Chaudhary Mahadeo Prasad College

(A CONSTITUENT PG COLLEGE OF UNIVERSITY OF ALLAHABAD)

E-Learning Module

Subject: Botany

(Study material for Post Graduate Students)

M.Sc. II Sem

COURSE CODE: BOT 508

Ecology and Phytogeography

Unit I: Topic Population Ecology

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Introduction to Ecology

Evolution of Definitions of Ecology

Ecology = from the Greek root OIKOS, “at home”, and OLOGY, “the study of”

Haeckle (1870): “By ecology we mean the body of knowledge concerning the economy of Nature - theinvestigation of the total relations of the animal to its inorganic and organic environment.”

Burdon-Sanderson (1890s): Elevated Ecology to one of the three natural divisions of Biology: Physiology Morphology -Ecology

Elton (1927): “Scientific natural history”

Andrewartha (1961): “The scientific study of the distribution and abundance of organisms”

Odum (1963): “The structure and function of Nature”

Definition**:** *“Ecology is the scientific study of the processes regulating the distribution and abundance of organisms and the interactions among them, and the study of how these organisms in turn mediate the transport and transformation of energy and matter in the biosphere (i.e., the study of the design of ecosystem structure and function).*

Beyond Fundamental Ecology

Applied Ecology: Using ecological principles to maintain conditions necessary for the continuation of present day life on earth.

Industrial Ecology: The design of the industrial infrastructure such that it consists of a series of interlocking "technological ecosystems" interfacing with global natural ecosystems. Industrial ecology takes the pattern and processes of natural ecosystems as a design for sustainability. It represents a shift in paradigm from conquering nature to becoming nature.

Ecological Engineering: Unlike industrial ecology, the focus of Ecological Engineering is on the manipulation of natural ecosystems by humans for our purposes, using small amounts of supplemental energy to control systems in which the main energy drives are still coming from non-human sources. It is the design of new ecosystems for human purposes, using the self-organizing principles of natural ecosystems.

[Note: The popular definition of ecological engineering is "the design of human society with its natural environment for the benefit of both.". *What is the logical flaw in this definition*?]

Ecological Economics: Integrating ecology and economics in such a way that economic and environmental policies are reinforcing rather than mutually destructive.

Urban ecology: For ecologists, urban ecology is the study of ecology in urban areas, specifically the relationships, interactions, types and numbers of species found in urban habitats. Also, the design of sustainable cities, urban design programs that incorporate political, infrastructure and economic considerations.

Conservartion Biology: The application of diverse fields and disciplines to the conservation of biological diversity.

Restoration Biology: Appllication of ecosystem ecology to the restoration of deteriorated landscapes in an attempt to bring it back to its original state as much as possible. Example, prarie grass.

Landscape Ecology: "Landscape ecology is concerned with spatial patterns in the landscape and how they develop, with an emphasis on the role of disturbance, including human impacts" (Smith and Smith). It is a relatively new branch of ecology, that employs Global Information Systems. The goal is to predict the responses of different organisms to changes in landscape, to ultimately facilitate ecosystem management.

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All these disciplines require an understanding of the "organizing principles" of ecosystems, i.e., their ecology. This involves the detailed study of the structure and function of ecosystems in their undisturbed state, and using their designs to:

− determine the resilience of ecosystem functions to human activities.
− design ecosystems which function in the service of human beings with minimal fossil energy input (ideally
none) and minimal waste. − design the industrial infrastructure. − integrate the value of "goods and services" of natural ecosystems into the global economic system.

What is "Sustainability"?: There are many definitions of this one, depending on your perspective. Here's ours: *Sustainability is a property of a human society in which ecosystems (including humans) are managed such that the conditions supporting present day life on Earth can continue.*

Ecology and The Future of Biology "However it is said, the future of biology lies not in the ongoing reduction of biology to molecular tidbits, but in studying biology in its essence; studying the organism and the environment as primary, not derived entities. Both, however, are facets of a single grand problem, the nature of biological organization. Such an emphasis brings to light an entirely different future for biology, one in which understanding the dynamic of the biosphere and the evolution and nature of cellular organization are central issues."

Carl Woese 2006

Levels of Studying Ecology

Biosphere: The earth's ecosystem interacting with the physical environment as a whole to maintain a steady state system intermediate in the flow of energy between the high energy input of the sun and the thermal sink of space (merges with atmosphere, lithosphere, hydrosphere…).

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Biome: Large scale areas of similar vegetation and climatic characteristics.

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***Ecosystem*:** Set of organisms and abiotic components connected by the exchange of matter and energy (forest, lake, coastal ocean). Or, "the smallest units that can sustain life in isolation from all but atmospheric surroundings."

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***Community*:** Interacting populations which significantly affect each other's distributions and abundance(intertidal, hot spring, wetland).

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Population: Group of interacting and interbreeding organisms
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Cell/Organism → Organelle → Molecule → Atom

Population Charachteristics
Introduction
2. Types of Population
3. Features of Population
3.1 Size and Density
3.2 Dispersion
3.2.1 Spatial Distribution
3.2.2 Temporal Distribution
3.2.3 Dispersal

1. Introduction

The common tendency of living beings to stay together in a suitable habitat is the basis of population ecology. Population ecology deals with various features of such groups. These aspects include properties of population, population's growth and regulation of population growth, each of which is essential to understand population's performance and status. Under population ecology, structure and dynamics of population are studied. Understanding population ecology is very important for planning conservation strategies. A population is a group of interbreeding individuals of a same species, occupying the same geographical area at a time.Berryman (2002) has modified this definition as "a group of individuals of the same species that live together in an area of sufficient size to permit normal dispersal and/or migration behavior and in which population changes are largely the results of birth and death processes"

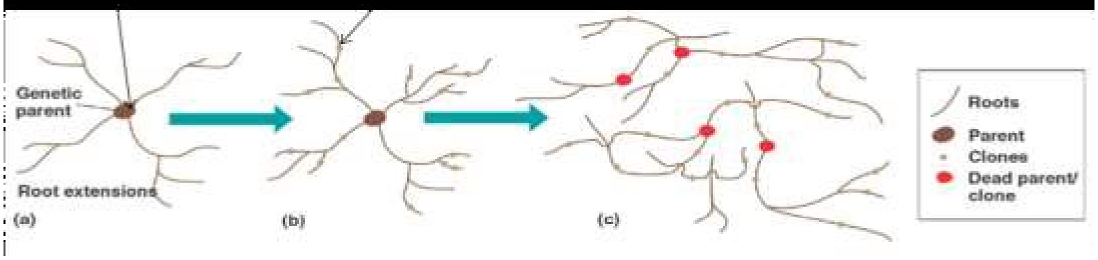
2. Types of Populations

Organisms which make the population may be unitary or modular depending on their reproductive pattern and thus populations are of two types:

2.1 ***Unitary Populations*** **-** In such populations, each individual are derived from zygote and thus are outcome of sexual reproduction. Identification and distinction of each individual of these populations is very easy, moreover the growth of these individuals is determinate and predictable. Most of the animal populations are unitary populations. For example, in a population of sheep it is very easy to identify and distinguish a sheep on the basis of its fixed morphological features like two legs, one head, two ears, its fur etc. and irrespective of age these features are constant and determinate.

