HABITAT AND NICHE, CONCEPT OF

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I. Contrasting the Habitat with the Niche
II. History of the Habitat and the Niche
III. Comparing Habitats and Niches
IV. Evolution of the Niche
V. The Habitat and Biodiversity
VI. Conclusions and New Frontiers

GLOSSARY

community An ecological term referring to a set of species that occur in the same location that have the potential to affect each other either directly or indirectly.

community structure The web of potential biological interactions among members of a community that may be characterized in terms of diversity, complexity, hierarchy, and stability.

ecotone A zone of transition between two different habitats that may contain a community of organisms distinct from either habitat.

habitat structure Analogous to community structure, but limited to the physical structural aspects of a habitat. The structure of habitats may be characterized by such measures as complexity, heterogeneity, regularity, stratification, and fractal dimensionality.

microhabitat Locations within a habitat where organisms may carry out important aspects of their lives, such as places for harvesting food, nesting, or taking shelter.

niche overlap The proportion of available resources that are shared by two species. Usually used in the context of a single resource that limits population growth.

WHY ARE SPECIES COMMON in some places but rare or absent in other places? Early attempts to answer this fundamental question led to the concept of the habitat. A habitat is simply where an organism can be found in nature. Habitats are described in terms of geography, geology, climate, as well as by other species commonly found within the same habitat. The habitat concept is very closely related to another concept used to characterize species, the niche. The niche of an organism can best be described as its role in the community of organisms around it. Among the many traits that may comprise a niche are the physical and climatic characteristics that an organism can tolerate, and the resources required for the species to persist, such as food and shelter. The habitat of a species is often treated as a subset of its niche, and in practice it has grown difficult to draw a distinct line between the two concepts, yet the study of habitats has a history distinct from that of the niche. Today, habitat descriptions are commonly used as a practical guide for locating and maintaining species, whereas the niche is a more abstract concept that forms the conceptual foundation for much ecological and evolutionary theory.

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I. CONTRASTING THE HABITAT WITH THE NICHE

As is the case with many ecological concepts, defining habitats and niches concisely and unambiguously is difficult. Habitat definitions are particularly prone to problems of scale. At the larger end of the scale is the biogeographical term *biome*. Some biomes may be considered the habitat of larger, well-traveled species such as large birds of prey, but usually the habitat is defined more narrowly. On the smaller end of the scale, the term microhabitat is used to describe the places where an organism spends part of its time. For instance, a fish may forage in the microhabitat that occurs near the banks of a river. Thus the concept of the habitat lies somewhere in between the biome and the microhabitat.

An ecological community is a suite of species that occur in the same location that at least have the potential to interact and affect each another either directly or indirectly. These effects are usually measured in terms of population growth or changes in the density of individuals. Different communities of organisms will generally reside in different habitats. If most species in one community have little chance of affecting the populations of other species in a different community, then these communities probably occur in different habitats. In this way, microhabitats refer to places within a community, and biomes encompass a number of different habitat types. Definition of habitat and community boundaries will depend on the exact species under consideration. For instance, it may be reasonable to distinguish the small mammal communities of grassland from nearby riparian forest, though an individual jaguar may prey on species in both habitats.

The habitat concept was originally applied to single species, but because many species share similar habitats, some general habitat descriptions are applied to many species. Habitat descriptions used in this fashion often incorporate the dominant species commonly found in that habitat. In nature, borders between different kinds of habitats are often not very distinct. Generally, one habitat type will gradually give way to another creating a zone of transition. Communities in the transition zone may be qualitatively different from communities that occur within one habitat type or another.

The primary habitat preferences of a species can be displayed graphically. Ordination is the process of characterizing a species with regard to habitat gradients. Gradients can be displayed as axes on a graph. Usually, some measure of density or population growth is plotted, and the portion of the gradient that is occupied by the species is referred to as the habitat breadth of the species. Figure 1 shows how two species of plankton can be compared according to a single habitat dimension, depth in the water column. There are potentially limitless gradients or factors that may be involved in characterizing the habitat of a species. Graphical representation of more than three variables in a single graph is difficult, but the concept easily extends into multiple dimensions.

