An investigation into the relationship between the stability of a biological community and both community complexity and environmental heterogeneity.

Thesis

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An investigation into the relationship between the stability of a biological community and both community complexity and environmental heterogeneity.

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Abstract

The aim of this dissertation is to study two aspects of the stability properties of a biological community. These are firstly their relationship with the structural complexity of the community and secondly the effect of spatial heterogeneity of the environment in which the community lives.

Chapter 1 introduces the subject of population dynamics and discusses the reasons for using mathematical models to study it.

The first part of Chapter 2 defines the terminology, especially the meaning of stability. The second part considers the biological evidence for a relationship between stability and complexity while the third part investigates the stability properties of mathematical models of communities of varying complexities. It is concluded that there is no general relationship, but that the more complex a community the more unlikely it is to be stable.

The first part of Chapter 3 discusses the bioligical evidence for the importance of the effect of spatial heterogeneity on stability and proposes a definition of this term. The second part describes different ways of modelling community population dynamics in spatially heterogeneous environments. It is concluded that spatial heterogeneity is not likely to make a community less stable.

Contents

Chapter 1 Introduction

1.1. Aim of the dissertation

The aim of this dissertation is to study two aspects of biological population dynamics.

These are i) the relationship between the stability of a biological community and the structural complexity of that community

and ii) the relationship between the stability of a biological community and spatial heterogeneity of the habitat in which that community exists.

1.2. Reasons for studying Population Dynamics

A biological population might be defined as a number of individuals of a single species in one place. The study of population dynamics involves investigating how a population changes through time and why. The value of such studies is manifold and depends on the type of population under consideration.

When the populations of particular plants and animals grow above a certain size, they become what are known as pest species.

Examples of pest species include the cottony cushion scale (Icerya purchasi) which attacks Citrus trees by sucking the sap from leaves and twigs, the froghopper (Aeneolamia varia saccharia) which attacks sugar cane in Trinidad and the larch saw-fly (Pristiphera erichsonii) which has been a serious pest of larch trees in Canada since the last century.

Control of pest populations is important both economically, especially to farmers, and in the prevention of the spread of diseases such as malaria for which the mosquito (Anopheles spp) is a vector and rabies for which the red fox and lately domestic dogs are vectors.

A control strategy may involve the use of an expensive pesticide or the introduction of a natural enemy of the particular pest species. Whatever method is chosen, a good understanding of the underlying population dynamics of the community involved is essential if an expensive waste of resources or undesirable side effects, such as outbreaks of other pest species which hitherto had been under control, are to be avoided.

A good review article discussing the importance of studying population dynamics to pest control strategies is given by May (1976).

The study of human populations is called demography. It is important economically and sociologically for those such as governments, sociologists and town planners to be able to estimate confidently how the human population is likely to change over a period of years. For instance, if the birth rate in a particular country begins to fall, it is likely that the number of teachers and even schools required in a number of years time will be reduced.

The study of human populations on a world scale is also important, especially studies concerning the under-developed countries. A good discussion of world demography is given in Krebs (1972) while an introduction to demography is given by Bogue (1969).

Another aspect of population dynamics is epidemiology, the study of epidemic diseases and in particular how to control them. A good review of the population biology of infectious diseases is given by Anderson and May (1979).

1.3. The use of Mathematics

In order to study population dynamics it is often necessary to count or estimate the number of individuals in a population at a particular time. The use of mathematics naturally follows

in attempting to determine how the numbers change through time. The appropriate mathematics involve constructing mathematical models.

In general mathematical models tell us what may be not what is. This is true even in physics. For instance, Newton's Laws of Motion do not hold exactly, especially for small values of mass and distance. However measurements from physical experiments tend to be relatively constant from replicate to replicate. This is certainly not so in biological experiments.

Biological data is renounced for its variability. This is especially apparant in many sets of data concerning population biology, whether it be, for example, estimates of the number in a population, estimates of the number of species in a particular habitat, or the number of eggs laid by a female housefly per day.

The fitting of any model to biological data is therefore likely to be a formidable task. Confidence in the mathematical models is often low and conclusions drawn are open to extensive criticism. However there have been some notable successes in the field of population dynamics which encourage mathematicians to persevere. For instance, the use of mathematical models in the fishing industry has proved very useful. In particular, one early model developed for its economic importance for the dynamics of exploited fish populations by trawling in the North Sea is that of Beverton and Holt (1957).

1.4. Types of Mathematical Models

Many different types of mathematical models have been employed in population dynamics. These include differential equations, difference equations, probabalistic models and simulation models.

Differential equations are often used to model populations (and communities) which exhibit continually overlapping generations, that is populations in which birth is effectively a continuous process through time, as in humans. Such models tend to break-down at low populations levels, but have proved useful in numerous cases. The Lotka-Volterra coupled differential equations

$$\frac{dh}{dt} = h(r-\alpha p) \qquad 1.1$$

$$\frac{dp}{dt} = p(-s+\beta h) \qquad 1.2$$

is a classical example of such a model for a predator (p) - prey (h) relationship.

Difference equations can be used to describe populations of species which have non-overlapping generations. Insect parasitoids (hymenoptera and diptera) that attack the insect herbivores (mostly lepidoptera) have a generation time the same length as that of their hosts, so that for instance, if a hymenopterous adult female attacks the second instar larva of a species of lepidepteran, the development of that hymenopteran is timed so that the next generation of females is flying at the time the next second instar of the lepidopteran is available. Difference equations have been used extensively to model host-parasitoid relationships. An investigation of the stability of such models is given by Hassell and May (1973).

The restriction to large numbers is still important.

If the parameters in such equations are constant, the models are deterministic. A random element may be introduced by allowing the parameters to vary at random through time.

If small population numbers are to be considered, growth in integral units can be described by probabalistic methods.

Continuous growth is modelled by considering the probability of a birth or death in an infinitesimal time interval while in discrete growth a fixed time interval is chosen.

Markov chain type models have been used by for example Zeigler (1977) to model spatial heterogeneity of the environment and its effect on the community dynamics. The habitat is divided into a definite number of patches each of which can take on a number of states. The transition between states of a particular patch is then made to depend on the number of patches in each state at a particular time. Transition may be continuous or discrete.

Another popular way of describing population dynamics is by simulation models. These models can be very detailed and are usually applied to specific populations or communities. They are run on a computer (digital or analogue) and are very flexible, especially when investigating the effects of discrete events such as natural catastrophies (e.g. a sudden change in the environment) or control strategies (application of an insecticide). One example of the use of simulation models in population dynamics is presented by Meek (1981) who modelled the liver fluke in sheep interaction and in particular investigated control strategies.

One further way of classifying mathematical models is into general or specific models. Both types of model may be empirical or complicated, however the latter type describes particular species or communities, as in the example by Meek referred to above, while the former type is used in an attempt to establish general ecological theories. It is the general approach and the difficulties associated with it which are considered mostly in this dissertation and mainly deterministic models are used.

1.5. Why Study Stability?

The two aspects of population biology considered in this dissertation both involve community stability. For the purpose of this section stability will be defined to be a property a population has if its numbers tend to remain at a more or less steady value for a period of time. Stability will be defined more carefully, as indeed it has to be, in the next chapter, however it is useful at this point to consider why it is necessary to study stability in mathematical models of biological populations.

There are a number of important questions to be answered concerning population biology. For instance, why do some species persist? Why do some species become extinct? Why do some species remain at low population numbers, then suddenly reach epidemic values? The spruce budworm (E. choristoneura fumiferana) is an example of one such species. Why does the addition of a natural enemy to a pest population sometimes control the number of pests to a tolerable but persistent level? Why does this control strategy often fail?

In order to answer these general questions by means of mathematical models and in particular to determine certain key factors such as number and type of links in the food chain or heterogeneity of the environment, it is useful to have a reference point from which to work. While populations in nature will always be subject to fluctuations due to a possibly uncountable number of factors, a convenient and I feel appropriate reference point to investigate is the equilibrium point (or points) of the mathematical model. A model can be considered to be at equilibrium if the populations numbers do not change through time unless they are perturbed. The stability of the model can then be investigated

by perturbing the numbers from their equilibrium values and monitoring whether they return to equilibrium. In this way the importance of the various parameters in the model concerning the above questions might be determined.

1.6. The Importance of Definitions

One important consideration when applying mathematical models to describe the real world is the consistency of terminology. For instance, what do we mean by stability of a biological population and how does this compare to the stability of a mathematical model? One essential way of avoiding confusion over terminology is to define all terms clearly and to demonstrate how the properties of a model may be related to the real world.

I hope that this will be evident throughout this dissertation.

Chapter 2 The relationship between the stability of a natural community and its structural complexity

2.1. Introduction

The object of this chapter is to demonstrate whether or not there is a general relationship between the stability of a natural community and the structural complexity of that community. We will do this both by studying evidence from field observations and by studying general mathematical models of community population dynamics.

We will need to define a number of terms and answer a few preliminary questions, namely:

i) what is a population?

ii) what is a community?

iii) how can a population change in size?

iv) how can we model this?

v) what do we mean by stability of mathematical models?

vi) how can we relate this definition to natural populations?

vii) what do we mean by complexity of a community?

We will then consider what types of relationship there may be between stability and complexity and will refer to evidence from field experiments and the literature for and against these relationships.

Finally we will compare the conclusions from field observations with results obtained by considering the relationship between the stability of solutions of simple mathematical models of communities and the complexity of these communities.

2.2. Definition of a population

I propose the following definition of a population ;

a population is a group of individuals of the same species

in the same place at the same time.

A number of other definitions have been used in the literature. For instance, Williamson (1972) defines a population as a 'group of individuals of the same species in one place' and Krebs (1972) uses the definition 'a group of individuals of the same species in a particular place at a particular time'. Both these definitions can be criticised because they exclude groups of individuals which move location, e.g. during migration. Krebs definition also implies that the same group of individuals forms a different population at different times whereas it is actually the same population with different population characteristics (e.g. size).

Solomon (1962) defines a population as a group of individuals of the same species. This definition is essentially identical to the one I have used, the 'same place at the same time' being implied. My definition automatically includes herds and flocks which are groups of individuals of the same species which move around together. The exact meaning of the 'same place' has to remain somewhat hazy, but fortunatly this does not really matter. Den Boer (1968) attempts to include this in his definition: a population is a group of indivuduals of one species living in a specified locality whose limits are spatially determined by natural barriers or are arbitrarily set by the ecologist. For instance, we may consider the populations of field mice in a particular field, in Hertfordshire, in England or in the world. What one must do is to specify the location. Individuals may migrate out of or into the location and hence may leave or join the population at any time.

2.3. Definition of a community

I propose the following definition of a community:

A community is a group of populations in the same place at the same time.

As for the definition of a population there are a number of different definitions of a community used in the literature. For instance, Krebs (1972) defines a community as an 'assemblage of populations living in a prescribed area' while Fager (1963) uses the somewhat looser definition 'a group of species which are often found living together.'

Fager's definition hints that there may be something more fundamental about the concept of a community and indeed in nature community patterns do occur. That is, certain groups of species do tend to be found living together more often than others. This has led to two schools of thought as to the biological significance of the community. On the one hand ecologists such as F.E.Clements and A.G.Tawley consider the community to be essentially a biological organism or superorganism. On the other hand the community may merely be a haphazard collection of species with the same physical resource requirements.

These arguments do not concern our theme however. What is important is that when a group of species live together in the same place, however that place is defined, they interact and because they interact the population sizes of the individual species depend on the structure of the community.

2.4. Why does the size of a population change through time?

The size of a population may change over a period of time due to at least one of the following reasons. Some individuals may be born, some may die, some may emigrate to another population of the same species, and some may immigrate into the population

from another population of the same species.

The effect of these events on the size of the population can be represented by what Williamson (1972) describes as the fundamental equation of population dynamics.

$$X_{t+\Delta t} = X_t + B - D + I - E \qquad 2.1.$$

where X_t = number of individuals in population at time t

$X_{t+\Delta t}$ = number of individuals in population at time $t+\Delta t$

B = number of births during time interval Δt

D = number of deaths during time interval Δt

I = number of immigrants during time interval Δt

E = number of emmigrants during time interval Δt

The numbers of events, B, D, I and E, tend to be functions of time, physical parameters and what might be termed 'living parameters'. Physical parameters include such factors as weather and amount of physical (inorganic) resource available (e.g. water). 'Living parameters' may include the numbers of individuals of cohabiting species present and behavioural aspects of these species (e.g. predator-prey relationships).

Many physical factors tend to be continually changing through time and indeed space. Consequently the rates of change of individual populations are likely to be continually changing, and, because population change depends also on the so called 'living parameters', communities are continually changing in size.

2.5 How can we model population dynamics?

In Section 1.3 it was stated that it is natural to use mathematics to attempt to explain how the size of a population changes through time (and indeed space), and a number of different types of mathematical model that might be suitable were briefly mentioned.

Most of these models are based on the fundamental equation of population dynamics:

$$x_{t+\Delta t} = x_t + B - D + I - E$$

which is described in the previous section (equation 2.1).
Here it is presented in the form of a difference equation.
The equation has a parallel formulation as a differential equation.

i.e. $$\frac{dx}{dt} = b - d + i - e \qquad 2.2$$

where $x = x(t)$ is the size of the population at time t and b, d, i and e respectively are the instantaneous rates of births, deaths, immigration and emigration at time t. As before these rates may be functions of time, 'physical' and 'living' parameters.

i.e. $$\frac{dx_i}{dt} = b(t,\underline{x},\underline{p}) - d(t,\underline{x},\underline{q}) + i(t,\underline{x},\underline{r},) - e(t,\underline{x},\underline{s}) \qquad 2.3$$

where x_i is the size of the i^{th} population,

$$\underline{x} = (x_1, \ldots, x_n)$$

where there are n species in the community,

and $\underline{p}$, $\underline{q}$, $\underline{r}$ and $\underline{s}$ are sets of parameters.

Equation 2.3 may be written in the more general form

$$\frac{dx_i}{dt} = f(\underline{x}, \underline{u}) \qquad 2.4$$

The simplest differential equation which has been used to model population dynamics is the exponential growth (decay) equation.

$$\frac{dx}{dt} = \alpha x \qquad 2.5$$

where $\alpha = b - d + i - e$ and is a constant.

The rate of growth (decay) of the population at time t is directly proportional to the size (x) of the population at time t. The constant of proportionality is in effect a lumped parameter describing the net effect of the four fundemental factors of population change. This equation has proved to be a good model to describe the dynamics of a population growing in an extremely favourable environment (Figure 2.1).

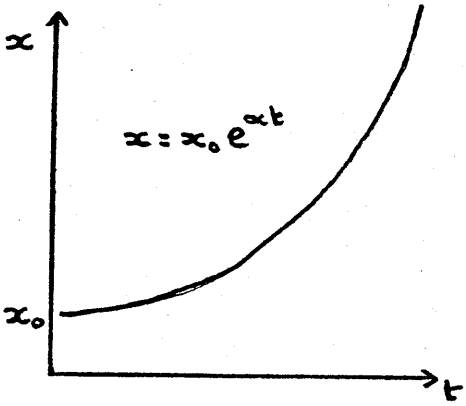

Figure 2.1: Example of exponential growth.

A slightly more sophisticated differential equation model of population growth is the logistic equation. This was first proposed by Verhulst as far back as 1838 as a model to describe human population growth, and was derived independently in 1920 by Pearl & Reed, again to model human population dynamics.

The equation is

$$\frac{dx}{dt} = rx\frac{(k-x)}{k} \qquad 2.6$$

Here r is the intrinsic rate of natural increase, that is, the maximum rate of increase the population can obtain under given conditions. It is assumed that there is no migration

k is often called the carrying capacity of the environment. Essentially the model assumes that there is a limited resource available in the environment, so that it can only support a maximum number (k) of individuals (Figure 2.2)

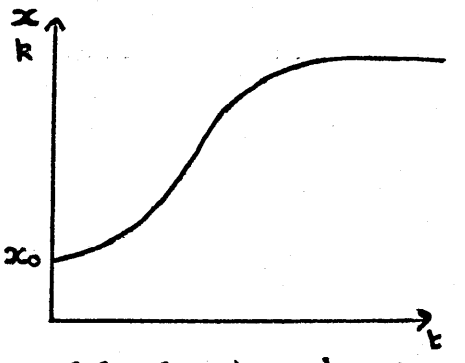

Figure 2.2: Example of logistic growth.

The logistic equation has frequently been used to model 'sigmoid' growth curves. For instance, G. F. Gause carried out a number of experiments with laboratory populations of microorganisms during the 1930's, and he fitted the logistic curve to describe the population growth of some individual species (Gause (1937)).

The suitability of the logistic curve to fitting such responses has been questioned by various authors (Williamson (1972), Sang (1950), and Feller (1940)),however it has certainly proved a very useful first approximation in the past.

Community population dynamics can be modelled by systems of differential equations.

One of the simplest and most famous examples is the predator-prey model which was derived independently by Lotka (1925) & Volterra (1926):

$$\frac{dh}{dt} = (r-\alpha p)h \qquad 2.6a$$

$$\frac{dp}{dt} = (-s+\beta h)p \qquad 2.6b$$

The prey species h is assumed to grow exponentially in the absence of predators p, while the predator population size is assumed to decay exponentially in the absence of prey. When both species are present, αph is essentially the rate at which predators meet and successfully kill prey and βph is the consequent increase in the instantaneous growth rate of the predator population.

The prediction of the equations is that the population size of both the predator and the prey oscillates, the amplitude of the oscillations being dependent entirely on the initial population sizes. This model is clearly not very realistic and has perhaps surprisingly been used a great deal as the basis for more elabourate mathematical models (e.g. Zeigler (1977)). However again it has proved to be a very useful approximation (Figure 2.3).

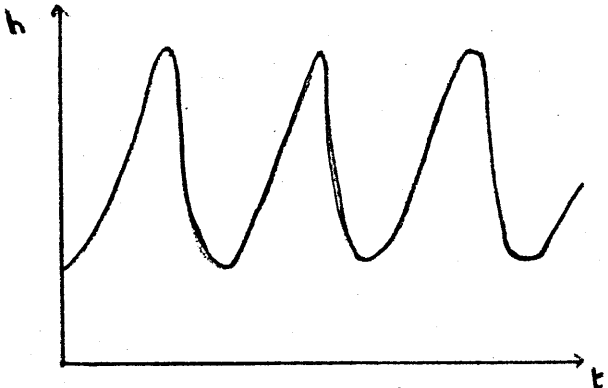

Figure 2.3 Prey oscillations predicted by the Lotka-Volterra equations

In general a community containing n species might be modelled by a system of n differential equation.

e.g. $$\frac{dx_i}{dt} = x_i \left(r_i - \sum_{j=i}^{n} \alpha_{ij} x_j\right) \qquad i = 1, \ldots, n \qquad 2.7$$

The examples of differential equation models quoted above are relatively simple and correspondingly may be very unrealistic when it comes to applying them to particular examples. However they may be made more sophisticated in a number of ways.

i) Age structure

Often within a population individuals of different ages will have different population dynamics. Even so, it may still be reasonable to use differential equation models. For example, if the young of a particular species are attacked by a particular predator but the adults are not, the following system of equations may apply:

$$\frac{dy}{dt} = ra - (d + s)\, y - yp \qquad 2.8$$

$$\frac{da}{dt} = sy - ea \qquad 2.9$$

$$\frac{dp}{dt} = -tp + \beta yp \qquad 2.10$$

where y, a and p are the number of young prey, adult prey and predators respectively at time t, ra is the birth rate of the prey, dy is the death rate of young prey, sy is the rate at which young prey become adults, ea is the adult prey death rate, tp is the rate of decrease of the predator population in the absence of prey, and α_{yp} and β_{yp} are the instantaneous effects of the predators successfully meeting and eating prey on the young prey and the predator populations respectively.

ii) Time delays

One immediate criticism of the Lotka-Volterra predator-prey model is that the effect of the predators eating prey at the rate α_{hp} at time t on the predator population size will not be instantaneous. One way of overcoming this is to introduce time delays into the differential equations (equation 6a and 6b).

For example, the Lotka-Volterra equations may become

$$\frac{dh}{dt} = (r-\alpha_p)h \qquad 2.11$$

$$\frac{dp}{dt} = sp + \beta h(t-T)\ p(t-T) \qquad 2.12$$

where T is the time delay between when the predators ate the prey and when there is a consequent effect on the predator population growth rate.

This sophistication to the model is not in fact particularly realistic (for instance the time delay T is not likely to be constant), but serves to demonstrate one way in which time delays may be introduced into differential equation models. May (1972a) is one author who has discussed the effect of introducing time delays on the ensuing population dynamics.

iii) Spatial heterogeneity of the environment

The environment in which a population or community lives may offer a different set of conditions to each individual depending on its exact location within the environment, and this may affect the overall population dynamics. This is especially true for plants and for animals which do not move far relative to the environment under consideration. For instance, the environment may be a particular field which is on a hill, and a diversity in conditions within the field may be decreasing water content in the soil depending on distance up the hill.

Spatial heterogeneity is discussed in more detail in chapter 3.

As was pointed out in Section 1.3 differential equations are not the only type of mathematical model that might be used to describe population dynamics, and indeed it is often not applicable to use them. In particular it is not realistic to use differential equations to model populations which have non-overlapping generations. Also, because population change occurs in discrete steps, they do not apply when the size of the population is small. However such models can often be useful both in modelling specific populations and, more important from the point of view of this dissertation, they might be used to explore general ecological theories.

2.6 Definition of stability

The size of a natural population tends to be continually changing through time. Often, at least over short periods of time, these changes demonstrate some definite trend. For instance, the population size may be growing; it may be decreasing; or it may demonstrate regular or irregular cycles. These trends may occur for a number of reasons. A species may have invaded a habitat which is particularly favourable. It is clearly inconceivable that a population should continue to grow in size ad infinitum as there can only be a finite amount of resource (e.g. space) available. Therefore, either some regulation of the population growth will occur, or the resources will

be used up, the individual members of the population will starve, and the population size will be drastically reduced. In the latter case the population might be said to be 'unstable'. In the former case the population 'may' be 'stable'.

Many ecologists do not attempt to define stability in the literature. This may be because a satisfactory definition does not exist. However, much of the research into population dynamics using mathematics has concerned stability and therefore it must be necessary to be able to relate this stability to that of the biological populations being modelled.

Orians (1974) recognised this and complained 'concepts are normally discussed with poorly defined terms, reflecting an uncertainty about what concepts of stability are useful in ecology and, even more important, what we wish to understand about natural ecosystems'. He is supported by Margalef (1968) who went as far as saying 'it is perhaps questionable whether the term stability should be retained, as it has been used too much in different and divergent speculation'.

Krebs (1972) suggested that a population is stable if it persists in the face of fluctuations or if it demonstrates a lack of or only small fluctuations. Elton (1958) defined a population to be unstable if it is 'more subject to destructive oscillations', while Williamson (1972) implied a similar definition and suggested further that some measure of population size variability might also measure stability.

The unsuitability of Kreb's definition is clearly shown by the example he used to demonstrate what he considers to be a stable population. This is the tawny owl population near Oxford, England between 1947 and 1959, the graph of which is shown in Figure 2.4. The population certainly demonstrates only minor fluctuations and persists over the period of time studied, and if this is to be a reasonable definition of stability, then the population is stable. However the population size is clearly increasing with time and in the spirit of the opening paragraph of this section, it is not intuitively stable.

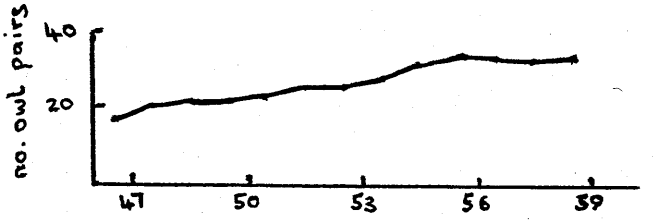

Figure 2.4: Abundance of tawny owls near Oxford (p.265 Krebs (1972)).

Intuitively a population is stable if its size remains constant over a period of time, and this constant level is maintained even when factors on which the population depends are subjected to perturbations.

At this point it is sensible to define mathematical stability.

2.6.1 Mathematical stability

Let P be a mathematical model of a biological population.

Let $x(t)$ measure the predicted size of this population at time t.

Then $x(t)$ is generated by the model P and therefore depends on the parameters of the model. These parameters will measure some of the factors discussed in Section 2.4 and the model will be some formulation of the fundamental equation of population dynamics (Equation 2.1).

For example, the model may be the logistic equation (Equation 2.6) in which r (>0) is a measure of the maximum (or intrinsic) rate of increase of the population and k (>0) is a measure of the carrying capacity of the environment, that is the maximum number of individuals that the habitat can support.

There are two types of stability to be discussed: local and global. A population which is globally stable is automatically locally stable, but a population which is locally stable is not necessarily globally stable.

A population model is locally stable if

i) there is a population size x^* (>o) such that if the population attains that size, it will remain at that size unless disturbed.

and ii) if the population size is disturbed slightly from this equilibrium size, the model will drive the size back to this value, though it may take infinite time.

For example, in the logistic model (Equation 2.6) the values $x^* = o$ and $x^* = k$ are both equilibrium points.

First consider the point $x^* = o$.

Let $x(t) = x^* + \xi(t)$ denote a small disturbance from this equilibrium.

Then $$\frac{d\,x(t)}{dt} = \frac{d\,\xi(t)}{dt} = r\xi(t)\,\frac{(k - \xi(t)}{k} \qquad 2.13$$

If we neglect all terms of order two and higher in $\xi(t)$, this equation reduces to

$$\frac{d\,\xi(t)}{dt} = r\,\xi(t) \qquad 2.14$$

and the solution of this gives

$$\xi(t) = \xi(o)\, e^{rt}$$

Clearly if the population size is disturbed from a value of zero by a small amount, then the size will tend to grow. The equilibrium size $x^* = o$ is therefore locally and hence globally unstable.

