

ECOLOGICAL SYSTEMS COURSE

For 1/5/01

Environmental variability, succession and invasion.

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Introduction

In this lecture we will be discussing the effects of environmental variability and disturbances on ecological communities, and how this impacts on how we study them. We will also be considering how communities change over time (succession), and the related topic of species invasions.

1. *Environmental variability and disturbance* (BHT Chapter 21)

Spatial vs. Temporal environmental variability

Environmental conditions can vary in both **time** and **space**. For example rainfall and temperatures change between years (Figure 1). Also, the environment is never even in space, some locations within an area (a whole water catchment, a forest patch, the bottom of a valley...) may have richer or wetter soils, more shade, different fire history etc. Such variable conditions will affect organism growth rates, food supply for animals, survival probabilities etc.

As a consequence of this variability, population sizes will fluctuate in both space and time (**spatio- temporal variability**).

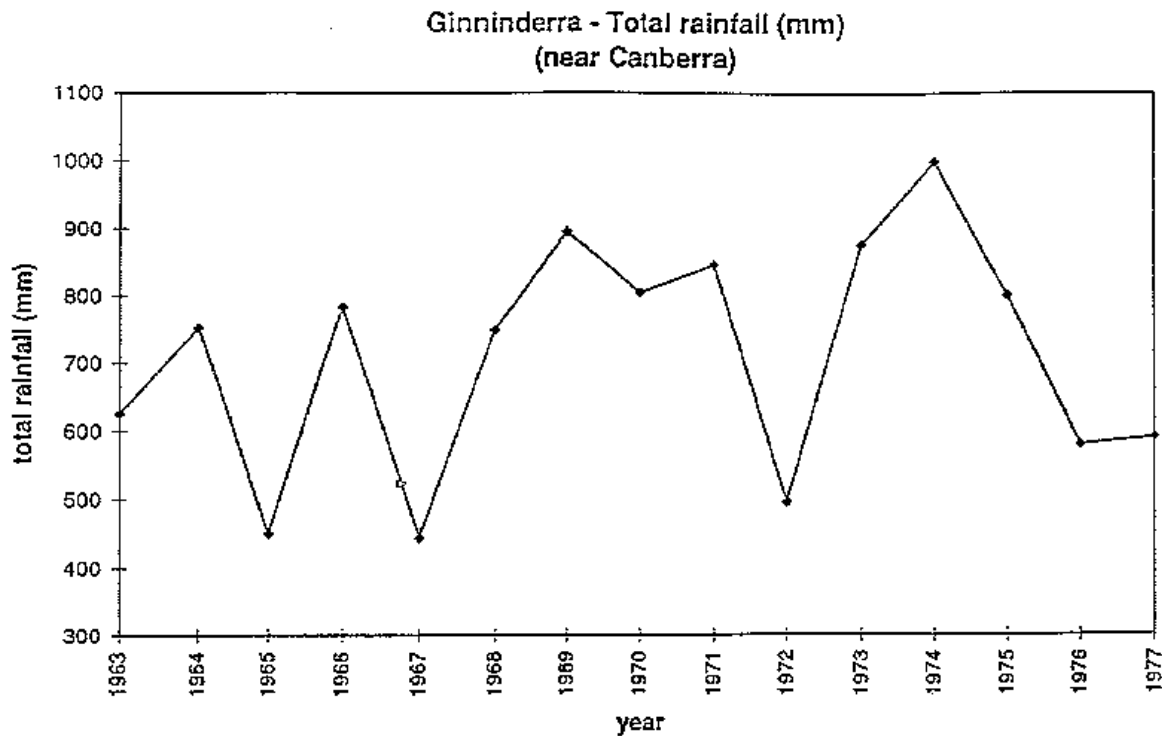


Figure 1. Temporal variability in rainfall at Ginninderra (near Canberra).

Disturbances

Disturbances are a particular source of environmental change. A **disturbance** is defined as 'any relatively discrete event in time that removes organisms and opens up space which can be colonised by individual of the same or different species' (BHT p. 754). Fires, cyclones, floods and windthrow (trees being blown down in forests) are disturbances. Predation can also be considered a disturbance when viewed from the position of the prey population. When discussing disturbance it is worthwhile keeping mind the following concepts from the previous lecture: **stability** (the ability of the community to recover following disturbance), **resilience** (the speed of recovery following disturbance) and **resistance** (the ability to remain unaffected by a disturbance).

2. Consequences of environmental variability on ecological systems

Disequilibrium

The traditional view of ecological systems (and in particular classic models of population dynamics) has been in terms of **equilibrium** between the species and the environment, and between the species themselves. It is easy to envisage that when the environment changes, the responses of the organisms take some time, and ecological systems will in fact spend most of the time in a **disequilibrium** state (Figure 2).

It is important to keep in mind that the notions of equilibrium and disequilibrium depend on the scales on which they are viewed. For example if we observe a 10m x 10m forest patch, the dynamics of the species within that plot might be very high - some individuals may perish, whilst others may become established. However, at a larger spatial scale of 1000m x 1000m these small scale dynamics may cancel each other out, resulting in

constancy at this larger scale. Similar concepts apply for temporal variation - many species are more abundant in the summer than the winter (and *vice-versa*), but overall abundances between years (summer to summer, or winter to winter) may be consistent (Figure 3).