2.2 ***Modular Populations*** **-** In these populations single or few individuals arise from zygote and then produce other individuals/modules by asexual means. Individuals of these populations exhibit variation in their morphological features. Plants and few animal groups like sponges and corals are examples of modular population. In a plant population, no two individuals will have the same number of branches leaves, flowers or fruits. The auxiliary buds or floral buds from where these plant parts developed are known as vertical modular units. Grasses and many plant species like pennywort are also examples of modular populations, which propagate vegetatively by means of horizontal stems or roots. Individuals which are produced by sexual reproduction are known as genets while the ones derived from genets are termed as ramet

[redacted]



3. Features Of Population

A population is a group of interbreeding individuals and thus the properties of a population are assessed as of a group, rather than that of an individual. These properties include:

3.1 *Size and Density*

Population size depends upon the geographical area/range occupied by the population and is the total number of individuals in that population. Density of a population is the number of its individuals per unit area. It is an important parameter of a population and is also one of the important indicators of species adaptability to that particular area. It varies with time at one area. Ecologists differentiate density in two types

3.1.1 ***Crude density***: It describes the measure of density for the whole area under consideration, e.g. number of ferns in a rain forest

3.1.2 ***Ecological density***: In measurement of ecological density only that area is considered which actually is occupied by the species like in previous example, most of the ferns grow on the forest floor, where humidity is abundant and only shade-tolerant plants can survive and in that case the density of ferns will be counted only for such areas and not for the other areas of forest where chances of their occurrence are nil. Ecological density concept is based on the assumption that the habitats are heterogeneous and populations do not occupy all the space of the available area, rather they occupy the area that is suitable to them. Though the ecological density measurement is ecologically realistic, in common practice measurements are done for crude density.

3.2 *Dispersion*

It is defined as the placement of individuals and groups of individuals within the habitat they occupy and the process by which this is brought about. Dispersion includes species distribution as well as dispersal movements. Species distribution or dispersion is the pattern of distribution of individuals in a population over space (spatial) and time (temporal). Habitats consist of a spatial – temporal mosaic of many different elements. Exact location of an individual is a major determinant of its immediate fitness.

3.2.1 ***Spatial Distribution*** – It is distribution of individuals over a geographical area and can occur in three patterns:

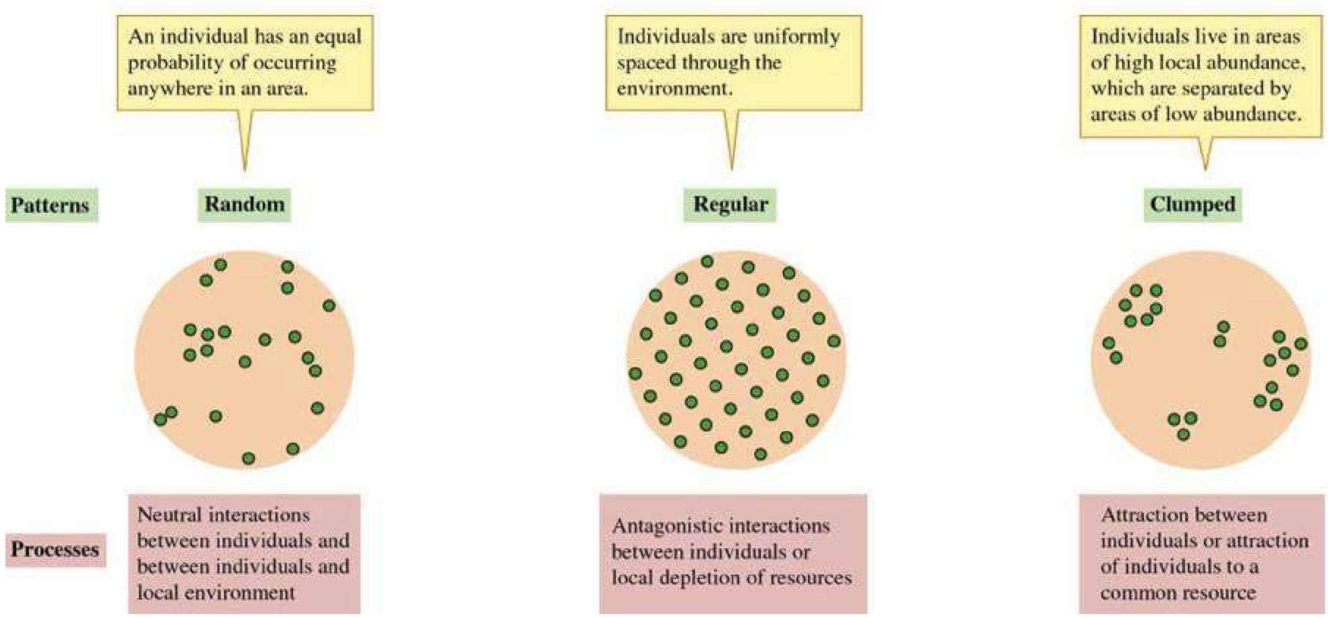
a. Random distribution-A random distribution means position of each individual of a population is independent of the other and chances of occurrence of the individuals is anywhere in the given area and spacing between two individual is unpredictable. This type of dispersion is rare in nature. It can occur only where the environment is uniformly consistent and there is no strong attraction or repulsion among individuals of a population. Seed dispersal through wind may result in random distribution as chances of seed germination and seedling establishment are anywhere:

b. Uniform or regular distribution -In uniform distribution, individuals are equidistantly distributed. It generally occurs because of intraspecific competition. This competition may be for space or for a resource such as moisture or nutrients. For example, trees in a forest are spaced in a way that their canopies do not overlap aboveground and roots do not overlap belowground.

Regular distribution may also occur because of allelopathy , the phenomenon in which toxic exudates released from an individual, do not allow other individual of the same or different species to grow near them. When the inhibition is towards same species, it is known as autotoxicity, alfalfa exhibits phenomenon of autotoxicity . Other example of allelopathy is black walnut; roots of black walnut produce a substance known as juglone which does not allow many plants such as tomato, potato, blueberry to grow within the root zone of this tree. Among animals, Penguins often exhibit uniform spacing by their territorial defense.

