Chapter 13
Species Competition and Predation

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Glossary

Apparent competition	The tendency for an increase in the density of a species to increase the impact of a natural enemy on that same species or other species.
Competition	The tendency for an increase in the density of a species to have a negative effect on the survival or reproduction of individuals of the same species or of other species by reducing resource abundance, reducing access to resources, or by direct harm of one individual organism on another associated with resource acquisition.
Density dependence	The tendency for an increase in the density of a species to have a negative effect on the survival or reproduction of individuals of the same or different species. As used in this essay, the species in question are in the same guild. Competition and apparent competition are special cases of density dependence.
Feedback loop	A chain of species interactions from one member of a guild, through other species, back to a species in that same guild. Feedback loops transmit density dependence.
Guild	A group of species potentially co-occurring in the same locality and having similar ecology in the sense of depending on the same or similar resources, often seeking

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	those resources in similar ways, and susceptible to the same or similar natural enemies. The standard of similarity in this definition is not precise, and varies depending on the purpose of the investigator.
Natural enemy	An organism that benefits its own reproduction or survival by harming the individuals of a given species, commonly by feeding on them.
Niche overlap	For any pair of species, the degree to which density dependence through feedback loops is concentrated between species compared to within species. It is measured by the quantity ρ which varies between zero for no overlap (no interspecific density dependence) and 1 for complete overlap (interspecific density dependence is on average equal to intraspecific density dependence).
Predator	A species that gains food by killing and consuming individuals of the species in the ecological guild in question.
Species average fitness	For a given species in a guild, it is a numerical measure of how well that species is adapted to the environment with the property that it predicts which species would dominate if the niche overlaps, ρ, were all equal to 1. It is normally related to the long-term average per capita growth rates of the species measured at fixed levels of competition and apparent competition. In this essay, the fitnesses κ are obtained from per capita growth rates at zero levels of competition and apparent competition, which are achieved by setting all members of a guild at zero density. These growth rates are then divided by scaling factors that correct for differences between species in their levels of sensitivity to competition and apparent competition.
Stable coexistence	The tendency of the members of a guild to recover when individually perturbed to low density, allowing their long-term persistence in the presence of interactions with other guild members.

Definition of the Subject

Competition and predation are key interactions between species, and are major foci of thought and study in community ecology. They are believed to be major forces structuring natural communities, having critical roles in the determination of species diversity and species composition, and are regarded as important drivers of evolutionary processes. The relationships between the niches of different species determine how they interact through competition and predation, which then have key roles in assembly of local communities, and their reassembly following perturbations. Niches define patterns of linkages between species, their resources, and their natural enemies. These patterns include how linkages change over time, and between different spatial locations, and define mechanisms by which similar species are able to coexist by their effects on competition and predation relationships. The human element in the environment has profound effects on these phenomena. Changing the environment shifts interactions between species, and profoundly modifies the structure of food webs. In the modern day, there is much community reassembly, potentially involving major shifts in competition and predation. Humans transport invasive species that act as predators, prey, and competitors with potentially major effects on the community reassembly process.

Introduction

Competition and predation are key species interactions that are believed to structure natural ecosystems and to have major roles in systems dominated by humans. Both of these interactions involve consumer–resource relationships in one form or another [1]. The relationship between a predator and one of its prey species is of necessity a consumer–resource relationship with the predator being the consumer and the prey its resource. Competition is mostly commonly resource competition, where several consumer species share one or more resources and compete for these resources [2–4]. A resource may or may not be a biological species. When the resources are biological species that are killed by the consumer, competition necessary involves predator–prey relationships. However, resource species may instead be grazed or browsed, parasitized or infected. In these cases, the consumer species are natural enemies of their resources, harming them without necessarily killing them, which generalizes the idea of a predator–prey relationship to a species–enemy relationship.

The resources of plants are generally not biological species, and indeed this is the case with the resources of most plants, which are instead broadly light energy, water, and chemical elements [5]. Plants are often thought of as requiring space to grow as a resource [4]. Space then provides their other needs. In general, not all space is equal, and plant species tend to be somewhat specialized, leading to the concept of safe sites [6] (places that satisfy the requirements for establishment, growth, and reproduction for a particular species), and the regeneration niche [5] (an elaboration of the idea of a safe site with a particular view to how species compete with one another). Sedentary animal species that either settle in a particular place and do not move, or establish territories, can also be regarded as having space as a resource [7]. Animal species require particular places for particular uses, such as nest holes and wallows, and use various dead organic and inorganic materials in their lives. These all count as resources if they are used or occupied by an individual to its benefit.

Both competition and predation are assumed to involve harm. In the case of predation, of course the predators benefit from the relationship, and prey are harmed because individual prey are killed. This does not, however, preclude some positive benefits of predation, or more generally of natural enemies, on species that are attacked, as these species may well be adapted to their natural enemies, and suffer some negative effects when natural enemies are removed. For example, grasses may be adapted to grazers that remove old, less productive biomass as well as enhancing nutrient recycling [8]. In the case of competition, harm is mutually negative for the participant species, though it is often lopsided with some species being harmed much more than others.

Resource consumption may reduce resource availability to individuals in species that depend on the resource. In this case, harm occurs when lowered resource availability leads to reduced fitness of individuals because they suffer directly by consuming less resource, have to expend more energy or materials to obtain the resource, take greater risks to obtain it, or have to divert time from other beneficial activities to do so. Competition is also assumed to occur by direct negative interactions between individuals seeking the resource. It is not necessary in such instances for resource consumption to lower resource availability, but the presence of other individuals decreases the ability of a given individual to consume resources, or in the process of seeking resources, individuals harm each other in other ways, for instance through fighting [9, 10].

Predation and species–enemy relationships necessarily have strong effects in ecosystems, as they form the paths of energy and material flows [1]. The role of competition between species is less obvious, often indirect, and frequently controversial [11]. Although it is easy to verify that a predator consumes a prey species, it is much more difficult to demonstrate that one consumer species harms another consumer species through their resource consumption activities. While numerous rigorous experimental studies have firmly established that competition between species is frequently a strong force in nature, the effects of interspecific competition on various community properties have been difficult to establish. An abundance of theoretical work provides hypotheses, but rigorously testing of them in nature has proved to be difficult and often controversial [12–14]. Thus, although competition as a strong force is well established, the effects of that force are not.

Several difficulties arise in the study of competition. First, the consequences of competition between species (interspecific competition) do not rest with its absolute strength but with its strength relative to competition within species (intraspecific competition) [15]. Competition within species constrains the tendency of one species to harm another. Second, competition can be constrained by other interactions, such as predation, in some cases limiting its effects, but potentially interacting with competition in complex ways [16, 17]. Third, the natural world is extremely variable in time and space. This variability not only makes clear trends difficult to discern, it potentially interacts with competition modifying the outcome [15]. Thus, although competition can be shown to be present and strong, and is believed to have important implications for numerous community phenomena, clear tests of predictions have often been elusive.

The predictions from predation are most often of a different character from those of competition, yet they need not be. Competition comes from the interactions between consumers as a result of consumption of shared resources. Turning that on its head, when the resources are prey, they affect each other indirectly by providing food for common predators, potential increasing danger from those predator species. This indirect interaction between prey species is known to have analogous effects to competition, and has thus been termed apparent competition [18]. Although first suggested in a single-species context many years ago [19], it has only recently been generally understood, and so has received far less direct study than competition, but it is also likely that studies of competition have inadvertently included the effects of apparent competition: protocols to cleanly separate the two effects have yet to be developed.

Conceptual difficulties have plagued understanding of how competition and predation structure communities owing to the intrinsic complexity of the subject. The theory, however, has been making steady progress, and a much more comprehensive theoretical framework is available now than even a few years ago. The body of this essay explains the fundamentals of how competition and predation are hypothesized to structure communities in the light of these recent advances. Included are the intricacies introduced by the complex behavior organisms, and the often conceptually difficult area of how predictions about competition and predation can be made in the face of temporal and spatial variation in the physical environment, and in the presence of fluctuations in the populations of the organisms themselves. Applications to a theory of invasive species are then presented. Invasions of alien species represent perturbations to natural systems that can lead to a process of reassembly of communities of organisms. Competition and predation are believed to have large roles in this reassembly process, and explaining it is a critical challenge in community ecology. Because of the impacts of alien species on native communities, there are major implications for conservation biology also. Finally, challenges in the study of competition and predation, and promising future directions, are presented.