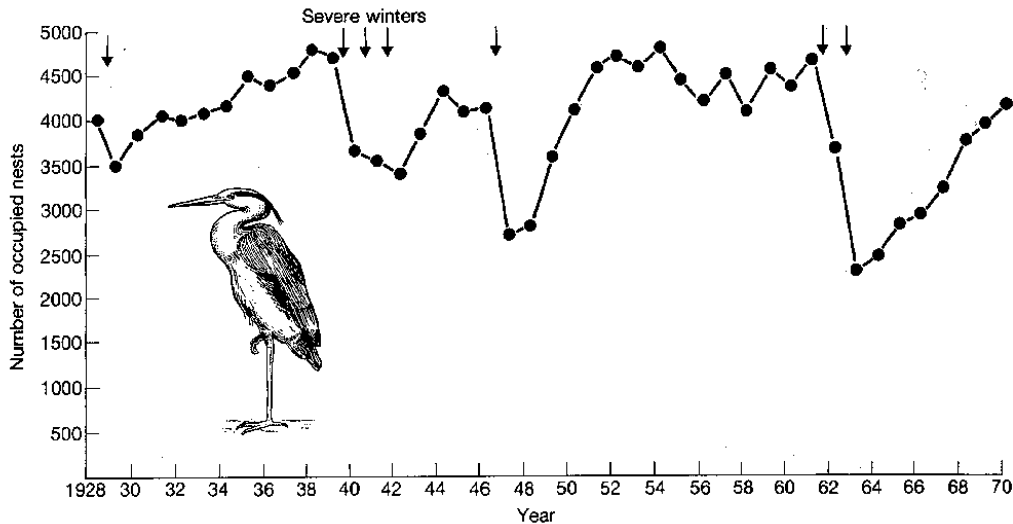


Figure 10.13. Changes in the abundance of herons (*Ardea cinerea*) in England and Wales (measured by the numbers of nests occupied) are readily attributable to changes in environmental conditions (particularly severe winters). (After Stafford, 1971.)

Figure 2. The response of heron populations in England and Wales to variations in environmental conditions (from BHT).

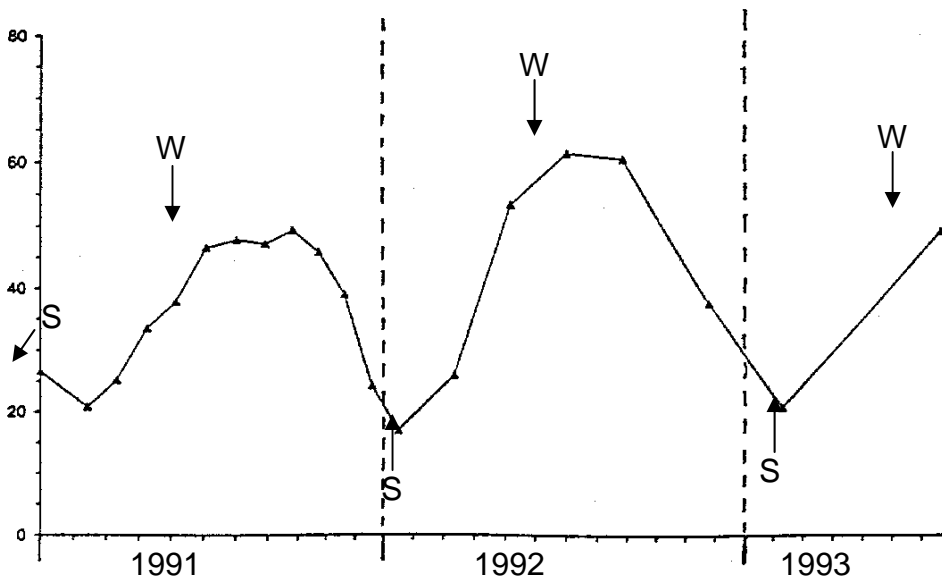


Figure 3. Consistent seasonal changes in the abundance of the moss *Eurynchium* in a mown lawn over 2.5 years. S = mid-summer. W = mid-winter (from Roxburgh 2000).

The implications of environmental variability on community structure

The principle of competitive exclusion does not seem to work in ecological systems: quite often we can observe very similar species coexisting quite happily. This is particularly the case with plants, where their basic requirement for growth (light, water, mineral nutrients)

do not appear to differ much between species. As an example, over 450 tree species (greater than 10cm diameter at breast height) have been recorded in one ha. of tropical rainforest.

Environmental variation can act to prevent competitive exclusion, and hence enhance coexistence and promote biodiversity. Two ways in which this can occur are given below.

Patch dynamics (BHT pp. 752-755)

Disturbances can be important driving forces of community dynamics. Each disturbance event resets colonisation and competition processes. As disturbances are not synchronised in space, different patches will be disturbed at different times. Species that are good colonisers but poor competitors (for example herbaceous weeds) can persist in the community by being able to colonise and reproduce as the patches are produced. These processes where there is a dynamic mosaic at different stages after disturbance belong to what is called **patch dynamics**.

Environmental variability and competition (BHT pp. 750-752)

In a more general manner the interaction between environmental fluctuations and the different competitive abilities of species can lead to species coexistence and hence high diversity. Different species can be favoured by different sets of conditions, and we know that conditions can change between years and between places. Imagine a plant species that performs well under drier conditions and another species that does better in rainier years. In a dry year the first species will produce a large population and many seeds, while the second species will have very few individuals. When conditions become moist the performances are reversed and the second species gets its turn to produce lots of seeds. During that time all the seeds from the first species remain dormant in the soil until the next dry year. The continual fluctuation between wet and dry years gives each species opportunities at different times, i.e. each species takes advantage of the different environmental conditions, hence opportunities for competitive exclusion are reduced. We can say that the ability of the organisms to partition their use of spatial and temporal variability defines spatial and temporal niches for the species (think about why this might be so).

It is important to remember that different places may have different histories in terms of disturbance, or in terms of the seeds which landed (or succeeded) there first. In this case community compositions will differ although environments may be equivalent. Such **historical effects** can make the interpretation of ecological data extremely difficult.

3 Succession (BHT pp. 628-647)

Introduction

Definition

Succession is the 'non-seasonal, directional and continuous pattern of colonisation and extinction on a site by species populations' (BHT p. 628). Succession is often associated with the recolonisation of an area following disturbance, although disturbance *per se* is not a prerequisite for succession to occur. For example the development of a forest from open water (Figure 4) and the sequence of fungi which invade dead organic matter (Figure 5) are also successions.

Types of Succession (BHT pp. 630-632)

The successional process has traditionally been divided into two types:

Primary succession is the recolonisation of bare substrate; for example bare rock following a volcanic eruption or glacial retreat, cessation of mining activity, and newly formed sand dunes.