The niche is a more abstract term than the habitat. It encompasses all possible interactions that a species has with the environment and other species in the community. Conceptually, the niche is richer than the habitat and forms the foundation for much ecological theory. Because of the abstract nature of the concept, the definition is perhaps even more difficult to formulate for all species. There are striking similarities in the way niches and habitats are displayed. Like a habitat, a niche is often defined by axes, and there are multiple axes that can be compared.

The most common type of axes used to characterize a niche include those that define environmental tolerances and resource requirements. Humidity, sunlight, temperature, wind exposure, and pH are examples of environmental axes that help to define a niche. Resource axes may include food resources (insects, seeds, bacteria, nutrients), space requirements (breeding sites, ref-

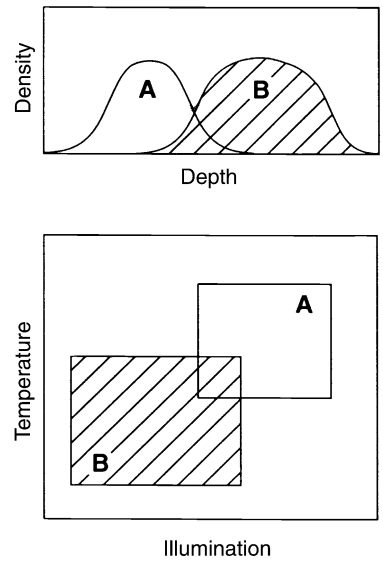

FIGURE 1 Two hypothetical species of plankton compared along the habitat axis of depth in the water column (top panel). This single habitat axis is correlated with two different niche axes, temperature and illumination. Species B is found in shallower, brighter, and warmer areas.

uges, foraging zones). Figure 1 also compares the two plankton species in two niche dimensions, illumination and temperature, which are correlated with the habitat axis, depth. This highlights the similarity of habitat and niche axes, which are often difficult to distinguish clearly.

In practice, ecologists focus on a subset of niche dimensions that are the most important in determining the role of a species in the community. Among these are food resources that are essential for survival. These factors *limit* the population size of the species and therefore determine the distribution and abundance of the population.

In spite of the more limited role of the habitat in theory, the physical nature of habitat axes make them useful tools for practical purposes. Habitats can often be adequately described with relatively few variables, whereas to fully document the niche of a species requires careful study and a great deal of time. Yet if the habitat can be accurately captured, it is likely that many the complex niche requirements and interconnections will be contained within the same habitat. As stated earlier, communities tend to map one to one onto habitats. The utility of this relationship is exploited for management when there is insufficient time to study all aspects of an organism's ecology before an action needs to be taken. To preserve a single species, one must also preserve its niche requirements and the complex interconnections with the rest of the community. Preserving adequate habitat will often achieve this goal. This principle is important not only for managing target species, but for preserving and restoring biodiversity in general.

The primary habitat and niche for a number of species is given in Table I. These brief characterizations are typically used as a shorthand way to describe where to find species and the basic role played by each in the community. Habitat descriptions include geographical information and often refer to the dominant species present (e.g., grassland, coral reef). Niche descriptions for a species usually begin with the main food items consumed.

As one moves through this list of very diverse species, the differences in the scales and roles are readily apparent. Trees may define different successional stages of a forest, each of which may be considered a different habitat. A jaguar may routinely cross into different successional stages on a daily basis, making it difficult to clearly define a jaguar's habitat. In contrast, certain trees, birds, and lichen are limited to only a certain successional stage, while specialized insects, parasites, and pathogens may even be limited to a single species of host. These differences make broad comparisons of niches and habitats difficult, but at any single scale, these concepts can be applied to facilitate meaningful comparisons among similar species.

II. HISTORY OF THE HABITAT AND THE NICHE

A. Niche Origins

It is tempting to think of a niche as a physical place. This is the common usage of the word, and there are examples in the early ecological literature that use the term *niche* in the purely physical sense. However the origins of the ecological niche reside in the more general observation that no two species are exactly alike.

Many naturalists in the latter part of the 19th century turned their attention toward documenting the traits that distinguish one species from another. When two species appeared very similar, it was thought that eventually differences could be found that would distinguish the unique role of each in the community. This idea was evident even in the writings of Darwin, and over time it has evolved into a very general principle: the principle of competitive exclusion. Exploring the implications of this relatively simple notion has dominated the study of ecology for much of the 20th century.

