

# SPECIES COEXISTENCE

Robert D. Holt

*Museum of Natural History and Center for Biodiversity Research, University of Kansas*

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## GLOSSARY

**coexistence** The state of two or more species being found in the same place at the same time.

**community** The assemblage of species found in a defined area, in which these species can interact.

**competition** The most widely used definition: use or defense of a resource by an individual which reduces resource availability to other individuals. Alternative definition: a reduction in one species' growth rate because of the effects of another species.

**food web** The pattern of feeding relationships among organisms.

**Lotka–Volterra competition model** A model describing the per-capita growth rates of two competing species as linear, declining functions of the abundances of each species.

**mechanistic models of population dynamics** Models which are explicit about resource consumption, the relationship of consumption to demography, and mortality factors.

**microcosm studies** Laboratory experiments involving population dynamics of small organisms with short generation lengths.

**natural enemy** Any species which consumes or parasitizes another species; a general term that includes predators, herbivores, parasites, pathogens, and parasitoids.

**niche** (Grinnellian/Hutchinsonian) The range of resources and conditions within which populations of a species are expected to persist. (Eltonian) The role of a species in a community.

**open communities** Communities which receive immigrants from external sources and may export emigrants as well.

**permanence** A property of communities that ensures long-term coexistence of species because community trajectories (variation in numbers through time) have no species approaching very low numbers.

**zero-growth isocline** In a graph with axes describing factors important to population growth (e.g., resource abundance), a line along which a population's growth rate is zero.

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*THE OXFORD ENGLISH DICTIONARY* states that to “coexist” is “to live together in the same place, at the same time, with another.” The topic of “coexistence” focuses on how biological species are organized into communities, in space and through time. Identifying the factors that influence coexistence is fundamental to understanding biodiversity. Important factors that influence coexistence include interspecific interactions, spatial and temporal scales, and historical contingencies. Insights into coexistence come from laboratory and field experiments, historical reconstructions and observational studies, and theoretical explorations. The topic of coexistence has had a long history in community ecology, some appreciation of which is necessary to understand contemporary perspectives. After a few general remarks about how scale, interactions, and the notion of permanence are related to coexistence, I provide a survey of the “phenomenology” of coexistence and exclusion, and lessons derived from field and classic lab studies. I then discuss key ingredients in both historical and current theoretical interpretations of species coexistence, emphasizing conceptual generalities rather than model details, and conclude with suggestions regarding significant unanswered questions about coexistence.

## I. GENERAL ISSUES

### A. The Importance of Scale

In some sense, all the species in the teeming plenitude of life present on Earth coexist because they are found in one place (Earth) at one time (now). However, from the perspective that matters most to an individual organism such as a vampire bat, a tulip, or a flatfish—the perspective defined by the space that an individual occupies or moves within over its life span—populations of any given species co-occur with only a tiny fraction of all living things. The same holds for community samples, for instance, those gathered in the quadrats beloved of plant ecologists or the towed plankton nets of limnologists; the number of species recorded is always much less than the potential number. That is, what counts as “coexistence” varies with the scale of ecological inquiry. Viewed at small spatial scales, tailored to the ecology of individual organisms or seen through the lenses of conventional field methods, most species in the global flora and fauna do not coexist. However, even at this scale many (and sometimes very many) species can coexist. Species coexistence is also temporally bounded. In the long term most species face extinc-

tion, and even in the short term coexistence may be transient rather than permanent.

### B. The Importance of Interactions

Species (like ships passing in the night) may either coexist or fail to do so for reasons having nothing to do with each other. A null model of community organization is that communities arise from the independent responses of species to the environment. However, coexistence often reflects the impact of interactions among species. Familiar categories of interactions include competition for resources, natural enemy–victim interactions (e.g., predator–prey and host–pathogen interactions), commensalisms and mutualisms (e.g., plant–pollinator relationships), allelopathy (poisoning), and a broad range of environmental modifications (collectively called “ecological engineering”). In the study of coexistence, competition has received by far the most attention, but there has also been considerable work on how natural enemy–victim interactions influence coexistence. Interactions are not fixed properties of species, or pairs of species, but can vary in their strength and pattern as a function of the physical environment and many contingent details of community structure. If species A affects species B, and species B in turn influences species C, then one says there is an indirect interaction between A and C. A complete understanding of coexistence requires one to consider indirect and direct interactions. Interspecific interactions may be strongly asymmetrical, and indeed, interactions frequently cause species exclusion (constraints on coexistence). Analyzing mechanisms of coexistence and exclusion forms the conceptual core of the discipline of community ecology.

### C. Coexistence and Permanence

Historically, coexistence is an outcome of the assembly of communities by colonization from species pools at larger spatial scales. If rules describe the historical process of community assembly, these rules must in large measure reflect the importance of species’ interactions in determining coexistence rather than extinction as assembly occurs.

The paleontological record shows that species’ distributions are not stable but move in concert with climate change, fluctuations in sea level, and the stately movement of the continents. Moreover, for many species, chance vicissitudes of dispersal provide a small trickle of potential colonists “testing the waters” outside their normal range. Local coexistence at the very least re-

quires species' geographical ranges to overlap. Many species do not coexist together today in local communities because of historical factors preventing them from ever encountering one another.

Within a species' geographical range, for that species to be a resident member of a local community, at one time it must have colonized, increasing from very low numbers. Once present, given the vagaries of climate and fluctuations in the abundance of other species, it is likely that resident species experience times of low abundance and thus extinction risk. To persist, a species must be able to rebound from these dangerous troughs of low population size. These observations suggest that a robust form of coexistence is ensured if each species can increase when rare. If all trajectories describing fluctuations in abundance in a community are bounded away from zero, all species in the community will coexist. This criterion for coexistence is called "permanence" in the jargon of mathematical ecology. Examining conditions for increase when rare provides a natural protocol for experimental studies of coexistence and analysis of mathematical models of interacting species. Permanence is always assessed relative to a certain spatial and temporal scale. A given pair of species may not coexist indefinitely in any single site but nonetheless coexist at larger scales in ensembles of sites.

