Competition

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Introductory article

Article Contents

Competition is the all-pervasive interaction between organisms in which each reduces the performance of the other, either by depleting mutually required resources or by directly inflicting damage. Competition is an important factor that controls the distribution and abundance of many if not most plants and animals. More generally, it has been a potent force driving natural selection and is a major factor (along with stress, disturbance, predation and mutualism) in shaping the structure of biological communities. Too often, competition is assumed to be occurring without sufficient evidence. Carefully designed experiments are one of the best sources of evidence for competition. Different kinds of experiments uncover different views of competition. In general, plants are organised into competitive hierarchies in which light is often the key resource. Mathematical models allow us to explore how competition might lead to either coexistence or exclusion.

Introduction

All life forms require resources. The challenge to find, harvest, transport and retain possession of resources is part of the struggle for survival. This contest between organisms for access to resources is called competition. Competition has two components. First, organisms consume resources, thereby depleting the resources available to neighbours. Second, organisms will sometimes directly interfere with their neighbours in order to maintain access to resources.

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Competition, along with predation and mutualism, is one of three fundamental forces that connect organisms into living systems. Competition may have the same importance in ecological systems that gravity has in planetary systems. One common definition of competition is

> the negative effects that one entity has upon another by consuming, or controlling access to, a resource that is limited in availability.
>
> (Keddy, 2001)

Historical Development

Prescientific period

Long before the formal scientific study of competition, there was an intuitive appreciation of its importance. Julius Caesar, for example, understood that competition between neighbours had two components: control of resources and direct interference with survival (these are now called exploitation and interference competition). At the siege of Uxellodunum in Gaul in 51 BC, Caesar surrounded the town by earthworks, and built a second ring of trenches with pitfalls and sharpened stakes facing outwards to prevent any attempts at rescue by neighbouring Gauls. He then cut off an essential resource: water. The town surrendered.

Early agriculture also required an inherent understanding of competition, whether in choosing sowing densities or dealing with weeds. Says the Bible (Matthew 13:3–7), 'Behold a sower went forth to sow; And when he sowed … some [seeds] fell among thorns; and the thorns sprung up and choked them'.

Scientific study of competition

By the mid-1800s, scholars began to appreciate that all organisms have the innate capacity to multiply exponentially until reaching limits set by natural resources. Thomas Malthus (1766–1834) was an English economist and clergyman whose writing, particularly his *Essay on the Principle of Population* in 1798, influenced both Charles Darwin and Alfred Wallace, who in turn were the co-discoverers of evolution through natural selection. All three saw that all organisms, from houseflies to elephants, given sufficient time, could multiply rapidly enough to entirely cover the Earth. Such explosive growth was constrained by other factors, usually disease or a shortage of resources that killed most young of a species. For example, each elm tree in a forest may produce millions of seeds but only one need reach adulthood for each tree to be replaced and the forest to remain intact. The other millions of young must therefore perish. Darwin (1868) reported that he saw

> on reading Malthus on *Population* that natural selection was the inevitable result of the rapid increase of all organic beings . . . . (p. 10)

Competition was an important mechanism of this natural selection.

Early in the twentieth century, research on competition flourished. Charles Elton published *Animal Ecology* in 1927. Raymond Pearl popularised the logistic equation (developed by P.F. Verhulst in 1838) to describe how intraspecific competition limits population growth. A.J. Lotka and Vitto Volterra independently arrived at equations for interspecific competition (the Lotka–Volterra equations; see Lotka–Volterra), which could be extended to *n* species to describe an entire community. By 1934, G.F. Gause had published his book *The Struggle for Existence*.

Professor A.G. Tansley carried out one of the first experiments on competition, a greenhouse experiment on two species of *Galium* (Tansley, 1917). By then, Clements had already described competition as one of the most important factors affecting plant communities. In the 1970s, there was a resurgence of interest in properly controlled field experiments for the study of competition.

For convenience, the different kinds of competition can be delineated on the basis of (1) the mechanisms of interaction, (2) the kinds of organisms that are competing and (3) the relative impacts of the competitors upon one another.

