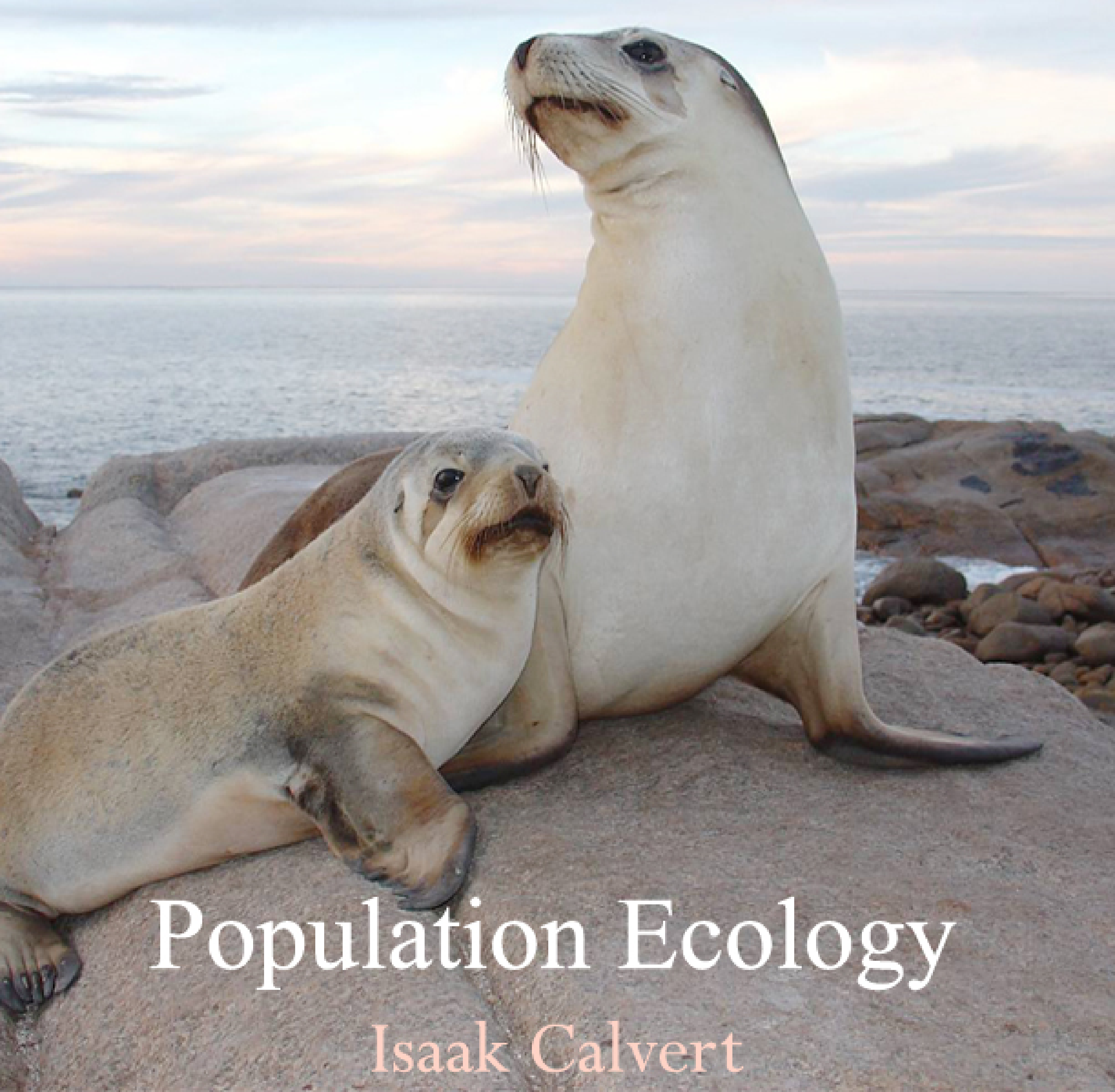


# Population Ecology

Isaak Calvert

First Edition, 2012

ISBN 978-81-323-3356-2



*Published by:*
**Research World**
4735/22 Prakashdeep Bldg,
Ansari Road, Darya Ganj,
Delhi - 110002
Email: info@wtbooks.com

# Table of Contents

## Chapter- 1

# Population Ecology

**Population ecology** is a major sub-field of ecology that deals with the dynamics of species populations and how these populations interact with the environment.

The first journal publication of the Society of Population Ecology, titled *Population Ecology* (originally called Researches on Population Ecology), was released in 1952. Population ecology is concerned with the study of groups of organisms that live together in time and space. One of the first laws of population ecology is the Thomas Malthus' exponential law of population growth. This law states that:

"...a population will grow (or decline) exponentially as long as the environment experienced by all individuals in the population remains constant."

At its most elementary level, interspecific competition involves two species utilizing a similar resource. It rapidly gets more complicated, but stripping the phenomenon of all its complications, this is the basic principal: two consumers consuming the same resource.

This premise in population ecology provides the basis for formulating predictive theories and tests that follow. Simplified population models usually start with four key variables including death, birth, immigration, and emigration. Mathematical models used to calculate changes in population demographics and evolution hold the assumption (or null hypothesis) of no external influence. Models can be more mathematically complex where "...several competing hypotheses are simultaneously confronted with the data." For example, in a closed system where immigration and emigration does not take place, the per capita rates of change in a population can be described as:

$$\frac{dN}{dT} = B - D = bN - dN = (b - d)N = rN,$$

where $N$ is the total number of individuals in the population, $B$ is the number of births, $D$ is the number of deaths, $b$ and $d$ are the per capita rates of birth and death respectively, and $r$ is the per capita rate of population change. This formula can be read as the rate of change in the population ($dN/dT$) is equal to births minus deaths (B - D).

Using these techniques, Malthus' population principle of growth was later transformed into a mathematical model known as the logistic equation:

$$\frac{dN}{dT} = aN\left(1 - \frac{N}{K}\right),$$

where $N$ is the biomass density, $a$ is the maximum per-capita rate of change, and $K$ is the carrying capacity of the population. The formula can be read as follows: the rate of change in the population ($dN/dT$) is equal to growth ($aN$) that is limited by carrying capacity $(1-N/K)$. From these basic mathematical principles the discipline of population ecology expands into a field of investigation that queries the demographics of real populations and tests these results against the statistical models. The field of population ecology often uses data on life history and matrix algebra to develop projection matrices on fecundity and survivorship. This information is used for managing wildlife stocks and setting harvest quotas

Terms used to describe natural groupings of individuals in ecological studies

| Term | Definition |
|---|---|
| **Species population** | All individuals of a species. |
| **Metapopulation** | A set of spatially disjunct populations, among which there is some immigration. |
| **Population** | A group of conspecific individuals that is demographically, genetically, or spatially disjunct from other groups of individuals. |
| **Aggregation** | A spatially clustered group of individuals. |
| **Deme** | A group of individuals more genetically similar to each other than to other individuals, usually with some degree of spatial isolation as well. |
| **Local population** | A group of individuals within an investigator-delimited area smaller than the geographic range of the species and often within a population (as defined above). A local population could be a disjunct population as well. |
| **Subpopulation** | An arbitrary spatially-delimited subset of individuals from within a population (as defined above). |

An important concept in population ecology is the r/K selection theory. The first variable is *r* (the intrinsic rate of natural increase in population size, density independent) and the second variable is *K* (the carrying capacity of a population, density dependent). An *r*-selected species (e.g., many kinds of insects, such as aphids) is one that has high rates of fecundity, low levels of parental investment in the young, and high rates of mortality before individuals reach maturity. Evolution favors productivity in r-selected species. In contrast, a *K*-selected species (such as humans) has low rates of fecundity, high levels of parental investment in the young, and low rates of mortality as individuals mature. Evolution in *K*-selected species favors efficiency in the conversion of more resources into fewer offspring.

Populations are also studied and conceptualized through the "metapopulation" concept. The metapopulation concept was introduced in 1969:

"as a population of populations which go extinct locally and recolonize."

Metapopulation ecology is a simplified model of the landscape into patches of varying levels of quality. Patches are either occupied or they are not. Migrants moving among the patches are structured into metapopulations either as sources or sinks. Source patches are productive sites that generate a seasonal supply of migrants to other patch locations. Sink patches are unproductive sites that only receive migrants. In metapopulation terminology there are emigrants (individuals that leave a patch) and immigrants (individuals that move into a patch). Metapopulation models examine patch dynamics over time to answer questions about spatial and demographic ecology. An important concept in metapopulation ecology is the rescue effect, where small patches of lower quality (i.e., sinks) are maintained by a seasonal influx of new immigrants. Metapopulation structure evolves from year to year, where some patches are sinks, such as dry years, and become sources when conditions are more favorable. Ecologists utilize a mixture of computer models and field studies to explain metapopulation structure.

The older term, autecology (from Greek: αὐτο, *auto*, "self"; οίκος, oikos, "household"; and λόγος, logos, "knowledge"), refers to roughly the same field of study, coming from the division of ecology into autecology—the study of individual species in relation to the environment—and synecology—the study of groups of organisms in relation to the environment—or community ecology. Odum (1959, p. 8) considered that synecology should be divided into population ecology, community ecology, and ecosystem ecology, defining autecology as essentially "species ecology." However, for some time biologists have recognized that the more significant level of organization of a species is a population, because at this level the species gene pool is most coherent. In fact, Odum regarded "autecology" as no longer a "present tendency" in ecology (i.e., an archaic term), although included "species ecology"—studies emphasizing life history and behavior as adaptations to the environment of individual organisms or species—as one of four subdivisions of ecology.

The development of the field of population ecology owes much to the science of demography and the use of actuarial life tables. Population ecology has also played an important role in the development of the field of conservation biology, especially in the development of population viability analysis (PVA) which makes it possible to predict the long-term probability of a species persisting in a given habitat patch (*e.g.*, a national park).

While essentially a subfield of biology, population ecology provides many interesting problems for mathematicians and statisticians, who work mainly in the study of population dynamics.

## Chapter- 2

# Effective Population Size

In population genetics, the concept of **effective population size** $N_e$ was introduced by the American geneticist Sewall Wright, who wrote two landmark papers on it (Wright 1931, 1938). He defined it as "the number of breeding individuals in an idealized population that would show the same amount of dispersion of allele frequencies under random genetic drift or the same amount of inbreeding as the population under consideration". It is a basic parameter in many models in population genetics. The effective population size is usually smaller than the absolute population size ($N$).

## *Definitions*

Effective population size may be defined in two ways, variance effective size and inbreeding effective size. These are closely linked, and derived from F-statistics.

### Variance effective size

In the Wright-Fisher idealized population model, the conditional variance of the allele frequency $p'$, given the allele frequency $p$ in the previous generation, is

$$\operatorname{var}(p' \mid p) = \frac{p(1-p)}{2N}.$$

Let $\widehat{\operatorname{var}}(p'|p)$ denote the same, typically larger, variance in the actual population under consideration. The variance effective population size $N_e^{(v)}$ is defined as the size of an idealized population with the same variance. This is found by equating $\widehat{\operatorname{var}}(p'|p)$ with $\operatorname{var}(p'|p)$ and solving for $N$ which gives

$$N_e^{(v)} = \frac{p(1-p)}{2\widehat{\operatorname{var}}(p)}.$$

## Inbreeding effective size

Alternatively, the effective population size may be defined by noting how the inbreeding coefficient changes from one generation to the next, and then defining $N_e$ as the size of the idealized population that has the same change in inbreeding. The presentation follows Kempthorne (1957).

For the idealized population, the inbreeding coefficients follow the recurrence equation

$$F_t = \frac{1}{N}\left(\frac{1+F_{t-2}}{2}\right) + \left(1-\frac{1}{N}\right)F_{t-1}.$$

Using Panmictic Index $(1 - F)$ instead of inbreeding coefficient, we get the approximate recurrence equation

$$1 - F_t = P_t = P_0\left(1-\frac{1}{2N}\right)^t.$$

The difference per generation is

$$\frac{P_{t+1}}{P_t} = 1 - \frac{1}{2N}.$$

The inbreeding effective size can be found by solving

$$\frac{P_{t+1}}{P_t} = 1 - \frac{1}{2N_e^{(F)}}.$$

This is

$$N_e^{(F)} = \frac{1}{2\left(1-\frac{P_{t+1}}{P_t}\right)}$$

although researchers rarely use this equation directly.

## *Examples*

## Variations in population size

Population size varies over time. Suppose there are $t$ non-overlapping generations, then effective population size is given by the harmonic mean of the population sizes:

$$\frac{1}{N_e} = \frac{1}{t}\sum_{i=1}^{t}\frac{1}{N_i}$$

For example, say the population size was $N = 10, 100, 50, 80, 20, 500$ for six generations ($t = 6$). Then the effective population size is the harmonic mean of these, giving:

$$\frac{1}{N_e} = \frac{\frac{1}{10}+\frac{1}{100}+\frac{1}{50}+\frac{1}{80}+\frac{1}{20}+\frac{1}{500}}{6}$$

$$= \frac{0.1945}{6}$$

$$= 0.032416667$$

$$N_e = 30.8$$

Note this is less than the arithmetic mean of the population size, which in this example is 126.7.

Of particular concern is the effect of a population bottleneck.

### Variance in reproductive success

With increased variation in family size, Ne is reduced: $N_e = (4N)/(V_k + 2)$ Where $V_k$ is the variance in family size.

### Dioeciousness

If a population is dioecious, i.e. there is no self-fertilisation then

$$N_e = N + \tfrac{1}{2}$$

or more generally,

$$N_e = N + \tfrac{D}{2}$$

where $D$ represents dioeciousness and may take the value 0 (for not dioecious) or 1 for dioecious.

When $N$ is large, $N_e$ approximately equals $N$, so this is usually trivial and often ignored:

$$N_e = N + \tfrac{1}{2} \approx N$$

## Non-Fisherian sex-ratios

When the sex ratio of a population varies from the Fisherian 1:1 ratio, effective population size is given by:

$$N_e^{(v)} = N_e^{(F)} = \frac{4N_mN_f}{N_m + N_f}$$

Where $N_m$ is the number of males and $N_f$ the number of females. For example, with 80 males and 20 females (an absolute population size of 100):

$$N_e = \frac{4 \times 80 \times 20}{80 + 20}$$

$$= \frac{6400}{100}$$

$$= 64$$

Again, this results in $N_e$ being less than $N$.

## Unequal contributions to the next generation

If population size is to remain constant, each individual must contribute on average two gametes to the next generation. An idealized population assumes that this follows a Poisson distribution so that the variance of the number of gametes contributed, $k$ is equal to the mean number contributed, i.e. 2:

$$\operatorname{var}(k) = \bar{k} = 2.$$

However, in natural populations the variance is larger than this, i.e.

$$\operatorname{var}(k) > 2.$$

The effective population size is then given by:

$$N_e^{(v)} = \frac{4N - 2D}{2 + \operatorname{var}(k)}$$

Note that if the variance of $k$ is less than 2, $N_e$ is greater than $N$. Heritable variation in fecundity, usually pushes $N_e$ lower.

## Overlapping generations and age-structured populations

When organisms live longer than one breeding season, effective population sizes have to take into account the life tables for the species.

## Haploid

Assume a haploid population with discrete age structure. An example might be an organism that can survive several discrete breeding seasons. Further, define the following age structure characteristics:

$v_i$ = Fisher's reproductive value for age $i$,
$\ell_i =$ The chance an individual will survive to age $i$, and
$N_0$ = The number of newborn individuals per breeding season.

The generation time is calculated as

$$T = \sum_{i=0}^{\infty} \ell_i v_i = \text{ average age of a reproducing individual}$$

Then, the inbreeding effective population size is (Felsenstein 1971)

$$N_e^{(F)} = \frac{N_0 T}{1 + \sum_i \ell_{i+1}^2 v_{i+1}^2 (\frac{1}{\ell_{i+1}} - \frac{1}{\ell_i})}.$$

## Diploid

Similarly, the inbreeding effective number can be calculated for a diploid population with discrete age structure. This was first given by Johnson (1977), but the notation more closely resembles Emigh and Pollak (1979).

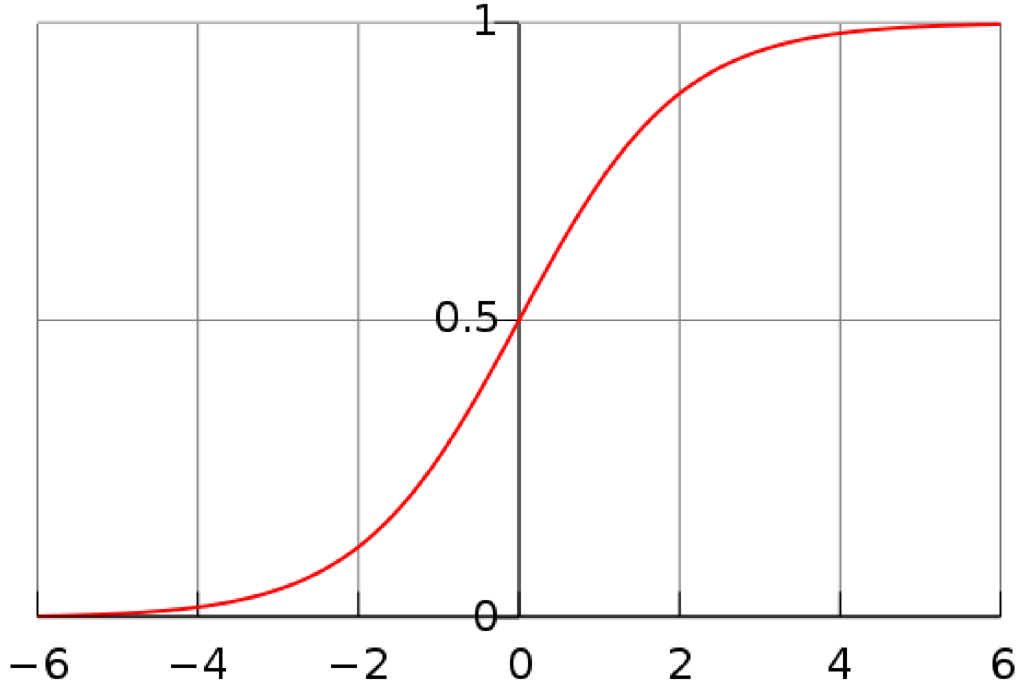
Assume the same basic parameters for the life table as given for the haploid case, but distinguishing between male and female, such as $N_0^f$ and $N_0^m$ for the number of newborn females and males, respectively (notice lower case $f$ for females, compared to upper case $F$ for inbreeding).

The inbreeding effective number is

$$\frac{1}{N_e^{(F)}} = \frac{1}{4T} \left\{ \frac{1}{N_0^f} + \frac{1}{N_0^m} + \sum_i \left(\ell_{i+1}^f\right)^2 \left(v_{i+1}^f\right)^2 \left(\frac{1}{\ell_{i+1}^f} - \frac{1}{\ell_i^f}\right) + \sum_i \left(\ell_{i+1}^m\right)^2 \left(v_{i+1}^m\right)^2 \left(\frac{1}{\ell_{i+1}^m} - \frac{1}{\ell_i^m}\right) \right\}.$$

## Chapter- 3

# Logistic Function




Standard logistic sigmoid function

A **logistic function** or **logistic curve** is a common sigmoid curve, given its name in 1844 or 1845 by Pierre François Verhulst who studied it in relation to population growth. It can model the "S-shaped" curve (abbreviated S-curve) of growth of some population *P*. The initial stage of growth is approximately exponential; then, as saturation begins, the growth slows, and at maturity, growth stops.

A simple logistic function may be defined by the formula

$$P(t) = \frac{1}{1 + e^{-t}}$$

where the variable *P* might be considered to denote a *population* and the variable *t* might be thought of as *time*. For values of *t* in the range of real numbers from −∞ to +∞, the S-curve shown is obtained. In practice, due to the nature of the exponential function $e^{-t}$, it is sufficient to compute *t* over a small range of real numbers such as [−6, +6].