Uniform distributionis rare in nature but is common in manmade systems like agricultural fields or planted forests.

c. Clumped distribution-In this type of distribution the individuals of a species are grouped in forms of patches or clumps. This distribution is also known as clustered, contagious or aggregated. It is the most common type of dispersion found in nature. It occurs because of common requirements of organism which are fulfilled at a common place/patch. It is distinctly visible in plant populations; aggregation in plants is affected by their propagative nature and their specific environmental requirements. Animal populations also show clumped distribution because of their reproductive pattern and social behavior. Co-operation, resource partitioning or protection also adds to clumped distribution pattern. Clumping or aggregation increases group survival value. Clumped distribution can again be random, uniform or clumped.



The spatial distribution of plant populations is an important feature of population structure and it determines the population's ecological preferences, biological characteristics and relationships with environmental factors. In a population the distribution patterns are result of a long- term interaction between the population and environment (Gray and He 2009).The distribution pattern of a population of a plant population differs among species, and the distribution pattern of a single species may vary in diverse habitats, it is scale dependent, for a species it may be clumped at one spatial scale and may be uniform or random at the other scale (Zhang et.al.,2012). Normally random distribution indicates homogenous environment while clumped pattern is indicative of heterogeneity and wide variation of microclimatic regions in a large scale.

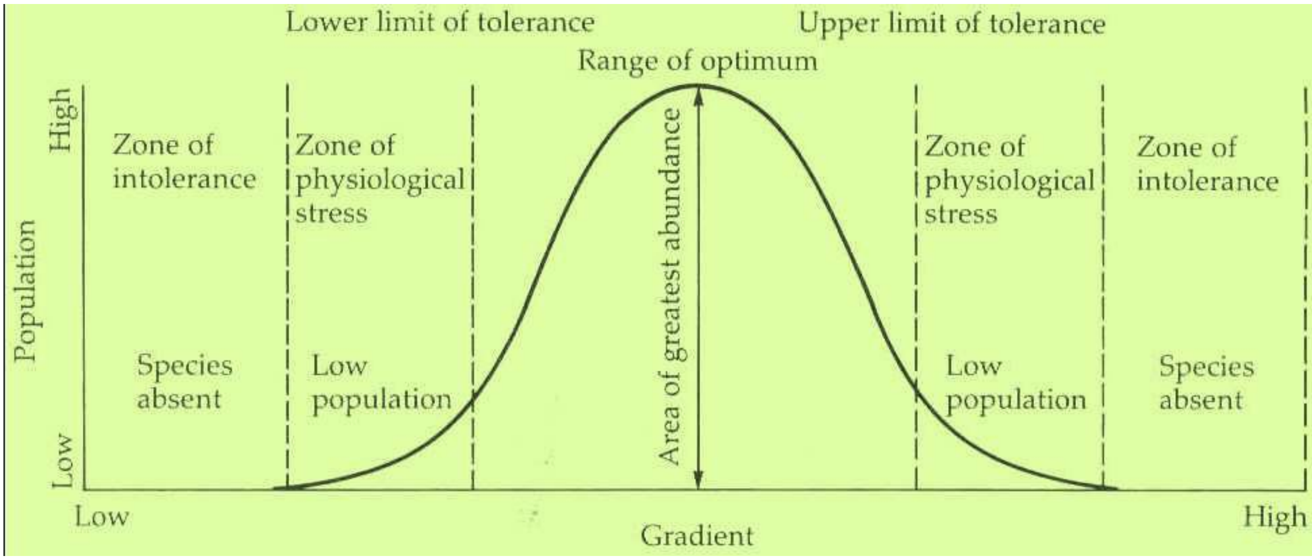
Fig. 4.Distribution Patterns of Individuals in Population

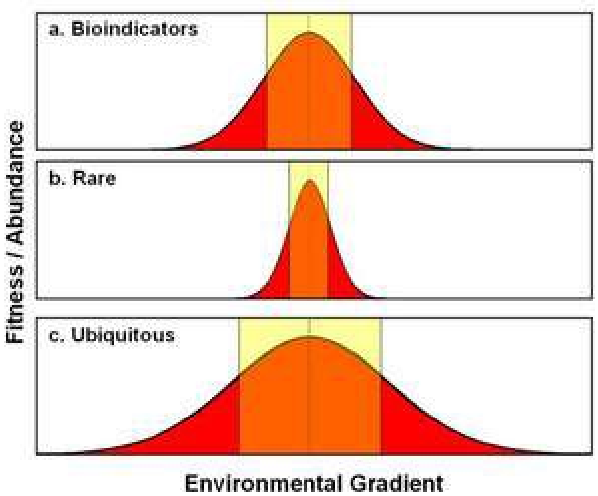
The distribution pattern of species can be determined by using various methods. The Clark-Evansnearest neighbor method can be used to determine if a distribution is clumped, uniform or random .In this method the distance of an individual to its nearest neighbor is recorded for each individual in the sample, enough number (minimum 50) of distance measurements are recorded. The average distance between nearest neighbors is compared to the expected distance to get the ratio R. Values of R give idea about the distribution pattern if R=1the pattern is random , if R > 1 pattern is uniform and if R<1 the pattern is clumped. The Variance/Mean ratio is also one such method, in this method, data is collected from several random samples of a given population. The number of individuals present in each sample is compared to the expected counts in the case of random distribution. The expected distribution can be found using Poisson distribution. If the V/M ratio = 1, the distribution is random. If V/M >1, it is clumped distribution and, if V/M<1, the population is evenly distributed. Test of significance has to be applied in both the methods. The point pattern analysis method of Ripley can also be used to study distribution pattern as well as interspecific relationships of populations at different scales ,it is especially important in plant population studies (Perry et.al,2006)

3.2.2 ***Temporal Distribution*** - It deals with pattern of population distribution over time. The scale of time may be a day, a season, a year or so on. The circadian movements of planktons, change in type of blooming flowers in an area and visit and return of migratory birds, are examples related to temporal dispersion. These examples clearly indicate that status of population at a place changes with time.

3.2.3 ***Dispersal*** **-**Dispersal includes movement of individuals or their offspring's/ propagules away from their originally occupied area to a new habitat. It is movement oforganism beyond its distribution limit.

Most of the organisms follow this process at some stage of their life. The process is important for their survival, growth and reproduction. It also helps in widening the distribution range of the species, as it leads to colonization of new areas. Lack of dispersal among populations impacts a species over a long time,if the species does not spreadto newer areas chances of it becoming endemic rise. It is fundamental process of biogeography. Dispersal, along with natality and mortality, regulates population growth, and plays an important role in evolution through mixing of genes between populations. Successful Dispersal depends on "long distance" transport, withstanding unfavorable conditions during travel and upon early arrival and establishing a viable population. The distribution of species is ruled by Shelford's law of tolerance according to which first the presence and then the success of an organism depend on the completeness of a complex of conditions , each organism--whether the individual or the species population--is subject to an ecological minimum, maximum, and optimum for any specific environmental factor or complex of factors. The range from minimum to maximum represents the limits of tolerance for the factor or complex. Efficient dispersal and successful establishment decide the geographical distribution of species, consequently putting them into category of rare, endemic or ubiquitous species.





