

# ECOLOGICAL SYSTEMS COURSE

For 3/4/01

## What are ecological communities?

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### Introduction

In today's session we consider the question 'What are ecological communities?'. We will discuss how communities are defined, and how ecologists go about studying them. We will also spend some time discussing biodiversity and its measurement.

#### 1. What are ecological communities?

##### **Definition** (BHT<sup>1</sup> pp. 611-615)

A *community* is a collection of populations of all the organisms which occur together in a given place and time. *Community ecology* is the study of the *interactions between these organisms*, and the *interactions between the organisms and their environment*. Communities can have emergent properties which arise from these interactions - properties which could not be predicted by studying the individual populations in isolation.

Traditionally, the term 'community' has had restricted use to describe the activities of the populations only, whereas when these are combined with the physical environment (e.g. nutrient dynamics and energetics) the term *ecosystem* has been used. However it is not possible to consider the biological 'community' in isolation

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<sup>1</sup> 'BHT' refers to page references in the textbook 'Ecology: Individuals, Populations and Communities' by Begon, Harper and Townsend, 2<sup>nd</sup> edn.

from its environment, therefore the traditional distinction between 'community' and 'ecosystem' will not be recognised in these lectures.

The term 'community' is also commonly used to refer to a subset of populations within the whole community, for example we talk about *plant communities*, *insect communities*, *arthropod communities*, *small mammal communities*, etc.

### **Species interactions**

Within communities there are a variety of ways in which organisms can interact with each other. There are also a variety of ways in which these interactions have been classified by ecologists.

#### 1. Competition (BHT pp. 197-209, 240-247)

Competition occurs when the interaction between organisms results in a reduction of growth, survival or reproduction for both partners of the interaction. **Exploitation competition** commonly involves the use of a **limiting resource** - some factor which is in short supply and is required for growth etc. by each competitor. Limiting resources for plants include light, water and nutrients, for animals they include food, shelter and nesting sites. **Interference competition** occurs when individuals directly interact, such as two animals fighting for a territory, or **allelopathy** - the production of chemicals by one organism which are toxic to another.

Competition can be of two types: **Intraspecific** competition occurs between individuals of the same species/population (figure 1), e.g. self thinning in crops or forest plantations, competition for females among kangaroo males. **Interspecific** competition involves individuals from different species/populations (figure 2), e.g. weeds and the crop in an agricultural field, marsupials and birds competing for nesting sites in dead trees.

#### 2. Predation (BHT pp. 279-281)

Predation is the consumption of one living organism (prey, plant or host) by another (predator, grazers or parasite). The key idea is that one member (the predator) benefits to the detriment of the other (the prey). Note that this definition does not include *detritivores* - those organisms which consume dead organic matter.

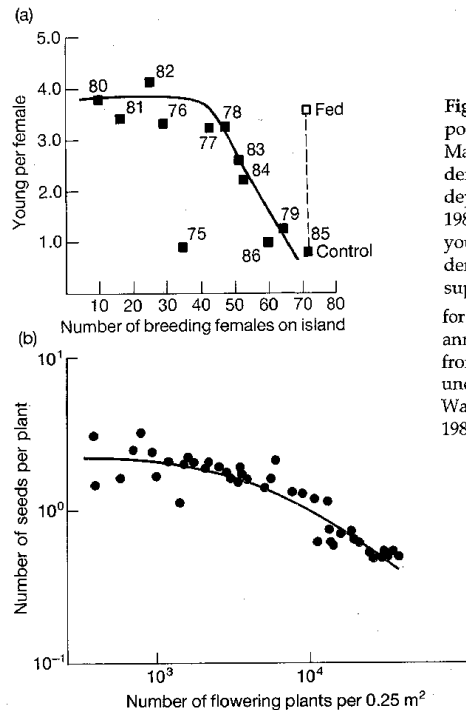
Below are three classes of interaction which come under the category of predation.

*'True' Predation:* This is predation in the ordinary sense where a predator kills and consumes a prey species. True predators are such organisms as tigers and birds of prey. Animals which kill and eat other animals are called *carnivores*. Insectivorous plants can also be considered true predators.

*Herbivory:* Herbivory is the consumption of plant material by plant eating animals (*herbivores*). In this case the herbivores are the predators, and the plants are the prey. Large herbivores such as kangaroos, sheep and cattle are usually called *grazers*. Other herbivores include insects, molluscs (slugs, snails) and fish.

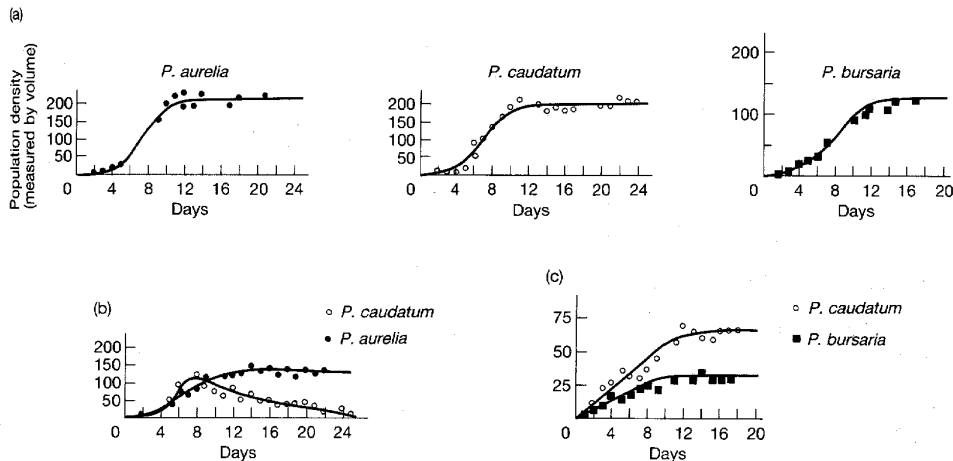
*Parasitism:* Parasites are generally much smaller than their host and grow and/or reproduce inside (endoparasites) or on the surface (ectoparasites) of the

living host. They directly divert some of the resources (water, food) from the host. Many parasites are animals, e.g. flatworms (Platyhelminthes) and roundworms (Nematodes), but there are also parasitic plants (e.g. mistletoes, *Euphrasia* sp.) and some species of fungi.



**Figure 1.** Density-dependent fecundity. (a) In the population of song sparrows, *Melospiza melodia*, on Mandarte Island, BC, Canada, fecundity changes from density-independence to overcompensating density-dependence as density increases, over the years 1975–1986. (For instance, at a density of 40, the total number of young produced was roughly  $40 \times 4 = 160$ , whereas at a density of 70 it was roughly  $70 \times 1 = 70$ .) Providing supplementary food in 1985 suggested that competition for food was the cause (Arcese & Smith, 1988). (b) In the annual dune plant *Vulpia fasciculata*, fecundity changes from approximate density-independence to undercompensating density-dependence. (After Watkinson & Harper, 1978. From Watkinson & Davy, 1985.)

**Figure 1.** Intraspecific (=within-species) competition (from BHT).



**Figure 7.2.** Competition in *Paramecium*. (a) *P. aurelia*, *P. caudatum* and *P. bursaria* all established populations when grown alone in culture medium. (b) When grown together, *P. aurelia* drives *P. caudatum* towards extinction.

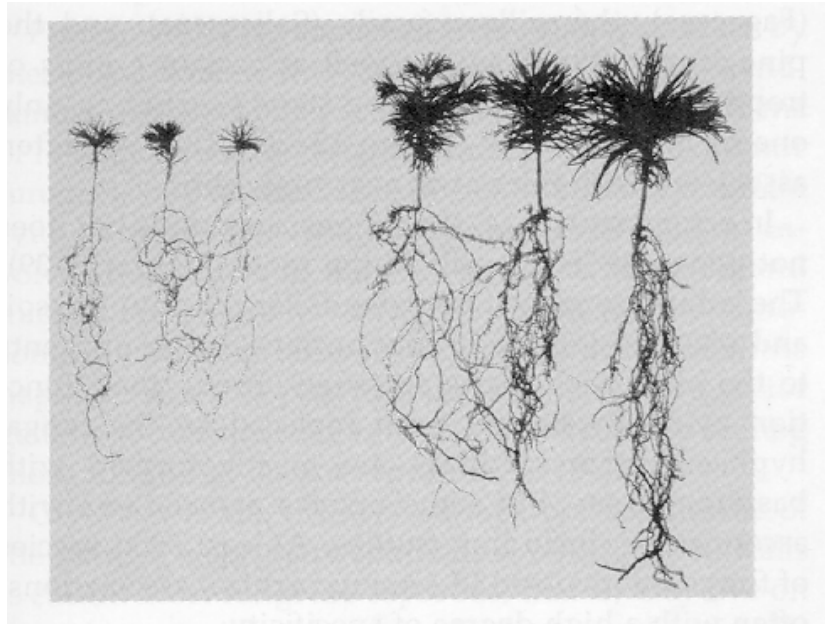
(c) When grown together, *P. caudatum* and *P. bursaria* coexist, though at lower densities than when alone. (After Clapham, 1973. Data from Gause, 1934.)

**Figure 2.** Interspecific (=between-species) competition (from BHT).

### 3. Mutualism (BHT Chapter 13)

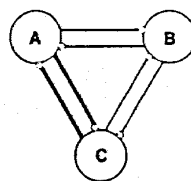
Mutualism occurs when both populations/individuals benefit from the presence of each other. For example many plants have a mutualistic interaction with *mycorrhizal*

fungi which live on, or in, the root surface. The fungi provide mineral nutrients to the plant, and in return receive carbon compounds from the plant (Figure 3).