## II. CONSTRAINTS ON COEXISTENCE: EXAMPLES FROM INTRODUCED SPECIES

In recent times, humans have greatly accelerated movements of species into novel habitats, both via deliberate introductions (e.g., most of the lowland birds found in Hawaii) and as incidental "hitchhikers" tracking human transport (e.g., most benthic invertebrates in San Francisco Bay are exotics released as by-products of ship ballast water dumps). Analyses of introductions suggest species interactions can constrain coexistence.

### A. Competition

Classical biological control involves deliberate introductions of species that one hopes will control a pest species. Between 1947 and 1952 the Hawaii Agriculture Department released parasitoid species to control the oriental fruit fly, an economically significant pest. (Parasitoids are insects, e.g., braconid wasps, whose larvae live within and ultimately kill their host, such as caterpillars.) Three wasps in the genus *Opius* were consid-

ered to be potential control agents. The first species established, *Opius longicaudatus*, parasitized approximately 20% of the fruit fly hosts. The second species introduced, *O. vandenboschi*, was more effective, parasitizing about 30% of the hosts; as *O. vandenboschi* increased, *O. longicaudatus* decreased toward extinction. The third species, *O. oophilus*, was even more effective, parasitizing up to 80% of the hosts and replacing in turn *O. vandenboschi*. This system provides an example of competitive exclusion in exploitative competition, where species dependent on a single limiting resource (here, host insects) cannot coexist. Increasing parasitism reduces the availability of unattacked hosts. The competitive dominant in this pattern of competitive displacement is the parasitoid species that persists at the lowest host abundance—an example of a simple rule of dominance in resource competition. Understanding how multiple species can persist on a limited resource base is a perennial theme in the study of coexistence.

### B. Natural Enemies

Very effective control agents can, after introduction, eliminate the target species (and thus themselves) over broad areas. The floating fern *Salvinia molesta* from Brazil escaped from a garden in Sri Lanka and became a serious aquatic pest in much of the Old World wet tropics. The beetle *Cyrtobagous salviniae* was introduced in Australia and proved highly successful at limiting the fern, which (with the beetle) is now found in only a few scattered populations. This example illustrates another species coexistence problem; that is, how effective natural enemies manage to coexist with their prey without overexploiting them and thus driving themselves to extinction.

### C. Community and Spatial Contexts

Many game departments routinely introduce game species. Failed introductions reveal constraints on species coexistence. Caribou were once common in the Maritime Provinces but declined during the 1800s to extinction by 1915. Attempted reintroductions have failed because the caribou pick up a widespread nematode parasite (carried by snails and incidentally consumed as the caribou forage on vegetation). The nematode lodges in the caribou brain and is fatal within a few months. The nematode population is sustained by another host, white-tailed deer, which tolerate parasitism. Deer are abundant because land practices by European settlers in the nineteenth century increased the area of

the second-growth habitats that deer favor; this may explain the disappearance of caribou. Caribou herds wander very widely, which makes it likely that they will encounter nematode-laden snails. Another ungulate species, moose, coexists with deer, even though infected moose also quickly die. Moose and deer overlap in diet and can compete; in contrast, caribou and deer do not overlap in diet. Nonetheless, it is caribou, not moose, which have been indirectly excluded by deer. Moose are relatively sedentary (for their body size) and can occupy patches of highland forests with deep winter snows, where deer do not penetrate. At the coarse scale of North America, caribou and white-tailed deer coexist but with little spatial overlap among populations. Moose and deer, in contrast, overlap geographically, coexisting at the level of landscapes, but at a finer scale they have considerable spatial segregation in habitat use.

This example illustrates several points. First, natural enemies (a term that refers to any species which consumes a species of interest) can prevent coexistence. Second, coexistence or exclusion may arise from complex webs of multispecies interactions. The nematode directly causes exclusion of caribou, but viewed more expansively exclusion is caused by the entire vegetation–snail–deer ensemble, which collectively governs nematode abundance and hence caribou infection rates. Third, movement patterns can influence interspecific interactions. Moose and white-tailed deer coexist at the landscape scale because moose have spatial refuges from infection, whereas caribou do not and are thus excluded.

### III. COEXISTENCE AND EXCLUSION: MESSAGES FROM BOTTLES

The previous examples strongly suggest the importance of species interactions in determining coexistence but are not conclusive. Without detailed observational studies tied to parameterized models or rigorous manipulative field experiments, it is difficult to persuade skeptics that other hypotheses are not also plausible. As an alternative, one simple but illuminating approach to the study of coexistence is to put together a few species in a confined setting and see what happens.

The study of “nature in a bottle” simplifies the world in important respects (e.g., a few species in closed and temporally constant environments), and such experiments are viewed skeptically by some ecologists. Despite these limitations, a wealth of important messages

about species coexistence emerged from classic bottle experiments—messages which have proven robust when applied to natural communities. Microcosm studies of ecological processes are now enjoying a renaissance in community ecology.

#### A. Competition Experiments

The term “competition” usually refers to an interaction among individuals (within or among species) that arises because they seek a resource in short supply. If this involves direct harm, the interaction is referred to as “interference competition.” If instead competition involves depletion of a resource, one refers to “exploitative competition.”

##### 1. Protozoa

Most ecology textbooks (Hutchinson, 1978) recount experiments by the Russian ecologist G. F. Gause, who as a young man in the 1930s put mixed cultures of protozoa into vials full of liquid media to study species coexistence. Gause’s famous competition experiments compared populations of the ciliate protozoans *Paramecium aurelia* and *P. caudatum* grown separately and together on a nutritive medium containing their essential resource (bacterial food). Both species thrived when alone, but *P. aurelia* usually displaced its congener in joint cultures within 30–50 generations. This outcome was reversed if the medium was completely replenished with fresh nutrient on a regular basis. Gause argued that metabolic by-products were building up in the experiments, and that part of the dominance of *P. aurelia* may involve its resistance to the chemical by-products of metabolic activity as well as its superior ability to exploit the food base. Here, competition combines environmental modification and exploitation of a limiting food resource.

In other experiments Gause found that *P. aurelia* could coexist with another species, *P. bursaria*, even in the confines of a closed culture. *Paramecium bursaria* contains symbiotic algae, which release oxygen in photosynthesis. In incompletely mixed cultures, bacteria accumulate on the bottom, creating a zone slightly depleted of oxygen. The protozoan with the algae in effect carries its own oxygen supply into this anoxic habitat and so can use a food source unavailable to the other, competitively superior species. Here, coexistence depends on both the availability of different habitats and differential species’ abilities to utilize those habitats.

