Population Ecology, Community Ecology, and Ethology

Alexandra Duan and Alex Pan

July 2023

Table of Contents

1 Introduction

Population and community ecology comprise the interactions between organisms and their environment. Population ecology examines how and why populations—groups of individuals of a single species—change over time, while community ecology focuses on the interactions between species which determine community structure.

2 Population Ecology

A **population** is a group of individuals of a single species that live in the same general area. Members of a population rely on the same resources, are influenced by similar environmental factors, and have a high likelihood of interacting and breeding with one another.

Population ecology is the study of populations in relation to their environment, including biotic and abiotic influences on population density, distribution, size, and age structure. Populations increase through birth and **immigration** (the influx of new individuals from other areas) and decrease through death and **emigration** (the movement of individuals out of a population).

2.1 Population Characteristics

Three fundamental characteristics of a population are **density**, **dispersion**, and **demographics**.

2.1.1 Density

Population density is the number of individuals per unit area or volume. Ecologists may estimate population size by counting individuals in randomly-selected plots and extrapolating, counting indices of population size (e.g., number of nests, calls, or fecal droppings), or using the **mark-recapture method**:

1. A random sample of individuals is captured, marked with a tag, and released.
2. After a period of time has elapsed, traps are set again, and a second sample of individuals are captured and identified.
3. Assuming each marked individual has the same probability of being captured as each unmarked individual, $M/N = m/n$, where M is the size of the first sample, N is the estimated total population size, m is the number of marked individuals in the second sample, and n is the size of the second sample.

2.1.2 Dispersion

Population dispersion is the geographic distribution of individuals within a population. Variations in local density provide insight into individuals' environmental and social interactions.

- **Uniform dispersion**: individuals are evenly spaced, often due to territoriality in animals or harmful chemicals secreted by plants (*Example:* sage plants, which secrete toxins)

- **Random dispersion**: individuals are spaced unpredictably; occurs in the absence of strong attractive or repulsive factors, or when resources are distributed homogenously (*Example:* dandelions, which have wind-dispersed seeds)
- **Clumped dispersion**: individuals aggregate in patches, often where natural resources are abundant (*Example:* oak trees, which drop their seeds directly to the ground)

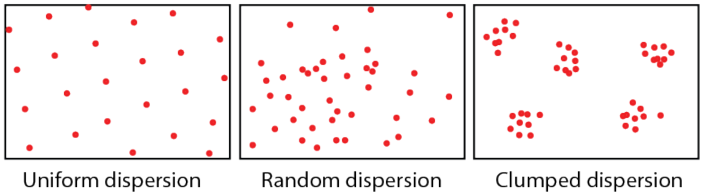

Figure 1: Patterns of population dispersion. (Source: Khan Academy)

2.1.3 Demography

Population demography is the study of the vital statistics of populations, particularly birth and death rates, and how they change over time.

- A **life table** is an age-specific summary of the survival pattern of a population. Life tables follow a **cohort**, a group of individuals of the same age, from birth to death, recording the proportion of the cohort that survives from one age to the next.
- **Survivorship curves** plot the proportion of a cohort alive at each age on a logarithmic scale. Natural populations exhibit several patterns of survivorship.

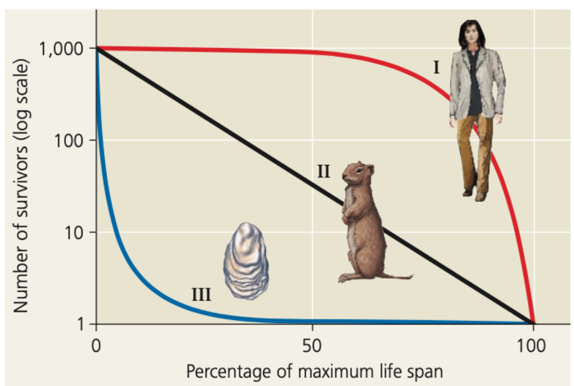

Figure 2: Survivorship curves. (Source: *Campbell Biology)*

1. **Type I**: Low death rates in early and middle life and high death rates in later life. Exhibited by humans and many other large mammals.
2. **Type II**: Constant mortality over an organism's lifespan. Exhibited by many rodents, various invertebrates, and some annual plants.
3. **Type III**: High death rates in early life and low death rates in later life. Exhibited by organisms that produce large numbers of offspring but provide little parental care, such as fish, long-lived plants, and marine invertebrates.
4. Many species show intermediate or more complex curves.

- Some invertebrates, such as crabs, show a "stair-stepped" curve, with increased mortality during molts.
- In birds, mortality is often high among chicks (Type II) but is fairly constant among adults (Type III).

- A **reproductive table** summarizes the reproductive rates of a population from birth to death. For sexually-reproducing species, a reproductive table tallies the number of female offspring produced by each age group (because only females give birth to offspring).

