

MSc- I, Semester VI, Paper III, Unit III**The Environment, Biogeography and Population Ecology****Contents:**

1. Population Ecology: Population demography; survivorship curves; population growth curves; population regulation; life history strategies (r and K selection).
2. Theory of island bio-geography.

Population Demography:

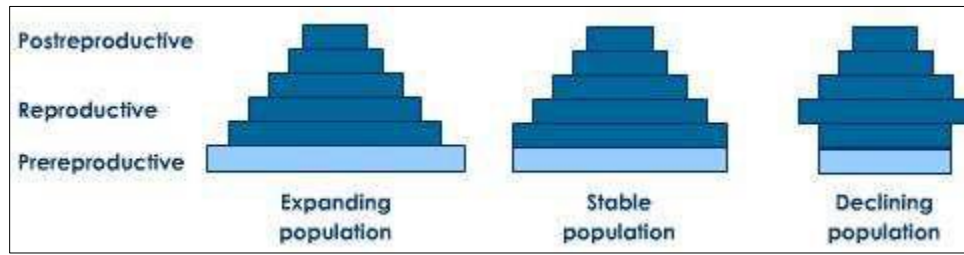
Demography is the study of population structure in relation to size, age, sex, natality, mortality, migration, age structure and survivorship. Population dynamics can vary drastically depending on the age structure of the population, ratio of male and females, addition of off springs through birth, deletion through death and so on. Demography is the study of the characteristics of populations. It incorporates statistical measurement of how these characteristics change over time. It is a useful tool for ecologists, economists and sociologists. In ecology it is applicable to all living beings while economists and sociologists make use of these studies only for human populations.

Demographic Parameters:

Age Structure: Age structures define ratio or proportion of individuals in a population following under different age groups. These age groups are: Pre-reproductive, Reproductive, Post- reproductive which correspondingly can also be termed as young, adult and old. The age structure represents the population status and also helps in determining the future of the population. Age structure is usually illustrated by an age pyramid, a graph in which horizontal bars represent the percentage of the population in each age group. Each age group is called a cohort. The longer a bar is, the greater the proportion of individuals in that age group. Age pyramids are useful for tracing the history of a population and for projecting future population trends. There are 3 forms of the age structure: according to which the populations can be:

- i. Expanding: The expanding population show higher ratios of pre-reproductive group of individuals. More number of offspring are produced than parents. It is pyramid shaped. It generally is found in lower organisms like algae, Bacteria and so on.
- ii. Stable: The stable population on the other hand has almost same ratio of all the 3 age groups. Number of off springs is just equal to number of parents. The pyramid shows almost straight sides and is bell shaped.
- iii. Diminishing: The ratio of pre-reproductive age group is minimum and of post reproductive is maximum in diminishing population. Number of offspring produced is less than parents. The base of pyramid is narrow and is urn shaped.

The age structure also helps in judging the consequences of a typical type of population and if needed a strategy can be defined to take a remedial measure so that the population does not decrease. In study of plant population demography, age structure has been included comparatively later. Determining age in plants is difficult plants show modular structure and asexual reproduction which is not dependent upon age. Uneven growth of same aged individuals also imposes difficulty, for example, trees of same age may not show exactly the same growth and at the same time, some may show same growth even if they are not of same age. Measuring girth of the stem, counting growth rings or taking account of the one cohort and then following it strictly are some parameters by which age structure in plant population is built up.



Survivorship curves:

Survivorship curves are graphical representation of a population growth form and they help in viewing the population future and status. The graph is plotted from the data of the life span and demarcating the different age groups, at different times during this life span.

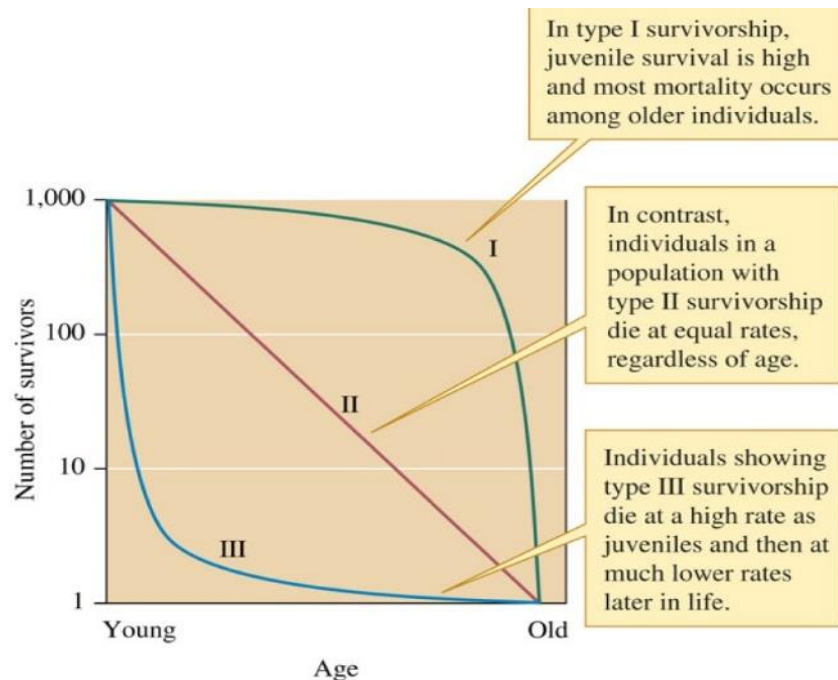
The Survivorship curve is drawn by taking into account the percentage of living individuals at every age or life stage. The number of survivors (density) is plotted on vertical axis on a log scale. Three types of graphs are obtained from different groups of plants and animals (Fig.2&3):

Type I: It indicates high mortality rate at old age, most individuals of the population live their full life. Eg. Mammals (especially human beings)

Type II: It indicates a steady mortality rate throughout the life span. Eg. Birds

Type III: It indicates high mortality in the young phase. Eg. plants, insects and invertebrates

The Survivorship curve helps in identifying the critical stage of the population or life cycle of the individuals at which mortality is high.



