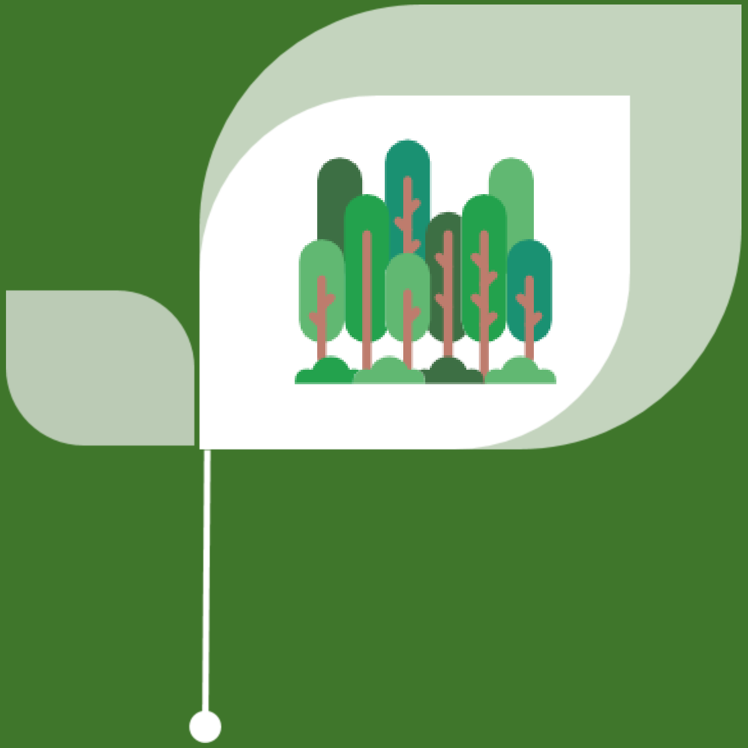


Chapter 7
Communities

Overview

Community ecology is a growing field that aims to understand the factors that influence biodiversity, community structure, and the distribution and abundance of species. These factors include interactions with the abiotic world and the diverse array of interactions that occur between species.

Many good conservation decisions rely on an intimate understanding of community ecology, including the abundance and distribution of food resources, habitat needs and predation pressure.

In this chapter we are going to look at how communities are structured, how they can be described, and what factors affect community structure and dynamics.

This branch of ecology is community ecology.

Contents

7.1

Community structure

Community Structure

A **community** is a group or association of populations of two or more different species occupying the same geographical area and in a particular time. A community's structure is the composition of a community, including the number of species in that community and their relative numbers. Community structure is influenced by many factors, including abiotic factors, species interactions, level of disturbance, and chance events.

Some species, such as **foundation species** and **keystone species**, play particularly important roles in determining their communities' structure.

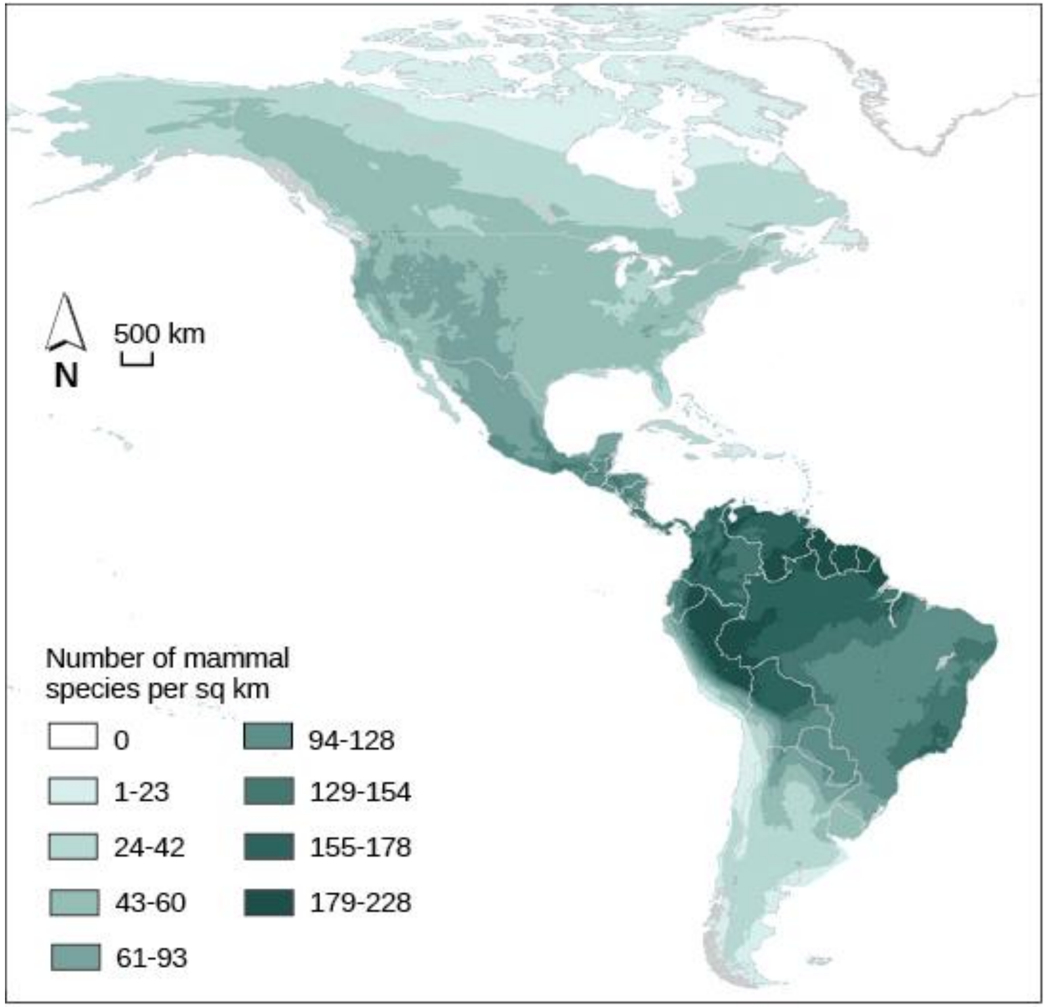
Two important measures ecologists use to describe the composition of a community are **species richness** and **species diversity**

Species Richness

Species richness is the number of different species in a particular community. If we found 30 species in one community, and 300 species in another, the second community would have much higher species richness than the first. Species richness is a measure of biodiversity often used in conservation planning.

Communities with the highest species richness tend to be found in areas near the equator. This is because of:

- lots of solar energy (supporting high primary productivity)
- warm temperatures
- large amounts of rainfall
- little seasonal change



Global species richness as calculated for mammal species. Image credit: "Community ecology: Figure 14," by OpenStax College, Biology, CC BY 4.0.

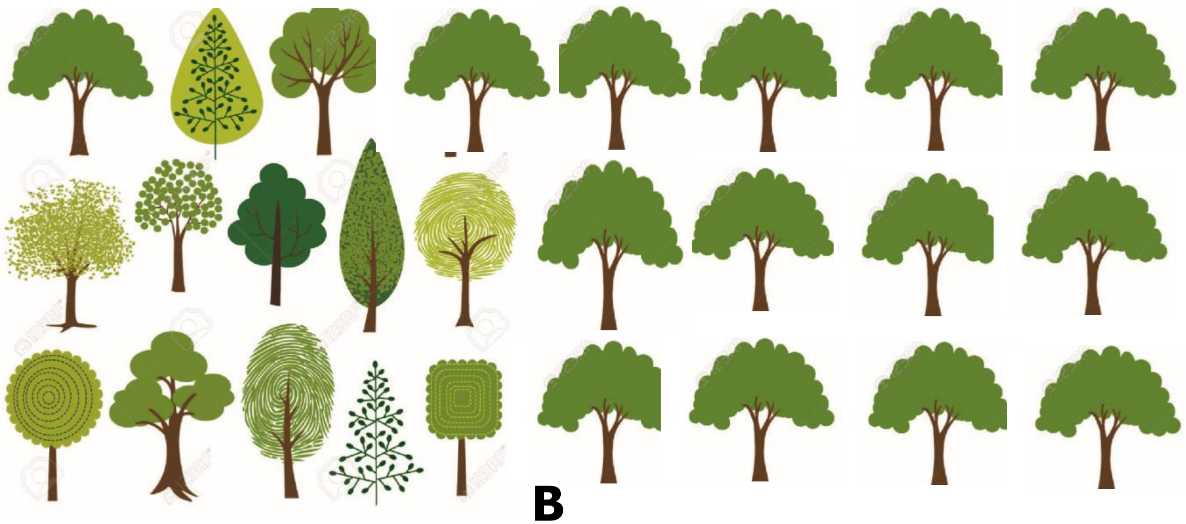
Species Diversity

Species diversity is a measure of community complexity. It is a function of both the number of different species in the community (species richness) and their relative abundances (species evenness).