##### 2. Beetles

Many ecologists have examined the dynamics of mixtures of beetle species competing for grain stored in

containers. L. C. Birch examined several species combinations that fed on wheat or maize under different conditions of temperature and moisture. Usually, one species won. The criterion for dominance was simple: The winner always had the highest intrinsic growth rate (the maximal rate of population growth when a species is rare and growing alone). However, the identity of the winner depended on both resource type and physical conditions. Moreover, competitive exclusion sometimes required many generations; in one experiment, the apparent loser survived until the experiment had to be terminated.

Experiments by T. Park with a different set of stored grain pests (*Tribolium castaneum* and *T. confusum*) also showed that the species identity of the winner varied with temperature and humidity. However, for some abiotic conditions the outcome was indeterminate; either species could win, with the winner tending to be the species initially most abundant. The net interaction between these beetles combines several mechanisms, including exploitation of a shared resource and cannibalism (both within and between species). In one set of experiments, Park intriguingly observed that when a coccidian parasite, *Adelina* sp., was present, the normal dominant *T. castaneum* became a weak competitor, thus permitting the persistence of *T. confusum* (and even its dominance).

Sometimes, coexistence in microcosms reflects very subtle biological differences between species. Crombie raised two grain beetles (*Rhizopertha dominica* and *Oryzaephilus surinamensis*) in vats of cracked wheat and found indefinite persistence, despite the fact that there seemed to be just a single resource. The main difference in the two species seemed to be in larval feeding habits; larvae of *Oryzaephilus* lived and fed from outside the wheat grains, whereas larvae of *Rhizopertha* were sufficiently small to live and feed from within the grains. This slight difference sufficed for the competitors to coexist.

### 3. Key Insights

Several insights emerged from "bottle" studies of competition. First, species competing in a closed homogeneous medium for a single limiting resource typically do not coexist. Second, the winner depends on environmental conditions, and the outcome can change if the environment is altered—there is no universally superior competitor. Third, exclusion is not instantaneous and may require many generations; this leads to the possibility of transient coexistence. Fourth, indefinite coexistence occurs but requires heterogeneity in the environment as well as differences in species' responses

to this heterogeneity. However, the species' differences permitting coexistence can be quite subtle. Fifth, pairs of species can interact in many distinct mechanistic ways (e.g., via impacts on resource levels or on levels of pollution from metabolic waste). It is difficult to generalize among studies if one has not clearly identified and characterized specific mechanisms of interaction. Finally, the outcome of competition can vary due to effects of other species, including parasites or mutualists.

## B. Predation

In classic literature, compared to studies of competition, somewhat less attention was given to predator-prey and host-parasite interactions (and essentially none to mutualism). Gause did carry out experiments with the predatory protozoan *Didinium nasutum* and a prey protozoan, *P. caudatum*. The predator quickly overexploited its prey and went extinct. To achieve coexistence, Gause concluded that there needed to be a spatial refuge for prey, inaccessible to the predator, or recurrent immigration. A qualitatively similar message emerged from experiments by C. Huffaker and colleagues, who studied an intrinsically unstable interaction between a voracious predatory mite (*Typhlodromus*) and a prey mite (*Eotetranychus*) living on oranges. In single oranges, the predator rapidly drove its prey to extinction. In contrast, in a large "universe" of oranges laid out in a grid, separated by barriers to dispersal, the interaction persisted over many generations, with complex patterns of spatial occupancy for the two species. Luckinbill reexamined the unstable predator-prey pair studied by Gause but reduced the encounter rate between predators and prey by adding methyl cellulose (a thickener) to the medium so as to slow predator movement. Reducing movement rates in effect expands the size of the spatial arena of the interaction (scaled by the distance a predator moves per unit time). This led to stable coexistence. The qualitative message of these microcosm experiments on predation is that patchiness, localized dispersal, and spatial heterogeneity (e.g., refuges) may facilitate the coexistence of effective specialist predators and their vulnerable prey.

## IV. CONSTRAINTS ON COEXISTENCE: RULES OF DOMINANCE

### A. The Competitive Exclusion Principle

The experimental observation that in homogeneous well-mixed environments it was often difficult to

achieve coexistence between similar species became enshrined in ecology as Gause's principle, or the "competitive exclusion principle." Another way to state this principle is to note that, to coexist, different species must have distinct ecologies.

Assume we are examining a local community defined by a spatial scale in which all individuals can reach all sites over a single generation. The basic logic of the competitive exclusion principle is impeccable (Levin, 1970): Consider two species with continuous generations, where both species respond to the same environmental factors, denoted by  $E$ . The quantity  $E$  could be many things (e.g., resource availability, predator abundance, or a weighted sum of the competitors' own numbers). The growth rate of species  $i$  is  $dN_i/dt = N_i f_i(E)$ , where  $N_i$  is the density of species  $i$ . We make three assumptions: (i) There is a single limiting factor, (ii) the species interact in a closed habitat (i.e., no immigration), and (iii) each species when alone settles down to an equilibrium at constant densities (i.e., the environment is temporally constant).

For species  $i$ , there will be some value of the environmental factor,  $E^*$ , at which that species equilibrates. It is a biological truism that any two species will almost surely differ in some way. Hence, it is very improbable that they will have exactly the same value of  $E$  at which they reach equilibrium. In other words, there should be no long-term persistence of two species limited by a single factor in a constant, closed environment. For this argument to work, there should be some effect of the species themselves on the magnitude of  $E$ , leading to either direct or indirect density dependence in demographic parameters such as birth or death rates. For example, if two species are consuming a single resource, then consumption should depress resource levels.