The logistic function finds applications in a range of fields, including artificial neural networks, biology, biomathematics, demography, economics, chemistry, mathematical psychology, probability, sociology, political science, and statistics. It has an easily calculated derivative:

$$\frac{d}{dt}P(t) = P(t) \cdot (1 - P(t)).$$

It also has the property that

$$1 - P(t) = P(-t).$$

In other words, the function *P - 1/2* is odd.

### *Logistic differential equation*

The logistic function is the solution of the simple first-order non-linear differential equation

$$\frac{d}{dt}P(t) = P(t)(1 - P(t))$$

where *P* is a variable with respect to time *t* and with boundary condition *P*(0) = 1/2. This equation is the continuous version of the logistic map.

The qualitative behavior is easily understood in terms of the phase line: the derivative is 0 at *P*=0,1, and the derivative is positive for *P* between 0 and 1, and negative for *P* above 1 or less than 0 (though negative populations do not generally accord with a physical model). This yields an unstable equilibrium at 0, and a stable equilibrium at 1, and thus for any value of *P* greater than 0 and less than 1, *P* grows to 1.

One may readily find the (symbolic) solution to be

$$P(t) = \frac{e^t}{e^t + e^c}$$

Choosing the constant of integration $e^c = 1$ gives the other well-known form of the definition of the logistic curve

$$P(t) = \frac{e^t}{e^t + 1} = \frac{1}{1 + e^{-t}}$$

More quantitatively, as can be seen from the analytical solution, the logistic curve shows early exponential growth for negative $t$, which slows to linear growth of slope 1/4 near $t$ = 0, then approaches $y$ = 1 with an exponentially decaying gap.

The logistical function is the inverse of the natural logit function and so can be used to convert the logarithm of odds into a probability; the conversion from the log-likelihood ratio of two alternatives also takes the form of a logistic curve.

The logistic sigmoid function is related to the hyperbolic tangent, A.p. by

$$2\,P(t) = 1 + \tanh\left(\frac{t}{2}\right).$$

### *In ecology: modeling population growth*


Pierre-François Verhulst (1804–1849)

A typical application of the logistic equation is a common model of population growth, originally due to Pierre-François Verhulst in 1838, where the rate of reproduction is proportional to both the existing population and the amount of available resources, all else being equal. The Verhulst equation was published after Verhulst had read Thomas Malthus' *An Essay on the Principle of Population*. Verhulst derived his logistic equation to describe the self-limiting growth of a biological population. The equation is also sometimes called the *Verhulst-Pearl equation* following its rediscovery in 1920. Alfred J. Lotka derived the equation again in 1925, calling it the *law of population growth*.

Letting $P$ represent population size ($N$ is often used in ecology instead) and $t$ represent time, this model is formalized by the differential equation:

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right)$$

where the constant $r$ defines the growth rate and $K$ is the carrying capacity.

In the equation, the early, unimpeded growth rate is modeled by the first term $+rP$. The value of the rate $r$ represents the proportional increase of the population $P$ in one unit of time. Later, as the population grows, the second term, which multiplied out is $-rP^2/K$, becomes larger than the first as some members of the population $P$ interfere with each other by competing for some critical resource, such as food or living space. This antagonistic effect is called the *bottleneck*, and is modeled by the value of the parameter $K$. The competition diminishes the combined growth rate, until the value of $P$ ceases to grow (this is called *maturity* of the population).

Dividing both sides of the equation by $K$ gives

$$\frac{d}{dt}\frac{P}{K} = r\frac{P}{K}\left(1 - \frac{P}{K}\right)$$

Now setting $x = P / K$ gives the differential equation

$$\frac{dx}{dt} = rx(1 - x)$$

For $r = 1$ we have the particular case with which we started.

In ecology, species are sometimes referred to as r-strategist or K-strategist depending upon the selective processes that have shaped their life history strategies. The solution to the equation (with $P_0$ being the initial population) is

$$P(t) = \frac{KP_0e^{rt}}{K + P_0\left(e^{rt} - 1\right)}$$

where

$$\lim_{t\to\infty} P(t) = K.$$

Which is to say that $K$ is the limiting value of $P$: the highest value that the population can reach given infinite time (or come close to reaching in finite time). It is important to stress that the carrying capacity is asymptotically reached independently of the initial value $P(0) > 0$, also in case that $P(0) > K$.

### Time-varying carrying capacity

Since the environmental conditions influence the carrying capacity, as a consequence it can be time-varying: $K(t) > 0$, leading to the following mathematical model:

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K(t)}\right)$$

A particularly important case is that of carrying capacity that varies periodically with period $T$:

$$K(t+T) = K(t).$$

It can be shown that in such a case, independently from the initial value $P(0) > 0$, $P(t)$ will tend to a unique periodic solution $P_*(t)$, whose period is $T$.

A typical value of $T$ is one year: in such case $K(t)$ reflects periodical variations of weather conditions.

Another interesting generalization is to consider that the carrying capacity K(t) is a function of the population at an earlier time, capturing a delay in the way population modifies its environment. This leads to a logistic delay equation, which has a very rich behavior, with bistability in some parameter range, as well as a monotonic decay to zero, smooth exponential growth, punctuated unlimited growth (i.e., multiple S-shapes), punctuated growth or alternation to a stationary level, oscillatory approach to a stationary level, sustainable oscillations, finite-time singularities as well as finite-time death.

## *In neural networks*

Logistic functions are often used in neural networks to introduce nonlinearity in the model and/or to clamp signals to within a specified range. A popular neural net element computes a linear combination of its input signals, and applies a bounded logistic function to the result; this model can be seen as a "smoothed" variant of the classical threshold neuron.

A common choice for the activation or "squashing" functions, used to clip for large magnitudes to keep the response of the neural network bounded is

$$g(h) = \frac{1}{1 + e^{-2\beta h}}$$

which we recognize to be of the form of the logistic function. These relationships result in simplified implementations of artificial neural networks with artificial neurons. Practitioners caution that sigmoidal functions which are symmetric about the origin (e.g. the hyperbolic tangent) lead to faster convergence when training networks with backpropagation.

### *In statistics*

Logistic functions are used in several roles in statistics. Firstly, they are the cumulative distribution function of the logistic family of distributions. Secondly they are used in logistic regression to model how the probability $p$ of an event may be affected by one or more explanatory variables: an example would be to have the model

$$p = P(a + bx)$$

where $x$ is the explanatory variable and $a$ and $b$ are model parameters to be fitted.

An important application of the logistic function is in the Rasch model, used in item response theory. In particular, the Rasch model forms a basis for maximum likelihood estimation of the locations of objects or persons on a continuum, based on collections of categorical data, for example the abilities of persons on a continuum based on responses that have been categorized as correct and incorrect.

### *In medicine: modeling of growth of tumors*

Another application of logistic curve is in medicine, where the logistic differential equation is used to model the growth of tumors. This application can be considered an extension of the above mentioned use in the framework of ecology. Denoting with $X(t)$ the size of the tumor at time $t$, its dynamics are governed by:

$$X' = r\left(1 - \frac{X}{K}\right)X$$

which is of the type:

$$X' = F(X)\,X, F'(X) \leq 0$$

where $F(X)$ is the proliferation rate of the tumor.

If a chemotherapy is started with a log-kill effect, the equation may be revised to be

$$X' = r\left(1 - \frac{X}{K}\right)X - c(t)X,$$

where *c*(*t*) is the therapy-induced death rate. In the idealized case of very long therapy, *c*(*t*) can be modeled as a periodic function (of period *T*) or (in case of continuous infusion therapy) as a constant function, and one has that

$$\frac{1}{T}\int_0^T c(t)\,dt > r \Rightarrow \lim_{t\to+\infty} x(t) = 0$$

i.e. if the average therapy-induced death rate is greater than the baseline proliferation rate then there is the eradication of the disease. Of course, this is an over-simplified model of both the growth and the therapy (e.g. it does not take into account the phenomenon of clonal resistance).

### *In chemistry: reaction models*

The concentration of reactants and products in autocatalytical reactions follow the logistic function.

### *In physics: Fermi distribution*

The logistic function determines the statistical distribution of fermions over the energy states of a system in thermal equilibrium. In particular, it is the distribution of the probabilities that each possible energy level is occupied by a fermion, according to Fermi-Dirac statistics.

### *In linguistics: language change*

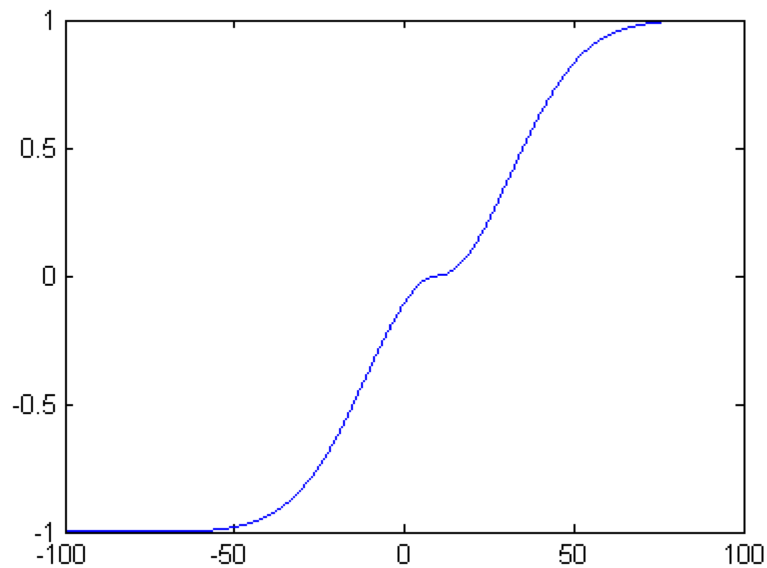
In linguistics, the logistic function can be used to model language change: an innovation that is at first marginal begins to spread more quickly with time, and then more slowly as it becomes more universally adopted.

### *In economics: Diffusion of innovations*

The logistic function can be used to illustrate the progress of the diffusion of an innovation through its life cycle. This method was used in papers by several researchers at the International Institute of Applied Systems Analysis (IIASA). These papers deal with the diffusion of various innovations, infrastructures and energy source substitutions and the role of work in the economy as well as with the long economic cycle. Long economic cycles were investigated by Robert Ayres (1989). Cesare Marchetti published on long economic cycles and on diffusion of innovations. Arnulf Grübler’s book (1990) gives a detailed account of the diffusion of infrastructures including canals, railroads, highways and airlines, showing that their diffusion followed logistic shaped curves.

Carlota Perez used a logistic curve to illustrate the long (Kondraeiev)business cycle with the following labels: beginning of a technological era as *irruption*, the ascent as *frenzy*, the rapid build out as *synergy* and the completion as *maturity*.

### *Double logistic function*




Double logistic sigmoid curve

The double logistic is a function similar to the logistic function with numerous applications. Its general formula is:

$$y = \operatorname{sgn}(x-d)\left(1-\exp\left(-\left(\frac{x-d}{s}\right)^2\right)\right),$$

where $d$ is its centre and $s$ is the steepness factor. Here "sgn" represents the sign function.

It is based on the Gaussian curve and graphically it is similar to two identical logistic sigmoids bonded together at the point $x = d$.

One of its applications is non-linear normalization of a sample, as it has the property of eliminating outliers.

## Chapter- 4

# Maximum Sustainable Yield

In population ecology and economics, **maximum sustainable yield** or **MSY** is, theoretically, the largest yield (or catch) that can be taken from a species' stock over an indefinite period. Fundamental to the notion of sustainable harvest, the concept of MSY aims to maintain the population size at the point of maximum growth rate by harvesting the individuals that would normally be added to the population, allowing the population to continue to be productive indefinitely. Under the assumption of logistic growth, resource limitation does not constrain individuals' reproductive rates when populations are small, but because there are few individuals, the overall yield is small. At intermediate population densities, also represented by half the carrying capacity, individuals are able to breed to their maximum rate. At this point, called the maximum sustainable yield, there is a surplus of individuals that can be harvested because growth of the population is at its maximum point due to the large number reproducing individuals. Above this point, density dependent factors increasingly limit breeding until the population reaches carrying capacity. At this point, there are no surplus individuals to be harvested and yield drops to zero. The maximum sustainable yield is usually higher than the optimum sustainable yield and maximum economic yield.

MSY is extensively used for fisheries management. Unlike the logistic (Schaefer) model, MSY has been refined in most modern fisheries models and occurs at around 30% of the unexploited population size. This fraction differs among populations depending on the life history of the species and the age-specific selectivity of the fishing method.

However, the approach has been widely criticized as ignoring several key factors involved in fisheries management and has led to the devastating collapse of many fisheries. As a simple calculation, it ignores the size and age of the animal being taken, its reproductive status, and it focuses solely on the species in question, ignoring the damage to the ecosystem caused by the designated level of exploitation and the issue of bycatch. Among conservation biologists it is widely regarded as dangerous and misused.

## *History*

The concept of MSY as a fisheries management strategy developed in the early 1930s. It increased in popularity in the 1950s with the advent of surplus-production models with explicitly estimate MSY. As an apparently simple and logical management goal, combined with the lack of other simple management goals of the time, MSY was adopted as the primary management goal by several international organizations (e.g., IWC, IATTC, ICCAT, ICNAF), and individual countries.

Between 1949 and 1955, the U.S. maneuvered to have MSY declared the goal of international fisheries management (Johnson 2007). The international MSY treaty that was eventually adopted in 1955 gave foreign fleets the right to fish off any coast. Nations that wanted to exclude foreign boats had to first prove that its fish were overfished.

As experience was gained with the model, it became apparent to some researchers that it lacked the capability to deal with the real world operational complexities and the influence of trophic and other interactions. In 1977, Larkin wrote its epitaph, challenging the goal of maximum sustained yield on several grounds: It put populations at too much risk; it did not account for spatial variability in productivity; it did not account for species other than the focus of the fishery; it considered only the benefits, not the costs, of fishing; and it was sensitive to political pressure. In fact, none of these criticisms was aimed at sustainability as a goal. The first one noted that seeking the absolute MSY with uncertain parameters was risky. The rest point out that the goal of MSY was not holistic; it left out too many relevant features.

Some managers began to use more conservative quota recommendations, but the influence of the MSY model for fisheries management still prevailed. Even while the scientific community was beginning to question the appropriateness and effectiveness of MSY as a management goal, it was incorporated into the 1982 United Nations Convention for the Law of the Sea, thus ensuring its integration into national and international fisheries acts and laws. According to Walters and Maguire, an ‘‘institutional juggernaut had been set in motion’’, climaxing in the early 1990s with the collapse of northern cod.

## *Modelling MSY*

### Population growth

The key assumption behind all sustainable harvesting models such as MSY is that populations of organisms grow and replace themselves – that is, they are renewable resources. Additionally it is assumed that because the growth rates, survival rates, and reproductive rates increase when harvesting reduces population density, they produce a surplus of biomass that can be harvested. Otherwise, sustainable harvest would not be possible.

Another assumption of renewable resource harvesting is that populations of organisms do not continue to grow indefinitely; they reach an equilibrium population size, which occurs when the number of individuals matches the resources available to the population (i.e., assume classic logistic growth). At this equilibrium population size, called the carrying capacity, the population remains at a stable size.

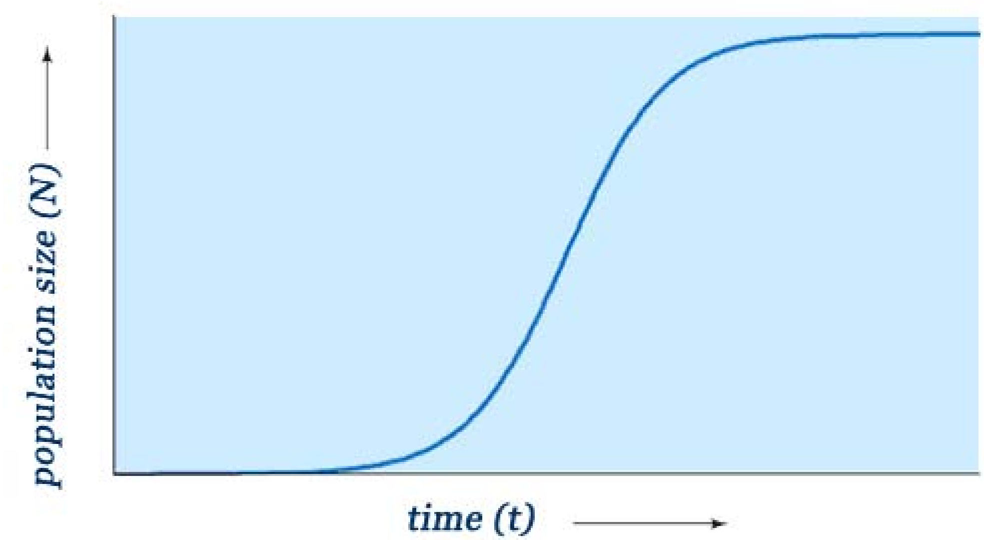



Figure 1

The logistic model (or logistic function) is a function that is used to describe bounded population growth under the previous two assumptions. The logistic function is bounded at both extremes: when there are not individuals to reproduce, and when there is an equilibrium number of individuals (i.e., at carrying capacity). Under the logistic model, population growth rate between these two limits is most often assumed to be sigmoidal (Figure 1). There is scientific evidence that some populations do grow in a logistic fashion towards a stable equilibrium – a commonly cited example is the logistic growth of yeast.

The equation describing logistic growth is:

$$N_t = \frac{K}{1 + \frac{K - N_0}{N_0} e^{-rt}} \quad \text{(equation 1.1)}$$

The parameter values are:

$N_t$=The population size at time t
$K$=The carrying capacity of the population
$N_0$= The population size at time zero
$r$= the intrinsic rate of population increase (the rate at which the population grows when it is very small)

From the logistic function, the population size at any point can be calculated as long as $r$, $K$, and $N_0$ are known.

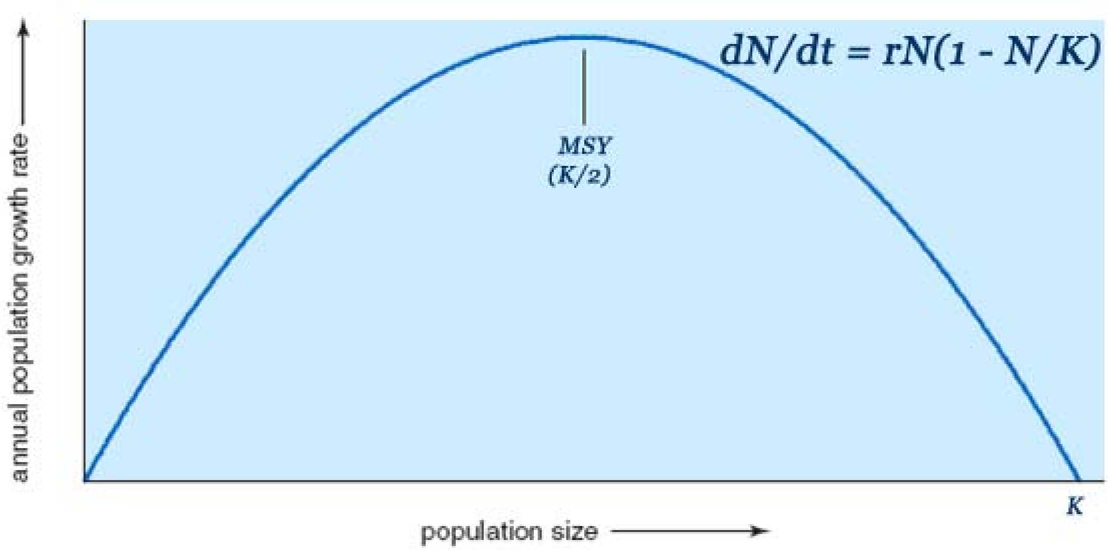



Figure 2

Differentiating equation 1.1 give an expression for how the rate of population increases as t increases. At first, the population growth rate is fast, but it begins to slow as times goes on, until it levels off to zero and then begins to decrease (figure 2).