A forest community with 20 different kinds of trees in even abundances would have greater species diversity than a forest community with the same number of species in very uneven abundances (for instance, with 90% percent of the trees belonging to a single species).

*Forest A has the same species **richnes**s as forest B, but a higher species **diversity***

A



B

Alpha, beta and gamma diversity

There are three terms for measuring biodiversity over different spatial scales: alpha, beta and gamma diversity.

Alpha diversity refers to the average diversity within one site (e.g. particular habitat, area or ecosystem), and is usually expressed by the number of species (i.e., **species richness**) and their proportion within that site. It is a local measure. Some commonly used indices to describe alpha diversity include Shannon' index (H), Simpson's index (D) and Renyi entropy.

Beta diversity is the dissimilarity in species diversity between two sites (or samples or ecosystems). A higher beta diversity means that two communities are more dissimilar. Some commonly used beta diversity indices include Bray-Curtis dissimilarity, percent similarity index (PSI) and Jaccards index (qualitative index).

Gamma diversity is a measure of the overall diversity for the different ecosystems within a region.

Alpha, beta and gamma diversity

To illustrate with a very simple example, if we are monitoring the effects of road construction on the diversity of native birds in a particular area, then we might want to compare species diversity within 3 different ecosystems, such as a woodland, a hedgerow and a large field.

The **alpha diversity** is obtained by recording the number of species in each ecosystem (here, 9, 7 and 3 species respectively)

Beta diversity is the difference in species diversity between ecosystems. It is the total number of species that are unique to each of the ecosystems being compared. In our example there are a total of 11 species found in woodland and hedgerow, but 5 are found in both, so the beta diversity is (11 – 5) = 6. The two ecosystems that are most dissimilar (woodland and field) share no species in common and have the highest beta diversity (12 – 0 = 12).

Gamma diversity is the total number of species recorded for the 3 ecosystems, which is 13 in our example.

Species	Woodland	Hedgerow	Field
A	X		
B	X		
C	X		
D	X		
E	X	X	
F	X	X	
G	X	X	
H	X	X	
I	X	X	
J		X	
K		X	X
L			X
M			X
Alpha diversity	9	7	3
Beta diversity	Woodland v Hedgerow (6)	Hedgerow v field (8)	Field v Woodland (12)
Gamma diversity	13		

What factors shape community structure?

The structure of a community is affected by many interacting factors, both abiotic and biotic. These include:

Climate patterns. Broad scale patterns of species richness are correlated with climate, and in particular, temperature. Basically, the warmer it is, the greater the diversity. High proportions of terrestrial and freshwater species occur in the tropics, whereas low species richness is found in deserts, at high latitudes (colder regions) and at high altitudes. The effect of temperature is seen most prominently at a community level, when many taxa are involved: the more taxa are looked at together, the greater the significance of temperature is in explaining biodiversity.

Geography. Geographical features of an area can affect community structure. For example, species richness on island communities is affected by the size of the island and its distance from the mainland, because that in turn affects immigration and extinction rates. This is explored in more detail in section 7.3 (island communities).

What factors shape community structure?

Habitat patchiness (heterogeneity). A patch of habitat that has a wider range of elevation, soil types, topography, etc provides more variation in a community's environment. This in turn may allow for higher species richness because there are more distinct habitats to be occupied. Habitat heterogeneity is also linked to habitat size, since a large area is more likely to contain more heterogeneity than a small one.

Disturbances. The frequency, intensity and even sequence of disturbances (e.g. storms, tsunamis, drought, wildfires and landslides) have the potential to greatly affect community structure (see section 7.4- Ecological Succession). At very high levels of disturbance (e.g. deforestation) many species are at risk of going extinct. However, disturbance also precipitates a progressive increase in species richness as species gradually recolonise the disturbed area during succession. When disturbances happen too frequently, communities may not be able to progress past the pioneer phase, but without disturbance, species richness will reach a climax according to the **competitive exclusion principle** (see section 7.2- Ecological Niches). This idea is behind the **intermediate disturbance hypothesis** (IDH) that suggests that communities with a medium (intermediate) level of disturbance may have greater species diversity than communities with very frequent or very rare disturbances. The IDH is not accepted by all ecologists, and evidence exists for and against it.

What factors shape community structure?

Biotic interactions. Inter-specific interactions between organisms (e.g. competition, predation and symbiosis) all have the potential to shape a community. The interactions between predators and their prey, the distribution and availability of limited food resources, the efficiency of seed dispersers and the abundance of parasites all affect which species can survive and thrive in a community. This is explored in more detail in sections 7.5 – 7.7. In addition, certain species in the community play an outsized role in ecosystem functioning, and their removal can precipitate trophic cascades. We will look at this in more detail in the following slides.

Chance events. A community's structure may also be shaped by chance events. For example, a particularly heavy storm blows a ripe seed far from its parent plant, into a patch of suitable habitat where the species was previously absent. The seed germinates, establishes and eventually becomes dominant. This chance event has shaped the community’s structure.

Foundation and keystone species

As mentioned in the previous slide, some species have unusually strong impacts on community structure. **Foundation species** play a unique, essential role in creating and defining a community- they are key to the resilience of the community. They are often called 'ecosystem engineers'. Foundation species can occupy any trophic level in the food web, but are often primary producers. Foundation species physically modify the environment and produce and maintain habitats that benefit other species.

The North American beaver harvests trees, removing undergrowth and maintaining an open forest understory. Their dams create habitat for aquatic organisms and a water source for terrestrial organisms

The exoskeletons of living and dead coral make up the reef structure, providing habitat and protection for many species from waves and ocean currents.

Brown algae (kelp) forests off the Californian coast. Kelp provides shelter and habitat for other species in the community.

Foundation and keystone species

Keystone species have a disproportionally large effect on community structure compared to their abundance. They play a crucial role in maintaining the structure of an ecological community, affecting many other species within that community. When keystone species are removed, both community structure and ecosystems dramatically change. Examples include pollinators, top predators and staple foods. Bees make one of the most important keystone species in the world, responsible for a third of plant pollination worldwide.

Ochre seastars (*Pisaster ochraceus*), a keystone predator

Honeybees (*Apis mellifera*) a keystone pollinator

Tiger sharks (*Galeocerdo cuvier*), an apex predator and keystone species

The story of the Yellowstone Wolf

The story of the Yellowstone wolf is a good example of how the removal of a single keystone species can have dramatic effects on community structure and ecosystem processes. Wolves are native to Yellowstone National Park, USA, but were exterminated in 1926. Their removal caused a trophic cascade. Without wolves to prey on elk, elk numbers increased, and also stopped moving around so much without fear of predation. Over-grazing led to a reduction in willow, aspen and cottonwood, vegetation that is important for soil and riverbank structure. Beavers, that also rely on willow, died off. Rivers changed course and the landscape suffered erosion.

In 1995 a reintroduction programme was started, and there are now about 100 wolves. Very rapidly, the ecosystem recovered and community structure was restored. Elk populations declined, grazing pressure on woody plants was reduced, stream structure and function improved. There was more habitat for birds, berries attracted bears back, beaver populations increased and the dams attracted other species such as otters, muskrat and reptiles.

Other species terms

Other terms are often used to describe the role of species in the community. These include:

Dominant species

The dominant species in a community is the species that is present in the greatest numbers—in other words, the species with the largest population in the community. For example, the ectomychorrizal legume *Dicymbe corymbosa* is the dominant tree in the Pakaraima mountaints of western Guyana, where it can represent up to 60% of all trees in the forest. In the northeastern United States, the dominant species of the eastern deciduous forest is the maple.

Macedonian pine (*Pinus peuce*) forests, Bulgaria

Other species terms

Flagship species.

