

ECOLOGICAL SYSTEMS COURSE

For 8/5/01

Population dynamics and landscape ecology.

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Introduction

Two topics will be covered in this lecture. In the first we will look at the methods used to study single-species populations. In the second part of the lecture we will be discussing the topic of landscape ecology.

Population dynamics

1. Introduction to population dynamics

Why study population dynamics?

To study or manage populations we first need to know what their present size is, how that size is changing with time (whether the population is increasing, decreasing or is

constant), and if changing, how fast those changes are occurring. Ecologists have developed a number of tools for investigating these changes (=dynamics) of populations, and we will be investigating a few of the most important of these in this lecture.

Demographic processes (BHT CHAPTER 4)

To investigate the dynamics of a population we need know how much it gains or loses per unit of time (of our choice). If the system is **closed**, meaning our population of interest is isolated and there are no **migration**, then population growth can only come from the **birth** of new individuals (**B**), and losses from **death** (**D**). If there is migration then growth can also come from the **immigration** (**I**) of new individuals from other populations, and losses from **emigration** (**E**) of individuals to other populations. **B**, **D**, **I** and **E** are called **demographic** parameters. To summarise these ideas we can combine them in the simple equation

$$N_{(t+1)} = N_{(t)} + B - D + I - E$$

where $N_{(t)}$ is the population size at time t and $N_{(t+1)}$ is the population size one time-step later. This equation simply states that the number of organisms expected to be living in the population at time $t + 1$ is equal to the number of births between now and then, minus the number of deaths between now and then, plus the number of immigrations, minus the number of emigrations.

The simple equation above suggests that all one has to do to study population dynamics is measure the appropriate parameters (**B**, **D**, **I** & **E**) to make a statement about the dynamics of the population. However, in reality the translation of this into practice is rarely straightforward. For example, the four basic parameters often rely upon several other processes, most species have a number of life stages which need to be addressed separately (e.g. eggs, larvae and adults in insects), and in many cases the simple counting of organisms can be quite problematical.

Measuring population sizes

The most straightforward way to determine population size is to count every individual present. This can be relatively easy for plants and sessile animals if the population is small, but complete enumeration is usually unpractical for animals that move, are small, or when the population sizes are large. Instead the most common method is to sub-sample. Samples are taken over known areas from one or several small portions of the population, which are usually selected at random and are assumed to be representative of the whole population. For plants and sedentary animals **quadrats** are commonly used. For animals **capture-recapture** methods can be used. These involve catching a random sample of the population, marking them, and releasing them again back into the population. By catching a further random sample the proportion of marked individuals in the second sample can be used to estimate the total population size. Many of these methods assume that the population is **closed**, that is, there is no **emigration** or **immigration**. Elaborate capture-recapture designs have been used to estimate demographic parameters.

A further problem is *what* to count. For species where individuals are easily identified this is not usually a problem, e.g. buffalo, grasshoppers, fish. However there are many organisms where it is not possible to determine where one 'individual' ends,

and the other begins. Examples include plants which can reproduce by vegetative spread (clonal growth) and clonal animals such as hydrozoans and corals. In these cases an investigator has to define the unit of study. For example with clonal plants we can count the number of leaves present in a given area, or the number of ramets (nodes along a stem which produce leaves), or it may be sensible to express abundance as a proportion of the ground covered by a species.

Life cycles (BHT PP. 131)

Birth and death patterns are a reflection of an organisms life cycle. Life cycles can be classified into five main types based on a number of characteristics (Figure 1).

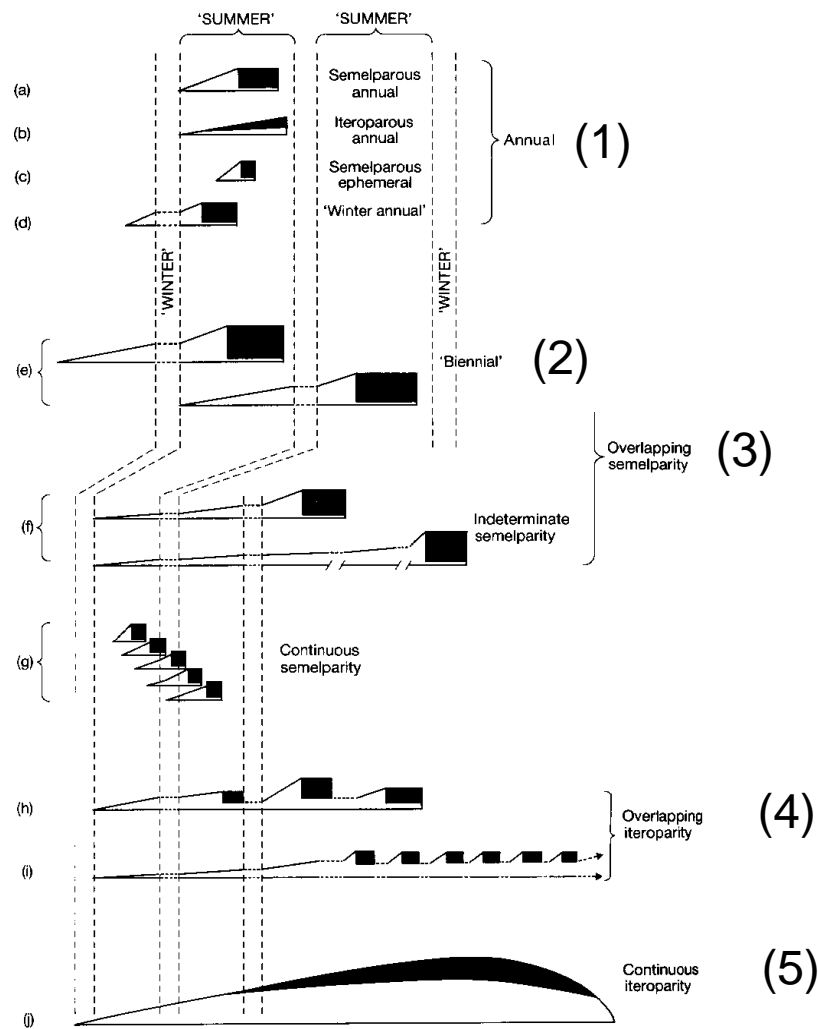


Figure 4.5. A range of life cycles. In each case, the length of a bar represents the length of an individual's life. The height of a bar represents individual size (though on a logarithmic scale, so that the exponential growth of an individual early in life appears linear). The shaded region indicates the proportion of available resources allocated to reproduction in comparative rather than exact terms, i.e. semelparous species, when they reproduce, allocate a large proportion of resources to reproduction and die soon thereafter; iteroparous species tend to allocate less to current reproduction but may survive for further reproductive bouts. Most life cycles should be self-explanatory. In overlapping semelparity, species may have a strict 2-year (or 3-year, etc.) cycle (e.g. part (e)), or they may have a cycle of indeterminate length. In overlapping iteroparity, species may be relatively short-lived (h) or long-lived (i).

Figure 1. The five main types of life-cylce (From BHT).

The main characteristics on which the life-cycles are defined are:

- (a) How long the organism lives. Organisms which complete their whole life cycle in one year or less are called **annuals**. **Perennial** species live for more than one year.
- (b) How many times the organism reproduces during a lifetime. **Semelparous** organisms reproduce only once in their lifetimes, **iteroparous** organisms reproduce more than once.
- (c) Whether reproduction is restricted to certain times (**breeding seasons**) or is continuous.

Birth and death patterns are often dependent on the age or stage of development of the organisms. Such patterns are commonly examined using **life-tables** which split the population up into age-classes or **cohorts** (Figure 2). 'Life tables' can be either tables such as Figure 2a, or diagrams such as Figure 2b. Life tables can be used to construct **survivorship curves** that trace the pattern of mortality over time (Figure 3). Alternatively, it might be more relevant to examine the population in terms of *stages* rather than *ages*. For example with insects the stages could be eggs, larva, nymphs and adults; with trees they could be seeds, seedlings, saplings and adults.