### 1. Exploitative Competition: The $R^*$ Rule

What counts as a "limiting factor" needs to be interpreted quite broadly and is often quite difficult to identify in practice. Nonetheless, sometimes one can observe a single, simply characterized limiting factor, which then defines a rule of species' dominance. For instance, the Hawaiian parasitoids fit the " $R^*$  rule" proposed by David Tilman; that is, the dominant species, given exploitative competition for a single resource, is the species persisting at the lowest resource level. (The asterisk denotes equilibrium, and  $R^*$  is the equilibrium resource level at which a given consumer species is in demographic equilibrium.) A virtue of this dominance rule is that one can measure  $R^*$  of each species when alone and then predict the outcome of competition. A species may have a low  $R^*$  and be competitively superior either

because it is efficient at resource consumption or because it has low mortality (e.g., it can escape predation).

The  $R^*$  rule successfully predicts the outcome of competition among phytoplankton competing for nutrients in microcosms and also characterizes competition in some natural systems. For example, in the nitrogen-poor soils of Cedar Creek, Minnesota, plant species compete for nitrogen. Wedin and Tilman showed that species with low  $R^*$  for nitrogen won in pairwise competition experiments. If two species had similar values for  $R^*$ , the rate of competitive displacement was greatly reduced, as expected by theory.

### 2. Apparent Competition: The $P^*$ Rule

Analogous "rules of thumb" arise in other situations. For instance, Sharon Lawler carried out a microcosm experiment in which a predatory protozoan (*Euplotes patella*) coexisted with either of two prey protozoans (*Tetrahymena pyriformis* and *Chilomonas paramecium*) grown alone. However, when all three species were together, *Chilomonas* was driven extinct. In the single-prey cultures, *Tetrahymena* sustained four times the number of predators as did *Chilomonas* cultures. In the mixed cultures, the latter species suffered higher predation than it could sustain. The limiting factor is the abundance of a shared predator, which can respond numerically to its prey. Let  $P^*$  be the abundance of the predator sustained (and tolerated) by a prey species. A " $P^*$  rule" now describes dominance: The winning prey species is the one with greater  $P^*$ . This form of indirect competition between species arising from shared natural enemies (including parasites) is called apparent competition (Holt and Lawton, 1994); the word "apparent" is used because the interaction has the same consequences for coexistence as does classical exploitative competition for resources but may occur even between species with totally different resource requirements. Dominance in apparent competition may occur because of different vulnerabilities to a natural enemy (as in the caribou example) or because one prey is highly productive and sustains an abundant enemy population (as in Lawler's experiment).

## V. MECHANISMS OF COEXISTENCE

The previous discussion emphasized constraints on species coexistence arising from interspecific interactions. Rules of dominance are important conceptual tools which quantify these constraints and help identify biological traits leading to dominance. However, even in simple microcosms coexistence can occur, and most

natural communities are rich in species. To understand coexistence, the competitive exclusion principle is reconsidered (Crawley, 1997; Grover, 1997; Tokeshi, 1999). Species may coexist when any of the assumptions leading to the competitive exclusion principle are violated. This suggests three classes of mechanisms promoting species coexistence of potentially competing species in a local community:

1. Species may coexist in a closed, temporally constant world if they experience different limiting factors at the spatial scale of the local community; this includes classical niche partitioning of resources, as well as mechanisms involving predation and parasitism, and direct interference.

2. Species may coexist, even though they experience the same limiting factor, if the environment is temporally variable and species respond differently to this temporal variation (temporal niche partitioning).

3. Species may coexist if the environment is spatially open; this includes spatial niche partitioning at scales broader than the local community and mechanisms such as colonization–competition tradeoffs in metapopulations.

From the 1950s to the mid-1970s, stimulated largely by G. E. Hutchinson and his brilliant student Robert MacArthur, most community ecologists emphasized classical niche partitioning in studies of species coexistence. In recent years, the balance of attention has shifted markedly to a broader range of coexistence mechanisms. Ecologists now believe that maintenance of diversity—coexistence writ large—often depends on spatial dynamics in open communities, food web interactions (including predation and parasitism), and nonequilibrium dynamics reflecting either extrinsic temporal variation or the endogenous instability of complex ecological system.

## VI. TRADITIONAL APPROACHES TO COEXISTENCE

### A. Classical Niche Partitioning

Competitive exclusion is expected if growth rates of two (or more) species are determined by a single limiting factor. Species may coexist, even in an unvarying and spatially confined bottle, given multiple limiting factors, such that each species is limited more strongly by its own distinct set of factors. When species coexist, one sensible approach to begin to understand this coexistence is to

map their niche requirements against the spectrum of limiting factors present in the environment. This basic methodology has been a source of significant insights for much of the history of ecology and continues to be fruitful. The classic paper in this genre is the 1958 study by Robert MacArthur of wood warblers in a New England boreal forest. Five warbler species in the genus *Dendroica* occurred in the same tract of forest; all five species have similar body sizes and eat the same range of insect taxa. MacArthur found that the species segregated with respect to microhabitat (with one species feeding at treetop, another in low branches, and so on). He argued that because of this microhabitat partitioning, each species consumed an independent pool of insect prey, thereby reducing the potential for competitive exclusion. Following publication of this study, there was a proliferation of field studies of niche partitioning patterns.

### B. Lotka–Volterra Competition Model

MacArthur's study was motivated in part by Gause's experiments on competitive exclusion, which in turn were stimulated by theoretical models of interacting species explored by the Italian mathematician Vito Volterra. In the usual textbook formulation (the famous Lotka–Volterra equations), the competitive effect of one species on another is expressed as a direct, density-dependent reduction in abundance:

$$\frac{dN_1}{dt} = r_1 N_1 (K_1 - N_1 - \alpha_{12} N_2) / K_2$$

where  $N_1$  and  $N_2$  are the abundance of competing species 1 and 2, respectively,  $K_1$  is the carrying capacity of species 1,  $r_1$  is its intrinsic rate of increase, and  $\alpha_{12}$  is a competition coefficient (the equation for species 2 is the same, with the subscripts 1 and 2 switched). The quantity  $\alpha_{12}$  measures the effect an individual of species 2 has on reducing the per capita growth rate of species 1 compared to the effect of an individual of 1 on its own species. Both species increase when rare and hence coexist if

$$\frac{1}{\alpha_{21}} > \frac{K_1}{K_2} > \alpha_{12}$$

The outer inequalities imply  $1 > \alpha_{12}\alpha_{21}$ . This necessary condition for coexistence states that one (or both) of the competing species experiences stronger intraspecific than interspecific competition. If the inequalities are reversed, either species can exclude the other if it is initially sufficiently abundant (as in Park's experiments with *Tribolium*). If the competition coefficients are near

unity (i.e., density dependence occurs uniformly within and between species), the species with higher carrying capacity wins.