The equation for figure 2 is the differential of equation 1.1 (Verhulst's 1838 growth model):

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \text{(equation 1.2)}$$

$\frac{dN}{dt}$ can be understood as the change in population (N) with respect to a change in time (t). Equation 1.2 is the usual way in which logistic growth is represented mathematically and has several important features. First, at very low population sizes, the value of $\frac{N}{K}$ is small, so the population growth rate is approximately equal to $rN$, meaning the population is growing exponentially at a rate r (the intrinsic rate of population increase). Despite this, the population growth rate is very low (low values on the y-axis of figure 2) because, even though each individual is reproducing at a high rate, there are few reproducing individuals present. Conversely, when the population is large the value of $\frac{N}{K}$ approaches 1 effectively reducing the terms inside the brackets of equation 1.2 to zero. The effect is that the population growth rate is again very low, because either each individual is hardly reproducing or mortality rates are high. As a result of these two extremes, the population growth rate is maximum at an intermediate population or half the carrying capacity ($N = \frac{K}{2}$).

### MSY model

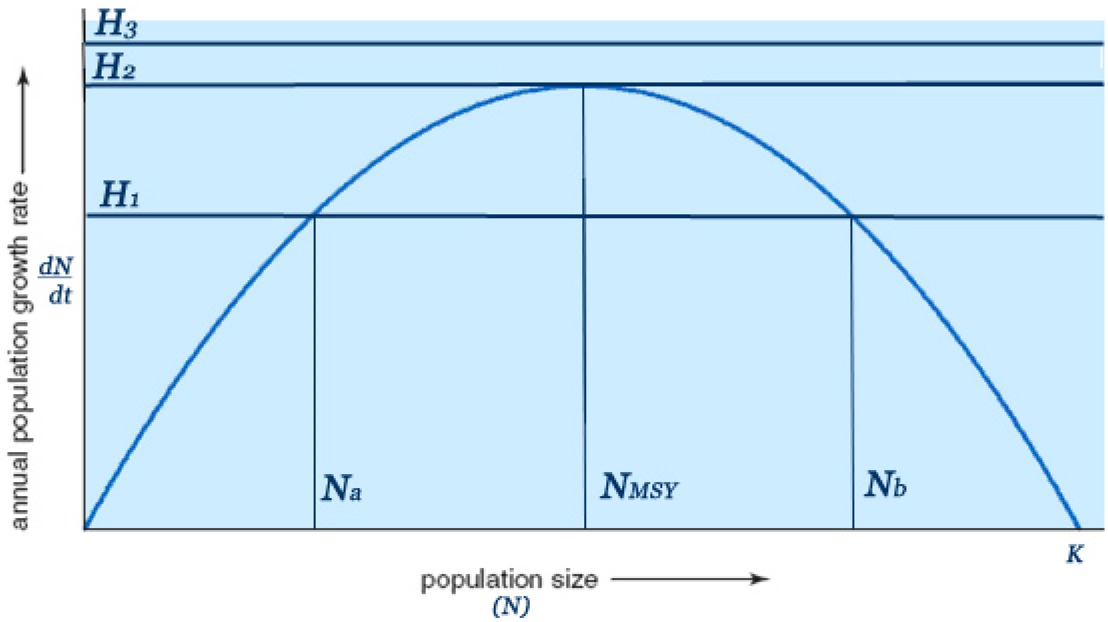



Figure 3

The simplest way to model harvesting is to modify the logistic equation so that a certain number of individuals is continuously removed:

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) - H$$ (equation 1.3)

Where H represents the number of individuals being removed from the population – that is, the harvesting rate. When H is constant, the population will be at equilibrium when the number of individuals being removed is equal to the population growth rate (figure 3). The equilibrium population size under a particular harvesting regime can be found when the population is not growing – that is, when $\frac{dN}{dt} = 0$. This occurs when the population growth rate is the same as the harvest rate:

$$rN(1 - \frac{N}{K}) = H$$

Figure 3 shows how growth rate varies with population density. For low densities (far from carrying capacity), there is little addition (or “recruitment”) to the population, simply because there are few organisms to give birth. At high densities, though, there is intense competition for resources, and growth rate is again low because the death rate is high. In between these two extremes, the population growth rate rises to a maximum value ($N_{MSY}$). This maximum point represents the maximum number of individuals that can be added to a population by natural processes. If more individuals than this are removed from the population, the population will decline to extinction. The maximum number that can be harvested in a sustainable manner, called the maximum sustainable yield, is given by this maximum point.

Figure 3 also shows several possible values for the harvesting rate, H. At $H_1$, there are two possible population equilibrium points: a low population size ($N_a$) and a high one ($N_b$). At $H_2$, a slightly higher harvest rate, however there is only one equilibrium point (at $N_{MSY}$), which is the population size that produces the maximum growth rate. With logistic growth, this point, called the maximum sustainable yield, is where the population size is half the carrying capacity (or $N = \frac{K}{2}$). The maximum sustainable yield is the largest yield that can be taken from a population at equilibrium. In figure 3, if $H$ is higher than $H_2$, the harvesting would exceed the population’s capacity to replace itself at any population size ($H_3$ in figure 3). Because harvesting rate is higher than the population growth rate at all values of $N$, this rate of harvesting is not sustainable. An important feature of the MSY model is how harvested populations respond to environmental fluctuations or illegal offtake. Consider a population at $N_b$ harvested at a constant harvest level $H_1$. If the population falls (due to a bad winter or illegal harvest) this will ease density-dependent population regulation and increase yield, moving the population back to $N_b$, a stable equilibrium. In this case, a negative feedback loop creates stability. The lower equilibrium point for the constant harvest level $H_1$ is not stable however; a population crash or illegal harvesting will decrease population yield farther below the current harvest level, creating a positive feedback loop leading to extinction. Harvesting at $N_{MSY}$ is also potentially unstable. A small decrease in the population can lead to a positive feedback loop and extinction if the harvesting regime ($H_2$) is not reduced. Thus, harvesting at MSY is unsafe on ecological and economic grounds. The MSY model itself can be modified to harvest a certain percentage of the population or with constant effort constraints rather than an actual number, thereby avoiding some of its instabilities.

The MSY equilibrium point is semi-stable – a small increase in population size is compensated for, a small decrease to extinction if H is not decreased. Harvesting at MSY is therefore dangerous because it is on a knife-edge – any small population decline leads to a positive feedback, with the population declining rapidly to extinction if the number of harvested stays the same.

The formula for maximum sustained harvest ($H$) is one-fourth the maximum population or carrying capacity ($K$) times the intrinsic rate of growth ($r$).

$$H = \frac{Kr}{4}$$

### Implications of MSY model

Starting to harvest a previously unharvested population will always lead to a decrease in the population size. That is, it is impossible for a harvested population to remain at its original carrying capacity. Instead, the population will either stabilize at a new lower equilibrium size or, if the harvesting rate is too high, decline to zero.

The reason why populations can be sustainable harvested is that they exhibit a density-dependent response. This means that at any population size below K, the population is producing a surplus yield that is available for harvesting without reducing population size. Density dependence is the regulator process that allows the population to return to equilibrium after a perturbation. The logistic equation assumes that density dependence takes the form of negative feedback.

If a constant number of individuals is harvested from a population at a level greater than the MSY, the population will decline to extinction. Harvesting below the MSY level leads to a stable equilibrium population if the starting population is above the unstable equilibrium population size.

### Uses of MSY

MSY has been especially influential in the management of renewable biological resources such as commercially important fish and wildlife. In fisheries terms, **maximum sustainable yield** (MSY) is the largest average catch that can be captured from a stock under existing environmental conditions. MSY aims at a balance between too much and too little harvest to keep the population at some intermediate abundance with a maximum replacement rate.

Relating to MSY, the maximum economic yield (MEY) is the level of catch that provides the maximum net economic benefits or profits to society. Like optimum sustainable yield, MEY is usually less than MSY.

### Limitations of MSY approach

Although it is widely practiced by state and federal government agencies regulating wildlife, forests, and fishing, MSY has come under heavy criticism by ecologists and others from both theoretical and practical reasons. The concept of maximum sustainable yield is not always easy to apply in practice. Estimation problems arise due to poor assumptions in some models and lack of reliability of the data. Biologists, for example, do not always have enough data to make a clear determination of the population's size and growth rate. Calculating the point at which a population begins to slow from competition is also very difficult. The concept of MSY also tends to treats all individuals in the population as identical, thereby ignoring all aspects of population structure such as size or age classes and their differential rates of growth, survival, and reproduction.

As a management goal, the static interpretation of MSY (i.e., MSY as a fixed catch that can be taken year after year) is generally not appropriate because it ignores the fact that fish populations undergo natural fluctuations (i.e., MSY treats the environment as unvarying) in abundance and will usually ultimately become severely depleted under a constant-catch strategy. Thus, most fisheries scientists now interpret MSY in a more dynamic sense as the maximum average yield (MAY) obtained by applying a specific harvesting strategy to a fluctuating resource.

### Orange roughy

An example of errors in estimating the population dynamics of a species occurred with in the New Zealand Orange roughy fishery. Early quotas were based on an assumption that the orange roughy had a fairly short lifespan and bred relatively quickly. However, it was later discovered that the orange roughy lived a long time and had bred slowly (~30 years). By this stage stocks had been largely depleted.

## *Overfishing*

All around the world, from the arctic to the tropics, there is a crisis in the world's fisheries. Until fairly recently it was assumed that our marine resources were limitless.

In recent years however, an accelerating decline has been observed in the productivity of many important fisheries. Fisheries which have been devastated in recent times include (but are not limited too) the great whale fisheries, the Grand Bank fisheries of the western Atlantic, and the Peruvian anchovy fishery. Recent assessments by the United Nations Food and Agriculture Organization (FAO) of the state of the world's fisheries indicate a levelling off of landings in the 1990s, at about 100 million tons

In addition, the composition of global catches has changed. As fishers deplete larger, long-lived predatory fish species such as cod, tuna, shark, and snapper, they move down to the next level – to species that tend to be smaller, shorter-lived, and less valuable.

## *Optimum sustainable yield*

In population ecology and economics, **optimum sustainable yield** is the level of effort (LOE) that maximizes the difference between total revenue and total cost. Or, where marginal revenue equals marginal cost. This level of effort maximizes the economic profit, or rent, of the resource being utilized. It usually corresponds to an effort level lower than that of maximum sustainable yield. In environmental science, **optimum sustainable yield** is the largest economical yield of a renewable resource achievable over a long time period without decreasing the ability of the population or its environment to support the continuation of this level of yield.

**Chapter- 5**

# Population Cycle and Population Dynamics

## Population cycle

A **population cycle** in zoology is a phenomenon where populations rise and fall over a predictable period of time. There are some species where population numbers have reasonably predictable patterns of change although the full reasons for population cycles is one of the major unsolved ecological problems. There are a number of factors which influence population change such as availability of food, predators, diseases and climate.

### *Occurrence in mammal populations*

Olaus Magnus, the Archbishop of Uppsala in central Sweden, identified that species of northern rodents had periodic peaks in population and published two reports on the subject in the middle of the 16th century.

In North America, the phenomenon was identified in populations of the snowshoe hare. In 1865, trappers with the Hudson's Bay Company were catching plenty of animals. By 1870, they were catching very few. It was finally identified that the cycle of high and low catches ran over approximately a ten year period.

The most well known example of creatures which have a population cycle is the lemming. The biologist Charles Elton first identified in 1924 that the lemming had regular cycles of population growth and decline. When their population outgrows the resources of their habitat, lemmings migrate, although contrary to popular myth, they do not jump into the sea.

### *Other species*

While the phenomenon is often associated with rodents, it does occur in other species such as the ruffed grouse. There are other species which have irregular population explosions such as grasshoppers where overpopulation results in locust swarms in Africa and Australia.

### *Relationships between predators and prey*

There is also an interaction between prey with periodic cycles and predators. As the population expands, there is more food available for predators. As it contracts, there is less food available for predators, putting pressure on their population numbers.

# Population dynamics

**Population dynamics** is the branch of life sciences that studies short- and long-term changes in the size and age composition of populations, and the biological and environmental processes influencing those changes. Population dynamics deals with the way populations are affected by birth and death rates, and by immigration and emigration, and studies topics such as ageing populations or population decline.

The mathematical model often viewed as the best to govern the population dynamics of any given species is called the exponential model. With the exponential model, the rate of change of any given population is proportional to the already existing population.

## *History*

Population dynamics has traditionally been the dominant branch of mathematical biology, which has a history of more than 210 years, although more recently the scope of mathematical biology has greatly expanded. The first principle of population dynamics is widely regarded as the exponential law of Malthus, as modelled by the Malthusian growth model. The early period was dominated by demographic studies such as the work of Benjamin Gompertz and Pierre François Verhulst in the early 19th century, who refined and adjusted the Malthusian demographic model.

A more general model formulation was proposed by F.J. Richards in 1959, further expanded by Simon Hopkins, in which the models of Gompertz, Verhulst and also Ludwig von Bertalanffy are covered as special cases of the general formulation. The Lotka–Volterra predator-prey equations are another famous example. The computer game SimCity and the MMORPG Ultima Online, among others, tried to simulate some of these population dynamics.

In the past 30 years, population dynamics has been complemented by evolutionary game theory, developed first by John Maynard Smith. Under these dynamics, evolutionary biology concepts may take a deterministic mathematical form. Population dynamics overlap with another active area of research in mathematical biology: mathematical epidemiology, the study of infectious disease affecting populations. Various models of viral spread have been proposed and analysed, and provide important results that may be applied to health policy decisions.

## *Fisheries and wildlife management*

In fisheries and wildlife management, population is affected by three dynamic rate functions.

- Natality or birth rate, often recruitment, which means reaching a certain size or reproductive stage. Usually refers to the age a fish can be caught and counted in nets
- Population growth rate, which measures the growth of individuals in size and length. More important in fisheries, where population is often measured in biomass.
- Mortality, which includes harvest mortality and natural mortality. Natural mortality includes non-human predation, disease and old age.

If $N_1$ is the number of individuals at time 1 then

$$N_1 = N_0 + B - D + I - E$$

where $N_0$ is the number of individuals at time 0, B is the number of individuals born, D the number that died, I the number that immigrated, and E the number that emigrated between time 0 and time 1.

If we measures these rates over many time intervals, we can determine how a population's density changes over time. Immigration and emigration are present, but are usually not measured.

All of these are measured to determine the harvestable surplus, which is the number of individuals that can be harvested from a population without affecting long term stability, or average population size. The harvest within the harvestable surplus is considered compensatory mortality, where the harvest deaths are substituting for the deaths that would occur naturally. It started in Europe. Harvest beyond that is additive mortality, harvest in addition to all the animals that would have died naturally. These terms are not the universal good and evil of population management, for example, in deer, the DNR are trying to reduce deer population size overall to an extent, since hunters have reduced buck competition and increased deer population unnaturally.

## *Intrinsic rate of increase*

The rate at which a population increases in size if there are no density-dependent forces regulating the population is known as the *intrinsic rate of increase*.

$$(dN/dt)(1/N) = r$$

Where (dN/dt) is the rate of increase of the population and N is the population size, r is the intrinsic rate of increase. This is therefore the theoretical maximum rate of increase of a population per individual. The concept is commonly used in insect population biology to determine how environmental factors affect the rate at which pest populations increase.

## Chapter- 6

# Population Modeling and Population Size

## Population modeling

**Population modeling** is the application of mathematical models to the study of population dynamics.

Models allow us to better understand how complex interactions and processes work. Modeling of dynamic interactions in nature can provide a manageable way of understanding how numbers change over time or in relation to each other. Ecological population modeling is concerned with the changes in population size and age distribution within a population as a consequence of interactions of organisms with the physical environment, with individuals of their own species, and with organisms of other species.. The world is full of interactions that range from simple to dynamic. Many, if not all, of Earth's processes affect human life. The Earth's processes are greatly stochastic and seem chaotic to the naked eye. However, a plethora of patterns can be noticed and are brought forth by using population modeling as a tool.. Population models are used to determine maximum harvest for agriculturists, to understand the dynamics of biological invasions, and have numerous environmental conservation implications. Population models are also used to understand the spread of parasites, viruses, and disease. The realization of our dependence on environmental health has created a need to understand the dynamic interactions of the earth's flora and fauna. Methods in population modeling have greatly improved our understanding of ecology and the natural world.

### *History*

Late 18th-century biologists began to develop techniques in population modeling in order to understand dynamics of growing and shrinking populations of living organisms. Thomas Malthus was one of the first to note that populations grew with a geometric pattern while contemplating the fate of humankind. One of the most basic and milestone models of population growth was the Logistic model of population growth formulated by Pierre François Verhulst in 1838. The logistic model takes the shape of a sigmoid curve and describes the growth of a population as exponential, followed by a decrease in growth, and bound by a carrying capacity due to environmental pressures. Population modeling became of particular interest to biologists in the 20th century as pressure on limited means of sustenance due to increasing human populations in parts of Europe were noticed by biologist like Raymond Pearl. In 1921 Pearl invited physicist A.J. Lotka to assist him in his lab. Lotka developed paired differential equations that showed the effect of a parasite on its prey. Mathematician Vito Volterra equated the relationship between two species independent from Lotka. Together, Lotka and Volterra formed the Lotka–Volterra model for competition that applies the logistic equation to two species illustrating competition, predation, and parasitism interactions between species. In 1939 contributions to population modeling were given by Patrick Leslie as he began work in biomathematics. Leslie emphasized the importance of constructing a life table in order to understand the effect that key life history strategies played in the dynamics of whole populations. Matrix algebra was used by Leslie in conjunction with life tables to extend the work of Lotka. Matrix models of populations calculate the growh of a population with life history variables. Later, Robert MacArthur and Edward Wilson characterized island biogeography. The Equilibrium Model of Island Biogeography describes the number of species on an island as equilibrium of immigration and extinction. The Logistic population model, the Lotka–Volterra model of community ecology, life table Matrix Modeling, the Equilibrium Model of Island Biogeography and variations there of are the basis for ecological population modeling today.

### *Equations*

Logistic growth equation:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

Lotka-Volterra equation:

$$\frac{dN_1}{dt} = r_1 N_1 \frac{K_1 - N_1 - \alpha N_2}{K_1}$$

Island biogeography:

$$S = \frac{IP}{I + E}$$

Species area:

$$\log(S) = \log(c) + z\log(A)$$

# Population size

In population genetics and population ecology, **population size** (usually denoted *N*) is the number of individual organisms in a population.

The effective population size ($N_e$) is defined as "the number of breeding individuals in an idealized population that would show the same amount of dispersion of allele frequencies under random genetic drift or the same amount of inbreeding as the population under consideration." $N_e$ is usually less than *N* (the absolute population size) and this has important applications in conservation genetics.

Small population size results in increased genetic drift. Population bottlenecks are when population size reduces for a short period of time.

Overpopulation may indicate any case in which the population of any species of animal may exceed the carrying capacity of its ecological niche.

Chapter- 7

# Biodiversity

Some of the biodiversity of a coral reef

Rainforests are an example of biodiversity on the planet, and typically possess a great deal of species diversity. This is the Gambia River in Senegal's Niokolo-Koba National Park.

**Biodiversity** is the degree of variation of life forms within a given ecosystem, biome, or an entire planet. Biodiversity is a measure of the health of ecosystems. Greater biodiversity implies greater health. Biodiversity is in part a function of climate. In terrestrial habitats, tropical regions are typically rich whereas polar regions support fewer species.

Rapid environmental changes typically cause extinctions. One estimate is that less than 1% of the species that have existed on Earth are extant.

Since life began on Earth, five major mass extinctions and several minor events have led to large and sudden drops in biodiversity. The Phanerozoic eon (the last 540 million years) marked a rapid growth in biodiversity via the Cambrian explosion—a period during which nearly every phylum of multicellular organisms first appeared. The next 400 million years included repeated, massive biodiversity losses classified as mass extinction events. In the Carboniferous, rainforest collapse led to a great loss of plant and animal life. The Permian–Triassic extinction event, 251 million years ago, was the worst; vertebrate recovery took 30 million years. The most recent, the Cretaceous–Tertiary extinction event, occurred 65 million years ago, and has attracted more attention than all others because it killed the nonavian dinosaurs.

The period since the emergence of humans has displayed an ongoing biodiversity reduction and an accompanying loss of genetic diversity. Named the Holocene extinction, the reduction is caused primarily by human impacts, particularly habitat destruction. Biodiversity's impact on human health is a major international issue.