**Figure 3.** Mycorrhizae and tree nutrition. Nine-month-old seedlings of white pine (*Pinus strobus*) were raised for two months in a sterile nutrient solution and then transplanted to sterile soil. The seedlings on the left were transplanted directly. The seedlings on the right were grown for two weeks in forest soil containing fungi before being transplanted to the grassland soil (from Raven *et al* 1982).

The above categories are based on pairwise interactions, i.e. between a single predator and a single prey. In ecological communities there are usually many more than two species interacting at any given time. When more than two species interact, the nature of the pairwise interactions can be distorted or even reversed (Figure 4). Ecologists are still trying to understand the complexities and importance of such multi-species interactions.



**FIG. 1.**—Competition among 3 hypothetical species of consumers (modified after Levine [1976]). Line width is directly proportional to intensity of competitive interaction. Although the pairwise interaction between species C and B is competitive, C actually increases the population growth rate of B by suppressing that of A.

**Figure 4.** An example of how multi-species competition can give different result from those based only on pairwise comparisons (from Davidson 1985).

### **Do communities exist?** (BHT pp. 627-628)

The question of whether communities have properties of their own which are more than the sum of their parts has been debated for a long time. Much of this debate

has centred around the role that the species interactions play in determining the species composition of ecological communities. There are two extreme views.

The Clementsian or **superorganismic** view of communities (Clements 1916) sees them as being tightly organised entities, where the growth and development of whole communities is seen to be analogous to the growth and development of an individual. Under this view, communities exhibit properties which are more than the sum of the individual parts. Species interactions are assumed to play a major role in the development and regulation of communities.

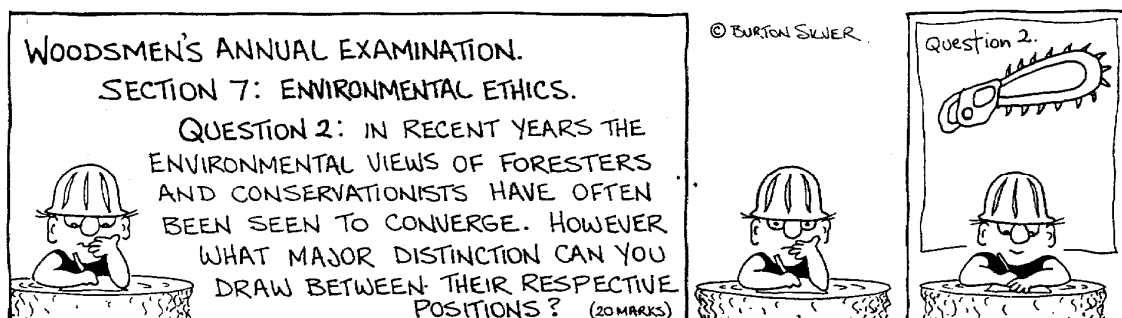
An alternative view is the **individualistic concept** of community structure, originally attributed to Gleason (1926). Under this view communities are not tightly structured, but are merely *coincidences* resulting from chance dispersal, environmental sorting and species interactions. Thus, communities are less predictable, and species interactions have a much reduced role in determining the structure of communities.

### **What is 'community structure'?**

'Community structure' is a general term used to describe a wide range of phenomenon resulting from the formation of ecological communities.

In ecology 'Community structure' is commonly used to refer to the limitations set by species interactions on which species can coexist with which others. These limitations to coexistence are called **assembly rules**, and they can apply to single species, as well as to groups of species such as guilds defined below. Of particular interest to ecologists has been the role that competition has played in the structuring of communities. This will be discussed in detail in the next section.

'Community structure' is also used to describe the physical arrangement of species in a community, such as the vertical arrangement of species in a forest (trees, shrubs and ground growing herbaceous (non-woody) plants (Figure 5).



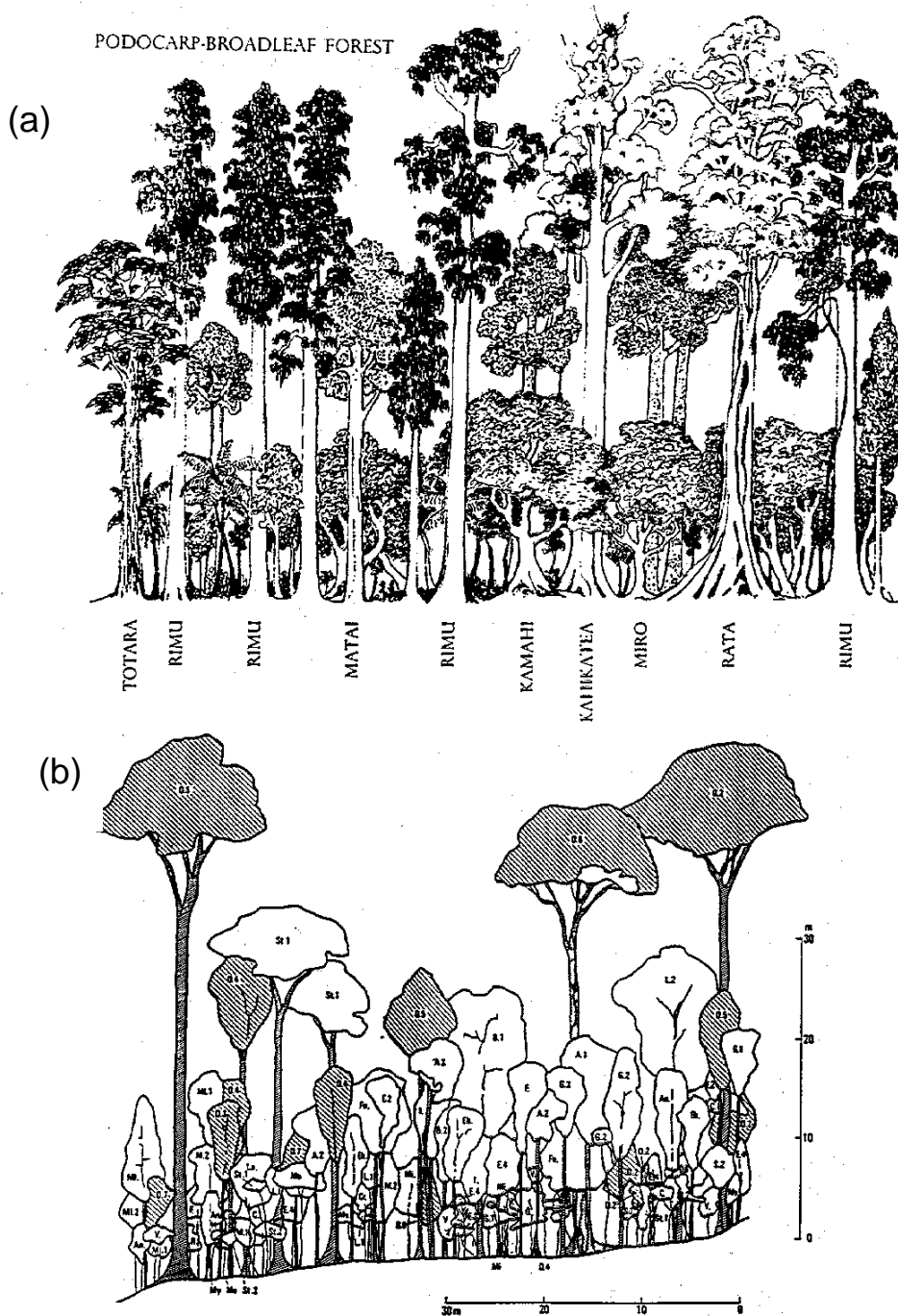


Fig. 27.2. Mature and building phases on ridge at Belalong, Brunei, in tropical lowland evergreen mixed dipterocarp rain forest. Plot area 60 m by 7.5 m, all trees over 4.5 m tall shown. Dipterocarps hatched.

**FIGURE 5.** Plant communities can be described by the vertical arrangement of the species in space. Figure 5a is a Podocarp-broadleaf forest in New Zealand. In this forest there is clear stratification, with a separation between the tall canopy and emergent species from the species which form the sub-canopy. In contrast, figure 5b is a profile of a typical Dipterocarpus forest in Brunei. Note that the species form a continuum of heights, with the result that there is little vertical stratification.

One further method of investigating community structure is by grouping organisms at levels higher than the species. Some common ways of grouping species are:

**Guilds:** A guild is a group of species which utilise resources in a similar way (Root 1967). For example a group of fruit eating birds in a rainforest, a guild of forest-floor dwelling herbs. Note that because species within a guild utilise the same resources, then we expect them to compete more strongly with each other than with species from different guilds.

**Functional types:** Functional types are groupings of organisms which respond similarly to a particular disturbance (Gitay and Noble 1997). The groupings can include species, or subspecies, or phenotypes which differentially respond to the disturbance, or even different stages in the life history of the same species. We will be returning to the concept of functional types later on.

**Trophic levels:** Community structure can be described by the use of food webs. A food web is a graph of the various trophic levels in a community (carnivores, herbivores, producers) and the links between them. Figure 6 is an example of an actual food web.