Feedback Loops

The fundamentals of competition and predation can be best understood in terms of feedback loops within a food web. Figure 13.1 shows a simplified food web, which should be considered as part of a food web rather than being any reasonably complete web that one might find in nature. It shows three trophic levels allowing understanding of how the middle trophic level is affected by the trophic levels above and below, which represent, respectively, predators and resources of that middle trophic level. Species in the same trophic level, by sharing trophic position, have strong similarities in their ecology. There may be other ecological similarities, and also differences within a trophic level, in the way the species relate to other trophic levels and to other elements in their environment. Species with similar ecology are commonly referred to as a *guild* and here the middle trophic level is the focus of discussion and is referred to as the focal guild, or just “the guild.”

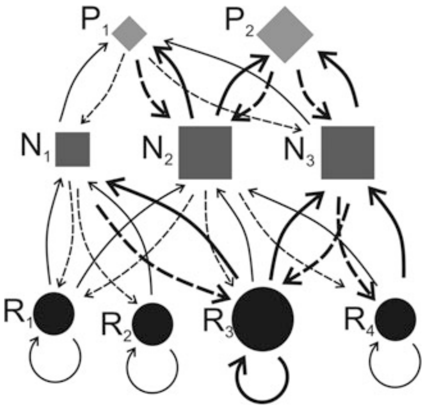

Fig. 13.1 Representation of a subset of a food web with arrows showing directions of effects from one species to another. Differences in the thicknesses of arrows are meant to indicate differences in the strengths of effects. The different symbols distinguish trophic levels, and their size differences are meant to imply differences between species in population size within a trophic level. The letters *R* and *P* indicate that they are respectively resources and predators of the species, *N*, in the middle trophic level, with subscripts labeling species within a trophic level. These subscripted letters serve simultaneously as species labels and as the population densities of the species. The recursive arrows for resources mean they experience direct intraspecific competition of some form giving density feedback to themselves, but not direct interspecific feedback within the resource trophic level. An assumption like this is common in the Lotka–Volterra models discussed in this essay, and may also be applied to the predators too

How species in a guild interact with each other, and ultimately coexist or instead exclude each other, leads to an understanding of how communities are structured, that is, an understanding of the relationships between the traits of different species that allow them to come together to form a long-lasting community, or in other words are assembled [20, 21]. Competition can be understood by considering the linkages between focal-guild species and their resources in the trophic level below. Linkages with the tropic level above lead to an understanding of apparent competition [22].

The arrows in the diagram show directions of effects. A species benefits from arrows pointing to it from a lower trophic level and suffers from arrows pointing to it from a higher trophic level. Chains of arrows define pathways of effects. Competition and apparent competition can be understood by pathways leading from the middle trophic level back to that level. For example, the species N_2 has pathways going from itself to each resource species, R, back to itself. These pathways contribute to intraspecific competition for N_2. The idea is that an increase in the density of N_2 leads to greater consumption of each resource species, R, reducing their densities and thereby reducing the availability of these resources for N_2. Pathways from these resources back to other species contribute interspecific competition. Thus, the pathways from N_2 through R_3 and R_4 back to N_3 lead to interspecific competition for N_2 on N_3. Through these various pathways, increasing the density of N_2 feeds back negatively to itself and to other species in the same trophic level. Critical to understanding of the ultimate effects of competition is the extent to which negative feedback of a species on itself limits its ability to increase and harm other species.

Apparent competition is understood by entirely analogous effects. In this case, we note that N_2 is preyed upon by P_1 and P_2. An increase in N_2 benefits both P_1 and P_2. These predators may therefore increase in abundance, and as a consequence, predation on the second trophic level will increase. Again, increasing the density of a species in the middle trophic level feeds back negatively to itself and to other species. Thus, in a food web, multispecies density dependence occurs when changes in the density of a species within a given trophic level feed back to that trophic level through linkages to other trophic levels, modifying the growth rates of the species. The term "density dependence" is traditionally used in ecology just for feedback from a species to itself, but understanding of the joint effects of predation and competition requires broadening of this concept to *interspecific density dependence* where increasing the density of one species affects the per capita growth rate of another species. Consistent with this usage, the traditional density dependence concept of ecology becomes *intraspecific density dependence*. Competition and predation both contribute to intraspecific and interspecific density dependence [17].

Basic understanding of the role of competition in ecological communities is usually represented by the Lotka–Volterra competition equations. Using the species labels to mean also their densities, these equations can be written in the form

$$\frac{1}{N_i}\frac{dN_i}{dt} = r_i\left(1 - \sum_{j=1}^{n} \alpha_{ij} N_j\right), i = 1, ..., n. \tag{13.1}$$

These equations define the per capita growth rate of each species in the focal guild, which reflect the average conditions that individuals of each species experience. The quantity r_i is the maximum per capita growth rate of species i, which is reduced by the terms representing density dependence inside the parenthesis. The coefficient α_{ij} measures density dependence of species j on species i. It measures how much the per capita growth rate of species i, as a proportion of its maximum value r_i, is decreased by increasing the density of species j by one unit. This coefficient measures interspecific density dependence if j is different from i, and intraspecific density dependence if $i = j$. The coefficient of intraspecific density dependence defines the so-called carrying capacity for a species: $K_i = 1/\alpha_{ii}$. Traditionally, the Lotka–Volterra competition equations have been parameterized with the competition coefficients defined as multiples of the carrying capacity, with the carrying capacity itself appearing explicitly in the equations, but this approach is now known to obscure the workings of the equations [15], and so is not done here.

Recent understanding shows that the Eq. 13.1 can also represent apparent competition, not just competition, and indeed they can represent the combined effects of competition and apparent competition. To do this, the equations are derived from a larger set of equations that take account of the direct interactions of the focal species with other species in the food web [17]. Thus, these equations have explicit formulae defining the effects of the arrows for a food web like Fig. 13.1. Equation 13.1 is then able to define the long-term growth of the species in the focal guild in terms of feedback loops from other species. The α_{ij} are given by formulae derived from this larger set of equations and depend specifically on how species forage for their resources, how they are preyed upon by their predators, and how these resources and predators change in density in response to density changes in the focal guild [17]. It is important to note, however, that Eq. 13.1 does not apply to short-term prediction, but to long-term outcomes such as long-term recovery of a population from low density, or eventual extinction [17]. Although the Lotka–Volterra competition equations are used generically in ecology, it should be appreciated that they are very specific, and can only be used to illustrate general principles, not to give precise outcomes in any given system. Fortunately, there are means of matching Lotka–Volterra models with models for particular systems that validate their use for general principles when treated appropriately [4, 15, 23].

The key issue to be addressed with the Eq. 13.1 is when species coexistence will occur, and when some species will be excluded from the community. This is easy and straightforward in the case of a guild of two species, and this case gives some key general principles [17]. The fundamental result in the two-species case is that species j can exclude i from a community if

$$\alpha_{ij} > \alpha_{jj}. \tag{13.2}$$

The reverse inequality means that species i is always able to invade the system when dominated by species j. The mutual invasibility criterion [24] then says that two species, labeled 1 and 2, will coexist stably whenever they are both able to recover from low density in the presence of the other species. In the two-species Lotka–Volterra equations, this criterion leads to the condition

$$\alpha_{11} > \alpha_{21} \text{ and } \alpha_{22} > \alpha_{12}. \tag{13.3}$$

Fundamentally, this means that for stable coexistence, each species must depress its own growth more strongly than it depresses the growth of the other species as it increases in population density. It is a very simple and general criterion that ensures stable coexistence [15]. If one of the inequalities in (Eq. 13.3) is reversed, then one species can exclude the other, and not vice versa. This means that one species always drives the other extinct. On the other hand, if both inequalities are reversed, then each species can exclude the other. This means that neither species can invade a system consisting of the other species. Whichever species establishes first remains the sole occupant in the guild in question in that locality.

The Lotka–Volterra competition Eq. 13.1 can be interpreted directly as meaning direct interference of individuals of all species with individuals of other species, harming them by reducing foraging time or in some cases by cannibalism or *intraguild predation*, which refers to predation by one species in a guild by another species in that guild [25]. In this case of direct interference, resource shortages or predators need not have a role [9–11]. Indeed, it is in this form that the

Lotka–Volterra equations are in principle most accurate, given that they do not explicitly represent the dynamics of resources or natural enemies outside the guild in question. In these cases, they are valid for short-term as well as long-term predictions. In these cases of direct interference, conditions (Eq. 13.2) and (Eq. 13.3) then apply, respectively, to exclusion and coexistence, showing in particular that coexistence requires each species to interfere more strongly intraspecifically than interspecifically.

When the Lotka–Volterra equations are used to represent trophic interactions such as those of the food web Fig. 13.1, the coefficients of density dependence α can be defined in terms of quantities that summarize the interactions in the food web: niche overlap, ρ, and species-level average fitness, κ [17]. The niche overlap, ρ, between any pair of species is a measure of the relative strength of the density-dependent feedback between versus within species through resources and through predators. This quantity takes the value 1 when there is complete overlap, and zero when then there is no overlap. No overlap occurs when the members of the pair of species under consideration do not share resources and do not share predators. Thus, they do not have arrows to or from any of the same resources or predators in Fig. 13.1. With complete overlap, they have arrows to and from all of the same resources and predators, and these predators and resources are of the same relative importance for each species in the guild. If the resources and predators vary in importance for different species, but nevertheless both species under consideration are affected by them, then ρ will be between 0 and 1. Figure 13.2 gives various scenarios for different strengths of niche overlap.