Classifications of Competition

Mechanism

‘Exploitation competition’ occurs solely through reduction of the pool of resources. Examples include plants damaging other plants by reducing the volume of water in a patch of soil or birds damaging other birds by reducing the number of seeds on trees during the winter. ‘Interference competition’ occurs when one individual directly interferes with another. Interference may include outright physical attack or subtler versions such as territoriality, threat behaviour or even chemical poisoning. Caesar’s attack on Uxellodunum (described earlier) has already illustrated these two components of competition. As is so often the case with living organisms, while the two extremes may seem clear, some cases may remain ambiguous: when a plant seizes space, thereby reducing the volume of soil available to a neighbour, should this be termed exploitation competition for space, territoriality or a combination of the two?

Type of organism

‘Intraspecific competition’ occurs between individuals within a species. Examples include territoriality among birds, competition for mates among apes or the race among sperm to fertilise eggs within female reproductive tracts. ‘Interspecific competition’ occurs between individuals of different species. Examples include competition among phytoplankton species in lakes for dissolved phosphorus or competition between maple and beech trees in forests for nitrogen and water in soil. **See also**: **Interspecific Competition**

Relative impacts of competitors

In most sports, games, battles or competitive interactions, there are winners and losers. ‘Symmetric competition’ describes one extreme, the rare case in which two competitors are equally matched. At the other extreme, ‘asymmetric competition’, there is a clear winner and loser. Symmetric competition is far less common than asymmetric competition, but scientists have tended to emphasise them in exactly the opposite degree to their occurrence in nature. When one species reduces the other to low abundance, the winning species is termed the dominant. Should the dominant species reduce the other to zero abundance, the absent species is said to be extirpated. Many times in nature, we do not witness the interaction, only the results. Hence, a species may be locally uncommon or absent because of competition that we no longer see. This is one reason that removal experiments are vital. In a removal experiment, the species thought to be the dominant is removed in order to measure the responses of nearby species. If they benefit from the removal, it is good evidence for competition.

The competition among nations for access to global resources such as food, oil or metal ores is similar to the competition among organisms for food, water or mineral nutrients.

Models Can Help Understand and Explore the Effects of Experiments

As competition is a process that takes time, and as experiments are difficult and expensive, models are sometimes used to explore possible interactions between organisms. A model is a way for scientists to explore the logical consequences of certain assumptions about how nature might work. We shall look at two examples. The first describes the possible interaction between two rather similar species. The second describes the possible interaction between two very different species where there is a clear dominant.

1. Lotka–Volterra

The Lotka–Volterra model invites us to think about how two (or more) competing organisms might change in population size as a function of time and population sizes of competitors. Lotka (1932) began with familiar exponential growth, where the rate of growth of a population (dN/dt) is a function of only three basic factors: the intrinsic rate of reproduction, r, the number of individuals, N and the elapsed time, t:

$$\frac{dN}{dt} = rN \tag{1}$$

This expression produces ever-expanding population sizes and ever-increasing rates of growth. Early scholars including Malthus, Darwin and Wallace understood that something must limit exponential growth. In the Lotka–Volterra models, the resource supply is assumed to set an upper limit to population size. We add this as a new term, K, for carrying capacity, in the form $[(K-N)/K]$:

$$\frac{dN}{dt} = rN\left[\frac{(K-N)}{K}\right] \tag{2}$$

The added term K sets an upper limit on population size. When population size is very small (N near zero), the population growth rate is close to that of eqn (1) and the population is growing exponentially. When population size is very large (N near K), then the population growth rate is nearly zero.

This still describes one population without a competitor. To include competition, we must add the effect of a second population. The growth rate of one population, N_1, is then limited both by its own population size N_1 and that of the competing population N_2. The effect of a species upon itself, a_{11}, is considered to be 1. A similar equation examines the growth of N_2:

$$\frac{dN_1}{dt} = r_1N_1\left[\frac{(K_1 - a_{11}N_1 - a_{12}N_2)}{K_1}\right] \tag{3}$$

$$\frac{dN_2}{dt} = r_2N_2\left[\frac{(K_2 - a_{22}N_2 - a_{21}N_1)}{K_2}\right] \tag{4}$$