Now let us consider the point $x^* = k$

Following the above procedure, let $x(t) = x^* + \xi(t) = k + \xi(t)$.

Then $$\frac{dx(t)}{dt} = \frac{d\xi(t)}{dt} = r\,(k + \xi(t))\quad\left(1 - \frac{K + \xi(t)}{k}\right)$$

$$= -\,r\,(k + \xi(t))\quad\frac{\xi(t)}{k} \qquad 2.15$$

Neglecting terms of order two or above in $\xi(t)$, this equation reduces to

$$\frac{d\,\xi(t)}{dt} = -r\,\xi(t) \qquad 2.16$$

and the solution of this gives

$$\xi(t) = \xi(o)\ e^{-rt} \qquad 2.17$$

This demonstrates that, if the population size is disturbed slightly from the value k, it will tend to return to k. This equilibrium point is therefore locally stable, though not necessarily globally stable.

A population is globally stable if

i) there is a population size x^* (>o) such that, so long as the population size is greater than 0 at some time t, the population is bound to attain that size and will stay there unless disturbed.

and ii) if the population is disturbed from x^*, so long as x(t) does not become o, the model will drive the population size back to x^*.

In particular, for differential equations of the general form

$$\frac{dx}{dt} = f(\underline{x}, \underline{p}) \qquad 2.18$$

where $\underline{p}$ is the parameter set, Lyapunov has shown that an equilibrium point is globally stable if there exists a function v(x) such that

i) $v(x) \leqslant 0$ for all x

and ii) $\frac{dv(x)}{dt}$ evaluated at $x=x^*$ is greater than 0.

For the logistic model let $v(x) = -(k-x)^2$

Clearly $v(x) \leqslant o$ for all x

and
$$\frac{dv}{dt} = 2(k-x)\ \frac{dx}{dt}$$

$$= 2rx\ (k-x)\ \frac{(k-x)}{K}$$

$$= 2rk\ (k-x)^2 > 0 \quad \text{for all } x > o \qquad 2.19$$

Therefore the equilibrium point $x^* = k$ is globally stable.

2.6.2 How can we relate this mathematical definition of stability to a natural population?

To answer this question it is necessary to consider what information is available concerning the size of the natural population. What the ecologist usually has or can obtain is a series of estimates of the population size over a period of time. These estimates may in fact be actual counts, in which case there is an accurate history of the results of the population dynamics over that period. More often, however, these estimates are relative counts. For example, the number of individuals in a small portion of the habitat is counted and an estimate of the total population size is calculated by multiplying this number by the number of such portions in the habitat. Southwood (1966) has described a number of methods of estimating the size of natural insect populations. Such estimates are subject to sampling errors and, such is the nature of biological data, these errors are likely to be large.

The ecologist can use the sort of data discussed above to decide whether or not the population size is stable, at least over a period of time, in the mathematical sense that I have defined. That is, he must decide whether the population size can be considered to be constant over the period of time, and, if so whether any fluctuations in the population size are of a reasonably small amplitude. The questions now are what do I mean by 'can be considered to be constant' and 'fluctuations are of a reasonable size'.

These questions are perhaps easier to answer if absolute counts are available, however, if we assume that sampling errors are either completely random or highly positively correlated with the absolute counts, then it is relatively simple in many cases to decide whether the size of a population is not constant over a period of time.

The population size cannot be considered to be constant if

i) the size demonstrates a significant increase (e.g. Figure 2.4)

ii) the size demonstrates a significant decrease (e.g. Figure 2.5)

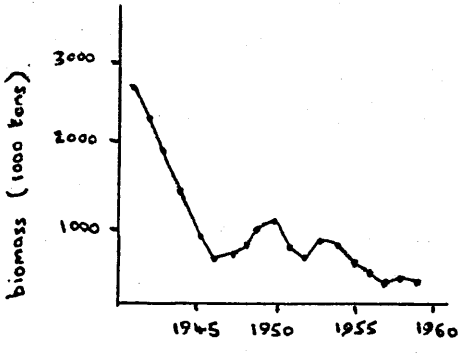

Figure 2.5 Estimated abundance of Pacific Sardines along Pacific Coast of N. America (p. 357 Krebs (1972)).

iii) the size demonstrates definite cycles of regular or irregular period and varying or constant amplitude (e.g. Figure 2. 6)

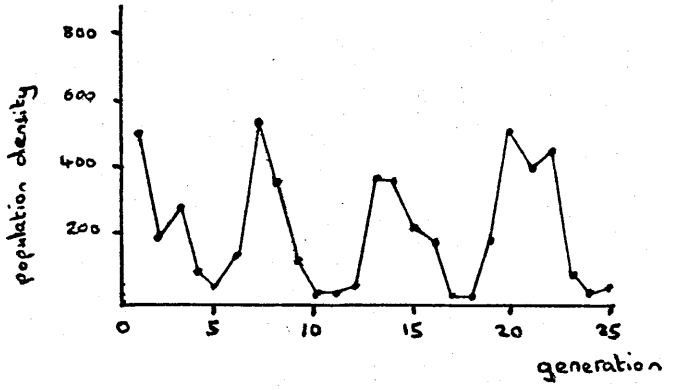

Figure 2.6 Fluctuations in population density of the azuki bean weevil (p. 254 Krebs (1972)).

In many other cases the population size will demonstrate no definite pattern or trend. Are such populations varying, due to a continual perturbation of the controlling parameters, about a constant equilibrium level or are such populations in a completely uncontrolled state?

From a practical point of view I suggest that the answer to this question depends to some extent on the value of the running mean of the population size and especially on the size of the observed fluctuations.

If the population is fluctuating, due to perturbations in the controlling factors, about a constant equilibrium level, then the running mean m(t) (that is, m(t) is the mean population count between the beginning of the time period and time t) is likely to be reasonably constant. Some sensible limits should be set such that, if the running mean goes outside these limits (and stays outside for some time), the population size can no longer be considered to be constant. These limits may be defined statistically, perhaps taking into account known sampling errors, or they may be set by the ecologist using his working knowledge (or indeed a Baysian approach).

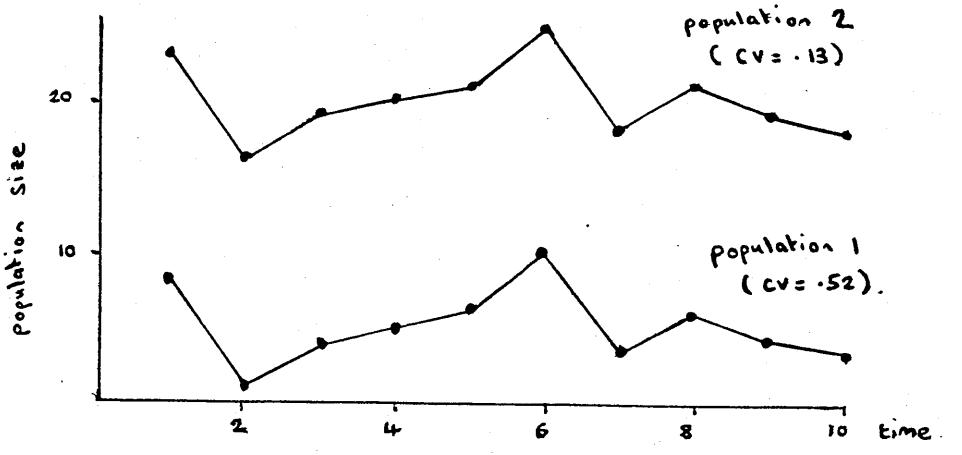

Figure 2.7 Two hypothetical populations (see text).

The value of the running mean determines the equilibrium level of the population size. The size of the fluctuations are the key to determining stability. Clearly different species and different conditions lead to differing potentials for increase, and it may be that species with high intrinsic rates of increase (sometimes labelled r-species) may be inherently more unstable.

However the size of fluctuations must be compared to the size of the mean level in order to give an indication of stability, that is it is the relative size of the fluctuations that is important. I suggest that the coefficient of variation is a suitable indicator of stability.

The coefficient of variation of the population size over a period of time is defined as one hundred times the standard deviation of the size divided by the mean size. The smaller this value, the more likely the population size is to be at a (locally) stable equilibrium.

For example, consider Figure 2.7. It is clear that the hypothetical population 2 is far more likely to be stable, than hypothetical population 1 and this is reflected by the difference in the coefficients of variation which is 52% for population 1 and 13% for population 2.

The coefficient of variation as a measure of variation can only be considered a crude practical guide to stability and may indeed be highly misleading in some cases. A more sophisticated way of measuring the stability of natural populations by assessing the variation of population numbers about mean levels can be provided by stochastic population models an introduction to the theory of which is presented by Bartlett (1960).

2.6.3 Conclusions

The type of population (and hence community) stability relevant to this dissertation is that which pertains to the size of the population (and to the size of the member populations of the community).

The mathematical definition of this stability is precise. In nature it is difficult to apply a parallel definition, but I suggest the following 'practical rule'.

The size of a natural population might be considered to be at a locally stable equilibrium level between times t1 and t2 if

i) the running mean size lies between certain limits

and ii) the coefficient of variation of the size between these times is less than a certain percentage.

The exact values of the critical limits in this rule need further thought and I do not feel qualified to make any suggestions without having examined a large amount of relevant data. However this is not relevant to this dissertation. What I have tried to do in discussing stability is to demonstrate how a particular mathematical definition of stability might be applied to natural populations, and I feel that it is this relationship which should be carefully assessed when interpreting the results from mathematical models.

2.7 Community Structure

In order to define the complexity of a community, it is first necessary to briefly discuss community structure. By community structure I mean the functional relationships within and between species in the community. Functional relationships involve how members of a species relate to their environment and, in particular, this means what food they eat and what physical resources they share with other species. These relationships determine the dynamics of the community population sizes.

If the population size of one species in the community is different in the absence than in the presence of a second species (all other population sizes being held constant), then we say the two species interact. Some interactions are obvious. For instance, individual A may eat individual B. If A and B are from different species, this is a predator-prey relationship. If they are from the same species, this is cannibalism.

Some interactions are not so obvious. For example, Birch (1957) defines competition as follows:

Competition occurs when a number of organisms (of the same or of different species) utilize common resources that are in short supply; or, if the resources are not in short supply, competition occurs when the organisms seeking that resource nevertheless harm one or other in the process.

Williamson (1972) argues that it is not the type of interactions that is important when studying population dynamics but the effect. Following Odum (1953) he lists the following effects:

+ + (e.g. symbiosis)
+ o (e.g. commensalism)
+ - (e.g. predator-prey)
o - (e.g. amensalism)
- - (e.g. competition)

A positive sign (+) indicates that the population size of that species increases in the presence of the other species, a negative sign (-) indicates a decrease and a zero indicates no effect.

Probably the most important effect is the +- effect which is caused by one species eating or living off another. Because species do not eat every other species, it is possible to divide the community into trophic levels. Species at the same trophic level have similar eating habits. For example the community may consist of plants, herbivors and carnivors, each type of organism constituting a trophic level. In practice this 'structuring' of the community is

not straightforward however (and the definition of a trophic level is not clear) and there may be several levels for a particular community.

Another important effect is that caused by competition. Because species in different trophic levels tend to differ biologically, they also tend not to compete. Competition occurs mainly within trophic levels either for food or space. However, many ecologists have argued that competition does not occur in nature, at least where some sort of equilibrium state has been achieved. Gause's (1934) famous experiments involving paramecium led him to suggest that two species with a similar ecology cannot live in the same community. This idea was developed further by Hardin (1960) who states that species in nature are not in competition. Unfortunately experimental and natural evidence for and against this argument are difficult to interpret.

2.8 Community complexity

Krebs (1972) lists five characteristics of a community:

i) species diversity
ii) growth form
iii) dominance
iv) relative abundance
v) trophic structure

Williamson (1972) lists many more properties of a community that may be measured and divides them into four classes:

Class A	Class B	Class C	Class D
richness	stratification	metabolism	vulnerability
diversity	periodism	energetics	stability
complexity	succession	success	
	climax	distribution	
	development		
	latitudinal variation		

Class A are properties related to the number of species. Class B are ecological properties of communities which change through either space or time. Class C relates to the flow of energy through a community. Class D are properties measured on the observed changes of numbers in time.

Notice that Williamson includes complexity as a property of a community that might be measured. At first sight it may appear that the complexity of a community depends on most of these properties. For example, it may be that the greater the stratification, the more complex the community might be considered to be. However, in this chapter we are concerned with investigating the relationship, if any, between community stability and complexity. We have already discussed that the way to investigate this mathematically is to consider the community to be in equilibrium and we have noted that, given the community structure, it is the population dynamics that determines the stability. We then discussed that community structure depends on the species present and how they react with themselves, with each other, and with their environment.

We should therefore include in any list of community properties

i) physical environment (habitat including climate)

and ii) species interactions (includes trophic structure, competition)

The physical environment determines the type and strength of the interactions. (e.g. whether competition occurs).

If a community is assumed to have reached some sort of equilibrium in terms of diversity and population sizes, then such properties as succession, climax and development can be considered to have reached a conclusion. Properties such as energetics and metabolism are contained in the strength of the community food links. Properties such as growth form, dominance, relative abundance, stratification and periodism are the results of the population or community dynamics.

The complexity of the community is therefore determined by

i) the number of species in the community

and ii) the number and the strength of species interactions.

Although in nature the number and strength of species interactions may be subject to great variability, this need not concern us when considering equilibrium conditions.

2.9 Evidence that stability increases as the community becomes more complex.

2.9.1 Introduction

The proposition that community stability increases as the community becomes more complex was widely (wildly?) supported by ecologists in the 1950's and early 1960's. In particular it is a view which was shared by Hutchinson (1959), Elton (1958), Allee, Emerson, Park and Schmidt (1949), and Odum (1953), and it is a theory which was 'proved' to be mathematically valid by MacArthur (1955). I will consider the arguments of three of these authors in more detail and then discuss a field experiment by Pimentel (1961) which was designed to test this proposition.

2.9.2 R.H. MacArthur (1955).

MacArthur (1955) is one of the few authors who has attempted to define community stability. He observed that in some communities the abundances of populations tend to remain quite constant while in other communities they tend to vary considerably. The first type of community we tend to call stable, the second unstable. This observation led him to offer the following qualitative definition of community stability.

Definition: if one species in the community has abnormal abundance at a particular time, the community is unstable if the population numbers of the other species in the community change markedly in abundance as a result of the first.

This definition might be considered identical to saying that if a community is disturbed from an equilibrium in some way, the community is unstable if it fails to return to equilibrium. If all fluctuations tend to die out, the community is stable.

MacArthur following Odum (1953) went on to put forward a qualitative condition for stability. The more choice of food species each species has, the more stable the community. That is, the more complex the community food web, the more stable the community. He rationalised this viewpoint by considering that if one species in the community is particularly abundant, then it will need many predators to dissipate the energy and hence dampen any adverse effects on community stability, and it will need a large number of prey, so that no one prey species is likely to be reduced to a dangerously low level.

MacArthur then attempted to prove mathematically that greater community complexity leads to greater community stability.

He made the following assumptions.

i) The more choice of food a species has, the more stable the community.

ii) If each species in the community has at most only one predator and one prey, stability is minimised.

iii) Community food webs which give identical choice in terms of probabilities have equal stability.

Consider for example the two food webs illustrated below (Figure 2.8) which, by the above assumptions, are required to demonstrate equal stability.

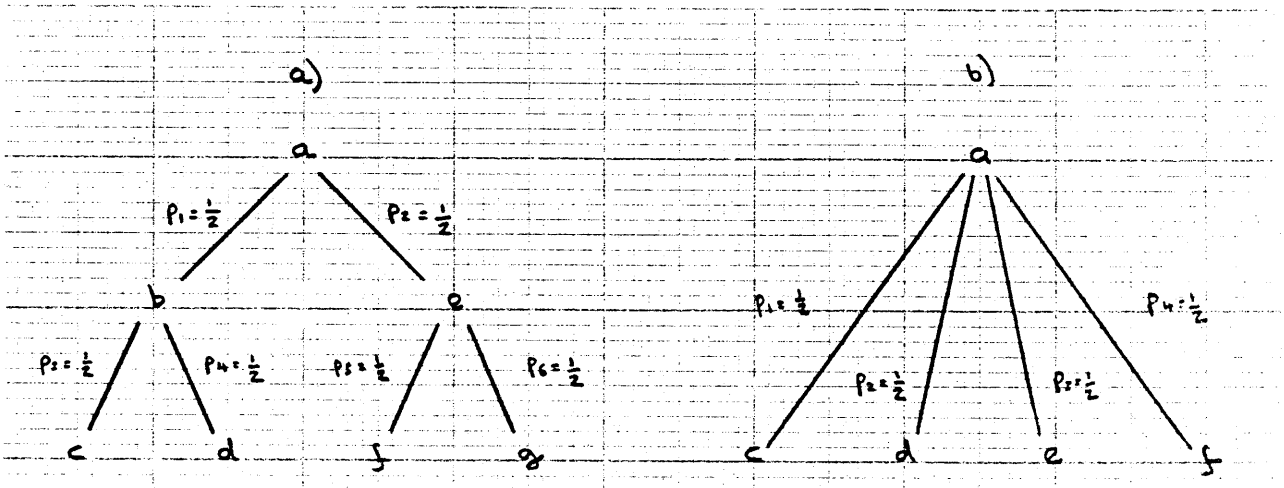

Figure 2.8 Two food webs (a) and b)) with equal stability. See text for explanation (from MacArthur (1955)).

The p_i's in the diagrams represent the proportions of the total number of the prey species of a particular predator formed by the prey species i. For instance, in Figure 2.8 a) p_1 is the fraction of the prey species b and e eaten by the predator a, that is $p_1=\frac{1}{2}$.

Based on these assumptions MacArthur determined to find a function which would measure stability. He realised that these are the assumptions that Shannon and Weaver (1949) used to define the entropy function in communication theory. This function is uniquely determined (apart from a constant) by the assumptions and can be written as

$$S = - \sum_{j=i}^{n} f_j \log (f_j) \qquad 2.20$$

Where S is stability and the f_j are the products of the p_i along each of the n paths through the food web.

For example, for the food web in Figure 2.8 a)

$$S = - (p_1p_3 \log (p_1p_3) + p_1p_4 \log (p_1p_4) + p_2p_5 \log (p_5p_5) + p_2p_6 \log (p_2p_6)$$
$$= \log (4).$$

If this measure of stability is reasonable, a number of interesting observations can be made.

i) Stability increases as the number of links increases.

ii) If the number of prey species for each species remains constant, an increase in the number of species in the community will increase the stability.

iii) A given stability can be achieved either by a large number of species with a fairly restricted diet, or by a smaller number of species each eating a wide variety of the other species.

iv) The maximum stability possible for n species arises when there are n trophic levels with one species on each, eating all species below. The minimum stability would arise with one species eating all the others, these all being on the same trophic level.

One cannot criticise the mathematics associated with MacArthur's argument, but one can argue with both his assumptions and his approach in general. MacArthur's first assumption is that greater choice of prey leads to greater stability. Surely this is just a statement of the 'theorem' he proceeds to prove and this is therefore not surprising.

Of greater significance I feel is that MacArthur based his arguments on statics rather than dynamics. It may be intuitively sensible to associate greater stability with greater choice, however what is also important is the actual numbers of each species present at a particular time. We have seen that these numbers tend to change through time due to unpredictable density independent factors and to density dependent factors. It is the stability of the dynamics of the community that is of interest and it may be that a simple system is far more stable than a complex one.

2.9.3 C. S. Elton

2.9.3.1 C. S. Elton (1958)

Elton (1958) collated six pieces of evidence which he claimed suggested that the 'balance of relatively simple communities of plants and animals is more easily upset than that of richer ones; that is, more subject to destructive oscillations in populations and more vulnerable to invasions'.

This evidence may be listed as follows:

i) mathematical models of simple two species communities tend to be unstable.

ii) laboratory experiments involving simple communities (for instance, Gause (1934)) often show them to be very unstable.

iii) natural habitats on small islands seem to be much more vulnerable to invading species than those of the continents.

iv) invasions and outbreaks most often happen on cultivated or planted land.

v) tropical rain forests, which may be described as having complex communities, do not tend to suffer outbreaks of pests.

vi) pesticides have caused outbreaks by the elimination of predators or parasites from the insect community of crop plants in particular orchards.

Elton concluded that complexity of populations is a property of the community to be studied and used in conservation and he stressed the importance of learning how to manage the environment, using general laws like this, for three ends:

i) to create refuges for wild animals.

ii) to make our surroundings interesting and satisfying.

and iii) to promote the stability of populations and a varied community in which all kinds of compensatory pressures will be exercised on populations.

2.9.3.2 Discussion of Elton's Ideas

Each piece of evidence on which Elton based his conclusions is either directly misleading or can equally well be interpreted in other ways. I shall consider each piece of evidence in turn.

i) Mathematical models of simple two species communities can indeed be unstable, but this is not necessarily so and, as we shall discover, mathematical models of more complex communities can be less stable.

ii) At the time Elton was writing many laboratory experiments including simple communities, especially those conducted by Gause using parameciae, had often shown such communities to be unstable. At the same time, there was little evidence from laboratory experiments that more complex communities were more likely to be stable. Further, laboratory communities are by their nature artificial and this, as we shall discuss later, may be important.

iii) Elton's third piece of evidence, that natural habitats on small islands tend to be more vulnerable to invasions than those of the continents, highlights another important point. Elton's 'definition' of stability includes resistance to invasion, whereas the definition I have decided upon essentially does not. The addition of a species to the community in effect initially makes that community more complex by creating new interactions and changing the strength of existing ones. What then happens to the community in terms of stability must surely depend on what

effect these changes have on the community population dynamics. It could thus be argued that invasion causes increased complexity which causes instability! It might also be argued that similar effects in continental habitats are difficult to measure because it is not easy to actually isolate communities in the same way.

iv) As indicated in ii) above, unnatural communities may tend to be unstable not because they are often simple but because they are artificial.

v) That tropical rain forests contain complex communities which do not tend to be subject to outbreaks has until lately appeared to have been true. The composition of such communities has evolved over a very long period of time in what is essentially a very stable environment (i.e. the environmental parameters remain relatively constant). Recently the stability of such habitats has been attacked (for instance, large areas of forest are being cleared) and consequently outbreaks and extinctions have occurred. So is it evolution, stability of environment, or complexity, or all of these which determine the stability of the community?

vi) The fact that the elimination of predators or parasites from insect communities of crop plants can lead to outbreaks can again equally well be attributed to the unnaturalness of crop communities, or indeed to the delicate balance of any community, regardless of its complexity. Removal of a species from a community will lead to the elimination of a number of interactions and the modification of others, and this may change the community population dynamics significantly. The community will need to find a new stable balance which, assuming little or no immigration of new species, will be a community containing less species!

2.9.4 G. E. Hutchinson

2.9.4.1 G. E. Hutchinson (1959)

In his presidential address to the American Society of Naturalists in December 1958 G. E. Hutchinson (1959) posed the question 'why are there so many species?' This question is, of course, fundamental to the theme of this chapter. Central to his discussion is the importance of food chains and, in particular, the importance of the interrelation of food chains.

A food chain consists of several species arranged in a hierachy such that each species eats the next species in the chain.

e.g. pine tree - aphids - spiders - warblers - hawks

Elton (1927) was one early ecologist who recognised that food chains tend to be interrelated with other food chains to form food webs.

If a predator has more than one prey to choose from, the predator is less likely to become extinct if its favoured prey becomes scarce. Hutchinson felt that, at the time of writing, ecological theory said that there is great diversity of organisms because communities of many diversified species are better able to persist than are communities of less diversified species. He also suggested that the addition of a new species to a community, although likely to reduce the average population of the species originally present in niches the new species may share, may reduce fluctuations and hence lead to greater community stability. Hutchinson went on to suggest that, because there are not more species than there are, there must be some limit to the complexity of food webs. This limit may be set by such factors as niche size and spatial heterogeneity.

2.9.4.2 Discussion

Hutchinson's paper clearly reflects the general view of the times that the more complex a community the more stable it is likely to be. It is strongly influenced by MacArthurs' apparent theorm, and can again be criticised for using aguments concerned with static

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relationships rather than dynamic. Further, although there is some discussion concerning food webs, there is no clear definition of either complexity or stability.

2.9.5 Pimentel

2.9.5.1 D. Pimentel (1961)

Pimentel (1961) proposed three hypotheses regarding the relationship between community stability and complexity which are based on the views and observations of such authors as Elton, Hutchinson and A. J. Nicholson (1933). They are as follows:

i) diversity of host or prey species provides alternative food for the parasites and predators, and this leads to greater stability.

ii) diversity in types of parasitic and predaceous species feeding on one species of herbivore leads to greater stability.

iii) increased diversity of feeding habits of the species members of the community leads to greater stability of the organisation.

Pimentel tested these hypotheses in the field by carrying out an experiment involving the animal community associated with the family of species Brassica oleracea L. (Cruciferae) which includes cabbage, collards, Brussels Sprouts and kale.

B. oleracea plants were planted in a 15-year fallow field in which approximately three hundred species of other plants and an estimated three thousand species of heterotrophs already existed. This plot constituted a 'mixed-species' planting or complex community. At the same time another field, which was separated sufficiently from the fallow field to minimise migration and which contained no other species, was planted with the same varieties of B. oleracea.

This plot constituted a 'single-species' planting or simple community.