The average fitness measure, κ, for any given species measures its ability to meet its energy needs and avoid predation when all species in the guild are at low density and thus not providing any feedback through density changes. This measurement is also expressed in special units, namely, in units of average sensitivity of the per capita growth rate of the species to changes in resources and predators. These quantities ρ and κ now relate to the coefficients of density dependence according to the relationship

$$\frac{\alpha_{ij}}{\alpha_{jj}} = \frac{\kappa_j}{\kappa_i}\rho. \tag{13.4}$$

Thus, the ratio of interspecific to intraspecific density dependence for species j's impact on species i is equal to the ratio of the fitness of species j to species i, multiplied by the overlap measure. This relationship is correct regardless of how many species are present in the guild in question. However, when there are just two species, the condition that the ratio (Eq. 13.4) be greater than 1 is the condition (Eq. 13.2) for species j to exclude species i. The ratio being less than 1 means that exclusion does not occur. These conditions in terms of the fitness ratio, multiplied by the overlap measure, are also strongly intuitive and instructive in terms of how stable coexistence occurs.

Consider the case of complete niche overlap, $\rho = 1$. Then the formula (Eq. 13.4) implies that whichever species has the larger fitness will exclude the other species.

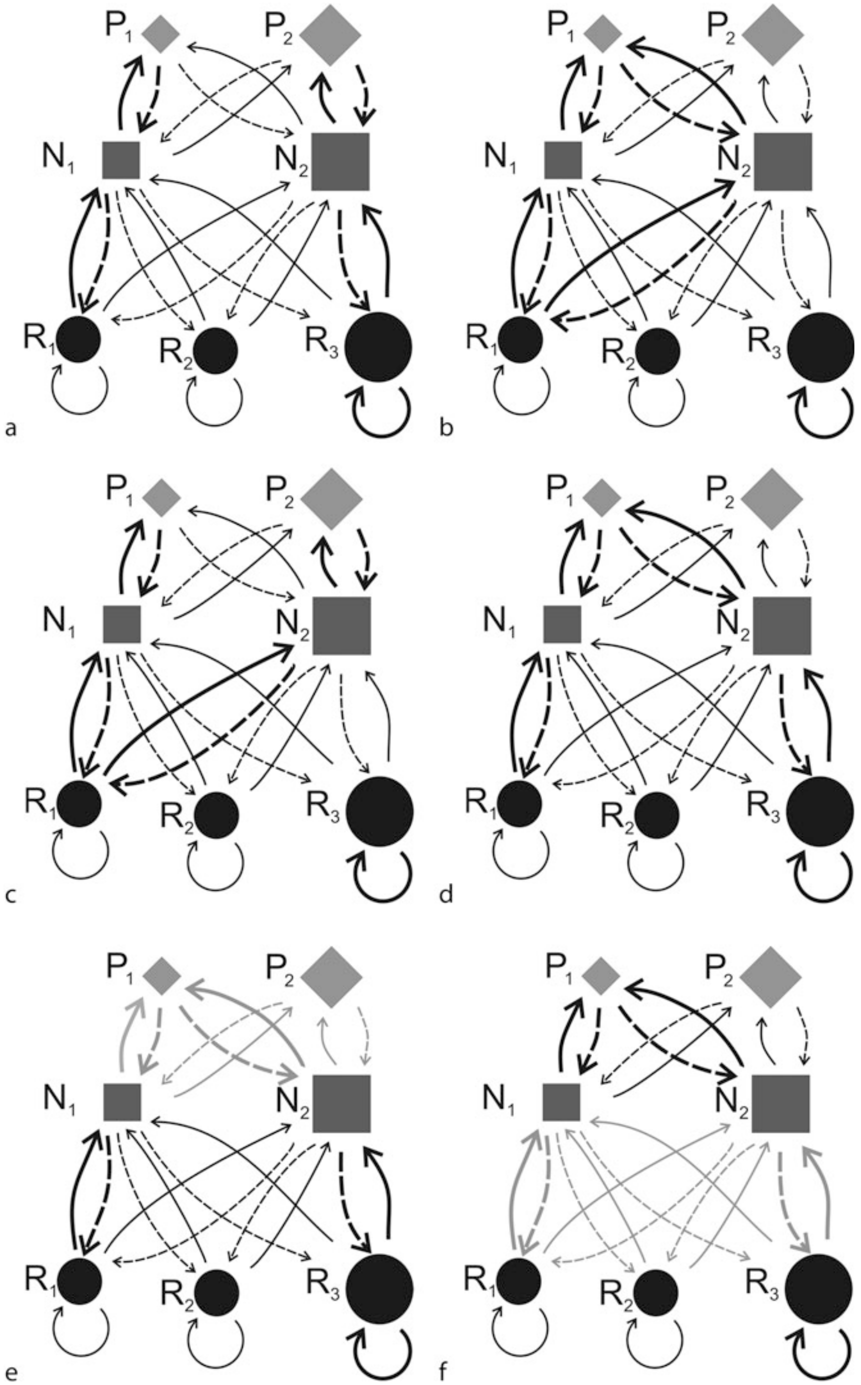

Fig. 13.2 Different scenarios for indirect linkages between the focal species, N_1 and N_2, through their resources and predators, leading to different degrees of niche overlap, ρ. Thick arrows

In other words, a simple fitness ratio greater than 1 is sufficient for one species to exclude the other. When $\rho < 1$, the fitness ratio is discounted by the overlap measure to determine if exclusion will occur. For example, if the overlap is ½, a species has to have fitness more than twice as high as the other to exclude it. The mathematics implies this outcome, but intuitively the idea is that the less species overlap in their niches, the more difficult it is for one species to exclude the other, but this can still occur if a species has a strong enough fitness advantage.

It is also worth noting that ρ is a symmetric measure of the ratio of interspecific to interspecific density dependence for any pair of species i and j, as formula (Eq. 13.4) implies that

$$\rho = \sqrt{\frac{\alpha_{ij}}{\alpha_{jj}} \cdot \frac{\alpha_{ji}}{\alpha_{ii}}}. \tag{13.5}$$

Thus, ρ can be thought of as niche overlap, and at the same time as the geometric mean of the ratios of interspecific versus intraspecific density feedback for any pair of species. Thus, it measures the potential for stabilization of coexistence without taking into account the fact the ratio might be different for one species compared with other and lead to dominance instead of coexistence. The formula (Eq. 13.4) shows how that bias changes as the fitness ratio changes, suggesting, as we shall see below, how changes in circumstances can change the opportunities for coexistence.

Niches and Species Coexistence Mechanisms

The results of the Lotka–Volterra equations can now be applied to see how a guild of coexisting species is constrained by trophic relationships. For two species to coexist, the conditions (Eq. 13.3) together with the formula (Eq. 13.4) imply that

$$\rho < \frac{\kappa_1}{\kappa_2} < \frac{1}{\rho}. \tag{13.6}$$

Fig. 13.2 (continued) indicate relatively strong linkages compared with thin arrows. A gray arrow indicates that although the linkage might be important, it is not a strong source of density-dependent feedback for focal species. (**a**) Low niche overlap because the strong links to both resources and predators differ between N_1 and N_2. (**b**) High niche overlap because the strength of the links between N_1 and the various resources and predators has the same pattern as the strength of the links between N_2 and these resources and predators. Although these two species do discriminate between these resources and predators, they do so in an identical way. (**c**) High niche overlap through resources, but low niche overlap through predators, leading overall to an intermediate level of niche overlap. (**d**) Low niche overlap through resources, but high niche overlap through predators, leading overall to an intermediate level of niche overlap. (**e**) As in **d**, but predation is not strongly density dependent, and so overall niche overlap is low due to the low overlap through resources. (**f**) As in **d**, but resource consumption is not strongly density dependent, and so overall niche overlap is high due to the high overlap through predators

Fundamentally, this says that species 1 and 2 will coexist stably if their fitness ratio lies between ρ and $1/\rho$. Thus, the less the niche overlap, the greater the difference in fitness that is tolerated compatible with species coexistence. These conditions involve two kinds of differences between species that affect species coexistence in opposite ways. First are fitness differences, which are measured in terms of the deviation of the fitness ratios from 1. This ratio fundamentally measures the overall relative degrees of adaptedness of the species to their common environment. A species with a larger value of κ can be thought of as a better performer, and therefore inequality in this respect understandably favors exclusion.