Flagship species is a non-biological concept used in conservation. It is a species that has been chosen to act as a focus for fundraising efforts for biodiversity conservation in a particular area or context. The concept relies on the idea that by raising money to protect a flagship species, many other species will also be protected
Flagship species need to be popular and to act as a symbol, attracting the public's attention. Thet tend to be iconic, charismatic large mammals, such as giant pandas, mountain gorillas, Bengal tiger and black rhinoceros.

Giant Panda (*Ailuropoda melanoleuca*)- a flagship species.

Other species terms

Indicator species.

Also called bioindicators, these are species whose presence, absence or abundance reflects a specific environmental condition.
Indicator species can signal a change in the biological condition of a particular ecosystem, and therefore may be used as a proxy to diagnose the health of an ecosystem. They are useful tools in conservation.
Indicator species are often species that are particularly sensitive to environmental change. Examples include spotted owls as indicators of the health of old growth forest in the USA, and butterflies as indicators of the state of biodiversity in the UK.

Caddisflies are used as an indicator of water quality.

7.2

Ecological Niches

Ecological Niche

Each species fits into an ecological community in its own special way and has its own tolerable ranges for many environmental factors. **Ecological Niche** describes the relational position of a species (or population) in an ecosystem.

The concept of niche encompasses all of the interactions between a species and it's biotic and abiotic environment . A species' **niche** is basically its ecological role, which is defined by the set of conditions, resources, and interactions it needs.

For example, for a fish this might be salinity, pH, temperature, and the types of food it can eat.

Ecological Niche

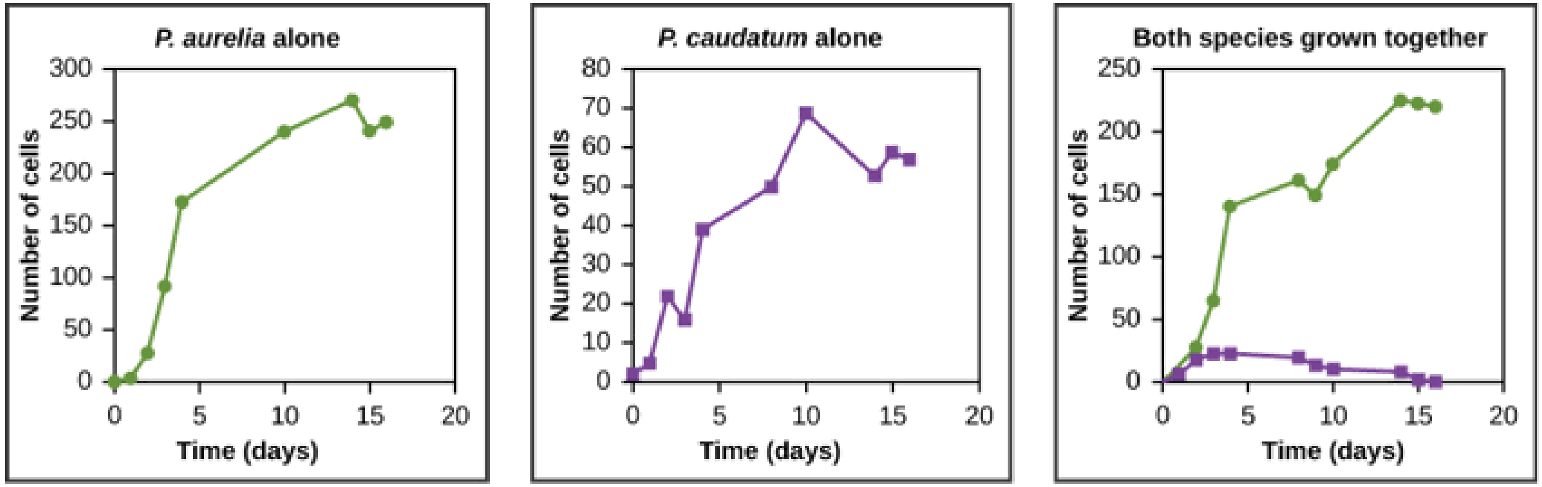
Ecological niche considers how a species responds to the abundance of its resources and enemies, for example, by growing when resources are abundant, or when predators, parasites and pathogens are scarce

It also concerns how a species affects those same factors, for example by reducing the abundance of resources through consumption and contributing to the population growth of enemies by falling prey to them.

The measurement of niches depends on first defining resource states (e.g. food and habitat resources). For example, measurements of niche **breadth** attempt to quantify the level of specialisation in plants and animals. This is measured by observing the distribution of individual organisms within a set of resource states. Niche **overlap** measures are a focus for ecologists interested in studying competition theory.

The Competitive Exclusion Principle

The **competitive exclusion principle** states that two species can't coexist if they occupy exactly the same **niche**, as they are competing for identical resources. It has been demonstrated experimentally with the micro-organism *Paramecium*. When the two species *Paramecium aurelia* and *Paramecium caudatum* are grown separately in test-tubes, each species thrives and the population size grows until resources become a limiting factor (see logistic growth in section 4.2). However, when grown together, only one species survives.

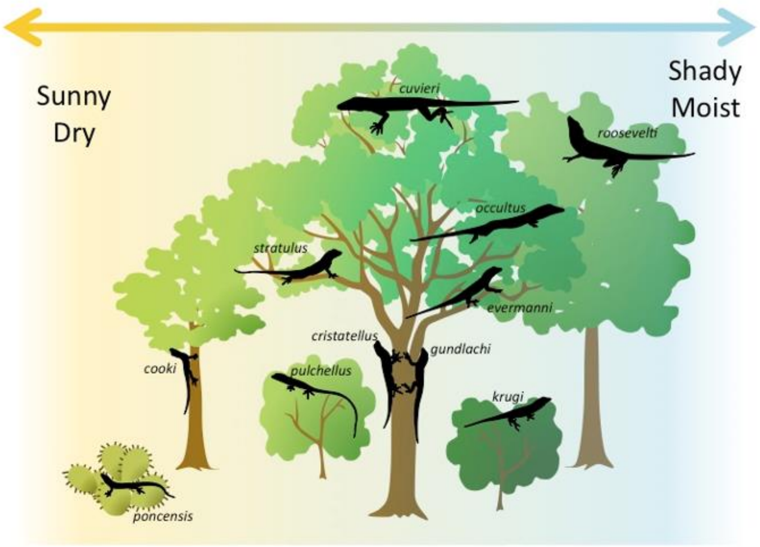


Although it has been shown experimentally, the Competetive Exclusion Principle, however, is rarely observed in natural ecosytems. The reasons for this are unclear, but it is observed that the greater the extent to which two species' niches overlap, the stronger the competition between them will tend to be.

Resource Partitioning

Two species whose niches overlap may evolve by natural selection to occupy a different part of the habitat- or to feed at different times of the day. Species end up with more distinct niches. This is known as **resource partitioning,** and it helps species to coexist because there is less direct competition between them.

An example comes from the island of Puerto Rico. Here, 11 species of Anole Lizard are found. Each species lives in its own preferred habitat, defined by type and height of vegetation, sunlight, moisture, other factors.



Resource Partitioning

Another example are Golden cats and leopards in the Congo Basin. They have 67% overlap in their dietary niche; however, Golden cats consume smaller and more arboreal prey than leopards and prefer to hunt diurnally. In contrast, Leopards consume larger prey and hunt nocturnally.

Resource Partitioning may take a very long time- Golden Cats and Leopards diverged around 11 million years ago!

7.3

Island communities

Island endemism

There are more than 100,000 islands on earth, accounting for nearly 1/6th planet's land surface area. Because of their isolation and high availability of empty niches, islands have led to increased speciation (also see Chapter 4.3). This means that the ecology of islands is often very different to mainland communities.

30% of the world's biodiversity hotspots are found in islands, and oceanic islands are known for their high levels of endemism: endemic richness is 9.5 times higher on islands than the mainland.

For example, the island of Socotra in the Arabian sea is described as the 'most alien looking place on earth'. Covering 3,800km^2, it contains 700 endemic species, including 37% of its plant species. New Zealand, isolated for 80 million years, counts 82% of its plant species, >90% freshwater fish and insects and 100% bat, amphibians and reptiles as endemic.

Proboscis monkey, endemic to the island of Borneo

North Island kōkako, endemic to New Zealand

The Socatran fig tree, *Dorstenia gigas*

Kier et al., 2009. A global assessment of endemism and species richness across island and mainland regions. PNAS, 106: 9322-9327

Island biogeography

The history of island formation is key to the biological characteristics of a given insular community.