Secondary succession is recovery of a community following partial or total removal of the organisms, but where well developed soil, seeds or other propagules remain.

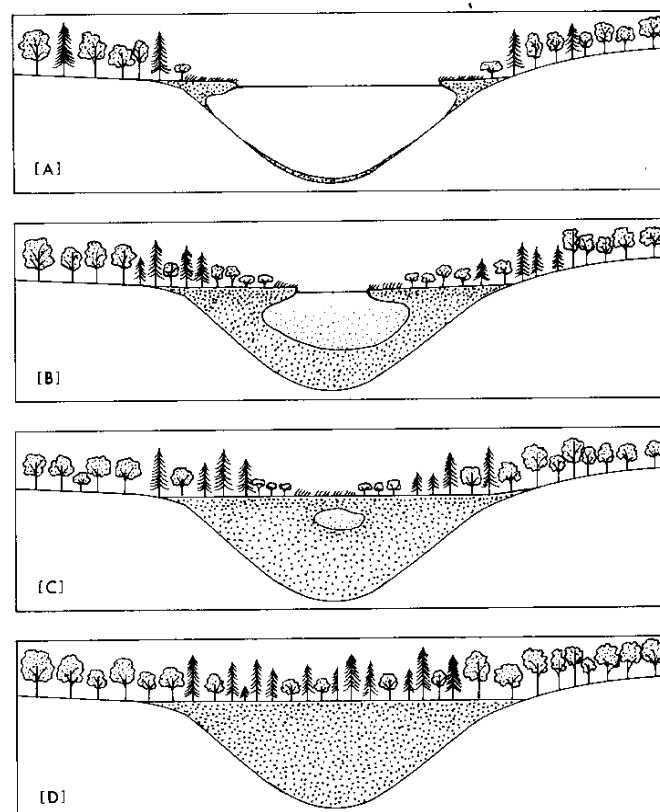


Figure 4.11. A bog lake succession. A floating mat of vegetation advances out over the water surface in a small lake in a cool, humid climate [A]. As the mat advances farther and the lake ages [B] and [C], scarcely decomposed organic matter (peat) accumulates in the lake basin, until after some thousands of years the lake will be converted to forest [D].

Figure 4. The successional development of forest from bare water (from Whittaker 1975).

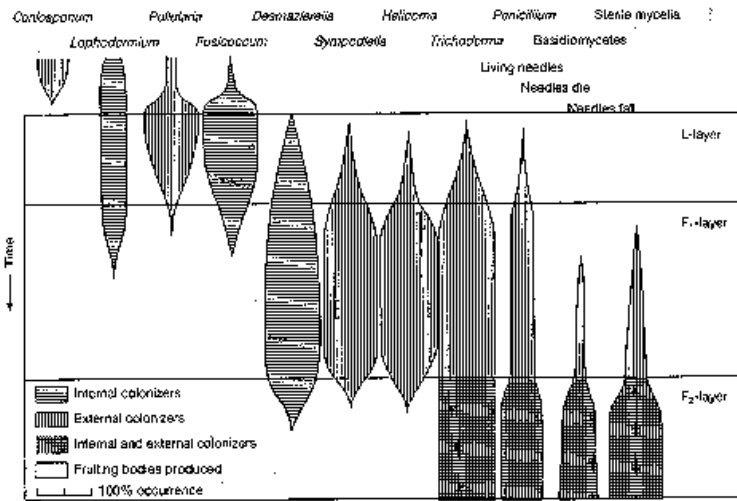


Figure 17.10. Temporal and spatial changes in fungal populations colonizing pine needles in litter layers beneath Scots pine (*Pinus sylvestris*) forest in England (After Kendrick & Burges, 1962. From S.N. Richards, 1974.)

Figure 5. The successional development of fungi colonising pine needles (from BHT).

Succession and species characteristics (BHT pp. 635-644, p. 838)

Species found early vs. late in successions share a certain number of characteristics (Figure 6). In general, early successional species have characteristics of good colonisers but poor competitors, while late-successional species are good competitors but poor colonisers.

Table 17.5. Physiological characteristics of early and late successional plants. (After Bazzaz, 1979.)

Attribute	Early successional plants	Late successional plants
Seed dispersal in time	Well dispersed	Poorly dispersed
Seed germination enhanced by		
light	Yes	No
fluctuating temperatures	Yes	No
high NO ₃ ⁻	Yes	No
inhibited by		
far-red light	Yes	No
high CO ₂ concentration	Yes	No?
Light saturation intensity	High	Low
Light compensation point	High	Low
Efficiency at low light	Low	High
Photosynthetic rates	High	Low
Respiration rates	High	Low
Transpiration rates	High	Low
Stomatal and mesophyll resistances	Low	High
Resistance to water transport	Low	High
Recovery from resource limitation	Fast	Slow
Resource acquisition rates	Fast	Slow?

Figure 6. Characteristics of early- vs. late-successional species (from BHT).