A complication arises due to the fact that when different focal species are present, the resource species or predator species maintained in the food web may be different [17]. When we ask if species 1 can exclude species 2, those resources and predators present when species 1 is present alone are used to calculate the fitnesses and niche overlap for both species 1 and 2. When we ask if species 2 can exclude species 1, a different set of resources and predators might be present. This means that in some cases, the ρ and κ ratio for each end of the inequality in (Eq. 13.6) will be different, and will have to be calculated based on which focal species is present. While, this complication does not alter the fundamentals as to whether a given species can exclude another species from a community, it is important to keep in mind that ρ and the κ's may change with the circumstances [26, 27].

What do these critical quantities measure? Although the κ's and ρ both involve aspects of resource consumption and predation, they measure independent aspects. In particular, the quantity ρ is independent of how well the species are adapted to the environment. Instead it compares species in terms of which trophic links (links to resources and predators) are most important to them, and how important they are, as illustrated in Fig. 13.2. Importance is measured in terms of the ability of that link to generate density-dependent feedback [17]. This comparison shows how much the species interact with each other through their resources and natural enemies and so how much conflict there is between them: the larger ρ is, the larger the conflict. Naturally, two individual organisms have greater similarity and therefore greater conflict through trophic relationships within species than between species (not counting the effects of overall fitness differences), and ρ is a relative measure comparing between-species interactions through trophic links to within-species interactions. In other words, it compares the strength of interspecific feedback loops with intraspecific feedback loops, in essence adjusted to equal overall fitness. Thus, the ratio κ_1/κ_2 and niche overlap ρ represent two different kinds of comparison between species.

Exclusion Principles

Recognition of these two separate kinds of ecological comparison between species resolves a conundrum about the competitive exclusion principle [28], which is often stated as “no two species can occupy the same ecological niche.” It has been a problematic principle because often the niche is not defined precisely enough to give the principle content. Indeed, there are many and various definitions of the niche [29], but perhaps the one most usefully behind the principle is the Eltonian niche which is about how an organism uses the environment [29]. However, when natural enemies are considered, the niche must include not just how a species uses the environment, but also how other organisms in the environment use that species. Thus, the niche needs to be defined as how an organism relates to the environment [15, 29]. Regardless of whether this idea can be measured in an absolute sense, the quantity ρ provides a relative sense in which two species relate to the environment. This definition specifically removes the overall level of adaptedness to the environment from the comparison between species, focusing on how they relate to it. This way of comparing niches differs markedly from what would be concluded from comparing niches according to the recent niche definition of Chase and Leibold [29]. Under their definition, the conditions in the environment defining zero per capita growth rates are the niche. That means species would only overlap completely if their growth rates were zero under exactly the same conditions. Species with $\rho = 1$ would overlap completely according to the approach here, but would not have zero growth under the same conditions unless their κ values were the same too.

The sense in which the competitive exclusion principle is correct is that no two species can coexist stably if their niches overlap completely, i.e., $\rho = 1$. The Lotka–Volterra approach defines this idea here, and makes it precise, but it is important to realize that it in fact emerges from a broad array of models, as will be discussed further below, without evidently any contrary models. More important, these ideas allow a quantitative approach to the competitive exclusion principle. A niche overlap value of $\rho = 1$ is an unlikely occurrence in nature, but a value near 1 is not unreasonable. Here condition (Eq. 13.6) shows that when species have high niche overlap, their fitnesses are very closely constrained to be more nearly equal. Thus, there is a more quantitative exclusion principle that relates not just to competition, but to apparent competition too, and states that species with high niche overlap must have correspondingly high similarity in average fitness if they are to coexist. This principle then replaces a statement with limited application to a more significant one about the difficulty of coexistence for species with strongly overlapping niches. That degree of difficulty is measured by how similar in average fitness the species must be to allow coexistence with that degree of overlap.

Stabilizing and Equalizing Mechanisms

The expanded exclusion principle defined here is broadened with the realization that there are two general but not equivalent ways in which species coexistence can be favored. First is low overlap in niches, and second is similarity in average fitness. Mechanisms that lead to low niche overlap are called stabilizing mechanisms, and those that lead to similar average fitnesses are termed equalizing mechanisms. The issue that distinguishes these two ways of achieving coexistence is the role of feedback loops. Niche overlap, ρ, is fundamentally about feedback loops. Low niche overlap means feedback loops between species are weak relative to those within species. As emphasized above, this is essential for coexistence to be stabilized. Thus, mechanisms that bring about low niche overlap are called stabilizing mechanisms. Stabilizing mechanisms vary from the obvious to the subtle. Specialization of the members of a guild on different resources is the stabilizing mechanism termed resource partitioning [30], which quite directly leads to low contributions to ρ (Fig. 13.2a, d, and e). Likewise, if the natural enemies of the guild members are specialists, feedback loops through predation are separated (Fig. 13.2a and c). This is natural enemy partitioning [17]. As we shall see below, these direct and obvious stabilizing mechanisms are far from the only ones. Likely involved in these scenarios are trade-offs that provide advantages to specialization. For instance, consumers well equipped to exploit a particular resource, or predators well equipped to attack a particular species, may not be so well equipped to exploit a different resource or attack a different species because the very equipment that works well in a specific situation does not work so well in another [11, 31].

Equalizing mechanisms do not have to involve the feedback loops at all. In the Lotka–Volterra model considered here, the fitnesses are measured at low density, and so density feedback has no direct role [17]. One can ask what mechanisms might lead species to be similar in average fitness in a given environment. It is clear that the laws of physics come in at the ultimate level and constrain performance differences between species. But there are still numerous ways in which species might differ in efficiency at a given task. Many trade-offs might be seen as equalizing mechanisms in that doing well in one respect might mean doing less well in another respect [29]. For instance, defense against predation or harsh physical environmental conditions might lead to lower growth rates of individual organisms and perhaps slower rates of reproduction. Thus, one species might have higher survival rates but suffer in reproduction relative to another species, thus limiting the fitness differences between species that are possible.

There is as yet no general theory of equalizing mechanisms, but one is likely to emerge from general principles of community assembly and natural selection. Natural selection drives species to the limits of what is possible: for instance, not being defended against harsh conditions, while not growing fast, are certainly possible in an organism, but if it is also possible through a genetic change to grow faster if expenditures on defense are low, or to be defended if growth is slow, then that character is likely to evolve. The constraint on what is possible is approached, which enforces the trade-off [4]. This process happens within species, as it involves natural selection at the individual level. The process of relevance between species is community assembly. More efficient species arriving in a particular locality are likely to displace others there, and that process will continue until constraints on efficiency are approached, trade-offs apply, and fitness differences are minimized.

It should be recognized that many constraints in nature may have both stabilizing and equalizing aspects to them. Trade-offs associated with resource partitioning may lead to stabilization as well as equalization, provided similar profit is derived from use of the various different resources involved. There is also a body of thought leading to the neutral theory of community ecology which says that highly diverse natural communities, such as tropical forests, behave as if all average fitnesses are equal, and stabilizing mechanisms are absent [32]. In terms of the theory here, this would mean that the average fitnesses, κ, are the same for all species and $\rho = 1$ for every species. Coexistence cannot be stabilized in these circumstances: invader growth rates are zero, and in the Lotka–Volterra model, the total abundance of all species is stabilized, but relative abundances are not. They are instead predicted to drift as a consequence of the chance processes of individual birth and death. However, there is no general reason to expect this extreme situation to arise in nature. The patterns that agree with those in nature can also be predicted by models with stabilizing mechanisms present [33], and fitness differences in systems without stabilizing mechanisms quickly lead to the collapse of diversity [34].

Competition-Based and Predation-Based Coexistence Mechanisms

Competition is often thought of as a major factor that limits species diversity, without a clear distinction being made between interspecific and intraspecific competition. That thought quickly leads to the idea that lower population densities will lessen the magnitude of competition and therefore promote the maintenance of species diversity [16]. In particular, that line of reasoning leads to the idea that high mortality rates, or harsh and stressful conditions, might generally promote species diversity [35]. However, as emphasized above, it is the ratio of interspecific competition to intraspecific competition that is critical to species coexistence and not the absolute value. Thus, lowering densities, and indeed lowering the intensity of competition, need not have any effect on the ratio of interspecific to intraspecific competition, and therefore need have not have any effect on species coexistence. In fact, competition can be important for stable coexistence. If competition is the only form of density dependence, then it is essential for stable coexistence. The challenge for species coexistence is not competition per se but interspecific competition that is strong relative to intraspecific competition. A pattern of species interactions that intensifies intraspecific competition relative to interspecific competition is a competition-based species coexistence mechanism [17].