Newly formed islands, such as those created by a volcanic eruption, can only gain species by **colonisation** and then the biota grows through colonization or **speciation.**

In contrast, islands created by fragmentation (e.g. climatic changes, water level rises) are formed with full biota, and will lose species and gain species. Given a long period of time on fragment islands, distinct species may form through speciation.

Island biogeography

Wilson's theory of "island biogeography" proposes that the number of species on any island reflects a balance between the rate at which new species colonize it and the rate at which populations of established species become extinct.

Those that are further away from a mainland tend to have smaller numbers of species than those that are closer to the mainland. This reflects that the chance event of a species arriving from the mainland is less likely when the island is more distant.

The rate of extinction once a species manages to colonize an island is affected by island size; this is the **species-area relationship**.

Larger islands contain larger habitat areas and opportunities for more different varieties of habitat. Larger habitat size reduces the probability of extinction due chance events.

Habitat heterogeneity increases the number of species that will be successful after immigration. Over time, the countervailing forces of extinction and immigration result in an equilibrium level of species richness.

Ecological island

Not all islands are those surrounded by water. An insular habitat can be defined as any discrete habitat that is isolated from other similar habitats by a surrounding inhospitable matrix. Both the habitat and the isolating matrix are relative to the organism in question. While water bodies present a stark barrier for terrestrial organisms; in the same way, intervening land around water bodies creates a barrier for aquatic organisms.

Any patch of habitat that is surrounded by areas of terrain that is unsuitable for an organism or group of organisms, whether that be vegetation, soil, altitude, shelter, temperature, salinity, pH etc, are insular habitats. Ecological islands may therefore include whale falls in the ocean, marshy clearings within a forest and forest fragments in a matrix of savannah.

The inselbergs of Gabon are ecological islands with completely different plant communities to lowland savannahs

7.4

Ecological Succession

Ecological Succession

Natural systems are not static, they are dynamic and constantly changing.

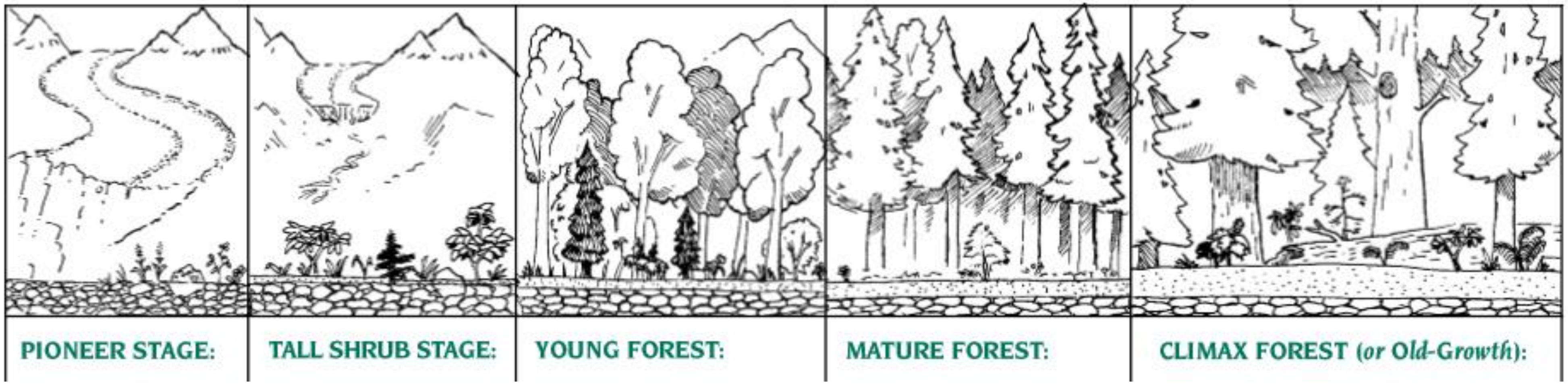
Ecological succession is the process by which the species structure of an ecological community changes and develops over time. It is usually thought of as a gradual process resulting in increased biological diversity and complexity, following an initial disturbance. The timescale can be short, i.e. decades, or it can span thousands – or even millions - of years.

There are two main types of succession: **primary** and **secondary succession.**

Primary Succession

Primary succession occurs in lifeless areas where some kind of perturbation has removed all living organisms and the soil layer. It follows major disturbances such as glacier retreats, volcanic eruptions, earthquakes, landslides or a newly created sand dunes. It can even occur on man-made structures such as ship-wrecks or oil rigs. What is required is a bare matrix- such as rock or lava- to provide the basis for which nutrients, organic matter and soil can accumulate, paving the way for different species to gradually colonize and for increasingly complex communities to develop.

Primary Succession



Following a disturbance, e.g. after the retreat of a glacier, a new environment without plant life is created. Weathering and other natural forces break down the substrate and rock.

Hardy pioneer species with few soil requirements (e.g. lichens, mosses, some grasses, orchids, algaei) are the first to establish. They 'normalise' the habitat with abiotic factors (water, wind). They help to further break down the mineral-rich lava/rock into soil by a process called **pedogenesis**.

This allows other species- vascular plants- e.g. grasses, shrubs- that can live in thin soils- to establish. Organic matter accumulates, enriching and adding to the soil layer.
The process repeats multiple times. At each stage, new species move into an area, often due to changes to the environment made by the preceding species.

Large trees and more shade-tolerant species eventually replace the community of sun-loving grasses and shrubs.
These young forests tend to be fast-growing but species poor, accumulating biomass rapidly with a large number of small-stemmed trees. Many tree species will be wind-dispersed.

As the forest matures, plant species diversity increases as insect and bird pollinator populations establish, and the proportion of animal-dispersed species may also increase. Stem density tends to decrease as trees get bigger.

This depends on the community but can take hundreds of years. The devlopment of old growth coastal rainforest following a glacier retreat in Alaska, for example, can take up to 600 years.

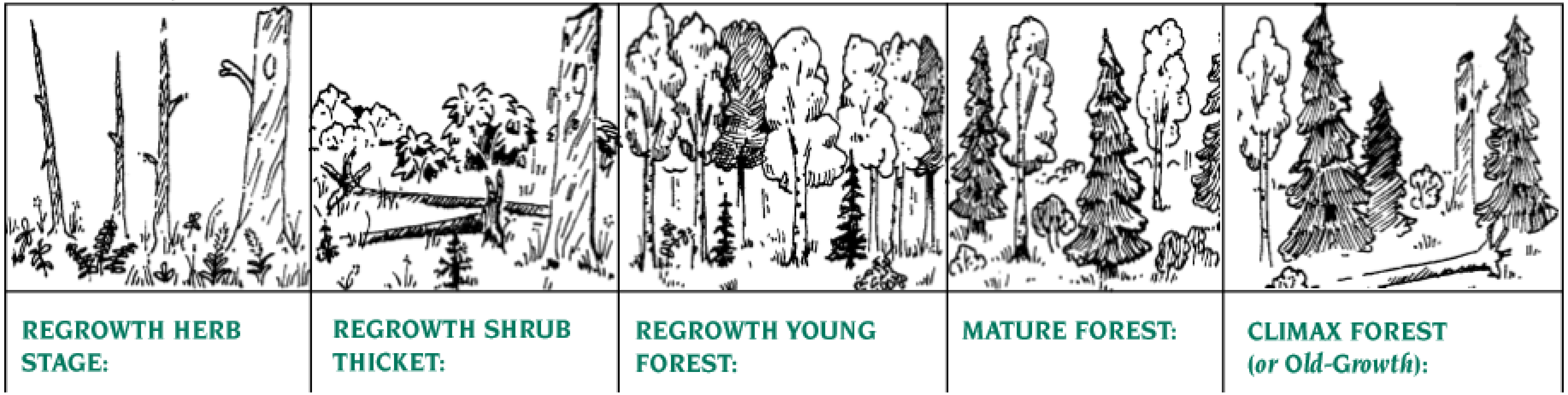
Source: http://www.adfg.alaska.gov/static/education/educators/curricula/alaskawildlifecurriculum/pdfs/alaskas_forests_wildlife_curriculum_insights.pdf

Secondary Succession

Secondary succession occurs after a disturbance has affected a community but not eliminated the soil matrix or all living organisms. Secondary succession follows disturbances such as fire, flooding, drought or even tsunamis. As there are usually nutrients, a soil matrix and some living organisms present, the ecosystem can be recolonised much faster than with primary succession.