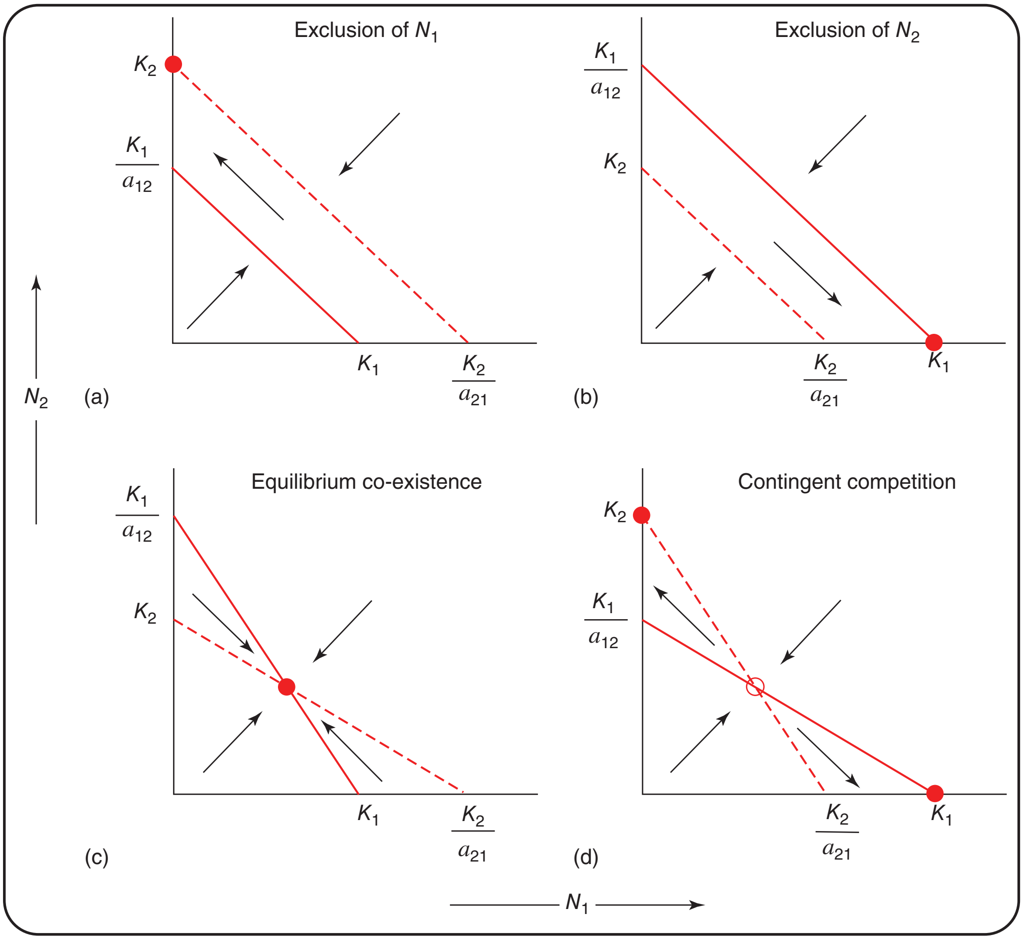

Figure 1 The Lotka–Volterra model is one traditional way of exploring competition between two populations, in this case labelled N_1 and N_2. As the text describes, the two axes are the population size of the two species and the lines show isoclines where population growth is zero. Depending on the nature of interspecific competition, four outcomes are possible. Cases (a) and (b) top show competitive dominance, where one species can predictably eliminate the other. In case (c), the two species reach a stable equilibrium, which allows long-term coexistence. In case (d), competitive dominance again occurs, but the winning species is entirely dependent on the starting size of the two populations, which is sometimes called contingent competition. The arrows show changes in population size with time. The solid dots represent the equilibrium points (expected outcomes) of these pairwise interactions. The open circle is an unstable equilibrium point.

As there are two competing populations, two outcomes are possible when these populations increase and interact: (1) one species becomes extinct and the other climbs to its own carrying capacity or (2) the species coexist. A principal objective of studying these equations is to determine whether the two species can coexist, and, if they fail to do so, which of the two will be the winner. As the only parameters to work with are the values for r_1, r_2, N_1, N_2, K_1, K_2 and a_{12} and a_{21}, the solution is given in terms of these.