Recent appreciation that density dependence from predation can play a similar role to competition leads to the idea of predation-based coexistence mechanisms. These are mechanisms that concentrate intraspecific apparent competition relative to interspecific apparent competition [17]. What then are the joint effects of competition and predation on species coexistence? Both natural enemy attack and resource competition are likely to be important in most guilds of coexisting species simply because it is difficult to avoid these phenomena. In discussions of species coexistence, predation has sometimes been viewed as important primarily as a cause of high mortality, and therefore not distinguished from harsh or stressful conditions in its effects [16]. However, as remarked above, such conditions need have no effect on species coexistence because they need not be associated with density-dependent effects, although they would alter species average fitness ratios if they were species-specific in effect.

The feedback loops expected with trophic interactions mean that predation would likely act in a density-dependent way. However, it is also possible that its density dependence might be weak relative to other sources and function on different spatial and temporal scales. For instance, predators that range over a much larger area than the focal guild might not be very responsive to the changes in the density of the focal guild. Predators might also live much longer and so change in density much more slowly than their prey in the focal guild, and they might also depend more heavily on species outside the focal guild and so not be so responsive to the focal guild even though they inflict mortality on them. Thus, it is not unreasonable to entertain the hypothesis that in some situations predation acts in an approximately density-independent way.

Density-independent predation would reduce the fitnesses κ of the species in the focal guild. From the two-species coexistence condition, it is clear that it would only affect coexistence if the ratio κ_1/κ_2 were affected, or in the multispecies case, if the ratio of any species' fitness to the guild average fitness were affected [15]. If fitnesses are unequal in the absence of predation, the same reduction for each fitness has the effect of making the fitness ratio deviate further from the value 1, which is more likely to lead to exclusion than coexistence. However, a trade-off that led to a disproportionately large reduction in fitness for the species with larger fitness ("selective predation on the competitive dominant") [16, 36] would make the fitness ratios more equal provided predation was not too strong. The requirement that the predation be not too strong leads to an intermediate predation prediction: predation promotes diversity for intermediate intensities of predation [16, 36].

Empirical studies have noted strong effects of predators in some guilds [37]. Of particular note are those consisting of sessile intertidal organisms, where the predator or herbivore is necessary for the maintenance of diversity [36, 38]. These predators are often termed keystone predators due to their essential role [38, 39]. Discussions of keystone predators often emphasize selective predation without regard for a density-dependent role of predation [37]. However, density-independent selective predation is purely equalizing and would be incapable of stabilizing coexistence in the absence of a separate stabilizing mechanism, such as resource partitioning [16].

It is reasonable to expect that a keystone predator would respond at least to some extent in a density-dependent way to its prey. A density-dependent but nonselective predator, i.e., one that does not affect the fitness ratio, would in fact have the effect of undermining competition-based coexistence, and thereby undermine coexistence overall. This would occur because such a predator adds equally to intraspecific and interspecific density dependence, diluting the effect of resource partitioning and increasing the value of ρ, weakening coexistence. A density-dependent but selective predator need not have negative effects on coexistence provided it is selective on the competitive dominant [40], but it would still be limited in its effects on coexistence without the presence of other stabilizing mechanisms, because alone it would not add the sort of structure to feedback loops able to separate many species [16, 35]. Indeed, the patterning of feedback loops would be quite limited. Lotka–Volterra theory in this case predicts that at most two species can coexist stably when species in the focal guild do not partition resources, and there is only one predator present, regardless of how the predator distributes its attacks [41].

Fundamentally, development of the keystone species concept has viewed predation and competition as very different kinds of interactions, and has not focused adequately on the true requirement that density dependence needs to be concentrated more strongly within species than between species to promote stable coexistence [16]. Simply reducing the magnitude of competition uniformly does not achieve this, and equalizing fitnesses alone does not achieve this in the absence of a separate and strong stabilizing mechanism [16]. Certainly it is conceivable that a keystone predator might focus its attacks in such a way that fitness is approximately equalized across species, which would achieve approximate neutrality, but there is no mechanism that makes this likely. Trade-offs between susceptibility to predation and competitive ability would work in the right direction [40], but there is no reason for these trade-offs to be sufficiently precise to yield approximate neutrality, which nevertheless would not stabilize diversity, just slow its loss. Though keystone predation can indeed be shown to have strong effects in some communities [16], the stabilizing mechanisms needed to make it effective have neither been identified nor sought.

The theory discussed above identifies predator partitioning as an important way in which predation can promote diversity. Indeed, predators and other natural enemies can have very strong effects on their prey populations, and it is not uncommon for predators to be relatively specialized [11]. In fact, if the predators of a guild partition their resources (the prey populations in the guild in question), it follows reciprocally that the prey are partitioning predators. Thus, predator partitioning should have about the same prevalence in nature as resource partitioning. If both predator partitioning and resource partitioning are present for any given guild (Fig. 13.2a), the reasonable expectation is that the strength of coexistence would be stronger than if only one of these were partitioned (Fig. 13.2c and d). Indeed, the evidence from models points in this direction [17]. However, this outcome applies when predators that partition their prey are substituted for predators that do not partition their prey. A situation of great importance in nature is removal, addition, or restoration of predators, as occurs with human activities, although human activities might sometimes substitute one kind of predator for another [42–44]. In this case, adding predators that partition the focal guild to a comparable extent to the partitioning of resources in the focal guild would not greatly change the strength of coexistence. The reason is that there would be little change in the ratio of interspecific to intraspecific density dependence. However, adding predators that do not partition would increase the ratio of interspecific to intraspecific density dependence, undermining resource partitioning and therefore undermining coexistence, as noted above.

These effects of adding or removing predators, or changing their properties, can be summarized in terms of changing values of ρ as the scenario changes. Note that ρ is the niche overlap measure, but is also a symmetric measure of the ratio of interspecific to intraspecific density dependence by Eq. 13.5. Defining the case under consideration in parentheses gives the following chain of inequalities:

$$\begin{aligned}\rho(R_{\mathrm{p}},P_{\mathrm{p}}) &\approx \rho(R_{\mathrm{p}}) \approx \rho(P_{\mathrm{p}})\\ &< \rho(R_{\mathrm{p}},P_{\mathrm{np}}) \approx \rho(R_{\mathrm{np}},P_{\mathrm{p}}) < \rho(R_{\mathrm{np}},P_{\mathrm{np}})\\ &= \rho(R_{\mathrm{np}}) = \rho(P_{\mathrm{np}}) = 1.\end{aligned} \tag{13.7}$$

Here R or P indicates the presence of resource competition or apparent competition, and the subscripts "p" and "np" indicate partitioned and not partitioned interactions. As smaller values of ρ mean stronger coexistence, the situations are ranked from strongest coexistence to no coexistence, from left to right. The approximate equality of $\rho(R_{\mathrm{p}})$ and $\rho(P_{\mathrm{p}})$ in (Eq. 13.7) is not a conclusion, but the assumption that resources and predators are partitioned about equally, specifying the scenario considered here. The rest of the inequalities and approximations are conclusions. When P or R is not listed in parentheses, predators or resources may still be present, but are not important sources of density dependence. For instance, strongly density-dependent predation can prevent resource competition from occurring even though resources are still consumed and contribute essentially to fitness.

When competition and apparent competition are both present, the value of ρ is intermediate between the values that occur when only one of these is present. Thus, when they are both partitioned in inequalities (Eq. 13.7), the value of ρ does not change much, regardless of whether competition and predation are both present, or only one is present (e.g., Fig 13.2a vs. 13.2e). When they are both present, but only one is partitioned, the value of ρ is necessarily higher than when they are both partitioned because then a smaller fraction of all density-dependent interactions are partitioned, reducing the distinction between interspecific and intraspecific density dependence (Fig. 13.2c and d vs. 13.2a). The reason is that there is less partitioning overall among the array of density-dependent interactions experienced. No partitioning leads to a value of ρ equal to 1 (Fig. 13.2b), regardless of which interactions are present, and therefore no possibility for stable coexistence.