Example 2.1 (USABO Semifinal Exam 2018) You are trying to determine how large a certain population of trout is. You capture 50 trout, mark them, then return them to the stream. Then, the next time you capture trout (some time later), you find that, out of the 100 you captured, only 7 are marked. About how many trout are in the stream?

(A) 500 trout
(B) 600 trout
(C) 700 trout
(D) 800 trout
(E) None of the above

Solution: This example describes the mark-recapture method and is derived directly from the proportion all marked/total = those marked of captured/captured. Solving this proportion, we get $50/x = 7/100$, so $x = 100 * 50/7$, which is about **(C) 700 trout**.

2.2 Life History

Life history comprises the traits that affect an organism's schedule of reproduction and survival. Life histories involve three basic variables: when reproduction begins, how often the organism reproduces, and how many offspring are produced during each reproductive episode.

- **Semelparity (big-bang reproduction)**: Semelparous organisms undergo a single reproductive episode before death (e.g., salmon, agaves). Semelparity is often an adaptation to harsh or unpredictable conditions.

- **Iteroparity (repeated reproduction)**: Iteroparous organisms undergo multiple reproductive cycles over their lifetime (e.g., lizards). Iteroparity is favorable in dependable conditions where competition for resources is intense.

- Some intermediate organisms repeatedly produce large numbers of offspring (e.g., oak trees, sea urchins).

In each of the above cases, trade-offs are made between survival and traits such as reproductive frequency, number of offspring, and parental investment.

2.2.1 Selection for Life History Traits

- ***K*-selection (density-dependent selection)**: Selection for traits advantageous at high densities; produces few, well-invested offspring. Found in populations living near K, the carrying capacity, where competition for resources is intense.
- ***r*-selection (density-independent selection)**: Selection for traits advantageous at low densities; produces many offspring with little parental investment. Maximizes r, the per capita rate of increase. Found in low-density populations and often in disturbed habitats, where individuals face little competition.

2.3 Models of Population Growth

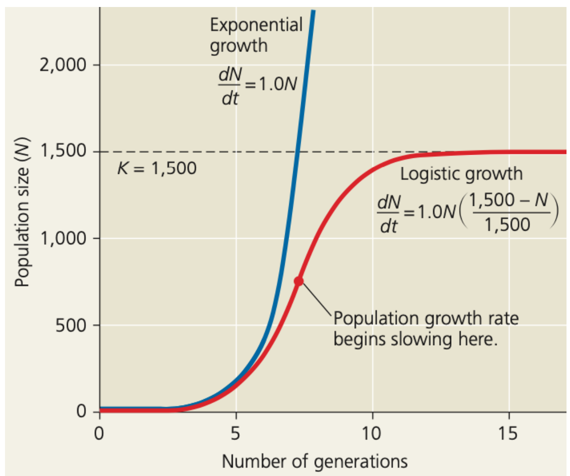

Figure 3: The exponential (blue) and logistic (red) population growth models. (Source: *Campbell Biology*)

2.3.1 Exponential Growth

The exponential model describes population growth in an ideal, unlimited environment. For simplicity's sake, we can ignore immigration and emigration and define a change in population size during a fixed time interval with the following equation:

Change in population size over time interval = Births in time interval - Deaths in time interval

$$\Delta N/\Delta t = B - D$$

The *per capita birth rate* (b) is the number of offspring produced per unit time by an average member of the population. Multiplying b by the population size N yields the exact number of births $B = bN$. We can thus replace B and D:

$$\Delta N/\Delta t = bN - dN$$

The difference between the per capita birth rate and the per capita death rate is the *per capita rate of increase*, or r, which indicates whether a population is growing ($r > 0$), declining ($r < 0$), or at zero population growth/ZPG ($r = 0$). We can replace $bN - dN$ with simply rN:

$$\Delta N/\Delta t = rN$$

Ecologists use differential calculus to express population growth instantaneously, as the growth rate at a particular instant in time. Exponential population growth occurs under ideal conditions, usually in rebounding populations or populations introduced to an unfilled environment. We may thus assume the maximum growth rate for the population (r_{max}), called the *intrinsic rate of increase*.

$$dN/dt = r_{max}N$$

2.3.2 Logistic Growth

However, most environments have a limited number of resources and cannot support unlimited population growth. As population density increases, populations approach the *carrying capacity* (K), the maximum stable population size that a particular environment can support. Carrying capacity is often determined by energy limitations, although factors such as shelters, nutrient availability, and suitable nesting sites can all be limiting.

In the **logistic population growth** model, the per capita rate of increase declines as the carrying capacity is reached. If the maximum sustainable population size (carrying capacity) is K, then $K - N$ is the number of additional individuals the environment can accommodate and $\frac{(K-N)}{K}$ is the fraction of K that is still available for population growth. By multiplying the intrinsic rate of increase r_{max} by $\frac{(K-N)}{K}$, we modify the growth rate of the population as N increases:

$$dN/dt = r_{max}N\frac{(K-N)}{K}$$

As N approaches K, the term $\frac{(K-N)}{K}$ decreases along with the rate of population growth. Population growth is greatest when the population is approximately half of the carrying capacity. The logistic model of population growth produces a sigmoid (S-shaped) growth curve over time.