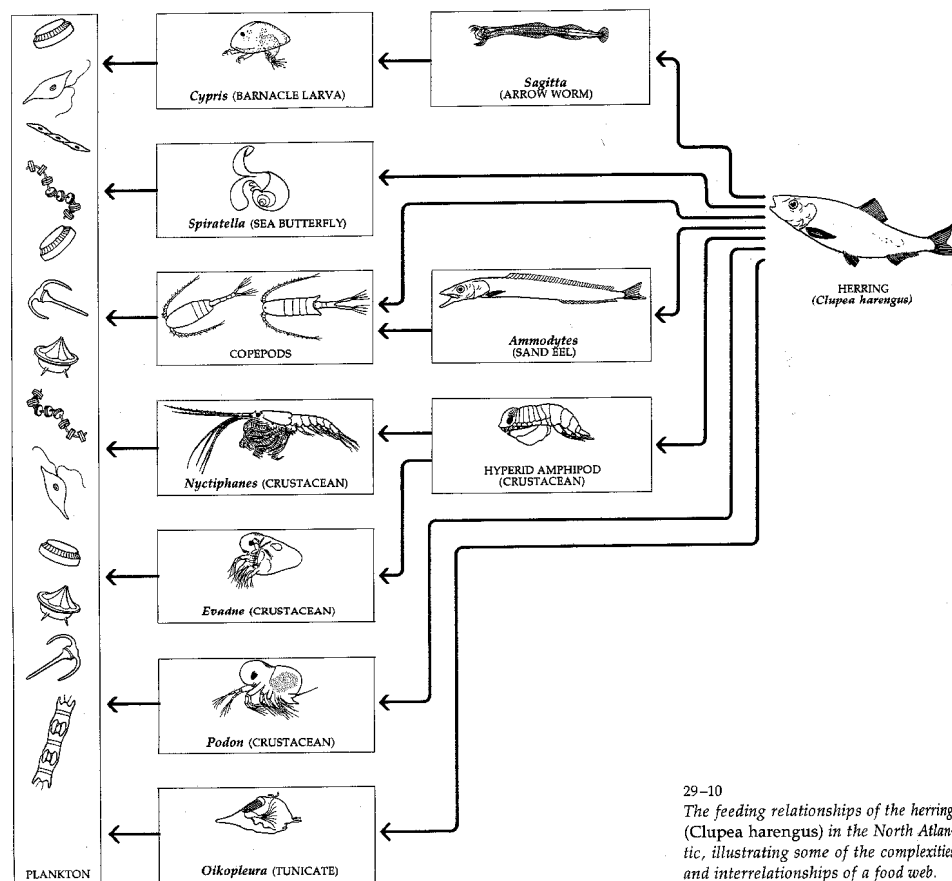


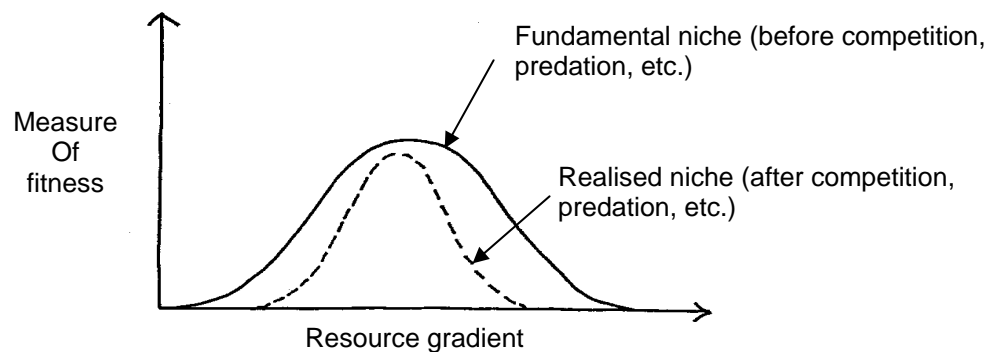
Figure 6. An example of a food web (from Curtis 1983).

## 2. Mechanisms structuring ecological communities

### **The ecological niche: definition and measurement** (BHT pp. 75-78)

The *ecological niche* of a species is a multidimensional description of its resource needs, habitat requirements and environmental tolerances (Hutchinson 1957).

The **fundamental niche** is the potential set of conditions which a species can occupy. It can be determined experimentally. However, in nature due to the effects of competition, enemies and biogeography, species do not occupy the niche entirely. What is observed is their **realised niche** (Figure 7).



**Figure 7.** The fundamental and realised niche.

The niche concept can be further split into two distinct aspects.

**Geographic niche, Conditions niche or Beta niche:** This simply states that some species live in different places due to differences in environmental tolerances. Therefore, species with differing beta-niches never physically come together to interact.

**Resource-specialisation niche or Alpha niche:** Here several species can co-occur in the same place, i.e. they have the same beta niche. For two species to have different alpha niches implies they are using different resources, or are using similar resources in such a way that overlap in their use is minimised. Figure 8 shows how desert plants can differ in their alpha-niches - plant A is able to capture water (the resource) most efficiently from the top layer of soil, whilst Plant B obtains most of its water from deeper underground.

### **The relationship between the ecological niche and species coexistence: the principle of competitive exclusion** (BHT pp. 251, 267-278)

“And Nuh is the letter I use to spell Nutches  
 who live in small caves known as Niches, for hutches.  
 These Nutches have troubles, the biggest of which is  
 The fact there are many more Nutches than Niches.  
 Each Nutch in a Nitch knows that some other Nutch  
 Would like to move into his Nitch very much.  
 So each Nutch in a Nitch has to watch that small Nitch  
 Or Nutches who havn't got Niches will snitch.”

[Dr. Seuss]



The **principle of competitive exclusion**, also known as **Gauss's principle**, states that no two species which share the same (alpha) niche can permanently coexist - the superior competitor will eventually exclude the weaker competitor. Coexistence between competitors is therefore related to the amount of overlap between species with similar niches (Figure 9). For example, in Figure 8 plants A and B might be expected to coexist because they utilise water from different depths, and hence competition for water is reduced.

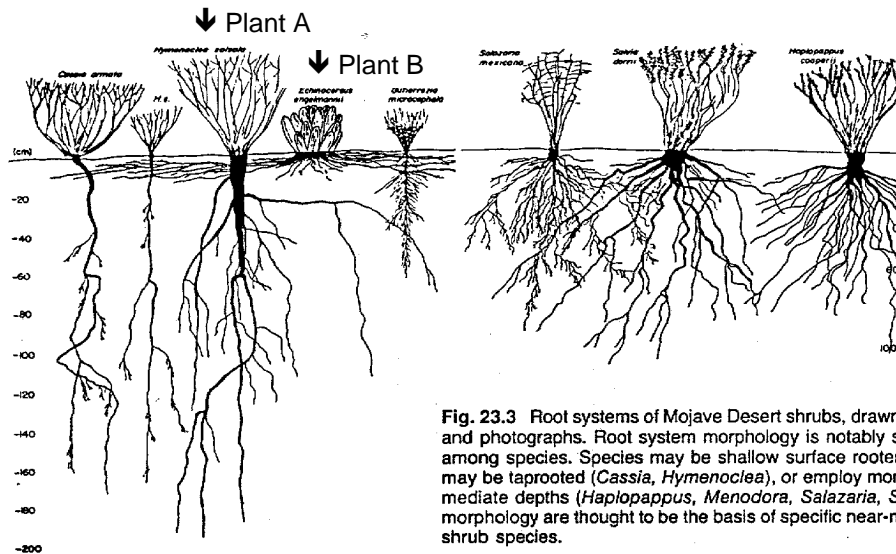


Fig. 23.3 Root systems of Mojave Desert shrubs, drawn from field excavations, diagrams, and photographs. Root system morphology is notably species-specific, but varies widely among species. Species may be shallow surface rooters (*Echinocereus*, *Hilaria*, *Yucca*), may be taprooted (*Cassia*, *Hymenoclea*), or employ more spreading roots at various intermediate depths (*Haplopappus*, *Menodora*, *Salazaria*, *Salvia*). Differences in root system morphology are thought to be the basis of specific near-neighbor preferences among these shrub species.

Figure 8. Rooting depths of different species of desert plants (from Cody and Diamond (1975).

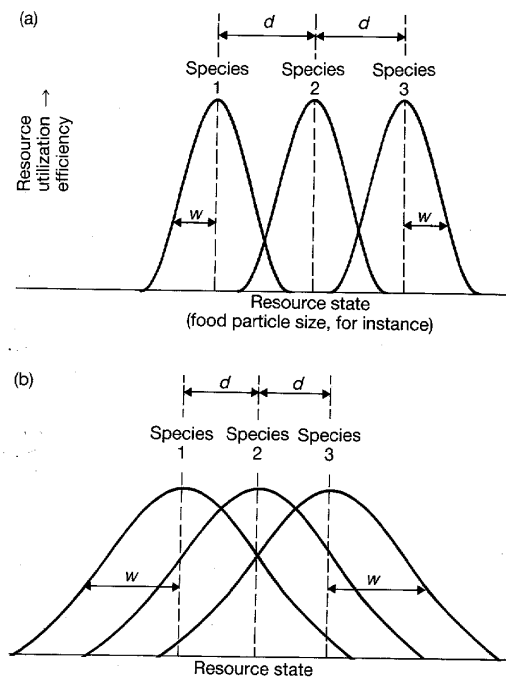
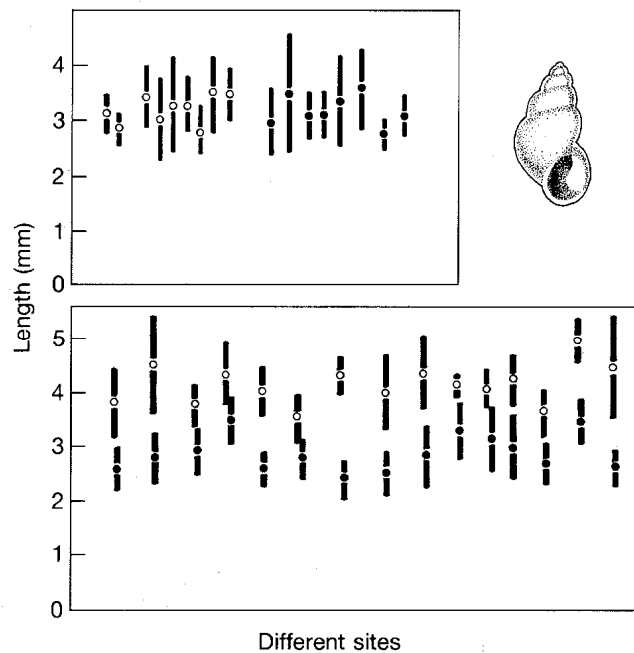


Figure 7.19. Resource utilization curves for three species coexisting along a one-dimensional resource spectrum.  $d$  is the distance between adjacent curve peaks,  $w$  is the standard deviation of the curves. (a) Narrow niches with little overlap ( $d > w$ ), i.e. relatively little interspecific competition. (b) Broader niches with greater overlap ( $d < w$ ), i.e. relatively intense interspecific competition.