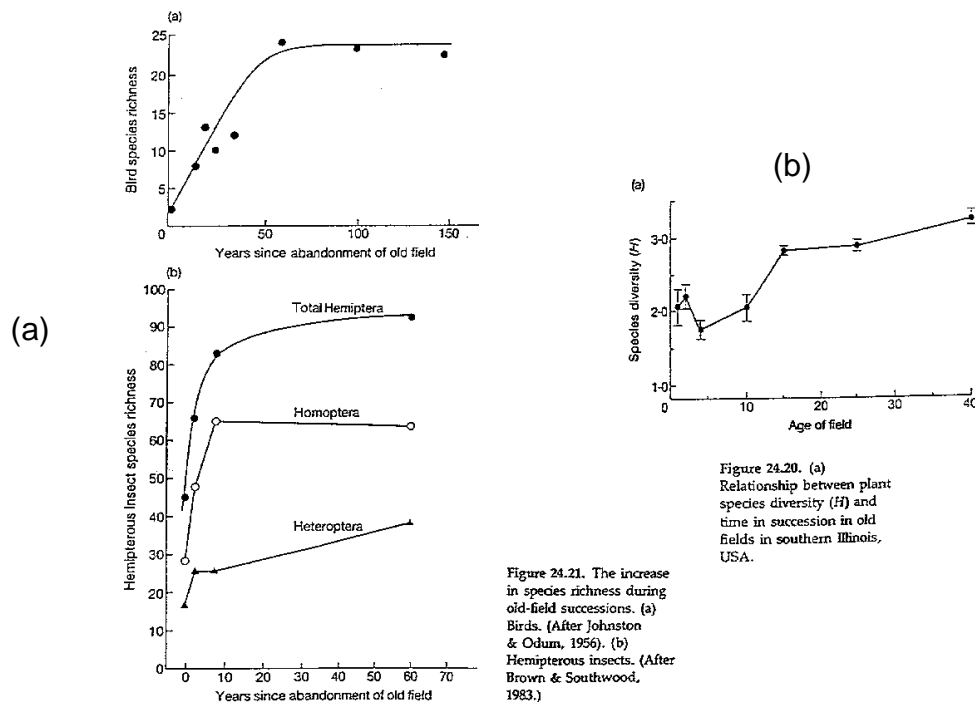


Figure 7. (a) The change in species diversity during succession of an abandoned agricultural field. The top graph is birds, the bottom graph insects. (b) The change in plant diversity during succession of an abandoned field in Illinois, US. (from BHT).

Species diversity is also known to change throughout succession (Figure 7a & b). Originally only a few colonisers establish. As more propagules arrive/establish, and possibly as the environment improves, more and more species accumulate. As species with superior competitive abilities assume dominance, diversity can stabilise or decrease.

Studying succession Succession can be studied by either observing changes through time at a given place (the **direct** approach) or by substituting time with space and looking at communities that are at different stages at a given time (the **indirect** approach). With the indirect approach the assumption is that the different patches are replicates in space of the same process, but asynchronous.

Historical Review of Succession Theory

The first theories of succession (organismic theories; Clements 1928) emphasised the interactive evolution of the environment and the community: in the course of succession the first species that arrive grow and alter the environment such that it becomes less attractive for themselves, and more attractive for the species which follow. This is called **facilitation** because the presence of the earlier species facilitates the subsequent entry of the later species. In this view succession ultimately leads to an equilibrium between the environment and the species, called a **climax** community.

An opposing view emphasises the independence of the behaviours of the individual species (Individualistic theories; Gleason 1926, Egler 1954). In particular, Egler called his theory the **Initial floristic composition** hypothesis (Figure 8). Under this theory there is

no facilitation; all the species that are likely to be involved in a succession are present at the beginning though some are predominant early on, and others later due to differences in their reproduction, dispersal germination and/or growth characteristics.

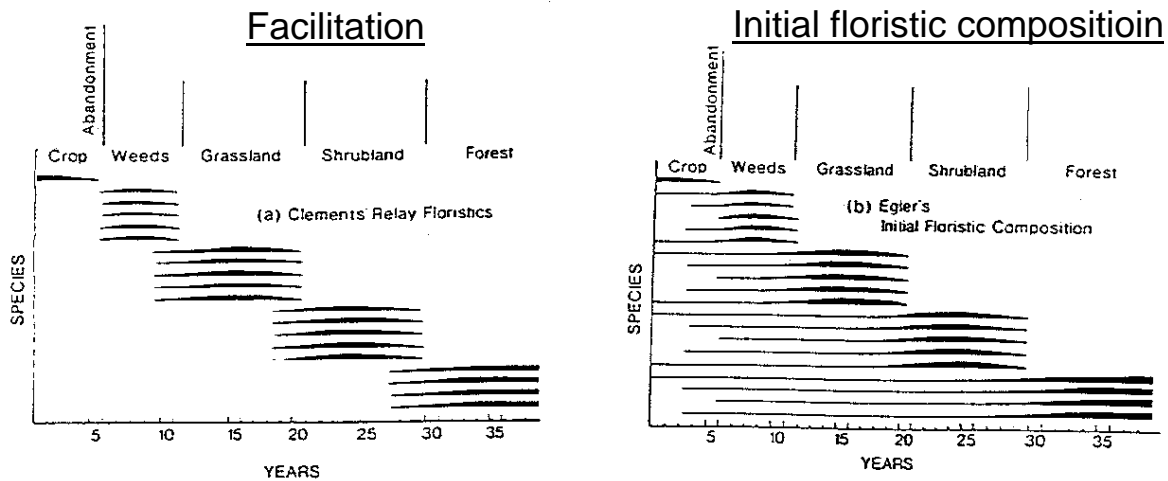


Figure 8. Figure illustrating the difference between the 'facilitation' and 'Initial floristic composition' models of succession (from Wilson *et al.* 1992).

Poised between these two extremes are the **tolerance** and **Inhibition** models (Figure 9). The *tolerance* model assumes that succession proceeds by the replacement of early, fast-growing species, by plants capable of regenerating in the conditions of depleted light and nutrient resources created by those earlier species. In contrast the *inhibition* model assumes that the early species prevent the establishment of the later species by site pre-emption. The later species gradually accumulate by replacing the early individuals when they die.