The logistic growth model assumes that populations approach the carrying capacity smoothly. However, most natural populations experience a lag time in which they briefly overshoot their carrying capacity. Some populations also show an *Allee effect*, in which individuals may have a more difficult time surviving or reproducing (finding mates) if the population is too small.

2.4 Population Dynamics

A birth rate or death rate that does not change with population density is **density-independent**, while a rate which does is said to be **density-dependent**. Density-dependent regulation provides negative feedback on population growth by reducing birth rates or increasing death rates. Competition for resources, increased rate of disease transmission, and intrinsic hormonal changes which increase aggression may all reduce population growth as population density increases.

- Some populations show cyclic population changes, such as the 10-year cycle of lynx and snowshoe hare in northern Canada and Alaska.
- A biological system in which a predator and a prey species interact can be described by the *Lotka–Volterra equations*, a pair of first-order nonlinear differential equations.

- A group of populations may be linked together to form a **metapopulation**. Local populations in a metapopulation occupy discrete patches of suitable habitat within a sea of unsuitable habitat. Individuals move among populations, and extinct populations' former patches may be recolonized through immigration.

2.4.1 The Human Population

To maintain stability, a regional human population can exist in one of two configurations:

1. Zero population growth = High birth rates-High death rates
2. Zero population growth = Low birth rates-Low death rates

The movement from the first toward the second state is called the **demographic transition**. Most population growth is centered in developing nations, while many developed nations have reproductive rates below the replacement level. **Age structure**, the relative number of individuals of each age, is illustrated as a pyramid showing the percentage of the population at each age. Age structure diagrams can predict a population's growth trends and future social conditions.

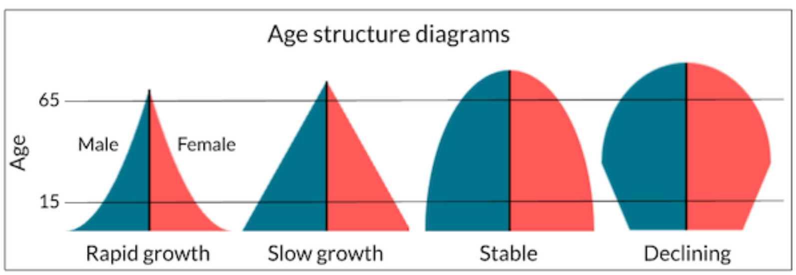

Figure 4: Age-structure pyramids for three countries. (Source: Khan Academy)

An **ecological footprint** is the aggregate land and water area required by each person, city, or nation to produce all the resources it consumes and to absorb all the waste it generates. If the area of all the ecologically productive land on Earth, excluding land for parks and conservation, is divided by the global human population, the result is 1.7 hectares (ha) per person.

3 Community Ecology

A **community** is a group of different species living close enough together for potential interaction. Ecologists define the boundaries of a particular community—for example, decomposers living on a rotting log or benthic organisms in Lake Superior—to fit their research questions.

3.1 Interspecific Interactions

Interspecific interactions, or interactions between species in a community, are classified by whether they help (+), harm (-), or have no effect on (0) the survival and reproduction of the species involved.

3.1.1 Competition

Interspecific competition (-/-) occurs when two species compete for a limited resource, harming one or both of the species involved.

A species' **ecological niche** is its sum total use of abiotic and biotic factors in its environment, which may include the temperature range it tolerates, the time of day when it is active, and the sizes and kinds of prey it eats.

- The **competitive exclusion principle** states that two species cannot coexist permanently in a community if their niches are identical.
- **Resource partitioning** is the differentiation of niches that allows two similar species to coexist in a community. As a result of competition, a species' *fundamental niche*, the niche potentially occupied by that species, may differ from its *realized niche*, the niche the species actually occupies.
- **Character displacement** is the tendency for characteristics to be more divergent in sympatric populations of two species than in allopatric populations of the same two species—for example, the variation in beak size between different populations of the Galápagos finches.