One hundred plant samples from each field were collected weekly during the summer months for two consecutive years, and the animal populations were identified and counted. These animals were mainly insects and included Lepidoptera, Homoptera, Hemiptera, Coleoptera, Diptera, Hymenoptera, Neuroptera and Arachnida.

The results can be summarised as follows:

i) In 1957, 27 taxa were associated with B. oleracea grown in the mixed-species planting and 50 taxa were associated with it in the single-species planting. In 1958, the figures were 39 and 50 respectively.

ii) There were three to four times as many parasitic and predaceous taxa present in the single-species planting than is the mixed-species planting.

iii) Aphids, flea beetle, and lepidopteran populations at times reached outbreak levels in the single-species planting, but never in the mixed-species planting.

iv) There were more host and prey type species present in the mixed-species planting.

v) There was a greater diversity of parasites and predators in the mixed-species planting.

vi) Predominant in the single-species planting were coccinellids and syrphids which are specific eaters which attack mainly aphids. In the mixed-species planting spiders existed. These are relatively non-specific feeders and tend to attack whatever is abundant at the time.

Pimentel concluded from results i)to iii)that the single-species planting was far less stable than the mixed species planting, and that results iv)to vi)lend support to his hypotheses i)to iii) respectively. Since these hypotheses are concerned with properties of complex communities and the mixed-species planting was essentially more complex than the single-species planting, Pimentel is suggesting that his results support the theory that, in general, increased community complexity gives increased stability.

2.9.5.2 Discussion of Pimentel's paper

At first sight Pimentel's conclusions may seem reasonable. However, I feel that the following criticisms are relevant.

The results do suggest that the 'simple' community is not at a stable equilibrium, but there is no clear evidence to suggest that the 'complex' community is anywhere near a stable equilibrium, and indeed it may be that this community is equally or even less stable. Further, both the 'simple' and 'complex' communities studied are infact subcommunities. They are the communities of animals associated with the family of species Brassica oleracea L. in each field. It is not clear how complex the complete communities were or how strong the links were between the subcommunity and the rest of the community in each case.

Also both communities were subject to invasion by other species. Essentially this means that the complexity of each community was continually changing and hence that the nature of the population dynamics involved were continually changing also. It will be seen later (Section 2.11) by using mathematical models what effect this might have on stability.

It is also important to note that Pimentel only studied two levels of complexity and hence his experimentwas inadequate to 'prove' any general relationship between stability and complexity.

Two less important points which perhaps did not have a significant effect on the results are firstly that the communities were both somewhat artificial and secondly that each community lived under different environmental conditions.

These criticisms essentially say two things about experiments like Pimentel's. Firstly it is important to define terms such as complexity and stability clearly, and secondly it is very difficult, perhaps impossible, to 'design' useful field trials to investigate any relationship between complexity and stability.

2.10 Evidence that the relationship between stability and complexity is not straightforward.

2.10.1 Introduction

By the mid-1960's the popular view discussed in Section 2.9 was being challenged far more strongly. Watt (1965) and Paine (1966) were two ecologists who put forward evidence and ideas which pointed to a less certain relationship between complexity and stability.

2.10.2 K. E. F. Watt

2.10.2.1 Watt (1965)

Watt (1965) discussed community stability and the strategy of biological control. He recognised two contrasting theories concerning the relationship between community structure and stability and the importance of the theories in determining an effective strategy for the biological control of pest species. On the one hand he pointed to the observations and theories of those such as Elton and MacArthur who advocate that stability increases as the number of links in the community increases. On the other hand in particular he quoted Zwölfer (1963).

Zwölfer analysed the structure of parasite complexes of six species of Lepidoptera. In each case that he considered the host species was attacked by at least one biologically specialised and synchronised parasite species, but in two of the six cases the parasites were

subjected to heavy competition by other parasites. In these two cases the mixture of parasites failed to control the host abundance to low levels, whereas in the other more simple cases the parasites reached a high efficiency against their hosts (i.e. the ratio of parasitised hosts to all hosts was high).

These observations caused Watt to note that there was a need to develop a more sophisticated theory of community stability. In an attempt to do this Watt looked to two sources of information. First he looked in the literature of pest population dynamics and found that in general most unstable pests, that is pests whose populations fluctuate widely, have a wide range of natural enemies, for example grasshoppers (Edwards (1964)). Secondly he analysed some data from the Canadian Insect Forest Survey (McGugan (1958), Prentice (1962, 1963)).

In particular Watt considered data concerning one particular type of insect, Macrolepidoptera (moths and butterflies), and attempted to determine

i) the effect of the number of tree host species on the stability and abundance of forest Macrolepidoptera.

and ii) the effect of the number of insect species eating the same host plants on the stability and abundance of a particular species of forest Macrolepidoptera.

Watt measured abundance by the mean arithmetric mean count (that is, the mean over all species of the mean counts for each individual species over time), and he measured stability by the mean standard error of logarithms of counts.

The statistics relating to i) above are plotted in Figures 2.9 and 2.10. Solitary and gregarious species are treated separately because both abundance and instability were generally greater for gregarious larval feeders than for solitary larval feeders. It it clear from these graphs that, for both solitary and gregarious species, mean abundance tended to be higher and stability to be lower in euryphagous species (that is, species which eat widely) than in

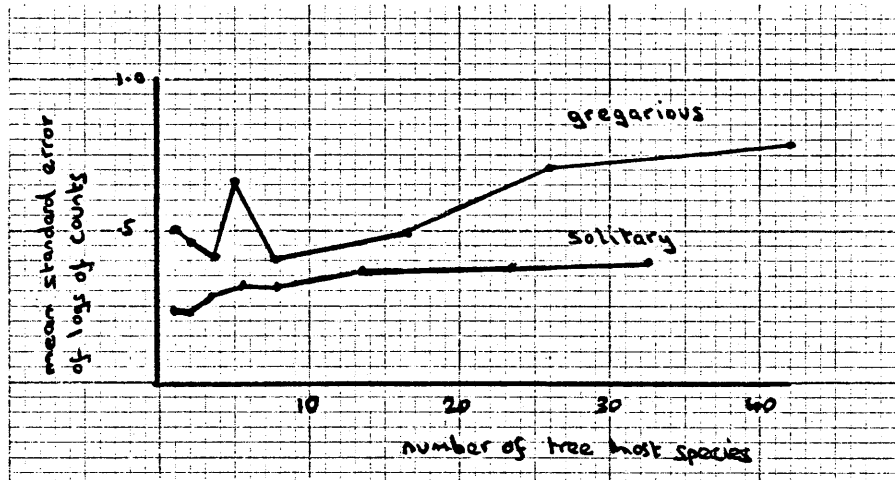


Figure 2.10 Effect of number of tree host species on stability of forest Macrolepidoptera.

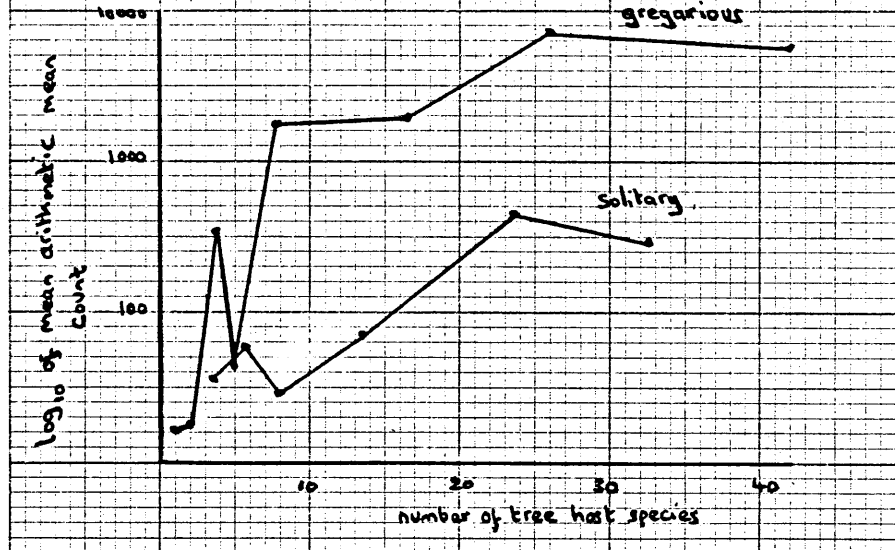
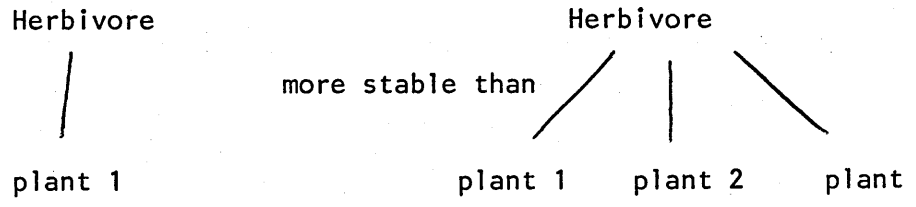


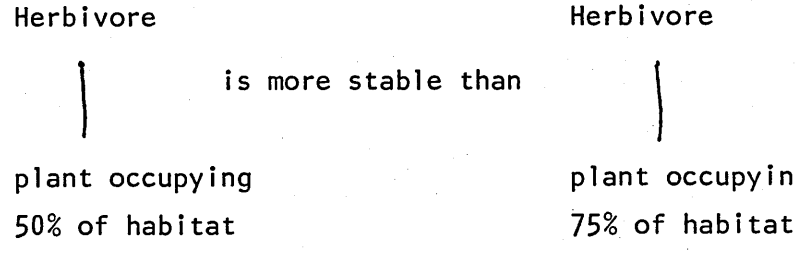
Figure 2.9 Effect of number of tree host species on abundance of forest Macrolepidoptera.

stenophagous species (that is, species which feed on a narrow range of food).

This suggests that the stability of a herbivore decreases as the number of links between it and its food increases. This is represented pictorially below.



This conclusion presented Watt with a dilemma because he was aware of a number of contrasting examples. For instance, the spruce budworm, which is a very unstable species, feeds principally on only two hosts, the balsam fir and the white spruce. However, these two species do fill a large proportion of the environment of the spruce budworm and hence Watt concluded that stability decreases with the proportion of the environment which is filled with food.



The statistics relating to ii) above are plotted in Figures 2.11 and 2.12. Watt considered the mean number of insect species eating the same host plant to be a measure of the number of different species that utilise the same food resources. He then assumed that whenever two or more species were known to eat the same host plant there was competition and that this competition was more intense the greater the number of species eating the same array of plants.

It thus follows from the graphs that, for both gregarious and solitary species, abundance was least where competition was most

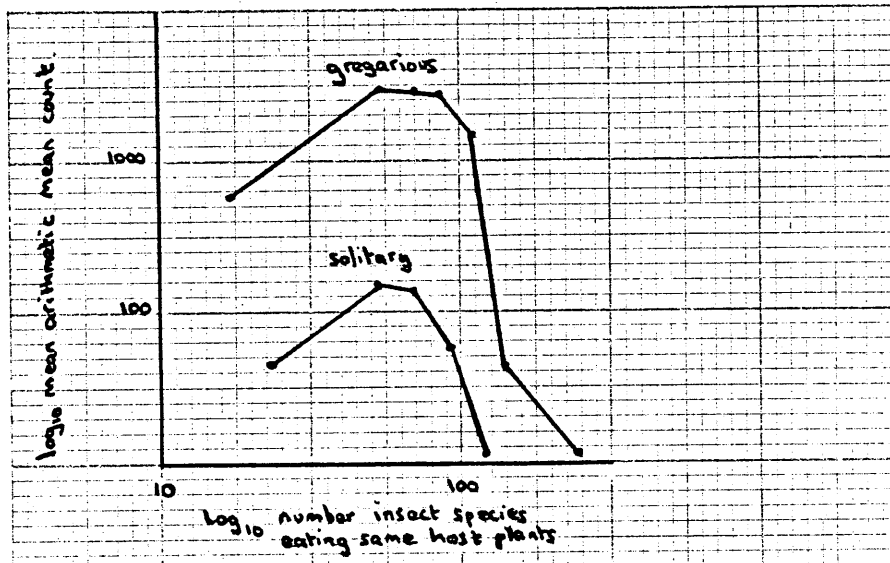


Figure 2.11 Effect of number of insect species eating same host plants on abundance of a particular species of forest Macrolepidoptera.

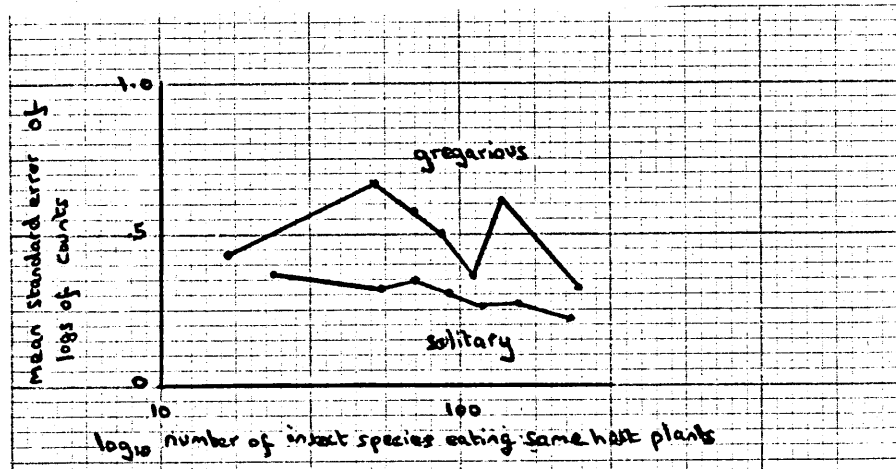


Figure 2.12 Effect of number of insect species eating same host plants on stability of a particular species of forest Macrolepidoptera.

intense but that stability of a species was greater the greater number of competing species it had.

Watt then put forward a hypothesis which aimed to explain both these results and observations and those of Zwölfer mentioned above. Essentially Zwölfer found that increased competition at the parasite trophic level caused instability of the host (the host escaped control). However Watt interpreted this result as being due to excessive competition within the parasite trophic level forcing excessive stability on that trophic level. Watt's hypothesis thus became three propositions.

i) Stability of a trophic level increases with the number of competing species at that level.

ii) Stability of a trophic level decreases with the number of competing species that feed on it.

iii) Stability of a trophic level decreases with the proportion o the environment containing useful food.

2.10.2.2 Discussion of Watt's ideas

It is essential to note firstly that Watt has investigated the effect of increased complexity within a particular trophic level on the stability of that trophic level or of a higher or lower trophic level. He did not look at a complete community and compare its complexity with its stability. Further we might criticise Watt's measurement of both stability and complexity. His measurement of stability firstly does not take into account the relative size of fluctuations when compared to the mean abundance and secondly does not contain an indication of how large the sampling errors were. His measurement of complexity does not take into account the relative strengths of interactions and his evidence that there is real competition for resources is somewhat vague.

In fact his proposition iii) is a good example of the importance of the strength of interactions because essentially it says that a few strong interactions (e.g. two plant species comprising 90% of a herbivore's food) may have the same effect on stability as many interactions of low strength (e.g. ten plant species comprising

90% of a herbivore's food).

However Watt's argument is useful to my main theme if we accept these above criticisms. Whenever a complexity effect has led to instability of a trophic level we know that the whole community was unstable. Whenever a complexity effect led to increased stability we are not quite so sure of the effect on the stability of the whole community. We therefore have evidence that the relationship between complexity and stability is not in general straightforward but depends very much on the strength, nature and number of interactions between trophic levels.

2.10.3 R. T. Paine

2.10.3.1 Paine (1966)

Paine (1966) offered some interesting observations and experimental evidence concerning the hypothesis that local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites by one species. This hypothesis is a modification of the complexity begets stability theme because it suggests that the actual composition of the community is important, that is the efficiency of the predators.

Paine defined a subweb as a group of organisms capped by a terminal carnivore and trophically interrelated in such a way that at higher levels there is little transfer of energy to co-occurring subwebs. He observed three such subwebs involving marine intertidal zones, one in a north temperate climate, one in a subtropical climate and one in a tropical climate.

The north temperate subweb, which was located at Mukkaw Bay, Washington is represented schematically below (Figure 2.13).

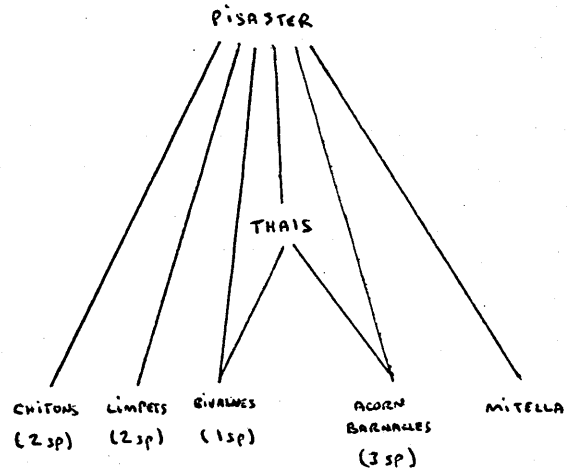


Figure 2.13 The Pisaster dominated subweb at Mukkaw Bay (from Paine (1966)).

There were two carnivorous species, Pisaster and Thais. Both these predators ate barnacles as their main prey, although the barnacles calorific value to Pisaster was only a third of bivalve or chiton.

Since 1963 a typical piece of the shoreline at Mukkaw Bay has been kept free of Pisaster and has been compared against a control area which was left unaltered. At first it was observed that the barnacle Balanus glandula spread to occupy between 60 and 80 per cent of the available space. There has since continued a successive replacement of species by more efficient utilisers of space. The control area did not change.

Paine observed the following from this field experiment.

i) The removal of Pisaster reduced the community from a fifteen species to an eight species system.

ii) The standing crop was increased.

iii) The area became trophically simpler.

iv) A food chain not containing Pisaster was removed. This indicates that a number of food chains may have been strongly influenced by Pisaster, but by an indirect method.

These observations tend to disagree with the complexity begets stability theory. In the absence of predation the community tends towards simplicity.

Paine then built on his theme that local diversity is related to the efficiency with which predators prevent monopolization of major environmental requisites by one species by comparing the three subwebs. All three subwebs contained one or two species capable of monopolising much of the space, but this only happened in the tropical subweb. In the other two areas there were top predators which ate masses of space-consuming species and therefore prevented monopolies. When a top predator was artificially removed, the systems converged towards simplicity.

This evidence again leads to a conclusion that stability increases/decreases with complexity is far to naive an argument and that the actual composition of the food web is important.

2.10.3.2 Discussion of Paine's paper

Although Paine only considered subcommunities, his observations and field experiments give particularly strong evidence that the actual composition of the food web is extremely important in determining stability. The removal of just one species (which is equivalent to removing a number of interactions and modifying the strength of others) from what appears to be a stable subcommunity led to the extinction of six other species before the subcommunity began to approach a further stable equilibrium.

In particular Paine observed the effect of predators, showing that species diversity within a subcommunity appears to depend on the number of predators and their efficiency in preventing other species from monopolizing some important, limiting, requisite. This efficiency is directly related to the strength and nature of the interactions between the predators and their prey (and each other) and hence his conclusions are likely to apply at all trophic levels. Again this is evidence that it is the actual structure of the community that is important in determining stability.

2.11 The use of mathematical models to investigate relationships between community stability and complexity.

2.11.1 Introduction

As discussed in Section 2.5 one way of modelling population dynamics is to use differential equations. In this Section we will investigate the relationship between the stability of differential equation models of community dynamics and the complexity of the community. We consider first an argument put forward by May (1971) that stability tends to be less the more species there are in the community model. This is clearly in direct conflict with the thoughts of MacArthur, et. al. We then consider some simple models in more detail and show that conclusions are not so straightforward.

Finally we will discuss the work of Gardner and Ashby (1970) and some further work by May (1972b) in an attempt to seek a general conclusion.

2.11.2 May's argument

May (1971) considered Elton's (1958) assertion that mathematical models of simple communities tend to be unstable whereas models of more complex communities are likely to be stable. May assumed that the type of model Elton was referring to was the Lotka-Volterra model of a predator-prey community (equations 2.6a and b), the equations of which are repeated here for convenience.

$$\frac{dh}{dt} = h\,(r - \alpha p) \qquad 2.21$$

$$\frac{dp}{dt} = p\,(-s + \beta h) \qquad 2.22$$

where h represents the prey population density and p the predator population density.

In order to determine whether these equations have any (non-trivial) equilibria we attempt to find h^* and p^* such that $\frac{dh}{dt}$ and $\frac{dp}{dt}$ are both equal to zero when evaluated at (h^*, p^*).

That is,

$$\left.\frac{dh}{dt}\right|_{(h^*,p^*)} = \left.\frac{dp}{dt}\right|_{(h^*,p^*)} = 0 \qquad 2.23$$

Let $A = \begin{pmatrix} 0 & -\alpha \\ \beta & 0 \end{pmatrix}$, 2.24

$$\underline{x} = \begin{pmatrix} h \\ p \end{pmatrix}, \qquad 2.25$$

and $\underline{r} = \begin{pmatrix} r \\ -s \end{pmatrix}$ 2.26

For $\frac{d\underline{x}}{dt} = \begin{pmatrix} \frac{dh}{dt} \\ \frac{dp}{dt} \end{pmatrix} = 0$

We require

$$\underline{r} + A\underline{x} = 0 \qquad 2.27$$

That is $$\underline{x} = -A^{-1}\underline{r} \qquad 2.28$$

Where A^{-1} is the matrix inverse of A

Thus

$$\underline{x^*} = \begin{pmatrix} h^* \\ p^* \end{pmatrix} = -\frac{1}{\alpha\beta}\begin{pmatrix} 0 & \alpha \\ -\beta & 0 \end{pmatrix}\begin{pmatrix} r \\ -s \end{pmatrix} \qquad 2.29$$

and hence the (unique) positive equilibrium population sizes are given by

$$h^* = s/\beta \text{ and } p^* = r/\alpha \qquad 2.30$$

We now need to determine whether the equilibrium values are stable.

We disturb the community from equilibrium by adding small perturbations ε and ψ to h* and p* respectively and investigate the ensuing population dynamics.

$$\frac{dh}{dt} = \frac{d}{dt}\ (h^* + \xi)$$

$$= \frac{d\xi}{dt}$$

$$= (h^* + \xi)\ (r - \alpha(p^* + \psi))$$

$$= (h^* + \xi)\ (-\alpha\psi) \qquad 2.31$$

since $r - \alpha p^* = 0$

Ignoring terms of order $\xi\psi$ we obtain

$$\frac{d\xi}{dt} = -\alpha h^* \psi \qquad 2.32$$

Similarly

$$\frac{d\psi}{dt} = \beta p^* \xi \qquad 2.33$$

We can combine equations 2.32 and 2.33 in a matrix equation

$$\frac{d\underline{\xi}}{dt} = A^* \underline{\xi} \qquad 2.34$$

where

$$\underline{\xi} = \begin{pmatrix} \xi \\ \psi \end{pmatrix} \qquad 2.35$$

and

$$A^* = \begin{pmatrix} 0 & -\alpha^* \\ \beta^* & 0 \end{pmatrix} \qquad 2.36$$

where $\alpha^* = \alpha h^*$ 2.37

and $\beta^* = \beta p^*$ 2.38

May calls A* the community matrix.

The solution of equation 2.34 may be written as

$$\underline{\xi} = \underline{c}\, e^{\lambda t} \qquad 2.39$$

where $$\underline{c} = \begin{pmatrix} C_1 \\ C_2 \end{pmatrix} \qquad 2.40$$

are constants which depend on the initial size of the perturbations and λ is an <u>eigenvalue</u> of the matrix A*.

For the equilibrium to be stable we require that the real part of the eigenvalue λ is negative (because in this case $e^{\lambda t}$ will approach zero at t becomes large).

λ is an eigenvalue of A* if the <u>characteristic equation</u>

$$|A^* - \lambda I| = 0 \qquad 2.41$$

where $$I = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \qquad 2.42$$

and $|A|$ denotes the determinant of A.

$$|A^* - \lambda I| = \begin{vmatrix} -\lambda & -\alpha^* \\ \beta^* & -\lambda \end{vmatrix} \qquad 2.43$$

The characteristic equation is thus

$$\lambda^2 + \alpha^* \beta^* = 0 \qquad 2.44$$

The solutions of this equation are

$$\lambda = \pm\, i\, (\alpha^* \beta^*)^{\frac{1}{2}} = \pm\, \omega\, i \qquad 2.45$$

and hence

$$\underline{\xi} = \begin{pmatrix} \xi \\ \psi \end{pmatrix} = \begin{pmatrix} C_{11} \sin(\omega t + C_{12}) \\ C_{21} \sin(\omega t + C_{22}) \end{pmatrix} \qquad 2.46$$

This means that the size of the predator and prey populations will oscillate about their equilibrium levels (equation 2.30) with constant amplitudes and period until further disturbed, the size of the amplitudes depending on the size of the initial perturbations.

This model is therefore not stable in the sense that the population sizes do not return to the equilibrium values after perturbation.

May then went on to consider a model of a community which contains n predators and n prey. The equations are as follows:

$$\frac{dh_i}{dt} = h_i \left(r_i - \sum_{j=1}^{n} \alpha_{ij} p_j\right) \qquad i=1,\ldots,n \qquad 2.47$$

$$\frac{dp_i}{dt} = p_i \left(-s_i + \sum_{j=1}^{n} \beta_{ij} h_j\right) \qquad i=1,\ldots,n \qquad 2.48$$

where h_i and p_i denote the population sizes of the i prey and predator species respectively.