One way to picture the outcomes of two-species interaction is using species isoclines (**Figure 1**). An isocline is simply all possible sets of conditions where the growth rate of a population is zero. Above an isocline, a population has exceeded the carrying capacity; thus, the population size declines with time. Below that isocline, the population size gradually increases. At any point along the isocline, the growth rate is zero and the population size remains constant. **Figure 1** shows the four possibilities, and each of these arrangements of isoclines has different consequences for the mixture of the two species.

In the top two cases in **Figure 1**, only one species survives at equilibrium; that is, there is a competitive dominant and a subordinate, with the dominant being the species with the isocline furthest from the origin. In the third case, the two species coexist, because each species is more negatively affected by intraspecific competition than by interspecific competition. In the final situation, the winner of the two-species competition can be predicted only when starting population sizes are known. The intensity of interspecific competition is such that, once a species begins to achieve numerical superiority, it damages the other so severely that the outcome becomes certain. Which population achieves this initial superiority depends solely on the assumed starting density.

The two-species situation can be expanded to as many species as needed. If there were n interacting species, the equation for population 1 would expand to

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1 \left[\frac{(K_1 - a_{11}N_1 - a_{12}N_2 - \cdots - a_{1n}N_n)}{K_1} \right] \qquad (5)$$

which includes a competition coefficient a_{1i} for each of the n species with which it is possible for species 1 to interact.

2. Skellam–Pielou

Competitive exclusion and the paradox of the plankton

If strong competitors always eliminate weaker ones, competition should lead to reduced biological diversity. This is often expressed as Gause's 'competitive exclusion principle': two species using the same resource in the same way cannot coexist indefinitely. Although this principle is now regarded as a truism, it has inspired a great deal of thought. Zoologists tend to conclude that competition forces organisms to use different resources, producing 'resource partitioning' where each species in an ecological community uses different food types, different feeding areas or different nesting sites (**Figure 2**).

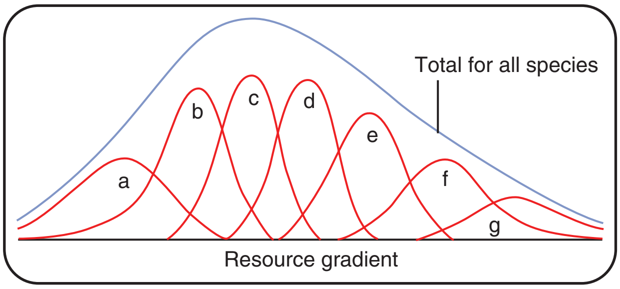

Figure 2 Resource partitioning occurs when a group of species (a) through (g) harvests different sizes or kinds of resources. At one time, in a simplistic way, the amount of overlap in resource use was thought to measure the amount of competition between each pair of species. The amount of overlap is, however, shaped by other factors including evolutionary history sometimes called 'the ghost of competition past', intensity of present-day competition and patterns in the availability of resources.

Plant ecologists have been less able to invoke resource partitioning, as most plants use only a few essential resources: nitrogen, phosphorus, water and carbon dioxide. The limits to competitive exclusion in plant communities can be illustrated by 'the paradox of the plankton'. Phytoplankton, said Hutchinson, share the same resources and occur in a relatively homogenous environment: water. Why, then, has competition not driven all but a few species to extinction, as predicted by Gause's principle? The answer seems to be that the environment in lakes changes continually, thereby preventing any single species from achieving competitive dominance. Hutchinson (1961) drew attention to seasonal changes in temperate lakes, where storms, ice cover and spring and fall overturn constantly change the environmental conditions. Simultaneously in America and England, other ecologists appreciated how disturbance limits the effects of competition. An American ecologist, Michael Huston (1979), reminded ecologists that disturbance defined as a factor that removes biomass can prevent a competitively dominant species from ever eliminating the weaker. He hypothesised that biological diversity tends to be highest at intermediate levels of disturbance, hence 'the intermediate disturbance hypothesis'. Similar arguments can be made to explain the high diversity of rain forests and coral reefs (Connell, 1978).