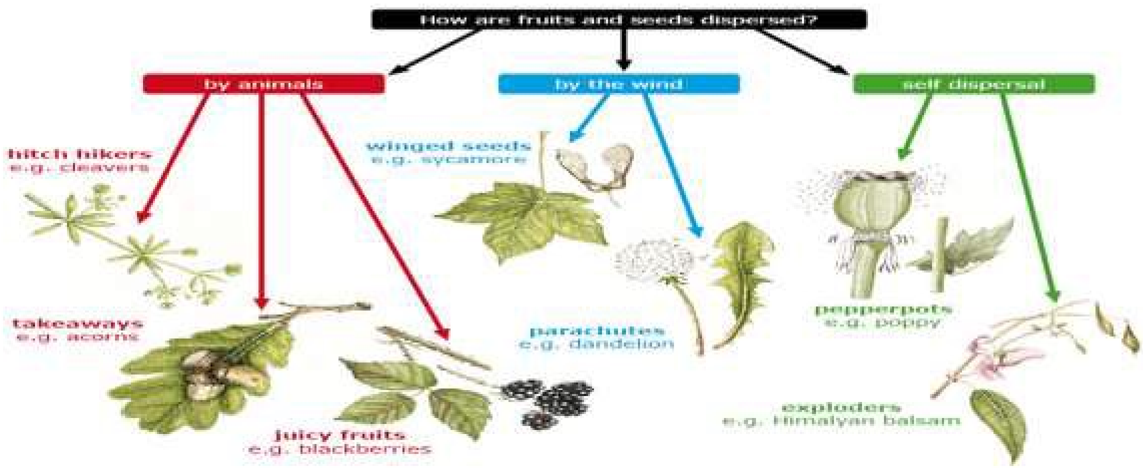
Dispersal movements

Movement of organisms or their propagules involves different ways viz.: Immigration - movement of new ones into a population leading to increase in population size. Emigration - movement of offspring's out of a population leading to decrease in population size. Migratio -periodic movement into or out of a population leading to temporary fluctuations in population size.

Dispersal Mechanisms

They are of two types active dispersal and passive dispersal. Active Dispersal is observed in mobile animals which have potential capacity to move to distant places, the degree of dispersal varies with species as well as with age within a species .These animals are known as vagile animals. Strong fliers like many species of birds, bats and large insects and large aquatic animals are examples of such vagile animals. The Monarch butterfly (Danaus plexippus) exhibits an ideal example of active dispersal, it is a highly vagile insect, capable of flying hundreds to thousands of kilometers moving from north to south America, in different seasons ,in its journey it reproduces and the returning individuals are new offspring.

Passive Dispersal: Plants and some animal groups like corals are not mobile and their dispersal is through their propagules (disseminules) ,these propagules in turn are dispersed by specific dispersal agents, , like wind, water, other animals etc. Such a dispersal is known as passive dispersal and the organisms as pagile.



Plants disperse through their fruits ,seeds, spores etc. Special modifications are observed in these disseminules which help them to successfully disseminate via respective agent. Dispersal of winged fruits by wind and of hooked or sticky seeds via other animals are examples of this phenomenon.

The major factors that influence dispersion patterns of population are 1. Edaphic and climatic features of the habitat 2.Impact of intra- and interspecific competition 3. Reproductive pattern of the population 4. Social behavior and 5. Dispersal movements.

Barriers to Dispersion

Limitations are imposed on dispersal of a species by various types of barriers ,there are physical barriers like drastic change in nature of habitat (e.g. land to water),physiological barriers like change in temperature range to which a species is not accustomed or anthropogenic barriers like construction of buildings ,roads etc. which block the dispersal. Successful dispersal depends on efficient transport and successful establishment.

These barriers modify the level of dispersal and consequently exert effects on population dynamics and genetic structure.

3.2.4 Cimate change and Dispersal

Dispersal processes are strongly affected by climate change and assessment of this is very essential for visualizing status of a species' population.It is the major decisive factor to decide the geographical range of a species because of its implications in the abilities of a speciesto cope with global environmental changes either in resisting reductions in available suitable conditions or in exploiting expansions in those conditions (Gaston, 2009).Climate change is posing a great impact on species range and ecologist are paying immense attention to it. Brooker et.al.(2007) have suggested that dispersal ability and species interactions are important biological processes useful in range modeling of a species.

Population Growth

1. **Introduction**
2. **Processes governing growth of population**:

Natality
Mortality
Immigration
Emigration

3. **Growth Models**

Exponential model
Logistic Model

4. **Time Lags**

Reaction time lag 'w
Reproductive time lag 'g'

1. Introduction

Populations are dynamic entities, the properties of populations change all the time, and the rate of change can vary from very low to high. Even in populations that do not change in density, the individuals change and are replaced. They take birth, grow, reproduce and die. The changes taking place during life span of individuals are not same for all, the performance and behavior changes more, when they are in groups. The growth of a population is dependent on many such changes. Processes like natality, mortality immigration and emigration are direct causes for the changes in the population's dimensions, composition and dynamics. Studying changes in populations' dimensions helps in predicting future changes in population sizes and growth rates. As the response varies with species, these studies help in predicting future compositional changes in community structure. Population growth studies of invasive and pathogenic species help in their management and eradication. Population growth studies help in predicting size of population to be achieved in due course of time.

2. **<u>Processes governing growth of population</u>:** The growth depends upon four important processes which are: Natality, Mortality, Immigration and Emigration. Among the four governing processes of population growth, natality and mortality are related to life history strategies while immigration and emigration are dispersal movements.

***Natality*:** It is the birth rate and is the prime factor leading to addition of new individuals to the population. It is also known as fecundity. The birth rate of the population is again influenced by various factors like type of species, environmental constraints or conditions and the number of reproducible individuals.It is an expression of the production of new individuals in the population. Natality is of two types:

i.Absolute/Potential/ Physiological natality: The maximum number of individuals that can be theoretically produced per individual under ideal environmental conditions is called as absolute natality. It is constant for a given population and expresses its biological limit. The absolute natality is calculated under conditionswhen there is no constraint upon the process; wild populations hardly reach this limit.

ii.Realized/ Ecological Natality: The amount of successful reproduction which actually takes place in due course of time is known asrealized natality. It is influenced by environmental conditions, resource availability and density of population.
The natality may also be expressed as **specific natality** that refers to population increase under specific conditions. It is not constant for a given population.
Natality rate is expressed in two ways **crude birth rate** and **specific birthrate**.Crude birth rate expresses total population growth per unit time, while specific birth rate is in relation to a specific criterion. Specific birth rate is used in calculating natality rate in animal populations, where it is expressed as an age-specific schedule of births. This is done by counting number and age classes of females present in a population. By calculating specific birth rate, the results are seen in an **age-specific schedule of births** i.e. the number of offspring produced per unit time by females in different age classes. It is also referred as fecundity in demographic studies.The expressions of natality are:

$\Delta N_n / \Delta t$= Absolute/ crude natality/birth rate

$\Delta N_n / N\,\Delta t$= specific natality/ birth rate i.e. the number of new Individuals added / unit time/ unit population

N = Total population or only the reproductive part of the population

Nn = New individuals added to the population

Δt = time lapsed during change in population

In plant populations determining natality is more difficult because various factors make it difficult to measure. Fluctuation in quantity of seed production, year to year and age class to age class are such factors, dormancy and unsuccessful germination also make it difficult to get a clear estimate of natality in plant populations.