The equilibrium levels are given by

$$\underline{h}^* = B^{-1} \underline{s} \quad \text{and} \quad \underline{p}^* = A^{-1} \underline{r} \qquad 2.49$$

where $\underline{h}^* = (h_1^*,\ldots,h_n^*)'$, $\underline{p}^* = (p_1^*,\ldots,p_n^*)'$

$$\underline{s} = (s_1,\ldots,s_n)' \quad , \quad \underline{r} = (r_1^*,\ldots,r_n^*)'$$

$$A = (\alpha_{ij}) \text{ and } B = (\beta_{ij}) \qquad 2.50$$

(The dash' denotes vector transpose)

May assumed that the values of the parameters are such that the equilibrium levels are all finite and positive. I feel that it is important to note that there are conditions on the values of the parameters which dictate whether such valid equilibriums exist. The more complex community may not be so likely to have a valid equilibrium.

The characteristic equation of this system is given by

$$\begin{pmatrix} -\lambda I & -A^* \\ +B^* & -\lambda I \end{pmatrix} = 0 \qquad 2.51$$

where $A^* = (\alpha_{ij} h_i^*)$, $B^* = (\beta_{ij} p_i^*)$ and I = the nxn identity matrix.

It can be shown that this equation is a polynominal of degree n in λ^2 and consequently it has n pairs of roots of the form

$$\lambda = \pm (x + iy)$$

It is clear therefore that either each pair of roots is pure imaginary (i.e. x=0) or there exists at least one root such that $x \neq 0$. In this case clearly one root of the pair will have a positive real part (i.e. either x>0 or -x>0)

This means that the more complex community described by equations 2.47 and 2.48 either has the same stability properties as the two species predator-prey community, that is the population sizes of each predator and each prey oscillate with constant amplitude through time, or there exists an eigenvalue with a positive real part and the community is unstable.

May then attempted to generalise this result by considering a n species community modelled by the following equations

$$\frac{dx_i}{dt} = k_i(\underline{x}) \quad , \quad i=1,\ldots,n \qquad 2.52$$

where $k_i(\underline{x}) = f_i(x_i)\, g_i(x_1,\ldots,x_{i-1}, x_{i+1},\ldots,x_n)$

and the equation $f_i(x_i) = 0$ has the unique solution $x_i = 0$.

Otherwise the functions f_i and g_i are completely arbitrary.

For there to exist an equilibrium set of finite and positive population sizes $x^* = (x_1^*, \ldots\ldots, x_n^*)$ we require that

$$g_i(x^*) = 0 \qquad \text{for all } i \in \{1, \ldots\ldots, n\} \tag{2.53}$$

Assuming that this is the case we can examine the stability of this equilibrium as follows:

Let $x_i = x_i^* + \varepsilon_i \qquad (i=1, \ldots\ldots, n)$ 2.54

Then $\frac{dx_i}{dt} = \frac{d\varepsilon_i}{dt} = k_i(x^* + \varepsilon)$ 2.55

where $\varepsilon = (\varepsilon_1, \ldots, \varepsilon_n)$

Thus $\frac{d\varepsilon_i}{dt} \doteq k_i(x^*) + \sum_{j=1}^{n} \varepsilon_j \frac{\partial k_i(x^*)}{\partial x_j}$ 2.56

(by expanding $k_i(x^* + \varepsilon)$ as a Taylor Series and neglecting terms in ε of order 2 and above)

$$= \sum_{j=1}^{n} \varepsilon_j \frac{\partial k_i(x^*)}{\partial x_j} \tag{2.57}$$

$$= \sum_{j=1}^{n} \varepsilon_j \left(\frac{\partial f_i(x_i^*)}{\partial x_j} g_i(x^*) + f_i(x^*) \frac{\partial g_i(x^*)}{\partial x_j} \right) \tag{2.58}$$

$$= \sum_{j=1}^{n} \varepsilon_j f_i(x_i^*) \frac{\partial g_i(x^*)}{\partial x_j} \tag{2.59}$$

The characteristic equation for this model can therefore be written as

$$|A - \lambda I| = 0 \tag{2.60}$$

where $A = (a_{ij}) \qquad (i,j=1, \ldots, n)$ 2.61

such that $a_{ii} = 0$ and 2.62

$$a_{ij} = f_i(x_i^*) \frac{\partial g_i(x^*)}{\partial x_j} \qquad 2.63$$

Because the diagonal elements of the community matrix A are all zero it can be shown that the coefficient of λ^{n-1} in the characteristic equation (equation 2.60) vanishes. Hence the sum of the n roots λ_k of the equation must vanish.

That is $$\sum_{k=1}^{n} \lambda_k = \sum_{k=1}^{n} x_k + iy_k = 0 \qquad 2.64$$

Therefore either

i) all the x_k are zero and the roots are pure imaginary

or ii) atleast one root has a positive real part
($x_i = - \sum_{k \neq i} x_k > 0$)

So this more general model displays similar stability properties to the n predator-n prey Lotka-Volterra model. May commented that, apart from the mild restrictions already mentioned, the general model may be arbitrarily complex. He commented further that the inclusion of such factors as time delay, predator saturation, predator switching and density-dependent fecundity are not likely to significantly alter the picture. He concluded that 'if we contrast simple few-species mathematical models with the analagously simple multispecies models, the latter are in general less stable that the former.'

I feel that this is a somewhat premature and unfair conclusion from this particular argument. Certainly May has achieved his main objective which was to demonstrate that Elton's assertion that mathematical models of complex communities tend to be more stable than models of simple communities is false. However his argument does not demonstrate that the converse is true.

What he does show is that, in general, differential equation models of n species communities with no species self-interaction are unstable (or at best purely oscillatory). He does not demonstrate that, for such models, as n increases the models become less stable in some way (e.g. the positive real part of the dominant eigenvalue increases as n increases). Also this result holds for n=1 and infact, when n=1, it is only when the interaction is predator-prey that the model is necessarily purely oscillatory. Therefore essentially May is demonstrating that differential equation models of predator-prey communities with no species self-interaction are unstable.

I feel that the most important inference from these results is that species self-interaction is essential for stability to be feasible. Therefore is order to investigate the relationship between stability and complexity it is sensible to include such interactions in the models.

This I attempt to do in the next section.

2.11.3 Models of communities consisting of only 1 species

2.11.3.1 Simple exponential growth

The model is

$$\frac{dx}{dt} = rx \qquad 2.65$$

where x is the size of the population at time t
and r is the intrinsic rate of increase (see Section 2.5)

The solution of this model is

$$x = x_o e^{rt} \qquad 2.66$$

where x_o is the size of the population at t=o

If r >o, the population grows uncontrolled.
If r =o, the population remains at x_o (i.e. is at equilibrium) but is unstable.
If r >o, the population becomes extinct.

These results are summarised in the following table.*

r	equilibrium	stable
>o	no	-
=o	yes	no
<o	no	-

Table 2.1 Equilibrium and stability properties of simple exponential growth.

* We ignore equilibrium values $\leq o$ throughout this discussion.

So the simplest differential equation model of the simplest community, that is one containing only one species and that species does not interact with itself, does not have a stable equilibrium. Infact it only exhibits an equilibrium value in the trivial case when r=o, and this is clearly unstable because every value of x is potentially an equilibrium point, but if the population size is disturbed from x it will remain at the new value until disturbed again.

2.11.3.2 Self-interaction

Now let us suppose that the one species in our community interacts with itself. We might model the population dynamics of this community with the following differential equation:

$$\frac{dx}{dt} = rx + \alpha x^2 = x(r+\alpha x) \qquad 2.67$$

We first determine any potential equilibrium values of x. If x* is an equilibrium value, then $\frac{dx}{dt}$ evaluated at x=x* is zero.

$$\text{i.e.} \quad \left.\frac{dx}{dt}\right|_{x^*} = 0 \qquad 2.68$$

But $\left.\frac{dx}{dt}\right|_{x^*} = x^*(r + \alpha x^*)$ 2.69

$\therefore$ $x^* = 0$ and $x^* = \frac{-r}{\alpha}$ are (potentially) equilibrium values.

For a positive equilibrium value to exist we require r and α to be of opposite signs.

To determine whether this equilibrium point is stable or unstable

Let $x = x^* + \xi$ where ξ is a small disturbance.

Then $\frac{dx}{dt} = \frac{d}{dt}(x^* + \xi) = \frac{dx^*}{dt} + \frac{d\xi}{dt}$ 2.70

$= \frac{d\xi}{dt}$ 2.71

$= (x^* + \xi)\ (r + \alpha(x^* + \xi))$ 2.72

$= (-\frac{r}{\alpha} + \xi)\ (r + \alpha(-\frac{r}{\alpha} + \xi))$ 2.73

$= (-\frac{r}{\alpha} + \xi)\ (r - r + \xi\alpha)$ 2.74

$\simeq -r\xi$ (ignoring terms in ξ of order 2 & higher) 2.75

Ignoring the trivial case r=o, the equilibrium is stable if r >o and unstable if r <o.

We can summarise the results in the following table:

		results from no interaction model		results from self-interaction model	
r	α	equilibrium	stable	equilibrium	stable
>o	>o	no	–	no	–
>o	<o	no	–	yes	yes
<o	>o	no	–	yes	no
<o	<o	no	–	no	–

Table 2.2 Equilibrium & stability properties of a one-species self-interaction model.

So the more complex community consisting of one species with self-interaction can have a stable equilibrium, and hence can be more stable than the one species with no interaction community. Making the simple community more complex by adding an interaction can lead to stability. Note, however, that we cannot demonstrate the converse, that is removing the interaction from an unstable situation might lead to stability, because the simpler model does not have an equilibrium.

2.11.4 Models of communities consisting of two species

Let our community now consist of two species initially obeying the following differential equations:

$$\frac{dx_1}{dt} = r_1 x_1 + \alpha_1 x_1^2 \qquad 2.76$$

$$\frac{dx_2}{dt} = r_2 x_2 + \alpha_2 x_2^2 \qquad 2.77$$

The two species do not interact with each other. The complexity of this community is described by the fact that there are two species and two self-interactions. The properties of the community in terms of equilibrium values and stability can be determined from Table 2.2

Suppose that we add an interaction between the two species. The equations might become:

$$\frac{dx_1}{dt} = r_1 x_1 + \alpha_1 x_1^2 + \beta_1 x_1 x_2 = x_1 (r_1 + \alpha_1 + \beta_1 x_2) \qquad 2.78$$

$$\frac{dx_2}{dt} = r_2 x_2 + \alpha_2 x_2^2 + \beta_2 x_1 x_2 = x_2 (r_2 + \alpha_2 x_2 + \beta_2 x_1) \qquad 2.79$$

Using the method of Section 2.11.2 we can determine whether there is a (non-trivial) equilibrium.

Let $$A = \begin{pmatrix} \alpha_1 & \beta_1 \\ \beta_2 & \alpha_2 \end{pmatrix} \qquad 2.80$$

$$\underline{x} = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \qquad 2.81$$

and $\underline{r} = \begin{pmatrix} r_1 \\ r_2 \end{pmatrix}$ 2.82

Then $\underline{x}^* = \begin{pmatrix} x_1^* \\ x_2^* \end{pmatrix} = \frac{1}{\Delta} \begin{pmatrix} \beta_1 r_2 - \alpha_2 r_1 \\ \beta_2 r_1 - \alpha_1 r_2 \end{pmatrix}$ 2.83

Where $\Delta = \alpha_1 \alpha_2 - \beta_1 \beta_2$ 2.83a

Clearly the signs of all the parameters will be important in determining whether positive equilibrium levels exist or not.

Where equilibrium values do exist we require to determine whether they are stable.

By perturbing both populations from their equilibrium sizes by amounts ε_1 and ε_2 respectively and using the method of Section 2.11.2 we find that

$$\frac{d\varepsilon_1}{dt} = \alpha_1^* \varepsilon_1 + \beta_1^* \varepsilon_2 \qquad 2.84$$

and $$\frac{d\varepsilon_2}{dt} = \beta_2^* \varepsilon_1 + \alpha_2^* \varepsilon_2 \qquad 2.85$$

where $\alpha_1^* = x_1^* \alpha_1$, $\alpha_2^* = x_2^* \alpha_2$, $\beta_1^* = x_1^* \beta_1$, and $\beta_2^* = x_2^* \beta_2$

The characteristic equation is

$$\lambda^2 - (\alpha_1^* + \alpha_2^*) + \alpha_1^* \alpha_2^* - \beta_1^* \beta_2^* = 0. \qquad 2.86$$

The roots of this equation are determined as follows:

$$\lambda = \frac{(\alpha_1^* + \alpha_2^*) \pm \left[(\alpha_1^* + \alpha_2^*)^2 - 4(\alpha_1^* \alpha_2^* - \beta_1^* \beta_2^*)\right]^{1/2}}{2} \qquad 2.87$$

ble 2.3 Equilibrium and stability conditions for a 2-species community with interactions

r_1 /-)	r_2 (+/-)	α_1 (+/-)	α_2 (+/-)	β_1 (+/-)	β_2 (+/-)	equilibrium (Y/N)	equilibrium condition	stable (Y/N)	stability condition
+	+	+	+	+	+	N			
+	+	+	+	+	-	N			
+	+	+	+	-	+	N			
+	+	+	+	-	-	Y	$\Delta<0$	N	
+	+	+	-	+	+	N			
+	+	+	-	+	-	N			
+	+	+	-	-	+	Y	E1	Y	S1
+	+	+	-	-	-	Y	E2	N	
+	+	-	+	+	+	N			
+	+	-	+	+	-	Y	E1	Y	S1
+	+	-	+	-	+	N			
+	+	-	+	-	-	Y	E3	N	
+	+	-	-	+	+	Y	$\Delta>0$	Y	
+	+	-	-	+	-	Y	E4	Y	
+	+	-	-	-	+	Y	E5	Y	
+	+	-	-	-	-	Y	C1	Y	$\Delta>0$
+	-	+	+	+	+	N			
+	-	+	+	+	-	N			
+	-	+	+	-	+	Y	E5	N	
+	-	+	+	-	-	Y	E1	N	
+	-	+	-	+	+	N			
+	-	+	-	+	-	N			
+	-	+	-	-	+	Y	$\Delta>0$	Y	S2
+	-	+	-	-	-	N			
+	-	-	+	+	+	Y	E3	N	
+	-	-	+	+	-	Y	$\Delta<0$	N	
+	-	-	+	-	+	Y	E1	Y	S1
+	-	-	+	-	-	Y	E2	N	
+	-	-	-	+	+	Y	E1	Y	$\Delta>0$
+	-	-	-	+	-	N			
+	-	-	-	-	+	Y	E4	Y	
+	-	-	-	-	-	N			

ble 2.3 (continued)

r_1 (+/-)	r_2 (+/-)	α_1 (+/-)	α_2 (+/-)	β_1 (+/-)	β_2 (+/-)	equilibrium (Y/N)	equilibrium condition	stable (Y/N)	stability condition
-	+	+	+	+	+	N			
-	+	+	+	+	-	Y	E4	N	
-	+	+	+	-	+	N			
-	+	+	+	-	-	Y	E1	N	
-	+	+	-	+	+	Y	E2	N	
-	+	+	-	+	-	Y	E1	Y	S1
-	+	+	-	-	+	Y	Δ <0	N	
-	+	+	-	-	-	Y	E3	N	
-	+	-	+	+	+	N			
-	+	-	+	+	-	Y	Δ >0	Y	S2
-	+	-	+	-	+	N			
-	+	-	+	-	-	N			
-	+	-	-	+	+	Y	E1	Y	Δ >0
-	+	-	-	+	-	Y	E5	Y	
-	+	-	-	-	+	N			
-	+	-	-	-	-	N			
-	-	+	+	+	+	Y	E1	N	
-	-	+	+	+	-	Y	E5	N	
-	-	+	+	-	+	Y	E4	N	
-	-	+	+	-	-	Y	Δ >0	N	
-	-	+	-	+	+	Y	E3	N	
-	-	+	-	+	-	N			
-	-	+	-	-	+	Y	E1	Y	S1
-	-	+	-	-	-	N			
-	-	-	+	+	+	Y	E2	N	
-	-	-	+	+	-	Y	E1	Y	S1
-	-	-	+	-	+	N			
-	-	-	+	-	-	N			
-	-	-	-	+	+	Y	Δ <0	N	
-	-	-	-	+	-	N			
-	-	-	-	-	+	N			
-	-	-	-	-	-	N			

Table 2.3 (continued)

Δ is given by equation 2.83a $(\alpha_1\alpha_2 - \beta_1\beta_2)$

Condition E1: if $\Delta > (<o)\ 0$ then $\beta_1\ r_2 - \alpha_2\ r_1 > (<o)\ o$

and $\beta_2\ r_1 - \alpha_1\ r_2 > (<0)\ o$

Condition E2: $\beta_1 r_2 - \alpha_2 r_1 < 0$

Condition E3: $\beta_2 r_1 - \alpha_1 r_2 < 0$

Condition E4: $\beta_2 r_1 - \alpha_1 r_2 > 0$

Condition E5: $\beta_1 r_2 - \alpha_2 r_1 > 0$

Condition S1: $\Delta > 0$ and $\alpha_1 + \alpha_2 < 0$

Condition S2: $\alpha_1 + \alpha_2 < 0$

In order for the real part of λ to be negative we require

$$i) \quad (\alpha_1^* + \alpha_2^*) < 0 \qquad 2.88$$

and $$ii) \quad (\alpha_1^* \alpha_2^* - \beta_1^* \beta_2^*) > 0 \qquad 2.89$$

Condition ii) reduces to $\Delta > 0$ since 2.90

$$\alpha_1^* \alpha_2^* - \beta_1^* \beta_2^* = x_1^* x_2^* (\alpha_1 \alpha_2 - \beta_1 \beta_2)$$

$$= x_1^* x_2^* \Delta \qquad 2.91$$

and x_1^* and $x_2^* > 0$.

We can now compile the equilibrium/stability table (Table 2.3).

Two important observations can be made concerning the results presented in Table 2.3

i. If the two species in a stable community without interspecific interactions ($r_i > 0, \alpha_i < 0$, i=1, 2) are allowed to interact (such that r_i remains >0 and α_i remains <0, i=1,2) the community, by definition, becomes more complex, but the table shows that the existence of a stable equilibrium now depends on the actual values of the parameters. In other words the more complex community is less likely to be stable.

ii. On the other hand, if the two species community without interspecific interaction is unstable, then, depending on the signs of r_i and x_i, the addition of an interaction term in the model makes a stable equilibrium possible. In this case the more complex community is more stable.

2.11.5 Models of communities consisting of three species

So far we have increased the complexity of the community by adding interactions only. Now let us examine what happens when we add one species to a community such that it interacts with only one other species.

Let the initial community be described by

$$\frac{dx_1}{dt} = x_1 (r_1 - \alpha_1 x_1 - \beta_1 x_2) \qquad 2.92$$

$$\frac{dx_2}{dt} = x_2 (r_2 + \beta_2 x_1 - \alpha_2 x_2) \qquad 2.93$$

where all the constants are positive.

This community has the stable equilibrium

$$x_1^* = \frac{r_1 \alpha_2 + \beta_1 r_2}{\Delta} \qquad 2.94$$

$$x_2^* = \frac{r_1 \beta_2 - \alpha_1 r_2}{\Delta} \qquad 2.95$$

if $r_1 \beta_2 > \alpha_1 r_2$ (See Section 2.11.4 and Table 2.3) 2.96

Now let a third species join the community

The model might become

$$\frac{dx_1}{dt} = x_1 (r_1 - \alpha_1 x_1 - \beta_1 x_2 + \gamma_1 x_3) \qquad 2.97$$

$$\frac{dx_2}{dt} = x_2 (r_2 + \beta_2 x_1 - \alpha_2 x_2) \qquad 2.98$$

$$\frac{dx_3}{dt} = x_3 (-r_3 + \gamma_3 x_1) \qquad 2.99$$

($r_3 > 0$, sign of γ_1, γ_3 to be determined).

Is there still an equilibrium point?

Equation 2.99 gives $x_1^* = \frac{r_3}{\gamma_3}$ 2.100

This leads to the necessary condition that $\gamma_3 > 0$.

Equation 2.98 gives

$$x_2^* = \frac{-r_2 + \beta_2 x_1^*}{\alpha_2}$$

$$= \frac{\beta_2 r_3 - r_2 \gamma_3}{\alpha_2 \gamma_3} \qquad 2.101$$

Since $\gamma_3 > 0$, this gives the further necessary condition

$$\beta_2 r_3 > r_2 \gamma_3 \quad (\text{i.e. } x_1^* > \frac{r_2}{\beta_2}) \qquad 2.102$$

Equation 2.97 gives

$$x_3^* = \frac{\beta_1 x_2^* + \alpha_1 x_1^* - r_1}{\gamma_1}$$

$$= \frac{\beta_1 \frac{\beta_2 r_3 - r_2 \gamma_3}{\alpha_2 \gamma_3} + \alpha_1 \frac{r_3}{\gamma_3} - r_1}{\gamma_1}$$

$$= \frac{\alpha_1 \alpha_2 + \beta_1 \beta_2}{\alpha_2 \gamma_1 \gamma_3} \left[r_3 - \gamma_3 x_1' \right]$$

$$= \frac{\Delta}{\alpha_2 \gamma_1} \left[\frac{r_3}{\gamma_3} - x_1' \right]$$

where x_1' is the equilibrium level of x_1 in the 2-species model.

$$= \frac{\Delta}{\alpha_2 \gamma_1} \left[x^* - x_1' \right] \qquad 2.103$$

This gives the further conditions:

$$\text{if } \gamma_1 < 0, \quad x_1' > x_1^* \qquad 2.104$$

$$\text{if } \gamma_1 > 0, \quad x_1' < x_1^* \qquad 2.105$$

Therefore adding one species to a stable two species community (equation 2.92 and 2.93) so that the population dynamics are described by equations 2.96, 2.97 and 2.98. gives three necessary conditions for there to be an equilibrium instead of only one.

What can we say about the stability of the three species model.

The characterstic equation is

$$\begin{vmatrix} -\alpha_1^* - \lambda & -\beta_1^* & \gamma_1^* \\ \beta_2^* & -\alpha_2^* - \lambda & 0 \\ \gamma_3^* & 0 & -\lambda \end{vmatrix} = 0 \qquad 2.106$$

i.e.
$$(-\alpha_1^* - \lambda)\left[-(-\alpha_2^* - \lambda)\lambda\right] + \beta_1^*\left[-\lambda\beta_2^*\right] + \gamma_1^*\left[\gamma_3^*(\alpha_2^* + \lambda)\right] = 0 \qquad 2.107$$

i.e.
$$\lambda^3 + (\alpha_1^* + \alpha_2^*)\lambda^2 + (\alpha_1^*\alpha_2^* - \beta_1^*\beta_2^* - \gamma_1^*\gamma_3^*)\lambda - \gamma_1^*\gamma_3^*\alpha_2^* = 0 \qquad 2.108$$

We can use the Routh-Hurwitz stability criteria (described in Section 2.11.6) to give three necessary and sufficient conditions for the roots of this equation to lie in the left half complex plane.

These equations are:

i) $\alpha_1^* + \alpha_2^* > 0$ 2.109

ii) $-\gamma_1^*\gamma_3^*\alpha_2^* > 0$ 2.110

iii) $(\alpha_1^* + \alpha_2^*)(\alpha_1^*\alpha_2^* + \beta_1\beta_2^* - \gamma_1^*\gamma_3^*) > -\gamma_1^*\gamma_3^*\alpha_2^*$ 2.111

In this case condition i) is satisfied automatically because α_1^* >0 and α_2^* > 0.

Condition ii) is satisfied if $\gamma_1^* \gamma_3^*$ < 0 because α_2^* > 0.

If condition ii) is satisfied, it is clear that condition iii) is automatically satisfied.

Therefore in this example a necessary and sufficient condition for stability is that $\gamma_1^* \gamma_3^*$ < 0, that is the new interaction is a predator-prey relation.

Combining this condition with the conditions determined above for there to be an equilibrium we see there are now four conditions for the 3-species model to have a stable equilibrium.

These are:

$$\text{i)} \quad \gamma_3 > 0 \qquad 2.112$$

$$\text{ii)} \quad \beta_2 r_3 > r_2 \gamma_3 \qquad 2.113$$

$$\text{iii)} \quad \gamma_1 < 0 \qquad 2.114$$

$$\text{iv)} \quad \frac{r_2 \alpha_2 + \beta_1 r_2}{\Delta} > \frac{r_3}{\gamma_3} \qquad 2.115$$

We might conclude from this example that, given a stable community of a particular complexity, then making this community more complex by adding a further species does not necessarily make the community more stable. It is evident that both the type and the strength of the new interactions are important in determining whether or not the more complex community will have a stable equilibrium.

We can also observe from this example that, even if the original two species model does not have a stable equilibrium (that is, condition 2.96 does not hold), the more complex community may still be stable.

2.11.6 The general case

2.11.6.1 Introduction

From the specific but simple examples given in Sections 2.11.3, 4 and 5 we might conclude that

i) a community which is at a stable equilibrium may become unstable if the complexity of the community is increased or decreased.

and ii) a community which does not have a stable equilibrium (or indeed an equilibrium) may become stable if its complexity is increased or decreased.

It is not hard to see that these conclusions hold for the equivalent n species differential equation models, but do they answer our question; that is, do they show that there is not a general relationship between community complexity and stability.

Let us consider a general differential equation model of a n species community.

$$\frac{dx_i}{dt} = f_i(x_1,\ldots,x_n) \qquad i=1,\ldots,n \qquad 2.116$$

where $f_i(\underline{x})$ is any function of the individual population sizes.

