

Liebig's Law of the Minimum

Liebig's Law of the Minimum was developed for the nutrition of agricultural plants, but can also be applied to populations.

Reproduction (birth of new organisms) and death are the fundamental processes regulating change in population size over time. Low abundance of resources, or other nonideal environmental conditions, reduces the reproduction rate or increases the death rate in a population, in addition to lowering rates of growth or activity for individual organisms. Reproductive rates are more sensitive to changes in the environment than metabolic rates or death rates since an individual can often survive under conditions under which it cannot reproduce. If a population grows, resources decline and some individuals will not obtain resources in adequate supply. This affects individual reproduction.

It is also an example of natural selection, since the individuals that are more successful at obtaining and using resources will make a greater contribution to the genetic makeup of the next generation. If the organisms within a population are members of the same species, this is "intraspecific competition."

For each species there is a gradient of habitat suitability that is determined by environmental conditions and resources. Ecologists need quantitative information on the suitability of habitats to predict population dynamics in other areas, in the future, and due to changes in community structure. The theoretical basis for these relationships was formalized by Pearl and Reed (1920), who promoted the logistic growth equation that had been previously described by P. F. Verhulst in 1838. The equation is an attempt to relate the specific growth rate of a population (m) to the environment. The probability of an individual reproducing (b) minus the probability of death (d) per unit time is equal to m and is a direct manifestation of the suitability of the habitat. The differential equation for logistic growth is

$$\frac{dN}{dt} = \mu \cdot N$$

where

$$\mu = r \cdot \left(\frac{K - N}{K} \right)$$

and where N is the number of individuals in the population, t is time, and dN/dt is the change in N over time. The intrinsic growth rate of the population (r) is the value m approaches when resources are not limiting growth and there is no intraspecific competition. The effects of environmental conditions other than resources, for instance temperature, are modeled by changes in r . The number of individuals that the resources of a habitat can support (K) is referred to as the carrying capacity, and

models intraspecific competition with a constant level of resource supply. Other impacts of the population on the environment, such as the accumulation of waste, are also modeled by K . As a population grows, the resources must be shared among many individuals, decreasing the reproduction rate and increasing the rate of death. In the equation, N approaches K , causing m to approach 0. If the population is above the carrying capacity, it cannot be supported by the resources present, m becomes negative, and the population declines. The relationship in which population growth rate is sensitive to population size is known as density-dependent population regulation.

The logistic growth equation is used by population ecologists mainly as a conceptual tool, rather than to forecast changes in population size, because the mechanisms of population regulation are not explicitly modeled in terms of reproduction and death rates. It is also rare in plant and animal populations for individuals of different ages to have the same rate of death or equal probabilities of reproduction. Intraspecific competition often affects certain classes of individuals more than others. The common method of forecasting population sizes is currently the use of structured demographic models that consider the effects of age, size, or developmental stage on probabilities of reproduction and death. Populations of each class of organism and the transition of individuals between classes are tracked separately in empirical models, using matrix algebraic methods.

a living cell requires that elements be supplied at specific ratios for growth. Liebig's law of the minimum has been applied to nutrient limitation of primary producer assemblages in aquatic systems with the assumption that all producers have equal nutrient requirements and nutrients are evenly distributed in space and time in the environment (i.e., a homogeneous equilibrium condition of nutrients exists). The law, combined with the idea of equilibrium nutrient availability, predicts that only one nutrient will limit primary production of a system.

Autotrophs in streams can also be limited by nitrogen, phosphorus, nitrogen and phosphorus, or neither. It is unwise to assume that any particular nutrient limits primary production in streams or that nutrients cannot be colimiting. CO_2 might also limit some primary producers in streams and silicon can limit epiphytic diatoms at times. Cases of no nutrient limitation are expected to be more common in streams than lakes or nonforested wetlands because of the greater influence of riparian canopy cover on light (light limitation) in streams and scouring floods that remove algal biomass. Bioassays of heterotrophic metabolism

upon nutrient enrichment versus stimulation of primary producers conducted in streams across the United States indicate that heterotrophs in streams can also be limited by nitrogen, phosphorus, both, or neither. These bioassays also indicate that autotrophic and heterotrophic responses often differ within the same stream.

Limitation of primary producers by more than one nutrient in wetlands, streams, and lakes raises the question of explaining colimitation that should not occur if Liebig's law is really a law of nutrient limitation. Given that streams are commonly far from equilibrium, the existence of colimitation in at least some streams is not surprising. Likewise, wetlands are structured by benthic processes, and it is easy to imagine that spatial variations in sediments and gradients created by different points of nutrient inflow and outflow lead to significant spatial heterogeneity in nutrient limitation. The concept of several nutrients limiting primary production in lakes is more difficult because lakes are more homogeneous than streams and wetlands.