The situation not considered in the inequalities (Eq. 13.7) is when there is partitioning between predation and competition (Fig. 13.3). In this case, although there is no partitioning of resources or predators, there is joint partitioning of them in that some species have strong predator feedback loops, being particularly susceptible to predation, and some species have strong resource feedback loops and therefore are particularly susceptible to resource competition [40]. This is a predation-competition trade-off. But without partitioning within these interactions, at most two species can coexist. The predator is selective in this case, and it is simply the keystone species case once again. It implies

$$\rho(R_{\mathrm{np}},P_{\mathrm{np}}) < \rho(R_{\mathrm{np}}) = \rho(P_{\mathrm{np}}) = 1 \tag{13.8}$$

as illustrated in Fig. 13.3. Although theoretically interesting in that it leads to coexistence in the absence of resource partitioning, it is not a serious solution

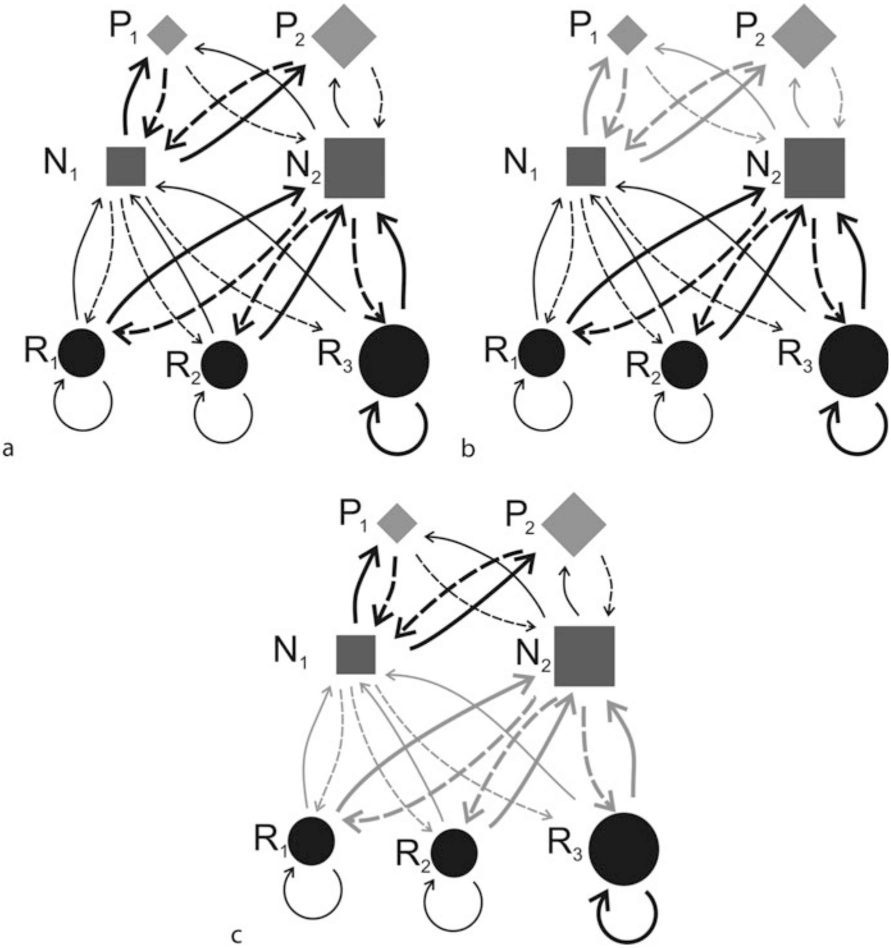

Fig. 13.3 General features as for Fig. 13.2. (**a**) Trade-off between competition and predation (apparent competition). Species 1 is more sensitive to predation, and species 2 is more sensitive to resources. Both resource consumption and predation are density dependent. Niche overlap is low. (**b**) As for (a), but only resource consumption is strongly density dependent. Niche overlap is high. (**c**) As for (a), but only predation is strongly density dependent. Niche overlap is high

to the maintenance of high diversity by means of predation because, by itself, it allows stable coexistence of at most two species as discussed in detail above.

Complexities of Foraging Behavior and Resource Acquisition

Predation and resource competition intimately involve the behavior of the organisms in seeking food and resources, or avoiding predation [45]. Interference competition is one behavior that is accounted for reasonably well in the

Lotka–Volterra competition equations, as discussed above, as direct contributions to the coefficients of density-dependence α. However, other aspects of the behavior of organisms are not accounted for well because all resource acquisition rates and foraging rates are assumed to be linear, i.e., the amount of any resource or prey consumed or captured by an individual organism per unit time is simply proportional to the abundance of that resource or prey [17]. One very simple and almost unavoidable deviation from the linearity of Lotka–Volterra equations occurs through the simple fact that an individual organism is generally limited in how much resource can be consumed per unit time, or how many prey can be captured and consumed. As a resource or prey becomes very abundant, the rate of consumption normally plateaus. Such plateaus weaken density-dependent feedback as densities increase, creating instabilities in population dynamics and promoting population fluctuations [1].

There is a vast literature on how these fluctuations might be stabilized and the extent to which they are indeed responsible for population fluctuations in nature [1]. Some scenarios involving population fluctuations provide further mechanisms of coexistence, because they enable population fluctuations to be partitioned by the various species, as discussed below (*environmental and population fluctuations*). However, when such nonlinearities are not strong enough to destabilize dynamics, and even in many cases when they do, the general principles for the Lotka–Volterra case continue to apply to the extent that they have been studied theoretically. For instance, a very general development of Levin [41], though lacking specific detail, is entirely consistent with the messages from the Lotka–Volterra development on partitioning resources and predators.

Resource-competition models where the resources do not regenerate in a Lotka–Volterra manner have also been studied [46], reproducing much of the detail, even quantitatively, for the Lotka–Volterra case. For plants, the key resources are light energy and simple inorganic compounds. Obtaining them in the right proportions is key to optimum plant growth, which makes the equations not just nonlinear, but nonadditive in the different resources. Despite these differences, the qualitative picture given here reappears in a different quantitative form [29, 31]. Nonlinear predation for equilibrium scenarios has been studied in limited situations [40, 47–49]. Quantitative variations on the results from the Lotka–Volterra case are found, but again in general the qualitative messages here remain intact. The reason is the fundamental nature of the requirement for coexistence that a species should inhibit its own growth more than it inhibits the growth of other species if it is to coexist with them. Thus, the requirement that intraspecific density dependence be stronger than interspecific density dependence is a robust requirement [15]. More complex nonlinear situations differ only in providing alternative ways of achieving this outcome. Partitioning of the environment, in one form or another, remains common among these alternative models. The major exception is for complex behaviors that lead to frequency dependence, as discussed next.

Some of the strongest effects occur when the per capita rates of foraging depend on the relative abundances of the species. The linear rates assumed in the Lotka–Volterra development mean that the fraction that any particular prey species represents in the diet of a predator is proportional to the abundance of that prey species. This makes intuitive sense as a prey species might be expected to be encountered at a rate proportional to its abundance. However, if a predator's efficiency at finding a prey species, or capturing it, increases with the rate at which it is encountered, then the actual rate of capture is super-proportional to the abundance of the prey species. The effect of this on the prey mortality rates is to make them increasing functions of intraspecific prey density, and possibly decreasing functions of the densities of other species. This phenomenon is known as frequency-dependent predation [50]. An important outcome is the intensification of intraspecific apparent competition relative to interspecific apparent competition. In models, frequency-dependent predation has been shown to be a powerful species coexistence mechanism. At a qualitative level, the outcome is similar to predator partitioning (or natural enemy partitioning) where each prey species has its own specialist natural enemy [50, 51]. Thus, frequency-dependent predation achieves with one natural enemy the same effect as several specialist natural enemies that do not have frequency-dependent behavior.

Frequency-dependent predation, which is also called "switching" in the ecological literature [52, 53] and "apostatic selection" in the evolutionary literature [54], has considerable empirical support to the extent that it has been studied [50]. Most studies reporting this phenomenon have been laboratory studies, with few prey species, and much less is known empirically from field studies. Moreover, the theoretical studies have only demonstrated multispecies coexistence from symmetrically acting forms of frequency-dependent predation: those that might be expected from increasing prey encounter and capture efficiency with increasing prey abundance [51]. The theory of optimal diet selection, however, leads to an asymmetrical form of frequency-dependent predation where the per capita predation rate on prey of low value to a predator depends on the absolute abundance of higher ranked prey, and not directly on the abundance of that prey itself [55]. Although coexistence can be promoted also by this form of behavior [56, 57], it is much less well investigated than symmetrically acting frequency dependence, and its performance in multispecies situations is not understood.

Environmental Variation and Population Fluctuations

Environmental fluctuations are often intuitively expected to undermine equilibrium perspectives such as those developed on the basis of Lotka–Volterra models [58]. In fact, however, rather than undermine them, they provide new contexts in which the critical phenomena considered here are realized. Fundamentally, they allow resource partitioning and predator partitioning to occur on large scales of time even though they do not occur on small scales [51, 59]. This is possible because different species in the same guild may have different responses to the physical environment, such as weather. Annual plant species, for instance, often have species-specific weather-dependent germination requirements. As weather patterns vary from year to year, and sometimes very markedly, this means that guilds of annual plants often show very marked variation from year to year in the relative abundances of the plants that successfully germinate, grow, and flower [59, 60]. Those that are not successful in given year can bide their time as dormant seeds in the soil, with good chances of success in some future year. In this way, intraspecific competition becomes concentrated relative to interspecific competition when a sequence of years of different environments are considered, as this behavior means that a given individual is likely to experience more intraspecific competition than interspecific competition from any given other species. The outcome is partitioning of resources over time [59]. Indeed, it is possible to derive Lotka–Volterra equations or very similar ones that represent the outcome of integration of short-term fluctuations over time, even based on random fluctuations on that short timescale [15, 23].