To determine whether a equilibrium exists we first need to find $\underline{x}^*$ such that

$$f_i(\underline{x}^*) = 0 \qquad i=1,\ldots,n. \qquad 2.117$$

For this to be a valid equilibrium we require further that $\underline{x}^* \in R_n^+$ where $R_n^+ = \{(x_1,\ldots,x_n) : x_i > 0 \text{ and } x_i \in R,\ i=1,\ldots,n\}$ and R is the set of real numbers.

Clearly in the most general case in which any or all of the f_i are non-linear, there may be several or no values of $\underline{x}$ which satisfy the conditions.

Whether a particular $\underline{x}^* \in R_n^+$ will usually depend both on the actual form of the functions f_i and also on the values of the parameters associated with the f_i.

For instance in the 'linear' case in which

$$f_i = x_i (r_i + \alpha_{i1} x_1 + \ldots + \alpha_{in} x_n) \qquad 2.118$$

we can say $\underline{x}^* \in R_n^+$ if and only if $\underline{\alpha} \in R_e$ 2.119

where $\underline{\alpha} = (r_1, \ldots, r_n, \alpha_{11}, \ldots, \alpha_{n1})$

and $R_e = \{ \underline{\alpha} : \underline{x}^* \in R_n^+ \}$

e.g. If n=1, $R_e = \{ (r_1, \alpha_{11}) : r_1 < 0, \alpha_{11} \geq 0 \} \wedge \{ (r_1, \alpha_{11}) : r_1 > 0, \alpha_{11} < 0 \}$

Returning to the general case we can examine the local stability of any $\underline{x}^*$ which satisfies 2.117 (but is not necessarily an element of R_n^+). Using our standard procedure we construct the community matrix A.

$$A = (\alpha_{ij}^*), \quad \text{where} \quad \alpha_{ij}^* = \frac{\partial f_i}{\partial x_j} \Big| \; \underline{x} = \underline{x}^* \qquad 2.120$$

$\underline{x}^*$ is locally stable if all the eigenvalues of A have non-positive real parts. Sufficient conditions for this to be so are given by the Routh-Hurwitz criteria. Essentially the eigenvalues of A are the roots of the characteristic equation.

$$|A - \lambda I| = 0 \qquad 2.121$$

This is a polynominal of degree n in λ:

$$\lambda^n + a_1 \lambda^{n-1} + \ldots + a_{n-1} \lambda + a_n = 0. \qquad 2.122$$

The Routh-Hurwitz criteria state that the system is stable if the following n conditions are true.

$$\begin{vmatrix} a_1 & 1 & 0 & 0 & \ldots & 0 \\ a_3 & a_2 & a_1 & 1 & \ldots & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a_{2i-1} & \cdot & \cdot & \cdot & \cdot & a_i \end{vmatrix} > 0 \quad i=1,\ldots,n \qquad 2.123$$

Whether these n conditions hold will depend on the values of the a_i. These are functions of the α^*_{ij} and these in turn depend on the functions f_i.

Let us again consider the linear case.

Clearly $\alpha^*_{ij} = \alpha_{ij} \; x_i^* \qquad i=1,\ldots,n \quad j=1,\ldots,n \qquad 2.124$

and $\underline{x}^*$ is locally stable only for particular values of the α_{ij} and r_i.

We can say $\underline{x}^* \in L$ iff $\underline{\alpha} \in R_s$ (iff ≡ if and only if) 2.125

where L denotes that $\underline{x}^*$ is locally stable

and $R_s = \{\underline{\alpha} : \underline{x} \in L\}$.

Therefore for $\underline{x}^*$ to be a valid locally stable equilibrium point we require

$$\underline{\alpha} \in R_e \cap R_s = S \qquad 2.126$$

Clearly similar regions can be defined for the more general case.

The question now is 'how does the size of the region of stable equilibrium S change with complexity?'

As discussed in Section 2.8 complexity is a function of the number of species in the community and the number and strength of interactions between these species. In the context of my argument each set of parameters $\underline{\alpha}$ has associated with it a particular stability. The more species there are, the more conditions need to be satisfied for there to be a stable equilibrium, and the more interactions there are, the more there are of parameters whose values are not zero.

It is not clear how to order parameter sets depending on the actual size of the parameters.

In the 'linear' example the parameter set is

$$\underline{\alpha} = (r_i, \alpha_{ij} \; ; \; i=1,\ldots,n; \; j=1,\ldots,n) \qquad 2.127$$

If we assume that $r_i \neq 0 \; \forall_i$, then a measure of complexity might be

$$C = n + \frac{\sum_{i,j} \delta_{ij}(\alpha_{ij})}{n(n+1) + 1} \qquad 2.128$$

where $$\delta_{ij}(\alpha_{ij}) = 1 \quad \text{if } \alpha_{ij} \neq 0 \qquad 2.129$$
$$= 0 \quad \text{if } \alpha_{ij} = 0.$$

Intuitively, therefore, the more complex the community, the less likely it is to be stable.

The problem is to calculate the size of the region S for the general differential equation model of a community with associated complexity C. In fact to formulate the problem in this way is perhaps not very meaningful because the size of S will not, in general, be comparable between communities of differing complexity because the parameter spaces are likely to be of different dimensions. However it is sensible to assume that not all the possible values of each parameter are equally likely. If we associate a probability density function g with the parameter set $\underline{\alpha}$ we can potentially calculate the probability that the community model is stable.

Indeed this probability is $$\int_S g(\underline{\alpha}) \; d\underline{\alpha} \qquad 2.130$$

In order to get an indication of the answer to our question it would be necessary to evaluate this expression for a wide range of the potentially infinite different forms the general differential equation model may take and for a wide range of

probability density functions g. Without some further simplification even for the linear case a computer would be hard-worked to give an answer.

2.11.6.2 M. R. Gardner and W.R. Ashby

Gardner & Ashby, while investigating the stability of general large dynamic systems, provide a simplification of this problem which gives some answers. Firstly Ashby (1952) has demonstrated using Monte Carlo techniques that for systems with n variables whose dynamics are described by the system matrix A every element of which is non-zero the probability of system stability decreases rapidly as n increases.

However in general not all the system variables are going to interact and therefore many of the elements of the matrix A will be zero. Gardner & Ashby (1970) postulated a method of measuring the average number of interactions per system variable and they term this measure 'connectance'. In their initial work they defined the connectance C as the percentage of non-zero elements in A and each non-zero non-diagonal element was selected from the uniform probability distribution U (-1,1). The elements of the main diagonal were all negative and selected from the uniform distribution U(-1,-0.1) - that is, each system variable alone is independently stable.

Gardner & Ashby then used a computer to estimate the probability of a system with n variables and connectance C being stable. Some of their results are summarised in Figure 2.14.

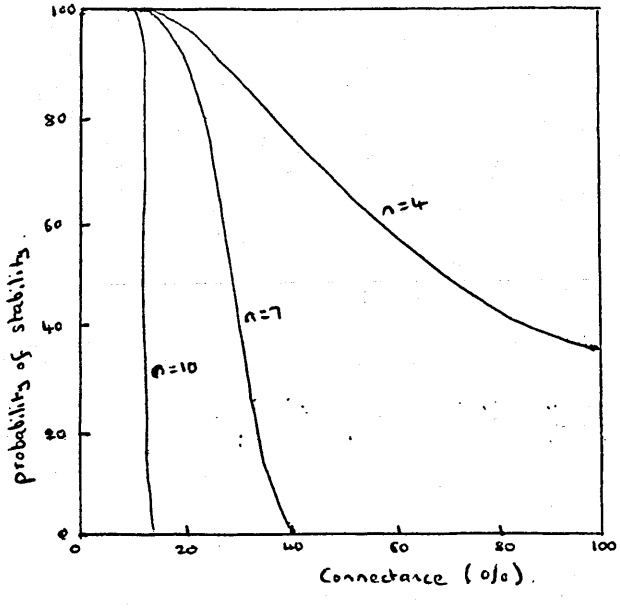


Figure 2.14 Variation of stability with connectance where n is the size of the system (from Figure 1 of Gardner and Ashby (1970)).

Essentially it appears that as n increases there is a rapid change in probability of stability from nearly 1 to nearly 0 as connectance passes a critical value. Also for a given connectance C the probability of stability decreases with increasing n and for a given n the probability of stability decreases with increasing connectance C.

Now Gardner & Ashby considered a general dynamic system. Clearly such a system could be the population dynamics of a biological community and the system matrix A could be the community matrix described above. C is a measure of the average number of interactions per species and hence, for given n, the larger C the more complex the community. Hence these results indicate that the more complex the community, the less is the probability of it being stable

Clearly Gardner & Ashby's results are limited to smallish values of n because of the size of the task on the computer. May (1972) uses analytical techniques to take this work a stage further.

2.11.6.3 May

May (1972b) had slightly different assumptions about the structure of the community matrix A. Firstly the diagonal elements are all fixed at -1 - i.e. each species alone is stable with unit damping time. Connectance is defined in a similar way but each non-zero element is assigned at random (from some statistical distribution) such that its expected value is zero and its mean square value is α^2. α can be considered to be a measure of interaction strength and in this case the expected strength is equal for all interactions.

May then followed the arguments and theories of Wigner (1959) to indicate the probability that a particular community with n (where n is large) species, connectance C and interaction strength α is stable.

He found that the community model is almost certainly stable if

$$\alpha < (nC)^{-\frac{1}{2}} \qquad 2.131$$

and almost certainly unstable if

$$\alpha > (nC)^{-\frac{1}{2}} \qquad 2.132$$

May's results confirm Gardner & Ashby's results that there is a sharp transition from stable to unstable behaviour as the complexity, as measured by the connectance C and the average interaction strength α, exceeds a critical value.

May concluded that, for this particular ensemble of mathematical models, too rich a web connectance or too large an average interaction strength leads to instability. The larger the number of species, the more pronounced the effect.

Clearly the assumptions made by both Ashby and Gardner and May restrict the conclusions from being completely general, the main assumptions being that each individual species is independently stable. However the results do tend to support our intuitive conclusions that stability is less likely the more complex the community.

2.12 Conclusions

The point of this Chapter has been to identify whether there is a general relationship between community stability and community complexity both by considering arguments put forward by ecologists (and especially their interpretation of field evidence) and by studying the stability properties of mathematical models of communities of varying complexity.

It was seen that ecologists such as MacArthur, Elton & Hutchinson had, during the nineteen fifties, put forward arguments that suggested that in general community stability increases with community complexity. It is my opinion that none of these arguments bear close scrutiny and that their conclusions are mostly based on intuitive ideas. The efforts of Pimentel were perhaps more positive but really only succeeded in demonstrating how difficult it is to set up field experiments to study such biological relationships. The observations of Watt & Paine, however, do tend to show that the relationship is not necessarily straight-forward.

It is important to note that none of the above workers gave a clear definition of what he meant by stability or complexity.

Evidence from studying some simple mathematical models of community population dynamics supports the observations of Watt and Paine, and indeed we may conclude:

> differential equation models of communities which are stable may be made unstable by either making the community more or less complex and, conversely, models of communities which are unstable may be made stable by either increasing or decreasing the community complexity.

However this is not a general relationship between stability & complexity. A consideration of the stability properties of general differential equation models of communities of arbitrary complexity shows that, if there is a relationship, it is not easy to demonstrate one. Intuitively stability is less likely the more conditions there are to be satisfied by the model parameters. The number of conditions grow with increasing complexity. Finally, arguments put forward by May support this conclusion that stability is less likely the more complex the community becomes.

How do these conclusions help for example the conservationist or the pest control manager. Well they probably tell such people what they have already discovered from experience. A particular community is either relatively stable or unstable and only a study of that community will guide the expert as to what strategy he should take. It is certainly dangerous to assume that increasing the complexity of the community by introducing a new species will neccessarily make the community more (or less) stable. Mathematical models, however, may be very useful in using the experts knowledge to simulate the population dynamics and hence evaluate potential solutions.

3. Environmental heterogeneity and community stability

3.1 Introduction

Ecologists have been aware for some time that variability of the actual characteristics of the environment in which the population of a particular species is living is likely to have a significant effect on the dynamics of that population and hence on its stability. For instance Hutchinson (1959) described what he termed the mosaic nature of the environment and clearly believed that this is an important factor in determining how many species can exist in a given environment and Den Boer (1968) in an interesting paper in which he described his concept of the 'spreading of risk' stressed the importance of heterogeneity of all factors which might determine population numbers.

More recently Levin (1974) claimed that 'the distribution of a species over its range of habitats is a fundamental and inseparable aspect of its interaction with its environment, and no complete study of population dynamics can afford to ignore it'.

The purpose of this chapter is to study the possible effect of environmental heterogeneity on the stability of the resident populations. Firstly I will present and discuss in some detail field and laboratory evidence which has been gathered by a number of workers to demonstrate that heterogeneity is important. We will observe from these discussions a number of definitions of environmental heterogeneity. I shall next attempt to combine these into a single definition. Thirdly I shall review the types of mathematical models that have been developed to study the effect of environmental heterogeneity on community stability.

3.2 Biological evidence of the importance of environmental heterogeneity in determining community stability

3.2.1 Introduction

From a survey of the literature it is clear that field and experimental evidence of the importance of environmental heterogeneity is somewhat limited. This is perhaps not surprising. Experiments designed to

study the effects of heterogeneity in general would have to be very extensive if they were to provide sufficient data, and field observations often tend to lack vital information regarding the exact nature of heterogeneity.

However a number of workers have reported useful observational evidence and this together with perhaps intuitive feelings and some further evidence provided by mathematical models at least suggests the importance of environmental heterogeneity.

In particular Huffaker (1958) was one of the first to set up sensible experiments in the laboratory in order to study heterogeneity and his work is now regarded as classic. More recently Smith and Dawkins (1971) have demonstrated that the hunting behaviour of great tits appears to depend on the distribution of food in the environment.

The comments and observations of Polyakov (1959), who is one of a number of Russian naturalists who were involved in setting up rodent control programmes in the 1950's, are valuable as are the more recent observations and theories of Hansson (1977, 1979).

Finally the work of Beddington, Free and Lawton (1978), who combined laboratory and field observations with evidence from various mathematical models, is reported.

3.2.2 C. B. Huffaker

Huffaker (1958) carried out a series of experiments the main aim of which was to establish an ecosystem in which a predator and a prey species could continue to live together for a reasonable period of time so that their interactions with each other could be studied in detail. The predator species used in the experiments was the predatory mite Typhlodromus occidentalis and the prey species was the phytophagous mite Eotetranychus sexmaculatus.

Each experiment involved arranging oranges, which provided the prey with food, and similar-sized waxed rubber balls on a tray and introducing individuals of the prey species and, at a later stage, of the predator species on selected oranges. The number of prey and

predator individuals in the universe (i.e. the tray) was estimated at certain points in time from samples until soon after one or other of the species became extinct.

The series of experiments was designed so that an arbitrary selection of different degrees of dispersion and segmentation of units of food for the prey was achieved without altering the total surfaces for the predators to search and, if desired, without altering the total food used. This was done by covering the oranges to varying degrees, so that only a proportion of each orange was exposed, and dispersing them among the rubber balls. The most complex universe constructed also included barriers to predator dispersion and aids to prey movement so that it was difficult for the predator to contact all the areas occupied by prey at any one time.

Control experiments were also carried out in which only the prey were introduced to the universes.

From the control experiments Huffaker observed that, if the oranges were more widely dispersed, the prey population tended to be more stable (i.e. exhibited smaller oscillations in size) although the mean density tended to be smaller.

When predators were introduced to universes in which the prey had easy access to food and hence no need for dispersal to obtain food, then more often than not both the predator and the prey populations became extinct. In experiments in which the food was widely dispersed it appeared that over-population of oranges by prey individuals as the reason for practically all movement from orange to orange. However, even with wide food dispersion it was chance whether the prey population survived or not.

In the largest and most complex universe studied coexistence of predator and prey was achieved for three oscillations in population sizes. In all other experiments only a single oscillation was achieved before extinction of atleast the predator species.

Huffaker concluded that in a given universe whether the participant populations survive is locally a matter of chance. As the universe increases in complexity so this chance increases. He concluded further that although the action of a predator may locally be insignificant at a given time, predation may be more significant throughout the larger sphere which can be reached by migrants from the over-populated areas.

What Huffaker described as universe complexity was the degree to which the prey food was dispersed, the amount of food there was in each area, the ease with which prey and predator individuals could migrate (physical barriers and aids) and the number and dispersion of refuges. Also, at any point in time the prey had a particular distribution of numbers throughout the universe and locally this may have affected the probability that predators found and killed prey.

So in effect the universes were heterogenous in both time and space.

Why should environmental complexity increase the chance of prey and predator survival? Many ecologists (eg Nicholson (1933), Nicholson & Bailey (1935)) had built mathematical models of predator-prey interactions which assumed that predators search completely at random throughout the universe so that the probability of locating and killing a prey depends only on the number of prey available and the predators efficiency at killing, and not on the actual distribution of the prey in the universe. Huffaker argued strongly that, due to the marked inconsistency of hazards from one microhabitat to another, such an assumption is difficult to visualise either in his experiments or in nature. The fact that the prey tended to clump together in various locations where food was concentrated meant that the predators also tended to concentrate in those areas. Some prey were able to migrate relatively easily to other parts of the universe which were predator-free and hence propagate. It would be some time before overexploitation of the food-rich areas forced the predators to disperse and hence to locate these other prey-rich areas.

Do Huffakers conclusions apply in natural conditions? Huffaker did acknowledge that conclusions drawn from observations on such artificial universes must have restricted value if the universes do not allow all the important natural parameters possibility of expression. He believed that, because he had succeeded in obtaining prolonged coexistence, he had achieved this. I am not convinced of this argument because the environments he constructed were still essentially artificial. What is certain though is that the experiments were carried out very carefully and the method of sampling was very accurate.

Artificial or otherwise, increased environmental complexity, that is heterogeneity, gave greater chance of prolonged coexistence.

3.2.3 J. N. M. Smith and R. Dawkins

Smith and Dawkins (1971) studied the hunting behaviour of individual great tits in relation to spatial variations in their food density. To do this they set up a particular experimental habitat which contained four separate possible feeding areas.

Initially Smith & Dawkins determined the preferred feeding area of each tit by releasing each individual, one at a time, into the experimental habitat for a period of time and observing how many times it visited each area. The four feeding areas were then set at different densities of food in such a way that for the particular bird under observation the lowest density of food was put in its preferred area and the highest in its least preferred area.

Invariably it was observed that the pattern of behaviour of each bird changed so that its new preferred area was the one with the highest food density. Smith & Dawkins concluded that tits are capable of determining areas of high prey (food) density and will visit that area more frequently.

Their experiment actually went further. At a fixed point through each trial the best area was swopped with the worst. In all but one case the birds did not reverse their behaviour although it was clear that they did visit the new best area and they were successful in finding prey there.

Smith & Dawkins pointed out that ideally the behaviour of tits should be investigated under field conditions to test whether the laboratory findings apply to wild birds, but this is very hard to achieve. They cited several examples of non-random distribution of prey in the wild.

In particular Gibb (1958) demonstrated significant variations in the intensity of the larvae of the eucosmid moth Enarmonia conicolana which inhabits pine cones and is preyed on during winter by coal and blue tits. The intensity of larvae per five pine cones showed up to sixteen-fold variation.

larval intensity (no. of larvae per 5 pine cones)	number of plots
<2	93
2-3	131
3-4	43
>4	15

Clearly the high intensities are less frequent. Gibb found infact that the concentration of tit predators on higher intensities was somewhat weaker than Smith & Dawkins predicted, but these were mainly non-terratorial birds searching over fairly large areas.

Also Goss-Custard (1970) studied flocks of red-shank (Tringa totanus) feeding in winter on burrowing eniphipod Corophium volutator in an estuarine habitat. He found that red-shank tended to feed in the more profitable areas and, in one particular transect under observation there was a suggestion that red-shank spent a disproportionate amount of time feeding at the highest Corophium density.

In conclusion what Smith & Dawkins experiments demonstrated was that tits may search for their prey in a non-random way. That is, their searching behaviour is affected by the distribution of the prey in its environment and the relationship between prey density and searching behaviour is not necessarily straightforward - the birds do not necessarily respond quickly to changes in prey density. In effect the non-uniform distribution of the prey in its environment makes the habitat spatially heterogeneous, and, since the prey distribution is likely to change with time, the habitat will infact be spatially and temporally heterogeneous.

3.2.4 I. J. Polyakov

Polyakov (1959) is one of a number of Russian naturalists who have indicated that environmental heterogeneity is important in determining population levels and fluctuations. He was particularly concerned with forecasting the size of vole populations so that farmers could take adequate control measures to protect their crops and pastures. He presented data which indicates that the amount and sort of food required by voles depends on the temperature and humidity of the immediate environment.

The spatial boundaries of the total rodent populations that Polyakov was studying were essentially the Russian borders, but clearly the actual distribution of the individuals within these borders is of critical value to the farmers. Polyakov observed that in locations where conditions are favourable and the vole numbers are increasing the voles tend to survive in areas where there are favourable conditions. During periods of unfavourable conditions voles tend to lose their viability, so that even when favourable conditions return the local populations tend to perish. These populations tend to be small in number and weight of individuals, do not propogate or propogate with lower intensity, have increased susceptibility to disease, a lower level of metabolic exchange and a narrow range of optimum temperatures. Further, the way in which predators affect the number of voles depends on the viability of the population and the environmental conditions.

So the environmental conditions can have a complicated effect on the population dynamics of rodents in Russia and the environment tends to vary both spatially and temporally. Russian naturalists have recognised this and have built both spatial and temporal observations of rodent populations into forecasting models in order to predict as accurately as possible the size and spatial distribution of such populations in Russia.

3.2.5 L. Hansson

Based on field evidence Hansson (1979) postulated a general hypothesis concerning the importance of what he terms landscape heterogenity in northern regions (i.e. Scandinavia) for the breeding population densities of homeotherms.

He pointed out that few communities are actually closed and that there will be a flow of individuals in and out. The neighbourhood between communities appears therefore to be important, as does the relative suitability of alternative habitats in a particular landscape. Hansson defines landscape ecology as the study of the effect of the composition of various ecosystems (communities) in a landscape on the local populations.

In particular Hansson (1977) described the behaviour of field voles in heterogeneous landscapes. Vole populations are found in a variety of densities throughout Scandinavia and this appears to depend to some extent on the particular local habitats. Voles do have a preferred habitat but this is not always available. Some habitats tend to be more permanent than others. Temporary habitats are often those areas which are flooded seasonally or leys which are cut once or twice annually.

Suitable habitats are often separated by large uninhabitable areas. Also suitable habitats may become unsuitable either seasonally or for irregular periods of time. So the landscape can be heterogenous in both space and time.

The pressure to move between suitable habitats depends on physical factors such as seasonal flooding and also on other factors such as the carrying capacity of a particular habitat. By observation some habitats appear to be donor habitats in that individuals tend to leave and seek other suitable habitats. Some habitats tend to be receptor habitats and will accept individuals from other habitats.

There is also evidence for movements of whole populations of field voles. For instance, seasonal flooding causes populations to seek out higher ground and there is similar movement out of leys in the middle of summer.

Voles are just one example of species whose population densities are affected by landscape heterogeneity. Hansson (1979) also cited field evidence concerning cervids, foxes, and others. In all cases the large difference between the seasons in terms of habitat suitability and the heterogeneity of the landscape has an effect on the population dynamics causing movements of individuals and even whole populations between habitats.

Hansson's general theory to account for the importance of landscape heterogeneity on homeotherm populations is presented diagrammatically in Figures 3.1, 3.2, 3.3 and 3.4.

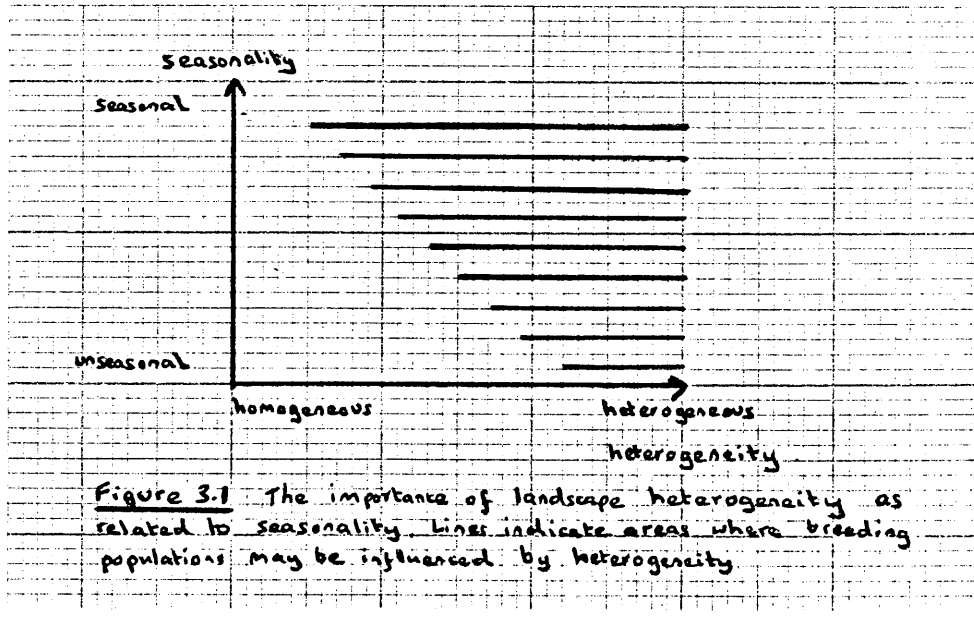


Figure 3.1 The importance of landscape heterogeneity as related to seasonality. Lines indicate areas where breeding populations may be influenced by heterogeneity.

