knowledge of relative competitive ability. Competitive ability is arguably a much more difficult parameter to estimate, given that complete knowledge of all the inter-specific interactions throughout a community are required before competitive ability can be derived. Important work by Paine (1992) has attempted to establish interaction strength experimentally, while McCann *et al.* (1998) also highlight the importance of interaction strengths in food-webs. The fact that abundance can be shown to provide sufficient information to allow predictions to be made about a community is once again important for conservation, especially the keystone species concept. Having showed that such aspects of communities (abundance and competitive ability) are inherently asymmetric and non-linear, I suggest that further emphasis should be made on gaining as much knowledge as possible of these factors for communities that are involved in conservation programmes.

Future Directions

This thesis only begins to address the outcome of incorporating biologically important factors into theoretical models, through the simulation of interactions at the level of both population and community. Below are some of other aspects of ecology that will undoubtedly be important influences on the life-history of organisms, that I am interested in studying further in the future.

Pacala & Silander (1985) devised a novel method of representing a discrete time continuous-space population, with interesting results. They outlined various failings within their own work, and strangely, little further attention has been paid to this intriguing approach. Representing continuous space heterogeneously is an obvious approach, which arguably simulates the natural conditions many organisms face within their environment. In general, the representation of populations in space provides an interesting avenue for future research.

While many previous models have addressed the trade-off between dispersal ability and population growth rate (often referred to as competitive ability), little consideration has been given to the specific costs associated with migration (e.g. increased mortality risk or a limit to the time allowed to sample the environment). I have shown that imposing different types of dispersal costs leads to different dynamical behaviours, and plan to incorporate this work into a study of the dispersal/colonisation trade-off.. This can be extended further by asking how maternal effects will affect dispersal decisions.

Closing remarks

While I have not discussed density-independent effects on dynamics in this thesis, they are of undoubted importance in regulating natural populations (Turchin 1995, Stenseth *et al.* 2002 and references therein). Bjørnstad *et al.* (2001) asked whether a single species' dynamics could provide information about species interactions within a community, when they are considered in isolation. They conclude, "an imprint of the interactions may be discerned within time-series data for component species of a system" (Bjørnstad *et al.* 2001, p.1001). In order to gain a full understanding of the role of density-dependence in governing population dynamics, I suggest that there are three levels of interaction that must be taken into consideration.

Firstly, it is imperative to understand the response of individuals to density-dependence in its different forms, whether this is in terms of competitive, Allee, or other effects that have not been addressed here. Secondly, the decisions that individuals take will impact at the level of the group or population, i.e. within-species interactions. Here, an individual's choices relating to, for example, competitive and/or Allee effects have obvious repercussions for those other individuals the focal individual has been, or will be, interacting with. Finally, between-species interactions connect all members in an ecosystem or community. Williams *et al.* (2002, p.12913) have recently emphasised that "the dynamics of species within ecosystems may be more highly interconnected and that biodiversity loss and species invasions may affect more species than previously thought". It is thus essential to appreciate individual, species, and ecosystem level reactions to changes in the environment in order to be able understand and predict responses of organisms in a useful manner.

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