(a)

Age (years) x	Proportion of original cohort surviving to the beginning of age-class x l_x	Proportion of original cohort dying during age-class x d_x
1	1.000	0
2	1.000	0.061
3	0.939	0.185
4	0.754	0.249
5	0.505	0.200
6	0.305	0.119
7	0.186	0.054
8	0.132	0.107
9	0.025	0.025

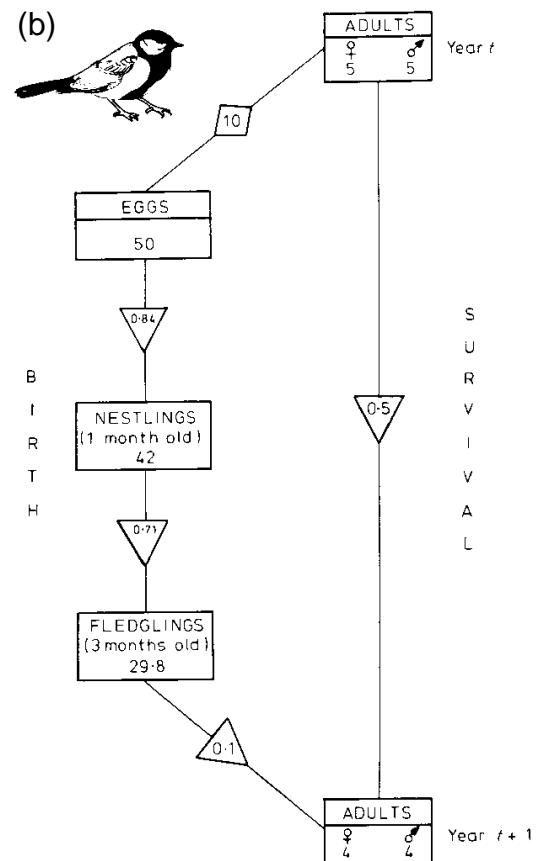


Figure 2. (a) Life-table for red deer hinds on the island of Rhum that were calves in 1957 (From BHT). (b) Diagrammatic life-table for a perennial bird (From Begon and Mortimer, 1986).

Fig. 1.5. Diagrammatic life-table of the perennial great tit, *Parus major*. (Population sizes are per hectare; data from Perrins 1965.)

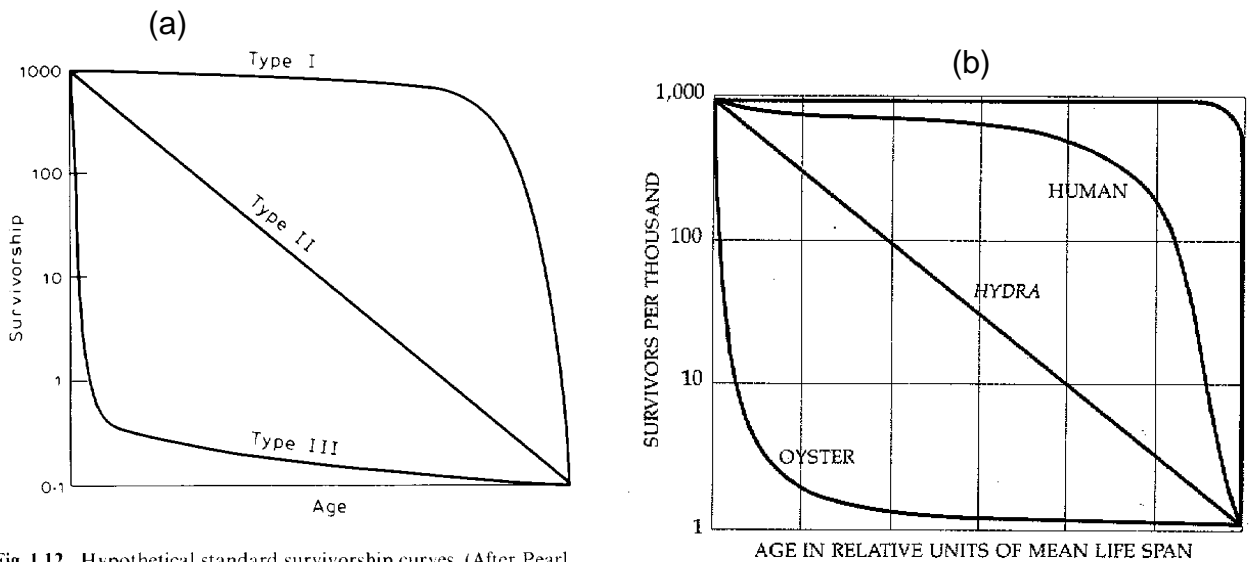


Fig. 1.12. Hypothetical standard survivorship curves. (After Pearl 1928.) For further discussion, see text.

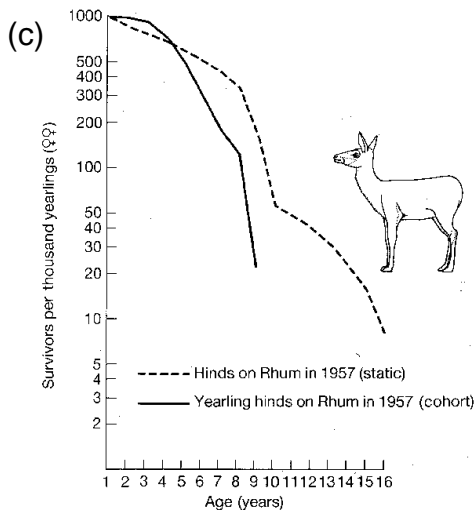


Figure 4.10. Two survivorship curves for red deer hinds on the island of Rhum. As explained in the text, one is based on the cohort life-table for the 1957 calves and therefore applies to the post-1957 period; the other is based on the static life-table of the 1957 population and therefore applies to the pre-1957 period. (After Lowe, 1969.)

Figure 3. (a) The three hypothetical standard survivorship curves (from Begon and Mortimer, 1986). (b) Survivorship curves for three organisms. In the oyster, mortality is extremely high during the early free-swimming larval stage. In the human population mortality is greatest during the latter stages of life. In the hydra, the mortality rate is the same at all ages (from Curtis, 1983). (c) Two survivorship curves for red deer hinds on the island of Rhum.

2. Modelling population growth (BHT pp. 224-226)

Ecologists use mathematical models as an aid to understanding the complexities of natural systems. Here we will consider a very simple model of population growth, often called the **logistic** model. Whilst this model has many limitations and simplifying assumptions, it has been used extensively in ecology for simple theoretical explorations, for clarifying thought and generating hypotheses, as well as

a simulation model of population growth. For better or worse, it is arguably the single most important model in ecology.

Exponential growth.

Before launching straight into the logistic model we will first consider how populations increase over time. We will illustrate this by working through an example.

The Russian scientist G. F. Gause performed several experiments with a single-celled organism called *Paramecium caudatum*. This organism reproduces by dividing itself in two after a certain time. Gause set up jars with a broth of bacteria as a food source; he then introduced a single *Paramecium* and followed the subsequent growth of the population. After the first division there are 2 cells (time-step 1 in the table below), these then divide to give 4 cells, then 8, 16, 32, 64 cells, and so on. Putting this information in a table we get:

Time step	0	1	2	3	4	5	6
No. cells	1	2	4	8	16	32	64

From one timestep to the next the population is increasing by a factor of 2. This value is often given the symbol R , called the **reproductive rate**. The reproductive rate can be thought of as a summary of the demographic parameters **B**, **D**, **I** & **E** - if R is greater than 1 then births and immigrations together outweigh deaths and emigrations and the population increases, and *vice versa* for R less than 1.

In cases where reproduction occurs in discrete jumps, as in our *Paramecium* example, it is possible to predict the population size at a given time by using the simple formula:

$$N_t = N_0 \times R^t \quad \text{Equation 1}$$

Where N_0 is the population size at time 0 (in our case $N_0 = 1$). For example the population size at time 7 is predicted to be

$$N_7 = 1 \times 2^7 = 1 \times (2 \times 2 \times 2 \times 2 \times 2 \times 2 \times 2) = 128 \text{ cells.}$$

The pattern of growth shown in the table is represented graphically in Figure 4. Note that growth is **discrete**, meaning that the population increases by a series of jumps because all the cells divide at the same time. Note also from *Equation 1* that the population will keep increasing indefinitely if R is greater than 1, and decrease to extinction if R is less than 1. The pattern of increase shown in Figure 4 is called **exponential growth**.

In many populations reproduction is not by discrete jumps as in the *Paramecium* example above (where at one time there may be four cells, then suddenly they all divide, and then there are eight) but is asynchronous and continuous, i.e. at any given instant some cells may be dividing, and some may not, so the population size increases smoothly and continuously. Such **continuous** exponential population growth with a reproductive rate $R=2$ is shown in Figure 5. Note the differences between Figures 4 and 5.