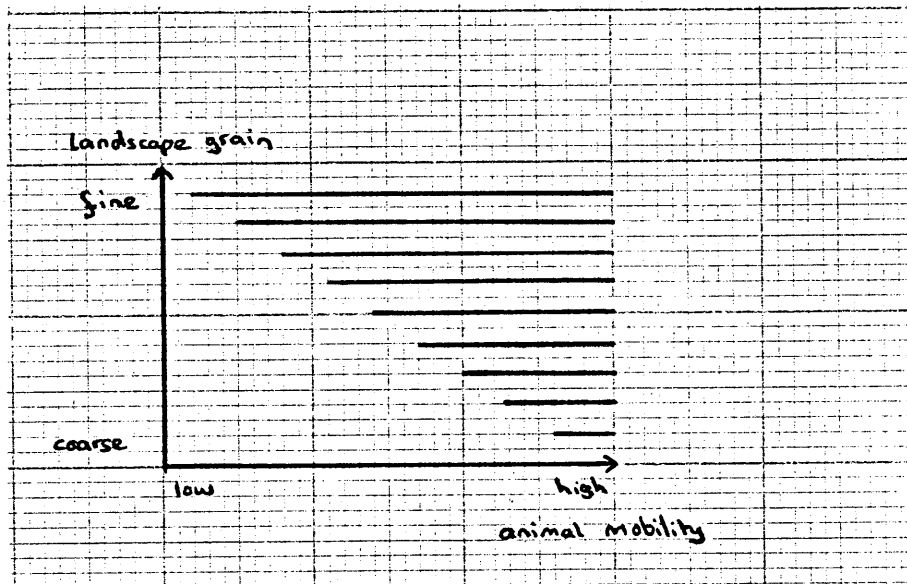


Figure 3.2 The importance of landscape heterogeneity as related to animal mobility and environmental grain size. Lines indicate favourable combinations.

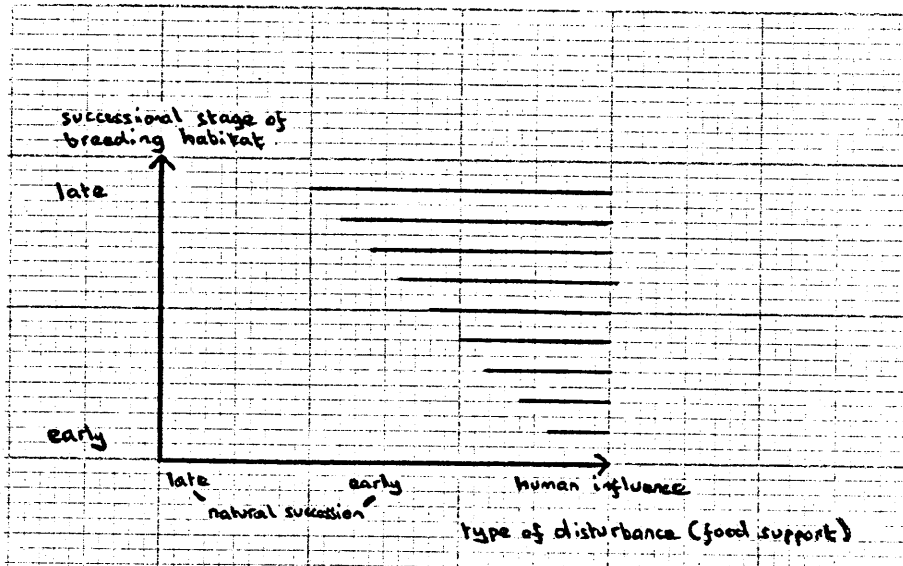


Figure 3.3 The importance of landscape heterogeneity as related to types of breeding habitat and of disturbance. Lines indicate favourable combinations.

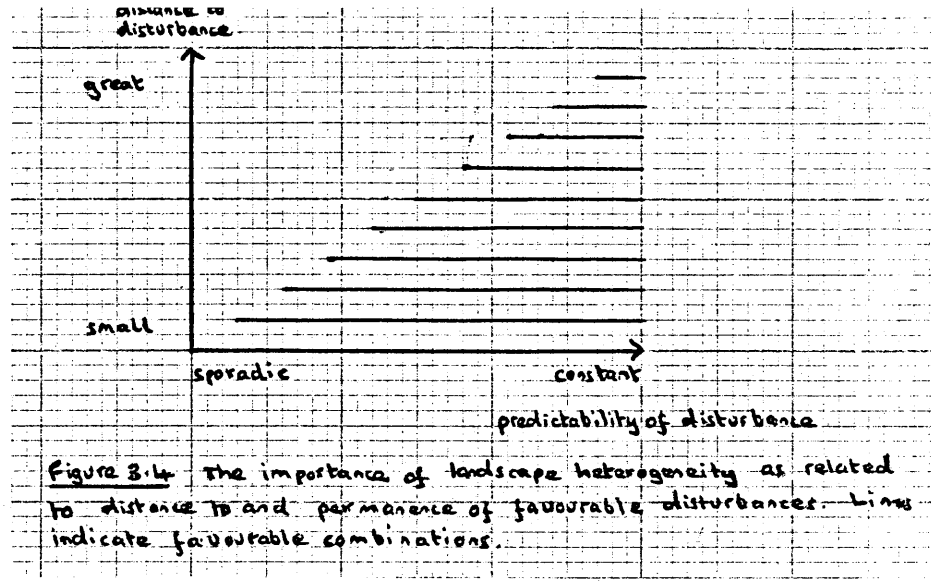


Figure 3.4 The importance of landscape heterogeneity as related to distance to and permanence of favourable disturbances. Lines indicate favourable combinations.

Figure 3.1 represents the proposed relationship between heterogeneity and seasonality. The more seasonal a species tends to be, the more likely heterogeneity will influence the breeding populations. (By seasonal Hansson means that the population breeds only at certain times in the year).

Figure 3.2 proposes a relationship between habitat dispersion and the mobility of the constituent species. For animals with low mobility only fine-grained landscapes tend to be suitable, that is landscapes which are relatively homogeneous, containing plenty of a limited range of food. Animals with high mobility can also exploit coarse-grained habitats, that is habitats providing a wide range of unevenly distributed food.

Figure 3.3 describes a relationship between the successional stage of the breeding habitat and disturbance in the habitat. (Succession is a term which describes the apparant maturation of an environment in terms of its complexity and constituent species). By disturbance Hansson means that new sources of food are introduced into the habitat. Naturally introduced disturbances of this kind only tend to affect mature communities whereas human disturbances can affect early or late successional stages.

Figure 3.4 represents the proposed relationship between distance to the disturbance and the predictability of the disturbance. Accidental sites of disturbance which increase the food supply only momentarily will affect a few animals temporarily and spatially constant areas of winter support may influence large populations of at least wide-ranging species. In habitats of the latter type there may eventually develop breeding populations from the invading species.

All the factors described are likely to interact strongly and the outcome for particular species and environments has to be examined separately.

Hansson admits that his hypothesis is very general and that it can only be tested when applied to particular species and environments. Of course it is virtually impossible to experimentally manipulate whole landscapes. Alternatively repeated field surveys and critical observations could be used but in practice this is a very difficult procedure.

However the importance of Hansson's theory is firstly that he believes that spatial heterogeneity is responsible for the observed behaviour and characteristics of certain homeotherm populations and secondly the interpretation of environmental heterogeneity. Two things are clear in Hansson's 'definition' of environmental heterogeneity. First the environment tends to consist of a landscape of habitats some of which are 'suitable' for the particular species to live in and some not. Secondly the number and nature of suitable habitats within the landscape may change with time. We will see later that this is a popular way of modelling environmental heterogeneity.

3.2.6 J. R. Beddington, C.A. Free and J.H. Lawton

Beddington, Free & Lawton (1978) presented a mixture of field, laboratory and mathematical evidence which suggests that environmental heterogeneity is important in determining community stability. In particular they were interested in the reasons for success or otherwise of attempts to control insect pests by the introduction of natural enemies, especially insect parasites (parasitoids).

One measure of the effect the introduction of a parasitoid has on its host is the ratio (q) of the population size of the host species in the presence of the parasitoid to that in the absence of the natural enemy. They obtained estimates of q for four laboratory host-parasitoid systems and a number of successful biological control programmes.

In all cases the laboratory values of q were significantly larger than the field values ($\sim$.3 compared to $\sim$.005). They attempted to reproduce these observed q values using mathematical models of the host-parasitoid relation.

In the simplest model explored (Nicholson & Bailey (1935) - see Section 3.4.5.2) the parasites were assumed to search completely at random for the hosts and the host growth rate was such that only a single equilibrium population level was possible. This model could be made more complicated by introducing density dependent effects on the per capita rate of increase of the parasitoid. In any case the smallest value of q which could be generated was .33. This compares with the values observed in laboratory experiments but is significantly larger than field values.

Further sophistication of the model (e.g. Hassell (1978)) to include such factors as unequal generation time between the host and parasitoid, non-constant searching efficiency due to time spent on handling the host, and fall-off of searching efficiency at low host densities failed to reproduce field q values.

One possible criticism of the models used by Beddington, Free & Lawton is that they are too unrealistic for modelling host depression in the field. Beddington, Free & Lawton refuted this by showing that there is a key parameter in the models which is a measure of parasitoid efficiency (i.e. how good the parasitoid is at catching and parasitising the host) and which is roughly related to q. They presented data from field experiments which show that the order of magnitude of the theoretical parasitoid efficiency compares with the field values and they argue that this signifies that the structure of the model is basically sound.

They then looked for alternative reasons why field q values should be so low. They observed that one difference between the laboratory and the field is the greater size and physical complexity of the field environment. The field environment is spatially heterogeneous.

Two ways in which spatial heterogeneity may affect the host-parasitoid community dynamics is i) by providing refuges for the host (i.e. locations in which the host is protected from parasitoid attack) and ii) by modifying the parasitoid attack rate.

Including refuges in the model led to q values of the order .1. Introducing modified attack rates, in particular by allowing the parasitoids to favour attacking 'patches' in the environment which have locally higher host densities than other patches, led to low q values being readily generated.

Beddington, Free & Lawton also described another way of generating low q values (due to May (1978)) which does not depend on spatial heterogeneity. This included varying the form of the host growth rate in the models so that two locally stable equilibrium population levels were possible. Some studies have show that this may be possible in the field due to background predation or parasitism (e.g. Takahashi (1964)). When the host is constrained at the lower equilibrium level the q value may be small.

They felt that what evidence there is supports heterogeneity as being commonly the most likely solution. This was mostly because models incorporating spatial heterogeneity predict that q is related to searching efficiency whereas if complex density dependence of the host growth rate were the reason, then the lower equilibrium value would largely be determined by background mortality. As discussed above, field values do appear to be related to efficiency. Also evidence from parasitoids which have been successful biological control agents suggested that they had high response to prey aggregation, high dispersal powers between patches and high effective searching efficiencies. These are exactly the powers needed in spatially heterogeneous environments.

One particular criticism of Beddington, Free & Lawton's argument is that the biological data, as so often is the case, are limited and what are available are subject to considerable uncertainty. However the difference between the field and laboratory q values is so significantly different that, all in all, this is powerfull evidence that environmental heterogeneity can have an important effect on

the community population dynamics and hence on the determination of species persistence within that community.

3.3 Definition of environmental heterogeneity

3.3.1 Introduction

From the work described in Section 3.2 it appears that there are a number of types of environmental heterogeneity which are important.

Huffaker's work was concerned both with the physical complexity of the environment and the effect of an uneven distribution of food on the population of a particular predator. The physical complexity was defined by the barriers and aids to individual movement which were included in the environment and was constant with time. The distribution of food varied in both space and time due to the individual movement and the results of interactions. Somewhat similarly Smith & Dawkins were concerned with the effect of an uneven distribution of food on the behaviour of a predator.

The heterogeneity discussed by Hansson and by Polyakov is a little different in that they were more concerned with the physical complexity of the environment. The environment may consist of a number of suitable habitats distributed between unsuitable areas. Populations of particular species will tend to concentrate in their particular suitable habitats. Each suitable habitat will have its own degree of suitability and the number of suitable habitats for each species and the degrees of suitability may change with time. Further, each suitable habitat may be physically heterogeneous in itself. For instance there may be a temperature gradient across the habitat and this gradient may change with time.

So an environment may be considered to be heterogeneous because there are non-constant physical properties in time and/or space, and/or because the distribution of a population within the environment is uneven. In either case this heterogeneity is only important if there is an effect on the community population dynamics.

This leads me to the following series of definitions.

3.3.2 Definition

It is important to define clearly what the term environmental heterogeneity means. There are three types of environmental heterogeneity to be considered, namely spatial, temporal and spatio-temporal heterogeneity. These terms are all often loosely covered by the term spatial heterogeneity in the literature, though Levin (1976) gives a reasonably clear description of each. The terms physical heterogeneity and landscape heterogeneity have also appeared as we have seen above.

If we refer to the definition of a community (Section 2.3) we see that at any point in time the community is living in a particular physical enivronment, the physical characteristics of which are likely to determine the strength and probability of interactions between individuals and hence the community population dynamics.

If each physical property which affects the population dynamics has (effectively) the same value at each location in the environment and throughout time, and the strength and probability of interactions between individuals is independent of time and location then the environment is homogeneous.

So in theory the whole community may move location and the environment still remain homogeneous by my definition. This is supported by Den Boer (1968) who defined the effective environment of a natural population as 'that subset of its environment whose components have a measurable influence on the statistics of the population at some time'. A population may migrate between environments which are effectively the same.

It may be that one or more of the physical properties of the environment may vary through time but at any point in time be constant in space, or the probability and strength of interactions between individuals may change with time (as well as the numbers of individuals present) but remain independent of space. In this case the environment is effectively temporally heterogeneous.

If at least one of the physical properties depends on the location but is constant with time or the strength and probability of an interaction depends on the location but is independent of time, then the environment is spatially heterogeneous.

An environment which is both temporally and spatially heterogeneous is spatio-temporally heterogeneous.

3.4 Approaches to modelling population dynamics in a heterogeneous environment

3.4.1 Introduction

In Section 3.3.2 we formally defined three types of environmental heterogeneity; temporal, spatial and spatio-temporal, although the latter term merely applies to an environment which is both temporally and spatially heterogeneous.

Temporal heterogeneity is relatively straight-forward to model by encorporating time-varying parameters into the equations. The variation may be deterministic or stochastic. Some simple examples are discussed in Section 3.4.2.

Modelling spatial heterogeneity is much more complicated The mathematics are immediately more difficult and there are also several different types of spatial heterogeneity to consider. In order to simplify the mathematics some people have included the effects of heterogeneity implicitly in what are essentially models of homogeneous situations. An example of this approach is given in Section 3.4.3.

However to understand more fully the effects of spatial heterogeneity on population and community dynamics it is necessary to develop more sophisticated models. The type of model appropriate (differential equation, difference equation or other) depends not only on the types of species and interaction between them (as in homogeneous models) but also on the type of spatial heterogeneity.

Four types of spatial heterogeneity are discernable from the discussions in Section 3.2 and the definition of heterogeneity.

TYPE A - environments which are essentially homogeneous except for example providing a number of refuges for particular individuals of species or physical barriers to the progress of predators.

TYPE B - environments in which important physical factors such as temperature vary with the position within the environment.

TYPE C - environments in which an uneven distribution of one species may affect the behaviour of others.

TYPE D - environments in which patches of suitable habitats are separated by areas of unsuitable habitats.

In reality a particular environment is likely to have a mixture of all four types of spatial heterogeneity plus other types not mentioned.

Type A can be relatively easily modelled by implicit methods. Some examples are given in Section 3.4.4.

Type A heterogeneity is strictly speaking an example of type B. In this case it may be that the values of certain important physical factors change significantly with spatial location. If so population density can be made a function of continuous space as well as time (discrete or continuous) and, for instance, partial differential equation models can be developed. A short discussion is given in Section 3.4.4.2. In some cases of type B heterogeneity the parameter values may change in such a way that the environment can be divided up into a number of discrete homogeneous patches. This technique has also been used in constructing models for types C and D. Choice of timescale and the measure of population or community size becomes important.

For type B and type C it is possible to develop models in which the population density in each patch or cell can be measured and the timescale can remain continuous (or in the discrete case the unit of time might be one generation). An example of such a model is given in Section 3.4.5.

In type D heterogeneity the environment is broken up into patches and the timescale often becomes the life-time of a community in such a patch. The population measure then becomes patch-occupancy, that is the proportion of patches occupied by each species.

As indicated above mathematical models which aim to describe community dynamics in spatially heterogeneous enviroments very quickly become extremely complicated and difficult to analyse. Indeed few results have been derived for communities with more than two species and even for two species models extensive use of simulation models run on computers has been made.

In the following Sections I present some models which have been developed to describe the various types of heterogeneity and in particular to investigate the effect of spatial heterogeneity on community stability.

3.4.2 Temporal environmental heterogeneity

It is unlikely that all of the environmental parameters which affect the dynamics of a population or a community will be constant through time (although they may be constant through space). Some parameters may indeed vary cyclically (e.g. seasonally) or in some other deterministic manner. Some parameters may vary randomly about a constant value or indeed a deterministic value. May (1974) considers briefly two ways of modelling temporal heterogeneity of the environment.

3.4.2.1 Deterministic temporal heterogeneity

Consider for example the simple exponential growth model

$$\frac{dx(t)}{dt} = r\,x(t) \qquad 3.1$$

Suppose that the intrinsic rate of increase r is infact a function of t, r = r(t).

It may be that r varies seasonally.

e.g. let $r = \sin(wt)$ 3.2

where w reflects a cycle of one year.

Clearly the solution of the differential equation is then

$$\begin{aligned} x(t) &= x(0)\exp\left(\int_0^t \sin(wt')dt'\right) \\ &= x(0)\exp\left(\frac{1-\cos(wt)}{w}\right) \end{aligned} \qquad 3.3$$

The population thus oscillates with a period of one year in a completely deterministic manner.

Such complexities can clearly be included in more sophisticated population models in a similar way.

3.4.2.2 Random temporal heterogeneity

Consider now the logistic equation

$$\frac{dx(t)}{dt} = x(t)\quad(k-x(t)) \qquad 3.4$$

and suppose that the environmental parameter k varies randomly with time.

i.e. $k = k_o + \gamma(t)$ 3.5

where k_o is the mean value of k

and $\gamma(t)$ is drawn from a random distribution of mean zero and variance σ^2.

The value of x(t) now depends on the probability distribution which determines $\gamma(t)$ and hence we need to talk about the probability of there being x individuals in the population at time t - f (x,t). When the stochastic term is white noise it has been shown that:

$$\frac{\partial f(x,t)}{\partial t} = -\frac{\partial}{\partial x}(m(x)\ f\ (x,t)) + \tfrac{1}{2}\frac{\partial^2}{\partial x^2}(v(x)\ f\ (x,t)) \qquad 3.6$$

where m(x) = the expected value of x (k-x) = $x\ (k_o - x)$ 3.7

and v(x) = the variance of $x(k-x) = \sigma^2 x^2$ 3.8

We can now talk about the equilibrium probability function $f^*(x)$ which is independent of time and is given by

$$\frac{\partial f(x,t)}{\partial t} = 0 \qquad 3.9$$

It can be shown that in this case

$$f^*(x) = \frac{C}{v(x)} \exp\left(2\int_o^x \frac{m(x')}{v(x')}\, dx' \right)$$

$$= \frac{C}{x^2 \sigma^2} \exp\left(2 \int_o^x \frac{k_o - x'}{\sigma^2 x}\, dx' \right)$$

$$= C \times^{2(k_o/\sigma^2)-2} \exp\left(-2x/\sigma^2\right) \qquad 3.10$$

provided $k_o > \frac{1}{2}\sigma^2$ where C is a normalising constant

This is infact a standard Pearson Type III gamma distribution.

If $k_0 < \frac{1}{2}\sigma^2$ there is no equilibrium solution.

The equilibrium solution shows that the equilibrium population is distributed about a mean $m^*(x)$ with relative variation $r^*(x)$ where

$$m^*(x) = \int_0^\infty x\, f^*(x)\, dx$$

$$= k_0 \left(1 - \frac{\sigma^2}{2k_0}\right) \qquad 3.11$$

and $$r^*(x) = \frac{\left(\int_0^\infty (x - m^*(x))^2 f^*(x)\, dx\right)^{\frac{1}{2}}}{m^*(x)}$$

$$= \left(\frac{\sigma^2/2k_0}{1 - \sigma^2/2k_0}\right)^{\frac{1}{2}} \qquad 3.12$$

If we parallel these results with the deterministic case in which the 'mean' is k_0 and the stability condition is purely that $k_0 > 0$, we can see that temporal heterogeneity has reduced the mean population level and that fluctuations about this mean level become more severe as the variance σ^2 approaches $2k_0$. For $\sigma^2 > 2k_0$ the population becomes unstable.

In general, for communities in homogeneous environments modelled by differential equations as in Section 2.11 the local stability of the equilibrium is determined by the value of the eigenvalue with the largest real part. In the equivalent temporally heterogeneous case in which environmental parameters are random it is apparant from the above example at least that the population numbers will vary about an equilibrium mean value in such a way that stability will also depend on the size of the variability. This variability will usually depend in turn on the variability σ^2 of the environmental parameters. For small σ^2 the population is likely to be stable. For large σ^2 the population may be unstable and indeed an equilibrium mean value may not exist.

Models for communities with more than one species living in a temporally heterogeneous environment can be developed along similar lines and indeed May considers specifically a two-species model and also a general n-species model in which certain environmental parameters are described randomly. In each case the ratio between the absolute value of the real part of the eigenvalue of the equivalent deterministic system with the largest real part and a measure of the environmental variance is important in determining whether the community is stable or not.

3.4.3 Approaches to modelling the effect of spatial environmental heterogeneity by implicit methods.

Rosenzweig and MacArthur (1963) used a general continuous-time model to investigate the effect of spatial heterogeneity of the environment on the dynamics of a predator-prey community.

$$\frac{dx}{dt} = f(x) - \phi(x,y) \qquad 3.13$$

$$\frac{dy}{dt} = -ey + k\phi(x,y) \qquad 3.14$$

where x is the prey density, y the predator density
f is the rate of change of prey in the absence of predators
ϕ is the rate of predation
k is the efficiency of converting prey into predators
e is the mortality rate of predators

They investigated several forms of the functions f and ϕ. In particular they simplified the equations by putting

$$\phi(x,y) = y\phi(x)$$

and discovered that the population dynamics are not fundamentally altered.

Hence $$\frac{dx}{dt} = f(x) - \phi(x)y \qquad 3.15$$

$$\frac{dy}{dt} = -ey + ky\phi(x) \qquad 3.16$$

The equilibrium population levels x* and y* are given by

$$f(x^*) - y\phi(x^*) = 0 \qquad 3.17$$

$$-ey^* + ky^*\phi(x^*) = 0 \qquad 3.18$$

Hence $$\phi(x^*) = e/k \qquad 3.19$$

$$y^* = \frac{f(x^*)}{\phi(x^*)} \qquad 3.20$$

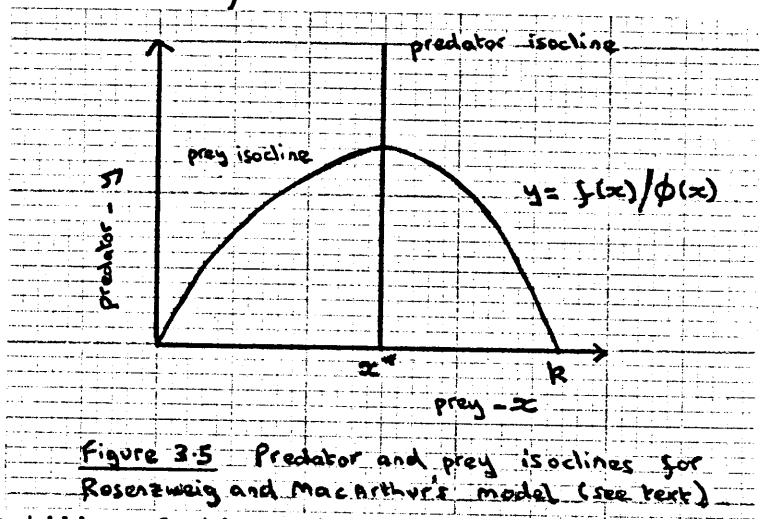


Figure 3.5 Predator and prey isoclines for Rosenzweig and MacArthur's model (see text)

The stability of this equilibrium can be investigated in the usual way.

The community matrix is

$$\begin{pmatrix} \frac{df}{dx} - y^*\frac{d\phi}{dx} & -\phi \\ k\frac{d\phi}{dx}\, y^* & 0 \end{pmatrix} \qquad 3.21$$

and hence the characteristic equation is

$$\lambda^2 - \lambda\left(\frac{df}{dx} - y^*\frac{d\phi}{dx}\right) + k\phi\frac{d\phi}{dx}\, y^* = 0 \qquad 3.22$$

where λ is an eigenvalue.