The principle of competitive exclusion and the concept of the niche developed in parallel through the early 1900s. Theoretical work by Volterra (1926) showed that if certain assumptions are met, only one species should be able to survive on a single resource. Gause (1934) demonstrated this principle experimentally with two species of *Paramecium* feeding on a common resource. Two species that consume the same resource in the same way simply cannot coexist.

The term niche was first used in the context of competitive exclusion by Grinnell, a superb naturalist of the North American west, as early as 1914. Grinnell's study of the California thrasher represents one of the first that specifically set out to characterize the ecological niche of a species, though he laid out the concepts of the niche and competitive exclusion 10 years earlier in a study on chickadees.

Grinnell's study of the California thrasher illustrates some of the most basic components of a niche (a) type of food consumed (mostly insects, berries at some times of the year), (b) microhabitat preference (beneath shrubby vegetation), (c) physical traits and behaviors used in gathering food (a long beak thrashed through the top layers of soil and leaves), and (d) resources

TABLE I

The Primary Habitat and Major Niche Components of Some Representative Species

Species	Habitat/Biome	Niche
California thrasher *Toxostoma redivivium*	Coastal chaparral; western North America	Generalist insectivore; territorial; sometimes a fruigivore
Cuban crown giant lizard *Anolis equestris*	Tropical forest tree crowns; Caribbean (Cuba)	Generalist insectivore; short pursuit predator; territorial
Spotted salamander *Ambystoma maculatum*	Ephemeral ponds in deciduous forest; temperate North America	Generalist carnivore, breeds in ponds with few large fish
Jaguar *Panthera onca*	Tropical forests of all types, savanna; Central and South America	Small animal carnivore; solitary stalking predator, keystone predator
Plains zebra *Equus burchelli*	Tropical savanna, Africa	Grazer of short grass; gregarious; migratory
Harvester ant *Pogonomyrmex rugosus*	Sandy regions of deserts; southwest North America	Scavenger of small seeds; makes terrestrial, colonial burrows
Tawny mining bee *Andrena fulva*	Temperate fields, gardens; Europe	Nectar/pollen harvester; solitary soil burrower; pollinator
Camel cricket *Ceuthophilus silvestris*	Caves, moist environments; North America	Scavenger, detrivore
Ghost crab *Ocypode quadrata*	Sandy marine beaches; temperate and tropical Nearctic	Scavenger; territorial; nocturnal
Mussel *Mytilus californianus*	Intertidal, rocky marine shores; western temperate North America	Filter feeds on Plankton; sessile; pelagic larvae
Tardigrade (water bear) *Echiniscus spp.*	Moist film on plants, moss, or lichen; cosmopolitan	Plant and moss cell predator; meiofaunal (0.4–1.0 mm)
Guanacaste tree *Enterolobium cyclocarpum*	Tropical savanna, dry forest; Central America	Large canopy tree; pioneer, keystone species
Flowering dogwood *Cornus florida*	Temperate deciduous forest, North America	Shade-tolerant, understory; pollen and nectar producer
Deuteromycota fungi *Arthrobotrys spp.*	Moist soil, pools; cosmopolitan	Sit-and-wait predator of roundworms, hoop-snare structures
Slime mold *Acrasiae spp.*	Moist soils, various habitats; cosmopolitan	Bacteria consumer, single and multicell stages
Schistosome	Humans and freshwater	Blood parasite in humans, gut
Schistosoma mansoni	Snails; tropical, Africa, South America	Parasite in snails

required for shelter and breeding (dense shrubs for night roosting and nesting). These four basic factors allow one to characterize the basic niche of most animals, and most animals differ with respect to one or more of these factors.

An analogous set of core niche dimensions may be constructed for plants, which tend to partition niche space along resource axes such as available light, soil moisture, and various soil nutrient gradients. Important niche dimensions for marine organisms may include temperature, substrate type, salinity, pH, and exposure to waves.