Figure 9. Resource utilisation curves illustrating the relationship between niche overlap and the intensity of competition (from BHT).

Competition between species with similar niches can lead to shifts in the niche space of a species through the action of evolution via natural selection (see Evolutionary Concepts lecture notes). When such a shift is associated with morphological changes it is referred to as *character displacement* (Figure 10).



**Figure 7.18.** Character displacement: average lengths (plus standard deviations) of *Hydrobia ulvae* (open circles) and *H. ventrosa* (filled circles) at various sites. When they live alone (above) their sizes are similar; but when they live together (below) their sizes differ. (After Fenchel, 1975.)

**Figure 10.** Character displacement in the snail *Hydrobia* (from BHT).

An example of the practical use of the ecological concepts of the niche and competitive exclusion is in 'mixed' or 'intercropped' agricultural systems. In such systems two or more crops are planted simultaneously. If the harvest of this mixture is somehow 'better' than if any of the component species were planted only by themselves (monoculture), then this is called **intercrop advantage**. Common intercropping combinations include sorghum & pigeonpea, corn & bean and corn and wheat. Biologically, intercrop advantage can result from two possible mechanisms. Firstly, the various crop species in the mixture can be chosen so that they do not compete strongly with each other, i.e. their *niche overlap* is sufficiently low. Secondly, an increase in crop performance can arise if the species are chosen so that one species modifies the environment in a positive way for a second species, for example one crop providing shelter for another that otherwise would not perform well in full sunlight. Note that the 'biological' reasons for intercropping, i.e. increasing productivity/yield may not be the most important in many situations. For example intercropping may result in more efficient use of resources such as land, water, time etc, and there may be socio-economic advantages such as improved human nutrition. The book by Vandermeer (1989) provides an excellent introduction to the topic.

### 3. **Methods used to describe ecological communities**

(BHT pp. 615-626)

#### **Spatial patterns, mosaics, gradients and ecotones**

Community composition changes in space. The way in which this happens is the **spatial pattern**. Community composition also changes in time. Temporal changes will be the topic of the next lecture. We can describe the spatial pattern with respect to any of the following:

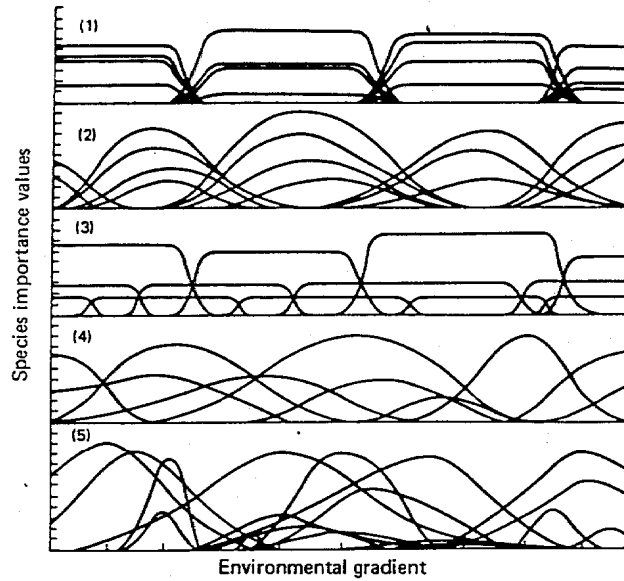
**Mosaic:** Mosaic patterns occur when there is a patchwork of communities with different compositions.

**Gradients:** Gradients are encountered when there is a gradual change in space of some environmental factor. This can either be reflected by a gradual or sharp change in the abundances of the species (Figure 11a). The most common pattern in nature is a gradual change in species composition along gradients, without sharp boundaries (Figure 11b). Examples of gradients include vegetation changes up mountains in response to an altitudinal gradient, and salinity gradients in estuaries which are associated with changes in the plant and fish communities.

**Ecotones:** Ecotones occur at the boundaries between different communities. They can be very sharp (Figure 12a) e.g. the boundary between the edge of a forest and a stream, or diffuse (Figure 12b) e.g. the transition between desert and savanna. They can be natural or human induced.

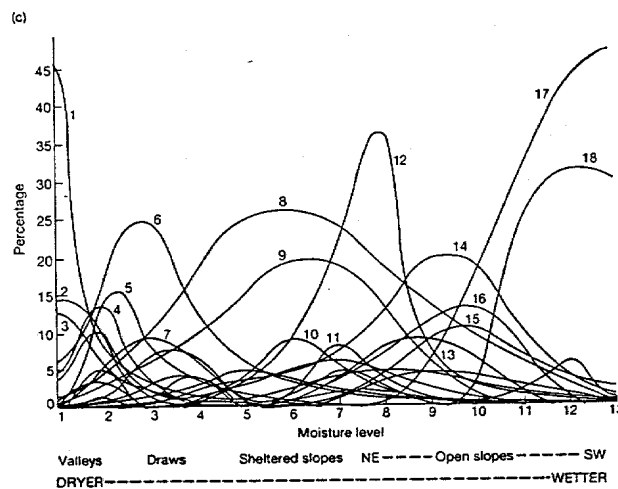
#### **Field surveys and multi-variate methods**

The description of communities is in general straight forward: one just needs to list and count the species which are present, usually also recording their spatial distributions. In practice it is surprisingly difficult because of species identification problems and because of sampling problems. An exhaustive count is not generally possible and one needs to devise an adequate **sampling strategy** taking into account variability in space, possibly time, and the differences in species abundances. Usually this involves selecting areas (**sampling units**) within communities in which to concentrate study, in the hope that through combining the results from several such areas a representative picture of the community will be obtained.



← (a) 5 theoretical predictions on how species composition might vary along an environmental gradient

Figure 4.6: Five Hypotheses of the Pattern of Change in Abundance of Species Along an Environmental Continuum (Environmental Gradient with Conditions Changing at a Gradual Uniform Rate from One Extreme to the Opposite). Panel 1, dominant species evenly spaced and sharply replacing each other with subordinate species distributions strongly correlated to those of dominants. Panel 2, dominant species evenly spaced but gradually replacing each other with subordinate species strongly correlated with dominants. Panel 3, dominant species evenly spaced and sharply replacing; patterns similar for subordinate species but not correlated with dominants. Panel 4, both dominant and subordinate species show bell-shaped abundance curves that tend to be non-coincident for species with similar requirements. Panel 5, both dominant and subordinate species show bell-shaped curves varying randomly in height, extent, and location. See text for further discussion. Source: Modified from Whittaker, 1970 after Collier, Cox, *et al.*, 1973.



← (b) Reality

Figure 11. (a) Hypothetical changes in species composition along an environmental gradient. (b) actual changes in forest composition along a moisture gradient (from BHT).

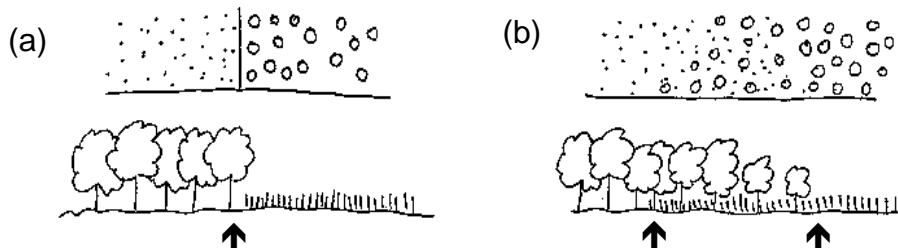


Figure 12. (a) Sharp ecotone. (b) diffuse ecotone.

Having obtained a list of species and their abundances within sampling units, there is usually so much information that it is impossible to draw conclusions about any general trends which may be apparent. What is required are methods to simplify and summarise this raw data. Two ways to analyse ecological data are:

**Indices:** Indices summarise the data into a single number (the index) by combining, and hence simplifying, the information. For example, the number of species in the community (species richness) is a very simple index. We'll see a number of such diversity indices below under section 4.

**Multi-variate methods:** These are statistical tools which allow us to identify species groupings according to their patterns of co-occurrence. An **Ordination** is a map which groups sampling units together on the basis of their similarity of species composition and abundance (Figure 13). The axes of the ordination are derived mathematically from the raw data, and they can be thought of as summaries of the community patterns. The scatter of the points in the ordination can then be used to see if the derived gradients correspond to gradients in environmental variables. Numerical **classification** is another method commonly employed by ecologists to summarise community patterns. With classification the sampling units are grouped together in sets and sub-sets corresponding to similarity in species composition. Performing a classification effectively imposes discrete boundaries to the communities (Figure 14). The literature on the use of multivariate methods in ecology is very large.....and often very confusing.

