

EVOLUTIONARY ECOLOGY

Evolutionary ecologists attempt to integrate the principles of population genetics and ecology by viewing ecological factors as selective agents that modify species characters over long time periods. We will now examine the influence of evolution on the different topics we have already discussed from a functional standpoint, namely, population ecology and interspecies interactions.

Evolution and Population Ecology

Suppose that the time axis for the logistic model of population growth (population ecology notes) was very long and encompassed hundreds of generations. This long time span would allow evolution to take place during the growth history of a single population.

You will recall that natural selection acts on individual variation to produce evolution. Those genetic variants that produce the most surviving offspring will leave more of their genes in the next gene pool than individuals not selected by the environment. We usually think of selection as acting on morphological traits to cause evolution, but any aspect of the phenotype that confers a reproductive advantage will be the object of natural selection. **During population growth history what aspects of the phenotype will be selected and what will be the selecting agent?**

During the early stages of population growth when density is low, the environment would be effectively **unlimited**. **Mortality** would come from **density-independent sources (e.g., weather) that are catastrophic and unpredictable**. Reproductive competition in such an environment would favor those individuals who channel all their energy into producing offspring. Since there is no way of predicting when a catastrophic change in the environment will occur, individuals who produced the greatest number of offspring would win out. This is the same rationale as buying lottery tickets: since the winner is determined by chance, the one who buys the most tickets has the highest probability of winning.

In an unlimited environment ruled by chance mortality, **life history characteristics** (which are phenotypic traits) such as **early age at first reproduction**, large number of eggs produced (**litter size**), little or **no parental care** and **short life span** would funnel all available energy into reproduction and so be favored by natural selection. Since these individual characteristics promote increased reproductive output, a high r would evolve and the population would grow exponentially. As the size of the population increased, however, **selection pressure would shift to favor individuals that could compete more effectively** for resources that were now becoming increasingly scarce. Mortality (due to competitive pressure) now becomes more predictable and parents can increase their reproductive yield by **producing fewer offspring but caring for them to insure their survival**. Life history characteristics, just the opposite of those cited above, would now be selected (**delayed reproduction**,

small litter size, high level of parental care and long life span) because individuals possessing these characteristics would now leave more **surviving offspring** as competition for the limited resources intensified. Thus, the change in density over many generations would result in a change in selective pressures, which in turn would produce a different set of characteristics in the population.

***r*- vs. *K*- selection**

The first set of characteristics adapted to low density situations is called the ***r*-strategy** and the evolution of this set is attributed to ***r*-selection**. **The selective pressure behind *r*-selection is catastrophic mortality.** The second set of characteristics constitutes the ***K*-strategy** whose evolution is driven by ***K*-selection**. The term *K*-selection specifies **intraspecific competition as the selective pressure behind the evolution of the *K*-strategy.**

Evolutionary ecologists suggest that **factors that control population size can act as selective pressures** and so account for interspecific variation in life history characteristics. Species adapted to life in fluctuating environments typically possess the life history features of the *r*-strategy (e.g., **opportunistic, colonizing, and fugitive species**) and so are called ***r*-selected species**; those adapted to stable environments have the *K*-strategy characteristics (e.g., **equilibrium species**) and so are called ***K*-selected species**. The *r*-*K* dichotomy is often applied to species comparisons (*r*-selected vs. *K*-selected species) but it must be noted that this is an inappropriate use of the terms *r*- and *K*-strategy. **The shift from *r*-selection to *K*-selection occurs within a single population** and so one would expect a continuum from *r*- to *K*-strategies to exist among species that currently exist at a single time period in the overall growth history. **Designating a species as *r*- or *K*-selected is very relative.** For example, a mouse may be *r*-selected relative to an elephant, but *K*-selected relative to a frog. Due to this relativity, classifying species in such a manner has little overall usefulness. The concepts do have importance heuristic value, however.

INTERSPECIFIC INTERACTIONS

Although we said little about it when we considered community ecology, recall that we stated that one way community ecologists work is to look at specific interactions between species in a community. The study of these sorts of interactions is one place where evolutionary and community ecology overlap significantly.

Given the sheer magnitude of species number, it is not possible to analyze all the complex interactions that involve all the species in a particular community. Community and evolutionary ecologists have therefore concentrated upon the different types of interactions between two species rather than attempt to disentangle the actual interactions among all of the species in a single community. These types of interactions are summarized below in terms of the

positive (+) and the negative (-) effects on the two species involved. The absence of an effect is designated by a value of zero.