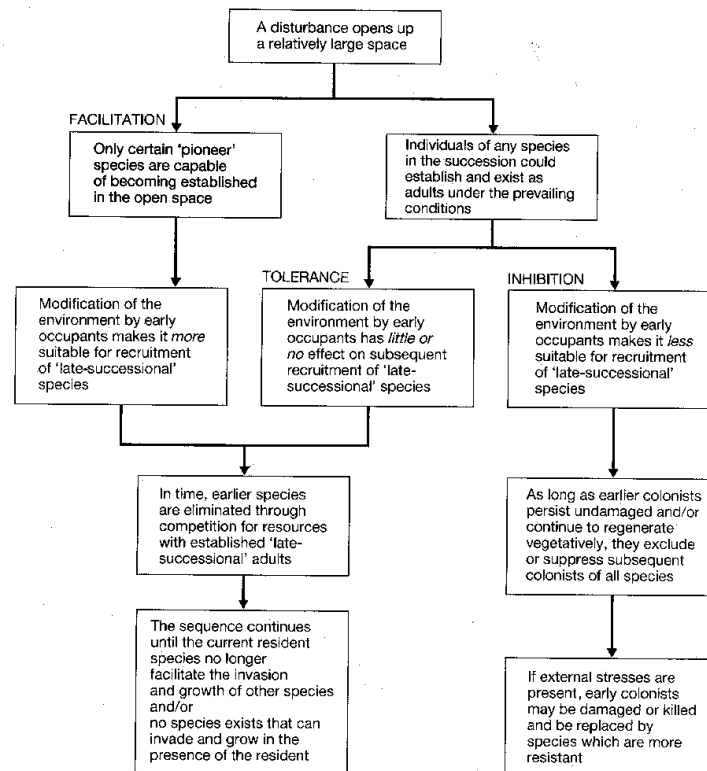


Figure 9. Three models of the mechanisms which underlie successions (from BHT).

Modelling Succession

For purposes of management of an area we need to take into account the successional changes that will occur. For that we need to use models to predict what the vegetation is likely to be in the future (5 yrs, 10 yrs, 500 yrs...). There exist a number of models which have been used to simulate the successional process. Most of them fall within three broad categories.

Life-history based models

Each species is characterised by properties which are thought to be important in determining their position in the successional sequence. These properties are known as **vital attributes** and include such things as the method of recovery following disturbance, capacity to reproduce in the face of competition and life history characteristics. Species are classified into groups based on the similarity of their vital attributes, and the model produces a set of replacement sequences between groups depending on conditions (e.g. occurrence of disturbance). In this way precise predictions about successional sequences can be produced (Figure 10).

TABLE 2. The division of plant function used in FATE, with the parameters required to describe each process. Cf table 1 in Pickett *et al.* (1987)

Plant function	Process	Parameters	Parameter domain	
Life history	Dispersal	Is functional group widely dispersed?	Yes/No	
		Does functional group have innate dormancy?	Yes/No	
	Dormancy/ propagule storage	If so, then:		
		—longevity of dormant pool†		
		—proportion of propagules moving from the dormant to the active pool as a result of each disturbance type		Proportion‡
		Longevity of active propagule pool		Age
Germination/ enforced dormancy	Germination rates at each resource level		None/Low/ Moderate/High: see table 3	
	Establishment	See environmental response		
Environmental response	Growth	Size‡ of immature plants as a proportion of the size of mature plants	Proportion	
		Maturation	Maturation time	Age
	Senescence	Lifespan	Age	
	Tolerance of environmental conditions	Strata of plants in immature and mature life stages		Small integer
		Survival/death of germinants, immatures and matures		Yes/No
Disturbance response	Niche relationships	Maximum abundance at the site	Low/Medium/ High¶	
		Escape	Proportions of each life stage meeting each of the three fates	Proportion¶¶
	Death	Resprouting	Ages of resprouting plants	Age

Figure 10. Life-history based models.

Markovian models

This class of models are statistical in nature. The community is described by a certain number of **states**, and by probabilities which summarise the chance, over a given time interval, of one state being replaced by another. The states can either be individual species, or groups of species characteristic of certain stages of the succession (called **seres**). Assuming that the community at time t depends only on the structure at the previous time step ($t-1$), it is possible to simulate changes in the succession over time (Figure 11).

Table 17.3. A 50-year tree-by-tree transition matrix from Horn (1981). The table shows the probability of replacement of one individual by another of the same or different species 50 years hence.

Present occupant	Occupant 50 years hence			
	Grey birch	Blackgum	Red maple	Beech
Grey birch	0.05	0.36	0.50	0.09
Blackgum	0.01	0.57	0.25	0.17
Red maple	0.0	0.14	0.55	0.31
Beech	0.0	0.01	0.03	0.96

This means that if there is an individual of Red Maple present today, in 50 years time there is a 14% chance that it would have been replaced by Blackgum.

Beginning with an observed distribution of the canopy species in a stand in New Jersey known to be 25 years old, Horn modelled the changes in species composition over several centuries. The process is illustrated in simplified form below (which deals with only four species out of those present). The progress of this hypothetical succession allows several predictions to be made. Red maple should dominate quickly, while grey birch disappears. Beech should slowly increase to predominate later, with blackgum and red maple persisting at low abundance. All these predictions are borne out by what happens in the real succession.