The United Nations designated 2010 as the International Year of Biodiversity.

## *Etymology*

The term **biological diversity** was used first by wildlife scientist and conservationist Raymond F. Dasmann in the 1968 lay book *A Different Kind of Country* advocating conservation. The term was widely adopted only after more than a decade, when in the 1980s it came into common usage in science and environmental policy. Thomas Lovejoy, in the foreword to the book **Conservation Biology**, introduced the term to the scientific community. Until then the term "natural diversity" was common, introduced by The Science Division of The Nature Conservancy in an important 1975 study, "The Preservation of Natural Diversity." By the early 1980s TNC's Science program and its head, Robert E. Jenkins, Lovejoy and other leading conservation scientists at the time in America advocated the use of "biological diversity".

The term's contracted form ***biodiversity*** may have been coined by W.G. Rosen in 1985 while planning the 1986 *National Forum on Biological Diversity* organized by the National Research Council (NRC). It first appeared in a publication in 1988 when entomologist E. O. Wilson used it as the title of the proceedings of that forum.

Since this period the term has achieved widespread use among biologists, environmentalists, political leaders, and concerned citizens.

A similar term in the United States is "natural heritage." It predates the others and is more accepted by the wider audience interested in conservation. Broader than biodiversity, it includes geology and landforms (geodiversity).

## Definitions

A Sampling of fungi collected during summer 2008 in Northern Saskatchewan mixed woods, near LaRonge is an example regarding the species diversity of fungi. In this photo, there are also leaf lichens and mosses.

"Biological diversity" or "biodiversity" can have many interpretations. It is most commonly used to replace the more clearly defined and long established terms, species diversity and species richness. Biologists most often define biodiversity as the "totality of genes, species, and ecosystems of a region". An advantage of this definition is that it seems to describe most circumstances and presents a unified view of the traditional three levels at which biological variety has been identified:

- species diversity

- ecosystem diversity
- genetic diversity

In 2003 Professor Anthony Campbell at Cardiff University, UK and the Darwin Centre, Pembrokeshire, defined a fourth level: Molecular Diversity.

This multilevel construct is consistent with Dasmann and Lovejoy. An explicit definition consistent with this interpretation was first given in a paper by Bruce A. Wilcox commissioned by the International Union for the Conservation of Nature and Natural Resources (IUCN) for the 1982 World National Parks Conference. Wilcox's definition was "Biological diversity is the variety of life forms...at all levels of biological systems (i.e., molecular, organismic, population, species and ecosystem)..." The 1992 United Nations Earth Summit defined "biological diversity" as "the variability among living organisms from all sources, including, 'inter alia', terrestrial, marine, and other aquatic ecosystems, and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems". This definition is used in the United Nations Convention on Biological Diversity.

One textbook's definition is "variation of life at all levels of biological organization".

Geneticists define it as the diversity of genes and organisms. They study processes such as mutations, gene transfer, and genome dynamics that generate evolution.

### *Linking biodiversity levels*

Measuring diversity at one level in a group of organisms may not precisely correspond to diversity at other levels. However, tetrapod (terrestrial vertebrates) taxonomic and ecological diversity shows a very close correlation.

### *Distribution*

A conifer forest in the Swiss Alps (National Park)

Selection bias amongst researchers may contribute to biased empirical research for modern estimates of biodiversity. In 1768 Rev. Gilbert White succinctly observed of his Selborne, Hampshire "all nature is so full, that that district produces the most variety which is the most examined."

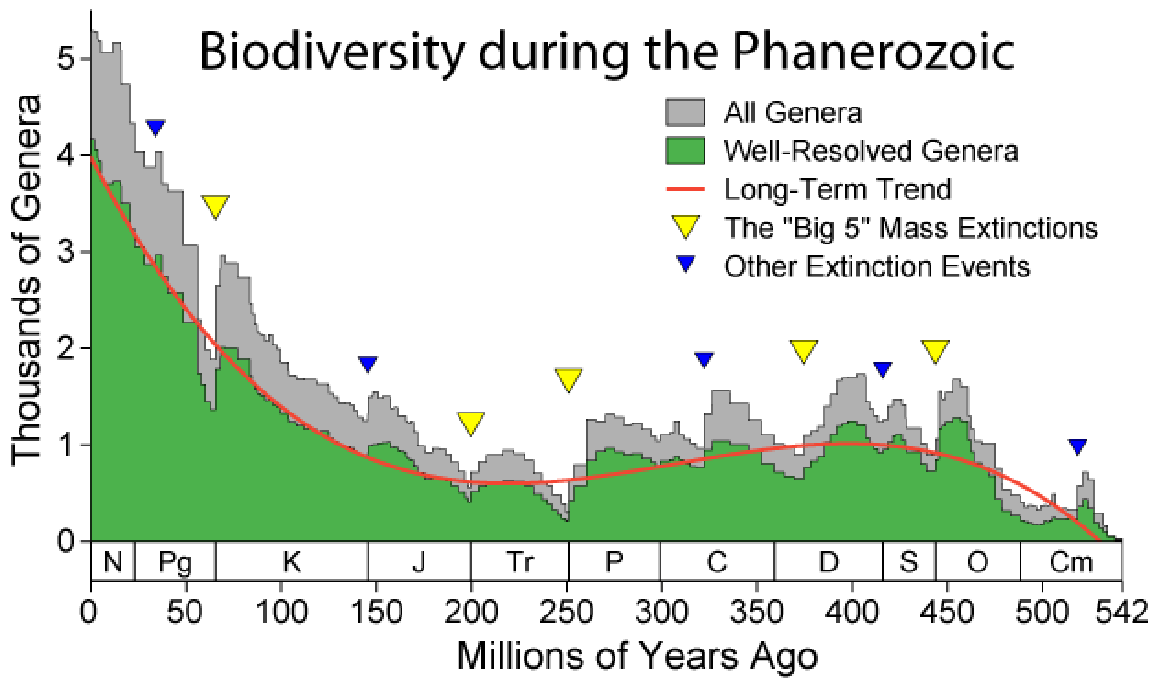
Biodiversity is not evenly distributed. Flora and fauna diversity depends on climate, altitude, soils and the presence of other species. Diversity consistently measures higher in the tropics and in other localized regions such as Cape Floristic Province and lower in polar regions generally. In 2006 many species were formally classified as rare or endangered or threatened; moreover, scientists have estimated that millions more species are at risk which have not been formally recognized. About 40 percent of the 40,177 species assessed using the IUCN Red List criteria are now listed as threatened with extinction—a total of 16,119.

Even though terrestrial biodiversity declines from the equator to the poles, this characteristic is unverified in aquatic ecosystems, especially in marine ecosystems. In addition, several assessments reveal tremendous diversity in higher latitudes. Generally terrestrial biodiversity is up to 25 times greater than ocean biodiversity.

A biodiversity hotspot is a region with a high level of endemic species. Hotspots were first named in 1988 by Dr. Norman Myers. Many hotspots have large nearby human populations. Most hotspots are located in the tropics and most of them are forests.

Brazil's Atlantic Forest is considered one such hotspot, containing roughly 20,000 plant species, 1,350 vertebrates, and millions of insects, about half of which occur nowhere else. The island of Madagascar, particularly the unique Madagascar dry deciduous forests and lowland rainforests, possess a high ratio of endemism. Since the island separated from mainland Africa 65 million years ago, many species and ecosystems have evolved independently. Indonesia's 17,000 islands cover 735,355 square miles (1,904,560 $km^2$) contain 10% of the world's flowering plants, 12% of mammals and 17% of reptiles, amphibians and birds—along with nearly 240 million people. Many regions of high biodiversity and/or endemism arise from specialized habitats which require unusual adaptations, for example alpine environments in high mountains, or Northern European peat bogs.

## *Evolution*




Apparent marine fossil diversity during the Phanerozoic

Biodiversity is the result of 3.5 billion years of evolution. The origin of life has not been definitely established by science, however some evidence suggests that life may already have been well-established only a few hundred million years after the formation of the Earth. Until approximately 600 million years ago, all life consisted of archaea, bacteria, protozoans and similar single-celled organisms.

The history of biodiversity during the Phanerozoic (the last 540 million years), starts with rapid growth during the Cambrian explosion—a period during which nearly every phylum of multicellular organisms first appeared. Over the next 400 million years or so, global diversity showed little overall trend, but was marked by periodic, massive losses of diversity classified as mass extinction events. A significant loss occurred when rainforests collapsed in the carboniferous. The worst was the Permo-Triassic extinction, 251 million years ago. Vertebrates took 30 million years to recover from this event.

The fossil record suggests that the last few million years featured the greatest biodiversity in history. However, not all scientists support this view, since there is considerable uncertainty as to how strongly the fossil record is biased by the greater availability and preservation of recent geologic sections. Corrected for sampling artifacts, modern biodiversity may not be much different from biodiversity 300 million years ago. Estimates of the present global macroscopic species diversity vary from 2 million to 100 million, with a best estimate of somewhere near 13–14 million, the vast majority arthropods. Diversity appears to increase continually in the absence of natural selection.

## Evolutionary diversification

The existence of a "global carrying capacity", limiting the amount of life that can live at once, is debated, as is the question of whether such a limit would also cap the number of species. While records of life in the sea shows a logistic pattern of growth, life on land (insects, plants and tetrapods)shows an exponential rise in diversity. As one author states, "Tetrapods have not yet invaded 64 per cent of potentially habitable modes, and it could be that without human influence the ecological and taxonomic diversity of tetrapods would continue to increase in an exponential fashion until most or all of the available ecospace is filled."

On the other hand, changes through the Phanerozoic correlate much better with the hyperbolic model (widely used in population biology, demography and macrosociology, as well as fossil biodiversity) than with exponential and logistic models. The latter models imply that changes in diversity are guided by a first-order positive feedback (more ancestors, more descendants) and/or a negative feedback arising from resource limitation. Hyperbolic model implies a second-order positive feedback. The hyperbolic pattern of the world population growth arises from a second-order positive feedback between the population size and the rate of technological growth. The hyperbolic character of biodiversity growth can be similarly accounted for by a feedback between diversity and community structure complexity. The similarity between the curves of biodiversity and human population probably comes from the fact that both are derived from the interference of the hyperbolic trend with cyclical and stochastic dynamics.

Most biologists agree however that the period since human emergence is part of a new mass extinction, named the Holocene extinction event, caused primarily by the impact humans are having on the environment. It has been argued that the present rate of extinction is sufficient to eliminate most species on the planet Earth within 100 years.

New species are regularly discovered (on average between 5–10,000 new species each year, most of them insects) and many, though discovered, are not yet classified (estimates are that nearly 90% of all arthropods are not yet classified). Most of the terrestrial diversity is found in tropical forests.

### *Human benefits*

Summer field in Belgium (Hamois). The blue flowers are *Centaurea cyanus* and the red are *Papaver rhoeas*.

Biodiversity supports ecosystem services including air quality, climate (e.g., $CO_2$ sequestration), water purification, pollination, and prevention of erosion.

Since the stone age, species loss has accelerated above the prior rate, driven by human activity. Estimates of species loss are at a rate 100-10,000 times as fast as is typical in the fossil record.

Non-material benefits include spiritual and aesthetic values, knowledge systems and the value of education.

## Agriculture

Amazon Rainforest in Brazil

The reservoir of genetic traits present in wild varieties and traditionally grown landraces is extremely important in improving crop performance. Important crops, such as potato, banana and coffee, are often derived from only a few genetic strains. Improvements in crop species over the last 250 years have been largely due to incorporating genes from wild varieties and species into cultivars. Crop breeding for beneficial traits has helped to more than double crop production in the last 50 years as a result of the Green Revolution. A biodiverse environment preserves the genome from which such productive genes are drawn.

Crop diversity aids recovery when the dominant cultivar is attacked by a disease or predator:

- The Irish potato blight of 1846 was a major factor in the deaths of one million people and the emigration of another million. It was the result of planting only two potato varieties, both vulnerable to the blight.
- When rice grassy stunt virus struck rice fields from Indonesia to India in the 1970s, 6,273 varieties were tested for resistance. Only one was resistant, an Indian variety, and known to science only since 1966. This variety formed a hybrid with other varieties and is now widely grown.
- Coffee rust attacked coffee plantations in Sri Lanka, Brazil, and Central America in 1970. A resistant variety was found in Ethiopia. Although the diseases are themselves a form of biodiversity.

Monoculture was a contributing factor to several agricultural disasters, including the European wine industry collapse in the late 19th century, and the US Southern Corn Leaf Blight epidemic of 1970.

Higher biodiversity also limits the spread of infectious diseases as many different species act as buffers to them.

Although about 80 percent of humans' food supply comes from just 20 kinds of plants, humans use at least 40,000 species. Many people depend on these species for food, shelter, and clothing. Earth's surviving biodiversity provides resources for increasing the range of food and other products suitable for human use, although the present extinction rate shrinks that potential.

## Human health

The diverse forest canopy on Barro Colorado Island, Panama, yielded this display of different fruit

Biodiversity's relevance to human health is becoming an international political issue, as scientific evidence builds on the global health implications of biodiversity loss. This issue is closely linked with the issue of climate change, as many of the anticipated health risks of climate change are associated with changes in biodiversity (e.g. changes in populations and distribution of disease vectors, scarcity of fresh water, impacts on agricultural biodiversity and food resources etc.) Some of the health issues influenced by biodiversity include dietary health and nutrition security, infectious disease, medical science and medicinal resources, social and psychological health. Biodiversity is also known to have an important role in reducing disaster risk, and in post-disaster relief and recovery efforts.

Biodiversity provides critical support for drug discovery and the availability of medicinal resources. A significant proportion of drugs are derived, directly or indirectly, from biological sources; At least 50% of the pharmaceutical compounds on the US market are derived from plants, animals, and microorganisms, while about 80% of the world population depends on medicines from nature (used in either modern or traditional medical practice) for primary healthcare. Only a tiny fraction of wild species has been investigated for medical potential. Biodiversity has been critical to advances throughout the field of bionics. Evidence from market analysis and biodiversity science indicates that the decline in output from the pharmaceutical sector since the mid-1980s can be attributed to a move away from natural product exploration ("bioprospecting") in favor of genomics and synthetic chemistry; meanwhile, natural products have a long history of supporting significant economic and health innovation. Marine ecosystems are particularly important, although inappropriate bioprospecting can increase biodiversity loss, as well as violating the laws of the communities and states from which the resources are taken.

## Business and Industry


Agriculture production, pictured is a tractor and a chaser bin

Many industrial materials derive directly from biological sources. These include building materials, fibers, dyes, rubber and oil. Biodiversity is also important to the security of resources such as water, timber, paper and fibre and food. As a result, biodiversity loss is a significant risk factor in business development and a threat to long term economic sustainability.

## Leisure, cultural and aesthetic value

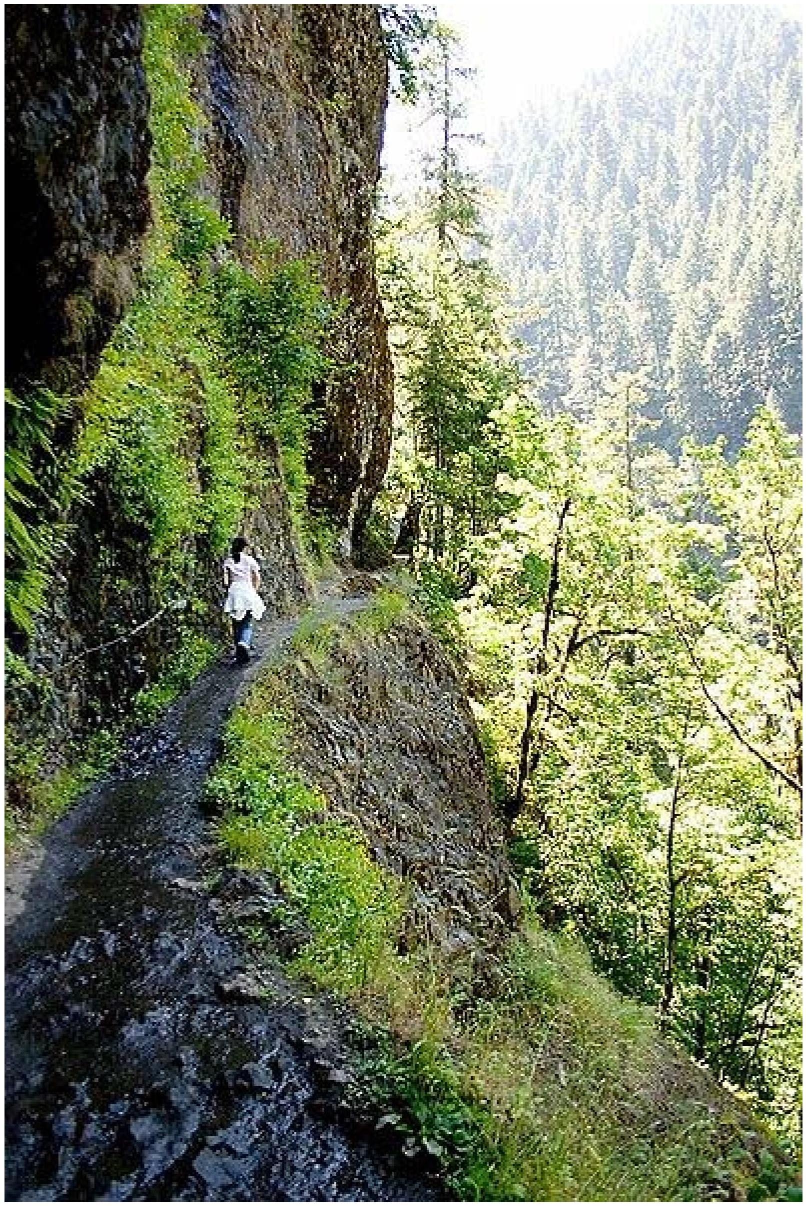
Biodiversity enriches leisure activities such as hiking, birdwatching or natural history study. Biodiversity inspires musicians, painters, sculptors, writers and other artists. Many cultures view themselves as an integral part of the natural world which requires them to respect other living organisms.

Popular activities such as gardening, fishkeeping and specimen collecting strongly depend on biodiversity. The number of species involved in such pursuits is in the tens of thousands, though the majority do not enter commerce.

The relationships between the original natural areas of these often exotic animals and plants and commercial collectors, suppliers, breeders, propagators and those who promote their understanding and enjoyment are complex and poorly understood. The general public responds well to exposure to rare and unusual organisms, reflecting their inherent value.

Philosophically it could be argued that biodiversity has intrinsic aesthetic and spiritual value to mankind *in and of itself*. This idea can be used as a counterweight to the notion that tropical forests and other ecological realms are only worthy of conservation because of the services they provide.