3.1.2 Predation

Predation (+/-) occurs when one species, the predator, kills and eats the other, the prey. Predators have evolved a variety of feeding adaptations, and prey animals in turn have evolved various adaptations to avoid being eaten:

1. **Adaptive coloration**: Some prey have *cryptic coloration* (camouflage).
2. **Mechanical and chemical defenses**: Some prey animals synthesize odors and toxins; others passively acquire them from their food. Animals with chemical defenses often exhibit bright warning *aposematic coloration*.
3. **Mimicry**: Many species mimic the appearances of others. Mimicry may be categorized into defensive mimicry, in which the prey acts as the mimic, and aggressive mimicry, in which the predator acts as the mimic.
   - Batesian mimicry: a harmless species mimics a harmful species.
   - Müllerian mimicry: two or more harmful species mimic each other.
   - Mertensian/Emsleyan mimicry: a harmful species mimics a less harmful species.
   - Browerian mimicry/automimicry: members of a species mimic each other; either (1) a less toxic individual mimics a more toxic individual or (2) a less vulnerable body part mimics a more vulnerable body part (e.g., eyespots).
   - Wasmannian mimicry: a mimic resembles a model organism that it lives along with in a nest or colony.
   - Vavilovian mimicry: weeds share characteristics to crops due to artificial selection.
   - Aggressive/Peckhamian mimicry: a predator or parasite mimics a harmless species to avoid detection ("wolf in sheep's clothing").

Herbivory (+/-) occurs when herbivores eat part of a plant or alga.

3.1.3 Symbiosis

Symbiotic relationships occur when individuals of different species live in direct and intimate contact with each other.

Parasitism (+/-) occurs between a parasite, which derives its nourishment from a host, and a host, which is harmed in the process. Many parasites feed on multiple hosts throughout their life cycle.

- *Endoparasites* live within the body of the host; *ectoparasites* live and feed on the external surface of the host. Parasitoid insects (usually small wasps) lay eggs on or in living hosts; the eggs hatch into larvae that feed on the host, eventually killing it.

Mutualism (+/+) is an interspecific symbiosis in which two species benefit from their interaction. In *obligate mutualism*, at least one species cannot survive without its partner; in *facultative mutualism*, both species can survive alone.

Commensalism (+/0) is an interaction that benefits one species but neither harms nor helps the other. **Amensalism (-/0)** is an interaction that harms one species but neither harms nor helps the other. **Synnecrosis (-/-)** is an interaction in which both species are harmed, resulting in the death of one or both of them.

Species with close ecological interactions (e.g., flowering plants and their pollinators) may undergo *coevolution*, in which two or more species experience reciprocal evolutional changes through natural selection.

> **Example 3.1** (USABO Open Exam 2018) Microbiologists from around the world travel to Hawaii to study the interaction of *Euprymna scolopes*, the Hawaiian squid, with the bacterium *Vibrio fischeri*. *Vibrio* bacteria live inside the light organ and obtain nutrients from the squid. The bacteria produce light through a process known as bioluminescence, providing a mechanism for camouflage for the squid in the ocean. This is an example of:
>
> (A) Commensalism.
> (B) Parasitism.
> (C) Behavioral imprinting.
> (D) Epigenetic modification.
> (E) Mutualism.

Solution: The bacteria and the squid are both benefiting from the interaction, so the scenario is an example of **(E) Mutualism**.

3.2 Community Structure

3.2.1 Species Diversity

Species diversity describes the variety of types of organisms that make up a community. Its components are:

1. **Species richness**: the total number of different species in the community.
2. **Relative abundance**: the proportion each species represents of the total individuals in the community.

Indices of diversity are based on species richness and relative abundance. One widely-used index is the Shannon diversity index (H):

$$H = -\sum_{i=1}^{S} p_i \cdot \log(p_i)$$

where S is species richness and p_i is the proportion of each species in the community.

Another index you may be asked to use is Simpson's diversity index (D). Here, the top formula is the **"finite" formula**, for small or finite populations, and the bottom is—you guessed it—the **"infinite" formula**, for extrapolating data to infinite populations or continuous data.

$$D = 1 - \frac{\sum_{i=1}^{s} n_i(n_i - 1)}{N(N-1)}$$

$$D = 1 - \sum_{i=1}^{s} \left(\frac{n_i}{N}\right)^2$$

where s is the total number of species in the sample, n_i is the number of individuals of species i, and N is the total number of individuals in the sample. Note that high scores (close to 1) indicate high diversity, while low scores (close to 0) indicate low diversity.

3.2.2 Trophic Structure

The **trophic structure** of a community is determined by the feeding relationships between organisms. Energy is transferred up trophic levels from plants and other autotrophs (primary producers) to herbivores (primary consumers) to carnivores (secondary and tertiary consumers) and eventually to decomposers in a **food chain**. Individual food chains in a community are linked together into **food webs**, which use arrows to link predator and prey.

The **energetic hypothesis** suggests that the length of a food chain is limited by the inefficiency of energy transfer along the chain.

- Only about 10% of the energy stored in the organic matter of each trophic level is converted to organic matter at the next higher trophic level. The rest is lost as heat or to metabolic processes.
- Most chains in a food web thus consist of only four or five links. Habitats with higher photosynthetic productivity generally have longer food chains than less productive ones.

The **dynamic stability hypothesis** suggests that long food chains are less stable than short chains. Population fluctuations at lower trophic levels are magnified at higher levels, making top predators vulnerable to extinction.

3.2.3 Ecological Pyramids

Pyramids of energy (or pyramids of productivity) represent the multiplicative loss of energy in a food chain.