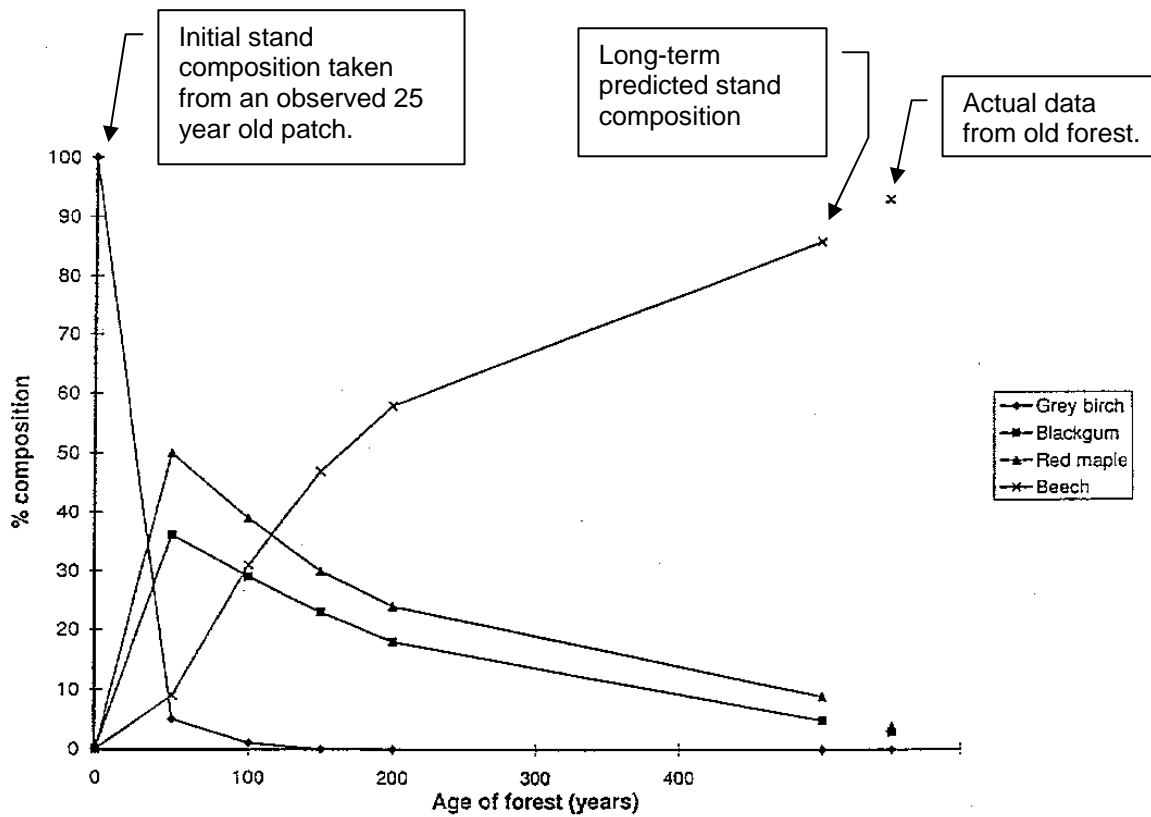


Figure 11. Markovian models (from BHT).

Patch (or gap) models

These models are widely used for predicting forest dynamics. The dynamics of the system are modelled at the scale of the patch (e.g. 1 ha of forest) and separated into compartments e.g. recruitment of seedlings, survival, growth. For each compartment mathematical equations relate the particular process to the physical environment (e.g. temperature), resource availability (e.g. water, nutrients), disturbances and competition. The model is run for a large number of such patches and the patterns can be described by the statistical properties of the whole set (Figure 12). This type of approach also includes **individual-based** models, where the fate of each individual in the patch is modelled through time, e.g. how many seeds each plant sets, how much wood it produces, if it dies etc.

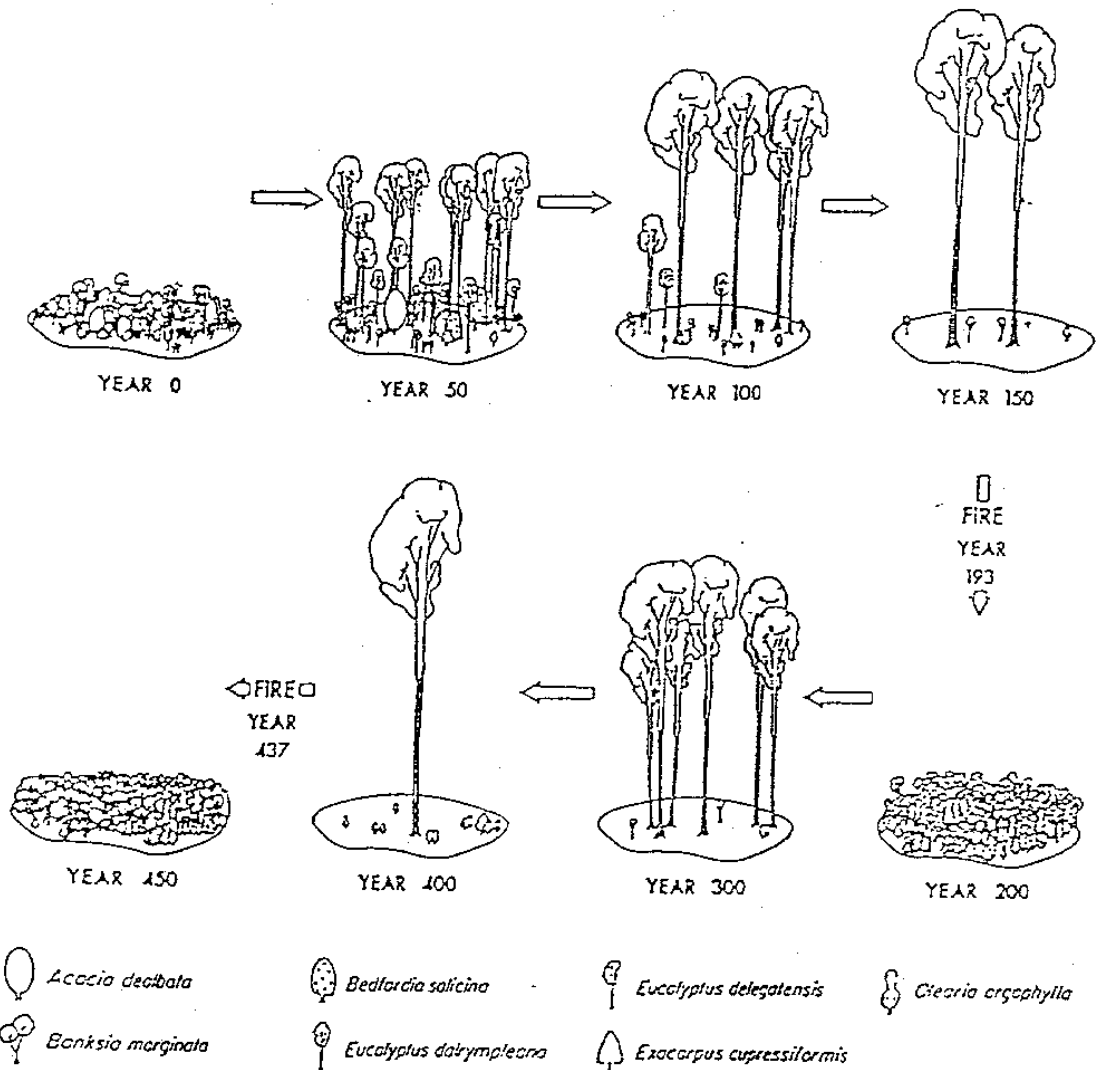


Figure 4.14. 450 years of change on a single simulated plot (BRIND model) for the alpine ash zone of the Brindabella Mountains. The species are drawn to scale by height, and the width of the plot is 32 meters.