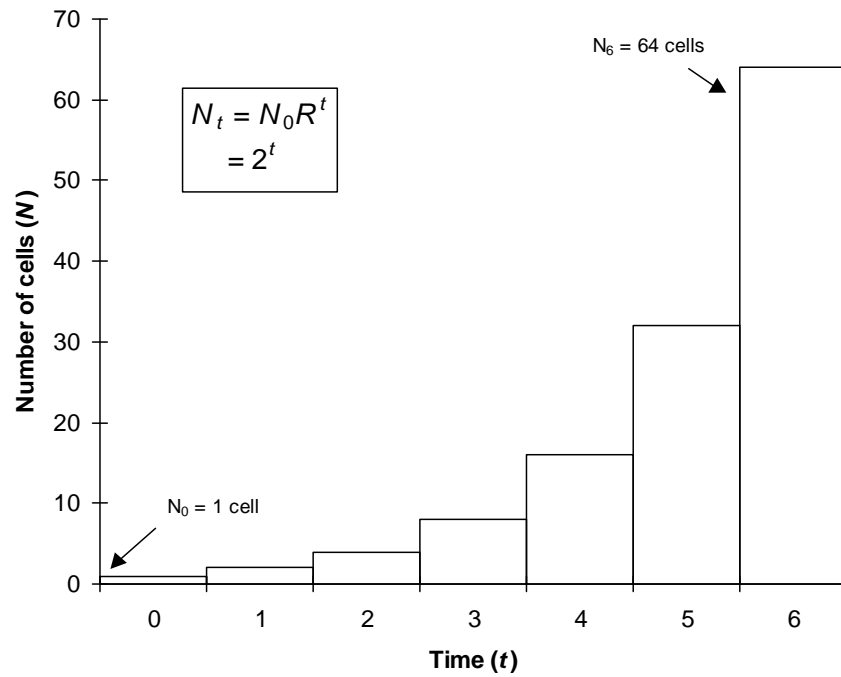


Figure 4. Exponential growth in discrete time

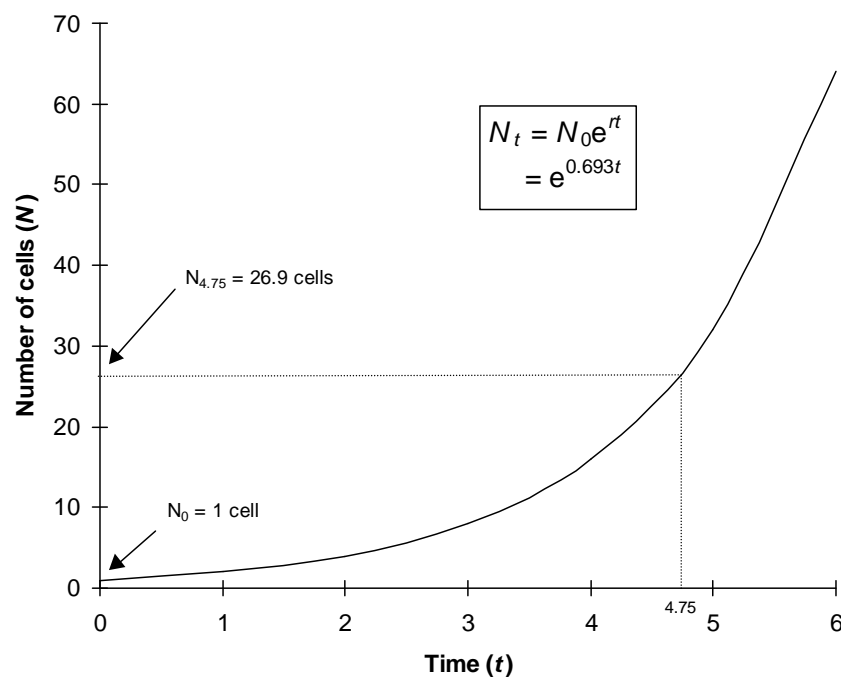


Figure 5. Exponential growth in continuous time.

In order to model continuous growth, as depicted in Figure 5, we can use the following equation, which describes the *speed* at which the population is changing rather than its size as in Equation 1:

$$\begin{aligned}\frac{dN}{dt} &= \ln(R) \times N \\ &= r \times N\end{aligned}\quad \text{Equation 2}$$

The left-hand-side (read as ‘dN by dt’) gives the slope of the curve in Figure 5 measured at a given time. Note in Figure 5 that when time is small the slope of the curve is also small, indicating that the population is increasing slowly, and as time progresses the slope of the curve increases, reflecting an increasing rate at which new individuals are added to the population. The most important aspect of Equation 5 is the value $\ln(R)$, usually replaced by the symbol r , which is known as the **intrinsic rate of increase**, or the **per capita rate of increase**. In our example $R = 2$, so $r = \ln(2) = 0.693$. For values of r greater than 0 population growth increases exponentially. For values of r less than 0 the population decreases towards extinction. We can ‘solve’ Equation 1 and convert it into a form where, instead of calculating the *rate* at which the population increases, we can calculate the actual population size (N) as in Equation 1. This is given by:

$$N_t = N_0 e^{rt} \quad \text{Equation 3}$$

Here N_0 is the initial population size, t is the time, and e is a constant (the base of the natural logarithms, 2.718...). E.g. in our example, to predict what the population size will be 3/4 of the time between at times 4 and 5 (time 4.75):

$$N_{4.75} = 1 \times e^{0.693 \times 4.75} = 26.91 \text{ cells}$$

This calculation is shown graphically in Figure 5. Note that we can have fractions of a cell, or fractions of an individual, as we are dealing with the *expected* number of cells, or to think of it another way, the number of cells we would expect to find if we performed the experiment many times, then took the average of the results.

Density dependence, equilibrium and logistic growth

Although exponential growth may be realistic for very young populations, or populations at a low density, in most cases populations cannot increase indefinitely. The organisms eventually become so numerous that the resources required for growth and reproduction are depleted and they begin to compete, or they become so numerous that they start polluting their own environment. Such changes are reflected by a decrease in fitness of the individuals in the population, which is equivalent to decreasing the value r as the total population size increases. Such a decrease in the growth rate with increasing population size or density is called **density dependence**. A consequence of density dependence is that there is an upper limit to the size of the population, which is traditionally called the **carrying capacity** and given the symbol K . If the population exceeds K , then the population growth rate becomes negative, and the population size decreases. If the population is below K , then the population growth rate is positive and the population increases. At K the population neither decreases nor increases. The carrying capacity is therefore a **stable equilibrium** for the population: no matter where the population

starts, either above or below K , over time the population eventually reaches this equilibrium (Figure 6).

Equation 2, the model for exponential growth, can be modified to include these more biologically reasonable constraints. This requires that as the population approaches K (i.e. as the population size increases), the intrinsic rate of increase r decreases. In addition, when the population is above K , r should be negative, and when the population is at K , r should be 0, indicating no net increase or decrease in the population size.

The simplest way to model this decrease in r as the population increases (as N increases) is to assume a linear relationship between r and N , or in other words, modify the model so the intrinsic rate of increase is **proportional** to the population size: Equation 2 can be modified in the following way to reflect this situation, and the result is shown graphically in Figure 6:

$$\frac{dN}{dt} = N \times r \times \left(\frac{K - N}{K} \right) \quad \text{Equation 4}$$

Note in Equation 4 that when the population size is small (N close to 0), the term in the brackets is approximately 1, therefore growth is approximately exponential as in Equation 2. At population sizes below K , the population will increase until it reaches K (curve A in Figure 6). At population sizes above K the population will decrease until it reaches K (curve B in Figure 6). At K , the population neither decreases nor increases, and is said to be at stable equilibrium. Equation 4 is the **logistic growth model**, and gives the characteristic S-shaped or **Sigmoid** curve in Figure 6.