Population growth curves:

In theory, any kind of organism could take over the Earth just by reproducing. For instance, imagine that we started with a single pair of male and female rabbits. If these rabbits and their descendants reproduced at top

speed, there would be enough rabbits to cover the entire land mass of the earth in 7 years! If we used *E. coli* bacteria instead, we could start with just one bacterium and have enough bacteria to cover the Earth with a 1-foot layer in just 36 hours. But that is not the case in reality. Why, then, don't we see these populations getting as big as they theoretically could? *E. coli*, rabbits, and all living organisms need specific resources, such as nutrients and suitable environments, in order to survive and reproduce. These resources are limited, and a population can only reach a maximum size that matches the availability of resources in its local environment. Population ecologists use a variety of mathematical methods to model **population dynamics** (how populations change in size and composition over time). Some of these models represent growth without environmental constraints, while others include "ceilings" determined by limited resources. Mathematical models of populations can be used to accurately describe changes occurring in a population and, importantly, to predict future changes.

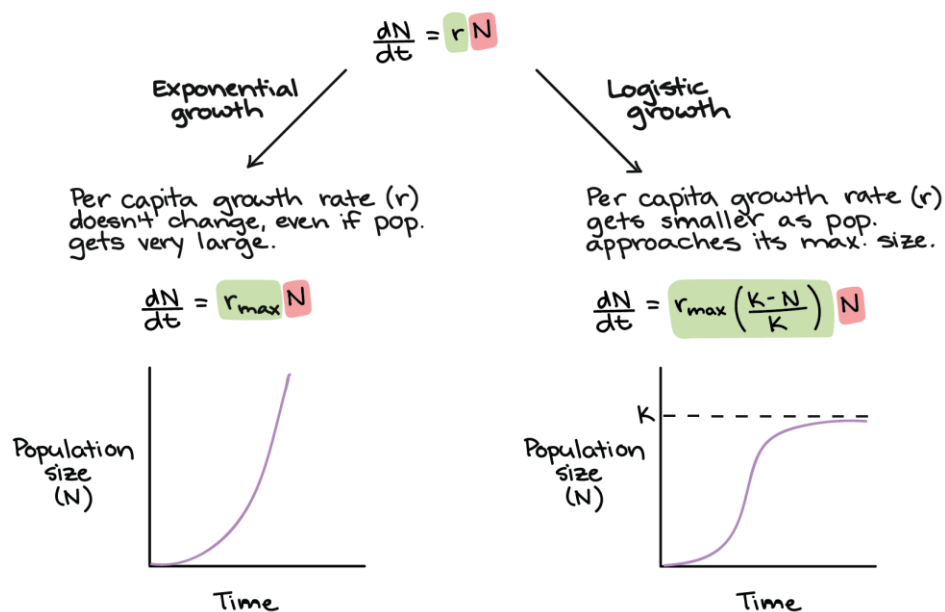
To understand the different models that are used to represent population dynamics, there is a general equation for the **population growth rate** (change in number of individuals in a population over time):

$$\frac{dN}{dt} = rN$$

In this equation, $\frac{dN}{dt}$ is the growth rate of the population in a given instant, N is the population size, T is time, and r is the *per capita* rate of increase (how quickly the population grows with respect to every individual already in the population.)

The equation above is very general, and we can make more specific forms of it to describe two different kinds of growth models: **exponential** and **logistic**.

- When the *per capita* rate of increase (r) has the **same** positive value regardless of the population size, then we get **exponential growth**.
- When the *per capita* rate of increase (r) **decreases** as the population increases towards a maximum limit, then we get **logistic growth**.



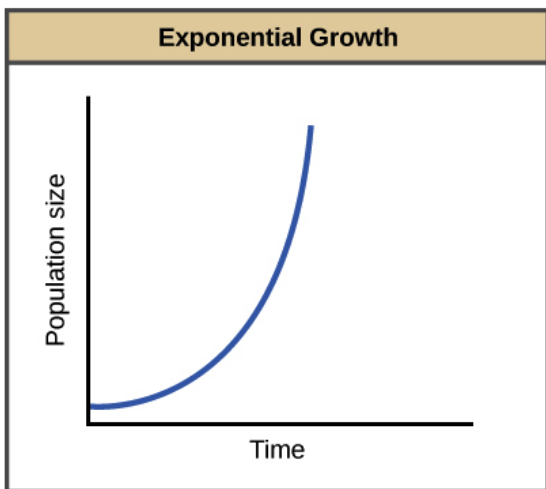
Exponential growth:

Bacteria grown in the lab provide an excellent example of exponential growth. In **exponential** growth, the population's growth rate increases over time, in proportion to the size of the population.

Let's take a look at how this works. Bacteria reproduce by binary fission (splitting in half), and the time between divisions is about an hour for many bacterial species. To see how this exponential growth, let's start by placing 1000 bacteria in a flask with an unlimited supply of nutrients.

- After 1 hour: Each bacterium will divide, yielding 2000 bacteria (an increase of 1000 bacteria).
- After 2 hours: Each of the 2000 bacteria will divide, producing 4000 (an increase of 2000 bacteria).
- After 3 hours: Each of the 4000 bacteria will divide, producing 8000 (an increase of 4000 bacteria).

The key concept of exponential growth is that the population growth rate—the number of organisms added in each generation—increases as the population gets larger. And the results can be dramatic: after 1 day (24 cycles of division), the bacterial population would have grown from 1000 to over 16 billion! When population size, N , is plotted over time, a **J-shaped** growth curve is made.