Mortality:It refers to the death of individuals in a population and is responsible for decrease in size of population. It is also of two types:

i. **Minimum / Physiological Mortality/ Physiological longevity:** When the individuals of the species attain full maturity and die according to their life span, their mortality is described asphysiological mortality.

ii. **Ecological/ Realized Mortality:** When the death rate is influenced by various factors like unfavorable conditions, lack of resources, competition or any epidemic, the mortality rate may increase and it is known as realized mortality.

Natality and Mortality both are species specific but the ultimate outcome is influenced by other pressure also.There are intrinsic and extrinsic factors that control natural mortality rates and these factors are linked with individual metabolism (McCoy &Gillooly,2008)

***Immigration*:** It is the movement of new ones into a population leading to increase in population size.

***Emmigration*:** It is the movement of offspring's out of a population leading to decrease in population size. These processes are very dominant and can be easily calculated for animal populations while in case of plant populations these processes are not distinctly visible. In Plant Population seeds or propagule dispersal play an important role in these processes especially in emmigration.

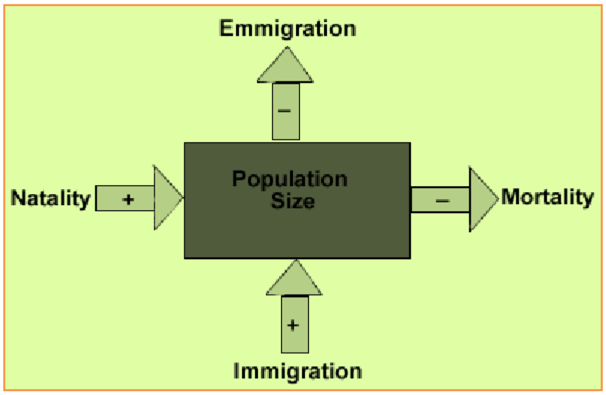


Fig.1 Influence of natality, immigration, mortality and emigration on population.

The Influence can be expressed as:

$$\mathbf{N_t = N_0 + B - D + I - E}$$

Where

N_0 = the population size at some arbitrary starting time (time zero)
Nt = the population size at some future time *t*
B = Birth rate / Natality
D = Death rate/ Mortality
I = Immigration
E = Emigration

3. **<u>Growth Models</u>:** Two most significant models of population growth based on reproduction of organisms are **exponential** and **logisticmodels** .Former is for situation where resources are essentially unlimited and therefore individuals do not compete, later is for situations where there are limited resources and therefore members of the population must compete for these resources.

***Exponential model*:** is associated with the name of Thomas Robert Malthus (1766-1834) who first realized that any species can potentially increase in numbers according to a geometric series. Main parameters to be considered are:

N -- the population size
N_0 -- the population size at starting time (time zero)
Nt -- the population size at some future time *t* (where *t* can have any positive value)

When the ratio of the population size in two adjacent time periods (for instance *t* =0 and *t* = 1) is taken, we obtain the factor by which the population increases during one unit of time, we call this factor **λ**. Thus:

$$\lambda = Nt/ N_0$$

If a population increase is double in one unit of time then λ is 2; if tripled then λ is 3 and so on. When population remains stable $\lambda = 1$ that means $Nt=N_0$, if increases $\lambda > 1$ and $Nt > N_0$ and if decreases $\lambda<1$ and $Nt < N_0$. When the rate of change of a population's size has to be calculated we can state that:

$$\Delta N/\Delta t = B + I - D - E$$

WhereΔN =Difference in population size in a time duration
Δt=Difference in time

If we assume that: I = E the equation will be

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

.
If **B** is replaced by ***b*** *i.e.* the birth rate for short time interval and **D** *by* ***d*** i.e. the death rate for a short time interval ,***b*** and *d* will be instantaneous birth and death rates respectively which are determined as *b*=B/N and *d*=D/N. In situation where time interval is very short and instantaneous rates are to be calculated Δ is replaced by a derivative d and the equation will be modified as

$$dN/dt = bN- dN =(b-d)*N$$

in the equation *(b-d)* is net addition of individuals and indicates the instantaneous rate of increase (***r***), putting this value in it , the equation will be

$$dN/dt = rN$$

When t is large and exponential growth has to be calculated the equation used is

$$Nt = N_0*\exp(r-t) = N_0^{ert}$$

There are three possible outcomes of this model viz.1. When r = 0, population will not change 2.when r >0,population will grow very fast and 3.when r < 0 population will decline suddenly. Exponential model assumes that all individuals of the population have same reproductive potential and there is no age structure, reproduction is continuous and resources are unlimited. There are different versions in which growth rates are expressed like

$$rN = \Delta N / N \Delta t \qquad \text{i.e. Specific Growth Rate}$$

$$rN = \Delta N / \Delta t \times 100 \quad \text{i.e. Percentage Growth Rate}$$

a version of r is $\mathbf{r_o/r_{max}}$ that is called as intrinsic rate of increase and is a measure of biotic potential of the population The difference between $\mathbf{r_{max}}$ and actual **r** gives measure of environmental resistance. The exponential growth is exhibited by short lived species like microbes, annual plants etc.