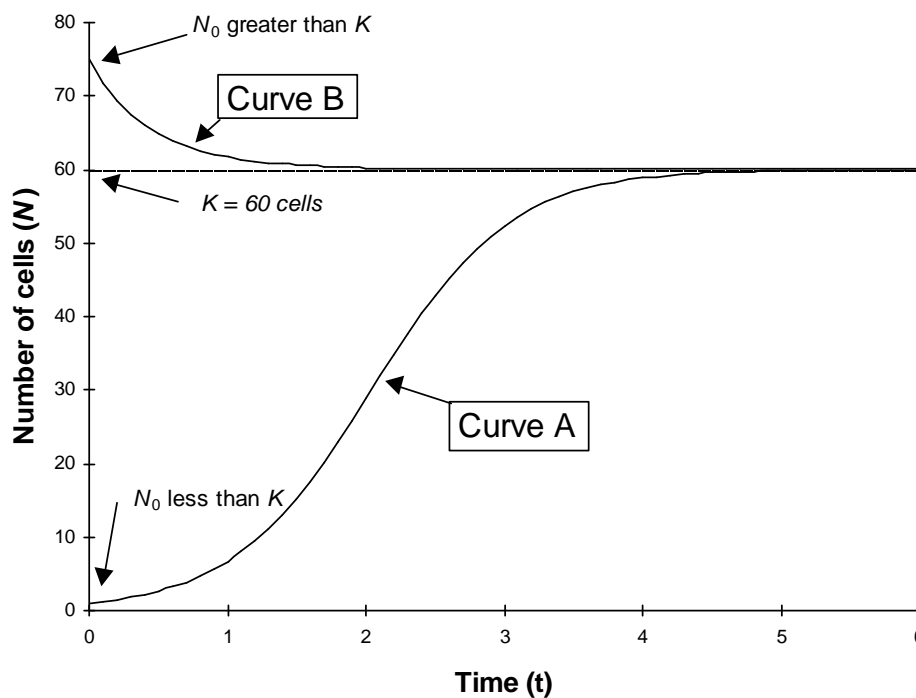


Figure 6. Logistic population growth for a hypothetical population of *Paramecium* cells

As before, we can solve Equation 4 and write it in a form where we can calculate the *actual* population size, rather than how fast it is increasing/decreasing at a given time. The appropriate equation is:

$$N_t = \frac{K}{1 + [(K - N_0) / N_0] \times e^{-rt}} \quad \text{Equation 5}$$

The parameter values used to draw the curves in Figure 6 are $K=60$ and $r=2$, with two different values for N_0 (1 and 75).

More complex versions of the logistic equation can take into account reductions of r that are faster or slower than increases in population size (rather than proportional as assumed above). In addition, this model is also capable of predicting a whole range of behaviours of a population, ranging from the smooth approach to equilibrium shown in Figure 6, to dynamics which have been described as chaotic (Figure 7). The logistic model of population growth can also be extended to models of community dynamics (two or more interacting species) by adding extra parameters which summarise the species interactions (competition, predation, etc.). To investigate the dynamics of a group of species interacting in a community involves simultaneously solving the appropriate equations which describe the growth of each species population.

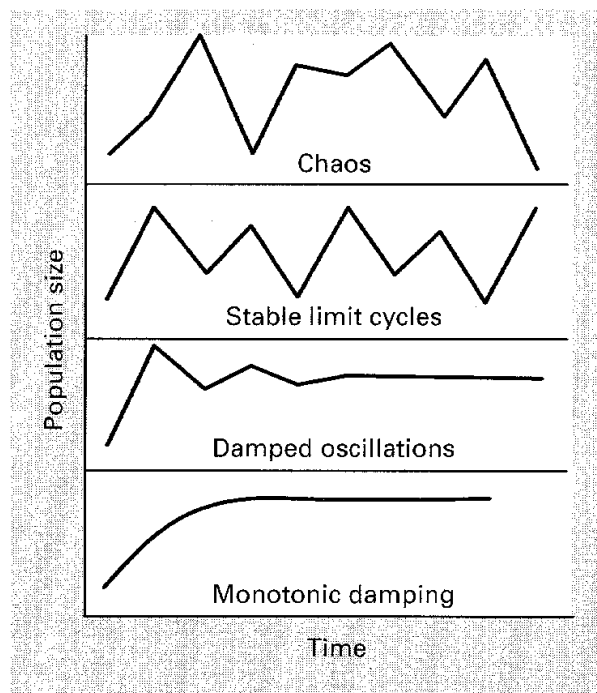


Figure 7. Simple logistic models are capable of predicting a wide range of behaviour, from a smooth approach to equilibrium (monotonic damping) to seemingly unpredictable ‘chaos’.

Logistic-based models have been shown to fit a wide range of ecological data for a variety of organisms and circumstances (Figure 8). Despite these successful

applications, there are several simplifying assumptions which are too unrealistic for many ecological applications. The two major ones are that all the individuals in the population are identical (i.e. that different ages or stages within the population have the same characteristics), and that the environment is homogenous. We will deal with this latter problem first.

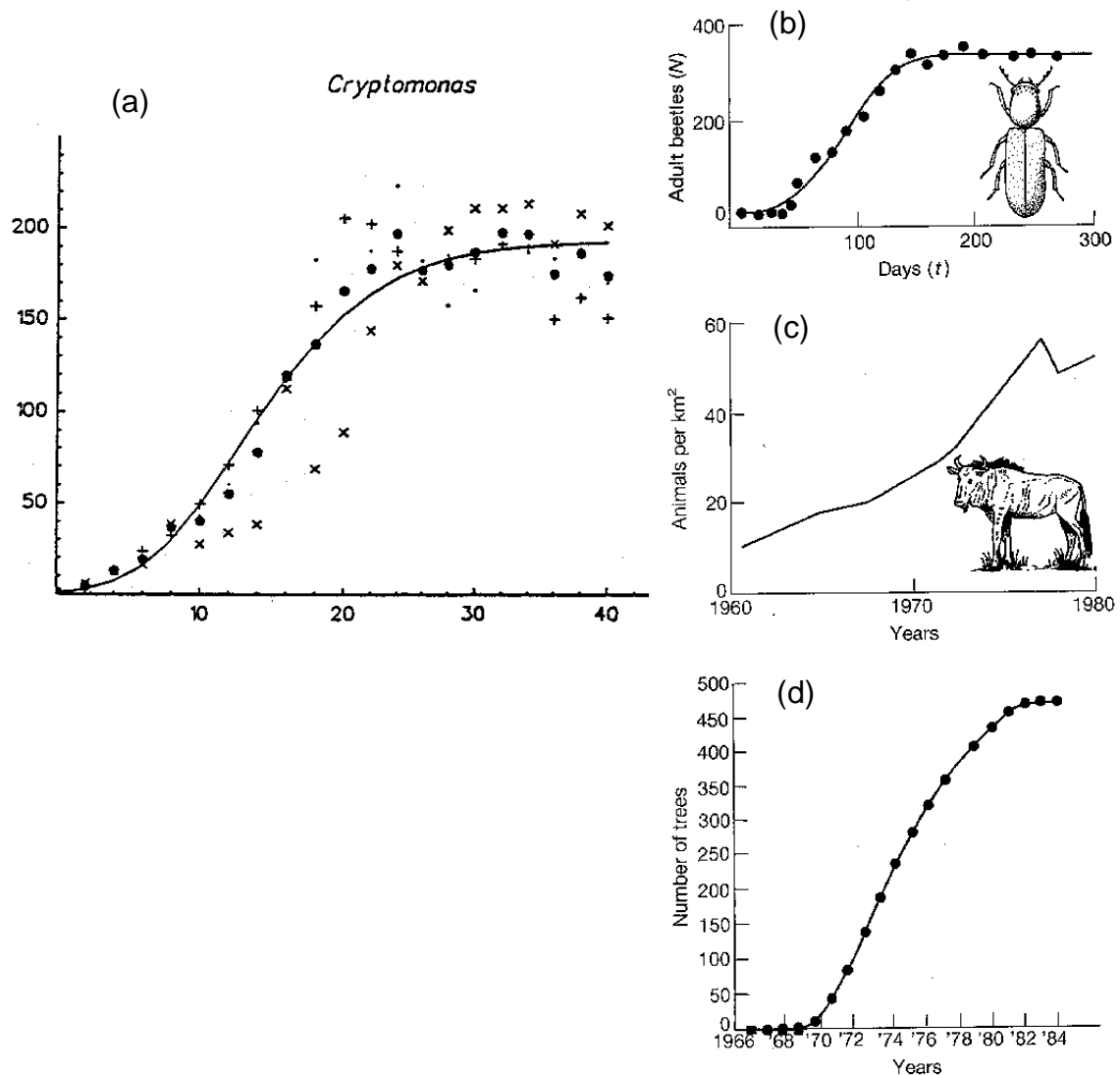


Figure 8. Real examples of 'S' –shaped population growth. (a) Growth of the single-celled alga *Cryptomonas* over 40 days (Roxburgh, unpubl. Data). (b) The beetle *Rhizophthera dominica* in 10g of wheat grains. (c) the growth of a population of wildebeest in the Serengeti following reduction to low density due to disease. (d) The increase in the willow tree in an area of land following the removal of grazing pressure by rabbits (from BHT).

Coping with environmental variability

Temporally variable environments

Depending on the seasons, or on years, the survival and reproductive rates might vary. In addition, the total amount of resources available and hence the carrying capacity can also vary. As a result populations fluctuate around their general trend (e.g. see Figure 2 in the *Environmental variability, succession and invasion* lecture handouts). The logistic model can be modified to incorporate such variability. This involves making r and K change as the conditions change, rather than treating them as 'constant' values as in the equations above.