The Lotka–Volterra model usefully describes competition, and multispecies extensions to it have been the focus of a rich body of theoretical work. However, the model is difficult to use predictively because competition coefficients and direct estimates of density dependence can only be measured during competitive trials rather than a priori. Moreover, taken literally, the model best describes systems in which competition is due to direct interference. Recognizing these limitations led to the development of a wide range of mechanistic models of resource–consumer and other interspecific interactions beginning in the late 1960s.

### C. Whither Limiting Similarity?

This development was concordant with interest in the important concept of “limiting similarity,” which is the notion that there might be a quantifiable limit to how similar species could be in their utilization of resources and still coexist. [To gain an understanding of the idea of limiting similarity, note that in Eq. (2) similar species should have competition coefficients near 1, so coexistence will not occur unless carrying capacities are finely balanced.] For a period in the history of the discipline, the goal of quantifying limiting similarity seemed to represent a “holy grail” for community ecology. Early theoretical explorations suggested simple rules might permit predictions of the maximal number of species which could persist on a defined resource base, providing a basic tool for understanding biodiversity. These studies were based on the Lotka–Volterra model coupled with assumptions about resource use. In some limiting cases, the Lotka–Volterra model emerges as a reasonable approximation of more complex resource–consumer interactions, and one can directly map niche overlap onto measures of competition. With simplifying assumptions about symmetry in resource use, the role of environmental variation, and other factors, a limiting similarity of competing species could be calculated and then compared against observed similarities. For instance, using MacArthur’s warbler data, it was assumed that spatial overlap in foraging was directly related to competition coefficients. Substitution into the model showed that observed overlap was consistent with long-term coexistence. More broadly, if niche overlap were proved to be closely related to the strength of competition, observational studies of overlap and niche partitioning would provide a powerful link between descrip-

tive analyses of community patterns and the dynamical forces of species interactions.

Further exploration has tempered the initial flush of enthusiasm for this approach to coexistence. After considerable grinding of mathematical gears, theoretical ecologists have concluded that limiting similarity, if it occurs at all, can only be characterized for models tailored to specific situations. Instead of a single general theory of limiting similarity and coexistence, there are many special theories. Moreover, there is a real sense in which increasing species similarity can facilitate, rather than hamper, coexistence. Equation (2) describes bounds on the permissible differences in the two species’ carrying capacities. If the  $\alpha_{ij}$  are less than unity, coexistence is more likely if carrying capacities are nearly equal rather than very different. The more similar species are in their demographic responses to the environment, the more similar their carrying capacities are likely to be. All else being equal, this kind of similarity promotes the coexistence of competing species.

### D. Manipulative Field Experiments

Recognizing the limitation of observational studies of niche overlap and partitioning as evidence for competition, ecologists have turned to manipulative field experiments, typically removing one species and monitoring changes in the abundance of others. Reviews of such experiments show that when species are suspected to compete (e.g., because of overlap in resource requirements and habitat use), they often in fact do compete. For instance, Hairston noted that in the Great Smoky Mountains two species of *Plethodon* salamanders had altitudinal ranges which were nearly mutually exclusive, with only a narrow range of overlap. In contrast, in the Balsam Mountains altitudinal overlap was extensive. Hairston hypothesized that this was due to stronger competition in the Smokies, and using reciprocal transplants and removals he demonstrated that competition (due to behavioral aggression) was indeed much stronger in the narrow overlap zone in the Smokies.

Unfortunately, relatively few field experiments have been directly tied to mechanistic models of competition, which makes it difficult to generalize among studies. Moreover, such experiments tend to focus on species which already coexist, at least to a degree; removals then assess the magnitude of competition, given coexistence, rather than coexistence or exclusion per se. One study which directly addressed coexistence was performed by Bengtsson, who studied three species in the zooplankton genus *Daphnia* (which compete exploitatively for algal food) on the coast of the Baltic Sea.



Observational studies suggested that usually just one, or more infrequently two, species was present in any given pool. Bengtsson added all possible combinations of the three species to artificial pools and found that there were no extinctions in the single-species pools. Yet high extinction rates occurred in the two- and three-species sets. This directly demonstrates the importance of competition in constraining coexistence in natural conditions.

## VII. MECHANISMS FOR LOCAL COEXISTENCE: CURRENT APPROACHES

### A. Mechanistic Models of Multiple Limiting Factors

Most theoretical studies of competition today focus on models in which the mechanisms of interaction are clearly described. Detailed analyses of mechanistic models of competition are often mathematically challenging, but important insights can often be gleaned from simple graphical analyses. A generalization of the competitive exclusion principle is that "coexistence of  $n$  species requires  $n$  limiting factors." Mathematically, one expresses the growth rate of each species as a function of a vector of limiting factors (e.g.,  $dN_i/dt = N_i f_i(E_1, E_2, \dots)$ ). For illustrative purposes, I discuss one example in detail (Tilman, 1982; Grover, 1997; Pacala as cited in Crawley, 1997).

Consider two species competing for two limiting resources. Assume exploitation depresses resources and that resource-consumer dynamics tend toward a stable equilibrium. For each species, there will be some combination of resources that allows equilibrium (with births matching deaths). On a graph with axes of resource abundance, assume this combination can be portrayed as a straight line, as in the line marked 1 in Fig. 1a (for species 1) (MacArthur, 1972). This line is the "zero-growth isocline" of species 1. The linear form of the isocline implies that resources are qualitatively substitutable so that a sufficient supply of one compensates for low abundances in the other. [Tilman (1982) examines exploitative competition for a broader range of resource types.] At equilibrium, resource abundances should lie along this line; if resources lie outside this line, species 1 should increase, depressing resource levels (with reverse dynamics inside the line). An equilibrium with coexistence requires resource levels at which both consumers have zero growth; graphically, the isoclines