Indeed, there are models that illustrate how regular disturbance can prevent competitive exclusion. Skellam's (1951) model (**Figure 3**) shows how recurring disturbance could lead to permanent coexistence of two species, even when one of them is clearly a better competitor than the other. To keep the arithmetic simple, imagine two competing species that reproduce once a year. Let A be the stronger competitor and B the weaker competitor. Wherever they coexist, A invariably wins. Therefore, the only habitat in which B can reproduce includes those sites in which it occurs alone. Assume that the landscape has N sites, or patches of habitat, and that at equilibrium the expected proportion of sites with a single A individual at the end of the growing season is Q. This means that NQ of the sites are dominated by species A. Therefore, only $N(1 - Q)$ remain for B to occupy. If we call this remaining portion of sites (those that allow B to survive) q, then q must be greater than zero for the competitive subordinate to survive in that landscape. We want to know how much better dispersal of B must be for this to occur. Therefore, let F and f be the number of seeds

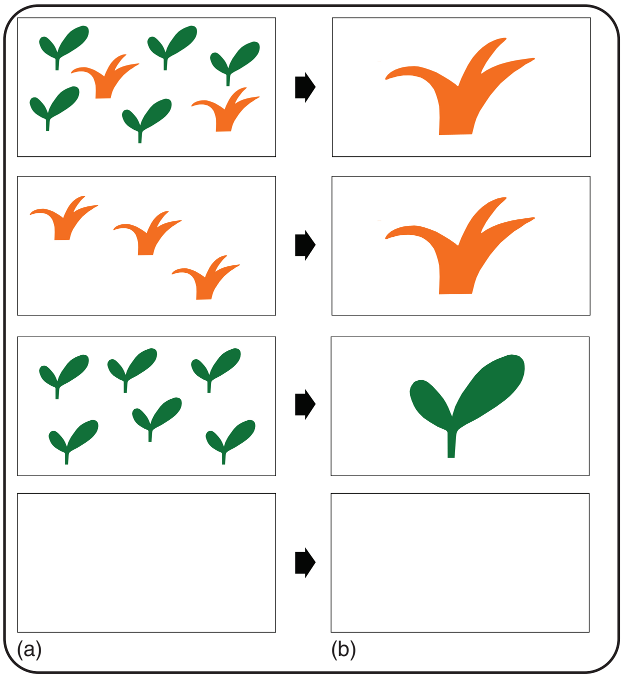

Figure 3 Weak competitors (green) may survive by escaping to habitat patches that are not occupied by stronger species (orange). Four possible combinations of seedlings are shown (a), and the outcome of adults is given (b) (from Keddy, in press after Pielou, 1975 and Skellam, 1951).

produced by species A and B, respectively. For species B to persist, f/F must be great enough to ensure that $q > 0$. It can be shown that, for this to occur,

$$f/F \text{ must exceed } -Q/[(1-Q)\ \ln(1-Q)]$$

Provided this condition is met, species B will continue to occur in the landscape in spite of its weak competitive ability.

Plant ecologists including Huston (1979) and Grime (1979) have emphasised that infertile sites, that is, sites lacking important nutrients, reduce the rate of recovery from disturbance, and hence might also enhance diversity by reducing the rate of competitive exclusion.

There is at least one other possible explanation for coexistence, that competition between nearly identical species may not be resolved simply because the competition, while intense, is symmetrical. This may, for example, explain how the Amazon has more than 10 000 species of trees. Even if competition is intense, the similarity in life form may lead to very slow rates of competitive exclusion (Hubbell and Foster, 1986). If this is the case, then rather small amounts of disturbance may be sufficient to allow long-term coexistence.

Is any generalisation possible at this point? Perhaps. Competition is probably less important among animals than plants, as plants cannot move away from neighbours. Competition may lead to resource partitioning, particularly among motile animals, and also in plants that grow along gradients. Competition in sessile organisms, particularly plants and corals, may be counterbalanced by natural disturbances. **See also**: Coexistence

Field Observations of the Presence and Consequences of Competition

Performance declines with increasing density

A negative relationship between performance and population density documents the presence of intraspecific competition. Performance (sometimes termed fitness) can be measured in many ways, depending on the organism and the circumstances – growth rates, survival rates and reproductive output are common examples. One classic study (Lack, 1966) examined a species of woodland bird – the Great Tit and found that (1) the higher the population density, the fewer the eggs per nest and (2) the greater the number of young in a nest, the smaller the mean weight of each nestling.