Spatially variable environments

Continuously variable environments: When there is a gradient of environmental factors (e.g. temperature, light) or resources (water, soil, nutrients), survival and reproductive capacity can vary along this gradient. It is possible to take these spatial trends into account to predict population dynamics over the range of the whole population. What we need to do is describe how the growth rate and carrying capacity varies along the gradient, then incorporate this variation into our model.

Patchy environments: Some environments consist of discrete patches. For example, for frogs, ponds are a suitable patch surrounded by a hostile environment. The parts of the population living in each patch are called subpopulations. Not all patches will provide the same degree of favourability for the population, hence the overall population dynamics will result from integration of all these local dynamics. Most simply, population dynamics can be described independently for each patch, and the total population growth is the sum over all the patches. Other things of interest include the variability of the growth rate between patches.

One particular case of patchy environments is where the different subpopulations are connected by migration. A set of subpopulations connected by migration is called a **metapopulation**. For example frogs might migrate from one pond to another each year, and seeds can disperse from one forest patch to another. Migration can influence the global population dynamics by having migrants going from growing subpopulations (called **sources**) to declining subpopulations (called **sinks**).

Coping with demographic variability

The second way in which the logistic model fails to capture reality is the assumption that all members of a population are identical, i.e. there is no distinction between juveniles and adults. In many cases we are interested in tracking the composition of the population in terms of the numbers of individuals per age or stage class. For example to manage a forest we need to know what proportions of different sizes of trees will be available at a given time. This can be achieved by utilising matrix algebra and constructing what is known as a **matrix** model, also known as the **Leslie matrix** model. This takes into account survival and reproduction within each age-class or stage-class, and also the transitions between classes. In its simplest form, to run the model all that is required is a list of the initial abundances of each age/stage, and a list of the **survivorship probabilities** of one age surviving to become the next, and also a list of the **fecundities** - the reproductive output of each age/stage. A practical application using this general method which also incorporates density dependence is shown in Figure 9 for different age classes of a grass. Don't worry too

much how the model works, the important thing to note is that it is possible to predict the number of individuals in each age class as the population grows.

We will finish off by considering a practical application which combines many of the theoretical ideas discussed in the previous sections, Population Viability Analysis.

1. The life cycle of the grass

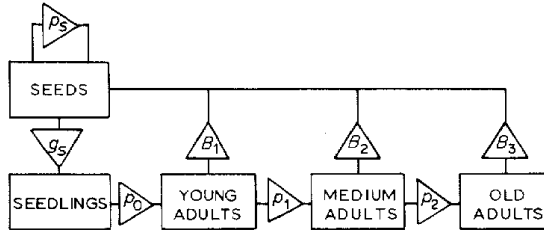


Fig. 3.13. The life cycle for annual meadow grass, *Poa annua*. (After Law 1975.) Proportions (ranging from 0 to 1): p_s = seeds surviving; g_s = seeds germinating; p_0 = seedlings surviving to become young adults; p_1 = young adults surviving to become medium adults; p_2 = medium adults surviving to become old adults. Fecundities (0 or > 0): B_1 , B_2 and B_3 = seed produced by young, medium and old adults respectively. All events occur over the time period t to $t + 1$.

Table 3.2 A transition matrix, \mathbf{P} , for a *Poa annua* population. (After Law 1975.)

2. The transition matrix corresponding to the above life cycle. Note that some of the fecundities (birth rates) and survivorships are density dependent, i.e. their values change as the population grows.

$$\begin{bmatrix}
 0.2 & 0 & B_1(N) & B_2(N) & B_3(N) \\
 0.05 & 0 & 0 & 0 & 0 \\
 0 & p_0(N) & 0 & 0 & 0 \\
 0 & 0 & 0.75 & 0 & 0 \\
 0 & 0 & 0 & 0.75 & 0
 \end{bmatrix}$$

3. The results of the model.

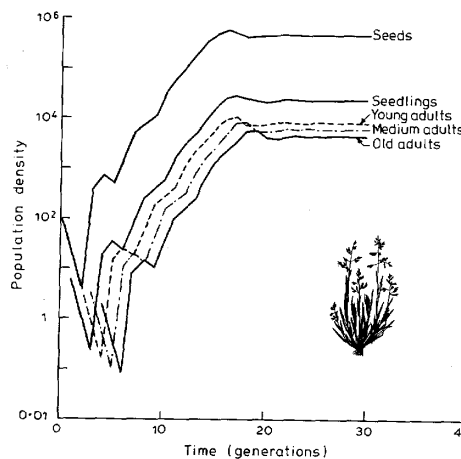


Fig. 3.15. Simulation of the density-regulated growth of five age-classes in a population of *Poa annua*. (From Law 1975.)

Figure 9. Application of a matrix population model using annual meadow grass (*Poa annua*) (From Begon and Mortimer, 1986).

Using the ideas of population dynamics for practical purposes - fisheries management

The concepts of logistic growth and the carrying capacity are often used in determining the catch size for marine fish. The first problem is to estimate the population of the fish concerned. This information often comes from the fishing industry, at times backed up by systematic surveys. The information collected includes the parameters referred to above (ie age, sex, maturity) as well as the catch per effort and the size of the fish. To estimate the change in the population, the growth rates of individual fish (from the “fish bone” or otolith, which can also be used to estimate the age of the fish), the recruitment rates (first age of maturity), the harvesting rate (human caused mortality) and other mortality. These are often calculated in terms of the catch effort or a particular time period. The future yields are determined by calculating the biomass of the fish (instead of numbers) that can be removed without changing the overall size class of the fish population and expressed as equivalent to dN by dt .

Some fish live to about 30 years or more, so they have to estimate the long-term and the short term potential yields. The above production estimate vary due to food availability, climate etc and thus long-term estimates are extremely variable. There has to be a good long-term monitoring to really suggest what the harvesting levels should be, but there are very few fish populations that are monitored in this way.

There are a lot of fish stocks that are in trouble around the world. Often the causes are overfishing, predation, bad sequences of climatic events leading to low growth rate and failure to reproduce, and pollution, amongst others. Sometimes, combinations of these events can be disastrous to the populations. If the fish species is an infrequent reproducer (case i of figure 2) then the population is slow to recover. For some good case studies see the web site <http://kingfish.ssp.nmfs.gov/olo.html>

The management of fish stocks is based on quite a bit of population dynamic theory as well as the economic returns. As you would have seen, getting reliable estimates for population size is difficult and the concept of carrying capacity is problematic.

3. *Population Viability Analysis (PVA)*

Definition

Population Viability Analysis (PVA) is a general term for a group of population models that attempt to assess the likelihood of a population going extinct subject to a range of conditions. These conditions can be different management options, fluctuating weather, random catastrophes, disease outbreaks, competition etc. A primary aim of a PVA is to determine the minimum conditions for the viability of a natural system. By viability we usually mean that the population will be self-perpetuating, without significant management or other interference from outside. This Minimum Viable Population size is often given the abbreviation MVP.

It is important to note that the definition of a MVP is likely to vary according to society's requirements, and vary according to who is the current decision maker. For

example some groups might consider a 50% probability of persistence for 100 years acceptable, whilst other groups a 95% probability of persistence for 500 years would be a minimum requirement. The important point is that there is no universal '*magic number*' which can be applied to all populations under consideration. Each situation is unique, both biologically and also socially.

What populations should we be trying to conserve?

Soulé (1987) suggested some rules for choosing candidate populations for which we might apply a PVA. Many of these are based on the assumption that there is one or a few **keystone** species in the system - species which are so important that there are the critical factors in determining the structure of the community.

- (1) Species whose activities create critical habitats for several other species.
- (2) Mutualist species whose behaviours enhance the fitness (e.g. reproduction, dispersal) of other species.
- (3) Predatory or parasitic species that regulate the populations of other species, and whose abundance would ultimately lead to a decrease in species diversity.
- (4) Species that have spiritual, aesthetic, recreational, or economic value to humans.
- (5) Rare or endangered species.

Factors affecting the viability of populations

In order to develop an ecologically realistic PVA, i.e. one where we are confident our predictions will be the correct ones, it is necessary to include in it all the factors thought to be influencing the population of interest. It is this aspect of PVA which brings together many of the population regulation factors that we have considered in this and previous lectures:

Demography: These are the birth and death processes discussed earlier this lecture, such as birth rates and death rates, and also the age/stage structure of the population.

Biotic Interactions: The importance of biotic interactions such as competition and predation on the target population need to be considered.

Environmental variation: We know that the environment varies in both space and time, in both a regular (e.g. seasonal) and irregular way (e.g. day-to-day or year-to-year variation), and that this variation can influence the demographic parameters.