### **Richness, abundance and dominance**

A community can be described by list of all the component species and their abundances. Although species are the most common 'currency', higher level groupings of species such as guilds (section 1.4) can also be used.

The total number of species is the **species richness**. **Abundances** can be quantified in terms of the number of individuals, biomass or cover. Abundances can be expressed either **absolutely** (e.g. how many individuals per species) or **relatively** (e.g. what proportion of the total for each species). Species can be ranked according to their abundances; the most abundant ones are said to be dominant, and the ranking is called a **dominance** ranking. The concept of diversity is considered in greater detail below.

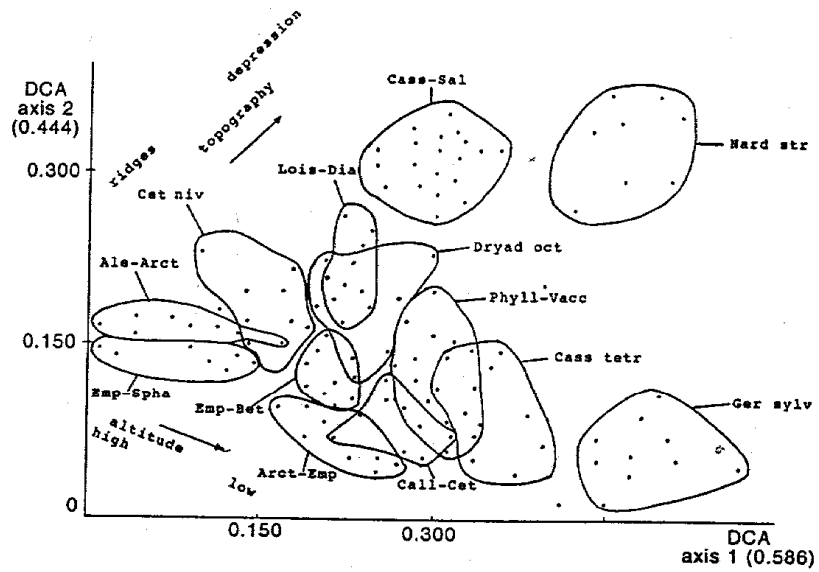
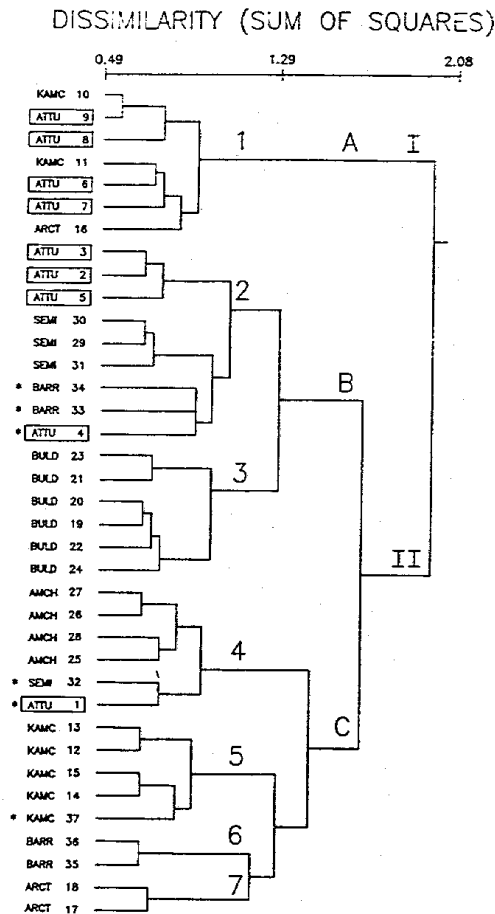


Fig. 3. DCA ordination of sample plots, axes 1 and 2. Association (community-) boundaries are indicated. For full community names, see text.

↑ Figure 13. An example of an ordination



← Figure 14. An example of a classification

Fig. 5. Classification dendrogram produced by minimum variance clustering of a similarity ratio matrix of 37 community types and 163 species from coastal Alaska and Kamchatka showing seven clusters, 1-7.

## 4. What is (bio)diversity?

### **Definition**

“Biological Diversity is the variety of all life forms: the different plants, animals and micro-organisms, the genes they contain and the ecosystems they form”<sup>2</sup>. Note the breadth of this definition; it covers not only diversity in terms of the number of species, but also the genetic information contained within individual organisms, as well as the diversity of habitats, natural communities and ecological processes in the biosphere.

### **The different levels of diversity**

Most commonly, the term diversity refers to **species diversity** which is a measure of how many species are present in a community and their relative abundances. Although the species is the most commonly used taxonomic level, studies at biogeographical scales also quantify diversity of genera (generic diversity) or families to compare regions. **Genetic diversity** is a similar measure which quantifies the variety of genotypes within a species or population. Humans have long been aware of the concept of genetic diversity through selection of crop plant varieties and domestic animals. More recently, the concept of **landscape diversity** has been developed to refer to the diversity of communities (or vegetation types) present at the scale of the landscape.

### **A. Genetic diversity (BHT pp. 34-39)**

#### Definition

Strictly speaking, genetic diversity refers to the diversity of **genotypes** within a population or species. The term can be used for a given trait (e.g. the colour of corn grains, resistance to disease). More generally, it is used to describe the total level of diversity for all traits. Populations which appear to be genetically distinct from other populations of the same species are referred to as a **subspecies** (a geographically recognisable population). Human modified genotypes are called **races** (for animals, Figure 15) and **varieties** (for plants, Figure 16). Indeed, the concept has been applied in agriculture and animal breeding for a long time, where breeders have been using the natural genetic diversity of wild ancestors and relatives of the cultivated varieties to produce new varieties.

#### Methods to measure genetic diversity

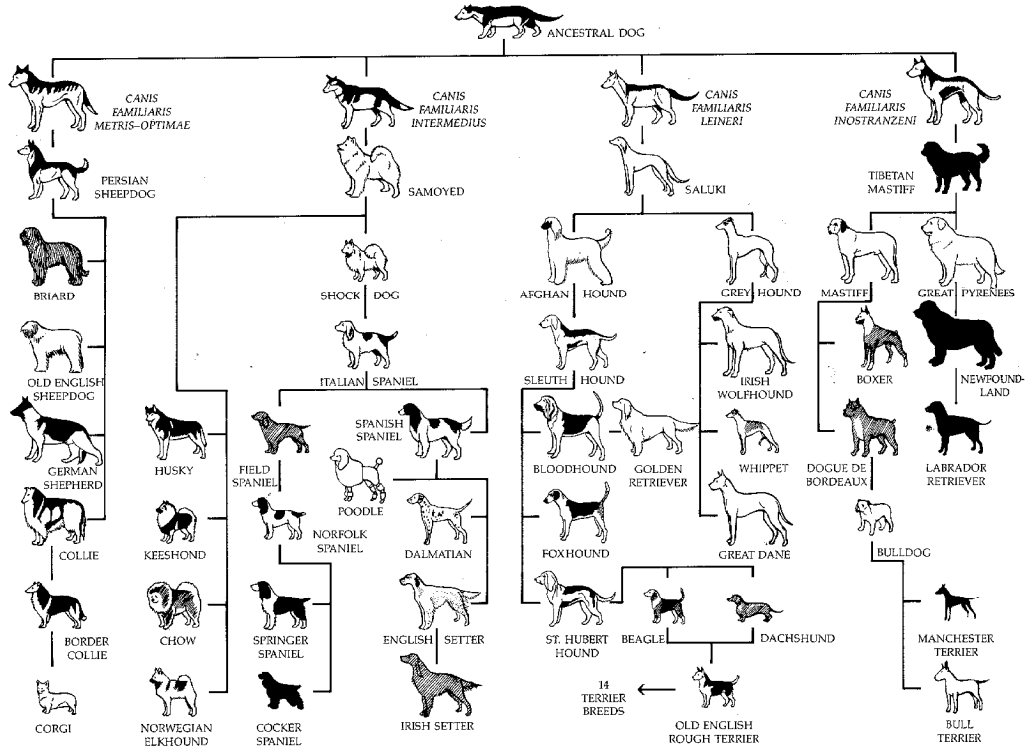
**Morphological studies:** If a trait has a simple genetic determinism (i.e. it is determined by one or a few genes), it is possible to study genetic diversity by simply measuring the frequencies of these different **phenotypes** present in the population. The existence of two or more phenotypes in a population is called **polymorphism** (Figure 17).

**Electrophoresis:** This is a chemical technique which allows the range of different forms of the same protein within a population to be measured. Because these different forms are a direct consequence of the variability in the underlying genetic code, measuring variability in these proteins indirectly measures the genetic diversity.

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<sup>2</sup> Taken from the Proceedings of the Fenner Environment Conference 1992 ‘Biological Diversity: Its future conservation in Australia’.

**Sequencing methods:** More recently, molecular biological techniques have been developed to directly investigate the composition of DNA. This between-individual variability in DNA composition gives a quantification of genetic diversity.



48-3  
All breeds of dogs have been produced by artificial selection, a demonstration of the tremendous potential for variability in a single species.

Figure 15. Races of domestic dogs (from Curtis 1983).