- The width of each tier in the pyramid is proportional to the net production of each trophic level, expressed in joules.
- he highest level, which represents top-level predators, contains relatively few individuals. Because populations of top predators are typically small and the animals may be widely spaced within their habitats, many predator species are highly susceptible to extinction.

Pyramids of biomass represent the ecological consequences of low trophic efficiencies.

- Each tier represents the *standing crop* (the total dry mass of all organisms) in one trophic level.
- Most biomass pyramids narrow sharply from primary producers to top-level carnivores because energy transfers are so inefficient.
- **In some aquatic ecosystems, the biomass pyramid is inverted** and primary consumers outweigh producers. This inversion occurs because the producers—phytoplankton—grow, reproduce, and are consumed by zooplankton so rapidly that they never develop a large standing crop.

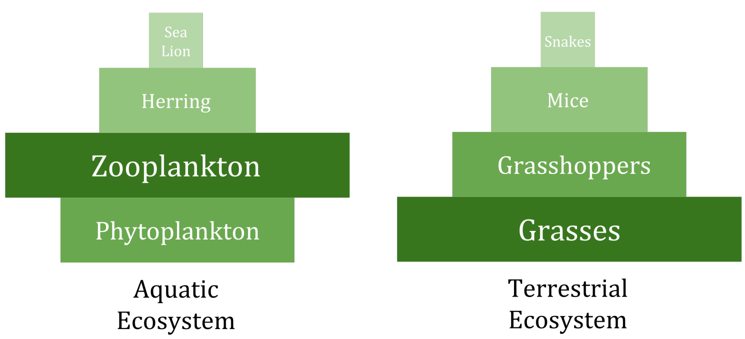

Figure 4: Pyramids of biomass for an aquatic and a terrestrial ecosystem. (Source: Wikipedia)

Pyramids of numbers represent the number of individual organisms involved at each level in a food chain (not their individual sizes or biomass). A pyramid of numbers may be inverted (e.g., in an ecosystem where many beetles feed from the output of a few forest trees).

Example 3.2 (USABO Open Exam 2017) You have been recently studying a small alien ecosystem that is near you. The ecosystem consists of trogs that eat brogs that eat progs. Progs produce energy from the sun. Given that there is 190kJ worth of biomass of progs, approximately how much energy does the biomass of trogs represent?

(A) 1900J
(B) 3800J
(C) 19000J
(D) 38000J

Solution: About 10% of the energy stored as biomass in a trophic level is converted to biomass at the next higher trophic level. A trog is two trophic levels higher than a prog, so the biomass of trogs represents approximately $0.1^2 * 190000\text{J} =$ **(A) 1900J**.

3.2.4 Influential Species

Certain species strongly affect community structure.

- **Dominant species** are the most abundant or have the highest biomass in a community.
  - **Invasive species** frequently achieve high biomasses in new environments in the absence of their natural predators and agents of disease.
- **Keystone species** are not necessarily abundant in a community, but due to their key ecological niches, they have a disproportionate influence on community structure.
  - *Example*: In rocky intertidal communities, the sea star *Pisaster ochraceous* maintains community structure by preying on mussels. When sea stars were removed, mussels were able to monopolize space, and species diversity declined to fewer than 5 species.
- **Foundation species**, or "ecosystem engineers," cause physical changes in the environment that affect community structure.

3.2.5 Bottom-Up and Top-Down Models

Simplified models based on relationships between adjacent trophic levels are useful for discussing community structure. Consider three possible relationships between plants (V for vegetation) and herbivores (H), where arrows indicate that a change in biomass at one trophic level causes a change in biomass at the other:

$$V \rightarrow H \quad V \leftarrow H \quad V \longleftrightarrow H$$

The **bottom-up model** postulates $V \rightarrow H$ linkages.

- A simplified bottom-up model is $N \rightarrow V \rightarrow H \rightarrow P$: the presence or absence of mineral nutrients (N) controls plant (V) numbers, which control herbivore (H) numbers, which control predator (P) numbers.
- Alterations in biomass at the lower trophic levels of a bottom-up community propagate up through the food web. In contrast, the effects of alterations to predator biomass should not extend to the lower trophic levels.

The **top-down model** postulates $V \leftarrow H$ linkages.

- A simplified top-down model is $N \leftarrow V \leftarrow H \leftarrow P$, or the **trophic cascade model**, named for its hypothesized "cascade" of effects: Predators (P) limit herbivores (H), which limit plants (V), which limit nutrient levels (N) through the uptake of nutrients during growth and reproduction.
- The effect of manipulation at higher trophic levels moves down the trophic structure as a series of +/- effects.

- *Example*: In a lake community with four trophic levels, removing the top carnivores increases the abundance of primary carnivores, in turn decreasing the number of herbivores, increasing phytoplankton abundance, and decreasing concentrations of mineral nutrients.
- Ecologists often use the trophic cascade model to alter an ecosystem by adding or removing species in a process called **biomanipulation**. For example, ecologists may alter the density of higher-level consumers in lakes to lower nutrient levels and prevent algal blooms.