The relationship between the size of the individuals and density has been extensively studied in plant populations, partly because of the obvious agricultural implications. All plants require the same few basic resources such as nitrogen, phosphorus, water and carbon dioxide to construct their tissues. If mean size is plotted against density, the negative slope shows the effect that each added individual has upon its neighbours (Watkinson, 1985). This line can be fitted by an equation of the following form:

$$w = w_m(1 + aN)^{-b}$$

where w is the weight of an individual plant, N is the density and w_m, a and b are parameters. The term w_m can be interpreted as the weight that a plant will attain if grown in isolation – that is, where intraspecific competition is zero.

Sperm competition is a driving force of intraspecific competition

In the foregoing example of intraspecific competition, resources are the raw materials necessary for growth and reproduction. However, mates can be viewed as the ultimate resource for intraspecific competition. Competition among sperm (and among the individuals producing them) for access to eggs is therefore intense and widespread (Birkhead and Hunter, 1990; Birkhead and Møller, 1998).

Competition for mates has its origins in anisogamy, the difference in sizes of gametes: vast numbers of sperm are produced by males relative to small numbers of eggs produced by females. Both exploitation and interference competition can occur among sperm cells. Exploitation competition can be involved as the selective force acting upon sperm anatomy and morphology to maximise success in the race up reproductive tracts to locate and fuse with eggs. Penis morphology and size can be seen as the result of selection to deposit sperm as close as possible to eggs. The chemical composition of seminal fluid may provide sperm with nutrition and induce uterine contractions in females to assist sperm movement. Mechanisms of interference competition are also well developed. Males may secrete plugs to block the female tract and prevent later successful matings; this is found in acanthocephalan worms, insects, spiders, mammals and snakes.

Similar kinds of competition can occur within flowers. Pollen tubes produced by each pollen grain must grow down the style to deliver sperm nuclei to the egg. As the number of pollen grains on the stigma may vastly outnumber the ovules, pollen tubes in stigmas appear to be in the same type of race as sperm cells within female reproductive tracts.

Removal experiments

The basic experimental procedure for detecting and measuring the effects of competition requires two steps: (1) removing individuals or species from a community and (2) measuring the performance of the remaining species or individuals relative to control plots. The greater the increase in performance in the removal plots, the greater the effects of competition. One classic study examined two shrubs that dominate some 70% of the Mojave Desert: *Larrea tridentata* the Creosote Bush and *Ambrosia dumosa* Burbage (Fonteyn and Mahall, 1981). In a desert, the limiting resource is almost certainly water, and the water status of plants can be determined by clipping off a branch, and measuring its water potential. **Figure 4** shows that competition significantly reduced the water potential of both species of plants. Removal experiments have been successfully carried out for many other organisms including barnacles, lizards, fish and birds. When, as in **Figure 4**, one removes all neighbouring species, one measures the total effects of competition, termed 'competition intensity'. Whether competition intensity changes in systematic ways, such as along environmental gradients, is still a matter of dispute.

Above- and belowground competition in vegetation

Competition among plants has two distinct components: competition above ground largely for light and competition below ground largely for water, nitrogen and phosphorus. It is not always possible to separate these experimentally. As one example, Putz (1992) tried to determine the relative importance of belowground as opposed to aboveground competition affecting slash pine *Pinus elliottii* seedlings in Florida forests. There were four treatments (**Figure 5**). The first group, C, were controls. In the second group, S, shade from neighbouring trees largely oaks was reduced by using guy wires to pull adjacent trees back from over-topping the seedlings, while leaving roots and presumably most belowground interactions present. In the third group, T, trenches were cut around plots to reduce root competition. A fourth group, ST, was trenched and guy-wired. After 2 years, the pines with trenching T nearly doubled in size, whereas those with guy wires S did not differ from the control plants C. Belowground competition apparently exceeded the aboveground component. Sixteen similar studies of competition among trees found that belowground competition was greater than aboveground competition in 9 of the 16 cases.