Thirteen years after Grinnell, the publication of Elton's *Animal Ecology* text (1927) established the term niche in the lexicon of ecology. However it was not until the work of Hutchinson (1957) that the concept of the niche was fully developed as a cornerstone of ecological theory. Hutchinson's niche is an *n*-dimensional hypervolume, implying that there are usually many factors, or dimensions, that define the role of a species in a given habitat. These included yet extended well beyond the basic niche dimensions described by Grinnell.

Other ecological concepts emerged from this founda-

tion. The resources that a species would use if it were isolated from all potential competitors is part of its fundamental niche. The realized niche is a subset of the fundamental niche that includes the resources actually consumed by the species in nature. The difference between the realized and fundamental niche can be attributed to competition from other species in the community.

B. Habitat Origins

Originally, the habitat of a species was not viewed as a part of its niche. In the early history of these terms they were treated separately. The habitat was seen more as a guide to the kind of community in which the organism played its role. For instance, the California thrasher occupies coastal chaparral of western North America, but this habitat description can be viewed as distinct from its niche within that habitat. Also, species were viewed as possessing suites of traits and physical tolerances that enabled them to be suitable only for specific habitats.

Over time, habitat axes were compared right alongside common niche axes, and the distinction became obscured. This change may be due in part to parallel development in the field of evolution and adaptation and increased knowledge of the processes involved. Today it is not difficult to imagine that two species may have evolved to occupy different habitats, whereas at a previous time only one species may have occupied both habitats.

The history of the habitat concept can also be traced back to the work of Grinnell and his contemporaries. In one of the earlier studies, Grinnell and Storer characterized the animals of Yosemite according to the elevations at which they occurred. In this mountainous region, species tend to be found in narrow elevational zones or bands.

At about the same time as the Yosemite study, Ramensky wrote that each species was unique and possessed adaptations that enabled it to tolerate a unique set of environmental conditions. This "principle of species individuality" bears strong resemblance to the early influences on the niche concept, except that in the habitat context, competitive exclusion was not at the core. Instead, species were seen to be adapted to certain conditions and habitats, and they independently sorted themselves out accordingly.

Subsequent work has confirmed that habitat boundaries are often determined by physical tolerances. However there are numerous examples where competition and other species interactions play an important role in determining the habitat breadth of a species in nature. This further illustrates how the habitat and the niche have converged over time. Therefore it is appropriate to treat the habitat and the associated gradients and axes as a subset of the niche.

III. COMPARING HABITATS AND NICHES

A. Multispecies Comparisons

The habitat and niche of any species can be characterized independently, but the true value of these concepts lies in comparing multiple species. The ability to display habitats and niches graphically greatly facilitates comparisons. Figure 2 shows how species can be ordered along a habitat gradient. Copepod species show different patterns of abundance with respect to the gradient from ocean to land in the intertidal region. While in this instance there is a large amount of overlap, each species has a characteristic distribution in this region.

Habitat boundaries are rarely sharply defined. *Ecotone* is the term used to refer to this zone of transition between habitats. Because this zone is somewhat different from either neighboring habitat, an ecotone may contain several unique species. This concept was proposed to help explain distributions of species that did not appear to coincide with habitat boundaries. In a unique test of this idea, Terborgh and Weske (1975) found little evidence that subsets of bird species along an elevational gradient were responding to ecotones. Instead, it appeared that the elevational ranges of many species were independently defined by the presence of other closely related species. In this case, competition appeared to be more important than habitat gradients for setting the actual limits of species distributions.

The niche framework is typically used to compare groups of closely related species that consumed similar resources but differed in one or a few important ways. Suites of species in a community that utilize the same general resource were termed guilds by Root (1967). Just as a guild of blacksmiths all work with iron yet have different specialties, assemblages of animals that specialize on seeds, fruits, or insects all have different ways of harvesting these resources.