Logistic Model: The population growth is under influence of many factors and thus there are limitations on the population growth. The exponential equation is applicable till the situations are unlimited. e.g. **r** is constant (rate of growth) and **N** does not decrease, enrollment is same and there is no immigration and emigration, but in nature it is not possible and to predict growth of population under limitations Logistic model was developed by Belgian mathematician Pierre-Francois Verhulst in 1838, who suggested that the rate of population increase may be limited, by population density.An identical model was proposed by Raymond Pearl and I.J.Reed in 1920 the logistic model is now knowns as Verhulst – Pearl logistic model. The model proposes that when a population starts growing, resources are ample but as the density increases, competition for resources arise and gets intensified with further increase in density. As a result population growth rate declines with population numbers, N, and reaches 0 when N = **K**. Parameter **K** is the upper limit of population growth and it is called carrying capacity It is defined as the maximum number of individuals of a certain population that can survive in a given habitat. It is assumed that any number of individuals beyond *K* simply cannot survive -- either they die or they immigrate to a better place.The dynamics of the population under this situation is described by the logistic equation which is a differential equation:

$$dN/dt = rN(K-N/K) = rN(1-N/K)$$

The (1-N/K) is the unutilized opportunity for population growth. Logistic model has two equilibria: N = 0 and N = K. The first equilibrium is unstable because any small deviation from this equilibrium will lead to population growth. The second equilibrium is stable because after small disturbance the population returns to this equilibrium state. The two ecologically important processes, reproduction and competition are involved in the logistic model .Both of these processes are density dependent .This type of growth is exhibited by long lived species and is mostly observed in established systems.

4. <u>Time Lags</u>: The logistic equation suggests that the populations function as a system which is regulated by positive and negative feedback. The positive feedback is mostly by resources and they stimulate the growth while the negative feedback is brought about by competition as the N approaches K the density dependency works. Even these feedbacks do not work smoothly and many a times K is not achieved and this occurs because of certain lags. The two important lags are:

Reaction time lag 'w':This was denoted by Kreb 1985.. It is the lag between environment change and corresponding change in the rate of population growth, including this in logistic equation the equation is modified as

$$dN/dt = rN\,(K- N_{(t-w)}/K)$$

Reproductive time lag 'g':It is the lag between environment change and consecutive change in the derivation of reproductive maturity, incorporation of this in the equation modifies equation as

$$dN/dt = rN_{t-g}\,(K- N_{(t-w)} / K)$$

both these time lags result in fluctuation of population growth and bring rise and fall from K.

5. <u>Summary</u> Populationshave an inherent capacity to grow,their growth depends upon their birth and death rate ,and on immigration and emigration of individuals .Growth of population can be predicted by the growth models .Exponential growth model is applicable to short lived and fast growing species ,while the logistic model is followed by long lived and slow growing species ,population growth of such species is controlled by the carrying capacity.

Population Regulation

1. Introduction

Population growth studies help scientists to understand what causes changes in population size and growth rates. Studying how and why populations grow or decline is important to know as it helps in predicting population's fate in future. It also helps in understanding how organisms interact with each other and with their environments. Impact of changing environment can be assessed, once we know its influential role on the population growth. Understanding population growth is important for predicting, managing, monitoring, and eradicating pest and disease outbreaks, in biodiversity conservation and in knowing fate of an invasive species. Population growth forms, strategies and regulations are important aspects of population growth studies.

2. Population growth forms

The growth of population is measured as increase in its size over a period of time and populations show characteristic patterns of growth with time. These patterns are known as population growth forms
There are two basic population growth forms.

2.1.*J - shaped population growth form*. - In this growth form, the population grows exponentially and after attaining the peak value, crashes abruptly.(Fig.1)The equation will be: $dN/dt = rN$; with the definite limit of N (the number of individual)

2.2.*S -shaped population growth form* -This form shows sigmoid growth curve, where population size changes against time, the population shows an initial gradual increase in population size, followed by an exponential increase and then a gradual decline to near constant level.(Fig.1). Sigmoid growth curve is formed of five phases.

i. Lag phase - Period where individuals adapt to the new environment.

ii. Positive acceleration phase - Period of slow increase in the population

iii. Logarithmic or exponential phase - Period of rapid rise in population due to availability of food and requirements in plenty and no competition.With abundance of resources the population expands exponentially into the habitat.

iv. Negative acceleration phase /Transition Phase - Period in which there is a slow rise in population as the environmental resistance increases. Resources are reduced and become limiting in the growth of the population. As the population grows, there will be increased competition between the individuals of that population for the same resources, resulting in survival of some and elimination of others, the rate of population increase is slow. Along with the reduced rate of population growth there will be selection (survival and reproduction) of those individuals within the population which are best suited to explore the resources.

v. Stationary phase/The Population plateau - where the population remains constant over considerable long time (may be for generations). Constancy in population growth indicates that Natality + Immigration = Mortality + Emigration. At this point in time the population size is determined by the **carrying capacity (K)** of the habitat.

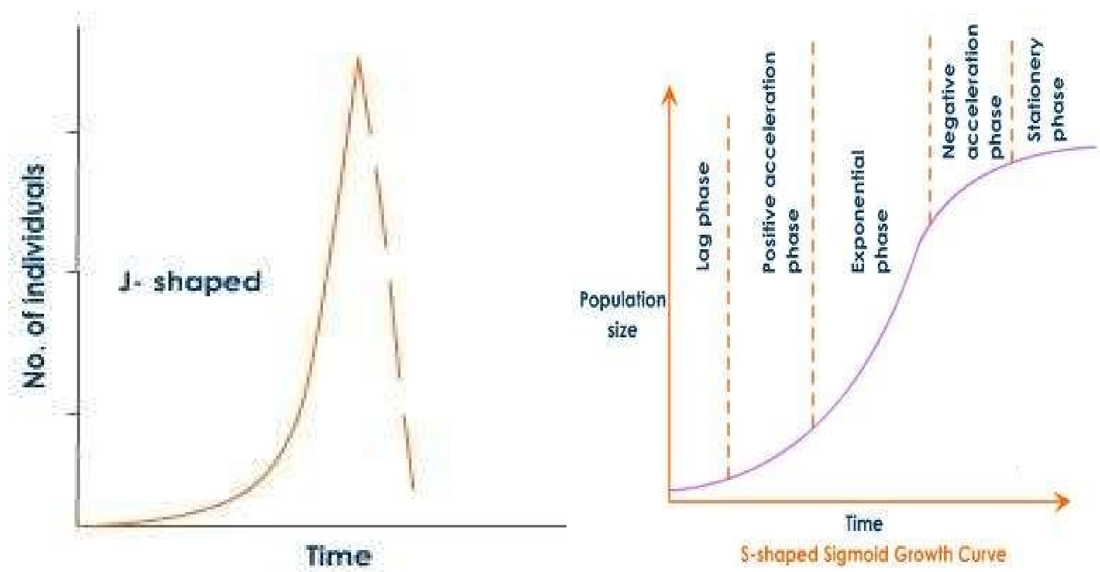


Fig. 1 – J&S shaped curves.

3. <u>**r & K Selected Populations**</u>

The growth curves and equations indicate that the growth rate depends mainly on two factors which are **r** the reproductive potential of organism and **K** the Carrying capacity or environment resistance .When growth curves are plotted, the r pushes the curve upward, while K after sometime pushes it downwards. Depending on the dominance of influence of these factors, populations can be named as **r/ K Selected Population** and species following these strategies are called as **r/ K Selected Species** correspondingly.