Genetics: For small populations, the amount of genetic material available to natural selection is correspondingly small. The implication is that if conditions change, there may be less genetic variability on which natural selection can act, resulting in a higher probability of extinction.

Catastrophes: In many systems, catastrophes can occur at unpredictable (random) intervals, e.g. floods, fires, droughts.

Landscape fragmentation: We know that the degree of fragmentation of the landscape can influence the viability of the population, for example some animal species are able to survive in small remnants of their natural habitat, whilst others require large continuous blocks of relatively undisturbed habitat. It may also be necessary to consider the nature of the corridors linking the patches, and their effects on population dynamics.

Metapopulation structure: If the population is fragmented, and there is migration between the patches, then it is also necessary to build this into our PVA as well.

Landscape ecology

1. What is a landscape? Why study it?

Definition - notions of scales and hierarchy

Many concepts in ecology are scale dependent, that is, we first need to define the spatial and temporal scales of interest. For example when we talk of persistence of a community we may mean that it remains unchanged over 100 years. However, if we look at a longer timescale, perhaps 1 000 000 years, then to expect the community to persist without change over this time-frame is clearly unreasonable; evolution can occur, the regional climate can change, and plate tectonics can alter the structure and position of land masses. How we view the world spatially is also dependent on the scale we choose to look at (recall the example using 10m² and 1000m² forest patches in the *Environmental variability, succession and invasion* lecture handouts - on page 2 under the heading 2.1 *Disequilibrium*).

Thus far we have been discussing the nature of *communities* (or ecosystems), the spatial limits of which are arbitrarily defined by the ecologist, but are usually small enough to include relatively homogenous areas, perhaps a few tens or hundreds of metres squared. For example, we may choose to study the plants and animals which live in a farm pasture, and call that our community. Alternatively, we may choose to study the plants and animals which live in an adjacent patch of remnant forest, or we may choose to study the plants and animals which live on a grassy bank bordering a road which runs through both the pasture and the forest.

When we increase the spatial scale of interest to include all three of our 'communities', then we can view all three systems as if they were one. We call this higher level of spatial scale a **landscape**, and the study of the landscape, and of the relationships between component systems, is known as **Landscape Ecology**.

As mentioned, the spatial scale of communities is often measured in terms of tens or hundreds of metres. On the other hand, landscapes are usually measured in units of kilometres. As such, remote sensing methods such as aerial photography and satellite imagery are often used to study landscapes.

A further characteristic of landscapes is the interactions between the various 'community types'; plants and animals may disperse and move among the roadside, forest and pasture. Similarly, many aspects of the physical environment also flow among the community types, e.g. heat, mineral nutrients, water and wind.

Description of landscape features

LANDSCAPE ELEMENTS

A number of features can be identified within landscapes, and because these features are common to all landscapes they provide a common language for comparison. Figure 10 shows a view of an agricultural landscape. Figure 11 shows a map of part of that landscape to illustrate the various components. In general, landscapes are made up of a number of basic, relatively homogenous **elements**. The map in Figure 11 shows five such elements, they are woods, dirt road, highway, farmyard, and field. Note that these elements can further be subdivided, for example

the fields may contain different crops. Note also that landscape elements can be lumped together, for example we may want to combine dirt road and highway into a common element 'road'. This ability to view the landscape at various scales by combining and splitting elements is due to its **nested** or **hierarchical** structure.



Figure 1.3 Agricultural landscape showing cluster of ecosystems repeated throughout. Contour planting of corn (*Zea*) and grain in center. Dodge County, Wisconsin, United States. (Courtesy of USDA Soil Conservation Service.)

Figure 10. A photograph of an agricultural landscape (from Forman and Godron, 1986).

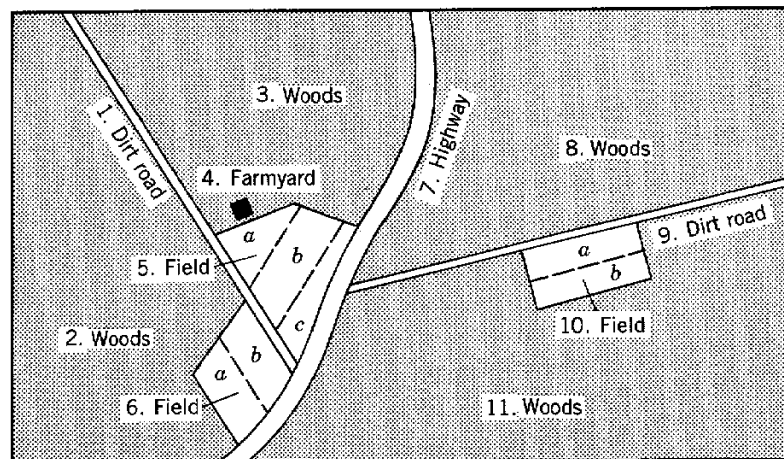


Figure 1.5 Landscape elements and tesseras. Five types of landscape element are present—woods, dirt road, highway, farmyard, and field. There are 11 specific landscape elements (numbered). Tesseras (a, b, and c) are visible within the fields.

Figure 11. A map of the agricultural landscape shown in Fig. 10, with the various landscape elements labeled (from Forman and Godron, 1986).

LANDSCAPE STRUCTURE

The structure of the landscape is defined by the spatial relationships, or linkages, of the different landscape elements. These elements are of three main types; matrix, patches and corridors.

1. Matrix

The matrix is the most extensive and connected landscape element (Figure 12). It can be thought of as the 'background' against which all of the other elements are placed. In some landscapes identifying the matrix presents few problems. For example the woods in Figure 11 are the matrix, with patches comprising fields and a farmyard embedded within this matrix. However in other cases, such as when there is a mosaic of distinct patches, the matrix may be less obvious, or even absent if there is no single dominant element.

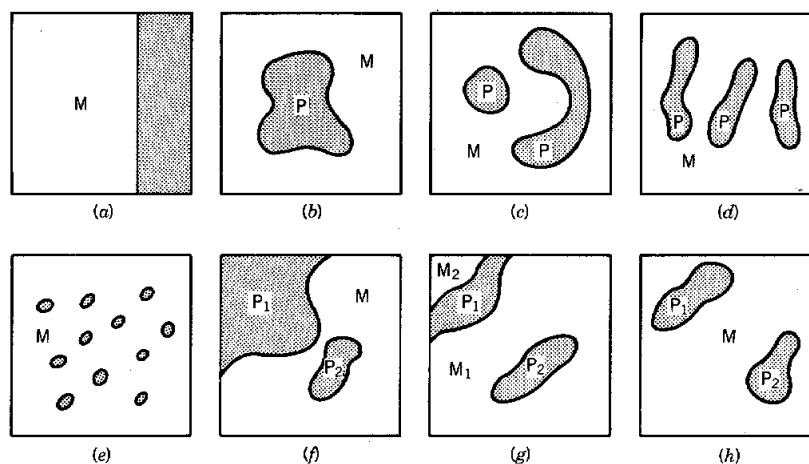


Figure 5.6 Porosity and connectivity of the matrix. M = matrix, P = patch. (a) The simplest case where porosity = 0. (b) Porosity = 1. (c) Porosity = 2. (d) Porosity = 3. (e) Porosity = 11. (f) Porosity = 2, and matrix connectivity is complete, but it is unclear whether type M or type P should be the matrix. (g) Porosity = 2, but connectivity is not complete. (h) Porosity = 2, and connectivity is complete.

Figure 12. The 'matrix' landscape element (from Forman and Godron, 1986).

2. Patches

A patch is defined as an area differing in appearance from its surroundings. Patches can be different assemblages of plants and animals, such as forest remnants in agricultural fields, or parks and gardens scattered throughout a city. Patches can also be predominantly lifeless such as car parks or buildings in a city. In figure 11 there are four patches, three fields and one farmyard. Recall in the *Ecological Communities* lecture that the overlap zone between a patch and its surroundings is called an *ecotone*.

Patch origins

Landscape patches have diverse origins.

Disturbance patches: These are patches produced by disturbances of the matrix. Disturbance patches can be produced by mudslides, avalanches, windstorms, mammal trampling etc. Recall from the *Environmental variability, succession and invasion* lecture that such disturbances initiate successions, keep populations in disequilibrium and in some cases can be the mechanism which allows many species to coexist. Disturbance patches can also be human induced, such as logging in forests, burning, and mining activity.