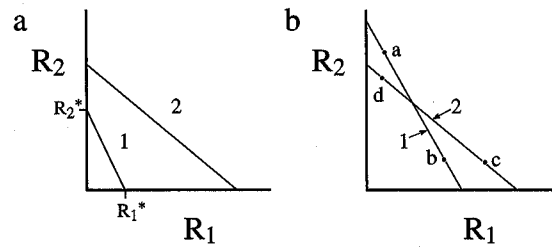


FIGURE 1 Graphical model of resource competition. The isocline of species  $i$  ( $=1,2$ ) is a combination of resource abundances where it has zero growth. At lower resources (toward the origin) a species declines. (a) Competitive exclusion of species 2 by species 1; (b) Potential coexistence. (See text for details.)

must cross. The isoclines do not intersect (Fig. 1a) species 1 has a lower  $R^*$  for each resource. If species 1 is resident and at equilibrium, and a few individuals of species 2 are introduced, the introduction will fail due to competitive exclusion. If isoclines cross (Fig. 1b) species 1 has a lower  $R^*$  for resource 1 than does species 2, and the converse is true for resource 2. Coexistence is now possible.

Crossing isoclines reflect differences in species' ecologies and the existence of two distinct limiting factors (here, linear combinations of resources). However, such niche differences do not suffice for coexistence. As in the Lotka-Volterra model, there must be broad similarities in how the two species respond to the environment. In Fig. 1a, exclusion occurs because the species are too different in their overall requirements for resources. Coexistence, in contrast, is permitted because overall resource requirements are approximately the same for the two species (Fig. 1b).

Having isoclines that cross does not guarantee coexistence. If species 1 is alone, and resources equilibrate at point a, species 2 invades. However, if resources instead equilibrate at point b, species 2 is excluded. If species 2 is resident, species 1 invades if resources are at point c but not at point d. Comparing these points to each species'  $R^*$  (for each resource) suggests a necessary requirement for coexistence: Given two resources, each competitor must have the greater impact on that resource for which it has the lower  $R^*$ . In effect, each species must limit itself (via resource consumption) more strongly than it limits the other species. Whether or not this occurs depends on both the intrinsic renewal rates of the resources and the rate of consumption of each resource. (A complete analysis of the conditions for coexistence requires a model with equations for dynamics of both consumers and each resource.)

This graphical model illustrates the important insight that coexistence depends on a balancing of overall similarities and differences in species' niche requirements, as well as differences in species' impacts on their environments. The former involves species' intrinsic properties, whereas the latter depends on the system in which the interaction is embedded, including ecosystem processes (e.g., resource renewal rates).

## B. Food Web Effects on Coexistence

This general approach can be extended in many ways, for instance, by including interactions among species at multiple trophic levels. With predation, herbivory, or parasitism inflicted on competing species, one greatly increases the number of potential limiting factors. This is a large and complex topic, and I briefly discuss some highlights here.

Specialist predators and parasites typically reduce the abundance of their favored species, freeing up resources for other nontarget species. This can facilitate coexistence if dominant competitors tend to attract more specialist predators or parasites than do subordinates. Generalist predators can have the same effect via differential fixed preferences for dominant competitors or if they reduce attacks on whichever species is temporarily rarest. However, predators or pathogens which attack two or more species can also hamper coexistence (as in the examples discussed previously). This is particularly likely if the prey species under attack do not strongly compete, and if some prey species are sufficiently productive to sustain high abundances of the predator or parasite (Holt and Lawton, 1994).

Whenever species interact via multiple mechanisms (providing different limiting factors), coexistence may occur. For instance, if two species compete for a single limiting resource, the species with higher  $R^*$  may nevertheless persist if it can also consume the superior competitor. This mixture of predation and competition is called intraguild predation.

## C. Local Habitat Heterogeneity

Traditional ecological models of interacting species such as Eq. (1) assume that populations are spatially well mixed and average over local environmental variation. Relaxing this assumption often promotes coexistence. As shown in Gause's experiments, even in the confines of a microcosm there can be spatial heterogeneity in abiotic conditions that influences coexistence. Assume that within the microcosm each species has a set of conditions in which it is superior. If competitive

interactions are sufficiently localized (e.g., because of limited movement or habitat selection), and each species spends more time in the microhabitat in which it is superior, one can readily generate coexistence. This simple mechanism for coexistence via local habitat partitioning is very important. A review by Schoener (1974) of resource partitioning studies following in the footsteps of MacArthur's warbler study revealed the ubiquity of habitat differences among potential competitors; subsequent years have not altered this basic message.

Competition for light is clearly important in plant communities, but it is not well understood. There is an asymmetry in that tall plants shade small plants but not the reverse. Because light absorption is imperfect, some light penetrates any canopy. Theoretical studies of light competition suggest that two (or more) plant species can coexist, given appropriate tradeoffs between size and the ability to use light at various levels. The physical structure of plants absorbing a directional flux of light almost inevitably leads to local gradients in light availability and quality (due to differential absorption of different wavelengths), which provides the opportunity for plant niche differentiation and coexistence.

In animals, habitat selection can be an important mechanism promoting coexistence with local spatial heterogeneity. If individuals of a species (when rare) can discriminate among local microhabitats and spend more time in those which provide the greatest fitness rewards, the rate of increase at low  $N$  will be increased, relative to that of a species which utilizes habitats at random. If local habitat heterogeneity permits each species to have a habitat in which it is competitively dominant, habitat selection will sharpen habitat partitioning and thereby make coexistence more likely. Habitat selection can permit subordinate species to withstand superior competitors. Recent studies in east Africa suggest that the fleetness of the cheetah helps it persist in the face of direct aggression by lions and hyenas (who kill cheetah cubs) by allowing it to seek out areas with low lion and hyena densities.

## D. Consequences of Individual Discreteness

Traditional ecological models also assume that populations are sufficiently large that abundances can be treated as continuous variables. The growth in computing power in recent decades has stimulated ecologists to analyze population dynamics by tracking the fates of individuals. This reveals novel mechanisms of coexistence. For many organisms (particularly terrestrial

plants), an individual occupies a small site and interacts with only a few neighbors during its lifetime. Probabilistic events of individual life histories (birth, death, and dispersal) lead to spatial variance in competition, even among sites with homogeneous physical conditions. Moreover, dispersal typically occurs over small spatial scales. Combining these two general facts together in models leads to nonuniform spatial patterns in which competition is typically stronger within species (because they tend to occur in clumps) than between species (which tend to become segregated spatially) (Pacala as cited in Crawley, 1997; Pacala and Levin as cited in Tilman and Kareiva, 1997). These effects are particularly strong for species that are relatively similar to each other. This mechanism may go a long way toward explaining the puzzling coexistence of large numbers of similar coexisting species in many plant communities.