The general shapes of the functions f and ϕ considered by Rosenzweig and MacArthur are shown in Figure 3.6

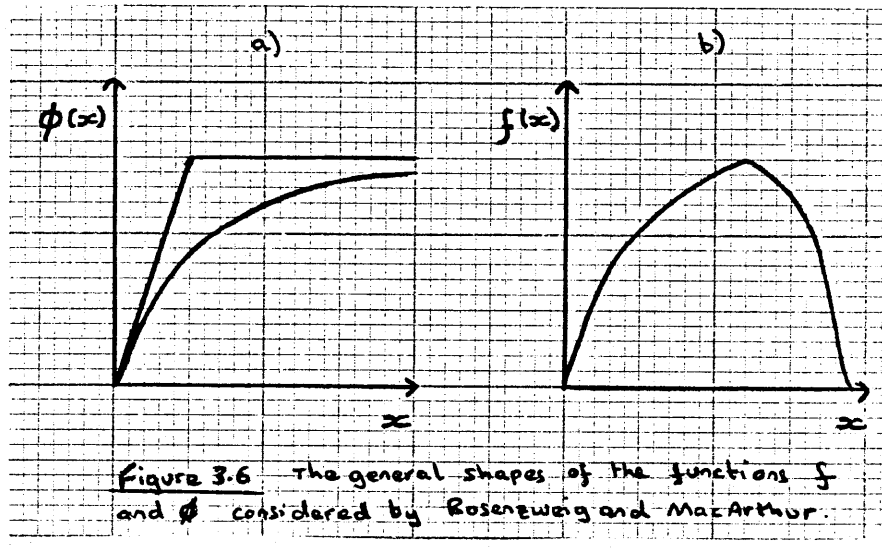


Figure 3.6 The general shapes of the functions f and ϕ considered by Rosenzweig and MacArthur.

For the equilibrium to be stable we require

$$k\phi\frac{d\phi}{dx}\,y^* \geqslant 0 \qquad 3.23$$

and $$\frac{df}{dx} - \overset{*}{y}\frac{d\phi}{dx} < 0 \qquad 3.24$$

Inequality 3.23 is clearly satisfied if ϕ is of the shape shown in Figure 3.6a.

Inequality 3.24 is satisfied if $\frac{df}{dx} \leq 0$. (though this is not a necessary condition)

Thus the equilibrium is stable if the predator isocline (equation 3.20) is crossed by the prey isocline (equation 3.19) to the right of its hump. Otherwise the equilibrium may be unstable. (See Figure 3.5).

Certain assumptions can be made about the values of the parameters in the model and on the forms of functions f and ϕ which may reflect the effect of spatial heterogeneity. For instance, Stenseth (1977) pointed out that population densities in homogeneous environments may be more variable for at least two reasons.

i) The supply of preferred food for the prey may be greater in homogeneous than in heterogeneous environments. This means that the carrying capacity K of the environment (that is the maximum density of prey that can be supported in the absence of predators - $f(K)=0$) is greater in homogeneous environments.

In this case the hump in Figure 3.5 is likely to be further to the right for homogeneous environments and hence the community less likely to be stable.

ii) It is easier for predators to find prey at low densities in homogeneous than in heterogeneous environments and thus the equilibrium density of the prey may be smaller.

So in this case the prey isocline is likely to cross the predator isocline further to the left in homogeneous conditions and again the community will be less likely to be stable.

So in both cases modelling spatial heterogeneity implicitly indicates that heterogeneous environments may be more stable than homogeneous ones.

3.4.4 Physical spatial heterogeneity

3.4.4.1 Cover and refuges (hiding places) - type A heterogeneity

An environment may be spatially heterogeneous purely because it offers a number of hiding places to the prey. In such a case it may be that at any point in time a constant density of prey is protected from attack by a predator.

Maynard-Smith (1974) used a differential equation model to investigate the effect of this as follows.

$$\frac{dx}{dt} = ax - hy(x-c) \qquad 3.25$$

$$\frac{dy}{dt} = -ey + khy(x-c) \qquad 3.26$$

where x and y are the prey and predator densities respectively and c is the constant number of hiding places per unit area.

The equilibrium densities x^* and y^* are given by

$$x^* - c = e/kh \qquad 3.27$$

$$y^* = \frac{ax^*}{h(x^*-c)} \qquad 3.28$$

The community matrix is

$$\begin{pmatrix} a - hy^* & -h(x^*-c) \\ khy^* & 0 \end{pmatrix} \qquad 3.29$$

and the characteristic equation is

$$\lambda^2 - \lambda(a-hy^*) + hey^* = 0. \qquad 3.30$$

So the equilibrium is stable if

$$a - hy^* < 0 \qquad 3.31$$

From equation 3.28 this is clearly always the case and hence the equilibrium is stable.

As we saw in Section 2.11.2 if c=0 (i.e. no hiding places) then constant but unstable oscillations about the equilibrium values ensue. The inclusion of hiding places makes the environment spatially heterogeneous and the equilibrium population densities stable by damping the oscillations.

3.4.4.2 Continuous heterogeneity - type B heterogeneity

In some situations the environment in which a community is living may be such that parameters which affect the community population dynamics (for example, temperature) may vary significantly with the exact location within the environment. This type of spatial heterogeneity may be particularly important for plant communities or plankton communities in the sea.

There are essentially two main approaches to modelling such a situation.

As suggested by for instance Levin (1976) the environment may be divided up into a large number of discrete patches. The community population dynamics can depend on the local conditions and migration between patches can be included. As the number of patches is increased the continuous case is approximated. This method is essentially similar to that described in Section 3.4.5 and 3.4.6 and the main advantage is that the mathematics is relatively easy to handle.

The alternative method is to use partial differential equations and I shall briefly consider this approach in more detail.

Let us start with a single species in a one-dimensional environment.

Suppose that the population size $x(s)$ at each point s in the environment grows independently of all other locations and that there is no migration.

A general partial differential equation model of this situation would be

$$\frac{\partial x(s,t)}{\partial t} = f(x,s,t) \qquad 3.32$$

e.g. $$\frac{\partial x(s,t)}{\partial t} = r(s)x(k(s)-x) \qquad 3.33$$

The size of the total population in the enviroment at time t would be given by

$$\int_S x(s,t)ds \qquad 3.34$$

where S defines the spatial limits of the environment.

It is more realistic to assume that some dispersion of individuals between locations will occur.

The appropriate partial differential equation model which takes this into account takes the following general form:

$$\frac{dx}{dt} = f(x,s,t) + \frac{\partial}{\partial s}\left(D(s)\frac{\partial x}{\partial s}\right) \qquad 3.35$$

where D(s) measures the diffusion potential at s.

This model can be extended to describe communities of interacting species in a m-dimensional spatial environment.

$$\frac{dx_i}{dt} = f_i(\underline{x}, \underline{s}, t) + \nabla . D_i(\underline{s})x_i \qquad 3.36$$

where $\underline{x} = (x_1, \ldots . x_n)$

$\underline{s} = (s_1, \ldots . s_m)$

and $\nabla . g(\underline{s}) = \frac{\partial g}{\partial s_1} + \ldots . + \frac{\partial g}{\partial s_m}$

The advantage of this method over the first (i.e. using discrete patches) is that the number of equations is greatly reduced however analysis of such equations can be extremely difficult even for the very simplest forms of f_i and D_i.

Since there appears to have been few useful results derived from such models I will not consider them further here. Partial differential equation models have been used relatively successfully to model plankton communities, for example Wroblewski, O' Brien & Platt (1975)

3.4.5 Non-random spatial distributions of populations - type C heterogeneity

3.4.5.1 Implicit refuges (May (1978)).

We have seen from the discussions of heterogeneity in Section 3.2 that environments often tend to be patchy in that some areas are more densely populated than others. If the prey population is distributed in such a way and the predators aggregate in areas of high prey density then the areas of low density will be, at least temporarily, refuges.

Too much of such refuge may lead to the prey increasing uncontrolled by the predators, while too little may not give any advantage to the prey over homogeneous environments.

Environmental patchiness (and it is important to note that such patchiness may develop by chance and not because of any physical heterogeneity of the environment) has been investigated in a number of ways as we shall see. One method of modelling patchiness without specifically modelling each individual patch was put forward by May (1978).

May's model is particularly applicable to arthropod host-parasitoid interactions. In such relationships each host (H) in any one generation is either parasitised by exactly one parasite(P) or escapes parasitism to give rise to F (>1) progeny which become the next generation of hosts.

The model is a difference equation one as follows:

$$H_{t+1} = F H_t (1 + a P_t/k)^{-k} \qquad 3.37$$

$$P_{t+1} = H_t - H_{t+1}/F \qquad 3.38$$

where $(1 + a P_t/k)^{-k}$ is the probability of a host escaping parasitism.

This probability is derived from the assumption that the probability for a given host to be discovered by a parasitoid d times during a generation is given by a negative binomial probability distribution with 'clumping' parameter k and mean attack rate given by aP (see Southwood (1966) for a description of the negative binomial distribution).

Such searching by the parasitoid is non-random and may result because the hosts are distributed unevenly (i.e. in patches) throughout the environment. May discussed experimental and field evidence which support that the negative binomial is an appropriate approximation in some cases. Griffiths & Holling (1969) carried out a series of experiments in which ichneumon Pleolophus Basizonus parasitoids attacked sawfly Neodiprion Sertifer hosts and the distribution of attacks per host was well described by the negative binomial, and

Hassell (unpublished) has gathered data on attacks of Cyzenis albicans on winter moths which also fitted the negative binomial distribution.

The equilibrium population levels H^* and P^* can be determined in the usual way by setting $H^* = H_{t+1} = H_t$ and $P^* = P_{t+1} = P_t$

Hence from equation 3.37

$$P^* = k\,(F^{1/k} - 1) / a \qquad 3.40$$

and from equation 3.38

$$H^* = F\,P^* / (F-1) \qquad 3.41$$

The stability of this equilibrium may be examined as follows:

Let $H_t = H^* + \varepsilon_t$ 3.42

and $P_t = P^* + \psi_t$ 3.43

where ε_t and ψ_t are small disturbances from the equilibrium values.

Then $H^* + \varepsilon_{t+1} = F\,(H^* + \varepsilon_t)\,(1 + a\,(P^* + \psi_t)/k)^{-k}$ 3.44

$$= F\,H^*\,(1 + a\,P^*/k)^{-k} + F\varepsilon_t\,(1 + a\,P^*/k)^{-k}$$

$$- F\,H^* a\,(1 + aP^*/k)^{-(k+1)}\psi_t \qquad 3.45$$

$$= H^* + \varepsilon_t - aH^*\,(1 + aP^*/k)^{-1}\,\psi_t \qquad 3.46$$

(by expanding equation 3.44 as a Taylor Series and ignoring terms of order 2 and above in ε, ψ).

and similarly $P^* + \psi_{t+1} = H^* + \varepsilon_t - (H^* + \varepsilon_{t+1})/F$ 3.47

That is

$$\varepsilon_{t+1} = \varepsilon_t - aH^* (1 + aP^*/k)^{-1} \psi_t \qquad 3.48$$

$$\psi_{t+1} = \varepsilon_t - \varepsilon_{t+1}/F \qquad 3.49$$

The solution of these coupled difference equations is necessarily of the form

$$\varepsilon_t = A\lambda^t \qquad 3.50$$

$$\psi_t = B\lambda^t \qquad 3.51$$

where λ is an eigenvalue of the system and A and B are constants determined by the initial sizes of the perturbations.

Substituting this solution into equations 3.48 and 3.49 gives

$$(\lambda - 1)\varepsilon_t + \Theta\psi_t = 0 \qquad 3.52$$

$$\left(\frac{\lambda}{F} - 1\right)\varepsilon_t + \lambda\psi_t = 0 \qquad 3.53$$

where $\Theta = aH^* (1 + aP^*/k)^{-1}$ 3.54

The community matrix is thus

$$\begin{pmatrix} \lambda - 1 & \Theta \\ \frac{\lambda}{F} - 1 & \lambda \end{pmatrix} \qquad 3.55$$

and the characteristic equation is

$$\lambda^2 - \lambda(1 + \Theta/F) + \Theta = 0 \qquad 3.56$$

There are two values of λ, λ_1 and λ_2, which satisfy this equation and hence the solution of equations 3.48 and 3.49 becomes

$$\varepsilon_t = A_1 \lambda_1^{\,t} + A_2 \lambda_2^{\,t} \qquad 3.57$$

$$\psi_t = B_1 \lambda_1^{\,t} + B_2 \lambda_2^{\,t} \qquad 3.58$$

where A_1, A_2, B_1, B_2, are constants determined by the initial sizes of the perturbations.

It is clear from the nature of this solution that in order for the perturbations ε_t and ψ_t to die away with time the moduli of λ_1 and λ_2 must both be less than one.

Solving equation 3.55 for λ we see that

$$2\lambda = (1 + \theta/F) \pm \{(1 + \theta/F)^2 - 4\theta\}^{1/2} \qquad 3.59$$

$$= b \pm (b^2 + 4c)^{1/2} \qquad 3.60$$

where $b = 1 + \theta/F$ 3.61

and $c = -\theta$ 3.62

It is straightforward to show that for the modulus of λ to be less than one the following conditions must be satisfied.

$$1 - b > c > -1 \qquad 3.63$$

and $$1 + b > c > -1 \qquad 3.64$$

Substituting the values of b and c (equations 3.61 and 3.62) into equations 3.63 and 3.64 we obtain the two conditions:

$$\theta/F < \theta < 1 \qquad 3.65$$

$$2 + \theta/F > -\theta > -1 \qquad 3.66$$

The left-hand side of both inequalities is satisfied automatically since F is greater than one by definition and θ is greater than zero from equation 3.54.

The stability conditions thus reduce to the single criterion

$$\theta < 1 \qquad 3.67$$

Substituting the values for H^* and P^* from equations 3.40 and 3.41 into equation 3.54 we see that

$$\theta = k\,(1-F^{-1/k}) \;/\; (1-F^{-1}) \qquad 3.68$$

is clearly a monotonic increasing function of k and θ equals one when k equals one.

Therefore

$$\theta < 1 \quad \text{if and only if} \quad k < 1$$

When k is less than one the negative binomial distribution is essentially overdispersed : and this means that there are enough patches relatively free of parasitoids to provide refuges for the host, and the host-parasitoid relationship may be stable.

3.4.5.2 Hassell and May (1973)

Hassell & May (1973) considered a series of mathematical models which they used to investigate the stability properties of host-parasitoid relationships. The general form of these models is

$$H_{t+1} = F\,H_t\,f\,(P_t, H_t) \qquad 3.69$$

$$P_{t+1} = H_t - H_{t+1}/F \qquad 3.70$$

where H_t, P_t and F are as defined in Section 3.4.5.1 and $f\,(P_t,H_t)$ is the probability of a host escaping parasitism during its lifetime.

Following the same argument as in Section 3.4.5.1 they investigated in particular the effect of a non-random searching strategy by the parasitoids in an environment in which the hosts are unevenly distributed. Further they did this by modelling more explicitly the 'exact' distribution of hosts and parasitoids in the habitat.

To do this they split the habitat into m patches and let α_i and β_i denote the proportion of the total number of hosts and parasitoids in the i^{th} patch.

Suppose that within each patch i the parasitoids search for hosts at random and with a searching efficiency (i.e. the average area searched by a single parasitoid in its lifetime) which is independent of the number of hosts and parasitoids.

The probability of a host escaping parasitism in a particular patch i is thus

$$\exp\ (-\ a\beta_i\ P_t) \qquad 3.71$$

The proportion of the total number of hosts H_t which escape parasitism in patch i is thus

$$\alpha_i\ \exp\ (-a\beta_i\ P_t) \qquad 3.72$$

and the total number of hosts escaping parasitism in the whole habitat is

$$H_t \sum_{i=1}^{m} \alpha_i\ \exp\ (-a\beta_i\ P_t) \qquad 3.73$$

The specific model is therefore

$$H_{t+1} = F\ H_t \sum_{i=1}^{m} \alpha_i\ \exp\ (-a\beta_i\ P_t) \qquad 3.74$$

$$P_{t+1} = H_t - H_{t+1}\ /F \qquad 3.75$$

The equilibrium population levels H^* and P^* are given by

$$F \sum_{i=1}^{m} \alpha_i \exp(-a\beta_i P^*) = 1 \qquad 3.76$$

$$P^* = H^* \left(\frac{F-1}{F}\right) \qquad 3.77$$

The stability of the equilibrium can be investigated by considering the effect of small pertubations.

Let $H_t = H^* + \varepsilon_t$ 3.78

$$P_t = P^* + \psi_t \qquad 3.79$$

By substituting these expressions in equations 3.74 and 3.75, expanding in a Taylor Series and ignoring terms of order two and higher in ε, ψ, the following equations may be derived:

$$\varepsilon_{t+1} = \left(1 + F H^* \frac{\partial f}{\partial H^*}\right)\varepsilon_t + F H^* \frac{\partial f}{\partial P^*}\psi_t \qquad 3.80$$

$$\psi_{t+1} = \varepsilon_t - \varepsilon_{t+1}/F \qquad 3.81$$

where $f = \sum_{i=1}^{m} \alpha_i \exp(-a\beta_i P^*)$ 3.82

Following the arguments of Section 3.4.5.1 the solution of these coupled difference equations is necessarily of the form of equations 3.57 and 3.58.

The characteristic equation of the system is

$$\lambda^2 - (1 + FH^* \frac{\partial f}{\partial H^*} - H^* \frac{\partial f}{\partial P^*})\lambda - FH \frac{\partial f}{\partial P^*} = 0 \qquad 3.83$$

The solution of equation 3.83 is given by

$$2\lambda = (1 + F H^* \frac{\partial f}{\partial H^*} - H^* \frac{\partial f}{\partial P^*}) \pm ((1+FH^* \frac{\partial f}{\partial H^*} - H^* \frac{\partial f}{\partial P^*})^2 + 4FH^* \frac{\partial f}{\partial P^*})^{1/2} \quad 3.84$$

and it is straightforward to show that for the modulus of λ to be less than one the following conditions must hold:

$$\frac{F}{F-1} H^* \frac{\partial f}{\partial H^*} < - H^* \frac{\partial f}{\partial P^*} < \frac{1}{F} \quad 3.85$$

$$2 + FH^* \frac{\partial f}{\partial H^*} > (F-1) \frac{\partial f}{\partial P^*} \quad 3.86$$

In this particular case

$$\frac{\partial f}{\partial H^*} = 0 \quad 3.87$$

and $$\frac{\partial f}{\partial P^*} = -a \sum_{i=1}^{m} \alpha_i \beta_i \exp(-a\beta_i P^*) \quad 3.88$$

and the stability criterion becomes

$$F \sum_{i=1}^{m} \alpha_i (a\beta_i P^*) \exp(-a\beta_i P^*) < \frac{F-1}{F} \quad 3.89$$

(since 3.86 is automatically satisfied).
Hence, for any particular set of values for the host and parasitoid distribution α_i and β_i and the host effective rate of increase F, the stability of the host-parasitoid relationship may be determined, although this may require extensive calculations for each particular set of parameter values.

In nature the distribution of hosts and parasites between the m areas might take any form. It will indeed be determined by the actual community population dynamics which in turn depend on a number of complicated factors.

In order to investigate the possible effect of aggregation of parasites in areas of high host density May used a simple relationship between α_i and β_i as follows:

$$\beta_i = C \alpha_i^{\mu} \qquad 3.90$$

where $$C = \left(\sum_{i=1}^{m} \alpha_i^{\mu} \right)^{-1} \qquad 3.91$$

and μ (≥ 0) is termed the aggregation coefficient.

i) Random search ($\mu = 0$)

If μ equals zero, then

$$\beta_i = \frac{1}{m} \quad \text{for} \quad i=1,\ldots,m \qquad 3.92$$

In this case there are an equal number of parasites in each area irrespective of the host distribution α_i - this is exactly the same as the situation in which the parasites search at random throughout the whole of the habitat.

In this case

$$f = \exp\left(- \frac{a P^*}{n} \right) \qquad 3.93$$

$$= 1/F \quad \text{(from equation 3.76)} \qquad 3.94$$

Hence the left-hand side of equation 3.89 becomes

$$\frac{a P^*}{n} = \ln (F) \qquad 3.95$$

It is easy to show that

$$\ln (F) > \frac{F-1}{F} \qquad 3.96$$

and hence the model is unstable.

The model has infact been reduced to the random search model first put forward by Nicholson (1933) and Nicholson and Bailey (1935) and the results support their conclusions that a community consisting of a parasite population which searches at random for individuals of a host population regardless of the way in which the hosts are distributed throughout the habitat is unstable.

ii) μ very large

As μ increases the aggregation of parasites in areas of highest host density becomes more marked.

When μ becomes very large the parasites aggregate in the area of highest host density.

In this case

$$f = (1-\gamma) + \gamma \exp(-aP^*) \qquad 3.97$$

where γ is the proportion of hosts in the area of highest host density.

From equation 3.76

$$F\left[(1-\gamma) + \gamma \exp(-aP^*)\right] = 1 \qquad 3.98$$

and hence

$$F(1-\gamma) < 1 \qquad 3.99$$

for an equilibrium to exist.

Further

$$aP^* = -\ln\left(\frac{\frac{1}{F} - (1-\gamma)}{\gamma}\right) \qquad 3.100$$

$$= \ln\left(\frac{F\gamma}{1-F(1-\gamma)}\right) \qquad 3.101$$

and $$F\gamma\exp(-aP^*) = 1 - F(1-\gamma) \qquad 3.102$$

(from equation 3.98)

Hence the stability criterion becomes

$$F\gamma aP^{*} \exp(-aP^{*}) < \frac{F-1}{F} \qquad 3.103$$

i.e. $$(1-F(1-\gamma)) \ln\left(\frac{F\gamma}{1-F(1-\gamma)}\right) < \frac{F-1}{F} \qquad 3.104$$

(from equations 3.101 and 3.102)

The inequalities 3.99 and 3.104 determine the pairs of values of γ and F for which a stable equilibrium exists.

The stability boundaries are sketched in Figure 3.7.

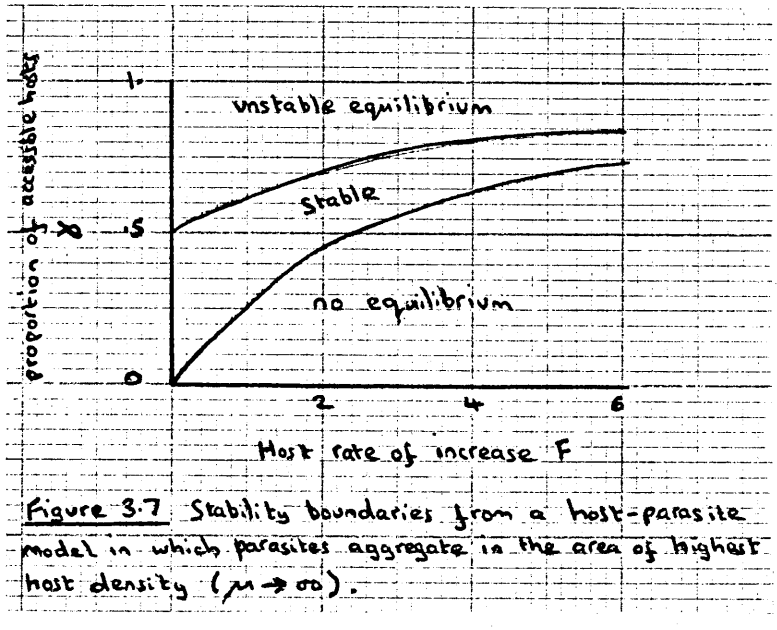


Figure 3.7 Stability boundaries from a host-parasite model in which parasites aggregate in the area of highest host density ($\mu \to \infty$).

The first point to note is that stability is now possible. However for low values of γ there is too much refuge and no equilibrium is possible, and for high values of F the range of values of γ for which a stable equilibrium exists is narrow. If the proportion of hosts accessible to parasitism is high then the equilibrium is likely to be unstable.

iii) $0 < \mu < \infty$

In order to easily evaluate the effect of μ between zero and infinity it is necessary to define more explicity the host distribution.

May chose the following form:

$$\alpha_i = \alpha \text{ for one patch } i. \qquad 3.105$$

$$\alpha_j = \frac{1-\alpha}{m-1} \text{ for } j \neq i. \qquad 3.106$$

$$\beta_i = \beta \qquad 3.107$$

$$\beta_j = \varepsilon\beta \qquad 3.108$$

where $$\varepsilon = \left(\frac{1-\alpha}{m-1}\right)^{\mu} \qquad 3.109$$

and hence $$\beta = (1 + \varepsilon(m-1))^{-1} \qquad 3.110$$

in order to satisfy equation 3.90.

Hence in this situation the hosts are distributed in such a way that there is one high density area and (m-1) low density areas, and the degree of aggregation of parasites in the high density area is determined by μ.

In this case

$$f = \alpha e^{-z} + (1-\alpha) e^{-\varepsilon z} \qquad 3.111$$

where $$z = \alpha\beta p^* \qquad 3.112$$

Hence (from equation 3.76)

$$F\left(\alpha e^{-z} + (1-\alpha)e^{-\varepsilon z}\right) = 1 \qquad 3.113$$

(note that f is clearly less than one and hence an equilibrium exists).

The stability criterion (equation 3.89) becomes

$$z F\left(\alpha e^{-z} + \varepsilon (1-\alpha)e^{-\varepsilon z}\right) < \frac{F-1}{F} \qquad 3.114$$

Given values for α and m (the number of patches) it is possible to determine from equations 3.112 and 3.114 a relationship between μ and F which in turn determines the stability of the host-parasitoid community.

A sketch of the stability boundaries is given in Figure 3.8.