Type of Interaction	Effect on Species #1	Effect on Species #2
Neutralism	0	0
Commensalism	+	0
Amensalism	-	0
(proto)-Cooperation (nonobligatory)	+	+
Mutualism (Obligatory)	+	+
Predation	+	-
	(predator)	(prey)
Parasitism	+	-
	(parasite)	(host)
Competition	-	-

The designation positive (+) and negative (-) is based on the effect one species has on the growth rate of the other species. Only two types of interaction have been extensively studied from the point of view of population dynamics and these will be discussed below.

Interspecific Competition and the Niche Concept

The inhibitory effect of two competing species on the population growth of each other has been modeled by extending the logistic equation (eq. 11) so that each individual of one species is included in the density of the other species. The model requires two growth equations: one for species 1 and one for species 2. Thus, for the growth of species #1:

$$\text{eq. 1: } \frac{dN_1}{dt} = \frac{r_1 N_1 (K_1 - N_1 - \alpha N_2)}{K_1}$$

where r_1 refers to the intrinsic rate of growth of species #1, N_1 is the population size of species #1, K_1 is the carrying capacity for species #1 and N_2 is the population size of species 2 and α is the interaction effect of species #2 on species #1. For a given competitor, **α has a value between 0 and 1**. The stronger the competitor, the closer the value comes to 1 and the greater the effect of the population size of species #2 on number 1. If $\alpha = 0$, species #2 does not interact on #1. Likewise, we could write a similar equation for the growth of species 2:

$$\text{eq. 2: } \frac{dN_2}{dt} = \frac{r_2 N_2 (K_2 - N_2 - \beta N_1)}{K_2}$$

where the only real difference is that β is a number between 0 and 1 that describes the effect of species #1 on number two. Notice that α will usually not equal β -- one species typically affects the other more strongly than the other.

The terms α and β are called the **coefficients of competition**. These coefficients translate the effect of an individual of one species in terms of the other species. Thus, a competition coefficient of 0.5 means that one individual of one species has one-half the effect on the population growth of the other species as has one individual of that other species. Consequently, if α equals 0.5, then two individuals of species 2 have the same effect as one individual of species 1 in depressing the growth rate of species 1.

The assumptions underlying this competition model are the same as those underlying the logistic model with one addition: the coefficients of competition are constants and don't vary with density. The **predicted outcome** of the model of interspecific competition is **the elimination of one species by the other**. Note that both species inhibit the growth of the other species, but when one species finally wins by increasing at the expense of the other, the winning species is limited by its own K value after the losing species becomes extinct.

This result has been called the **competitive exclusion principle** and exclusion has been documented in both laboratory and field experiments. The competitive exclusion principle (also known as **Gause's axiom** after the Russian ecologist who tested the model in the lab) can be stated as follows: ***No two species can indefinitely occupy the same ecological niche for the inevitable result is that one species will eliminate the other.*** Occupying the same ecological niche means that both species **use the same limited environmental resources in the same way**.

The term "niche" has been the object of much confusion. It is a **functional attribute** of a species and **not a spatial unit**. Hence, **niche**, a term that defines a species' role in the community, is not the same as the species' **habitat** that **defines its location in a community**. It has often been stated that the habitat of a species is its address while its niche is its profession. This distinction is useful in stressing the functional nature of niche.

In 1957 G. Evelyn **Hutchinson** attempted to clarify the meaning of niche by stressing that it described the **response of a species** in terms of survival and reproduction to the entire range of environmental forces which impact on the species. To define a species' niche one would have to plot the **range of tolerance**, i.e., survival ability, of the species for each environmental factor to which the species was exposed.

The range of tolerance is a unit of **physiological space** because it specifies the range of a parameter within which individuals can survive based on their physiological properties. Suppose we were to plot on one axis of a graph the tolerance range of a species to humidity and on the other its tolerance range

to temperature. The area where these two ranges overlap would be an area of physiological space.

The area where these two tolerance ranges intersect constitutes that species' response to a combination of temperature and humidity. If one were to plot a third variable, then the area of physiological space would become a volume of physiological space. The addition of a fourth variable would produce a hypervolume of physiological space. Hutchinson called his concept the species' **fundamental niche** that he defined as an **n-dimensional hypervolume** of physiological space. We could then add other dimensions associated with various biotic interactions and we end up with the fundamental niche being defined as an n-dimensioned hypervolume. The actual response of a species to the real environmental variables that it encounters in nature is called its **realized niche**.