Boreal pine forest disturbed by fire (left) and two years later (right).

Secondary Succession



Disturbances such as a wildfires will destroy most vegetation as well as all animals unable to flee the area.
Their nutrients are returned to the ground as ash or decaying organic matter.

After the disturbance, annual plants are the first pioneer species to establish. They are followed by grasses and perennial plant.

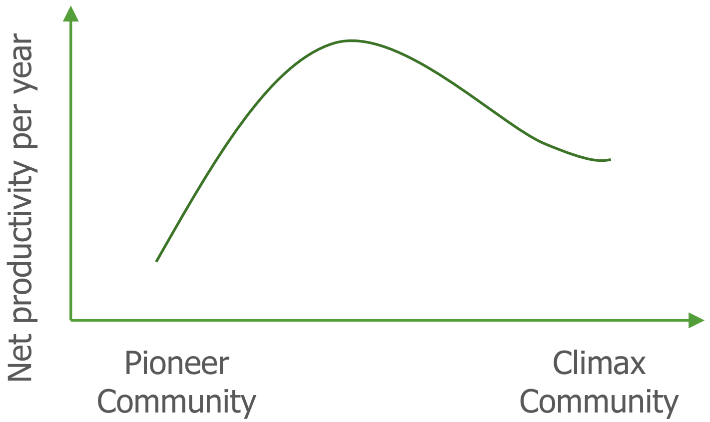
Over many years, shrubs and then trees can establish- eventually to pre-fire composition

Succession, productivity and diversity

Succession has an effect on **Productivity**, which is the rate of biomass production (see Section 8.4). During succession productivity tends to increase through the pioneer and early wooded stages and then decreases as the climax community reaches maturity. This increase in productivity is linked to growth and biomass.

Early successional stages are usually marked by rapid growth and biomass accumulation – grasses, herbs and small shrubs. As the community develops towards woodland biomass increases and so does productivity.

Studies have shown that standing crop (biomass) in succession to deciduous woodland reaches a peak within the first few centuries. Following the establishment of mature climax forest biomass tends to fall. This is because as trees age growths slows and an extended canopy crowds out ground cover. Also older trees become less photosynthetically efficient and more productivity is allocated to non- photosynthetic structural biomass such as root systems.



Succession, productivity and diversity

The early stages of succession also tend to be marked by few species within the community. As succession progresses the number of species also increases. Few pioneer species are completely replaced, instead they tend to get rarer within the community. Species diversity increases until a balance is reached between possibilities for new species to establish, existing species to expand their range and local extinction.

An example of this is found following the eruption of the mount St Helens volcano in 1980. Species diversity increased rapidly for the first 10 years after the eruption, but after 20 years very little additional increase in the diversity occurred.

Source: Carey et al., 2006. Ecography 29:866-872

7.5

Predator-Prey relationships

Predator-prey interactions

Predator-prey relations refer to the interactions between two species where one species is the hunted food source for the other. Such relationships are found in all ecoystems and exist among even the simplest life forms on Earth. Predation can have large effects on prey populations and therefore on community structure. Predators can increase diversity in communities by preying on competitive dominant species or by reducing consumer pressure on foundation species.

Predators and prey have evolved together, and so they can influence one another's evolution. Traits that improve a predator's ability to find and capture prey will be selected for in the predator, while traits that enhance the prey's ability to avoid being eaten will be selected for in the prey. The interaction of selective pressures will influence the dynamics of both the predator and prey populations. These kinds of interactions – and predicting their eventual outcomes- is important to ecologists trying to understand how communities are structured and maintained– and also to design optimal species protection plans.

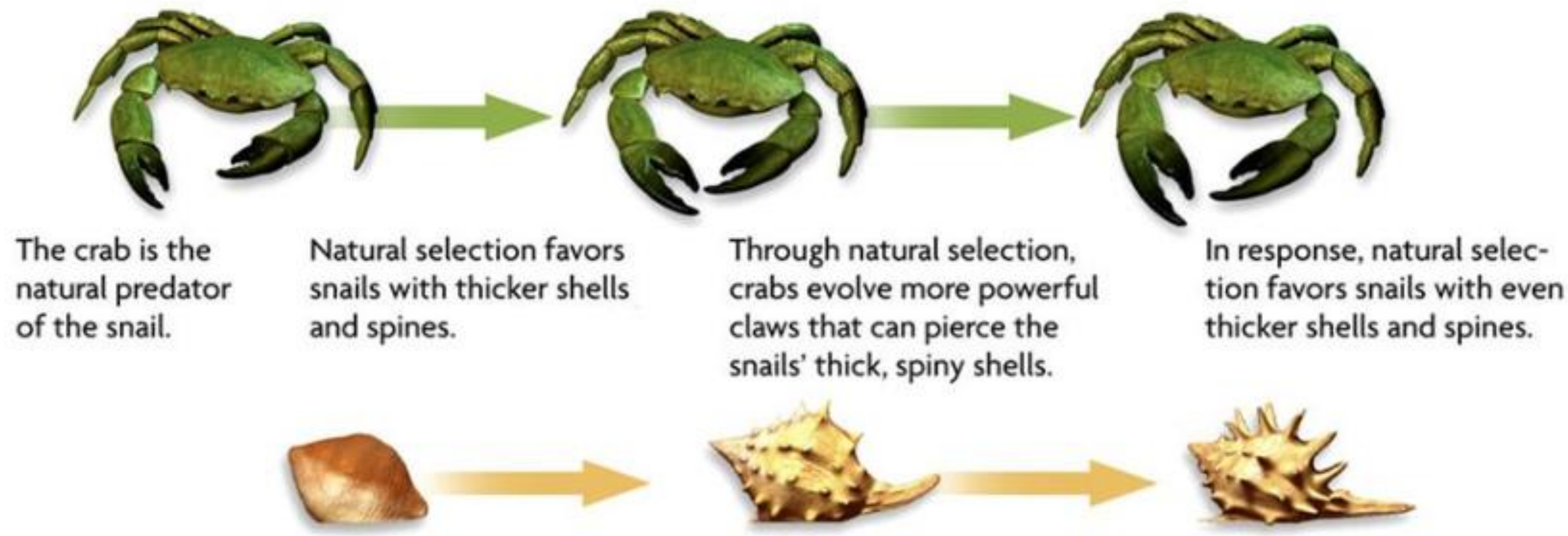
Predator-prey adaptations

Predation requires one individual, the predator, to kill and eat another individual, the prey. Usually predators and prey are both animals, but there are also predatory (carnivorous) plants. Herbivory is also a special form of predation (we will look at that a little later). Usually predation is an **inter-specific** interaction. Intra-specific predation is rarer, and is otherwise known as **cannibalism.**

Typical predatory adaptations include sharp teeth and claws; stingers or poison; quick and agile bodies; camouflage coloration ; excellent olfactory, visual or aural acuity. Prey species have evolved a variety of defenses including: camouflage, burrowing, spikes, evasive manoeuvers, alarm calls, nocturnal foraging and poison