### Other services



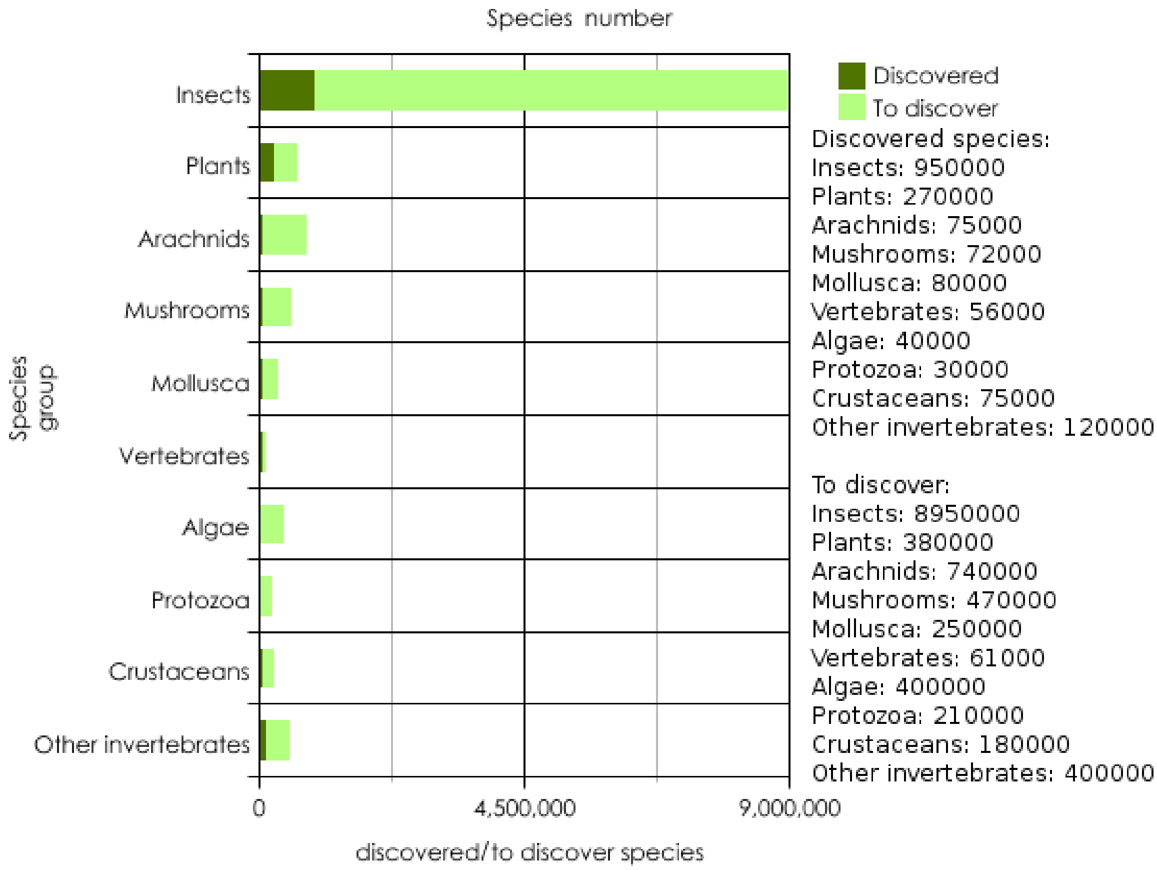
Eagle Creek, Oregon hiking

Biodiversity supports many ecosystem services that are often not readily visible. It plays a part in regulating the chemistry of our atmosphere and water supply. Biodiversity is directly involved in water purification, recycling nutrients and providing fertile soils. Experiments with controlled environments have shown that humans cannot easily build ecosystems to support human needs; for example insect pollination cannot be mimicked, and that activity alone represents tens of billions of dollars in ecosystem services per year to humankind.

Ecosystem stability is also positively related to biodiversity, protecting against disruption by extreme weather or human exploitation.

Polar bears on the sea ice of the Arctic Ocean, near the North Pole

### *Number of species*




Undiscovered and discovered species

According to the Global Taxonomy Initiative and the European Distributed Institute of Taxonomy, the *total* number of species for some phyla may be much higher than what was known in 2010:

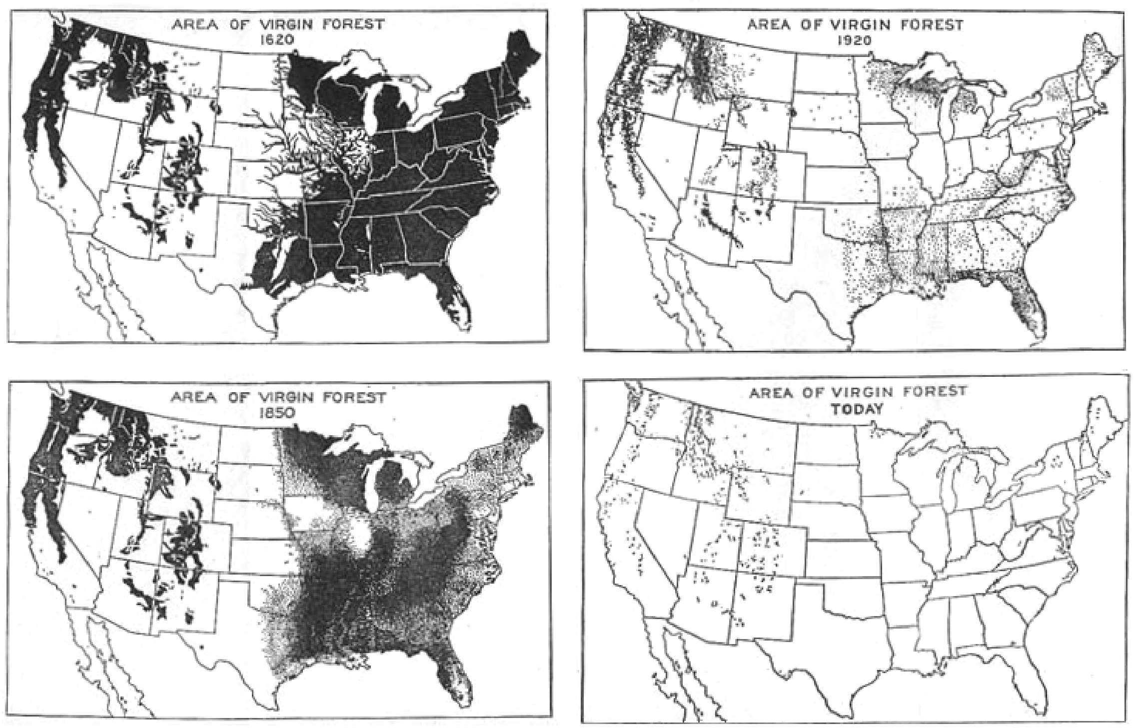
- 10–30 million insects; (of some 0,9 we know today )
- 5–10 million bacteria;
- 1.5 million fungi; (of some 0,4 million we know today )
- ~1 million mites
- The number of microbial species is not reliably known, but the Global Ocean Sampling Expedition dramatically increased the estimates of genetic diversity by identifying an enormous number of new genes from near-surface plankton samples at various marine locations, initially over the 2004-2006 period. The findings may eventually cause a significant change in the way science defines species and other taxonomic categories.

Since the rate of extinction has increased, many extant species may become extinct before they are described.

### *Species loss rates*

During the last century, decreases in biodiversity have been increasingly observed. In 2007, German Federal Environment Minister Sigmar Gabriel cited estimates that up to 30% of all species will be extinct by 2050. Of these, about one eighth of known plant species are threatened with extinction. Estimates reach as high as 140,000 species per year (based on Species-area theory). This figure indicates unsustainable ecological practices, because few species emerge each year. Almost all scientists acknowledge that the rate of species loss is greater now than at any time in human history, with extinctions occurring at rates hundreds of times higher than background extinction rates.

### *Threats*




**Loss of old growth forest in the United States; 1620, 1850, 1920, and 1992 maps:** *From William B. Greeley's, The Relation of Geography to Timber Supply, Economic Geography, 1925, vol. 1, p. 1–11. Source of "Today" map: compiled by George Draffan from roadless area map in The Big Outside: A Descriptive Inventory of the Big Wilderness Areas of the United States, by Dave Foreman and Howie Wolke (Harmony Books, 1992)*. These maps represent only virgin forest lost. Some regrowth has occurred but not to the age, size or extent of 1620 due to population increases and food cultivation.

Jared Diamond describes an "Evil Quartet" of habitat destruction, overkill, introduced species, and secondary extensions. Edward O. Wilson prefers the acronym **HIPPO**, standing for **H**abitat destruction, **I**nvasive species, **P**ollution, Human Over **P**opulation, and **O**verharvesting. The most authoritative classification in use today is IUCN's Classification of Direct Threats which has been adopted by major international conservation organizations such as the US Nature Conservancy, the World Wildlife Fund, Conservation International, and Birdlife International. The massive growth in the human population through the 20th century has had more impact on biodiversity than any other single factor. From 1950 to 2005, world population increased from 2.5 billion to 6.5 billion and is forecast to reach a plateau of more than 9 billion during the 21st century.

## Habitat destruction

Deforestation and increased road-building in the Amazon Rainforest are a significant concern because of increased human encroachment upon wild areas, increased resource extraction and further threats to biodiversity.

Habitat destruction has played a key role in extinctions, especially related to tropical forest destruction. While most threatened species are not food species, their biomass is converted into human food when their habitat is transformed into pasture, cropland, and orchards. It is estimated that more than a third of the earth's biomass is tied up in humans, livestock and crop species. Factors contributing to habitat loss are: overpopulation, deforestation, pollution (air pollution, water pollution, soil contamination) and global warming or climate change.

Habitat size and numbers of species are systematically related. Physically larger species and those living at lower latitudes or in forests or oceans are more sensitive to reduction in habitat area. Conversion to "trivial" standardized ecosystems (e.g., monoculture following deforestation) effectively destroys habitat for the more diverse species that preceded the conversion. In some countries lack of property rights or lax law/regulatory enforcement necessarily leads to biodiversity loss (degradation costs having to be supported by the community).

A 2007 study conducted by the National Science Foundation found that biodiversity and genetic diversity are codependent—that diversity among species requires diversity within a species, and vice versa. "If any one type is removed from the system, the cycle can break down, and the community becomes dominated by a single species." At present, the most threathened ecosystems are found in fresh water, according to the Millennium Ecosystem Assessment 2005, which was confirmed by the "**Freshwater Animal Diversity Assessment**", organised by the biodiversity platform, and the French Institut de recherche pour le développement (MNHNP).

Co-extinctions are a form of habitat destruction. Co-extinction occurs when the extinction or decline in one accompanies the other, such as in plants and beetles.

## Introduced and invasive species

Male *Lophura nycthemera* (Silver Pheasant), a native of East Asia that has been introduced into parts of Europe for ornamental reasons

Barriers such as large rivers, seas, oceans, mountains and deserts encourage diversity by enabling independent evolution on either side of the barrier. Invasive species occur when those barriers are blurred. Without barriers such species occupy new niches, substantially reducing diversity. Repeatedly humans have helped these species circumvent these barriers, introducing them for food and other purposes. This has occurred on a time scale much shorter than the eons that historically have been required for a species to extend its range.

Not all introduced species are invasive, nor all invasive species deliberately introduced. In cases such as the zebra mussel, invasion of US waterways was unintentional. In other cases, such as mongooses in Hawaii, the introduction is deliberate but ineffective (nocturnal rats were not vulnerable to the diurnal mongoose!). In other cases, such as oil palms in Indonesia and Malaysia, the introduction produces substantial economic benefits, but the benefits are accompanied by costly unintended consequences.

Finally, an introduced species may unintentionally injure a species that depends on the species it replaces. In Belgium, Prunus spinosa from Eastern Europe leafs much sooner than its West European counterparts, disrupting the feeding habits of the Thecla betulae butterfly (which feeds on the leaves). Introducing new species often leaves endemic and other local species unable to compete with the exotic species and unable to survive. The exotic organisms may be predators, parasites, or may simply outcompete indigenous species for nutrients, water and light.

At present, several countries have already imported so many exotic species, that the own indigenous fauna/flora is greatly outnumbered. For example, in Belgium, only 5% of the indigenous trees remain.

## Genetic pollution

Endemic species can be threatened with extinction through the process of genetic pollution, i.e. uncontrolled hybridization, introgression and genetic swamping. Genetic pollution leads to homogenization or replacement of local genomes as a result of either a numerical and/or fitness advantage of an introduced species. Hybridization and introgression are side-effects of introduction and invasion. These phenomena can be especially detrimental to rare species that come into contact with more abundant ones. The abundant species can interbreed with the rare species, swamping its gene pool. This problem is not always apparent from morphological (outward appearance) observations alone. Some degree of gene flowis normal adaptation, and not all gene and genotype constellations can be preserved. However, hybridization with or without introgression may, nevertheless, threaten a rare species' existence.

## Overexploitation

Overexploitation occurs when a resource is consumed at an unsustainable rate. This occurs on land in the form of overhunting, excessive logging, poor soil conservation in agriculture and the illegal wildlife trade. Joe Walston, director of the Wildlife Conservation Society's Asian programs, called the latter the "single largest threat" to biodiversity in Asia. The international trade of endangered species is second in size only to drug trafficking.

About 25% of world fisheries are now overfished to the point where their current biomass is less than the level that maximizes their sustainable yield.

The overkill hypothesis explains why earlier megafaunal extinctions occurred within a relatively short period of time. This can be connected with human migration.

## Hybridization, genetic pollution/erosion and food security

The Yecoro wheat (right) cultivar is sensitive to salinity, plants resulting from a hybrid cross with cultivar W4910 (left) show greater tolerance to high salinity

In agriculture and animal husbandry, the Green Revolution popularized the use of conventional hybridization to increase yield. Often hybridized breeds originated in developed countries and were further hybridized with local varieties in the developing world to create high yield strains resistant to local climate and diseases. Local governments and industry have been pushing hybridization. Formerly huge gene pools of various wild and indigenous breeds have collapsed causing widespread genetic erosion and genetic pollution. This has resulted in loss of genetic diversity and biodiversity as a whole.

(GM organisms) have genetic material altered by genetic engineering procedures such as recombinant DNA technology. GM crops have become a common source for genetic pollution, not only of wild varieties but also of domesticated varieties derived from classical hybridization.

Genetic erosion coupled with genetic pollution may be destroying unique genotypes, thereby creating a hidden crisis which could result in a severe threat to our food security. Diverse genetic material could cease to exist which would impact our ability to further hybridize food crops and livestock against more resistant diseases and climatic changes.

## Climate Change

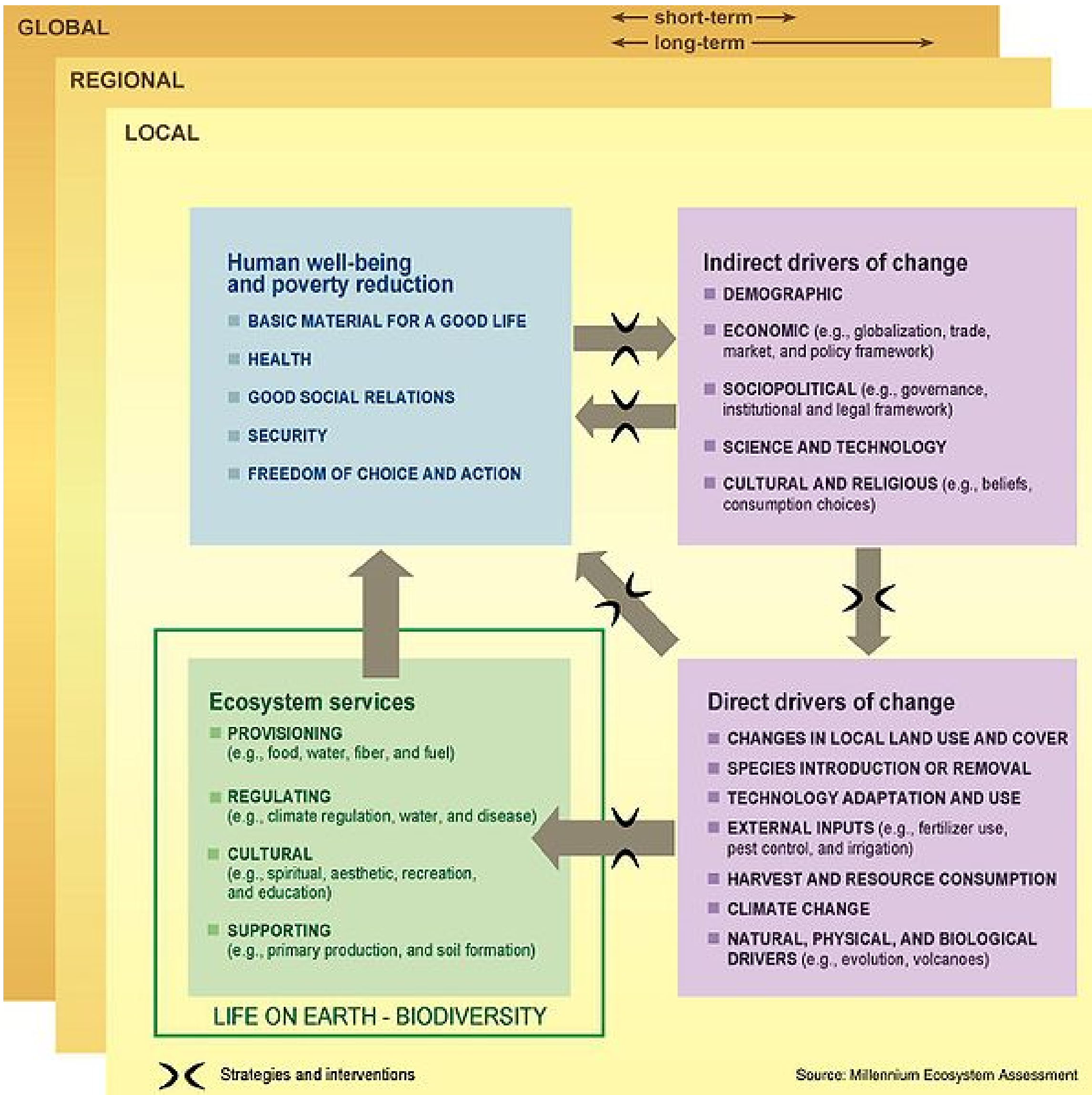
Global warming is also considered to be a major threat to global biodiversity. For example coral reefs -which are biodiversity hotspots- will be lost in 20 to 40 years if global warming continues at the current trend.

In 2004, an international collaborative study on four continents estimated that 10 percent of species would become extinct by 2050 because of global warming. “We need to limit climate change or we wind up with a lot of species in trouble, possibly extinct,” said Dr. Lee Hannah, a co-author of the paper and chief climate change biologist at the Center for Applied Biodiversity Science at Conservation International.

### *The Holocene extinction*

Rates of decline in biodiversity in this sixth mass extinction match or exceed rates of loss in the five previous mass extinction events in the fossil record. Loss of biodiversity results in the loss of natural capital that supplies ecosystem goods and services. The economic value of 17 ecosystem services for Earth's biosphere (calculated in 1997) has an estimated value of US$ 33 trillion ($3.3x10^{13}$) per year.

### *Conservation*




A schematic image illustrating the relationship between biodiversity, ecosystem services, human well-being, and poverty. The illustration shows where conservation action, strategies and plans can influence the drivers of the current biodiversity crisis at local, regional, to global scales.

The retreat of Aletsch Glacier in the Swiss Alps (situation in 1979, 1991 and 2002), due to global warming

Conservation biology matured in the mid-20th century as ecologists, naturalists, and other scientists began to research and address issues pertaining to global biodiversity declines.

The conservation ethic advocates management of natural resources for the purpose of sustaining biodiversity in species, ecosystems, the evolutionary process, and human culture and society.

Conservation biology is reforming around strategic plans to protect biodiversity. Preserving global biodiversity is a priority in strategic conservation plans that are designed to engage public policy and concerns affecting local, regional and global scales of communities, ecosystems, and cultures. Action plans identify ways of sustaining human well-being, employing natural capital, market capital, and ecosystem services.

## *Protection and restoration techniques*

The most powerful technique is to preserve habitat.

Exotic species removal allows less competitive species to recover their ecological niches. Exotic species that have become a pest can be identified taxonomically (e.g. with Digital Automated Identification SYstem (DAISY), using the barcode of life. Removal is practical only given large groups of individuals due to the econimic cost.

Once the preservation of the remaining native species in an area is assured. "missing" species can be identified and reintroduced using databases such as the *Encyclopedia of Life* and the Global Biodiversity Information Facility.