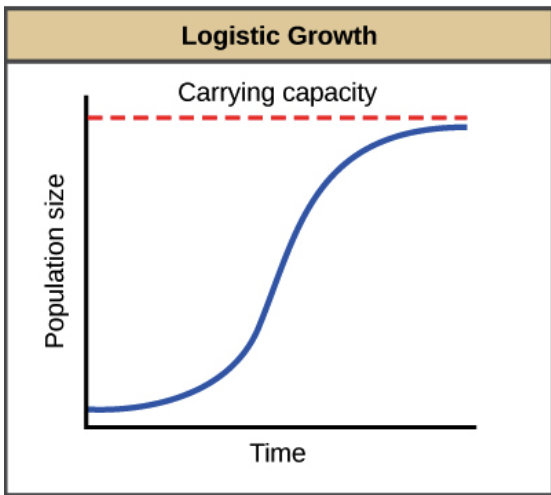
When a population shows exponential growth, the per capita growth rate (r) is represented by r_{\max} i.e. maximum per capita increase. This can vary from species to species. The r_{\max} of bacteria is often larger than that of humans, thus have a greater per capita increase in population under ideal conditions. The maximum population growth rate for a species, sometimes called its biotic potential, is expressed in the following equation:

$$\frac{dN}{dT} = r_{\max} N$$

Logistic growth:

Exponential growth is not very sustainable, since it depends on infinite amounts of resources (which do not exist in the real world).

Exponential growth may happen for some time, if there are few individuals and many resources. But when the number of individuals gets large enough, resources start to get exhausted, slowing down the growth rate. Eventually, the growth rate will **plateau**, or level off, making an **S-shaped curve**. The population size at which it levels off, which represents the maximum population size a particular environment can support, is called the **carrying capacity**, or **K**.



Mathematically, logistic growth can be represented by:

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

where, $K-N$ gives the number of individuals that can be added to the population in order to reach carrying capacity; the fraction of $(K-N)/K$ represents the fraction of carrying capacity that has not been used up.

When the population is tiny, N is very small compared to K . The $(K - N)/K$ term becomes approximately (K/K) i.e. 1, giving us back the exponential equation. This fits with our graph above: the population grows near-exponentially at first, but levels off more and more as it approaches K .

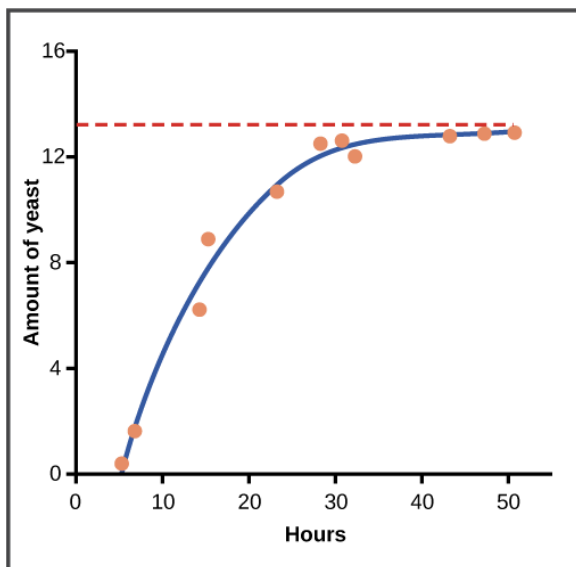
Factors affecting carrying capacity:

Any kind of resource important to a species' survival can act as a limiting factor. For plants, the water, sunlight, nutrients, and the space to grow are some key resources. For animals, important resources include food, water, shelter, and nesting space. Limited quantities of these resources results in competition between members of the same population, or **intraspecific competition** (*intra-* = within; *-specific* = species).

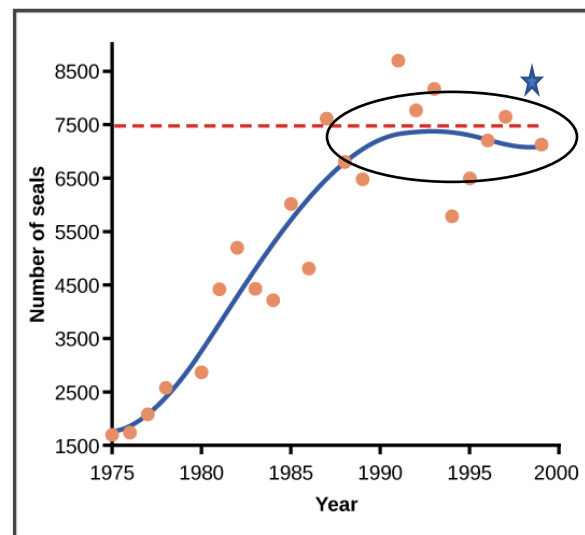
Intraspecific competition for resources may not affect populations that are well below their carrying capacity, where resources are plentiful and all individuals can obtain what they need. However, as population size increases, the competition intensifies. In addition, the accumulation of waste products can reduce an environment's carrying capacity.

★ The population of k -selected species tends to wobble as it approaches the carrying capacity. It can slightly dip below the carrying capacity line but it never touches the line. In reality, the exact value of carrying capacity is never met.

Examples of Logistic growth: Yeast



Population growth in harbor seals in Washington State



Population regulation:

*Limiting factors: A factor is defined to be a limiting factor if a change in the factor produces a change in the equilibrium or average density. For example, a disease may be a limiting factor for a fish population if fish population abundance is lower when the disease is present.

*Regulating factors: A factor is defined to be a regulating factor if the percentage mortality caused by the factor increases with population density; or, alternatively a factor is defined to be a regulating factor if the reproductive rate is reduced as the population rises. For example, a disease may be a regulating factor only if it causes a higher fraction of losses as fish density goes up.