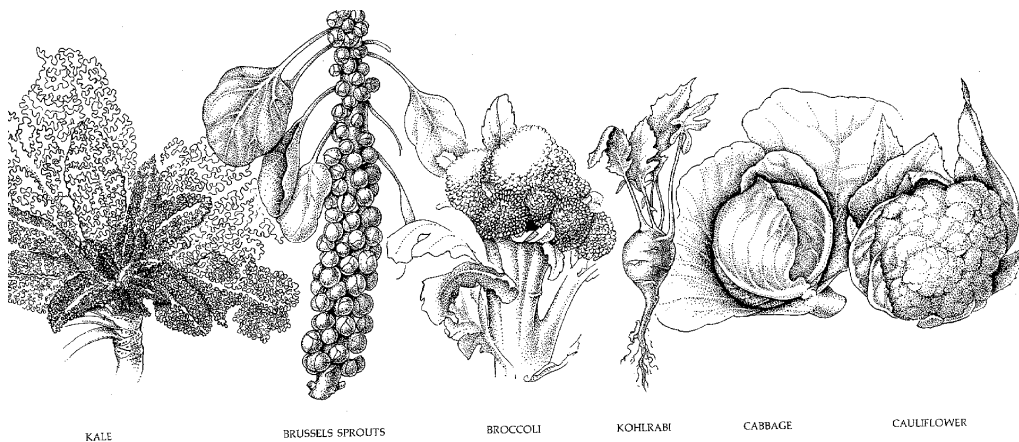
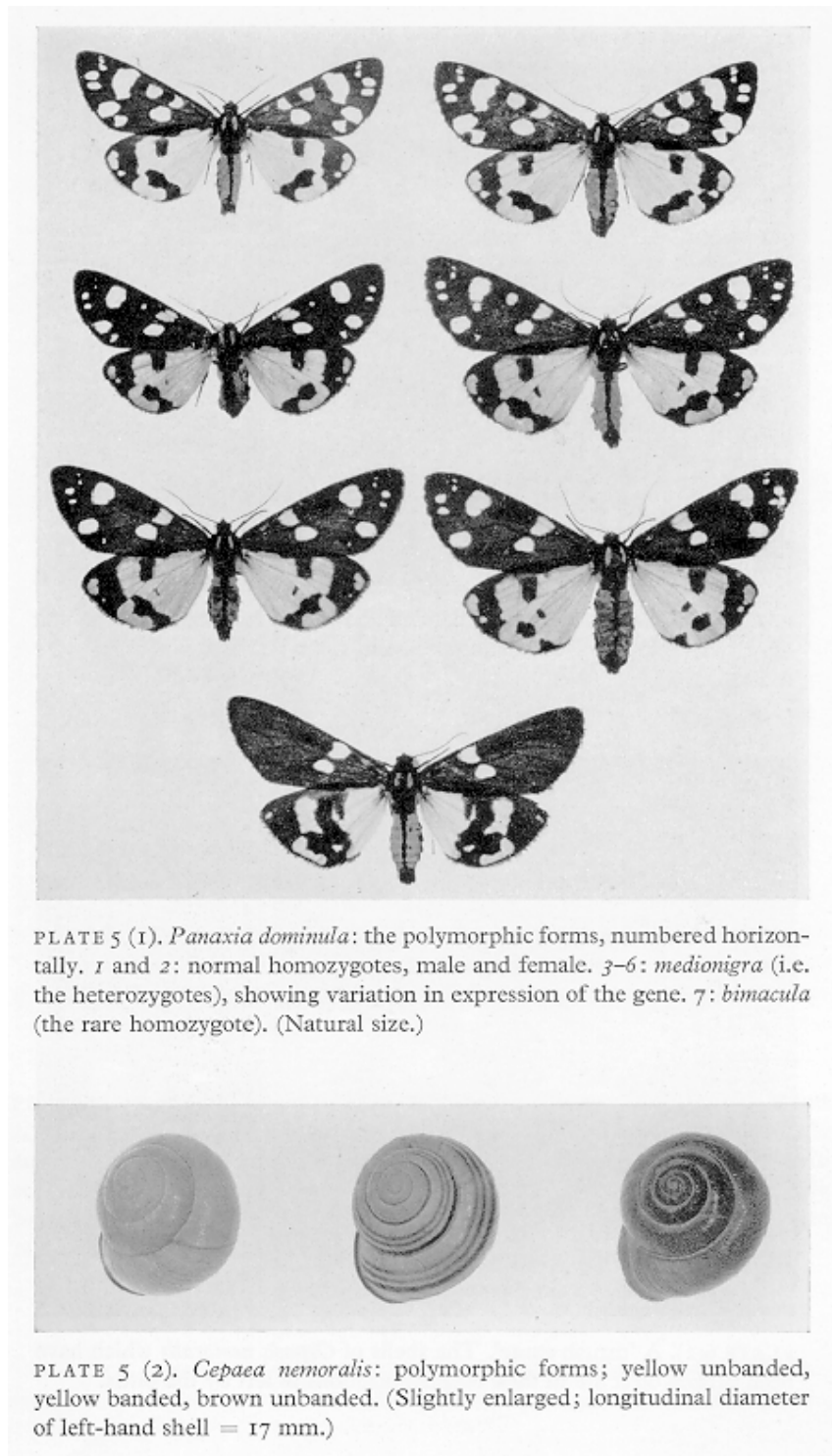


Figure 16. Varieties of *Brassica oleracea* (from Curtis 1983).





**Figure 17.** Polymorphism in the butterfly *Panaxia dominula* and the snail *Cepaea nemoralis* (from Ford 1965).

### Why is genetic diversity important?

The extent of genetic diversity in a population is a major determinant of its capacity for evolutionary change - it is effectively the species 'life insurance' against environmental change, accidental reductions in population size and attack from enemies such as disease and herbivores. Without such variability there is no raw material for natural selection to act (see Evolutionary Concepts lecture notes), and

environmental changes may result in extinction if individuals able to cope with such changes are absent from the population.

## B. Species Diversity (BHT pp. 615-620)

### Diversity indices

To compare different communities or different regions, a standardised measure of diversity is needed. The information contained in a list of species and their abundances can be summarised by a simple number: a **diversity index**. There are a number of such indices.

The most straightforward index is simply the total number of species in a community. This is usually called **species richness** and is often given the symbol **s** (or sometimes **n**).

Species richness has the disadvantage that the **abundances** of the species are not included. There are two commonly used indices which take species abundances into account.

Simpson diversity index:  $D = 1/\sum p_i^2$   
 Shannon diversity index:  $H = -\sum (p_i \times \ln p_i)$

Where  $p_i$  is the proportional abundance of each species. The effect of including abundances can be seen from an examination of Figure 18. Note that these indices incorporate both differences in *abundance* and *richness*. Sometimes we want to just consider the relative abundances of the species independent of the species richness, to see how *evenly* they are distributed. This can be done by expressing **D** or **H** as a percentage of the value that would be expected if all species were equally abundant. This is simply done by dividing **D** by the species richness (**s**), and dividing **H** by the logarithm of **s**. In particular, note that although communities 1 and 2 have the same number of species ( $s = 5$ ), community 1 is much more diverse (**D** = 5.0 cf. 1.06, **H** = 1.61 cf. 0.21). Also note that although communities 1 and 3 have different numbers of species, they have the same degree of evenness (**D/s** = 1, **H/ln(s)** = 1).

### Measures of diversity at different spatial scales

Different spatial scales are recognised when considering diversity. **Alpha-diversity** refers to the diversity *within* a single stand or community sample. **Beta-diversity** refers to the diversity *between* community samples.

Explaining beta-diversity generally poses few problems; we know that different species are often found in different environments. In contrast, explaining alpha-diversity can be extremely difficult. One of the most famous discussions of alpha-diversity is Hutchinsons (1961) 'paradox of the plankton', where he questioned how so many species of phytoplankton can coexist given that they all live in the same environment and they all **compete** for the same basic resources (e.g light & nutrients).

**Gamma-diversity** refers to diversity at the regional scale - i.e. the combination of *alpha*- and *beta*- diversity. Species diversity also varies temporally, as we will see in a later lecture (Environmental variability, succession and invasion).

COMMUNITY 1				
SPECIES (i)	<b>s = 5</b>			
	# INDIVIDUALS	PROPORTIONS ( $P_i$ )	$(P_i)^2$	$P_i \ln P_i$
A	30	0.20	0.04	-0.3219
B	30	0.20	0.04	-0.3219
C	30	0.20	0.04	-0.3219
D	30	0.20	0.04	-0.3219
E	30	0.20	0.04	-0.3219
	$\Sigma = 150$		$\Sigma = 0.2$	$\Sigma = -1.609$
			<b>D = 5.0</b> <b>D / s = 1</b>	<b>H = 1.609</b> <b>H / LN (s) = 1</b>

COMMUNITY 2				
SPECIES (i)	<b>s = 5</b>			
	# INDIVIDUALS	PROPORTIONS ( $P_i$ )	$(P_i)^2$	$P_i \ln P_i$
A	146	0.97	0.9474	-0.026
B	1	0.01	0.0001	-0.046
C	1	0.01	0.0001	-0.046
D	1	0.01	0.0001	-0.046
E	1	0.01	0.0001	-0.046
	$\Sigma = 150$		$\Sigma = 0.948$	$\Sigma = -0.211$
			<b>D = 1.055</b> <b>D / s = 0.211</b>	<b>H = 0.211</b> <b>H / LN (s) = 0.131</b>