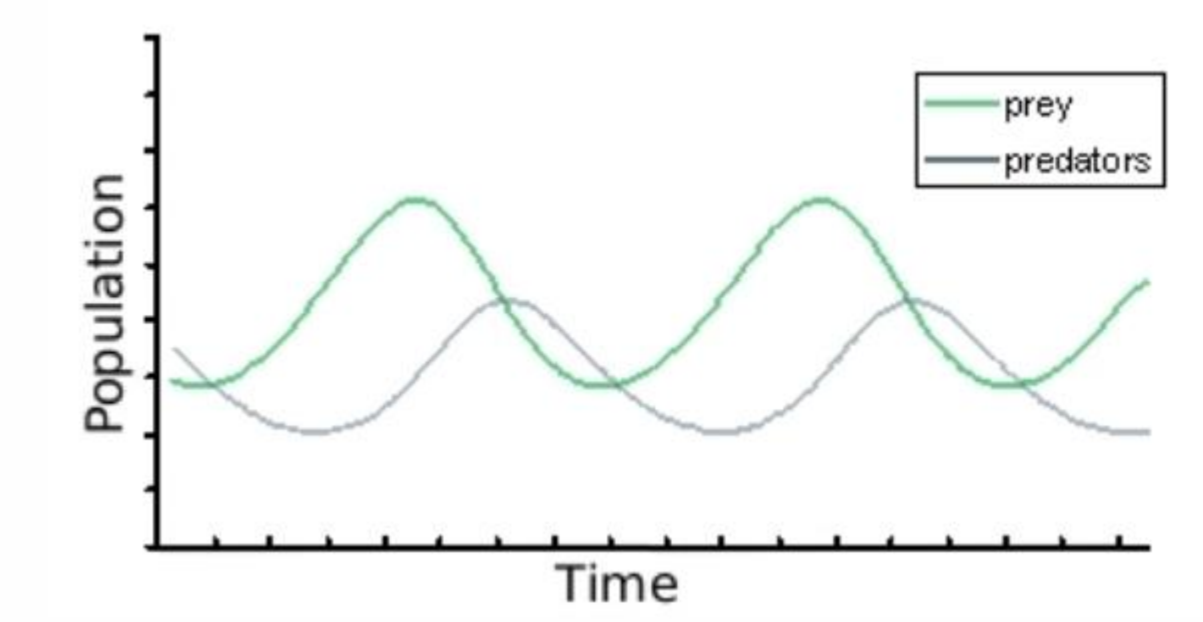
Evolutionary arms race

Predator-prey co-evolution can lead to an ‘evoluationary arms race’, where natural selection favours the evolution of adaptations and counter-adaptations between competing sets of genes. This is probably common in many plant-herbivore systems.



Predator-Prey Cycles

The interactions between predators and their prey have a direct effect on the population sizes of the two species in question. When there are few predators and many prey, conditions are favourable for predator populations to increase. As predators become more abundant, they will consume more prey, causing a decline in the prey populations. At some point prey will become too scarce to sustain the augmented predator population, predators will start to starve and their numbers will decline. As they do so, prey populations will be able to recover. A cyclic relationship forms, known as the predator-prey cycle, where the predator cycle lags behind the prey cycle.



Lotka-Volterra equations

These relationships are modelled by **Lotka-Volterra** equations, which are a pair of nonlinear differential equations that are often used in ecology to describe species interactions in biological systems.

In its simplest form the model makes several assumptions :

1) the prey population will grow exponentially when the predator is absent;
2) the predator population will starve in the absence of the prey population (rather than switching to another type of prey);
3) predators can consume infinite quantities of prey; and
4) there is no environmental complexity (in other words, both populations are moving randomly through a homogeneous environment).

Lotka-Volterra equations

The equations describe the predator-prey relationship as follows:

$$\frac{dx}{dt} = x(\alpha - \beta y)$$

Prey equation

$$\frac{dy}{dt} = -y(\gamma - \delta x)$$

Predator equation

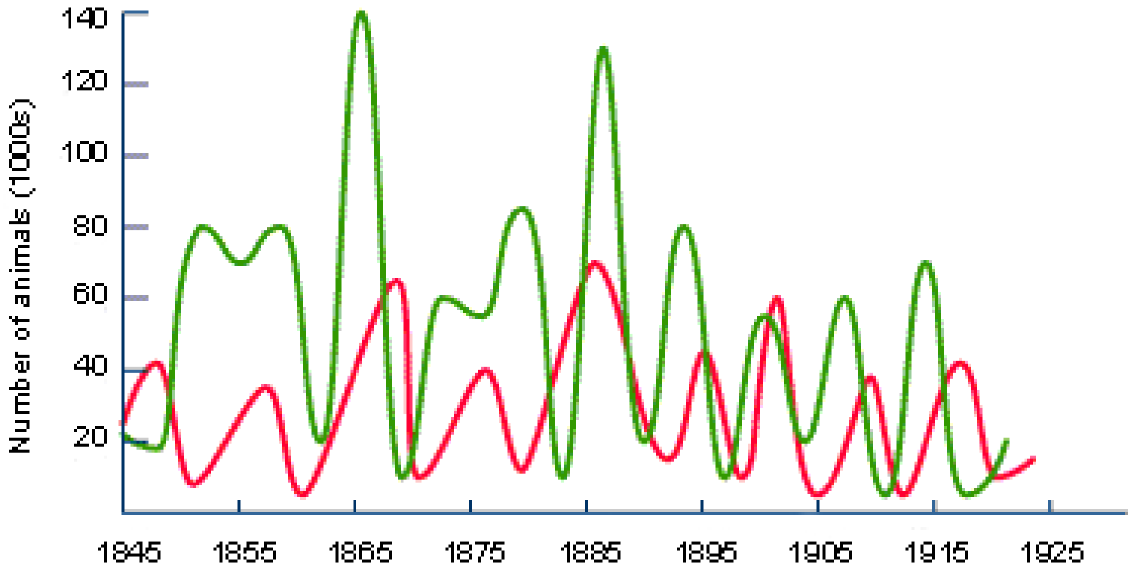
The **prey equation** tells us that the rate of change of the prey's population is given by its own growth rate minus the rate at which it is preyed upon.

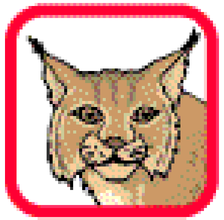
The **predator equation** says that the rate of change of the predator's population depends upon the rate at which it consumes prey, minus its intrinsic death rate.

In the equations, x and y are the numbers of prey and predators respectively; t is time; dx/dt and dy/dt represent instantaneous growth rates of the two populations and alpha, beta, gamma and delta are constants describing the interaction of the two species. These constants are based on empirical observations and depend on the particular species being studied.

Predator-Prey Cycles

A famous example of this relationship is seen in the snowshoe hare and canadian lynx.



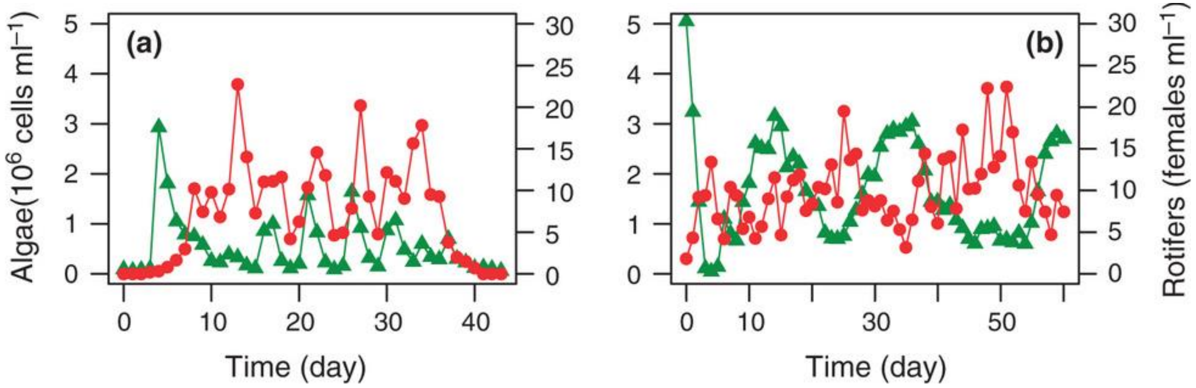


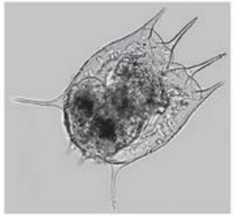
Predator-Prey Cycles

It has also been shown experimentally how evolution can affect ecological dynamics in predator-prey systems.

Rotifers are microscopic invertebrates that prey on algae. When an algal population of *Chlorella vulgaris* descended from a single cell is cultured with the predator rotifer *Brachionus calyciflorus,* the classic predator-prey cycle is observed (graph a). However, when the experiment is repeated with a prey algae population grown from multiple sources, the cycles are longer and the oscillations in predator and prey abundance are almost exactly out of phase.

What has happened is that in the first example, the single-cell algal population lacks genetic variability and less opportunity for beneficial algal genotypes to arise by mutation. In the second example the initial algal population has higher genetic variability, meaning more resilient prey are able to evolve to compete with the predators.