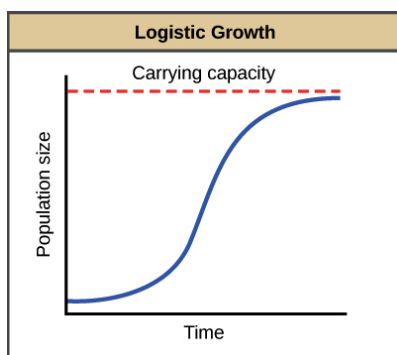
All populations on Earth have limits to their growth. Even populations of rabbits that reproduce very quickly, don't grow infinitely large. And although humans are reproducing very rapidly, we too will ultimately reach limits of population size imposed by the environment. What exactly are these environmental limiting factors? Broadly, the factors that regulate population growth can be split into two main groups: density-dependent and density-independent.

Density-dependent regulation:

For example, imagine a population of organisms - let's say, deer - with access to a fixed, constant amount of food. When the population is small, the limited amount of food will be plenty for every individual. But, when the population gets large enough, the limited amount of food may no longer be sufficient, leading to competition among the deer. Because of the competition, some deer may die of starvation or fail to have offspring, decreasing the per capita (per individual) growth rate and causing population size to plateau or shrink.

In this scenario, competition for food is a density-dependent limiting factor. In general, we define density-dependent limiting factors as factors that affect the per capita growth rate of a population differently depending on how dense the population is at that particular moment. Most density-dependent factors make the per capita growth rate go down as the population increases. This is an example of **negative feedback** that limits population growth.

Density-dependent limiting factors can lead to a **logistic** pattern of growth, in which a population's size levels off at an environmentally determined maximum called the carrying capacity. Sometimes this is a smooth process; in other cases, though, the population may overshoot carrying capacity and be brought back down by density-dependent factors (wobble seen in case of harbor seals population in Washington).



Density-dependent limiting factors tend to be biotic - living organism-related - as opposed to physical features of the environment. Some common examples of density-dependent limiting factors include:

- Competition within the population: When a population reaches a high density, there are more individuals trying to use the same quantity of resources. This can lead to competition for food, water, shelter, mates, light, and other resources needed for survival and reproduction.

- **Predation:** Higher-density populations may attract predators that were not attacking the previously sparser population. When these predators eat individuals from the population, they decrease its numbers but may increase their own population. This can produce interesting, cyclical patterns.
- **Disease and parasites:** Disease is more likely to break out and result in deaths when more individuals are living together in the same place. Parasites are also more likely to spread under these conditions.
- **Waste accumulation:** High population densities can lead to the accumulation of harmful waste products that kill individuals or impair reproduction, reducing the population's growth.

Density-dependent regulation can also take the form of behavioral or physiological changes in the organisms that make up the population. For example, rodents called Lemmings respond to high population density by emigrating in groups in search of a new, less crowded place to live. This process has been misinterpreted as a mass suicide because the lemmings sometimes die while trying to cross bodies of water.

Density-independent regulation:

The second group of limiting factors consists of *density-independent* limiting factors that affect *per capita* growth rate independent of how dense the population is. As an example, let's consider a wildfire that breaks out in a forest where deer live. The fire will kill any unlucky deer that are present, regardless of population size. An individual deer's chance of dying doesn't depend at all on how many other deer are around. Density-independent limiting factors often take the form of natural disasters, severe weather, and pollution.

Unlike density-dependent limiting factors, density-independent limiting factors alone can't keep a population at constant levels. That's because their strength doesn't depend on the size of the population, so they don't make a "correction" when the population size gets too large. Instead, they may lead to erratic, abrupt shifts in population size. Small populations may be at risk of getting wiped out by sporadic, density-independent events. Such events are very unpredictable and may have a massive impact on populations in some cases while they may leave entire populations unharmed in others.

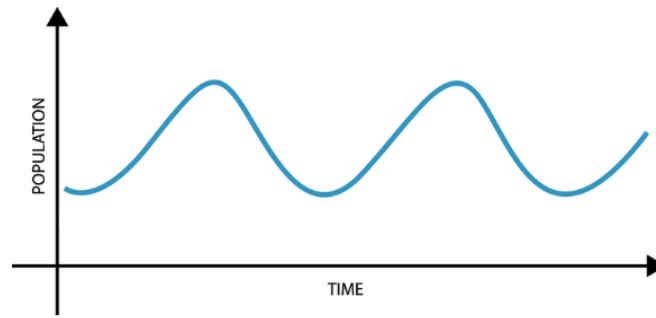
Population fluctuations

In the real world, many density-dependent and density-independent limiting factors can—and usually do—interact to produce the patterns of change we see in a population. For example, a population may be kept near carrying capacity by density-dependent factors for a period, then experience an abrupt drop in numbers due to a density-independent event, such as a storm or fire.

However, even in the absence of catastrophes, populations are not always stably at carrying capacity. In fact, populations can fluctuate, or vary, in density in many different patterns. Some undergo irregular spikes and crashes in numbers. For instance, algae may bloom when an influx of phosphorous leads to unsustainable growth of the population. Other populations have regular cycles of boom and bust.

Population cycles

Some populations undergo cyclical oscillations in size. Cyclical oscillations are repeating rises and drops in the size of the population over time. If we graphed population size over time for a population with cyclical oscillations, it would look roughly like the wave below.