3.3 Disturbances

Disturbances, such as floods, droughts, human activities, and overgrazing, change communities by removing organisms or altering resource availability. The **nonequilibrium model** proposes that communities constantly change following a disturbance. A high level of disturbance is generally the result of a high intensity *and* high frequency of disturbance, whereas a low level of disturbance can result from either a low intensity or a low frequency of disturbance.

The **intermediate disturbance hypothesis** suggests that moderate levels of disturbance foster greater species diversity than a low or high level of disturbance. Intermediate levels of disturbance open up habitats for occupation by less competitive species without fostering conditions so severe that they exceed the environmental tolerances or rates of recovery by potential community members. Human-caused disturbances, however, are more frequent than natural events and usually reduce species diversity.

3.3.1 Ecological Succession

Ecological succession is the transition in species composition in disturbed areas over time.

- **Primary succession** occurs in a lifeless area where soil has not yet formed (e.g., volcanic islands and moraines).
  - Initially, only autotrophic prokaryotes, heterotrophic bacteria, and protists may be present. Mosses and lichens then colonize by windblown spores and cause the development of soil, after which grasses, shrubs, and trees sprout from seeds blown or carried in from nearby areas.
- **Secondary succession** occurs where an existing community has been removed by a disturbance, such as a clear-cut or fire, but the soil is left intact.
  - Herbaceous species grow from windblown or animal-borne seeds, shrubs replace the herbaceous species, and forest trees replace the shrubs.

Early-arriving species may *facilitate* the appearance of later species by changing the environment, *inhibit* the establishment of later species, or neither hinder nor help the colonization of later species.

3.4 Biodiversity

A community's **biodiversity** (species diversity) is correlated with its geographic location and its size. Species richness generally declines along an equatorial-polar gradient: tropical habitats support many more species of organisms than do temperate and polar regions due to their longer evolutionary history and more ideal climates.

- **Evolutionary history**: Older communities generally undergo more speciation events, increasing species diversity. Tropical communities are older than temperate or polar communities, with a growing season about five times longer (and biological time five times faster) than that of a tundra.
- **Climate**: *Evapotranspiration*, the evaporation of water from soil plus the transpiration of water from plants, acts as a combined measure of solar energy input and water availability. Evapotranspiration is correlated with species richness and is much higher in areas with high temperature and precipitation.

The **species-area curve** shows that the larger the geographic area of a community, the greater the number of species.

3.4.1 Island Biogeography

In ecology, *islands* (oceanic islands, mountain peaks, woodland fragments, etc.) are defined as isolated patches of habitat surrounded by an environment unsuitable for the "island" species being studied. The number of species which inhabit a newly-formed island is determined by (1) the rate at which new species immigrate to the island, and (2) the rate at which species become extinct on the island.

Immigration and extinction rates are affected by islands' size and distance from the mainland.

- **Size**: Small islands have both *lower immigration rates* (because potential colonizers are less likely to reach them) and *higher extinction rates* (because they have fewer resources and less diverse habitats for colonizing species to partition).
- **Distance from the mainland**: Islands closer to the mainland have higher immigration rates than islands that are farther away.

The **theory of island biogeography** predicts that a dynamic equilibrium will eventually be reached, where the rate of species immigration equals the rate of species extinction. The number of species at this equilibrium point is correlated with the island's size and distance from the mainland.

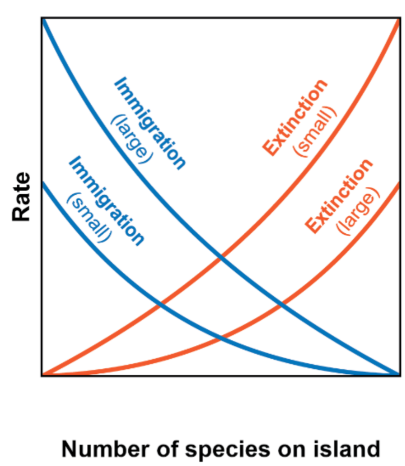

Figure 5: MacArthur and Wilson's theory of island biogeography. (Source: HMMI BioInteractive)

This model may apply in only a limited number of cases and over relatively short periods, where colonization is the main process affecting species composition. Nevertheless, it is widely applied in conservation biology as a starting point for predicting the effects of habitat loss on species diversity.

4 Ethology

Ethology is the study of animal behavior, which is crucial for understanding the basis of animal interactions and human society.

4.1 Specific Signals Stimulate Specific Behaviors

Fixed action patterns are specialized behaviors that some animals have in response to a certain **sign stimulus**. Humans do not have fixed action patterns, but a prime example comes from stickleback fish. Whenever they see the color red (sign stimulus), they immediately respond aggressively (fixed action pattern). Since male sticklebacks have red bellies, this fixed action pattern creates natural competition between males for territory.