As most plants and animals occupy a range of habitats, it is possible that the importance of competition and, in the case of plants, the relative importance of above- and belowground competition depend on where a study is carried out. This prospect was tested with removal experiments in two very different wetlands that represented extremes in habitat productivity, an infertile sandy shoreline and a fertile bay. In each habitat, transplants of two common marsh species were grown with no neighbours, with roots of neighbours only, and with roots and shoots of neighbours. In the fertile sites, there was an overall 60% reduction in growth rates from competition. Aboveground competition was greater in the fertile wetland, whereas belowground competition did not change among habits (Twolan-Strutt and Keddy, 1996). In general, it now

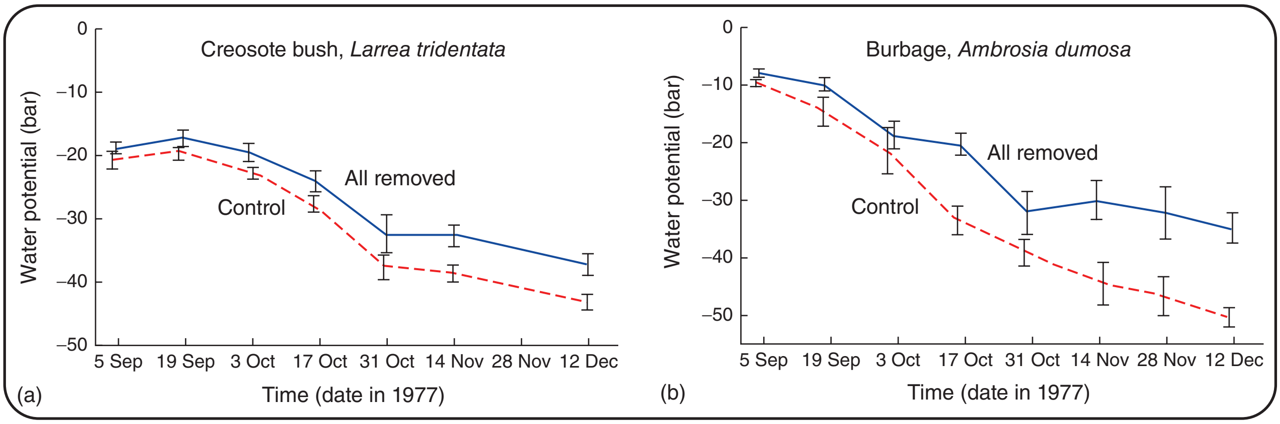

Figure 4 (a,b) Effect of competition upon two common species of desert shrubs was measured by comparing the water potential of plants having many neighbours line designated 'control' with plants where all neighbours of both species had been removed line designated 'all removed'. For both species, the removal of neighbours significantly improved their water potential ((a/b) after Fonteyn and Mahall, 1981).

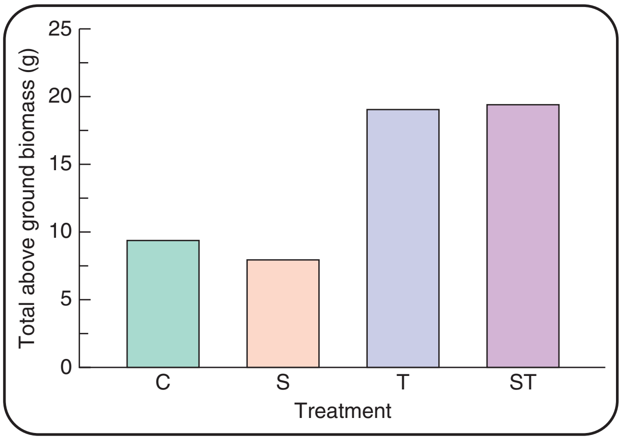

Figure 5 Effects of above- and belowground competition from hardwood trees upon slash pine *Pinus elliottii* were assessed in four types of plots, from left to right, C = controls, S = reduced shading, T = reduced root competition and ST = reduced shading and reduced root competition. See text for more details. As reduced shading S did not increase pine growth, but the reduced root competition T allowed plants to nearly double in size, belowground competition appears far more important than aboveground competition. Corroborating evidence comes from the treatment ST, where reduced shading combined with reduced root competition was no different from merely reduced root competition (after Putz, 1992).

seems that in sites with infertile soils, or in sites early in succession, belowground competition predominates. As soil fertility improves or as succession progresses, a denser canopy forms, and aboveground competition for light becomes more important. Hence, there is a change in the relative importance of below- and aboveground competition along natural gradients (**Figure 6**). **See also**: **Mutualism among Free-living Species**