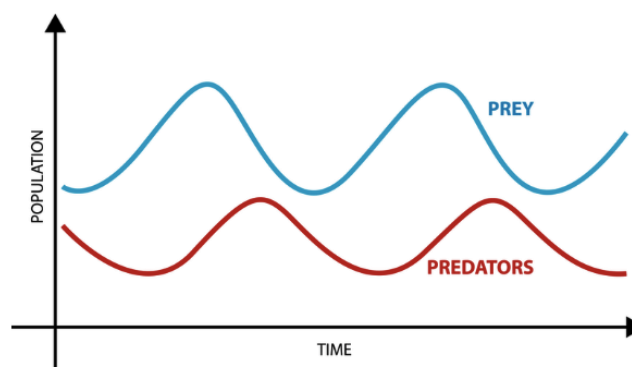
In many cases, oscillations are produced by interactions between populations of at least two different species. For instance, predation, parasite infection, and fluctuation in food availability have all been shown to drive oscillations. These density-dependent factors do not always create oscillations, however. Instead, they only do so under the right conditions, when populations interact in specific ways.

Case study: Lemmings

As an example, let's look at a population of lemmings found in Greenland. For years, this population had cyclical oscillations in size, with a period—the length of a full cycle—of about four years. Ecologists found that the cycle could be explained by interactions between the lemming and four predators: the owl, fox, skua (a bird) and stoat. The owl, fox, and skua are opportunistic predators that can use various food sources and tend to eat lemmings only when they are abundant. The stoat, in contrast, eats only lemmings.

Why does the cycle happen? We can start by following the lemmings at a low point in their cycle. Because the population density is low, the owls, skuas, and foxes will not pay too much attention to the lemmings, allowing the population to increase rapidly. As the lemming population grows, the stoat population also grows, but with a lag. This reflects that stoats reproduce only once a year—unlike lemmings, which reproduce more or less constantly—and can only leave numerous offspring after they've had a period in which their food source, lemmings, is abundant. As the lemming density increases, owls, foxes, and skuas are attracted and start preying on the lemmings more frequently than when they were scarce. This acts as a density-dependent limit to lemming growth, and it keeps lemmings from getting ahead of the stoats in numbers. The stoat population thus overshoots and becomes large enough that it kills off many of the lemmings, leaving few to reproduce and causing a lemming population crash. This crash is followed by a stoat crash with a one-year delay, as the stoats wind up with a greatly reduced food supply. And then the cycle begins again.

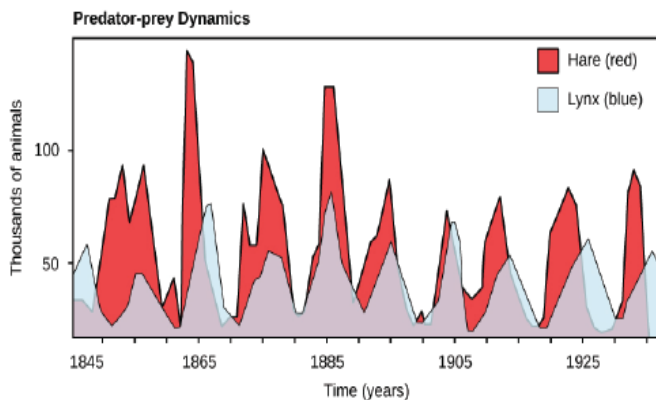
This general pattern of interaction is represented in the graph below. You can see that prey population numbers—such as those of lemmings—drop first and are then followed by predator numbers—such as those of the stoat.



Are other factors besides predator-prey interactions driving this pattern? It's possible, but ecologists were able to reproduce the oscillating pattern in a computer model based only on predation and reproduction data from the field, supporting the idea that predation is a driving factor.

Sad fact: some lemming populations are no longer oscillating. They peaked—per their usual cycle—in 1998 but never recovered from the crash that followed. Ecologists think this may be due to unusually warm winters and changes in snowfall in the Arctic, which may have reduced the snowpack that usually provides protection to the lemmings as they raise their young. As a result, species that are predators of lemmings may die out in regions where the lemming populations have crashed.

Case study: Lynx and Hares



One other famous example of this type of predator-prey interaction involves the Canada lynx- the predator and snowshoe hare- the prey - whose populations have been shown to co-vary in cycles, with a drop in hare numbers predicting a drop in lynx numbers. At first, scientists thought that lynx predation was the key factor that made the hare population drop. We now know that other factors are likely involved, such as availability of food for the hares. Either way, this is another example in which density-dependent factors produce cyclical changes in a population.

Life History Strategies: (r and k selection):

Life history means basic demographic features of a population or species. That includes when organisms first reproduce, how many offspring they have in each round of reproduction, and how many times reproduction occurs. For humans, life history involves a late start to reproduction, few offspring, and the ability to reproduce multiple times.

We can define the life history of a species as its lifecycle, and in particular, the lifecycle features related to survival and reproduction. Life history is shaped by natural selection and reflects how members of a species distribute their limited resources among growth, survival, and the production of offspring.

In the relay race of evolution, getting as many copies of your genes into the next generation as possible is the only goal. As you might imagine, there are many ways to be reproductively successful. One way is to become the dominant animal in a pack, and to monopolize mating opportunities, but another way is to be submissive and sneaky, mating with others when the dominant animal is not around to stop you. {There are no moral judgements. It's just biology} Now imagine that you are an animal faced with the following choice: given limited resources, would you put them all into producing one or a few offspring, and protect them with great ferocity, or would you put a small amount of effort into a much larger number of offspring, and let them each take their chances? Should you measure out your reproductive effort over many seasons, or save it all up for a one-time reproductive event? These **trade-offs** relate to the r/K selection theory of life history strategies.

r-selection: On one extreme are the species that are highly r-selected. '**r**' is for **reproduction**. Such a species puts only a small investment of resources into each offspring, but produces many such low effort babies. Such species

are also generally not very invested in protecting or rearing these young, hence parental care is absent. Often, the eggs are fertilized and then dispersed. The benefit of this strategy is that if resources are limited or unpredictable, you can still produce some young. However, each of these young has a high probability of mortality, and does not benefit from the protection or nurturing of a caring parent or parents. r-selected babies grow rapidly, and tend to be found in less competitive, low quality environments. r-selection is more common among smaller animals with shorter lifespans and, frequently, non-overlapping generations, such as fish or insects. The young tend to be precocial (rapidly maturing) and develop early independence.