Figure 12. Patch models.

4. Invasion

Introduction

Definition

'A biological invader is a species of plant, animal or micro-organism which, most usually transported inadvertently or intentionally by man, colonises and spreads into new territories some distance from its home territory.' (Di Castri 1990). If one looks at long time scales (geological) then invasions are probably a frequent phenomenon. However, human activity has increased the frequency of invasions dramatically by disrupting biogeographic barriers and increasing exchanges.

The importance of invasions Invading species can have enormous impacts on both the biological and economic aspects of the invaded area. For example, rabbits (*Oryctolagus cuniculus*), a native of Europe, reached plague proportions in Australia in the later part of the 1940's and the early 1950's. The impact this invader had was reflected both in its effects on the environment (e.g. problems with soil erosion) and also the economy through loss of farming productivity (Figure 13). Figure 14 shows the percentage of introduced plant species in various countries. They range from a low of 7% in Java to nearly 50% in New Zealand.

TABLE 2
VERMIN DESTRUCTION ON A PROPERTY, NORTHERN MIDLANDS (Tasmania)
(1600 Acres)

Year	Total Sheep	Lambs Bred	Wool Clip (lb)	Wool per Sheep (lb)	Total Cattle (Head)	No. of Rabbits Destroyed	Vermine Control Costs (£)	Cost per Acre (s. d.)
1952	1,808	895	11,770	7½	—	18,000	922	11 6
1953	1,830	1,055	18,027	9½	—	3,000	120	1 6
1954	2,060	1,206	21,320	9½	—	1,200	80	1 0
1955	2,025	1,241	20,484	10	23	900	60*	9
1956	2,175	1,253	23,047	10½	25	600	40	6
1957	2,344	1,297	25,644	10½	25	450	30	4½

*Estimated.

Figure 13. Table showing the increase in farm productivity with a decrease in the invading rabbit population (from Meldrum 1959).

Table 2.3. Percentages of introduced species in selected floras

Country	Native species	Introduced species	Percentage introduced
Antigua/Barbuda	900	180	10
Australia	15-20000	1500-2000	10
Sydney	1500	4-500	26-33
Victoria	2750	850	27.5
Austria	3000	300	10
Canada	3160	881	28
Ecuador			
Rio Palenque	1100	175	15
Finland	1250	120	10
France	4400	500	11
Guadeloupe	1668	49	9
Hawaii	12-1300	228	17.5-19
Java	4598	157	7
New Zealand	1790	1578	47
Spain	4900	758	15

Figure 14. Percentages of introduced species in selected floras (from Drake et al. 1989).

Figure 14. The percentage of introduced plant species in various countries

The Invasion Process

Stages of invasion

The successful invasion of a species requires the completion of four main stages (Figure 15).

Introduction: The various means by which a new species enters a new territory.

Colonisation: The establishment of the species into its new habitat.

Naturalisation: Reaching successful reproduction and population sustainability in the new area

Spread: The dispersal of the invader to new sites within the area. This spread can be of three types: **Phalanx**, **Guerilla**, and **Infiltration** (Figure 16a). Figure 16b shows infiltration invasion by a millipede in South Australia.

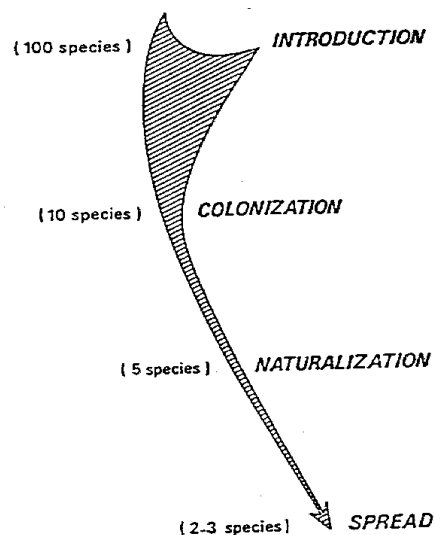


Figure 15. The stages of invasion (from di Castri 1990).

What makes a successful invader?

In order to predict which species have the potential to become successful invaders, attempts have been made to recognise common characteristics of invading species. Although it is possible to come up with a few characteristics such as rapid growth, high reproductive capability etc. they are in no way a safe predictor (figure 17). For example no species possess all characteristics, but rather an unpredictable proportion of them, hence there is large variability between invaders. There are many examples where invading species have characteristics opposite to those listed in figure 17, and many examples of species which we would expect to be successful invaders but are not. In general, lists of characteristics are of little help in recognising potential invaders.

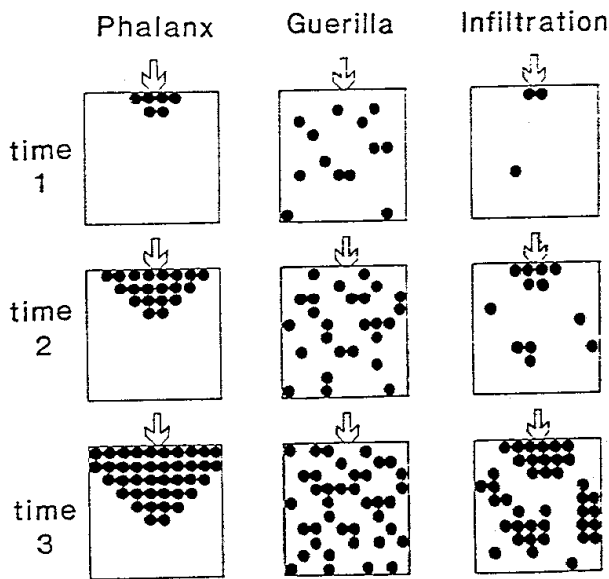


Figure 3. Map of the southern end of Eyre Peninsula, South Australia, showing the areas (shaded) in which the millipede *Ommatoiulus moreletii* was found to occur (after Baker 1976).