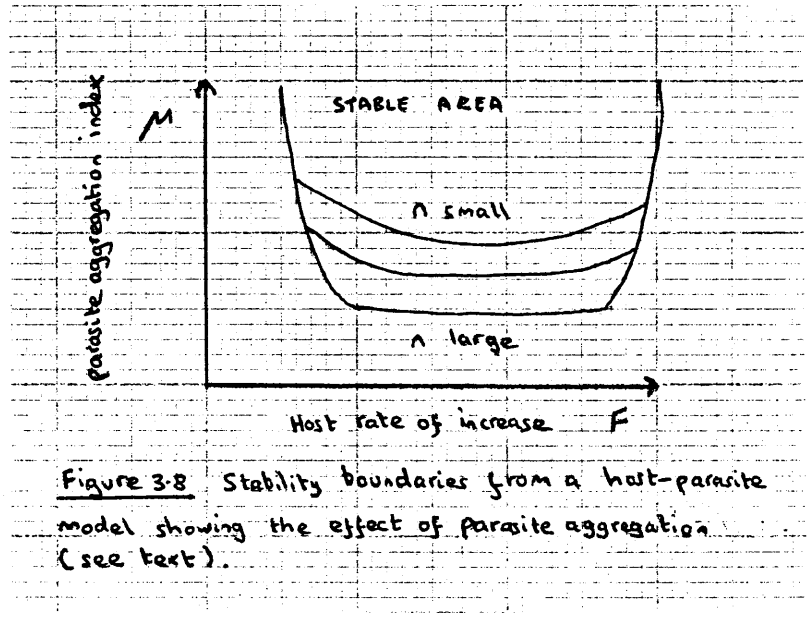


Figure 3.8 Stability boundaries from a host-parasite model showing the effect of parasite aggregation (see text).

May noted four trends:

- increasing parasite aggregation (μ) increases stability.
- stability is increased if there are more low density regions.
- there is a wider region of stability conditions when α is near 0.5 then when α is very small or very large.
- stability breaks down abruptly as F increases.

3.4.5.3 Discussion of Hassell and May's model

Hassell & May (1973) used a relatively simple model to demonstrate that, in a host-parasitoid relationship, if the parasitoids search completely at random for the hosts then the relationship will be unstable whereas if the parasitoids tend to aggregate in areas of high host density then the relationship may be stable. Although they chose a particular form of host distribution to demonstrate this, they have done further work which shows that similar results apply for other forms of distribution. In general the more uneven the host distribution, the more likely the relationship is to be stable.

There are two main criticisms of the model used.

Firstly, in nature it is likely that the searching efficiency (a) will depend on the numbers of hosts and parasitoids present and also on such factors as the time wasted by a parasitoid in unsuccessfully engaging a host. However Hassell & May's model E includes such factors and the results are not qualitatively different.

Secondly, in nature the distribution of hosts and parasites is not likely to remain constant but will depend on the local population dynamics, the physical heterogeneity of the environment and the amount of movement possible. Indeed Comins & Hassell (1979) have extended Hassell & May's model by allowing the parasitoids to be capable of instantly sensing which area of the environment has the highest density of unparasitised hosts. Hence at any time t all the parasitoids are found in the area with the highest density of healthy hosts.

They investigated the local stability properties of this model and found that they are not qualitatively any different from the 'fixed aggregation' model. In the real world the behaviour of the parasites is likely to lie somewhere between the two models and, as suggested above, other factors, such as locally different population dynamics, may have further effects.

However, since both 'extremes' lead to stable relationships under a wide range of conditions it seems reasonable to conclude that spatial heterogeneity resulting from an uneven distribution of hosts in the environment can stabilise a host-parasitoid relationship provided that the parasitoids aggregate in areas of higher host density.

3.4.6 Migration - type D heterogeneity

3.4.6.1 A. Hastings

Hastings (1977) considered a predator-prey community in an environment consisting of a large number of identical patches between which prey and predator individuals can migrate at any time.

He assumed that an any time t a patch could be in one of only three states: empty; containing only prey (prey); containing both prey and predator (predator).

The rate of change of state of a patch is determined by some simple rules:

i) An empty patch can only be invaded by prey, thus creating a prey patch.

ii) A prey patch remains so until it is invaded by a predator whence it becomes a predator patch.

iii) A predator patch becomes an empty patch after a fixed length of time (i.e. the presence of predators always causes the extinction of both prey and predator populations within the patch).

iv) The rate at which predators migrate to invade prey patches is directly proportional to the number of predator patches.

v) The rate at which prey migrate to invade empty patches is directly proportional to the number of prey plus predator patches.

All patches are assumed to be equally accessible from all other patches and the time it takes individuals to migrate between patches is assumed to be insignificant.

Let x be the fraction of prey patches and y be the fraction of predator patches at time t, and, without loss of generality, set the time it takes for a predator patch to return to the empty state to one.

From the assumptions the following differential-delay model can be formulated.

$$\frac{dx}{dt} = \alpha(1-x-y)(x+y) - \beta xy \qquad 3.115$$

$$\frac{dy}{dt} = \beta[x(t)\,y(t) - x(t-1)y(t-1)] \qquad 3.116$$

with initial conditions

$$\left.\begin{aligned} x(t) &= \phi_1(t) \\ y(t) &= \phi_2(t) \end{aligned}\right\} \quad -1 \leq t \leq 0 \qquad \begin{matrix} 3.117 \\ 3.118 \end{matrix}$$

Note that

$$0 \leq x \leq 1, \quad 0 \leq y \leq 1-x \qquad 3.119$$

and that at any time t the total number of predator patches is

$$y(t) = \beta \int_{t-1}^{t} x(s)\,y(s)\,ds \qquad 3.120$$

and hence the initial conditions must satisfy this equation.

We now consider whether this model provides any equilibrium population levels.

There are clearly two trivial equilibria

$$x^* = 0, \quad y^* = 0$$

and $$x^* = 1, \quad y^* = 0$$

The first is unstable since any small perturbation from it will clearly tend to grow.

The stability of the second depends on the values of α and β, but will not be considered further here.

Other possible equilibria may be determined in the usual way by setting $\frac{dx}{dt}$ and $\frac{dy}{dt}$ equal to 0.

$$\alpha(1-x^*-y^*)(x^*+y^*) - \beta x^* y^* = 0 \qquad 3.121$$

$$\beta(x^* y^* - x^* y^*) = 0 \qquad 3.122$$

The unique non-trivial solution is

$$x^* = 1/\beta \qquad 3.123$$

$$y^* = \frac{1}{2} - \frac{1}{\beta} - \frac{1}{2\alpha} + \frac{1}{2}\left(\left(\frac{1-1}{\alpha}\right)^2 + \frac{4}{\alpha\beta}\right)^{1/2} \qquad 3.124$$

provided that $\beta > 1$.

The local stability of this equilibrium can be examined by adding small perturbations ε and ψ to the equilibrium values x^* and y^* respectively and substituting these expressions into equations 3.115 and 3.116.

This leads to the following equations for ξ and ψ.

$$\frac{d\xi}{dt} = (\alpha - 2\alpha(1/\beta + y^*) - \beta y^*)\xi + (\alpha - 2\alpha(1/\beta + y^*) - 1)\psi \qquad 3.125$$

$$\frac{d\psi}{dt} = \beta y^* (\xi(t) - \xi(t-1)) + (\psi(t) - \psi(t-1)). \qquad 3.126$$

The standard way of solving such equations is to try solutions of the form

$$\xi = Ae^{\lambda t} \qquad 3.127$$

$$\psi = Be^{\lambda t} \qquad 3.128$$

where λ is an eigenvalue, and A and B are constants depending on the initial size of the perturbations.

This leads to the characteristic equation

$$s - K\lambda + Kc + d = 0 \qquad 3.129$$

where $K = (1-e^{-\lambda})/\lambda$ 3.130

$$C = \alpha - \frac{2\alpha}{\beta} - \alpha\beta y^* + 2\alpha\beta y^{*2} \qquad 3.131$$

$$d = -\alpha + \frac{2\alpha}{\beta} + 2\alpha y^* + \beta y^* \qquad 3.132$$

If all solutions of Equation 3.129 have negative real parts then the equilibrium is stable.

By using the method of D-partitions (El'sgol'ts and Norkin (1973)) the regions of stability for pairs of parameter values α, β may be determined.

Such regions are shown schematically in Figure 3.9

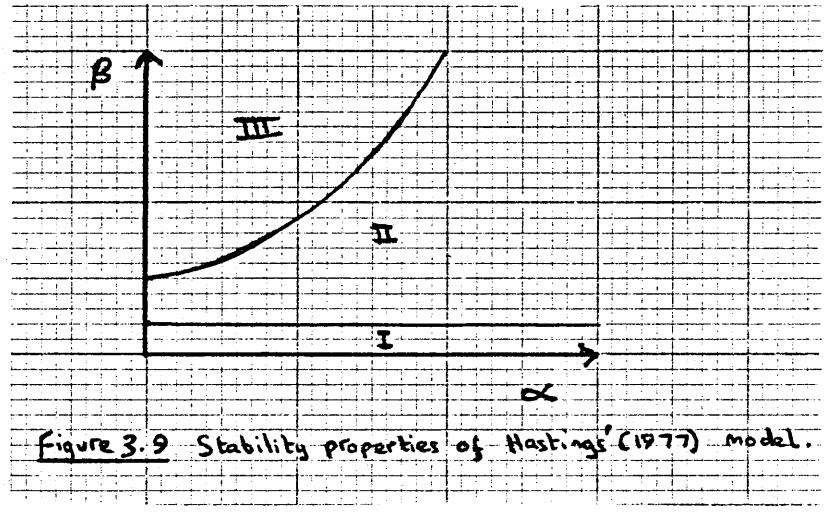


Figure 3.9 Stability properties of Hastings' (1977) model.

In region I the predator population becomes extinct. This is because β is less than I and hence the predators are unable to invade enough new patches in the time it takes the current predator patches to crash.

When β is large and α is small (region III) both species' populations have a low equilibrium density which is unstable since the prey patches are quickly invaded but new ones are not created quickly enough.

In region II there is a locally stable equilibrium of prey and predator patches. In this case both the mobility of the predator and prey is relatively high so that dispersion between patches becomes the stabilising factor.

There are a number of important points to note about Hastings' model, the main one being the relative timescale involved. Essentially the individual population dynamics within each patch are not modelled specifically. It is assumed that prey persist in a prey patch until that patch is invaded whence the local predator-prey community becomes extinct after a fixed period of time. The actual size of populations in each patch at time t is irrelevant and the important timescale of the model becomes the predator patch extinction time. Any time related results when comparing results from this model should be related to this timescale.

Many other mathematical ecologists have developed models along similar lines, a few involving more than two species and more sophisticated within-patch dynamics. The model of Zeigler described in Section 3.4.6.3 is such an example as are models by Caswell (1977) , Hilborn (1975) and Vandermeer (1973).

Another assumption which can be easily modified is that all patches are equally accessible. It may be more realistic to limit movement to between nearest neighbours (e.g. Zeigler (1977)).

However none of these modifications have been shown to disagree with the general conclusion that dispersion between patches in a spatially heterogeneous environment may lead to stability, although, as we shall see in the next sections, there is some debate as to whether continuous dispersion is actually stabilising.

3.4.6.2 J. Maynard Smith

Maynard Smith (1974) argued that continuous population exchange, such as that due to continuous migration of individuals between suitable patches within the total environment, cannot provide effective stabilisation.

Firstly Maynard Smith considered a continuous habitat broken up (somewhat contradictarily) into a number of homogeneous cells and assumed that migration of individuals between cells is instantaneous and that no deaths occur during migration.

Suppose that the population size of a particular species in a single cell is oscillating with large amplitude. Will migration reduce the size of this amplitude? If neighbouring cells oscillate in phase, Maynard-Smith argued that migration will have no effect.

This conclusion leads to a more significant question: does migration tend to bring neighbouring cells into or out of phase?

Maynard Smith considered four possible criteria for migration to occur in a predator-prey community:

i) prey migrate away from cells in which the number of prey is high.

ii) prey migrate away from cells in which the number of predators is high.

iii) predators migrate away from cells in which the number of predators is high.

iv) predators migrate away from cells in which the number of prey is low.

He argued that types i) and iii) tend to bring neighbouring cells into phase but ii) and iv) have no effect on phase. Hence migration does not tend to reduce population amplitudes and so has no effect on stability.

He recognised that this conclusion is at variance with the result of Huffaker's classic experiments (Section 3.2.2) in which slowing down the migration of the predators and increasing that of the prey increased the stability (persistence) of the system.

He therefore constructed a 'discrete population exchange' model in which each cell can be in one of a finite number of states (e.g. contain prey only, be empty) at time t, and each cell has a transition probability of changing state after each period of time T which depends in particular on the state of its nearest neighbours.

Simulation runs of this model on a computer demonstrated that persistent coexistence of predators and prey can occur with a wide range of parameter values.

Maynard Smith suggested that the following factors are important for stability

i) high capacity of prey for migration
ii) cover or refuge for prey
iii) predators only migrate during a restricted period
iv) large number of cells

3.4.6.3 B. P. Zeigler

Zeigler (1977) attempted to make Maynard Smith's model more rigorous.

Firstly he proposed that the local community population dynamics in each cell obey the Lotka-Volterra equations with prey self-limitation.

$$\frac{dx}{dt} = ax(1-x) - xy \qquad 3.133$$

$$\frac{dy}{dt} = -by + xy \qquad 3.134$$

where x and y denote the density of prey and predators respectively in the cell.

This model has the non-trivial equilibrium

$$x^* = b \qquad 3.135$$

$$y^* = a(1-b) \qquad 3.136$$

He then defined two positive numbers L_1 and L_2 called the prey and predator extinction level respectively. The cell is locally unstable if $x^* < L_1$ or $y^* < L_2$.

Zeigler then defined a stability effect as one which makes the expected lifetime of the overall predator-prey community significantly greater than that of the cells in isolation.

A cell can be in one of five states.

i) A cell is in the EMPTY state until it is invaded by $x \geq L_1$ prey when it enters the PREY state.

ii) The prey population grows according to the logistic equation until the carrying capacity is reached when the cell enters the PREY state (unless the cell is invaded by predators).

iii) If a PREY or PREY' cell is invaded by $y=L_2$ predators the cell enters the PRED state.

iv) After a certain amount of time (which is calculated from the elapsed time since the cell entered the PREY state) the density of prey will decline below L_1 and the cell enters the PRED' state.

v) The predator density will then decline below L_2 and the EMPTY state is entered.

If a cell is in state PREY' (lots of prey) or PRED' (too few prey, lots of predators) migration of prey or predators respectively may occur. Neighbouring empty cells may be converted to PREY cells with probability h and neighbouring PREY and PREY' cells may be converted to PRED cells with probability p. However this conversion/ migration may only occur at fixed points in time (defined by the invasion rate).

The number of neighbouring cells to which prey or predators may migrate is specified as a parameter of the model as is the rate at which migration may take place (i.e. the invasion rate), the time the prey population takes to reach the carrying capacity, the time the prey population takes to decline below L_1 in the PRED state, and the time the predator population takes to decline below L_2 in the PRED' state.

Simulation runs of this model on a computer demonstrated that persistence (defined as the non-vanishing of both prey and predator populations in a certain period of time) is possible for a wide range of values for p and h (shown schematically in Figure 3.10).

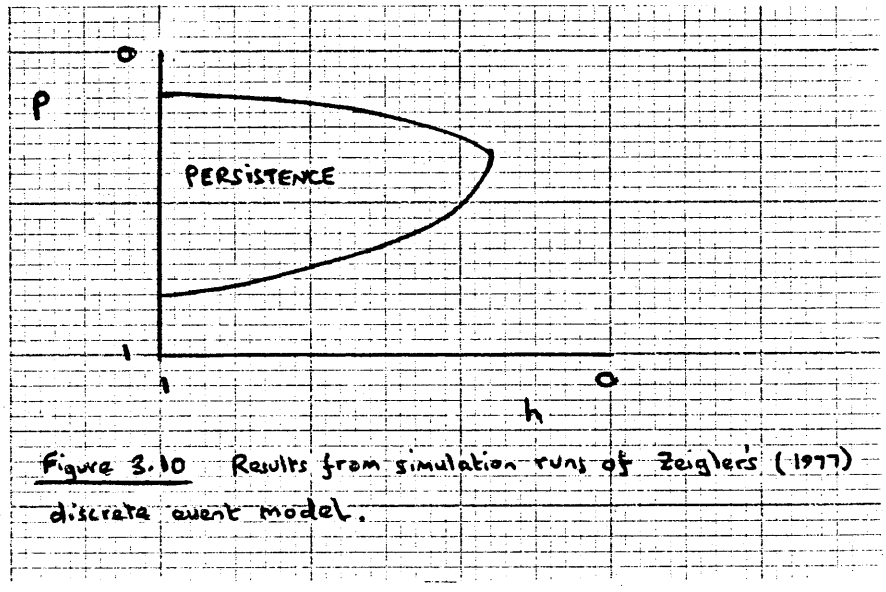


Figure 3.10 Results from simulation runs of Zeigler's (1977) discrete event model.

In comparison Zeigler then considered a continuous population exchange model.

He divided the environment into m cells and described the community population dynamics in each cell as follows:

$$\frac{dx_i}{dt} = a x_i (1-x_i) - x_i y_i + \sum_{j \in N_{PREY}} (x_j - x_i) \; D_{PREY} \qquad 3.137$$

$$\frac{dy_i}{dt} = y_i (x_i - b) + \sum_{j \in N_{PRED}} (y_j - y_i) \; D_{PRED} \qquad 3.138$$

where i=1,....,m denotes which cell,

N_{PREY} , N_{PRED} are the sets of cells to which or from which prey and predators respectively may migrate from or to cell i

and D_{PRED} , D_{PREY} measure the size of migration.

Zeigler considered what he terms randomised phase/space solutions of the above equation as follows:

Let C be a cycle of predator and prey population sizes and let L measure the arc length of C (see Figure 3.11).

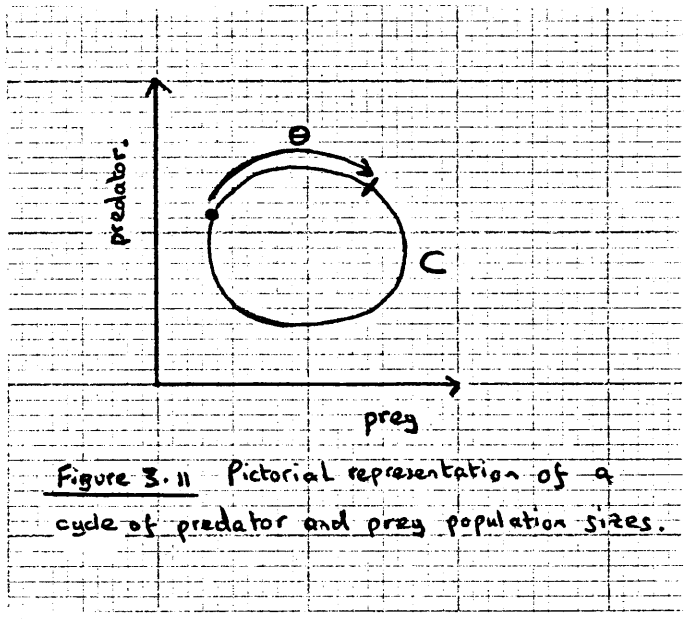


Figure 3.11 Pictorial representation of a cycle of predator and prey population sizes.

Let f be a probability distribution over $[0,L]$ such that

$$\int_0^L f(\theta)\, d\theta = 1 \quad , \quad f(\theta) \geq 0. \qquad 3.139$$

The distance θ measures the arc length along C from an initial population size to the current population size and is termed the phase of the cell.

If the number of cells is very large, then there is a random phase/space solution of the form (C,f) if there is a solution of equations 3.137 and 3.138 $[x_1(t), y_1(t), \ldots, x_m(t), y_m(t)]$ such that for $t \geq 0$.

i) The population sizes in every cell are found somewhere on C.

ii) The proportion of cells having phase in the interval $(\theta, \theta + d\theta)$ is $f(\theta)\, d\theta$

iii) The number of cells in the neighbourhood N_{PREY} (N_{PRED}) with phase in $(\theta, \theta+d\theta)$ is N_{PREY} (N_{PRED}) $f(\theta)\, d\theta$.

Since the number of cells m is large the diffusion terms in equations 3.137 and 3.138 can be written.

$$\sum_{j \in N_{PREY}} (x_j - x_i)\, D_{PREY} = \int_0^L (x(\theta) - x_i)\, f(\theta)\, N_{PREY}\, D_{PREY}\, d\theta \qquad 3.140$$

$$= D_{PREY}\, N_{PREY}\, (\bar{x} - x_i) \qquad 3.141$$

$$\sum_{j \in N_{PRED}} (y_j - y_i)\, D_{PRED} = \int_0^L (y(\theta) - y_i)\, f(\theta)\, N_{PRED}\, D_{PRED}\, d\theta \qquad 3.142$$

$$= D_{PRED}\, N_{PRED}\, (\bar{y} - y_i) \qquad 3.143$$

where $\bar{x} = \int_0^L x(\theta)\, f(\theta)\, d\theta$, $\bar{y} = \int_0^L y(\theta)\, f(\theta)\, d\theta$ 3.144

Hence the pair of population sizes $[x_i(t), y_i(t)]$ predicted by equations 3.137 and 3.138 for each cell i must each satisfy the following equations.

$$\frac{dx}{dt} = x(a-c-ax-y) + c\bar{x} \qquad 3.145$$

$$\frac{dy}{dt} = y\,(x-b-d) + d\bar{y} \qquad 3.146$$

where $c = D_{PREY}\, N_{PREY}$, $d = D_{PRED}\, N_{PRED}$ and $\bar{x}$ and $\bar{y}$ as defined by equation 3.144 are all non-negative constants.

These equations have a point equilibrium given by

$$y^* = a-c-ax^* + \frac{c\bar{x}}{x^*} \qquad 3.147$$

$$y^* = \frac{d\bar{y}}{(b+d-x^*)} \qquad 3.148$$

This equilibrium is locally stable and, basically from simulation runs, Zeigler claimed that it is also globally stable.

This suggests that the only random phase/space solution (C,f) of equations 3.137 and 3.138 is the trivial point cycle where C = (x^*, y^*) and f (0) = 1. In this case all the cells remain at the same point (x^*, y^*) and the contribution of continuous migration essentially vanishes.

Zeigler then argued, I believe falsely (see next section), that since the effect of diffusion vanishes the equilibrium reduces to the Lotka-Volterra equilibrium as predicted by equations 3.133 and 3.134 and this is unstable.

He therefore concluded that a randomised phase/space mode of persistence cannot be maintained by linear continuous diffusion.

3.4.6.4. Discussion

Hasting's model demonstrates that migration between patches in a patchy environment can be a stabilising factor. However the precise conditions for migration are not stated. The timescale of the model is set by the time a predator-prey relationship becomes extinct in an individual patch. Hence the invasion rates α and β do not necessarily describe continuous migration, only that a number of invasions occur in a unit time.

Although the conclusion of Maynard Smith's and Zeigler's arguments that continuous linear migration between patches cannot maintain stability is possibly correct, their actual arguments may be false.

It is probably biologically sensible to propose that migration in any significant numbers will only occur under certain conditions

and that these conditions will only occur for certain, relatively short, periods of time. The results of Maynard Smith's and Zeigler's simulations demonstrate that such population exchange can be stabilizing.

Maynard Smith's argument that continuous migration will not lead to stability is difficult to follow and appears to be based on intuition rather than mathematical fact.

Zeigler attempted to make Maynard Smith's argument more rigorous. However I feel that his analysis of the continuous population exchange model can be criticised on a number of counts.

Firstly he somewhat understandably assumed that the solutions of the model equations 3.137 and 3.138 will take the same form within each cell since the equations essentially are the same for each cell. However this assumption may exclude valid solutions of the equations, in particular the relative size of populations may depend on the initial population sizes which may be different for each cell.

Further Zeigler assumed that $\bar{x}$ and $\bar{y}$ in equations 3.145 and 3.146 are constants whereas their values depend on the actual solution (C, f) and hence on the values of x and y in equation 3.144.

Finally, even if $\bar{x}$ and $\bar{y}$ can be assumed to be constant, the solution (x^*, y^*) of equations 3.145 and 3.146 can only be maintained because there is continuous migration and it is therefore false to conclude that migration vanishes and that the equilibrium reduces to the Lotka-Volterra case.

3.5 Conclusions

The main aims of this chapter have been to define what is meant by the term environmental heterogeneity and to investigate the effect of such heterogeneity on community stability.

It is clear that there are a number of types of environmental heterogeneity to be considered.

Temporal heterogeneity is relatively straightforward to model and is not considered in any great detail. Results obtained by May in particular indicate that conditions for community stability are more stringent than for the equivalent time - homogeneous case.

Spatial heterogeneity may occur in a number of forms and perhaps one of the most important observations is that spatial heterogeneity may be created in a physically homogeneous environment by an uneven distribution of one species affecting the behaviour of another.

Ecologists, and indeed mathematical ecologists, have rarely fully defined the terms heterogeneity and use the term spatial heterogeneity very loosely. However, in most discussions of experiments and field observations concerning spatially heterogeneous environments the indications are that such heterogeneity is stabilizing.

We have seen that models of community dynamics in spatially heterogeneous environments can become very complex and difficult to analyse and indeed few results have been obtained for communities of more than two species, except by simulation.

Most of the models discussed in Section 3.4 support the theory that spatial heterogeneity is stabilizing. It certainly appears to be valid for communities in environments which physically provide refuges or cover for prey species, and for communities in environments in which individuals of prey species are distributed non-randomly and predators react to this by aggregating in areas of high prey density.

There is some debate about the stabilizing nature of migration between patches in a patchy environment. The model of Hastings demonstrates that continuous migration can lead to stabilization of a two-species community. Maynard Smith and Zeigler argue that migration which only occurs at discrete intervals in time is more likely to be stabilizing.

In all cases the general conclusion is that spatial heterogeneity of the environment in which a community is living is not likely to make the community less stable.

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