K-selection: On the other extreme are species that are highly K-selected. '**K**' refers to the carrying capacity, and means that the babies are entering a competitive world, in a population at or near its carrying capacity. K-selected reproductive strategies tend towards heavy investment in each offspring, are more common in long-lived organisms, with a longer period of maturation to adulthood, heavy parental care and nurturing, often a period of teaching the young, and with fierce protection of the babies by the parents. K-selected species produce offspring that each have a higher probability of survival to maturity. K-selection is more common in larger animals, like whales or elephants, with longer lifespans and overlapping generations. The young tend to be altricial (immature, requiring extensive care).

For example, elephants are highly K-selected, whereas mice are much more r-selected. Among the fishes, most, like the salmon, are r-selected. Some species will even inadvertently eat their own young if they are not immediately dispersed, but a few species, such as the cichlids, are K-selected and provide prolonged care and protection of the eggs and hatchlings. Even among humans, there are a range of strategies toward one or the other extreme. In one family, with ten children, for example, there is no way for the parents to put as much time, energy, or resources into all of them as could be done with an only child. But, with humans, it gets complicated by the fact that others, including siblings, grandparents, blood-relatives, and the larger community all play a role in the nurturing and education of children.

Even plants are capable of r- and K-selected reproductive strategies. Wind pollinated species produce much more pollen than insect pollinated ones, for example, because the pollen has to be carried at random by the wind to a receptive female flower. Eggs too, can be r- or K-selected. The amount of nutrient energy placed in an egg gives it a lesser or greater ability to survive in adverse conditions. One can even compare the reproductive strategies of males and females within a species, when sperm and egg represent different levels of energy investment. Often sperm are resource poor, and produced in large quantities, while eggs are resource rich and produced in smaller numbers. This can lead to differences in behavior between the sexes, often with the result that the female is the choosier sex when it comes to reproduction. This trend is further extended if the female also carries the young (in the case of internal fertilization) or has a greater role in parental care once the babies are born. There are some interesting exceptions that illustrate the rule. Male seahorses are the choosier sex, and they are the ones that incubate the young. In a small fish called the stickleback, the male is also choosier, it is believed, because the female lays her eggs in a nest he constructed and then leaves. The male guards the nest and tends the young for an extended period.

It should be noted that r- and K-selection are the extremes at both ends of a continuum and that most species fall somewhere in between.

Characteristic	r	K
Number of offspring	high	low
Parental care	low	high
Reproductive Maturity	early	late
Size of offspring	small	large
Independence at birth	early	late
Ability to learn	low	high
Lifespan	short	long
Early mortality	high	low

Island Biogeography:

One of the major topics in ecological biogeography is variation in the diversity of species among regions or habitats. Early observations of biogeography involved the examination of the geography of biodiversity around the globe. This was followed by recognition of the species-area relationship - as area increases, the number of species present (diversity) also increases. A great deal of conservation research has been done on islands, because they are small, replicated units of area, isolated from other habitats. They are very useful for species, community, and ecosystem studies. Islands are used as microcosms for studying evolutionary and ecological problems. Alexander Von Humboldt in 1807 stated that larger areas harbor more species than smaller ones.

Islands and Species–Area Relationships

What determines the number of species on an island? Islands typically have fewer species than patches of the same size on continents. Large islands tend to support more species than smaller islands. Preston (1962) formalized that if the area of the island is plotted against the number of species, on a logarithmic scale, the relationship should be a straight line as:

$$\begin{aligned}\log S &= \log c + z \log A \\ S &= cA^z\end{aligned}$$

Where, S= the number of species, c= constant meaning the number of species per unit area and A = the area of the island and z is a constant which varies little between taxa. The relationship between the number of species and area is called a **species area curve**. Two eminent ecologists, the late Robert MacArthur of Princeton University and E. O. Wilson of Harvard, proposed an equilibrium hypothesis to describe the relationship between the number of species found on an island and the area of the island. The traditional non equilibrium hypothesis was that most of the continental species have not reached the islands yet. MacArthur and Wilson (1967) proposed that “**the species composition of an island is a dynamic equilibrium, with the number of species resulting from a balance between colonization and extinction**”. That is, 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. The number of species on an island is increased by new colonisations, but decreased by

extinctions. As long as the rate of new colonisations exceeds the rate of extinction, the number of species goes up but when the rates become equal, the number no longer changes; it is at equilibrium. Wilson collected observations from birds and used these observations to draw island area species curves (Figure 1). Using these curves, MacArthur mathematically described the relationship between immigration and extinction rates of species on an island as a function of the numbers of species already present -- and identified the point where these curves cross as equilibrium, that point where immigration and extinction rates are equal (Figure 2).

When an island is nearly empty, the rate at which new species will establish populations will be high and the extinction rates will be low because few species are available to become extinct. As the resources are limited, the rate at which resident populations go extinct will be high when the island is relatively full. Thus, there must be a point where the two rates are equal -- where input from immigration balances output from extinction. That equilibrium number of species would be expected to remain constant as long as the factors determining the two rates did not change.