Early studies focused on guilds that differed mainly with respect to body size. Hutchinson (1959) observed that species within a guild often differed by a minimum size ratio. Known as Hutchinsonian ratios, these regular arrangements of species body sizes occur in a number

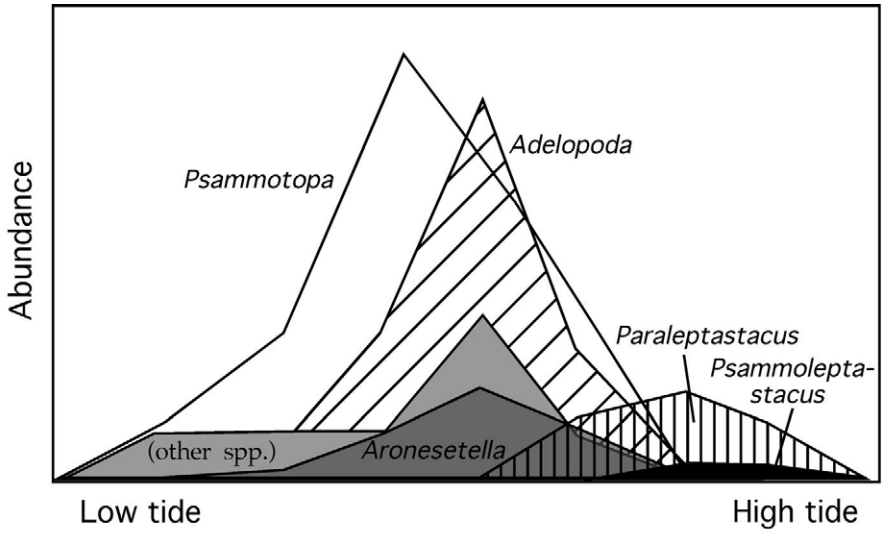

FIGURE 2 The distribution of copepod species along the sandy intertidal habitat gradient in Massachusetts (only genus names are given). From Pennak, 1951.

of vastly different communities consuming very different resources.

One example of the kind of pattern Hutchinson was attempting to explain is the assemblage of rodents that consume seeds in the deserts of North America. Figure 3 shows how similar assemblages of rodents in different communities contain a similar set of rodents. Each species differs from others in the same community mainly in terms of body size. Convergence is a term applied to organisms or communities that are not closely related historically that have members with similar physical features because they occupy similar niches. The implication is that parallel evolutionary trajectories were followed independently by different species because of similar selection pressures.

The underlying mechanisms that create such regular patterns can be explained because each species consumes resources of a size class that is proportional to its body size. Smaller rodents consume smaller seeds, while larger rodents eat larger seeds. In a different community, smaller fruit pigeons consume smaller fruits, while larger species primarily consume larger fruit. For a medium sized bird, small fruits take too long to gather and handle, and the bird can not eat them efficiently enough to sustain itself. Larger fruits may be too big to handle or crack open.

Many types of food resources such as seeds, fruit, or arthropods have a wide, flat distribution along a size gradient. These relationships can be displayed graphically with a single niche axis, food resource size (Figure 4). One curve represents the available resources, in this case seeds, and the narrower curves underneath represent the sizes and amounts of seeds consumed by each species. This division of available resources among members of a community is termed resource partitioning.

Utilization curves are often bell shaped (normal, Gaussian) to reflect the tapering ability of each species to consume seeds away from the "optimum" size. This type of niche representation allows direct comparison of the amount of overlap in resource consumption. If food is indeed the primary limiting resource, the overlap of species resource utilization curves directly represents the amount of competition that each species is experiencing. It is the regular spacing of curves to minimize overlap, or competition, that creates the pattern of regular size distributions of animals seen in natural communities. This simple framework forms the basis of niche theory.

The concepts of fundamental and realized niches can be clearly visualized within this framework of graphical representation of both habitat and niche dimensions. Mussels are capable of living in a wide range of elevations above the low tide mark, and they will move into these spaces in the absence of other species. However other animals, such as barnacles, are better adapted to occupy lower positions and can outcompete mussels in some zones. That is why in natural communities, the realized niche of mussels in terms of this habitat gradient is usually narrower than the fundamental niche.