Remnant patches: A remnant patch can be thought of as the converse of a disturbance patch. It is caused by the widespread disturbance of the matrix resulting in a remnant of the plant and animal community becoming embedded in the now disturbed matrix. Note that the only difference between disturbance and remnant patches is the spatial scale of the disturbance. Examples of remnant patches are areas of vegetation which have escaped the effects of a widespread fire, and the patches of natural vegetation which can be found in many agricultural landscapes.

Environmental resource patches: These patches are commonly unrelated to disturbance, and are formed by distinct differences in the environmental conditions or resources between the patch and its surroundings. Examples of environmental resource patches are the wet patches or depressions found in many bogs, oases in desert environments, and frost hollows in forests.

Planted patches: Planted patches are areas of introduced plants such as the crop fields in Figure 2, pine plantations and orchards. Planted patches also include sports fields, recreational parks and golf courses.

Habitations: Patches formed by habitations include houses and associated yards, courtyards, farm buildings, farmyards etc.

Patches may also be transient, meaning that they may only exist for short periods of time. For example, herds of grazing animals and temporary ponds formed as a result of heavy rain.

Patch size and shape

Patches vary in size and shape (Figure 13). In undisturbed landscapes the patches are usually large, and with increasing human interference they may become more numerous and smaller.

Patch size and shape is extremely important for conservation. Patch size has important implications for animals which require a minimum habitat size to live, and patch shape affects how much edge there is between the patch and the surrounding area relative to the interior area of the patch (Figure 13a). For example, long thin patches have more contact with their surroundings compared with circular or square patches (Figure 13b). These issues are mentioned only briefly here, and will be dealt with in detail in the lecture *Conservation Management and planning*.

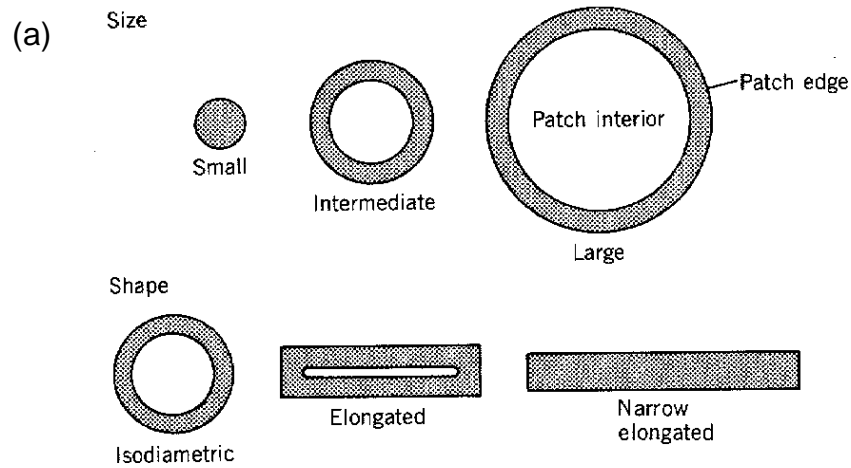


Figure 3.12 Interior and edge areas as affected by patch size and shape. (From Forman, 1981; courtesy of Pudoc–Centre for Agricultural Publishing and Documentation.)

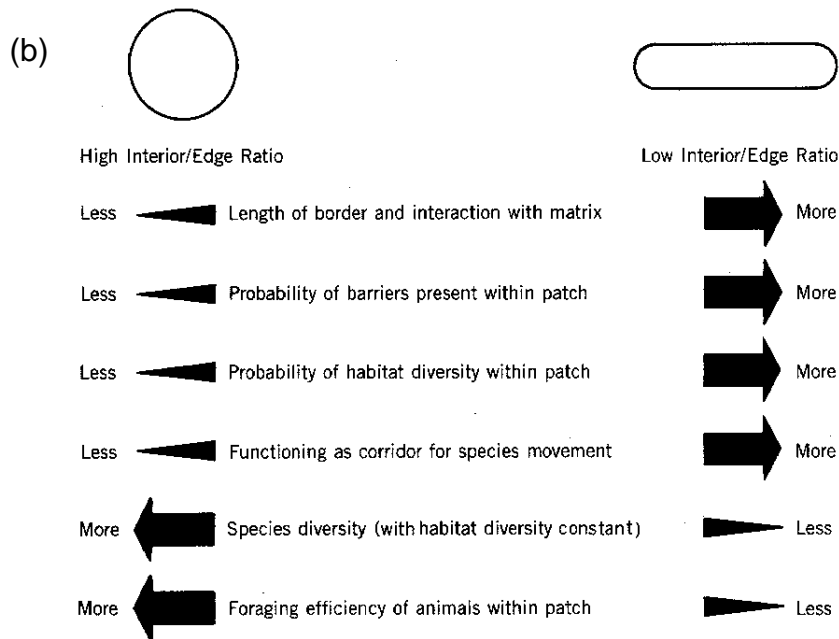


Figure 3.13 The interior-to-edge effect on several ecological characteristics. The pattern for foraging efficiency is a hypothesis.

Figure 13. The ‘patch’ landscape element (from Forman and Godron, 1986).

3. Corridors

Corridors are narrow strips of land which differ from the matrix on either side. Corridors may be isolated strips, but are more commonly found to link patches in the landscape. In Figure 11 the corridors are the highway and dirt road. There are several types of corridor.

Line corridors: Line corridors are narrow strips of habitat such as paths, hedgerows, drainage ditches roads and railways (Figure 14). Line corridors are

characterised by a lack of a distinct interior environment. Line corridors occur predominantly in modified landscapes, and are particularly important in human society for providing routes for transportation.

Strip corridors: Strip corridors include such things as cuttings for powerlines, wide strips of forest, and firebreaks (Figure 14). Strip corridors are wide enough so that they have a distinct interior environment. Like line corridors, they are also found predominantly in human-modified landscapes.

Stream corridors: Stream corridors occur in both natural and highly modified landscapes. A stream corridor includes not only the water, but also the band of vegetation along a stream bank (Figure 15). This vegetation is usually characterised by being tolerant of high soil moisture levels and flooding. Stream corridors have an important role in the functioning of the landscape; they regulate the movement of water and materials from the surrounding land, and thus affect transport in the stream itself. They also influence erosion, nutrient runoff, water runoff, flooding, sedimentation and water quality.

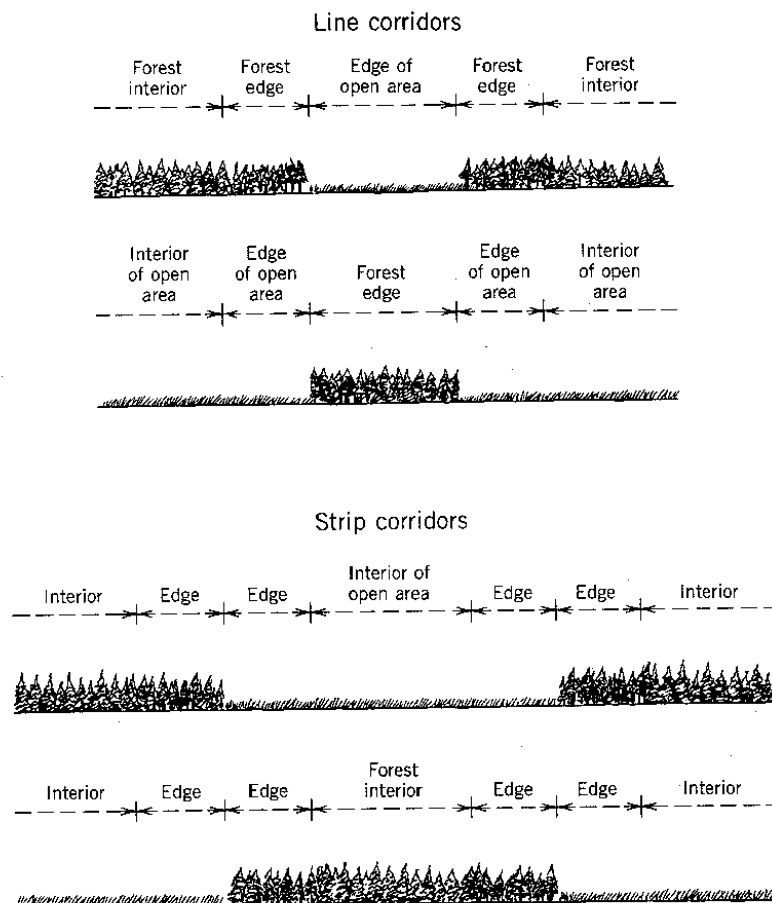


Figure 4.6 Comparison of line and strip corridors. From Forman (1983). (Courtesy of Ekologia CSSR.)