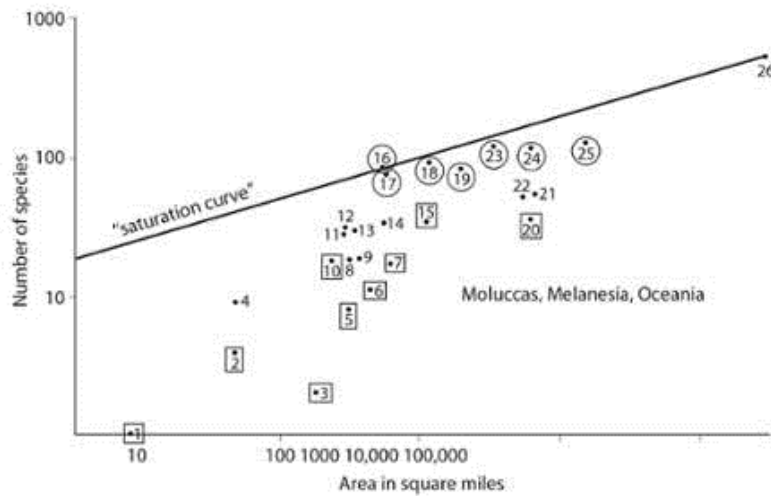


Figure 1: Area-species curves of birds showing area and distance effects (MacArthur and Wilson 1967)

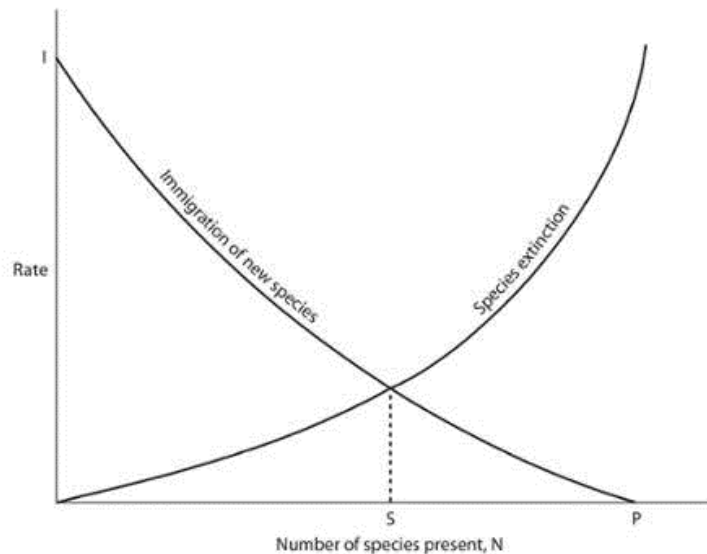


Figure 2: Equilibrium model of a single island showing crossed immigration and extinction curves. The equilibrium species number is reached at the intersection point, S.

Equilibrium Theory of Island Biogeography (ETIB)

The ETIB describes the theoretical relationship between immigration and extinction of species to islands, depending on their size and distance from the mainland. The theory builds on the first principles of population ecology and genetics to explain how distance and area combine to regulate the balance between immigration and extinction in island populations. Two major variables thought to affect extinction rate and immigration rate are: 1) Size of the island, 2) Distance from the mainland.

Island size

As the size of the island increases, immigration rate increases slightly, because the island is a bigger target for dispersing individuals. Extinction rate is lesser on the large islands because larger islands support large population of species which in turn provide buffer to stochastic extinction events.

Distance effect

As the distance from the mainland increases, the immigration rate decreases as the far away islands are more difficult to reach and fewer species are able to cross that barrier. Immigration is higher on near islands than on distant islands (in relation to the mainland), hence the equilibrium number of species present will be greater on near islands. Therefore, the number of species on near, large islands is higher than the number of species on distant, small islands (Figure 3). The theory predicts, everything else being equal, distant islands will have lower immigration rates than those close to a mainland, and equilibrium will occur with fewer species on distant islands. Close islands will have high immigration rates and support more species (Figure 4). By similar reasoning, large islands, with their lower extinction rates, will have more species than small ones -- again everything else being equal (which it frequently is not, for larger islands often have a greater variety of habitats and more species for that reason). Much of ETIB, which was founded on the study of true islands, can be extended to islands in fragmented habitat.