The details of these effects of temporal partitioning are important. It is critical for instance, that competition between individuals growing at different times does not occur [61]. For this to be the case, the resources cannot carry over in time. For instance, day and night foragers for a particular resource might still be competing strongly even though they capture the resource at different times. This would be the case if units of resource available at night are used by organisms in the day time if they are missed by night time foragers. The result is that temporal differences in foraging do not, in this case, concentrate intraspecific competition relative to interspecific competition.

What is possible in this context for competition is also possible with apparent competition, extending the essential symmetries for consideration of these processes before. However, differences do occur because of the potential that apparent competition works on a longer timescale [61]. For example, in annual plants with seed predators, when a good seed crop causes buildup of seed predators through high predator reproduction and survival, it is the seed crop the next year that experiences the higher predator density. The seed crop the next year will likely have different species composition due to species differences in response to the temporally varying physical environment. Thus, the species that cause the predator buildup are not necessarily the species experiencing higher predation. Intraspecific apparent competition is not necessarily concentrated relative to intraspecific competition in his case. When the environment varies randomly from 1 year to the next, predator buildup on good seed crops does not lead to effective temporal partitioning. However, behavioral changes in predation rates can be on short timescales with the potential that effective temporal partitioning can occur. Indeed, the theory implies that frequency-dependent behavior and other density-dependent behaviors can in some circumstances lead to temporal partitioning due to predation [50, 51]. In these cases, frequency-dependent behavior has two effects: an immediate and direct effect of frequency dependence on the ratio of intraspecific to interspecific density dependence, and a longer-term effect that involves an interaction between year to year temporal variation in the physical environment and temporal variation in foraging behavior as the prey species fluctuate in density in response to the environment.

These instances of temporal partitioning due to the responses of species to environmental variation are generally referred to as the storage effect, but another general mechanism termed relative nonlinearity of competition [15] works based on temporal fluctuations in the magnitude of competition and different nonlinear responses to competition by different species. Fundamentally, different species are more sensitive to competition over different ranges of competition. Under certain conditions, they can also generate the kinds of fluctuations that are disadvantageous to them when they are abundant. This mechanism continues the theme that coexistence stems from mechanisms that generate stronger intraspecific density dependence than interspecific density dependence when integrated over time. This mechanism works just as well for apparent competition [62], but it seems to be a relatively weak mechanism to the extent that at best two species can coexist this way in the absence of other mechanisms [15]. However, in the two-species case, models have suggested that it can have comparable strength to resource partitioning [63]. Moreover, there is some suggestion that when interacting with other mechanisms, it can be very powerful in multispecies settings, but there is as yet insufficient information on this possibility [64, 65].

Spatial Structure

Spatially varying environments have long been known to allow spatial partitioning of competition in a very similar way to temporal partitioning [66]. Thus, there are various spatial analogues to temporal partitioning by the storage effect for both competition [67–69] and apparent competition [22, 70]. Indeed, there is every indication that spatial variation powerfully fosters species coexistence due to the different responses that species have to environmental factors that vary in space. From time to time, the idea that species tend to be spatially aggregated intraspecifically is raised as a potential mechanism of species coexistence [71]. Such local aggregation naturally arises due to localized dispersal [72], can also be influenced by habitat selection. Although coexistence by aggregation has sometimes been claimed to be an entirely new mechanism [73], there are good reasons to believe that it functions primarily as a form of spatial resource partitioning [74], or as a form of competition–colonization trade-off [75], as discussed next.

Some spatial mechanisms do not have clear analogues with temporal mechanisms. Of particular note is the mechanism known as competition–colonization trade-offs [76]. In this case, species are assumed to be ranked very strictly in competitive ability such that any given locality will become dominated by just one species, the strongest competitor that has found that locality. In some cases, a locality is assumed to be a site only large enough to be occupied by a single plant individual. In other cases, it might be a local population of a plant or animal species [77]. Death of the individual, or extinction of the local population, vacates that space. The assumption is that there is a trade-off between competitive ability and colonizing ability, and this means that vacant space is likely to be taken by an inferior competitor. Ecological succession takes place as inferior competitors are replaced by later arriving superior competitors. Because local sites are vacated at different times, and recolonization and succession have stochastic timing, landscapes governed by these process will consist of a mosaic of sites in different successional stages. For this reason, this hypothesis is also known as the successional mosaic hypothesis [35]. It is one version of the intermediate disturbance hypothesis [78–80], and perhaps the version closest to the original intention of the idea [79].

In these discussions, disturbance is a natural process such as fire or extreme weather that destroys local populations patchily in space. In one version, predators are the agents that destroy local populations [37, 81], and thus maintain a patchy landscape in a mosaic of successional states. The competition–colonization trade-off hypothesis, however, can work without an agent of disturbance, but relying on chance mortality of individuals, dispersal and colonization [82]. This successional mosiac process can be modeled well by Lotka–Volterra competition equations with density measured at the landscape scale as the fraction of sites occupied by a species [76, 77, 83]. Its form is the same as an asymmetric interference competition model, but nevertheless governed by the coexistence conditions (Eq. 13.3) above, which mean that all species inhibit themselves more than they do other species. For superior competitors, this outcome occurs because inferior competitors are better at finding free species and so escape interspecific competition from superior competitors. This idea is also related to nonspatial models of exploitation of leftover resources, for example light not intercepted by a plant canopy, and so available to understorey species [84, 85]. Fundamentally, in the competition–colonization trade-off hypothesis and leftover resource models, superior competitors do not efficiently exploit all resources, leaving some to be exploited by those species that have lesser competitive ability but through a trade-off have achieved the ability to exploit the leftovers.

A final spatial mechanism involves natural enemies. Known as the Janzen-Connell hypothesis [86–88], it was originally proposed for tropical trees, but is closely related to the soil-feedback hypothesis for coexistence of species in grasslands [89]. The idea as applied to trees was that natural enemies specialized on a particular species would build up in abundance on or near a given tree. These natural enemies would then provide strong inhibition to the establishment of individuals of the same species there. Other species, however, would be able to establish. It is clear, however, that this is a form of natural enemy partitioning that does not require a spatial element, although it might well be enhanced by the spatial element. In the soil-feedback hypothesis, soil microorganism communities develop in the root zone of a particular individual plant. A preponderance of relatively species-specific harmful microorganisms leads to a net negative effect of establishment of the same species at that site, favoring others species to replace that individual or to thrive nearby [89, 90].

Applications

These ideas have applications in a number of other areas beyond the basic concept of how communities are structured, including invasion biology [91, 92], conservation biology [93, 94], and ecosystem functioning [95]. The focus here is on invasion biology. The biosphere is undergoing vast changes as a result of human activities. One activity is the introduction of new species to places where they were not previously found either deliberately or as an accidental by-product of commerce. Many transplanted species fail to perform well in a new environment, or if they do perform well enough to establish self-sustaining populations (to "naturalize"), they never become very abundant. However, a few species perform spectacularly well and become major pests or weeds, often displacing native species [96]. Although invasive species are not often responsible for regional extinction of native species, they can displace them locally and dramatically change the character of local communities. The local communities thus undergo a process of reassembly in response to the arrival of these invasive species. The ability of alien species to have these effects is often analyzed in terms of competition and predation, although other mechanisms, such as facilitation of one species by another can be expected to be important too [97]. The study of coexistence and exclusion mechanisms, as discussed here, fundamentally involves the question of whether a species can increase from very low density in the presence of other members of the guild, or to "invade." This invasibility analysis also applies to the question of how an alien invader successfully enters a local guild, and whether it displaces existing guild members.

The ability of an alien species to invade can be discussed in terms of the concept of niche opportunities [91]. Fundamentally, a niche opportunity means sufficient resources are available for the species in question to invade, given the risk from natural enemies that it will encounter. To some extent, lower risk from natural enemies can enable a species to invade at lower resource levels, as it would be able to do so at lower reproduction or survival based on those resources. A surfeit of resources is called a resource opportunity, while a low risk from natural enemies is an escape opportunity. The overriding question in invasion biology is why native species, in the eons of time, have not used up all opportunities to exploit a particular environment. There are a number of potential answers to this question.

First the local environment may have changed as a result of human activities or climate change, and the local community is therefore no longer well adapted to it, allowing the potential for a species from elsewhere to be better adapted than local species [91, 98]. This idea of change, however, should not be confused with a natural regime of disturbance or environmental variation that might be temporally partitioned by the native species. Like other persistent features of the environment, such environmental variation ought already be exploited by the native species, and so should not provide new opportunities. Unless, the natural regime of environmental variation has changed, there is no change that should be expected to facilitate invasion [98]. Pollution is an example of one common change that humans cause.