Figure 14. Comparison of line and strip corridors (from Forman and Godron, 1986).

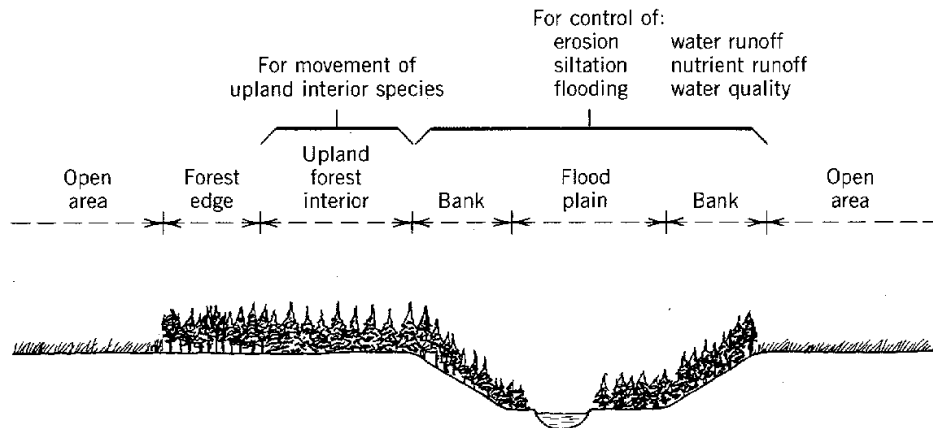


Figure 4.13 Structure and functions of a stream corridor. From Forman (1983). (Courtesy of Ekologia CSSR.)

Figure 15. Stream corridors (from Forman and Godron, 1986).

Networks: Networks are formed by the intersection of corridors, often resulting in the subdivision of the matrix (Figure 16). Other networks include the intersecting boundaries of agricultural paddocks, and networks of interconnected irrigation systems.

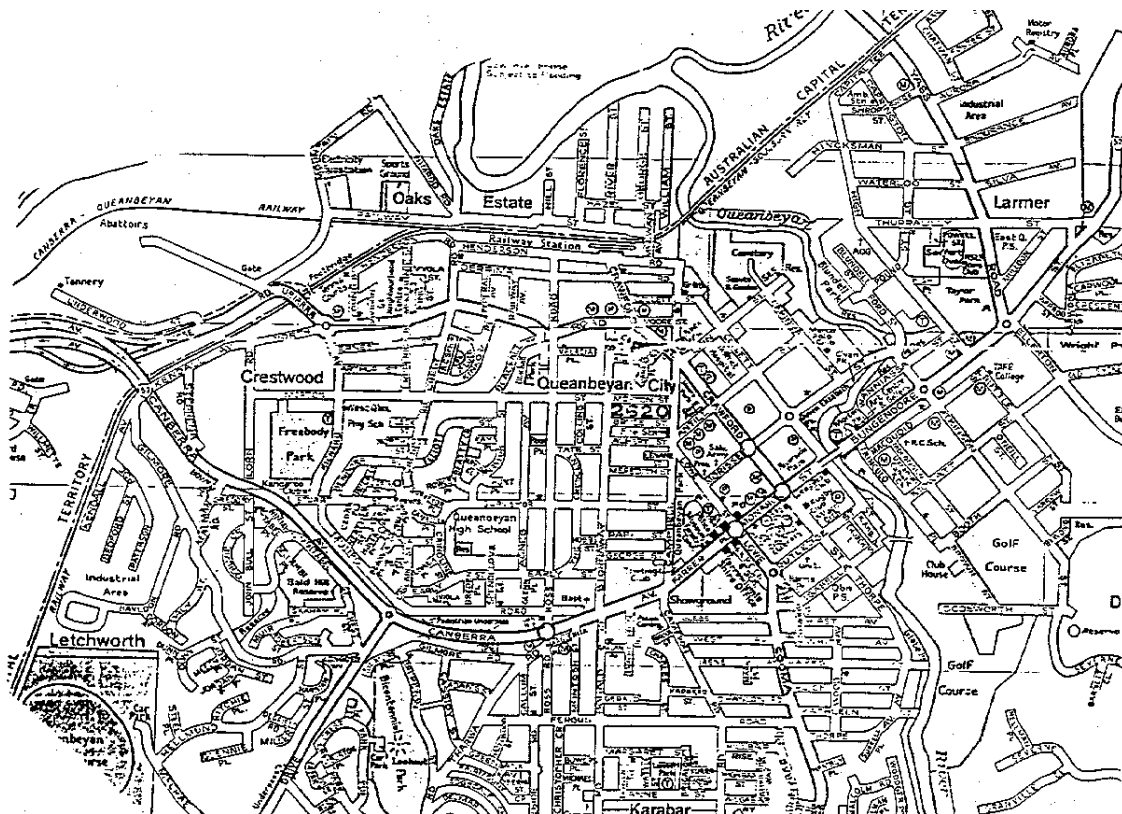


Figure 16. Queanbeyan (near Canberra), an urban landscape dominated by a network of inter-connecting roads.

Landscape dynamics

The functioning of the landscape is intimately tied in with the distribution patterns of the various landscape elements. To investigate this we can begin by asking a number of questions;

- How many patches of each element are there in total?
- How many patches of the same element are there?
- What is the variation in the size of these patches?
- How connected (by the various types of corridor) are these patches?
- How dissected is the matrix by the joining of corridors to form networks?
- How are the landscape elements arranged relative to each other in space?

All of these questions are relevant when we want to consider how the landscape functions, that is, when we want to consider the flows of energy, mineral nutrients and species between landscape elements.

The significance of the size and shape of patches for plants and animals was discussed briefly above. Also of importance for questions of conservation is how many patches there are, their spatial relationships, and how they are connected - either physically by the various types of corridor, or by the migration routes of animals (recall that a population which occurs in a number of patches which are linked by migration is called a **metapopulation**).

Corridors not only play a central role in the control of flows of species between landscape patches, but also the dynamics of matter and energy. In general there are four main functions of corridors

1. A channel to enable movement throughout the landscape.

Examples are the transportation of water, nutrients, sediment etc. along stream corridors, and human transportation along roads and railways. Of importance to living organisms is the movement of species along corridors to different patches of habitat.

2. A habitat for certain types of species

A notable example of corridors providing a habitat for particular species is roadside banks and verges. In many cases plant species are only able to persist in the landscape in this habitat, perhaps because the surrounding matrix is agricultural and they are excluded due to land management regimes, or because the surrounding matrix is natural vegetation and the species can only persist in the more disturbed habitat of the roadside.

3. A barrier or filter separating areas.

If vegetation corridors are aligned across hillsides then this type of corridor provides a barrier to water runoff, traps nutrients and helps reduce erosion. Other corridors such as shelterbelts are specifically designed to act as a barrier, in this case for wind. Some corridors also act to prevent the movement of species, for example certain forest birds and mammals will not cross even narrow roads cut through a forest, and many species are killed by traffic on roadways. Networks (linked corridors) can also act as a barrier for species attempting to cross the matrix.

4. A source of environmental/ & biotic effects on the surrounding matrix.

Examples of this include the thick coating of dust experienced by plants adjacent to high-use dirt roads, and pollution spread by traffic fumes on busy highways.

Mechanisms allowing flows within landscapes

There are five major **vectors** or **transport mechanisms** which allow the flow of energy, nutrients and species within landscapes. Keep in mind that the spatial arrangement of the various landscape elements has a direct effect on the effectiveness of all these mechanisms.

1. Wind

Wind can carry a wide range of items, including heat energy, water, dust, snow, pollution, sound, seeds, small elephants, spores and insects.

2. Water

Water, either on the ground surface or underground, carries (apart from more water) mineral nutrients, seeds, insects, sewerage, fertilisers and toxic chemicals.

3. Flying animals

Birds, bats, bees and other flying animals transport various seeds spores and insects.

4. Ground animals

These act similar to transportation by flying animals, except that some ground animals may be restricted by barriers, whereas flying animals may be able to avoid such obstacles

5. People

In developed areas the most important mechanism for transport may be human, either directly, or indirectly through the construction/formation of corridors.

Summary

Many of the concepts which are dealt with under the title of landscape ecology are already well known within others fields such as geography or ecology. Landscape ecology is a recent attempt to bring all of these ideas together under a common heading, and to provide a more structured framework within which we study the landscapes we live in.

Having this structured framework allows decisions regarding the management of landscapes to be made more effectively and more easily, it helps focus attention on the relationships between the various components of the landscape, and the terminology that has been developed e.g. elements, patches etc. has become the language of practical tools such as analysis by Geographic Information Systems (GIS).

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