Features of r/ K Selected Species

r-selected species are the ones whose populations are governed by their biotic potential (maximum reproductive capacity, r_{max}). Characteristics useful for r-selected species include small size, fast reproduction, short generation time, short life span and ability to disperse offspring widely. These species invade in disturbed habitats, such as freshly burnt grasslands , cut forests or any situation where vacancy is created. Under such conditions these organisms respond opportunistically, becoming the first ones to use the available resources, such as nutrients, light, and living space .Seasonal and annual plants ,the weedy species, bacteria, planktons, pest insects , few birds, rodents, and rabbits are examples of r selection. Many of these species show semelparity a reproductive pattern in which organisms produce all of their offspring in a single reproductive event. Population growth in *r*-selected species behaves according to the exponential growth equation.$\Delta N/ \Delta t = rN$and follows J shaped growth curve.

In K-selected species population growth is limited by carrying capacity (K) and is density dependent. Characteristic features of these species are larger body size, long life span; delayed reproduction, slow growth and poor dispersal .They produce fewer offspring, and provide great parental care. These species are excellent competitors and are equilibrium species. They do well in predictable environment. Examples of K-selected species are humans, tigers, elephants and trees. Many of these species show iteroparous pattern of reproduction where organisms reproduce in successive years or breeding seasons. Population growth in K-selected species is according to the logistic growth equation$\Delta N/ \Delta t = rN\ (1-K/N)$ and follows S shaped growth curve.

The concept of r &K species was developed by Robert MacArthur and E. O. Wilson (1967); the terms were used in their island biogeography theory, to distinguish between types of selection pressures imposed on the species colonizing the islands. The key idea of r/K selection theory is that evolutionary pressures tend to drive organisms in one of the two directions — towards quickly reproducing animals whose specialty is to adopt as many niches as possible using simple strategies, and slowly reproducing animals who are strong competitors in crowded niches and invest substantially in their offspring. The r/K selection theory suggests that r-selected species do best in unpredictable environments, they have the ability to make use of temporary habitats, while K-selected species are competitive species, they have ability to cope with physical and biotic pressures, among them selection favors genotypes, which show slow growth rate initially, even when the density is low and the growth rate is maintained at high density also.Both strategies are necessary for the biosphere. K-Selected populations help to maintain ecosystem constancy while r- Selected populations help in quick invasion of available niches.

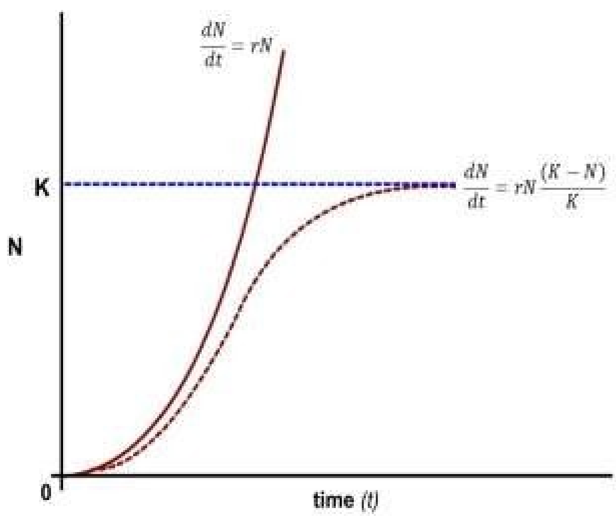


Fig. 2- Comparative expression of r & K selected population's growth

Table 1: Comparative features of r & K species

Feature	r selected	K selected
Growth Pattern	Exponential	Logistic
Growth curve	J shaped	S shaped
Survivorship curve	Type III in which most of the individuals die within a short time but a few live much longer	type I or II in which most individuals live to near the maximum life span
Energy utilization	Waste lot of energy	Efficient energy utilizers
Life span	Short	Long
Population size	Variable	Constant at K
Size of organism	Small	Large
Maturity	Early	Late
Parental care	Nil or very little	Much care for offspring
Mortality	Highly variable & density independent	Often regular & density dependent
Competition	Poor competitors	Good competitors
Environment	Unstable	Stable
Nature	opportunistic	equilibrium
Examples	Annual plants ,Weeds ,Microbe s ,Pest Insects etc.	Perennial trees ,Humans, Elephants

4. Population growth regulation

Populations experience many impositions during their growth which try to regulate or limit their growth.There are two basic categories of population regulating factors: Density dependent factors and Density independent factors.

Density dependent regulation - Density dependent effects influence a population in proportion to its size, as the size of the population increases, effect intensifies. This is due to the fact that individuals are competing for limited resources. Exhaustion of these resources by increasing density of population changes **K,** the carrying capacity, if resources increase K increases and correspondingly the population size. Density can also increase the mortality rate when overcrowding leads to physiological stress and decreased natality .Both these processes try to bring back the population at equilibrium (Fig.3) Intraspecific competitions play very important role in growth regulation and are solely density dependent. In plant populations especially in tree stands, self thinning is a common phenomenon. Clark (1990) demonstrated that even aged stands show density dependent mortality and there is relationship between individual plant growth and population mortality.

Density independent influences -Density-independent factors are those that affect the population in the same proportion irrespective of the population size. Many natural disasters such as storms, hurricanes, droughts or floods affect the population equally. These factors affect but not regulate populations.

W.C. Allee, an ecologist known for his extensive research on social behavior of animals, gave a concept known as Allee's principle. According to Allee, both under-crowding (low population density) and over-crowding (high population density) limit growth and survival of a population. There are a number of examples (in both plants and animals) where Allee's principle holds good. A number of plant species occur in groups, which may be in response to habitat preference or suitable climatic or environmental conditions or due to reproductive strategies.

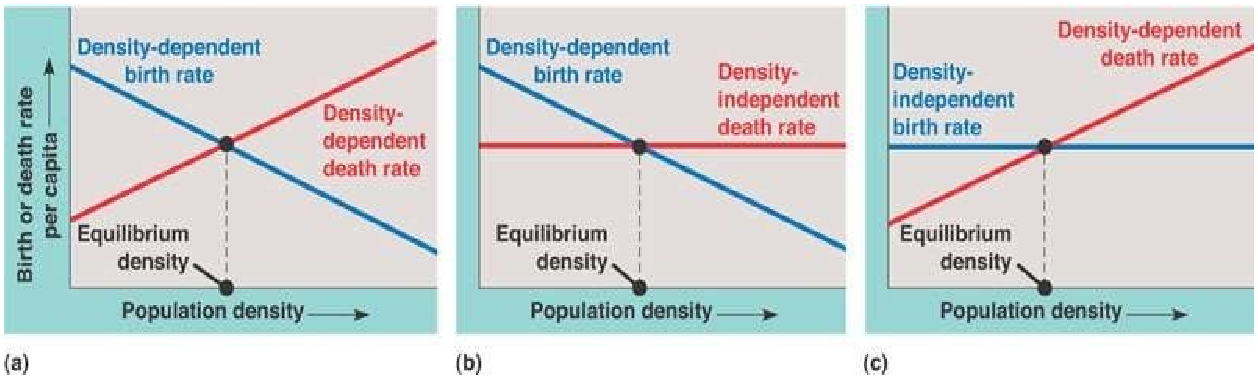


Fig. 3: Density- dependent regulation of birth rate and death rate. a) both the rates are density dependent and equilibrium is achieved when both the rates equate to each other. b) birth rate is density dependent and declines as density increases. c) death rate is density dependent and increases as density increases.