Source: Yoshida et al., (2003). Nature, 424: 303-306, cited in Chave (2013). Ecology Letters, 16: 4-16

Herbivory

Herbivory is a special kind of predation, when a **herbivore** feeds on all or part of a photosynthetic organism (plant or algae). The difference is that herbivory does not always lead to the death of the individual, unlike predation. Herbivory is often the foundation of food webs since it involves the consumption of primary producers. Herbivores are classified based on the part of the plant consumed. Grazers (e.g. sea urchins, rhinos, rabbits, antelopes) eat grasses, algea and low shrubs. Browsers (e.g. elephants, giraffes, red pandas) eat leaves, soft shoots, or fruits of high-growing, generally woody plants such as shrubs. Granivores (e.g. chaffinches, squirrels) eat and predate on seeds. Frugivores eat fruits – frugivores play an important ecological role in many ecosystems as they do not destroy the seeds they eat (unlike granivores) - instead they act as seed dispersers. This relationship is a kind of mutualism.

Herbivory

Plants have evolved adaptations to herbivory. **Tolerance** is the ability to minimize negative effects resulting from herbivory. **Resistance** means that plants use defenses to avoid being consumed.

Defenses may be **physical** (e.g., thorns, tough material, sticky substances) or **chemical** (e.g, irritating toxins on piercing structures, bad-tasting chemicals in leaves)

7.6

Competition

Competition

In ecology, competition refers to the negative interaction of individuals that vie for a common resource that is in limited supply. It occurs through the direct or indirect interactions of organisms that leads to a change in fitness when the organisms share the same resource. It can be inter-specific (between individuals of different species), or intra-specific (between individuals of the same species).

Three major forms of competition are recognised: **interference competition**, **exploitation competition** and **apparent competition.** Inteference competition occurs directly between individuals, whereas the other two are forms of indirect competition.

Interference Competition

Interference competition occurs when an individual directly alters the resource-attaining behaviour of other individuals. It is often expressed as “fighting for a scarce resource”.

An example of intraspecific interference competition is male-male competition for females in red deer.

An example of interspecific interference competition are desert ants *Novomessor cockerelli*, which plug the entrance holes of the red harvester ant (*Pogonomyrmex barbatus*) with small stones to delay the emergence of the other workers competing for the same resources (interspecific)

Exploitation competition

Exploitation competition occurs when organisms interact indirectly by consuming scarce resources. One organism has a superior ability to gather a resource than another, and the use of that resource by one individual will decrease the amount available for other individuals.

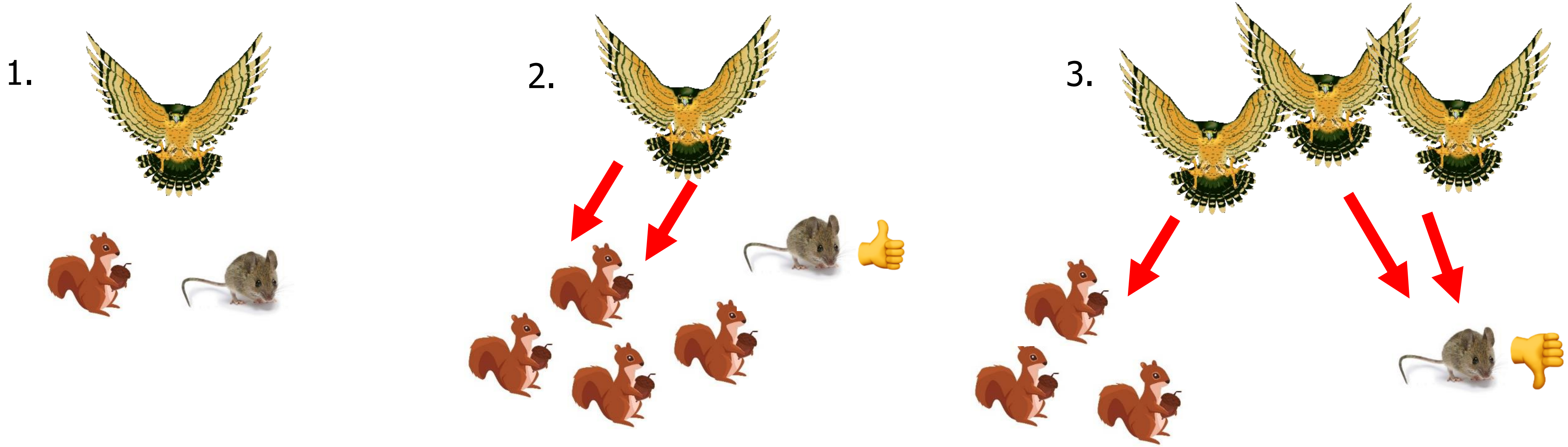
Examples of interspecific exploitation competition include plants that plants consume nitrogen by absorbing it into their roots, making nitrogen unavailable to nearby plants.

An example of intraspecific exploitation competition are nesting white storks- those living in proximity to many neighbours have to compete more for food – they have a lower foraging efficiency than those living with no/few neighbours and end up raising fewer chicks.

Apparent competition

Apparent competition occurs when two species affect each other indirectly by being prey for the same predator. When one prey species increases in number, this attracts more predators to the area. More predators in the area affect the second prey species too.

As an example, we can consider a predator (hawk) that preys both on squirrels and mice (1). If the squirrel population increases, then the mouse population may be positively affected since more squirrels will be available as prey for the hawks (2). However, an increased squirrel population may eventually lead to a higher population of hawks requiring more prey, thus, negatively affecting the mice through increased predation pressure as the squirrel population declines (3).



Outcomes of competition

The outcomes of competition between two species can be predicted using equations. One of the most well known is the Lotka-Volterra model. This model relates the population density and carrying capacity of two species to each other and includes their overall effect on each other.

The four outcomes of this model are:

1) species A competitively excludes species B;

2) species B competitively excludes species A;

3) either species wins based on population densities;

4) coexistence occurs.

Species can survive together if intra-specific is stronger than inter-specific competition. This means that each species will inhibit their own population growth before they inhibit that of the competitor, leading to coexistence.

7.7

Symbiosis

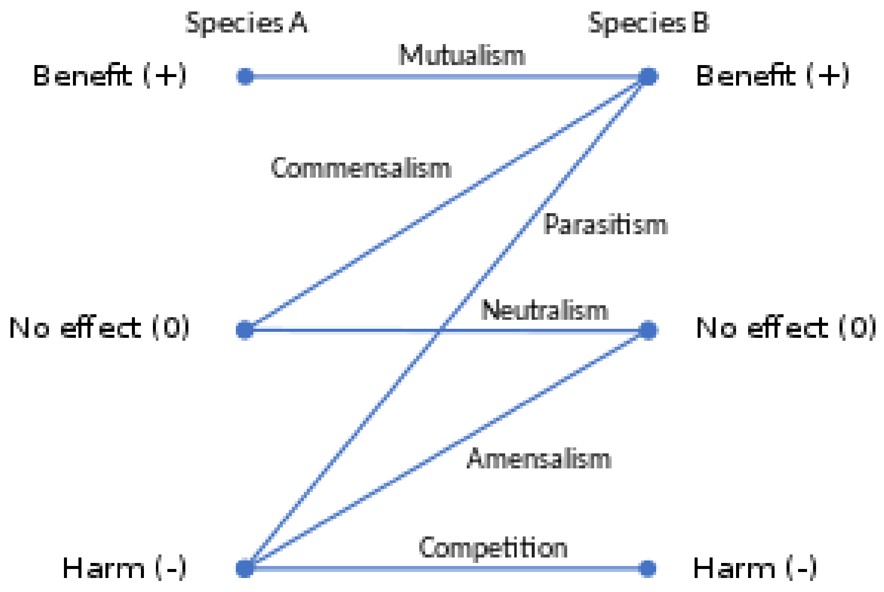
Symbiosis

Within communities, different types of interspecific interactions have different effects on the participating species, which may be positive, negative or neutral.

Symbiosis occurs when two or more species live **purposefully** in direct contact with each other. Although the term “symbiosis” is often used to mean mutually beneficial relationships, in ecology it is not always positive for both parties. Symbiosis can be obligatory, which means that one or both of the symbionts entirely depend on each other for survival, or facultative (optional) when they can generally live independently.