When this results in deposition of nitrogen in a nutrient-poor environment, it can have a large effect on local plant communities, facilitating the invasion of species adapted to exploit this resource [99]. The invasive species then potentially depress other resources that the native species depend on, harming them.

Second, the native community might have not existed for very long, or in the past was poorly connected to areas that might provide colonists or genetic diversity allowing adaptation to exploit all opportunities well. In a sense, such a local community is immature [91]. In these cases, niche opportunities exist, and species from elsewhere might have the adaptations allowing them to exploit the local environment more successfully than the native species. Islands that have been devastated by invasions might be in this category [96, 100], but so also might aquatic systems which suffer from the problem that dispersal from one place to another was historically much rarer than it is today. This idea has been applied on continental scale, suggesting that the Eurasian continent being larger contains species with stronger competitive ability than species in North America [101]. There is some evidence for this in plant species from Eurasian that use chemical interference successfully in competition with North American species [102]. The idea of biotic resistance says that localities with high species diversity ought to be more difficult to invade [103, 104], which makes sense to the extent that it means that more niche opportunities are foreclosed by the adaptations present in the more diverse community.

Third, invaders potentially arrive in the absence of their specialist natural enemies. Even if diseases, parasites, or predators are introduced with an invader at the same time, unless these natural enemies can exploit other species, they may well be lost early in the introduction because the invader in question was initially at too small a population size to sustain them. Such a species would have a strong natural enemy escape opportunity that would give it an advantage in a novel environment, especially if native species were attacked by natural enemies that do not affect the invader [97, 105]. Of course, native natural enemies do attack and inhibit invaders to varying extents, reducing their success [91, 97].

These various ideas can be analyzed within the Lotka–Volterra framework presented here [92, 106]. Fundamentally, if an invader has overall advantage such as novel competitive weapons for interfering with other species, is less susceptible to enemy attack, or is better overall in its adaptation to the environment, it will have an average fitness advantage over native species (κ ratios greater than 1), allowing it to invade, with the potential, if this advantage is large enough, to exclude native species, at least locally. Instead, it might not have an overall advantage, but simply an advantage under specific conditions, leading to low niche overlaps, ρ, with native species. This advantage might be that it can specialize better on a particular resource or particular environmental conditions, arising spatially or temporally, that native species are not fully exploiting. In many situations, it seems that elements of both are likely. It might for instance weakly partition resources or predators, but also have some fitness benefits, without average superiority over natives, but together this might be sufficient for invasion. On the other hand, the fact that even strongly successful invaders do not eliminate species in the same guild on a regional scale suggests that spatial partitioning, perhaps coupled with temporal partitioning, is sufficiently strong for natives to persist in a region even if they are eliminated or driven to low abundances locally [92, 107].

Invaders naturally interact with species outside their own guild also. As predators and diseases they have been more frequently the cause of extinctions of native species [44, 96]. However, they can also be the agents that enhance predators or diseases, damaging native species through apparent competition [43, 108]. Ways of controlling such invasives is therefore of substantial interest in conservation biology [43, 108].

Future Directions

The picture of community organization driven by competition and predation presented here has been developing for decades but it is relatively recently gelling on a new synthesis. It is now able to integrate competition, predation, temporal variation, and spatial structure in one common framework to gain understanding of not just individual mechanisms but their interactions as well [17, 51], as exemplified by the simple comparison presented above of how the strength of stabilization of coexistence changes with the circumstances. This picture now leads to comprehensive theoretical understanding that greatly clarifies a confusing picture of numerous potential mechanisms of a few years ago [109]. The most glaring lack now is in rigorous empirical study of mechanisms by which communities are structured, especially stable coexistence mechanisms [14].

Many empirical studies focus on features of mechanisms without truly testing whether they have a role in stabilizing diversity [13, 14]. Patterns of morphology of animals [11] and plants [110] that are related to how they gather resources or avoid predation can provide strong circumstantial evidence, but still leave open numerous possibilities as to the actual mechanisms [110]. One problem has been that the sort of data necessary to test mechanisms has not been clear because the mechanisms have not been truly understood, but that issue is now much less significant. One recent development is a theory of testing mechanisms [13] aimed to guide empirical studies. The key problem is to determine ways of testing whether density feedback loops do indeed concentrate intraspecific density dependence relative to interspecific density dependence in the manner proposed by a specific mechanism. In general, this is not an easy proposition, but it is also not infeasible for well-resourced project, given the right approach. Developing these approaches is the aim of the theory of testing mechanisms [13]. For example, to test for stabilization by temporal or spatial resource partitioning, the concept of covariance between environment and competition has been developed, which specifically measures how competition is linked to environmental factors [111]. Testing whether coexistence is stabilized by partitioning environmental conditions involves showing that covariance between environment and competition weakens as a species is reduced to low density in presence of unmanipulated competitors. More developments along these lines are needed to test other specific mechanisms.

New theoretical understanding has also revealed relatively basic deficiencies in empirical studies. For instance, frequency-dependent predation shows much promise as a strong coexistence mechanism, yet there are few rigorous field studies of this phenomenon [50]. It seems that the dominance of predation–competition tradeoffs, including keystone predation ideas, has led to the neglect of frequency-dependent predation as a coexistence mechanism in empirical studies. However, it is also true that studies of keystone predation assumed that the mechanism was powerful when acting alone, and this impression seems likely to have inhibited the search for the stabilizing mechanisms that must be present also for keystone predation to be effective in promoting multispecies coexistence.

Naturally, the theory, though rich and not rigorously tested, still has some glaring deficiencies. One issue that complicates the Lotka–Volterra theory presented above is that as parameters are changed gradually, species in the resource and predator guilds that interact with the focal guild may not be supportable [27]. This possibility leads to abrupt changes in the coefficients of density dependence and related parameters [26]. It is also true that depressing a given member of the focal guild to low density may mean that only a subset of the resource species or predator species is present [17]. These facts, however, do not alter the invasion criteria presented here provided they are based on the resources and predators actually present in a given invasion scenario. They do, however, complicate interpretation of the criteria as parameters are changed. It is not known how important these issues are, and a comprehensive theory of their effects is needed.

The integrated understanding of the roles of predation and competition in species coexistence and exclusion presented here also raises the critical question of what factors control density dependence through these two processes. Of potentially major significance are other species in food webs beyond those directly linked to the focal guild. For instance, if the major natural enemies of the focal guild are themselves subject to strong density dependence from their natural enemies, they will be limited in their ability to change in abundance in response changes in the density of the focal guild. This means that density-dependent feedback to the focal guild through their natural enemies would be limited to behavioral responses of the natural enemies to focal guild densities. The idea of trophic cascades has long postulated how various density-dependent effects permeate from one part of a food web to another [112–114]. Integration of trophic cascade research with species coexistence research has the potential to make important advances with major implications for understanding the broader impacts that humans are having on the planet through widespread disruption of food webs, especially the destruction of many large carnivorous species [115–117].

Most of the discussion here has been purely ecological focused on interactions between a few species. However, natural populations and communities are shaped by evolution and community assembly processes, of which the considerations discussed above form just a small part. It is now known that evolutionary change can be fast to the extent that ecological dynamics and evolutionary dynamics cannot be completely separated [118]. The field of adaptive dynamics tries to integrate ecological and evolutionary process, but nevertheless still tends to treat these two processes as functioning on different timescales [119]. At the same time, much study of species coexistence focuses on the conditions that allow species coexistence, without considering the processes by which species assemble in communities. A proper treatment of community assembly would include challenging a local community with invaders from the pool species present regionally. There have been only limited theoretical studies of this sort [83, 120, 121]. Without an adequate treatment of these processes of adaptation and assembly, there is no true prediction of the structure of natural communities, and a seriously incomplete understanding of the role of competition and predation in community structure.

Finally, future theoretical research will likely take on the challenge of long-term climate change. The planet faces relative rapid climate change at the hand of human activities, but long-term climate change has always been a feature of the environment. However, theoretical models normally assume that climate fluctuations have stable long-term frequencies. There is a critical need to strip away this assumption, and develop theory that allows predictions even though the climate is not statistically stable. A useful theory would couple long-term climate change with the ability of populations to move on a spatially structured landscape as climate shifts change the viability of parts of their habitat. With such migration, there is the potential that climate fluctuations realized by species will have stable long-term frequencies as species track the shifting climate, but there are bound to be numerous new issues arising due to the fact that different species are likely to track the environment at different rates and in different ways [122].

A few years ago, imagining developments in the directions discussed here would have been daunting given the challenges that simpler theory gave. However, recent progress augers major extensions beyond the current limited contexts.

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