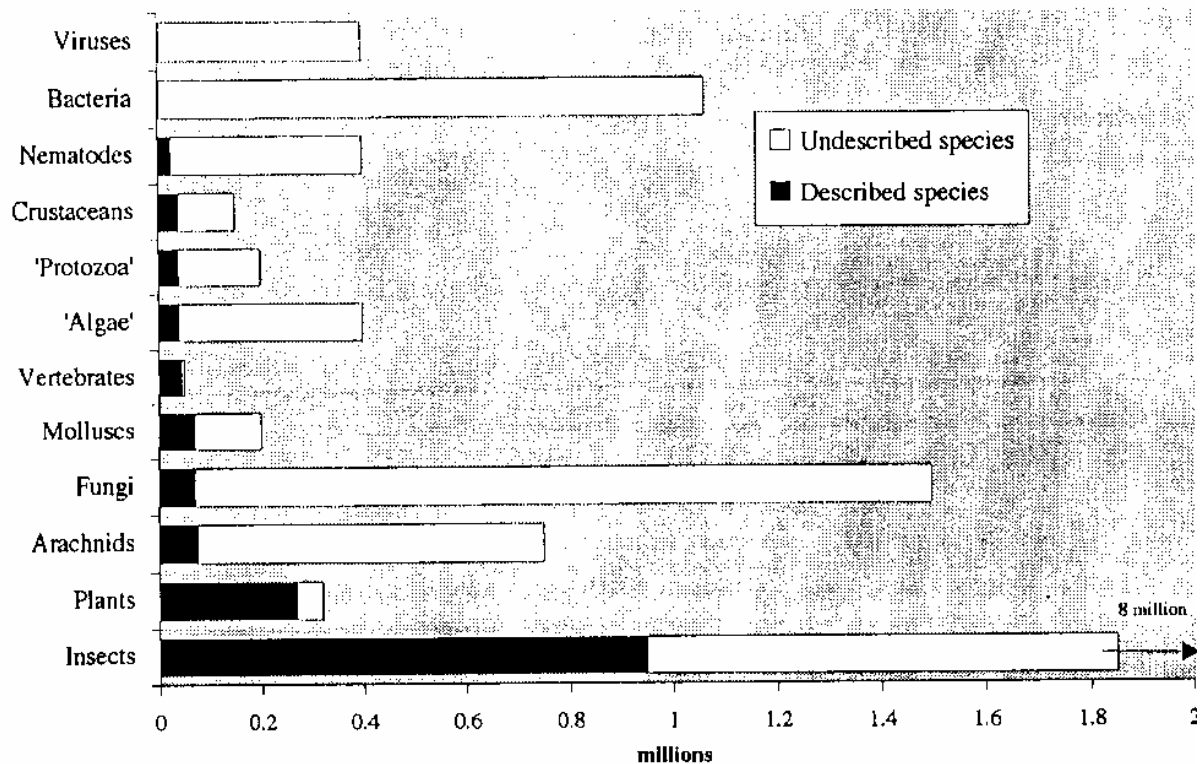
  

COMMUNITY 3				
SPECIES (i)	<b>s = 3</b>			
	# INDIVIDUALS	PROPORTIONS ( $P_i$ )	$(P_i)^2$	$P_i \ln P_i$
A	50	0.33	0.111	-0.366
B	50	0.33	0.111	-0.366
C	50	0.33	0.111	-0.366
	$\Sigma = 150$		$\Sigma = 0.333$	$\Sigma = -1.099$
			<b>D = 3</b> <b>D / s = 1</b>	<b>H = 1.099</b> <b>H / LN (s) = 1</b>

**Figure 18.** Three hypothetical communities illustrating the various measures of species diversity

### How many species?

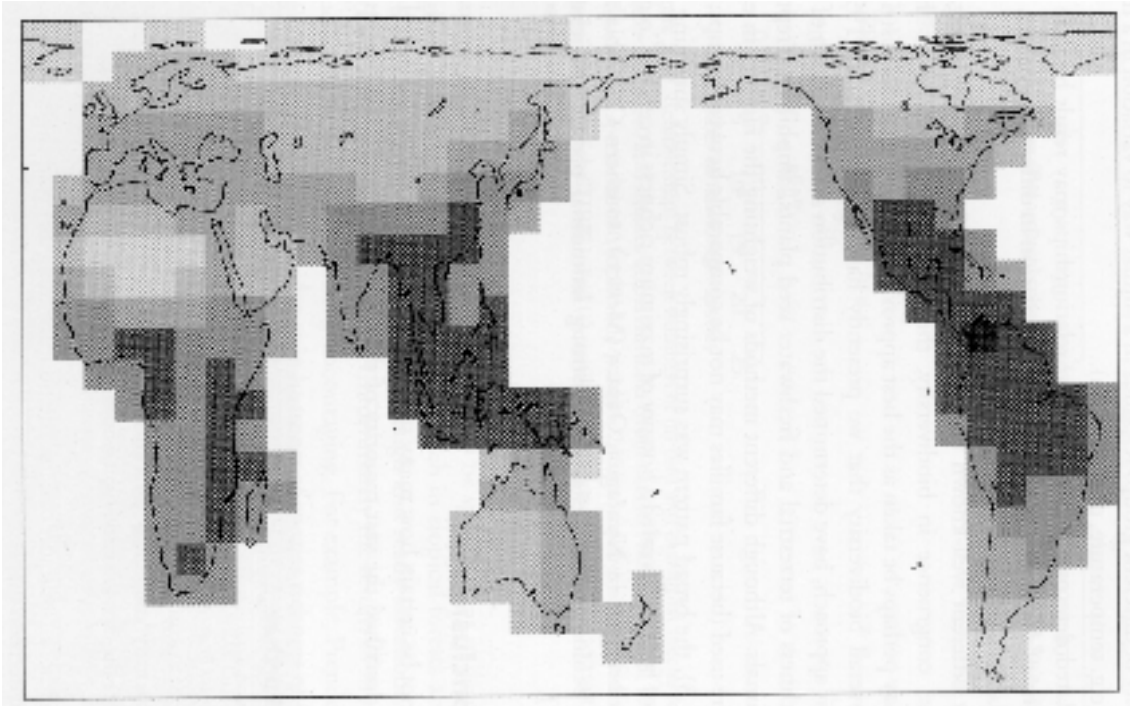
How many species are there in the world? This is a very difficult question to answer, because of the vast numbers of species that are still thought to be named (Figure 19), because of difficulties in collating such a vast amount of information, and because taxonomists are continually updating (and changing) species classifications. Current estimates put the figure at between 13-100 million, although many consider 30 million to be the current 'best guess'. As you can see, there is much uncertainty!



**Figure 19.** Numbers of species already described (black bars) and estimates of those yet to be described (white bars) for major groups of organisms. The estimates are conservative. Note that the bar for insects shoots off the page towards 8 million! (from Heyward 1995).

### ***Patterns of species diversity*** (BHT Chapter 24)

The diversity of communities can be related to a number of factors. There are **geographic** factors such as *altitude*, *latitude* and *depth* for aquatic environments which are correlated with species richness (Figure 20). Such *patterns* of species richness are easy to document, however explanations for *why* these patterns occur are much less convincing.



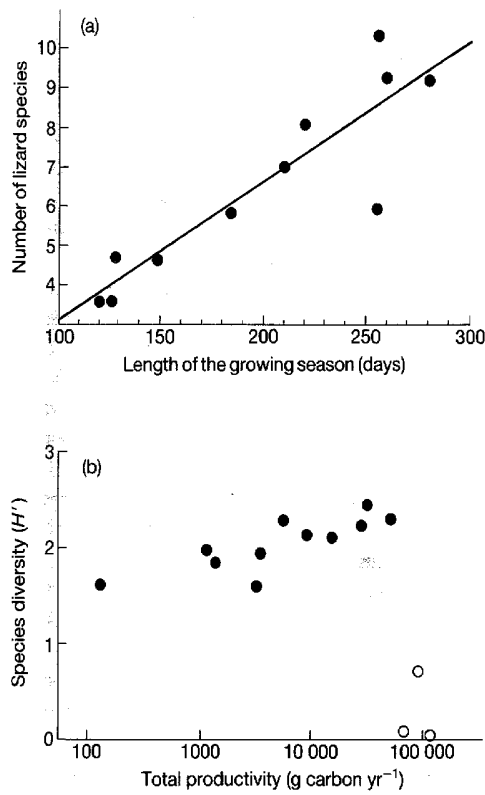
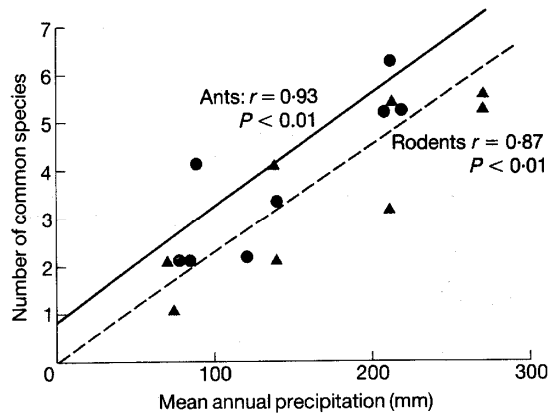
**Figure 20.** Map of worldwide family richness, combining terrestrial and freshwater plants, amphibians, reptiles and mammals. Darker squares mean higher richness. From Williams *et al.* (1997).

These geographic factors are not causal agents in their own right, there must be some other factors which change along the same gradient which have the actual effect on diversity. Examples of factors which can be correlated with the geographic factors and *may* be causal agents include *productivity of the environment* (the rate at which biomass is produced per unit area, Figure 21), in some cases the evolutionary age of the community, and *climatic variability*. Care needs to be taken when interpreting relationships such as these, as observing a correlation does not necessarily imply a causal connection.

A third group of factors are those that also vary geographically, but are uncorrelated with the geographic factors listed above. Such factors include the amount of *disturbance* a habitat experiences, the relative isolation of a habitat, and *heterogeneity* in physical and chemical factors (Figure 22).