There are two approaches to understanding animal behaviors: **proximate** and **ultimate** causation. Proximate causation involves the immediate effects of the action: in sticklebacks' case, to protect territory. This is the "how" of the action. On the other hand, ultimate causation involves the overarching "survival and reproduction" effects of this behavior (more aggressive males have a better chance of being the sole mate for females).

Figure 6: Male Stickleback Competition. (Source: Warren Photography)

Another animal behavior is **migration**. Normally in birds, it can be stimulated by changes in the sun, circadian rhythm, stars, and magnetism.

Animals also base behavior off of **behavioral rhythms**. For example, there are **circadian** rhythms that control the daily sleep-wake cycle and **circannual** rhythms that control behaviors like migration and hibernation. Another example of a behavioral rhythm is a **lunar** rhythm, which fiddler crabs (a type of crab) use to determine when to mate (due to tidal patterns, which are controlled by the moon).

However, animals may temporarily interrupt these rhythms and lower their baseline metabolism to survive stressful conditions. The best example of this is **hibernation**, which is a voluntary sleep-like state that animals enter during winter to conserve energy. **Torpor** is a similar state of reduced metabolism, except it is involuntary. Torpor during a hot, dry period (usually summer) is often known as (a)**estivation**.

4.1.1 Signals

Animals also produce **signals** (stimuli between two organisms) which allow them to **communicate** (signal transmission). In *Drosophila*, the male detects and sends visual (seeing the female), olfactory (detecting female-specific smells), tactile (touches female foreleg), and auditory (courtship song) signals to attract the female and eventually mate.

In order to communicate with others, bees use a "**waggle dance**" to communicate the location of nectar sources. The angle relative to the hive when a bee runs straight indicates the food angle relative to the sun, the sound indicates the amount of food, and the straight run distance indicates the distance to the food. Tight circle dances show chose nectar, while large circle dances indicate nectar that's far away.

4.1.2 Pheromones

Pheromones are secreted chemical factors that contribute to signaling. These substances can be extremely powerful and long-range – for example, a male silk worm can detect pheromones from females several kilometers away! Another function of pheromones is to alert nearby members about danger. Some fish like minnows and catfish release pheromones when threatened, helping other fish escape danger. In colony insects like bees and ants, the queen releases special "queen pheromones" to maintain the social order in the hive. It can attract workers and drones to the hive and also prevents worker ovary development, keeping them sterile.

4.1.3 Genetic Variation in the Same Species

Members of some species can have drastically different appearances and lifestyles due to different environmental conditions and behaviors. For example, coastal garter snakes are adapted to eating banana slugs while inland garter snakes lack this ability. This difference in diet is due to genetic variation of their scent receptors, leading to different behaviors. **Migration** can also be due to genetic variation. For example, the German blackcap migrates to either Spain or Britain based on genetic variation.

4.2 Learning

There are many different types of **learning** in the animal kingdom. Even though most traits are based on genetic information, experiments like the **cross-fostering** of California and White-footed mice (California mice are more aggressive while White-footed mice are less aggressive) have found that California mice cross-fostered with White-footed mice were less aggressive than usual (and vice versa).

Habituation is a type of learning where upon repeated exposure to a stimulus, the animal gets used to the stimulus. The opposite of this is **sensitization**, where repeated exposures to a stimulus cause the animal to become more responsive to the stimulus.

Imprinting is a type of learning with a sensitive period. When geese and cranes are born, they immediately imprint onto something moving away from them – this behavior evolved because the mother usually moves away from them first. However, with human interference, geese and cranes can actually imprint on to humans and other objects before the mother, which is problematic for the chicks' survival.

Animals such as digger wasps also use **spatial learning** to orient themselves. If a wasp uses the location of pinecones as markers for the location of its nest, scientists can move the pinecones, making the wasp go to the wrong location. Additionally, some use **cognitive maps**, which are visualizations of particular spatial settings in the animal's brain. In this way, the animal will be able to orient itself based on its previous memories.

These are all types of **associative learning**, in which external cues are associated with a certain response. There are two types of conditioning, **classical** and **operant** conditioning, that utilize associate learning. In classical conditioning, an unrelated stimulus is associated with a particular outcome (like ringing a bell before giving a dog food). Over time, the animal will begin to respond to that stimulus even if the outcome does not occur. On the other hand, operant conditioning makes the animal associate a particular behavior with a particular result (punishment or reward). This could come in the form of a dog getting a treat when it performs a trick correctly.

Some higher-level forms of learning are **cognition** and **problem-solving**. Cognition is the ability to recollect and judge. Even though this is seen as a human trait, many "lower-order" animals still possess some form of it. Problem-solving involves getting over some sort of obstacle. For example, corvids (crows and ravens), primates, and dolphins have advanced problem-solving skills. Remember the old fable of the crow putting pebbles in a bottle of water to reach it? That's problem solving.