Symbiosis

Definitions of symbiosis have evolved over time. Some definitions include all interspecific interactions, from mutual benefit through to mutual harm and including competition (see diagram below). In this section, we will consider symbiosis using a common “de Bary” definition, which includes **mutualism, commensalism** and **parasitism.**

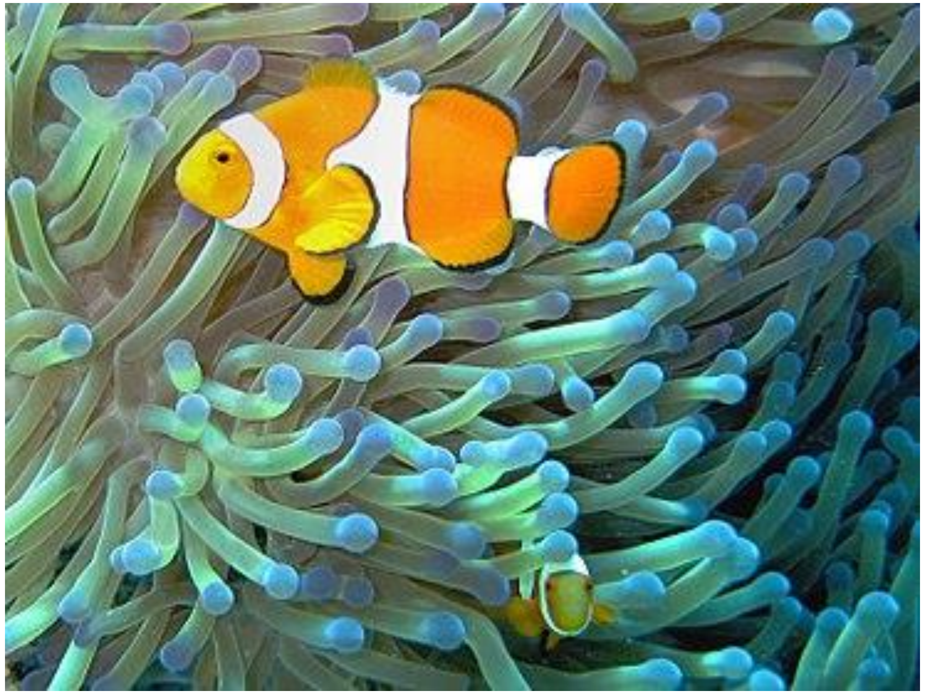


Mutualism

Mutualism is a symbiotic interaction where both or all individuals benefit from the relationship.

While the activities of each partner benefits the other species in some way, neither species behaves altruistically. Each species pursues its own selfish interest, and any benefit incurred by the mutualist partner is an unintended consequence of the interaction.

There are two kinds of mutualism : obligate and facultative.



The Clownfish feeds the sea anemone with its faeces and eats harmful invertebrates. In return, the anemone protects the clownfish against predators with its sting.

Obligate Mutualism

With obligate mutualism one species is entirely dependent on and cannot survive without the other. For example: leafcutter ants and certain fungi.

The ant larvae eat only one kind of fungi, and the fungi cannot survive without the constant care of the ants.

As a result, the colony activities revolve around cultivating the fungi. They provide it with digested leaf material, can sense if a leaf species is harmful to the fungi, and keep it free from pests

Facultative mutualism

Here species can survive individually but often not as well. An example is the tropical African tree *Barteria fistulosa* and the slender ant *Tetraponera aethiops*.

The *Barteria* tree provides the *Tetraponera* ant with shelter and food in hollow branches where they form colonies. *Tetraponera* ant s are aggressive and protect the tree from other insects and plant invasions.

It has been found that *Barteria* don't survive as well in areas where there are no *Tetraponera* , and are more prone to disease.

Mutualism and seed dispersal

Plants have very limited mobility and therefore rely on dispersal mechanisms to transport their propagules away from the parent plant. There are various kinds of seed dispersal syndrome available to plants (e.g. wind, ballistic, water, on the outside of animals), however, only two represent a co-evolved mutualistic plant-animal relationship. These are **endozoochory** and **synzoochory**, in which both plant and animal participants gain a benefit.

In **endozoochory**, the plant surrounds seeds with an edible, nutritious fruit as a good food for animals to consume. Birds and mammals are the most important seed dispersers, but a wide variety of other animals, including turtles, fish, and insects can transport viable seeds. Seeds or the seeds and fruit together (**diaspores**: the dispersal unit) pass through the gut passage and are expelled without being damaged, allowing the seed to germinate. In this case, diaspores are carriers of rewards or lures that result very attractive to animals. That is why fruits are usually fleshy, sweet and often have bright colours or emit scents to attract them.

In **synzoochory** seeds or fruits are collected by animals (often mammals, such as squirrels) in times of abundance and then are buried as a food storage to be used when needed. Often, not all seeds are found and eaten, so some are able to germinate.

Plant-pollinator mutualisms

Pollination is a very important kind of mutualism. Many plants are visited by animals seeking to feed on nectar, pollen or other sugars they produce in their flowers and, during this process, the animals carry pollen from one flower to others, allowing it to reach the stigma in a very effective way. Thus, the plant gets the benefit of fertilization with a lower cost of pollen production, which would be higher if it was dispersed through the air. And the animals, in exchange, obtain food. Therefore, a true relationship of mutualism is stablished between the two organisms.

Nearly three-quarters of all extant flowering plants (angiosperms) are pollinated by animals, and most pollinators receive food in the form of pollen or nectar. Some pollinators (e.g. bees) also use waxes and resins from flowers to build their hives.

The majority of animal pollinators are insects; bees, butterflies, moths, flies, wasps, and beetles are the most common insect pollinators. However, some bird groups (hummingbirds, spiderhunters, sunbirds, honeycreepers and honeyeaters) are pollinators, and many bats: over 530 plant species rely on bats for pollination!

Commensalism

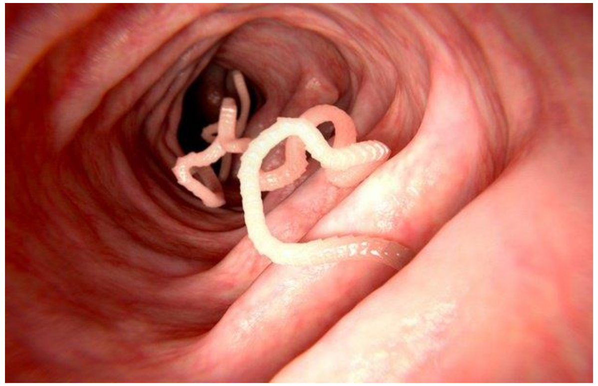
Commensalism describes interactions in which one individual benefits while the other is neither helped nor harmed.

For example, epiphytes (orchids, bromeliads) are plants found in tropical rainforests that grow on the branches of trees. The epiphytes benefit as they gain access to light, however their presence does not affect the trees. Barnacles growing on the bodies of whales benefit from food, dispersal means and a place to live, but their presence neither harms nor helps the whale.

Parasitism

Parasitism is a relationship when one individual, the parasite, benefits from another individual, the host, while reducing the fitness of the host in the process. Parasites feed on host tissue or fluids and can be found within (**endoparasites**) or outside (**ectoparasites**) of host bodies. Like predation, parasitism is a type of consumer-resource interaction, but unlike predators parasites are typically much smaller than their hosts, do not kill them, and often live in or on their hosts for an extended period. Parasites of animals are highly specialised and reproduce at a faster rate than their hosts.

Parasites can shape community structure through their effects on trophic interactions, food webs, competition, biodiversity, and keystone species, and can have a significant impact on population dynamics. As parasites may cause deleterious effects on their hosts, host and parasite are often forced to constantly adapt to one another, which may lead to host-parasite co-existence. Many animals have very high parasite loads, for example. Some animals have behavioural strategies to deal with parasites, like preening in birds or social grooming in mammals.



7.8

Resources

Suggested Reading

- Morin, P.J. (2011). Community Ecology, 2nd Edition. Wiley Online Library.
- MacArthur, R.H. and Wilson, E.O. (1967). The Theory of Island Biogeography. Princeton University Press.
- Galetti, Mauro. (2002). Seed dispersal and frugivory: Ecology, Evolution and Conservation. Cabi Publishing https://www.researchgate.net/publication/271706264_Seed_dispersal_and_frugivory_-_Entire_Book
- Howe, H.F. and Westley, L.C. (1990). Ecological Relationships of Plants and Animals. Oxford University Press.

Online Resources

- Online simulations of Lotka-Volterra:

https://www.geogebra.org/m/y746ry8g

https://www.ahahah.eu/trucs/pp/

https://observablehq.com/@mbostock/predator-and-prey

- Niche Measures and Resource Preferences: https://www.zoology.ubc.ca/~krebs/downloads/krebs_chapter_14_2017.pdf