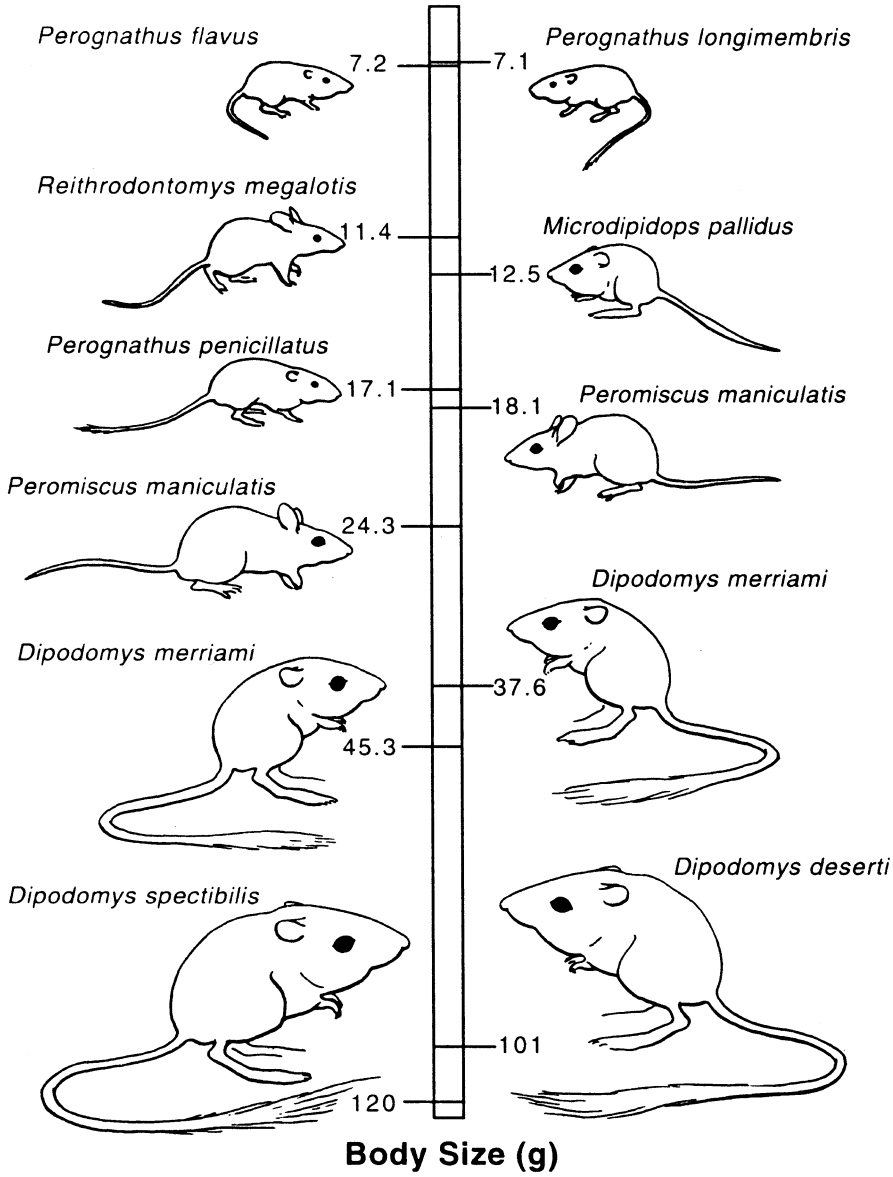

FIGURE 3 A comparison of the niche relations among Great Basin and Sonoran desert rodent guilds. From Brown, 1975. Different habitats support a different assemblage of rodents that show similar differences in body size.

A similar process may be operating in the granivorous rodent example presented earlier. Each rodent may be capable of consuming a wider range of seeds, albeit inefficiently. In nature, either there are fewer of these suboptimal resources available because of competitors, or each species deliberately chooses a narrower range of seeds to consume to avoid competition.

The effect of competition on realized niches can be seen by comparing island and mainland communities. Islands usually support fewer species than equivalent mainland habitats. It has been shown for many kinds of species that in these species-poor island communities, species tend to eat a wider array of foods and therefore have wider niches. This agrees with the expectation based on niche theory outlined earlier: there are fewer potential competitors on islands, and therefore there is less resource overlap with other species acting to constrain their niches.

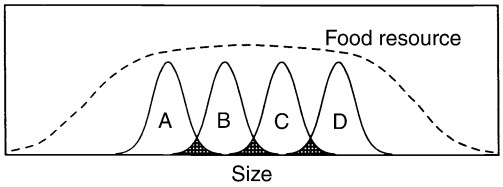

FIGURE 4 A hypothetical species assemblage. A nearly continuous spectrum of resources that differ mainly in size (top curve) are consumed and partitioned among different species that also differ mainly in size (A–D).