## VIII. TEMPORAL NICHE PARTITIONING

Outside the controlled confines of the lab, environments are rarely constant. Temporal variation occurs on scales ranging from diurnal cycles to climatic changes over millennia. Many ecologists have intuitively argued that temporal variability by itself weakens negative interspecific interactions and thereby facilitates coexistence. Theoretical studies (reviewed in Chesson and Huntly, 1997) have conclusively shown that this is not the case. Instead, temporal variation can provide a rich arena for differentiation among species in responses to the environments, which can promote coexistence. The basic idea is that if species A does better when the local environment is in state A' and species B does better when the local environment is in state B', and the environment alternates between A' and B', coexistence is possible. Two plausible scenarios are presented in the following sections.

### A. Nonlinear Consumption

Assume two consumer species exploit a single limiting resource and have saturating, nonlinear relationships between feeding rates and resource availability. Species A has a higher rate at low resource levels, whereas species B enjoys a higher feeding rate at high levels. In a constant environment the resource level will equilibrate at a constant level, and the species with lower  $R^*$  will win. However, because of large-scale seasonal variation in resource supply rates, resource levels may fluctuate between high and low levels. Such variation can permit coexistence of these two competitors on a

single resource. This mechanism hinges crucially on nonlinearity in species' responses to the shared limiting factor; if feeding rate were to increase linearly with resource availability in both species, then even in a variable environment one would observe competitive exclusion.

### B. The Storage Effect

In a desert, rain falls sporadically and at different times in different years, sometimes early in the spring when the air is cool and at other times later in the hot summer. At each rain, a mixture of plant species appear in abundance from the resting seed bank and compete for water and soil nutrients. These plants are short-lived as adults, often completing their entire aboveground life cycle in just a few weeks. Some species do disproportionately better following warm rains, whereas others do better following cold rains. The seeds each species produces enter the seed bank and germinate gradually during the following years (like a time-release capsule of past recruitment). The "storage" of good years of recruitment in a long-lived seed bank can facilitate coexistence of competitors. Again, it is not variability alone which allows coexistence. One also needs (i) niche partitioning, with different species being superior at different times; (ii) nonlinear effects of the environment on responses to competition; and (iii) correlations between the varying environmental factors and the strength of competition (Chesson and Huntly, 1997). The existence of distinct life stages (e.g., long-lived seeds) can induce the needed nonlinearity in responses to temporal variation that promotes the coexistence of competing species.

## IX. COEXISTENCE IN OPEN COMMUNITIES

In contrast to laboratory microcosms, many natural communities are open, coupled to the external environment via dispersal. Such coupling influences local coexistence of species in many distinct ways.

### A. Autecology and Population Size Effects

A consumer species which relies on a sparse or sporadic resource, or extracts different essential resources in different habitats, may need to be mobile to persist. If absolute population size is small, extinction is risked even in favorable environments. Specialist consumers are likely to go extinct if their resources are rare. All

these problems are aggravated when there are barriers to dispersal and habitable area is small. These considerations may help explain why food chains are often short on oceanic islands or isolated habitat patches. Moreover, as one increases the number of species which coexist deterministically on a fixed resource base, the abundance per species typically declines. Small population sizes have an increased risk of extinction; this can put a loose limit on coexistence.

## B. Colonization–Extinction Dynamics

It was previously mentioned that strong specialist predator–prey interactions are prone to local extinctions. Coexistence may require dispersal among habitats, with prey dispersing sufficiently fast so that they can find and reproduce within empty habitat patches before being discovered by predators. Similarly, if a guild of competitors utilizes a single resource, species with successively lower values of  $R^*$  should eventually colonize and displace species with higher  $R^*$ . If there are extinctions, asynchronous among patches, inferior competitors may have a temporary window of opportunity during which they can occupy habitat patches and reproduce sufficiently to colonize other patches. This metapopulation mechanism for coexistence can be promoted by a tradeoff between competitive ability and colonization ability, and in principle it can promote the coexistence of many competing species (Tilman and Lehmann as cited in Tilman and Kareiva, 1997). Even if the inferior competitor is not a superior colonizer, it may be able to persist if it has a lower basal extinction rate when it occurs in patches alone compared to that of the superior competitor.

## C. Landscape Heterogeneity

### 1. Spillover Effects

If a species can persist in one local community, then with emigration it can also be found in other nearby communities in which otherwise it would be excluded by local interactions. To model this “spillover” effect, assume the species when rare declines at rate  $r < 0$  because of competitive exclusion but immigrates from an external source community at rate  $I$ . Its local dynamics are thus described by  $dN/dt = I + rN$ , which implies  $N^* = I/|r|$  at equilibrium. A species which should be absent, considering only local interactions, may not just persist but even be abundant if (i) there is a large rate of immigration (e.g., from a productive source habitat into an unproductive habitat) and (ii) the rate of exclusion is slow. In this scenario, the answer to the species

coexistence problem ultimately requires analyzing population dynamics at the appropriate spatial scale, larger than the local community; spatial niche partitioning at this larger scale is responsible for coexistence.

### 2. Landscape Mechanisms of Exclusion

Spatial coupling can also generate novel mechanisms for exclusion. For instance, a predator sustained by a prey species in a productive habitat may move through another habitat and inflict mortality at a sufficiently high rate to exclude a prey species there. Likewise, a species which is a superior competitor in one habitat may be excluded by a species which is inferior there but sufficiently abundant elsewhere so that via dispersal it can “swamp” the local habitat. For instance, Ted Case and associates recently described impacts of an invasive ant species, the Argentine ant, on an entire community of ants in coastal southern California. In contrast to many ants, the Argentine ant shows little intercolonial hostility and so has a high carrying capacity; it competes exploitatively for food but also preys on the juvenile life stages of some ant species. The Argentine ant readily becomes established in disturbed habitats. It can then spread into fragments of natural habitat resulting from intense development. Case suggests that in these fragments many other ant species have declined to the point of extinction because of the sheer force of numbers. These effects are particularly dramatic in small fragments, and at the edges of large fragments, because of incursions from surrounding human-disturbed habitats in which the Argentine ant is abundant.