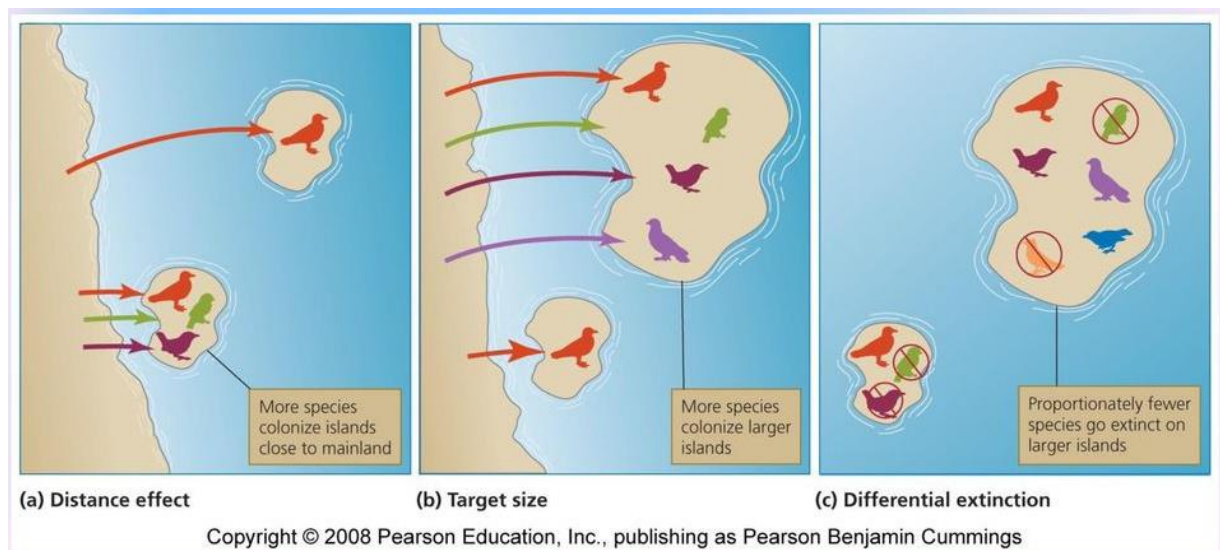
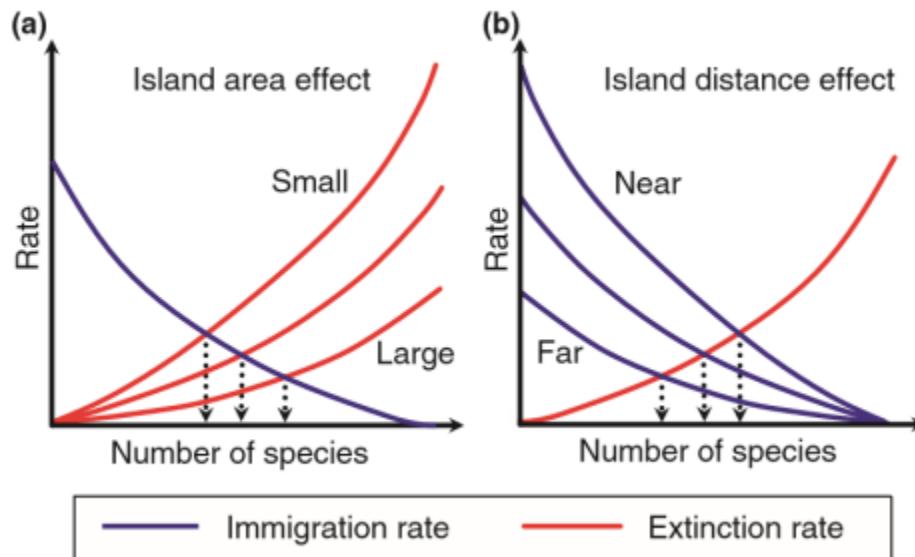


Figure 3: Diagrammatic illustration showing the effect of distance from mainland (a), size of the island (b) and differential extinction rates depending on the size of the islands (c) (From Pearson)



- a) Effect of area of island on species diversity and species richness
 b) Effect of distance of island from mainland on species diversity and richness

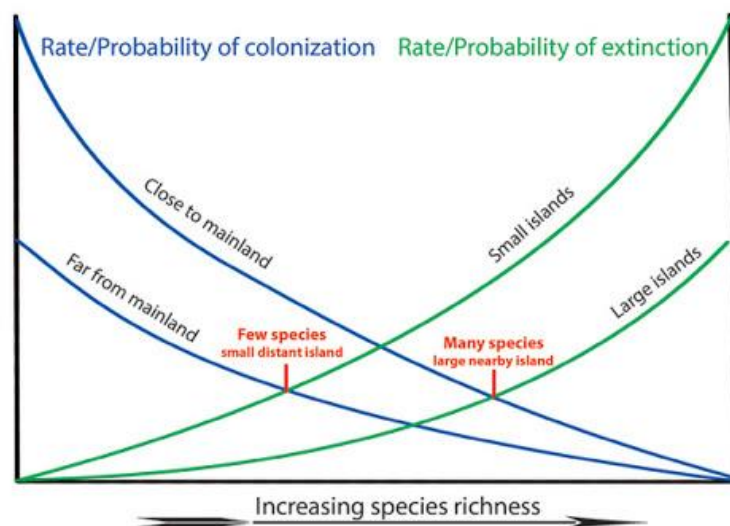


Fig 4: Equilibrium model of several islands of various sizes and distance from the mainland. An equilibrium of species richness occurs at each intersection point of the immigration and extinction curves

Evidence for the equilibrium theory of island biogeography

How well does it explain what we actually observe in nature?

One famous "test" of the theory was provided in 1883 by a catastrophic volcanic explosion that devastated the island of Krakatoa, located between the islands of Sumatra and Java. The flora and fauna of its remnant and of two adjacent islands were completely exterminated, yet within 25 years (1908) thirteen species of birds had recolonized what was left of the island. Between the explosion and 1934, thirty-four species actually became established, but five of them went extinct. By 1984-85, thirty-five species were present. During 1934-1985, a further fourteen species had become established, and eight had become extinct. As the theory predicted, the rate

of increase declined as more and more species colonized the island. In addition, as equilibrium was approached there was some turnover (MacArthur and Wilson 1963).

The authors also tested the theory against experimental data. Wilson & Simberloff (1969) artificially created “miniature Krakatoas” by fumigating small mangrove islets to exterminate all arthropods. Wilson and his colleagues then routinely surveyed the arthropod species that recolonised these islets. They found that the numbers of species on these “miniature Krakatoas” returned to pre-extermination levels within two years, where they remained stable thereafter, which demonstrated that species equilibria do exist. The predicted distance effect was also confirmed: the farther an islet was from the mainland, the fewer species it held.

Island Biogeography Theory and Conservation

Island biogeographic theory has been applied to many kinds of problems, including forecasting faunal changes caused by fragmenting previously continuous habitat. Island biogeographic theory can be a great help in understanding the effects of habitat fragmentation. Island biogeography has become an essential component of conservation biology, particularly in the analysis of preserve design (Diamond 1975). The fragmentation of natural habitats results in smaller patches surrounded by uninhabitable or hostile human environment (McCullough 1996). The remnant patches of habitat, national parks, and nature reserves can be considered islands. The key implications of the theory are that the ultimate number of species that a natural reserve will save is likely to be an increasing function of the reserve's area. The relation between reserve area and probability of a species' survival is characteristically different for different species. Explicit suggestions thus can be made for the optimal geometric design of reserves.