Other techniques include:

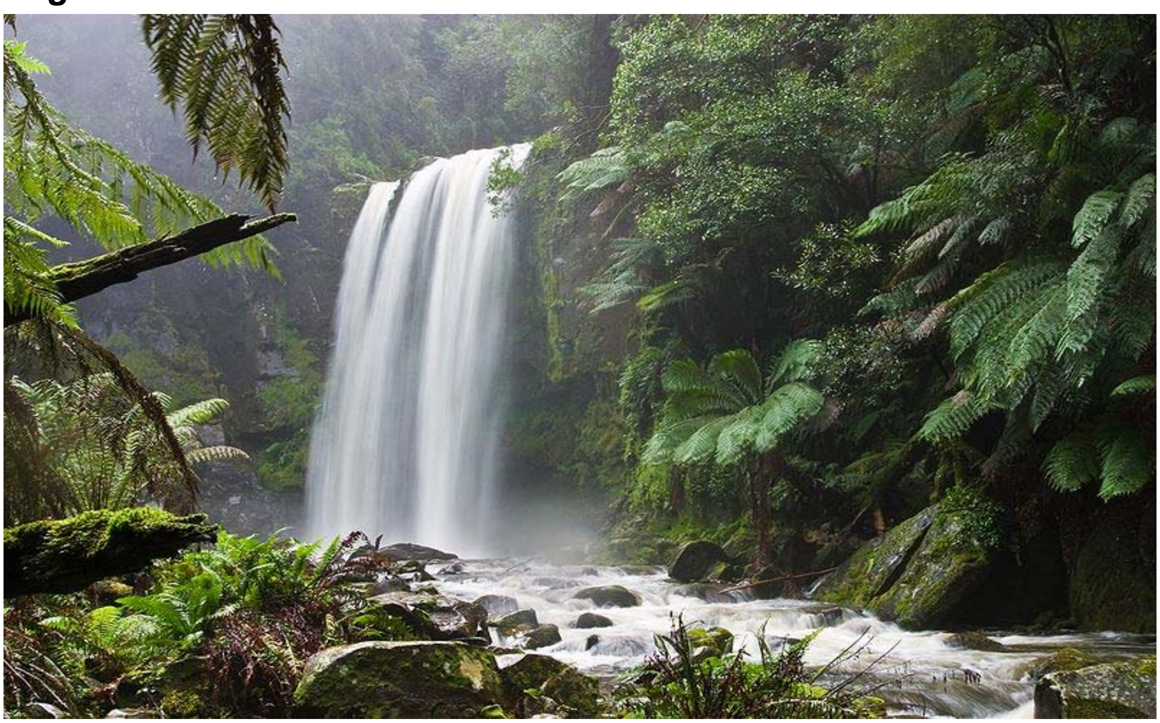
- Biodiversity banking places a monetary value on biodiversity. One example is the Australian Native Vegetation Management Framework.
- Gene banks are collections of specimens and genetic material. Some banks intend to reintroduce banked species to the ecosystem (e.g. via tree nurseries).
- Reducing and better targeting of pesticides allows more species to survive in agricultural and urbanized areas.
- Location-specific approaches are less useful for protecting migratory species. One approach is to create wildlife corridors that correspond to the animals' movements. National and other boundaries can complicate corridor creation.

## Resource allocation

Focusing on limited areas of higher potential biodiversity promises greater immediate return on investment than spreading resources evenly or focusing on areas of little diversity but greater interest in biodiversity.

A second strategy focuses on areas that retain most of their original diversity, which typically require little or no restoration. These are typically non-urbanized, non-agricultural areas. Tropical areas often fit both criteria, given their natively high diversity and relative lack of development.

## *Legal status*



A great deal of work is occurring to preserve the natural characteristics of Hopetoun Falls, Australia while continuing to allow visitor access.

Biodiversity is taken into account in some political and judicial decisions:

- The relationship between law and ecosystems is very ancient and has consequences for biodiversity. It is related to private and public property rights. It can define protection for threatened ecosystems, but also some rights and duties (for example, fishing and hunting rights).
- Law regarding species is more recent. It defines species that must be protected because they may be threatened by extinction. The U.S. Endangered Species Act is an example of an attempt to address the "law and species" issue.
- Laws regarding gene pools are only about a century old. Domestication and plant breeding methods are not new, but advances in genetic engineering has led to tighter laws covering distribution of genetically modified organisms, gene patents and process patents. Governments struggle to decide whether to focus on for example, genes, genomes, or organisms and species.

Global agreements such as the Convention on Biological Diversity), give **sovereign national rights over biological resources** (not property). The agreements commit countries to **conserve biodiversity**, **develop resources for sustainability** and **share the benefits** resulting from their use. Biodiverse countries that allow bioprospecting or collection of natural products, expect a share of the benefits rather than allowing the individual or institution that discovers/exploits the resource to capture them privately. Bioprospecting can become a type of biopiracy when such principles are not respected.

Sovereignty principles can rely upon what is better known as Access and Benefit Sharing Agreements (ABAs). The Convention on Biodiversity implies informed consent between the source country and the collector, to establish which resource will be used and for what, and to settle on a fair agreement on benefit sharing.

Uniform approval for use of biodiversity as a legal standard has not been achieved, however. Bosselman argues that biodiversity should not be used as a legal standard, claiming that the remaining areas of scientific uncertainty cause unacceptable administrative waste and increase litigation without promoting preservation goals.

## *Analytical limits*

### Taxonomic and size relationships

Less than 1% of all species that have been described have been studied beyond simply noting their existence. The vast majority of Earth's species are microbial. Contemporary biodiversity physics is "firmly fixated on the visible [macroscopic] world". For example, microbial life is metabolically and environmentally more diverse than multicellular life. "On the tree of life, based on analyses of small-subunit ribosomal RNA, visible life consists of barely noticeable twigs. The inverse relationship of size and population recurs higher on the evolutionary ladder—"to a first approximation, all multicellular species on Earth are insects". Insect extinction rates are high—supporting the Holocene extinction hypothesis.

Chapter- 8

# Ecosystem

Coral reefs are an example of a marine ecosystem.

Rainforests often have a great deal of biodiversity with many plant and animal species. This is the Gambia River in Senegal's Niokolo-Koba National Park.

An **ecosystem** is a biological environment consisting of all the organisms living in a particular area, as well as all the nonliving, physical components of the environment with which the organisms interact, such as air, soil, water, and sunlight. It is all the organisms in a given area, along with the nonliving (abiotic) factors with which they interact; a biological community and its physical environment.

## *Overview*

The entire array of organisms inhabiting a particular ecosystem is called a community. In a typical ecosystem, plants and other photosynthetic organisms are the producers that provide the food. Ecosystems can be permanent or temporary. Ecosystems usually form a number of food webs.

Ecosystems are functional units consisting of living things in a given area, non-living chemical and physical factors of their environment, linked together through nutrient cycle and energy flow.

1. Natural
    1. Terrestrial ecosystem
    2. Aquatic ecosystem
        1. Lentic, the ecosystem of a lake, pond or swamp.
        2. Lotic, the ecosystem of a river, stream or spring.

2. Artificial, ecosystems created by humans.

Central to the ecosystem concept is the idea that living organisms interact with every other element in their local environment. Eugene Odum, a founder of ecology, stated: "Any unit that includes all of the organisms (ie: the "community") in a given area interacting with the physical environment so that a flow of energy leads to clearly defined trophic structure, biotic diversity, and material cycles (i.e.: exchange of materials between living and nonliving parts) within the system is an ecosystem."

## *Etymology*

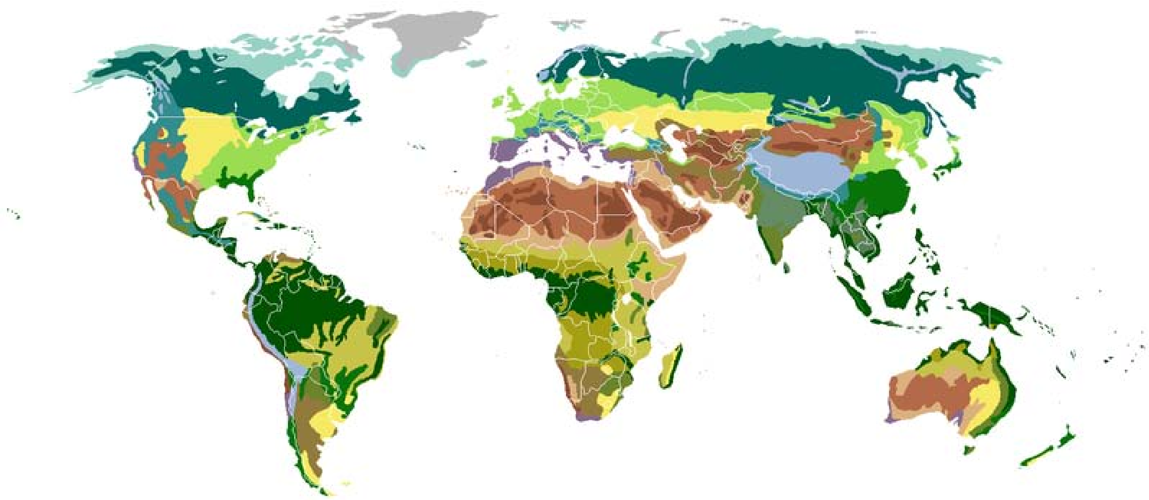
The term ecosystem was coined in 1930 by Roy Clapham to mean the combined physical and biological components of an environment. British ecologist Arthur Tansley later refined the term, describing it as "The whole system, … including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment". Tansley regarded ecosystems not simply as natural units, but as mental isolates. Tansley later defined the spatial extent of ecosystems using the term ecotope.

## *Examples of ecosystems*

- agro-ecosystems
- Agroecosystem
- Aquatic ecosystem
- Chaparral
- Coral reef
- Desert
- Forest
- Greater Yellowstone Ecosystem
- Human ecosystem
- Large marine ecosystem
- Littoral zone
- Lotic
- Marine ecosystem
- Pond Ecosystem
- Prairie
- Rainforest
- Riparian zone
- Savanna
- Steppe
- Subsurface Lithoautotrophic Microbial Ecosystem
- Taiga
- Tundra
- Urban ecosystem

A freshwater ecosystem in Gran Canaria, an island of the Canary Islands

## Biomes



Map of Terrestrial biomes classified by vegetation

Biomes are a classification of globally similar areas, including ecosystems, such as ecological communities of plants and animals, soil organisms and climatic conditions. Biomes are in part defined based on factors such as plant structures (such as trees, shrubs and grasses), leaf types (such as broadleaf and needleleaf), plant spacing (forest, woodland, savanna) and climate. Unlike ecozones, biomes are not defined by genetic, taxonomic or historical similarities. Biomes are often identified with particular patterns of ecological succession and climax vegetation.

A fundamental classification of biomes is:

1. Terrestrial (land) biomes.
2. Freshwater biomes.
3. Marine biomes.

### *Classification*

Summer field in Belgium (Hamois). The blue flower is Centaurea cyanus and the red one a Papaver rhoeas.

The High Peaks Wilderness Area in the 6,000,000-acre (2,400,000 ha) Adirondack Park is an example of a diverse ecosystem.

Flora of Baja California Desert, Cataviña region, Mexico

Ecosystems have become particularly important politically, since the Convention on Biological Diversity (CBD) - ratified by 192 countries - defines "the protection of ecosystems, natural habitats and the maintenance of viable populations of species in natural surroundings" as a commitment of ratifying countries. This has created the political necessity to spatially identify ecosystems and somehow distinguish among them. The CBD defines an "ecosystem" as a "dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit".

With the need of protecting ecosystems, the political need arose to describe and identify them efficiently. Vreugdenhil et al. argued that this could be achieved most effectively by using a physiognomic-ecological classification system, as ecosystems are easily recognizable in the field as well as on satellite images. They argued that the structure and seasonality of the associated vegetation, or flora, complemented with ecological data (such as elevation, humidity, and drainage), are each determining modifiers that separate partially distinct sets of species. This is true not only for plant species, but also for species of animals, fungi and bacteria. The degree of ecosystem distinction is subject to the physiognomic modifiers that can be identified on an image and/or in the field. Where necessary, specific fauna elements can be added, such as seasonal concentrations of animals and the distribution of coral reefs.

Several physiognomic-ecological classification systems are available:

- Physiognomic-Ecological Classification of Plant Formations of the Earth: a system based on the 1974 work of Mueller-Dombois and Heinz Ellenberg, and developed by UNESCO. This classificatie "describes the above-ground or underwater vegetation structures and cover as observed in the field, described as plant life forms. This classification is fundamentally a species-independent physiognomic, hierarchical vegetation classification system which also takes into account ecological factors such as climate, elevation, human influences such as grazing, hydric regimes and survival strategies such as seasonality. The system was expanded with a basic classification for open water formations".
- Land Cover Classification System (LCCS), developed by the Food and Agriculture Organization (FAO).
- Forest-Range Environmental Study Ecosystems (FRES) developed by the United States Forest Service for use in the United States.

Several aquatic classification systems are available, and an effort is being made by the United States Geological Survey (USGS) and the Inter-American Biodiversity Information Network (IABIN) to design a complete ecosystem classification system that will cover both terrestrial and aquatic ecosystems.

From a philosophy of science perspective, ecosystems are not discrete units of nature that simply can be identified using the most "correct" type of classification approach. In agreement with the definition by Tansley ("mental isolates"), any attempt to delineate or classify ecosystems should be explicit about the observer/analyst input in the classification including its normative rationale.

Two Giant Sequoias, Sequoia National Park. Note the large fire scar at the base of the right-hand tree; fires do not kill the trees but do remove competing thin-barked species, and aid Giant Sequoia regeneration.

## *Ecosystem services*

Ecosystem services are "fundamental life-support services upon which human civilization depends,"[i] and can be direct or indirect. Examples of direct ecosystem services are: pollination, wood and erosion prevention. Indirect services could be considered climate moderation, nutrient cycles and detoxifying natural substances.

The services and goods an ecosystem provides are often undervalued as many of them are without market value. Broad examples include:

- regulating (climate, floods, nutrient balance, water filtration)
- provisioning (food, medicine, fur)
- cultural (science, spiritual, ceremonial, recreation, aesthetic)
- supporting (nutrient cycling, photosynthesis, soil formation).

### *Ecosystem legal rights*

Ecuador's new constitution of 2008 is the first in the world to recognize legally enforceable Rights of Nature, or ecosystem rights.

The borough of Tamaqua, Pennsylvania passed a law giving ecosystems legal rights. The ordinance establishes that the municipal government or any Tamaqua resident can file a lawsuit on behalf of the local ecosystem. Other townships, such as Rush, followed suit and passed their own laws.

This is part of a growing body of legal opinion proposing 'wild law'. Wild law, a term coined by Cormac Cullinan (a lawyer based in South Africa), would cover birds and animals, rivers and deserts.

### *Function and biodiversity*

Savanna at Ngorongoro Conservation Area, Tanzania

The side of a tide pool showing sea stars (*Dermasterias*), sea anemones (*Anthopleura*) and sea sponges in Santa Cruz, California.

From an anthropocentric point of view, some people perceive ecosystems as production units that produce goods and services, such as wood by forest ecosystems and grass for cattle by natural grasslands. Meat from wild animals, often referred to as bush meat in Africa, has proven to be extremely successful under well-controlled management schemes in South Africa and Kenya. Much less successful has been the discovery and commercialization of substances of wild organism for pharmaceutical purposes. Services derived from ecosystems are referred to as ecosystem services. They may include

1. facilitating the enjoyment of nature, which may generate many forms of income and employment in the tourism sector, often referred to as eco-tourisms,
2. water retention, thus facilitating a more evenly distributed release of water,
3. soil protection, open-air laboratory for scientific research, etc.

A greater degree of species or biological diversity - commonly referred to as Biodiversity - of an ecosystem may contribute to greater resilience of an ecosystem, because there are more species present at a location to respond to change and thus "absorb" or reduce its effects. This reduces the effect before the ecosystem's structure is fundamentally changed to a different state. This is not universally the case and there is no proven relationship between the species diversity of an ecosystem and its ability to provide goods and services on a sustainable level: Humid tropical forests produce very few goods and direct services and are extremely vulnerable to change, while many temperate forests readily grow back to their previous state of development within a lifetime after felling or a forest fire. Some grasslands have been sustainably exploited for thousands of years (Mongolia, Africa, European peat and mooreland communities).

### *The study of ecosystems*

Forest on San Juan Island

## Ecosystem dynamics

Loch Lomond in Scotland forms a relatively isolated ecosystem. The fish community of this lake has remained unchanged over a very long period of time.

Introduction of new elements, whether biotic or abiotic, into an ecosystem tend to have a disruptive effect. In some cases, this can lead to ecological collapse or "trophic cascading" and the death of many species within the ecosystem. Under this deterministic vision, the abstract notion of ecological health attempts to measure the robustness and recovery capacity for an ecosystem; i.e. how far the ecosystem is away from its steady state.

Often, however, ecosystems have the ability to rebound from a disruptive agent. The difference between collapse or a gentle rebound is determined by two factors—the toxicity of the introduced element and the resiliency of the original ecosystem.

Ecosystems are primarily governed by stochastic (chance) events, the reactions these events provoke on non-living materials and the responses by organisms to the conditions surrounding them. Thus, an ecosystem results from the sum of individual responses of organisms to stimuli from elements in the environment.The presence or absence of populations merely depends on reproductive and dispersal success, and population levels fluctuate in response to stochastic events. As the number of species in an ecosystem is higher, the number of stimuli is also higher. Since the beginning of life organisms have survived continuous change through natural selection of successful feeding, reproductive and dispersal behavior. Through natural selection the planet's species have continuously adapted to change through variation in their biological composition and distribution. Mathematically it can be demonstrated that greater numbers of different interacting factors tend to dampen fluctuations in each of the individual factors.

Spiny forest at Ifaty, Madagascar, featuring various Adansonia (baobab) species, Alluaudia procera (Madagascar ocotillo) and other vegetation

Given the great diversity among organisms on earth, most ecosystems only changed very gradually, as some species would disappear while others would move in. Locally, sub-populations continuously go extinct, to be replaced later through dispersal of other sub-populations. Stochastists do recognize that certain intrinsic regulating mechanisms occur in nature. Feedback and response mechanisms at the species level regulate population levels, most notably through territorial behaviour. Andrewatha and Birch suggest that territorial behaviour tends to keep populations at levels where food supply is not a limiting factor. Hence, stochastists see territorial behaviour as a regulatory mechanism at the species level but not at the ecosystem level. Thus, in their vision, ecosystems are not regulated by feedback and response mechanisms from the ecosystem itself and there is no such thing as a balance of nature.

If ecosystems are governed primarily by stochastic processes, through which its subsequent state would be determined by both predictable and random actions, they may be more resilient to sudden change than each species individually. In the absence of a balance of nature, the species composition of ecosystems would undergo shifts that would depend on the nature of the change, but entire ecological collapse would probably be infrequent events.


Arctic tundra on Wrangel Island, Russia

The theoretical ecologist Robert Ulanowicz has used information theory tools to describe the structure of ecosystems, emphasizing mutual information (correlations) in studied systems. Drawing on this methodology and prior observations of complex ecosystems, Ulanowicz depicts approaches to determining the stress levels on ecosystems and predicting system reactions to defined types of alteration in their settings (such as increased or reduced energy flow, and eutrophication.

In addition, Eric Sanderson has developed the Muir web, based on experience on the Mannahatta project. This graphical schematic shows how different species are connected to each other, not only regarding their position in the food chain, but also regarding other services, i.e. provisioning of shelter, ...

## Ecosystem ecology

Ecosystem ecology is the integrated study of biotic and abiotic components of ecosystems and their interactions within an ecosystem framework. This science examines how ecosystems work and relates this to their components such as chemicals, bedrock, soil, plants, and animals. Ecosystem ecology examines physical and biological structure and examines how these ecosystem characteristics interact.