I now return to the lab and field case studies of competition discussed previously. In light of what we now know about mechanisms of coexistence, it is easy to see why competitive exclusion was often observed in the classic bottle experiments with protists and grain beetles. The design of these experiments included most of the elements assumed in the syllogism leading to the competitive exclusion principle. The lab environments were climatically controlled, and the culture bottles were spatially closed, precluding two of the major classes of coexistence mechanisms. The culture media and conditions (e.g., stirring) were set up to have a restricted number of limiting resources (ideally, one) and little within-culture spatial heterogeneity in limiting food resources; the communities are very simple, so there is little opportunity for complex food web interactions. The most interesting result of these experiments may be that coexistence is observed at all. In the field study of introduced parasitoids, these species were specialized to the same host species, and the environment was relatively constant in time and homogeneous

in space (the lowlands of tropical islands such as Hawaii have very stable climates, and the habitat is a deliberately homogenized landscape—plantations with regularly spaced fruit trees). It is likely that the communities are simple (islands tend to be low in species richness, particularly in heavily disturbed habitats dominated by introduced species). Most natural systems, in contrast, are temporally variable and spatially heterogeneous, and they harbor rich, complex communities; therefore, it should not be surprising that it is often difficult to document competitive exclusion in the wild.

## X. FUTURE DIRECTIONS

There are many important themes relevant to species coexistence which have not been addressed in-depth by ecologists but are likely to receive considerable attention in the near future.

### A. Transient Coexistence

Ecological theory has traditionally emphasized equilibrium community states and the development of criteria for exclusion and indefinite persistence. However, exclusion takes place over some timescale. If this is long (e.g., relative to climate change), communities may exhibit transient dynamics and be far from equilibrium. This is particularly likely when considering interactions among species which are very similar in their niche requirements and environmental effects; their abundances can vary through time in an essentially random fashion (a process known as community “drift,” championed by Steve Hubbell). An important task for future ecological theory and empirical work is to derive a deeper understanding of transient dynamics and the drift hypothesis.

### B. Allee Effects and Coexistence

Most ecological theory applies literally only to clonal, asexual organisms. However, most species of concern to ecologists are sexual. At very low population sizes, outcrossed sexual species should have depressed growth rates simply because the two sexes have to get together to reproduce—an “Allee” effect (positive density dependence in growth rates at low densities). Allee effects can influence coexistence. For instance, consider two sexual species with identical ecologies in a landscape with many habitat patches. If colonization is infrequent, whichever species arrives first in a patch should be able to dominate there because the first colonist increases until births just match deaths. When the second species

appears, its potential birth rate will then also just match its death rate (because its ecology is the same as that of the resident), but its realized birth rate will be depressed because it has difficulties in pair formation at low numbers. Hence, in this patch the second species to arrive will be excluded. In the landscape as a whole, the two species may coexist if by chance each species is the first to occupy a subset of patches. In some patches, both species may by chance appear initially in sufficient numbers so as not to experience the Allee effect; in these patches, abundances should drift through time. Over the entire landscape, patterns in abundance will not be correlated with any discernible factors in the external environment. The magnitude of the Allee effect varies greatly among species, depending on details of the mating system and mate-finding strategies (e.g., selfing in plants should greatly weaken Allee effects). This influence of mating ecology on coexistence may provide an as yet poorly understood source of variation among taxa in community structure.

### C. Speciation Mode and Coexistence

Over long timescales, all species originate from other species. Understanding the mode of speciation may provide insight into coexistence. For instance, sympatric speciation occurs when a lineage diverges within a single community. Most models of sympatric speciation depend on substantial ecological differentiation being present from the beginning; as speciation unfolds, ecological differences between the two emerging species must be sufficient to withstand cross-mating. In other words, with this mode of speciation, mechanisms of coexistence (e.g., substantial habitat or resource segregation) are built into the very branching pattern of the phylogenetic tree. In contrast, allopatric speciation requires geographical isolation. This can occur without any ecological difference arising between the daughter lineages (although speciation should occur more rapidly if correlated with ecological divergence). Dispersal can later bring the daughter species together, with essentially any degree of ecological difference being possible at this stage. Speciation may also often involve changes in sexual selection and mating systems, which can occur with no change in ecological requirements. After speciation, when these species' ranges begin to overlap, relative abundances should be particularly prone to community drift.

## XI. CONCLUSIONS

In conclusion, understanding the factors which promote or constrain the coexistence of species is an ongoing en-

terprise at the intellectual core of the study of biodiversity. Community ecologists have a rich smorgasbord of hypotheses to explain both species coexistence and exclusion. In most natural communities it is likely that many mechanisms operate simultaneously. A challenging problem is to ascertain the relative contribution of these ecological mechanisms of coexistence to explain major patterns in biodiversity in space and time. There is much work to be done in analyzing mechanisms of coexistence in the context of food web dynamics and metapopulations. Moreover, very little mention was made in this article about commensalism, mutualism, and nontrophic interactions, all of which can be crucial to coexistence. An improved understanding of the factors governing species coexistence is needed to address many applied problems, particularly the conservation of natural communities. Given the importance of spatial openness for coexistence, the anthropogenic alteration and simplification of landscapes pose particular dangers to the continued coexistence of many species. Indeed, the basic unstated problem of conservation is how to structure our activities and modify our impacts so that most of the world's biota can manage to coexist (at some spatial scale and, it is hoped, over long timescales) with just a single species, namely, ourselves.

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### See Also the Following Articles

COEVOLUTION • FOOD WEBS • MUTUALISM, EVOLUTION OF • INTRODUCED SPECIES, EFFECT AND DISTRIBUTION • LANDSCAPE DIVERSITY • PARASITISM • PREDATORS, ECOLOGICAL ROLE OF • POPULATION DYNAMICS • SCALE, CONCEPT AND EFFECTS OF

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