5. <u>Population Fluctuations</u>

Density dependence tends to push populations toward carrying capacity, *K*. Because the environment is variable, K isalso variable and hence populations often don't rest at *K* too, which means density dependence doesn't always lead to a static equilibrium. Populations show ups and downs and always try to reach K; these ups and downs are referred as population fluctuations. Population fluctuations can be erratic (irruptive) or they can be periodic (cyclic). Erratic fluctuations are mostly due to variation in density-independent environmental factors that have a large, immediate impact on population size (e.g., fires, catastrophes).While cyclic fluctuations also known as oscillations are the result of **time lags** in responses of populations to their own density.Populations acquire "momentum" when high birth rates at low densities cause the populations to overshoot *K,* whichcauses very low survival and birth rates, consequently population falls below *K*, recovery occurs when birth rates again increase due to lowered density conditions. Population cycles result from time delaysin the responses of birth and death rates to current environmental conditions which try to either under compensate or overcompensate for population size. The nature of the cycle depends on population's resilience. Resilience decides how fast the population will regain the equilibrium. Reproductive rate has very strong influence on resilient capacity of the population.. Population fluctuations occur over many different time scales, ranging from millions of years on a geological time scale to years, seasons or weeks, on a short time scale. Fluctuations at short time scales are important to be studied in population dynamics.

Types of fluctuations

i. Stable: population size fluctuates around carrying capacityslightly aboveand below and is characteristic of many species living under fairly constant environment, like conditions in Tropical rain forest.

ii. Irruptive: population is normally fairly stable,itoccasionally explodes (*irrupts)* to peakthen crashes tolevelbelow carrying capacity. This occurs due to a factor (e.g. a resource availability) that temporarily increases carrying capacity. This is characteristic of short-lived, rapidly reproducing species.

iii. Irregular: no apparent recurring pattern is observed an irregular, chaotic behavior is seen in population size .The cause for this behavior is poorly understood, some scientists attribute irregular behavior to chaos in the system.

iv. Cyclic: fluctuationsoccur over a regular time period, generally a multiple year cycle.

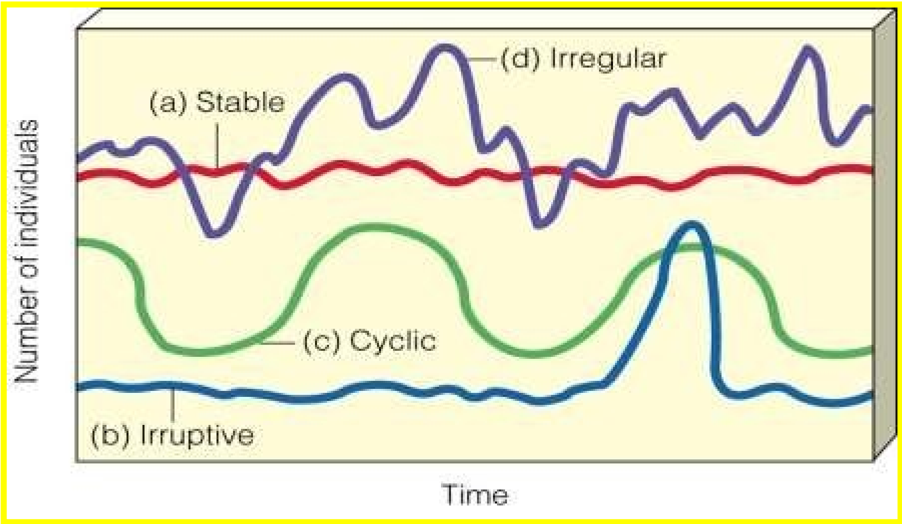


Fig. 4: Types of population fluctuations.

6. <u>Population Fluctuations and Species Conservation</u>

The climate change is imposing a huge pressure on biosphere. Species are either getting extinct or are under threat of extinction. Habitat destruction is occurring at a very fast rate on a global scale. The populations left out on the fragmented islands are isolated populations which fluctuate markedly and may disappear ultimately; its replacement by recolonization is unlikely. A frequent fluctuation in such conditions, increases risk of extinction and it becomes urgent to support the processes of dispersal and interbreeding. Preserving the largest possible population size becomes a prime requirement as it will not succumb to extinction even if normal fluctuations occur.

References:

1. Begon, M., & M. Mortimer. 1986. *Population Ecology, 2nd edition*. Blackwell Scientific Populations.

2. Clark, J.S.1990.Integration of Ecological Levels :Individual Plant growth ,Population Mortality and Ecosystem Processes. *The Journal of Ecology*,78:275-299.

3. Crawley, M.J. 1997. Sex. In: *Plant Ecology, 2nd edition*. M.J. Crawley (ed.). Blackwell Scientific Publications, Oxford.

4. Davison, R., H. Jacquemyn, D. Adriaens, O. Honnay, & H. de Kroon. 2010. Demographic effects of extreme weather events on a short-lived calcareous grassland species: stochastic life table response experiments. *Journal of Ecology* 98: 255-267.

5. Gibson, D.J. 2002. *Methods in Comparative Plant Population Ecology.* Oxford University Press.
6. Rockwood, L.L. 2006. *Introduction to Population Ecology.* Blackwell Publishing,Oxford.
7. Silvertown, J., Franco, M., Pisanty, I., & Mendoza, A. 1993**.** Comparative plant demography-relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. Journal of Ecology 81: 465-476.
8. Silvertown, J. & Dodd, M. 1997. Comparing plants and connecting traits. In: Plant Life Histories: Ecology, phylogeny and evolution, p. 3-16. Ed. by Silvertown, J., Franco, M., & Harper, J.L. Cambridge University Press, Cambridge.
9. Silvertown, J.W., & Charlesworth. 2001. *Introduction to Plant Population Biology, 4th edition.* Blackwell Science.

10. Smith, R.L., & T.M. Smith. 2001. *Ecology and Field Biology,6th ed. Chapter 11.* Benjamin Cummings.
11. Turner, B.D., & L.R. Taylor. 1979. *Population Dynamics*. Blackwell