# Chapter- 9

# Resilience

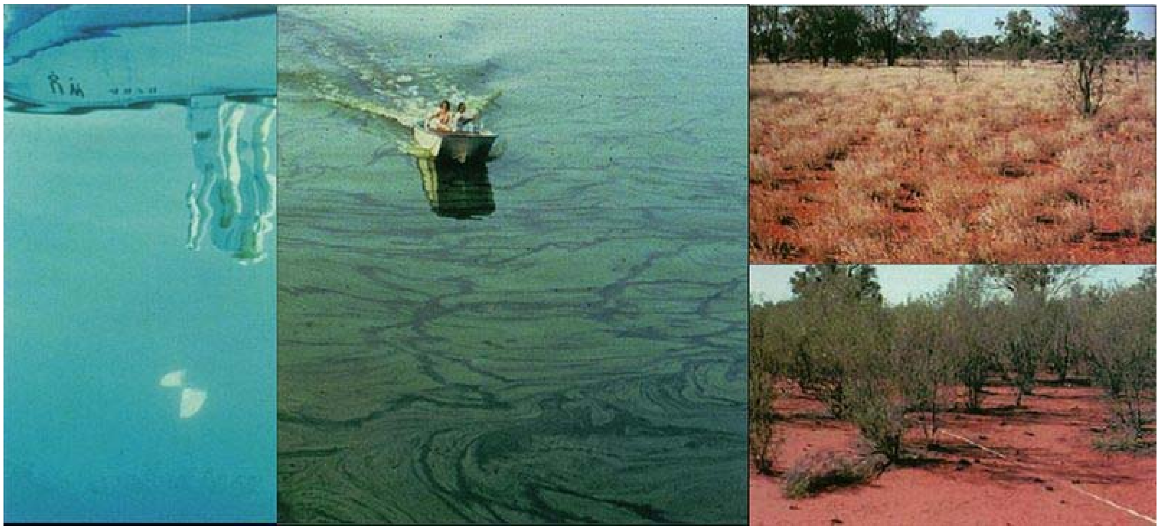
In ecology, **resilience** is one possible ecosystem response to a perturbation or disturbance. A resilient ecosystem resists damage and recovers quickly from stochastic disturbances such as fires, flooding, windstorms, insect population explosions, and human activities such as deforestation and the introduction of exotic plant or animal species. Disturbances of sufficient magnitude or duration can profoundly affect an ecosystem and may force an ecosystem to reach a threshold beyond which a different regime of processes and structures predominates. Human activities that adversely affect ecosystem resilience such as reduction of biodiversity, exploitation of natural resources, pollution, land-use, and anthropogenic climate change and are increasingly causing regime shifts in ecosystems, often to less desirable and degraded conditions. Interdisciplinary discourse on resilience now includes consideration of the interactions of humans and ecosystems via socio-ecological systems, and the need for shift from the maximum sustainable yield paradigm to environmental management which aims to build ecological resilience through "resilience analysis, adaptive resource management, and adaptive governance".

## *Definitions and theory*

The concept of resilience in ecological systems was first introduced by the Canadian ecologist C.S. Holling in order to describe the persistence of natural systems in the face of changes in ecosystem variables due to natural or anthropogenic causes. Resilience has been defined in two ways in ecological literature:

1. as the time required for an ecosystem to return to an equilibrium or steady-state following a perturbation (which is also defined as stability by some authors). This definition of resilience is used in other fields such as physics and engineering, and hence has been termed ‘engineering resilience’ by Holling.
2. as "the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks".

The second definition has been termed ‘ecological resilience’, and it presumes the existence of multiple stable states or domains.



Lake and Mulga ecosystems with alternative stable states

Temperate lakes can exist with clear water providing many ecosystem services, or turbid water with toxic algae blooms and reduced ecosystem services. The regime or state is dependent upon lake phosphorous cycles, and either state can be resilient dependent upon management.

Mulga woodlands of Australia can exist in a grass-rich state that supports sheep herding, or a shrub-dominated state of no value for sheep grazing. Changes in regime or state are driven by the interaction of fire, herbivory, and variable rainfall. Either state can be resilient dependent upon management.

## Aspects of resilience

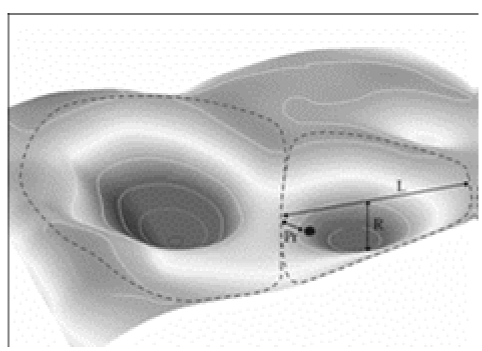


Figure 1a: Original stability landscape

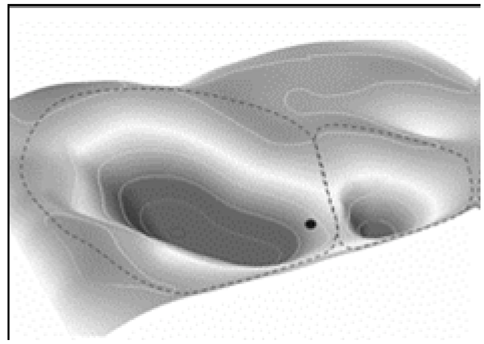


Figure 1b: Altered stability landscape

Aspects of resilience and changes in stability landscapes

Ecologists Brian Walker, Holling and others describe four critical aspects of resilience: *latitude*, *resistance*, *precariousness*, and *panarchy*.

The first three can apply both to a whole system or the sub-systems that make it up.

1. Latitude: the maximum amount a system can be changed before losing its ability to recover (before crossing a threshold which, if breached, makes recovery difficult or impossible).
2. Resistance: the ease or difficulty of changing the system; how "resistant" it is to being changed.
3. Precariousness: how close the current state of the system is to a limit or "threshold.".
4. Panarchy: the degree to which a certain hierarchical level of an ecosystem is influenced by other levels. For example, organisms living in communities that are in isolation from one another may be organized differently than the same type of organism living in a large continuous population, thus the community-level structure is influenced by population-level interactions.

These four dimensions are most easily understood through mathematical representation of an ecosystem and its variables in phase space. A phase or state space diagram is one in which each axis represents a variable of a system with any number of variables, so a point in this space describes the system's total state. A state space diagram of an ecosystem would contain several attractors, or "*basins of attraction*" which are representations of ecosystem process configurations or regimes. Moreover, these configurations or regimes can change over time as a result of both internal and external processes.

Figure 1a. depicts a three-dimensional stability landscape with two basins of attraction showing, in one basin, the current position of the system and three aspects of resilience, L = latitude, R = resistance, Pr = precariousness.

In Figure. 1b., changes in the stability landscape have resulted in a contraction of the basin the system was in and an expansion of the alternate basin. Without itself changing, the system has changed basins.

Closely linked to resilience is *adaptive capacity*, which is the property of an ecosystem that describes change in stability landscapes and resilience. Adaptive capacity in socio-ecological systems refers to the ability of humans to deal with change in their environment by observation, learning and altering their interactions.

## *Human impacts on resilience*

Resilience refers to ecosystem's stability and capability of tolerating disturbance and restoring itself. If the disturbance is of sufficient magnitude or duration, a threshold may be reached where the ecosystem changes state, possibly permanently. Sustainable use of environmental goods and services requires understanding and consideration of the resilience of the ecosystem and its limits. However, the elements which influence ecosystem resilience are complicated. For example various elements such as the water cycle, fertility, biodiversity, plant diversity and climate, interact fiercely and effect different systems.

There are many areas where human activity impacts upon and is also dependent upon the resilience of terrestrial, aquatic and marine ecosystems. These include agriculture, deforestation, pollution, mining, recreation, overfishing, dumping of waste into the sea and climate change.

### Agriculture

Agriculture can be seen as a significant example which the resilience of terrestrial ecosystems should be considered. The organic matter (elements carbon and nitrogen) in soil, which is supposed to be recharged by multiple plants, is the main source of nutrients for crop growth. At the same time, intensive agriculture practices in response to global food demand and shortages involves the removal of weeds and the application of fertilisers to increase food production. However as a result of agricultural intensification and the application of herbicides to control weeds, fertilisers to accelerate and increase crop growth and pesticides to control insects, plant biodiversity is reduced as is the supply of organic matter to replenish soil nutrients and prevent run-off. This leads to a reduction in soil fertility and productivity. More sustainable agricultural practices would take into account and estimate the resilience of the land and monitor and balance the input and output of organic matter.

### Deforestation

The term deforestation has a meaning that covers crossing the threshold of forest's resilience and losing its ability to return its originally stable state. To recover itself, a forest ecosystem needs suitable interactions among climate conditions and bio-actions, and enough area. In addition, generally, the resilience of a forest system allows recovery from a relatively small scale of damage (such as lightning or landslide) of up to 10 per cent of its area. The larger the scale of damage, the more difficult it is for the forest ecosystem to restore and maintain its balance.

Deforestation also decreases biodiversity of both plant and animal life and can lead to an alteration of the climatic conditions of an entire area. Deforestation can also lead to species extinction, which can have a domino effect particularly when keystone species are removed or when a significant number of species is removed and their ecological function is lost.

## Climate change

Climate change is threatening coastal communities in a variety of ways such as rising sea levels, increasingly frequent large storms, tidal surges and flooding damage. One of the main results of climate change is rising sea water temperature which seriously effect on coral reefs through thermal-stress related coral bleaching. Between 1997-1998 the most significant worldwide coral bleaching event was recorded which corresponded with the El Nino Southern Oscillation, with significant damage to the coral reefs of the Western Indian Ocean.

## Overfishing

It has been estimated by the United Nations Food and Agriculture Organisation that over 70% of the world's fish stocks are either fully exploited or depleted which means overfishing threatens marine ecosystem resilience and this is mostly by rapid growth of fishing technology. One of the negative effects on marine ecosystems is that over the last half-century the stocks of coastal fish have had a huge reduction as a result of over-fishing for its economic benefits. Blue fin tuna is at particular risk of extinction. Depletion of fish stocks results in lowered biodiversity and consequently imbalance in the food chain, and increased vulnerability to disease.

In addition to overfishing, coastal communities are suffering the impacts of growing numbers of large commercial fishing vessels in causing reductions of small local fishing fleets. Many local lowland rivers which are sources of fresh water have become degraded because of the inflows of pollutants and sediments.

## Dumping of waste into the sea

Dumping both depends upon ecosystem resilience whilst threatening it. Dumping of sewage and other contaminants into the ocean is often undertaken for the dispersive nature of the oceans and adaptive nature and ability for marine life to process the marine debris and contaminants. However, waste dumping threatens marine ecosystems by poisoning marine life and eutrophication.

## Poisoning marine life

According to the International Maritime Organisation oil spills can have serious effects on marine life. The OILPOL Convention recognized that most oil pollution resulted from routine shipboard operations such as the cleaning of cargo tanks. In the 1950s, the normal practice was simply to wash the tanks out with water and then pump the resulting mixture of oil and water into the sea. OILPOL 54 prohibited the dumping of oily wastes within a certain distance from land and in 'special areas' where the danger to the environment was especially acute. In 1962 the limits were extended by means of an amendment adopted at a conference organized by IMO. Meanwhile, IMO in 1965 set up a Subcommittee on Oil Pollution, under the auspices of its Maritime Safety committee, to address oil pollution issues.

The threat of oil spills to marine life is recognised by those likely to be responsible for the pollution, such as the International Tanker Owners Pollution Federation:

The marine ecosystem is highly complex and natural fluctuations in species composition, abundance and distribution are a basic feature of its normal function. The extent of damage can therefore be difficult to detect against this background variability. Nevertheless, the key to understanding damage and its importance is whether spill effects result in a downturn in breeding success, productivity, diversity and the overall functioning of the system. Spills are not the only pressure on marine habitats; chronic urban and industrial contamination or the exploitation of the resources they provide are also serious threats.

## Eutrophication and algal blooms

The Woods Hole Oceanographic Institution calls nutrient pollution the most widespread, chronic environmental problem in the coastal ocean. The discharges of nitrogen, phosphorus, and other nutrients come from agriculture, waste disposal, coastal development, and fossil fuel use. Once nutrient pollution reaches the coastal zone, it stimulates harmful overgrowths of algae, which can have direct toxic effects and ultimately result in low-oxygen conditions. Certain types of algae are toxic. Overgrowths of these algae result in harmful algal blooms, which are more colloquially referred to as "red tides" or "brown tides". Zooplankton eat the toxic algae and begin passing the toxins up the food chain, affecting edibles like clams, and ultimately working their way up to seabirds, marine mammals, and humans. The result can be illness and sometimes death.

## *Resilience and environmental management*

Ecological resilience and the thresholds by which resilience is defined are closely interrelated in the way that they influence environmental policy-making, legislation and subsequently environmental management. The ability of ecosystems to recover from certain levels of environmental impact is not explicitly noted in legislation, however, because of ecosystem resilience, some levels of environmental impact associated with development are made permissible by environmental policy-making and ensuing legislation.

Some examples of the consideration of ecosystem resilience within legislation include:

- *Environmental Planning and Assessment Act 1979* (NSW) – A key goal of the Environmental Assessment procedure is to determine whether proposed development will have a significant impact upon ecosystems.
- *Protection of the Environment (Operations) Act 1997* (NSW) – Pollution control is dependent upon keeping levels of pollutants emitted by industrial and other human activities below levels which would be harmful to the environment and its ecosystems. Environmental protection licenses are administered to maintain the environmental objectives of the POEO Act and breaches of license conditions can attract heavy penalties and in some cases criminal convictions.
- *Threatened Species Conservation Act 1995* (NSW) – This Act seeks to protect threatened species while balancing it with development.

There is increasing awareness that greater understanding of the ecosystem resilience is required to reach the goal of sustainable development. Scientific research associated with resilience is beginning to play a role in influencing policy-making and subsequent environmental decision making.

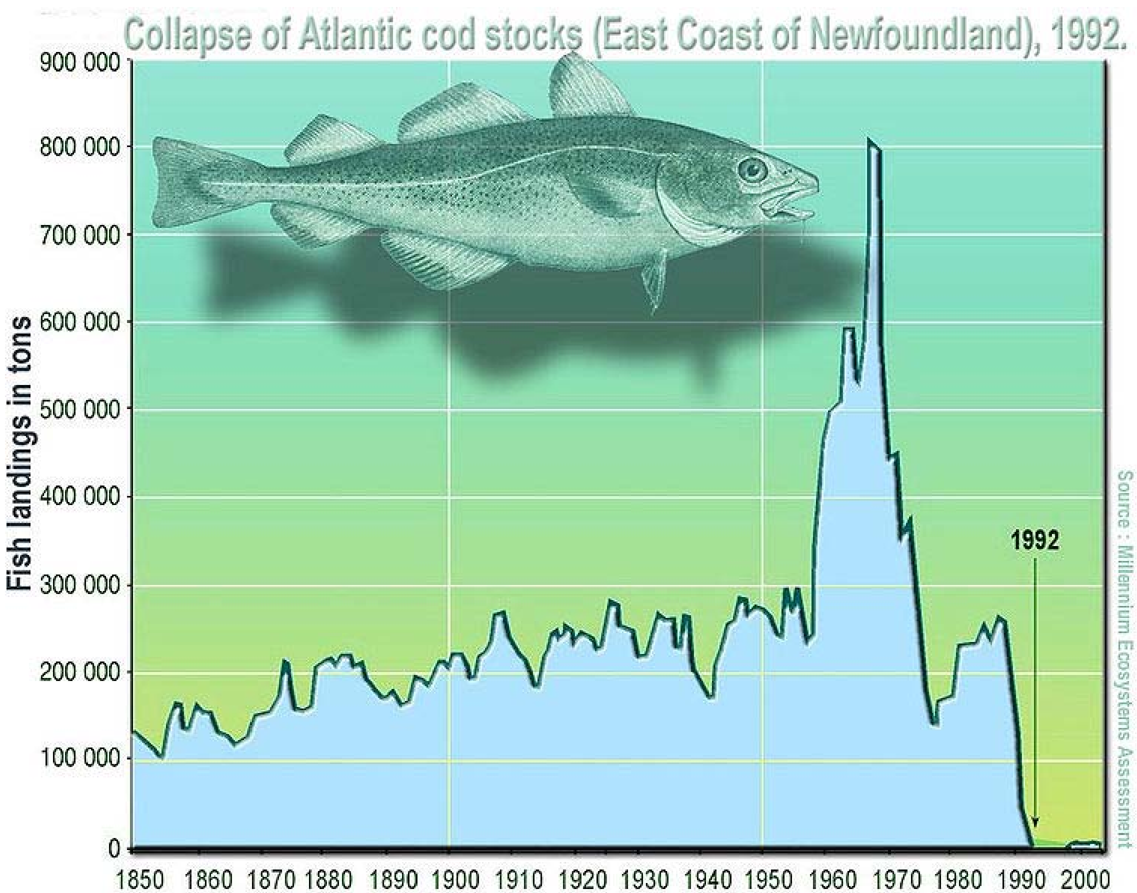
This occurs in a number of ways:

- Observed resilience within specific ecosystems drives management practice. When resilience is observed to be low, or impact seems to be reaching the threshold, management response can be to alter human behavior to result in less adverse impact to the ecosystem.
- Ecosystem resilience impacts upon the way that development is permitted/environmental decision making is undertaken, similar to the way that existing ecosystem health impacts upon what development is permitted. For instance, remnant vegetation in the states of Queensland and New South Wales are classified in terms of ecosystem health and abundance. Any impact that development has upon threatened ecosystems must consider the health and resilience of these ecosystems. This is governed by the *Threatened Species Conservation Act 1995* in New South Wales and the *Vegetation Management Act 1999* in Queensland.
- International level initiatives aim at improving socio-ecological resilience worldwide through the cooperation and contributions of scientific and other experts. An example of such an initiative is the **Millenium Ecosystem Assessment** whose objective is "to assess the consequences of ecosystem change for human well-being and the scientific basis for action needed to enhance the conservation and sustainable use of those systems and their contribution to human well-being". Similarly, the **United Nations Environment Programme** aim is "to provide leadership and encourage partnership in caring for the environment by

inspiring, informing, and enabling nations and peoples to improve their quality of life without compromising that of future generations.

## Chapter- 10

# Overexploitation




Atlantic cod stocks were severely overexploited in the 1970s and 1980s, leading to their abrupt collapse in 1992

**Overexploitation**, also called **overharvesting**, refers to harvesting a renewable resource to the point of diminishing returns. Sustained overexploitation can lead to the destruction of the resource. The term applies to natural resources such as: wild medicinal plants, grazing pastures, fish stocks, forests and water aquifers.

In ecology, overexploitation describes one of the five main activities threatening global biodiversity. Ecologists use the term to describe populations that are harvested at a rate that is unsustainable, given their natural rates of mortality and capacities for reproduction. This can result in extinction at the population level and even extinction of whole species. In conservation biology the term is usually used in the context of human economic activity that involves the taking of biological resources, or organisms, in larger numbers than their populations can withstand. The term is also used and defined somewhat differently in fisheries, hydrology and natural resource management.

Overexploitation can lead to resource destruction, including extinctions. However it is also possible for overexploitation to be sustainable, as discussed below in the section on fisheries. In the context of fishing, the term overfishing can be used instead of overexploitation, as can overgrazing in stock management, overlogging in forest management, overdrafting in aquifer management, and endangered species in species monitoring. Overexploitation is not an activity limited to humans. Introduced predators and herbivores, for example, can overexploit native flora and fauna.

## *History*

When the giant flightless birds called moa were overexploited to the point of extinction, the giant Haast's eagle that preyed on them also became extinct

Overexploitation is not a new phenomenon. It has been observed for millennia. For example, ceremonial cloaks worn by the Hawaiian kings were made from the mamo bird; a single cloak used the feathers of 70,000 birds of this now-extinct species. The dodo, a flightless bird from Mauritius, is another well known example of overexploitation. As with many island species, it was naive about certain predators, allowing humans to approach and kill it with ease.

From the earliest of times, hunting for wild mammals and birds has been an important human activity as a means of survival. There is a whole history of overexploitation in the form of overhunting. The overkill hypothesis (Quaternary extinction events) explains why the megafaunal extinctions occurred within a relatively short period of time. This can be traced with human migration. The most convincing evidence of this theory is that 80% of the North American large mammal species disappeared within 1000 years of the arrival of humans on the western hemisphere continents. Again, in New Zealand, ten species of the giant moa birds were hunted to extinction by the Māori by 1500 AD. A second wave of extinctions occurred later with European settlement.

In more recent times, overexploitation has resulted in the gradual emergence of the concepts of sustainability and sustainable development, which has built on other concepts, such as sustainable yield, eco-development and deep ecology.

## *Overview*

Overexploitation need not necessarily lead to the destruction of the resource, nor is it necessarily unsustainable. However, depleting the numbers or amount of the resource can change its quality. For example, footstool palm is a wild palm tree found in Southeast Asia. Its leaves are used for thatching and food wrapping, and overharvesting has resulted in its leaf size becoming smaller.