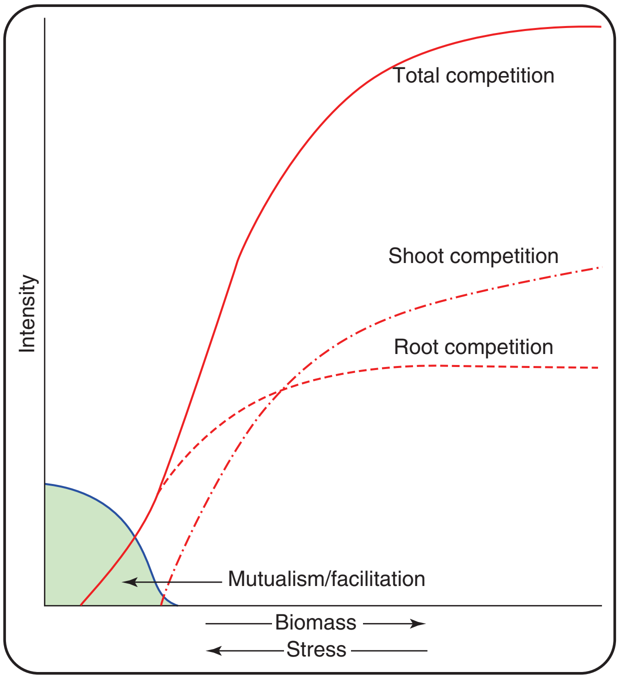

Figure 6 The importance of different ecological factors probably changes along environmental gradients. Total competition likely increases from left to right, as biomass accumulates and small plants are increasingly shaded. The relative importance of root and shoot competition, that is, below- and aboveground competition, probably shifts as light becomes increasingly limited. Mutualism may be important at the far left where plants may ameliorate harsh conditions for their neighbours. Thus, the importance of mutualism, and competition, and above- and belowground competition, may depend on the location of an organism (after Keddy, 2001).

Role of Competition in Changing Life-table Elements

Competition has costs. These costs show up as increased metabolic rates, which have further effects such as reduced rates of production of young, reduced growth rates or increased mortality. The most obvious currency for measuring such costs is rates of energy consumption. The more energy that must be diverted merely to survive, the less that remains for growth and reproduction. Abiotic conditions such as cold or drought already impose metabolic costs upon individuals. When neighbours further reduce resource levels, the costs of competition add to the costs created by abiotic conditions. The greater these costs, the lower the performance of individuals and the lower the probabilities of survival and reproduction.

As one illustration, consider frogs, toads or salamanders that breed in temporary ponds. As the ponds dry out during the summer, there is an advantage associated with early metamorphosis: the sooner an amphibian leaves the pond, the lower the probability that it will be killed by desiccation when the pond dries. Further, the larger the amphibian at metamorphosis, the greater its probability of survival as an adult. Competition from neighbouring tadpoles has been shown to (1) increase the time to complete metamorphosis, (2) reduce mean size at metamorphosis and (3) reduce the rate of survival. These effects might be caused by either reduced food supplies or growth inhibitors released by neighbouring tadpoles. In a remarkable convergence, it has also long been suspected that plants can poison the roots of their neighbours.

Conclusion

Competition is an all-pervasive force in nature. Its importance in ecological systems corresponds to the central role of gravity in physical systems. As it is very difficult to see competition in action, except in relatively trivial cases of aggression, competition can only be detected and measured with carefully designed experiments. In such experiments, neighbours are usually removed, and the consequences if any compared to controls where the neighbours are still present. Each experiment can take many years. The outcome of such experiments is likely to vary with both abiotic factors such as soil fertility and biotic factors such as the presence of predators. These should be considered, and where possible included, when designing competition experiments.

Although competition is very important, in real ecological communities, species are influenced by other factors, including (1) stress, for example, cold, low nitrogen supplies, (2) disturbance, for example, storms, fires, (3) mutualism, for example, mycorrhizae, pollinators and (4) predation that includes the effects of herbivores. It is thus often very difficult to separate out any single factor as the sole cause of the patterns seen in natural communities.

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