Another form of learning is birdsong. Some species have sensitive periods (similar to imprinting), while others have flexible songs.

The highest level of learning is **social learning**. In this process, more inexperienced members of a population will watch and copy the behaviors of older members. This results in **culture**, a system of information that influences a population's behavior.

4.3 Foraging

Foraging is another important animal behavior – it's how they obtain nutrients. In *Drosophila* larvae, two alleles called "*Rover*" (R) and "*sitter*" (s) control a fly's foraging behavior. Rover flies are prevalent in high-density populations where they forage for further distances to obtain food (high risk, high reward). On the other hand, sitter flies are prevalent in low-density populations – they forage at shorter distances to minimize energy cost – foraging for long distances is unnecessary.

Ecologists have developed a model called the **optimal foraging model** in order to interpret and predict foraging behaviors. In this model, the animal tries to minimize energy costs while maximizing nutritional benefits. An important aspect of the model is **predation**, which results in a compromise for the prey. They have to sacrifice high food-density areas in order to escape predation, eventually finding a balance between these two phenomena.

4.4 Mating Systems

There are three main mating systems: monogamy (one male, one female), polygamy (one male, multiple females), and polyandry (multiple males, one female). The most notable distinction between these mating systems is **sexual dimorphism**, which is exaggerated in polygamous species and decreased in monogamous species due to sexual selection and competition.

In most animals, the **certainty of paternity** is a factor in the male's care for young. For example, fish have a relatively high certainty of paternity compared to animals with internal fertilization because mating and egg-laying occur around the same time. For animals with internal fertilization, the male engages in behaviors like guarding the female and removing other males' sperm during copulation. Thus, the certainty of paternity is associated with male care, which is higher in external than internal fertilization.

Inter- and intra- **sexual selection** is an important factor in mate selection. In **mate-choice copying**, an individual conforms to the population in their preferred mate choice. The most famous example of mate-choice copying is in guppies. Females will prefer to mate with males who have already mated with other females. Mate-choice copying can mask genetic preferences for specific traits – in short, the copier usually settles for less than its genetic standards. In general, sexual selection reduces variation and selects for the "best" phenotype. But there's still high variation in males, so what gives? Game theory!!

4.4.1 Example of Game Theory

Let's take the example of the Side-blotched lizard. There are three types of lizards: large territory (orange throat), small territory (blue throat), and sneakers (yellow throat). One would expect one of these subtypes to dominate, but a continuous game of existential rock-paper-scissors game of mating keeps all phenotypes balanced. When the population of orange-throated lizards increases, the "sneaker" yellow-throated lizards have an easier infiltrating and mating with females. When the yellow-throated lizards increase, blue-throated lizards which defend smaller groups of females can successfully defend against these sneaker lizards. And when blue-throated lizards increase, they get outcompeted by the more aggressive orange-throated lizards. In this way, these lizards form a constant cycle of phenotypic dominance.

Select genes control mating in different organisms. In *Drosophila*, the *fru* gene (master regulatory for a group of genes that regulate courtship) controls the courtship ritual. Mutations in *fru* result in males that don't mate. In voles, **ADH** is used to establish pair-bond relationships and parental care cues. This deviates from the normal function of ADH in water reabsorption.

4.5 Altruism and Sociobiology

Why are worker bees, ants, and naked mole rats sterile? Why do ground squirrels and prairie dogs put themselves in danger to alert the group? These questions can be answered by a behavior known as altruism: reducing one's own fitness to increase the fitness of other members of the population. For instance, **inclusive fitness** is the phenomenon in which non-parental relatives help care for offspring. Even though the individual isn't parenting their own offspring, it still maximizes their own DNA in the population.

A subset of inclusive fitness is **kin selection**, which are behaviors that increase the reproductive success of relatives. If a particular relative is in danger, an individual may choose to save (or not save) the relative. This choice can be mathematically represented by **Hamilton's Rule**, which is covered in the "Genetics" handout.

Altruism can still occur without relatedness. **Reciprocal altruism** is the act of altruism between non-related individuals with the hope of reciprocation. It's kind of like a "tit-for-tat" system in which individuals will help each other if the precedent is set. There are a special subset of individuals called **cheaters** who don't reciprocate the behavior. Their advantage is that they get free help and benefit, but the disadvantage is that most individuals will not trust them after the first altruistic event.

Sociobiology is the idea that our biology affects social interactions. With the development of human society and culture in the recent past, reciprocal altruism and cooperation have become more important than ever.

Some scientists study **play**, which has been likened to preparing individuals for unexpected situations. Play is hypothesized to have evolved to help juvenile animals get familiar with their environments in a low-risk manner.

5 Conclusion

This handout covered the interactions between organisms at the community and population levels, as well as the animal behaviors which govern those interactions. To learn about ecological interactions concerning the abiotic factors of an ecosystem, read the Climates, Biomes, and Ecological Restoration handout.