### *Tragedy of the commons*

Cows on Selsley Common. The tragedy of the commons is a useful parable for understanding how overexploitation can occur

The tragedy of the commons refers to a dilemma described in an article by that name written by Garrett Hardin and first published in the journal *Science* in 1968.

Central to Hardin's essay is an example which is a useful parable for understanding how overexploitation can occur. This example was first sketched in an 1833 pamphlet by William Forster Lloyd, as a hypothetical and simplified situation based on medieval land tenure in Europe, of herders sharing a common on which they are each entitled to let their cows graze. In Hardin's example, it is in each herder's interest to put each succeeding cow he acquires onto the land, even if the carrying capacity of the common is exceeded and it is temporarily or permanently damaged for all as a result. The herder receives all of the benefits from an additional cow, while the damage to the common is shared by the entire group. If all herders make this individually rational economic decision, the common will be overexploited or even destroyed to the detriment of all. However, since all herders reach the same rational conclusion, overexploitation in the form of overgrazing occurs, with immediate losses, and the pasture may be degraded to the point where it gives very little return.

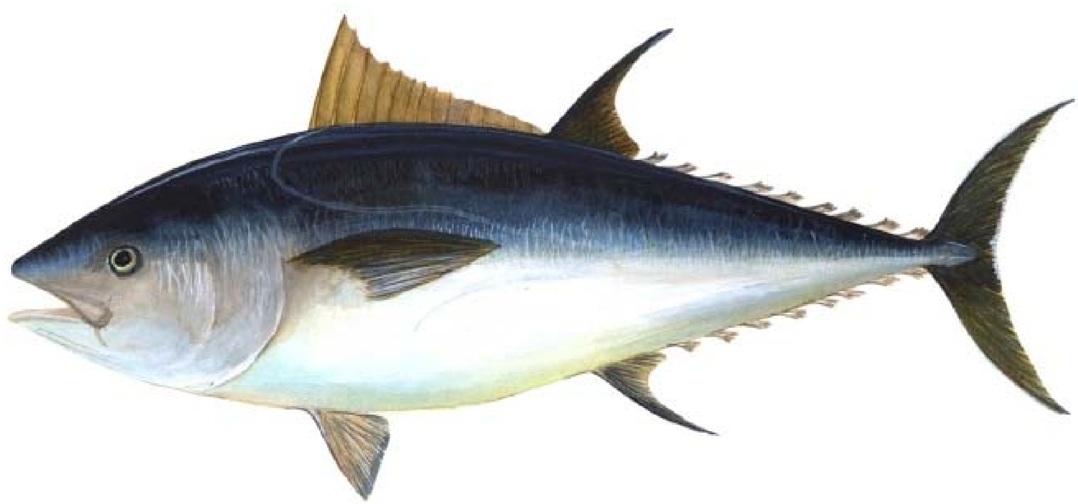
"Therein is the tragedy. Each man is locked into a system that compels him to increase his herd without limit - in a world that is limited. Ruin is the destination toward which all men rush, each pursuing his own interest in a society that believes in the freedom of the commons." (Hardin, 1968)

In the course of his essay, Hardin develops the theme, drawing in many examples of latter day commons, such as national parks, the atmosphere, oceans, rivers and fish stocks. The example of fish stocks had led some to call this the "tragedy of the fishers". A major theme running through the essay is the growth of human populations, with the Earth's finite resources being the general common.

The tragedy of the commons has intellectual roots tracing back to Aristotle, who noted that "what is common to the greatest number has the least care bestowed upon it", as well as to Hobbes and his leviathan. The opposite situation to a tragedy of the commons is sometimes referred to as a tragedy of the anticommons: a situation in which rational individuals, acting separately, collectively waste a given resource by underutilizing it.

The tragedy of the commons can be avoided if it is appropriately regulated. Hardin's use of "commons" has frequently been misunderstood, leading Hardin to later remark that he should have titled his work "The tragedy of the unregulated commons".

### *Fisheries*



The northern bluefin tuna is currently seriously overexploited. Scientists say 7,500 tons annually is the sustainable limit, yet the fishing industry continue to harvest 60,000 tons.

In wild fisheries, overexploitation or overfishing occurs when a fish stock has been fished down "below the size that, on average, would support the long-term maximum sustainable yield of the fishery". However, overexploitation can be sustainable.

When a fishery starts harvesting fish from a previously unexploited stock, the biomass of the fish stock will decrease, since harvesting means fish are being removed. For sustainability, the rate at which the fish replenish biomass through reproduction must balance the rate at which the fish are being harvested. If the harvest rate is increased, then the stock biomass will further decrease. At a certain point, the maximum harvest yield that can be sustained will be reached, and further attempts to increase the harvest rate will result in the collapse of the fishery. This point is called the maximum sustainable yield, and in practice, usually occurs when the fishery has been fished down to about 30% of the biomass it had before harvesting started.

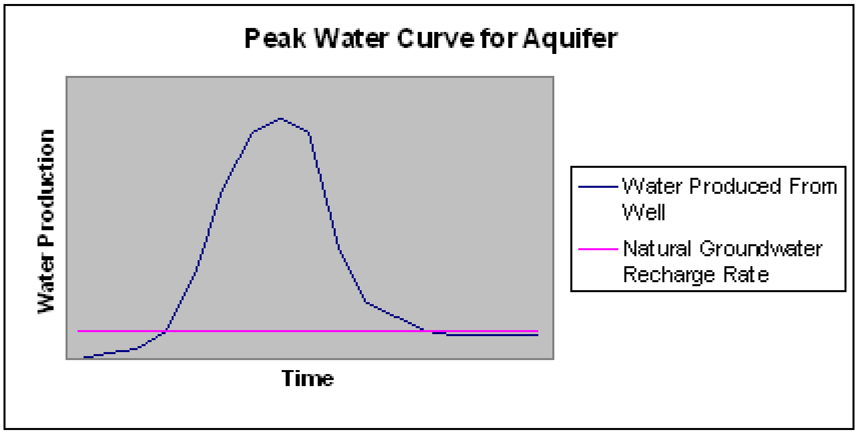
It is possible to fish the stock down further, to say 15% of the pre-harvest biomass, and then adjust the harvest rate so the biomass remains at that level. In this case, the fishery is sustainable, but is now overexploited, because the stock has been run down to the point where the sustainable yield is less than it could be.

Fish stocks are said to "collapse" if their biomass declines by more than 95 percent of their maximum historical biomass. Atlantic cod stocks were severely overexploited in the 1970s and 1980s, leading to their abrupt collapse in 1992. Even though fishing has ceased, the cod stocks have failed to recover. The absence of cod as the apex predator in many areas has led to trophic cascades.

About 25% of world fisheries are now overexploited to the point where their current biomass is less than the level that maximizes their sustainable yield. These depleted fisheries can often recover if fishing pressure is reduced until the stock biomass returns to the optimal biomass. At this point, harvesting can be resumed near the maximum sustainable yield.

The tragedy of the commons can be avoided within the context of fisheries if fishing effort and practices are regulated appropriately by fisheries management. One effective approach may be assigning some measure of ownership in the form of individual transferable quotas (ITQs) to fishermen. In 2008, a large scale study of fisheries that used ITQs, and ones that didn't, provided strong evidence that ITQs help prevent collapses and restore fisheries that appear to be in decline.

### *Water resources*




Overexploitation of groundwater from an aquifer can result in a peak water curve.

Water resource, such as lakes and aquifers, are usually renewable resources which naturally recharge (the term fossil water is sometimes used to describe aquifers which don't recharge). Overexploitation occurs if a water resource, such as the Ogallala Aquifer, is mined or extracted at a rate that exceeds the recharge rate, that is, at a rate that exceeds the practical sustained yield. Recharge usually comes from area streams, rivers and lakes. An aquifer which has been overexploited is said to be overdrafted or depleted. Forests enhance the recharge of aquifers in some locales, although generally forests are a major source of aquifer depletion. Depleted aquifers can become polluted with contaminants such as nitrates, or permanently damaged through subsidence or through saline intrusion from the ocean.

This turns much of the world's underground water and lakes into finite resources with peak usage debates similar to oil. These debates usually centre around agriculture and suburban water usage but generation of electricity from nuclear energy or coal and tar sands mining is also water resource intensive. A modified Hubbert curve applies to any resource that can be harvested faster than it can be replaced. Though Hubbert's original analysis did not apply to renewable resources, their overexploitation can result in a Hubbert-like peak. This has led to the concept of peak water.

## *Forest resources*

Beech forest – Grib Skov, Denmark

Forests are overexploited when they are logged at a rate faster than reforestation takes place. Reforestation competes with other land uses such as food production, livestock grazing, and living space for further economic growth. Historically utilization of forest products, including timber and fuel wood, have played a key role in human societies, comparable to the roles of water and cultivable land. Today, developed countries continue to utilize timber for building houses, and wood pulp for paper. In developing countries almost three billion people rely on wood for heating and cooking. Short-term economic gains made by conversion of forest to agriculture, or overexploitation of wood products, typically leads to loss of long-term income and long term biological productivity (hence reduction in nature's services). West Africa, Madagascar, Southeast Asia and many other regions have experienced lower revenue because of overexploitation and the consequent declining timber harvests.

## *Biodiversity*

The rich diversity of marine life inhabiting coral reefs attracts bioprospectors. Many coral reefs are overexploited

Overexploitation is one of the five main activities threatening global biodiversity. The other four activities are pollution, introduced species, habitat fragmentation and habitat destruction.

One of the key health issues associated with biodiversity is drug discovery and the availability of medicinal resources. A significant proportion of drugs are derived, directly or indirectly, from biological sources. Marine ecosystems are of particular interest in this regard. However unregulated and inappropriate bioprospecting can be considered a form of overexploitation which has the potential to degrade ecosystems and increase biodiversity loss, as well as impacting on the rights of the communities and states from which the resources are taken.

### *Endangered species*

It is not just humans that overexploit their resources. Overgrazing can occur naturally, caused by native fauna, as shown in the upper right.

Overexploitation threatens one-third of endangered vertebrates, as well as other groups. Excluding edible fish, the illegal trade in wildlife is valued at $10 billion per year. Industries responsible for this include the trade in bushmeat, the trade in Chinese medicine, and the fur trade. The Convention for International Trade in Endangered Species of Wild Fauna and Flora, or CITES was set up in order to control and regulate the trade in endangered animals. It currently protects, to a varying degree, some 33,000 species of animals and plants. It is estimated that a quarter of the endangered vertebrates in the United States of America and half of the endangered mammals is attributed to overexploitation

All living organisms require resources to survive. Overexploitation of these resources for protracted periods can deplete natural stocks to the point where they are unable to recover within a short time frame. Humans have always harvested food and other resources they have needed to survive. Human populations, historically, were small, and methods of collection limited to small quantities. With an exponential increase in human population, expanding markets and increasing demand, combined with improved access and techniques for capture, are causing the exploitation of many species beyond sustainable levels. In practical terms, if continued, it reduces valuable resources to such low levels that their exploitation is no longer sustainable and can lead to the extinction of a species, in addition to having dramatic, unforeseen effects, on the ecosystem. Overexploitation often occurs rapidly as markets open, utilising previously untapped resources, or locally used species.

The Carolina parakeet was hunted to extinction

Today, overexploitation and misuse of natural resources is an ever present threat for species richness. This is more prevalent when looking at island ecology and the species that inhabit them, as islands can be viewed as the world in miniature. Island endemic populations are more prone to extinction from overexploitation, as they often exist at low densities with reduced reproductive rates. A good example of this are island snails, such as the Hawaiian *Achatinella* and the French Polynesian *Partula*. Achatinelline snails have

15 species listed as extinct and 24 critically endangered while 60 species of partulidae are considered extinct with 14 listed as critically endangered. The WCMC have attributed over-collecting and very low lifetime fecundity for the extreme vulnerability exhibited among these species.

As another example, when the humble hedgehog was introduced to the Scottish island of Uist, the population greatly expanded and took to consuming and overexploiting shorebird eggs, with drastic consequences for their breeding success. Twelve species of avifauna are affected, with some species numbers being reduced by 39%.

Where there is substantial human migration, civil unrest, or war, controls may no longer exist. With civil unrest, for example in the Congo and Rwanda, firearms have become common place and the breakdown of food distribution networks in such countries leaves the resources of the natural environment vulnerable to whoever can exploit them. Animals are even killed as target practice sometimes, or simply to spite the government. Populations of large primates, such as gorillas and chimpanzees, ungulates and other mammals, may be reduced by 80% or more by hunting and certain species may be eliminated all together. This decline has been called the bushmeat crisis.

Overall, 50 bird species that have become extinct since 1500 (approximately 40% of the total) have been subject to overexploitation, including:

- Great Auk- The penguin-like bird of the north, hunted for its feathers, meat, fat and oil.
- Carolina parakeet - The only parrot species native to the eastern United States, was hunted for crop protection and its feathers.

Other species affected by overexploitation include:

- The international trade in fur: chinchilla, vicuña, giant otter and numerous cat species.
- Insect collectors: butterflies
- Horticulturists: New Zealand mistletoe (*Trilepidia adamsii*), orchids, cacti and many other plant species.
- Shell collectors: Marine molluscs
- Aquarium hobbyists: tropical fish
- Chinese medicine: bears, tigers
- Novelty pets: snakes, parrots and primates

### *Cascade effects*

Overexploiting sea otters resulted in cascade effects which destroyed kelp forest ecosystems

Overexploitation of species can result in knock-on or cascade effects. This can particularly apply if, through overexploitation, a habitat loses its apex predator. Because of the loss of the top predator, a dramatic increase in their prey species can occur. In turn, the unchecked prey can then overexploit their own food resources until population numbers dwindle, possibly to the point of extinction.

A classic example of cascade effects occurred with sea otters. Starting before the 17th century and not phased out until 1911, sea otters were hunted aggressively for their exceptionally warm and valuable pelts, which could fetch up to $2500 US. This caused cascade effects through the kelp forest ecosystems along the Pacific Coast of North America.

One of the sea otters' primary food sources is the sea urchin. When hunters caused sea otter populations to decline, an ecological release of sea urchin populations occurred. The sea urchins then overexploited their main food source, kelp, creating urchin barrens, areas of seabed denuded of kelp, but carpeted with urchins. No longer having food to eat, the sea urchin became locally extinct as well. Also, since kelp forest ecosystems are homes to many other species, the loss of the kelp caused other cascade effects of secondary extinctions.

In 1911, when only one small group of 32 sea otters survived in a remote cove, an international treaty was signed to prevent further exploitation of the sea otters. Under heavy protection, the otters multiplied and repopulated the depleted areas, which slowly recovered. More recently, with declining numbers of fish stocks, again due to overexploitation, killer whales have experienced a food shortage and have been observed feeding on sea otters, again reducing their numbers.

**Chapter- 11**

# Ecological Stability and Small Population Size

# Ecological stability

**Ecological stability** can refer to types of stability in a continuum ranging from resilience (returning quickly to a previous state) to constancy to persistence. The precise definition depends on the ecosystem in question, the variable or variables of interest, and the overall context. In the context of conservation ecology, stable populations are often defined as ones that do not go extinct. Researchers applying mathematical models from system dynamics usually use Lyapunov stability.

## *Types of ecological stability*

Local stability indicates that a system is stable over small short-lived disturbances, while global stability indicates a system highly resistant to change in species composition and/or food web dynamics.

### Constancy and persistence

Observational studies of ecosystems use **constancy** to describe living systems that can remain unchanged.

### Resistance and inertia (persistence)

*Resistance* and *inertia* deal with a system's inherent response to some perturbation.

A perturbation is any externally imposed change in conditions, usually happening in a short time period. **Resistance** is a measure of how little the variable of interest changes in response to external pressures. **Inertia** (or persistence) implies that the living system is able to resist external fluctuations. In the context of changing ecosystems in post-glacial North America, E.C. Pielou remarked at the outset of her overview, "It obviously takes considerable time for mature vegetation to become established on newly exposed ice scoured rocks or glacial till...it also takes considerable time for whole ecosystems to change, with their numerous interdependent plant species, the habitats these create, and the animals that live in the habitats. Therefore, climatically caused fluctuations in ecological communities are a damped, smoothed-out version of the climatic fluctuations that cause them."

### Resilience, elasticity and amplitude

*Resilience* is the tendency of a system to return to a previous state after a perturbation. *Elasticity* and *amplitude* are measures of resilience. Elasticity is the speed with which a system returns. Amplitude is a measure of how far a system can be moved from the previous state and still return. Ecology borrows the idea of neighborhood stability and a domain of attraction from dynamical systems theory.

# Small population size

**Small populations** behave differently from larger populations. They often result in population bottlenecks, which have harmful consequences for the survival of that population.

### *Demographic effects*

The influence of stochastic variation in demographic (reproductive and mortality) rates is much higher for small populations than large ones. Stochastic variation in demographic rates causes small populations to fluctuate randomly in size. The smaller the population the greater the probability that fluctuations will lead to extinction. They are subject to a higher chance of extinction because they are more vulnerable to genetic drift, resulting in stochastic variation in their gene pool, their demography and their environment.

One demographic consequence of a small population size, the probability that all offspring in a generation are of the same sex, and where males and females are equally likely to be produced, is easy to calculate: it is given by $1 / 2^{n-1}$ (The chance of all animals being females is $1 / 2^{n}$; the same holds for all males, thus this result). This can be a problem in very small populations. In 1977, the last 18 Kakapo on a Fiordland island in New Zealand were all male, though the probability of this would only be 0.0000076 if determined by chance (however, females are generally more predated than males and kakapo may be subject to sex allocation). With a population of just three individuals the probability of them all being the same sex is 0.25. Put another way, for every four species reduced to three individuals (or more precisely three individuals in the effective population), one will go extinct within one generation just because they are all the same sex. If the population remains at this size for several generations, such an event becomes almost inevitable.

### *Environmental effects*

Stochastic variation in the environment (year to year variation in rainfall, temperature) can produce temporally correlated birth and death rates (i.e. 'good' years when birth rates are high and death rates are low and 'bad' years when birth rates are low and death rates are high) that lead to fluctuations in the population size. Again, smaller populations are more likely to go extinct due to these environmentally generated population fluctuations than are large populations.

### *Genetic consequences*

Conservationists are often worried about a loss of genetic variation in small populations. There are two types of genetic variation that are important when dealing with small populations.

- The degree of homozygosity within individuals in a population; i.e. the proportion of an individual's loci that contain homozygous rather than heterozygous alleles. Many deleterious alleles are only harmful in the homozygous form.
- The degree of monomorphism/polymorphism within a population; i.e. how many different alleles of the same gene exist in the gene pool of a population. Polymorphism may be particularly important at loci involved in the immune response.

There are two mechanisms operating in small populations that influence these two types of genetic variation.

- Genetic drift — Genetic variation is determined by the joint action of natural selection and genetic drift (chance). In small populations the relative importance of genetic drift (chance) is higher; deleterious alleles can become more frequent and 'fixed' in a population due to chance. Any allele, deleterious, beneficial or neutral is more likely to be lost from a small population (gene pool) than a large one. This results in a reduction in the number of forms of alleles in a small population and in extreme cases to monomorphism where there is only one form of the allele. Continued fixation of deleterious alleles in small populations is called Muller's ratchet, and can lead to mutational meltdown.
- Inbreeding — In a small population, related individuals are more likely to breed together. The offspring of related parents have a far higher number of homozygous loci than the offspring of unrelated parents.

There are two types of potential consequence of loss of genetic variation:

- Inbreeding depression — Inbreeding depression is usually taken to mean any immediate harmful effect, on individuals or the population, of a decrease in either type of genetic variation. Inbreeding depression can almost never be found in declining populations that were not very large to begin with; it is somewhat common in large populations *becoming* small though. The reason is purging selection, most efficient in populations that are strongly but not dangerously inbred.

- The ability of the population to adapt/evolve to changing conditions, “without variability evolution is impossible”. It is obvious that the absolute size of a population limits the absolute degree of allelic diversity. On the other hand, should an advantageous mutation arise, it is likely to show its effect sooner and more thoroughly.