Hutchinson's model has conceptual value but no practical force for measuring a niche. The reason is that the factors are too numerous to graph and not all can be conveniently ordered in a linear fashion (which is essential for constructing such a graph). In practice, a niche is measured by selecting one or two variables and comparing two or more different species with respect to these variables. Usually, this is enough to demonstrate **resource partitioning** among the species that prevents them from entering competition. Resource partitioning allows coexistence of closely related species that are potential competitors by dividing the resources between them. For seed eating birds this could result in one species eating smaller seeds than the other, and so the two species would occupy different ecological niches.

Evolution and Interspecific Competition

Evolutionary ecologists view **interspecific competition as a selective pressure that can promote something called niche diversification between two competing species** and so allows them to coexist. To coexist two species must be sufficiently different in their ecological characteristics to eliminate the possibility of competition. This differentiation can evolve due to competition itself provided that **some individuals in both species are already sufficiently different to avoid competition**. Selection will favor the non-competitive individuals in both species over those who are in competition and so over time both species will diverge in niche range so that they don't overlap. The result of this process is called **niche diversification**.

Since the parameters of a niche are difficult to measure, ecologists use morphological characteristics indicative of resource use to support the reality of the concept of niche diversification. Beak size and shape in birds correlates well with the type of food eaten and can be used as an indirect measure of niche difference. Congeneric bird species that live together **do not overlap** in beak morphology. Yet, when these same species are allopatric, their beak characteristics **exhibit broad overlap**. This pattern of overlap when allopatric and no overlap when sympatric has been interpreted as the result of natural

selection eliminating individuals in both species which had the same beak characteristics in the area of sympatry. This observed pattern of **character displacement** (see the *Speciation* note package) is then taken as evidence of selection producing niche diversification due to the relationship between beak morphology and food preference.

Evolution and Predation

Predators control prey populations by increasing the prey species' mortality rate, thus keeping the prey species below its K level. On the other hand, the prey population can control the number of predators since prey constitute the food of the predator, which sets the predator's K level.

A mathematical model, analogous to the ones presented above for intraspecific and interspecific competition, which explains predator-prey interactions as a density-dependent interaction has not been experimentally verified. Because this model has proven inadequate, we need not discuss its details other than mention its prediction: an oscillatory pattern of first prey and then predator abundance. The model, however, is too oversimplified and so coexistence between predators and prey in laboratory populations can only be maintained if (1) **spatial heterogeneity** (=complexity) is introduced to provide a refuge for the prey, or (2) an **alternate prey species** is made available to predators when their primary prey species is in low abundance. Without these modifications the result of laboratory experiments is always the same: the predator eliminates the prey species and then dies from starvation.

Despite the complexity of the predatory-prey relationship that makes modeling very difficult, there is sufficient field and laboratory evidence to support the claim that predators influence the size of the prey population. When predators are removed, as has been the case in western North America with the extinction of wolves, coyotes and cougars, prey populations (deer) increase dramatically up to and beyond their K limit with the result that massive starvation ensues. The only way deer populations can be managed so that they are not always on the verge of extinction due to overexploitation of their food supply is by human intervention with humans acting as predators.

The predator-prey interaction, as well as the closely related herbivore-plant and parasite-host interactions, provide examples of the phenomenon of **convolution** wherein a change in one species exerts a selective pressure on another species which interacts with it. This results in an adaptive response on the part of the second species that, in turn, creates a selective pressure on the first species. Consequently, **the two species evolve together**.

An example of coevolution can be seen in the interaction between plants and their herbivores. Should a new herbivore enter a plant population and feed off it, any plant that possessed some characteristic that resisted the herbivore would reproduce better than those more susceptible to herbivore foraging. The result would be that in successive generations the plant population would evolve some measure of resistance to the herbivore. This change in the plant would

favor any variation in the herbivore to overcome the plant's defenses, and so the race would continue with the **eaten always being a step ahead of the eater**. Should the eater win out, both species will suffer as extinction of the plant will cause extinction of the herbivore, unless the herbivore has another food supply.

The phenomenon of coevolution is not restricted to associations wherein one species benefits at the expense of another. In species of plants pollinated by insects coevolution between the plant and its insect vector can result in a mutual dependence of one species upon the other. The floral arrangement of some orchid species is specialized to attract certain insect pollinators that in turn become specialized to extract pollen and nectar from the orchid. Coevolution can result in protocoevolution (which is nonobligatory) evolving into an obligatory mutualistic association.

In summary, evolutionary ecologists study how ecological factors can act as agents of natural selection to modify characteristics and relationships within and between species over long periods of time. In so doing they attempt to explain how ecological factors are involved in what we learned at the start of the semester is often called **ultimate causation** – questions that deal with evolutionary history. A formal treatment of evolution will be our next topic.