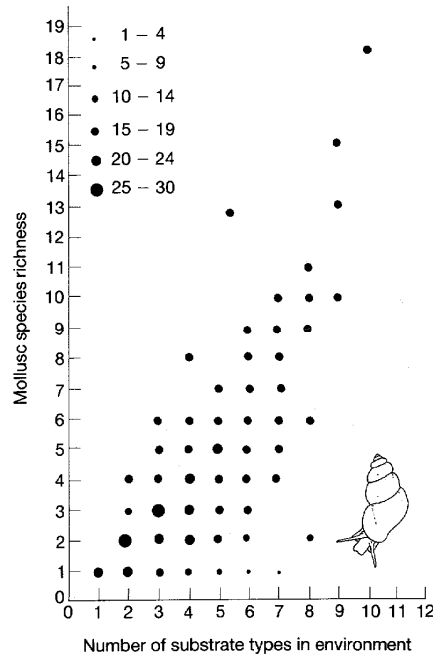
Finally, **biotic** factors also influence diversity. These include the amount of *predation* or *competition*, or the complexity of the *vertical structure* of the community (Figure 23).

**Figure 24.3.** Patterns of species richness of seed-eating rodents ( $\blacktriangle$ ) and ants ( $\bullet$ ) inhabiting sandy soils in a geographic gradient of precipitation and productivity. (After Brown & Davidson, 1977.)



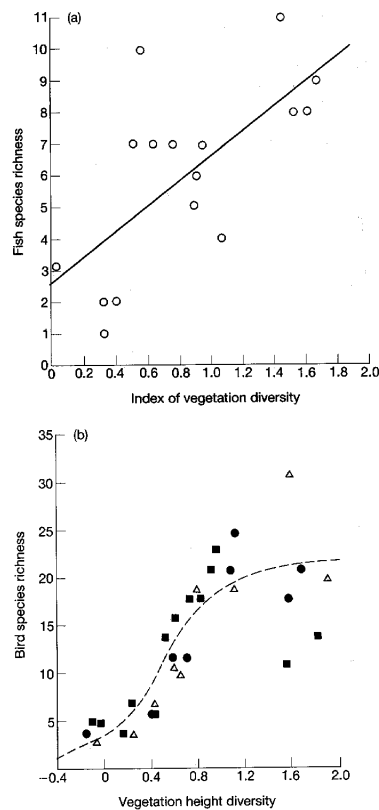
**Figure 24.4.** (a) Species richness of lizards at 11 sites in the south-western USA plotted against length of the growing season. (After Pianka, 1967.) (b) Relationship between species diversity ( $H'$ ) of chydorid cladocerans and primary productivity (expressed as g carbon year<sup>-1</sup> per entire lake) in 14 lakes in Indiana, USA. Open circles show three heavily polluted lakes. (After Whiteside & Harmsworth, 1967, re-analysed in Brown & Gibson, 1983.)

**Figure 21.** Relationships between diversity and environmental productivity (from BHT).



**Figure 24.8.** Relationship between species richness of freshwater molluscs and spatial heterogeneity, assessed in terms of the number of substrate types present. The size of the plotted points reflects the number of study sites which fall into that category. (After Harman, 1972.)

**Figure 22.** Relationship between diversity and environmental heterogeneity (from BHT).



**Figure 24.9.** Relationships between animal species richness and an index of structural diversity of the vegetation for: (a) freshwater fish in 18 Wisconsin lakes. (After Tonn & Magnuson, 1982.) (b) birds in Mediterranean-type habitats in California ( $\Delta$ ), central Chile ( $\bullet$ ) and south-west Africa ( $\blacksquare$ ). (After Cody, 1975.)

**Figure 23.** Relationship between diversity and biotic factors (from BHT).

In summary, there appear to be several generalisations that can be made about the species richness of communities e.g. that communities nearer the equator tend to contain more species (Figure 20); that communities of more productive environments tend to contain more species (Figure 21). However, because there are many exceptions to these generalisations, and many possible additional factors which can interact to influence diversity, in most cases patterns in species diversity are difficult to explain in a causal way.

### **Diversity and Stability** (BHT Chapter 23)

Ecologists have long been interested in community **stability** - the ability of a community to recover following a disturbance, and the related concepts of **resistance** - the ability of the community to persist without change (loss of species) in the face of disturbance, and **resilience** - the speed at which the community recovers following disturbance.

In the 1950's - 60's the 'conventional wisdom' in ecology was that *increased diversity within a community leads to increased stability*. However all of the arguments used to develop this 'conventional wisdom' have been shown to be flawed (Figure 24).

**Table 23.1.** Summary of Elton's arguments (1958) in support of the 'conventional wisdom' prior to 1970 that complexity begets stability in communities. Each observation is consistent with the complexity/stability hypothesis. However, each can be explained in terms of reasonable alternative hypotheses or questioned because of lack of a control.

Statement	Assessment
1. Mathematical models of interactions between two or a few species are inherently unstable	No longer held to be true after recent development of two-species models (see Chapter 10). In any case, there was no evidence at the time that multi-species models would be any more stable (none had been developed)
2. Simple laboratory communities of two or a few species are difficult to maintain without extinctions	True, but no evidence that multi-species laboratory communities would be more stable. The probable reason that laboratory cultures are difficult to set up and maintain is because it is virtually impossible to reproduce the natural environmental conditions
3. Islands, which usually possess few species, are more vulnerable to invading species than are species-rich continents	There have also been well-documented and remarkable examples of introduced species assuming pest proportions on continents (see Chapter 17). Nevertheless, statement 3 may be true. However, vulnerability to invasion has only a tenuous link with more conventional definitions of stability and resilience
4. Crop monocultures are peculiarly vulnerable to invasions and destruction by pests	Differences between natural and agricultural communities could derive from the long periods of coevolution to which natural associations may have been subject (Maynard Smith, 1974). Note also that arable crops are typically early successional species, naturally subject to rapid change. Natural monocultures such as salt-marsh and bracken seem to be stable (May, 1972)
5. Species-rich tropical communities are not noted for insect outbreaks when compared to their temperate and boreal counterparts	Such a pattern, if real, could be due to the destabilizing effects of climatic fluctuations in temperate and boreal communities (Maynard Smith, 1974). Wolda (1978) has produced evidence suggesting that insect abundances fluctuate just as markedly in the tropics

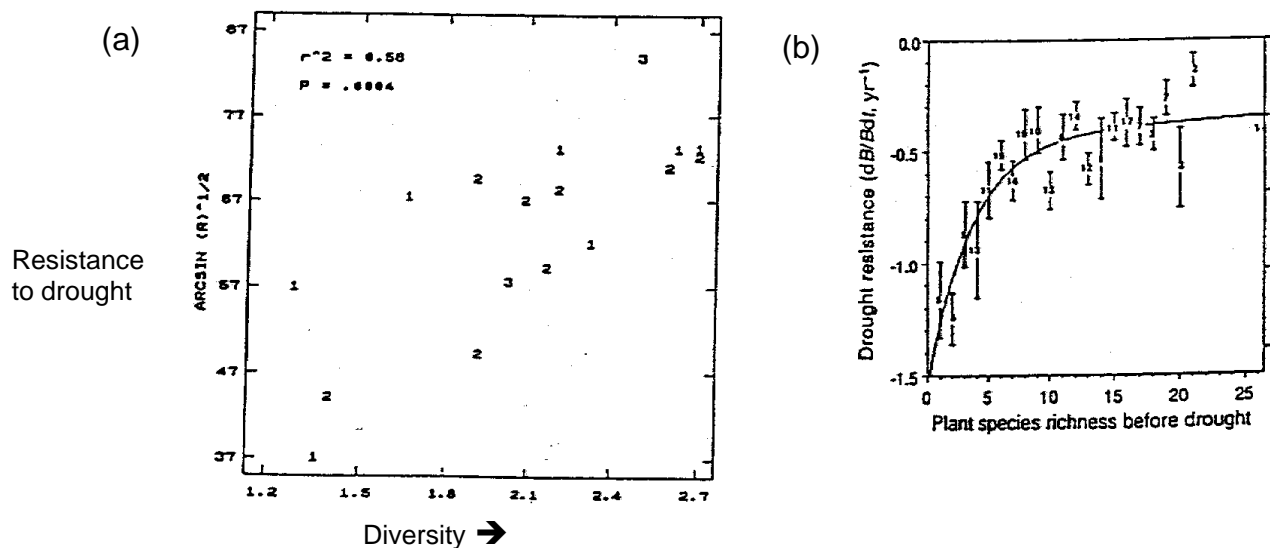
**Figure 24.** Elton's evidence for his claim that community stability should increase with complexity (from BHT).



More recently, mathematical analyses have (in general) predicted the opposite trend - that communities with *less* species tend to be more stable. However, depending on the assumptions used in these models the opposite prediction can also be generated.

Unfortunately, the evidence from natural communities is both sparse and inconclusive. Figure 25 shows the results from two recent studies, both of which imply that the species-rich plant communities studied were more resistant to disturbance than comparable species-poor communities, suggesting that preservation of biodiversity is essential for the maintenance of these communities.

To conclude, the relationship between complexity and stability cannot be conveniently generalised, as was originally hoped. It depends on the type of disturbance applied, and the particular characteristics of the community to which it is applied.



**Figure 25.** Two studies which suggest that community resistance to drought increases with increasing diversity in two different grasslands in the USA. (a) Frank and McNaughton (1991). (b) Tilman and Downing (1994).

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