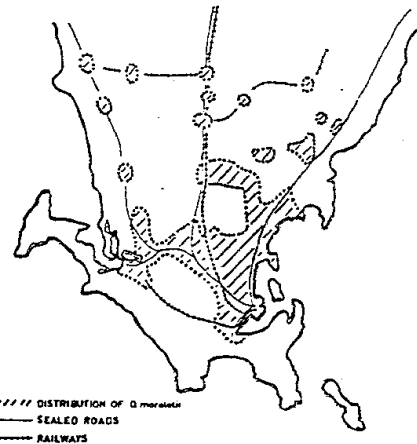


Figure 16. (a) Three different types of dispersal, at three times during the spread of the species (from Wilson and Lee 1989). (b) Infiltration invasion of a millipede in south Australia (from Browning 1973).

Table 1. Some biological attributes of a possible invader.

Related to ecology and physiology	Related to morphology and behaviour	Related to genetics and population dynamics
Wide potential niche	Small body size	Subject to <i>r</i> -selection
Non-specialized germination and regeneration patterns	High mobility	High fecundity
Non-specialized pollination patterns	High vagility	High population growth
Dormancy	Apt to phoresis	Short and simple life-cycle
Rapid growth	High resistant spores	High genetic variation
High resource allocation to reproduction	Seed morphology (spiny seeds or burr, plumed seeds, winged seeds or samara) suitable to long dispersal by wind or animals	Uniparental reproduction
Longevity of seeds able to create seed banks		Polyploidy
Edible fruits and seeds transported by animals		

Figure 17. Some biological attributes of a possible invader (from Di Castri 1990).

Predicting the risk for target systems

In order to predict the risks of invasion, and to reduce them, one may want to ask whether some characteristics of systems make them more susceptible to invasions. Figure 18 summarises three main types of conditions:

- Experiencing the right kinds of conditions (pressures) in the home environment can **pre-adapt** species to become successful invaders.
- Opportunities for introduction to the new area.
- Local conditions which favour the establishment and spread of invaders.

While it is true that species can more easily invade regions or habitats that are similar to their own, this is not always the case. The lack of competition, predation, and pathogens can also facilitate successful colonisation.

The (unfortunate) conclusion is that there are probably no general principles which we can use to predict whether species X will/will not become a successful invader in area Y. The interaction of chance, historical factors and the interactions between the invaders biology and ecosystem properties may combine to produce outcomes which are often case-specific.

Table 2. Conditions facilitating the potential to invade new territories.

Historical conditions in the home territory	Facilities for transportation and/or migration	Local conditions facilitating colonization by new invaders
Geological and evolutionary history of recent natural disturbance (e.g. glaciations, regional tectonic pulses, frosts, droughts)	Intensive exchanges of people and their products because of trade, colonization or war Rapid transportation systems	Existence of open spaces and spare resources Ecosystems subject to frequent natural disturbances
Early man-related history of exogenous disturbance (e.g. grazing pressure by large herbivores, fires)	High vagility of invaders Phoresis (active transportation of small animals by larger insects, birds, etc.)	Man-disturbance of ecosystems similar to that of the home territory Absence of pathogens, parasites, predators, competitors left behind in the home territory
Domestication by man and commensalism	Longevity of seeds, resistance of spores and possibility of long dispersal (by oceanic currents, wind, etc.)	Homoclimatic and mostly homocultural (similar land-use patterns) conditions as compared to home territory 'Insularity' conditions (evolutionary history with isolation patterns) in islands, southernmost tips of continents (South America, South Africa, Australia) and western fringes of continents

Figure 18. Predicting the risk for invasions (from Di Castri 1990).

The control of invading species (BHT P. 551-582)

The aim of controlling invaders is not total eradication, which is virtually impossible and very costly, but to reduce them to a 'tolerable level'. This level needs to be set by managers taking into account numerous factors (ecological, socio-economic, political).

Methods of control include:

Physical methods such as shooting and trapping for animals and hand weeding and fire for plants.

Chemical methods such as pesticides, herbicides and poisoning programs.

Ecological manipulations such as promoting the increase of natives to competitively exclude the invaders and maintaining or even increasing diversity.

Biological control. The introduction of natural enemies e.g. insects, fungi or viruses.

Legislative control. The prevention of entry into a country of by legal means, and tight control over imports.

The most effective and viable strategy is to combine several different methods, which is called **integrated control**. The success is never predictable, but it is recognised that control needs to start early in the invasion, and that once initiated the control methods have to be maintained, and that good monitoring and flexibility of the program are necessary.

To illustrate some of the features of biological invasions (and to show you it is not all doom and gloom) I will present two case studies during class. The first is the invasion of the tree species *Myrica faya* into Hawaii. The second is the story of the control of an invasive tropical water-weed species (*salvinia molesta*).

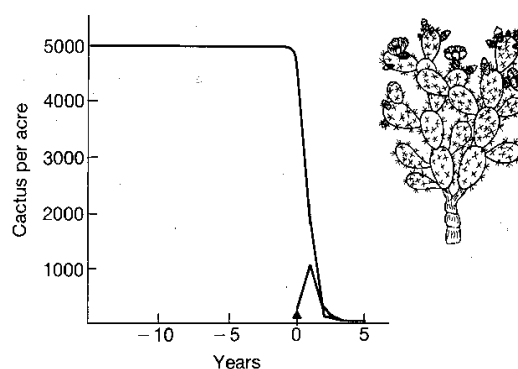


Figure 15.26. The control of *Opuntia* by *Cactoblastis*. The model derived by Caughley and Lawton (1981) accurately describes the crash of the cactus population from its pre-release level of 5000 plants per acre to a stable density of only 11 plants per acre within 2 years. Upper curve indicates cactus abundance; lower curve indicates moth numbers after introduction at year 0.

Figure 19. An example of the potential effectiveness of biological control (from BHT).

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