Species that have very high overlap in many niche dimensions often have little or no overlap in one key dimension. This principle, called niche complementarity, lies at the heart of the guild concept. In previous examples, similar species consumed the same general resource and had high niche overlap, but they showed little overlap with respect to a single dimension: body size. Typical niche axes where complementary species can be found include size, light (nocturnal/diurnal), benthic/pelagic, and canopy/ground or coniferous/deciduous microhabitat.

In many instances niche differences among species are clear, but sometimes niche differences are extremely subtle and require careful study to be revealed. For instance, five species of *Dendroica* warblers can all be found in the very same tree in temperate zone coniferous forest habitat. All glean similar types of prey, primarily lepidopteran larvae, from the surfaces of the tree. Only careful study by MacArthur (1958) revealed that each species favors different parts of the tree, and each tends to move about the tree in different ways (Figure 5). Thus it is not only the type of food resource that is limiting the population growth of each species, but where and how that food resource was harvested. There are enough subtle differences in microhabitat use and behavior to allow coexistence of species that at first glance appear to share equally the same limiting resource.

Niches can change through time. For instance, the larval forms of many organisms often have completely different niches from adult forms. Thus, the term ontogenetic niche has been applied to amphibians, arthropods, and a wide variety of marine organisms. The great versatility of the niche concept allows incorporation of these temporal changes by simply adding a temporal axis to the species niche. The realized niches of species in a community can also change through time if the community undergoes change. Extinctions and invasions cause rapid community changes that in turn result in niche shifts among other community members.

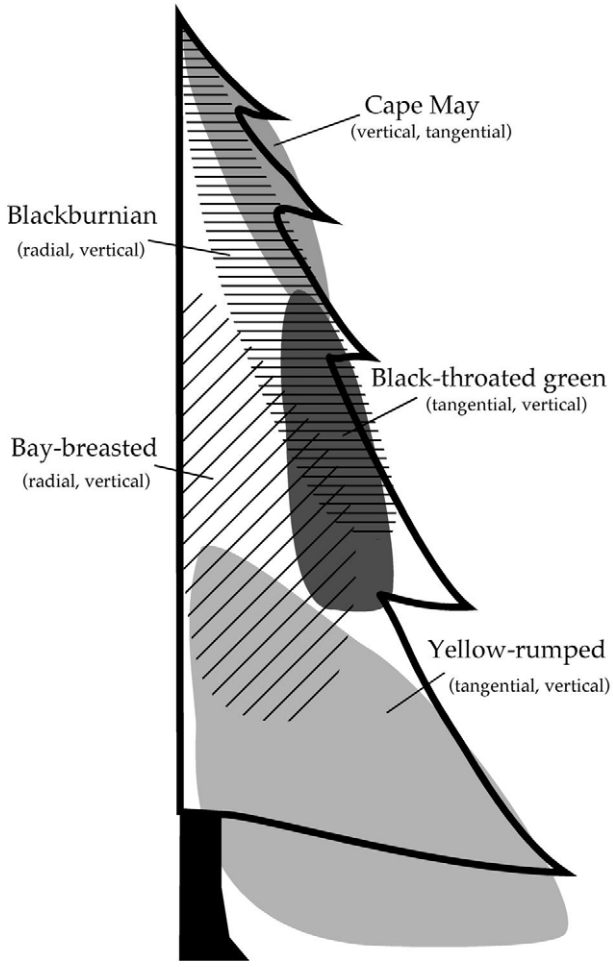

FIGURE 5 Niche relations among some North American warblers that forage in coniferous forests. Species differ according to microhabitat (parts of the tree most frequently visited) and foraging behavior. From MacArthur, 1958.

Niche theory is the branch of ecology that has taken these informal graphical models and extended them mathematically to model the process of competition and community organization. The origins of niche theory can be traced back to the early work of Volterra, and has grown and undergone dramatic changes. Complex interactions among members of a community are very difficult to measure, and the approach of studying theoretical models has greatly enhanced our knowledge of the factors that influence community dynamics.

B. Other Niche Dimensions

The classical context of niche comparisons is mainly restricted to niche axes characterizing habitat and food

resources. Some ecologists have even considered the definition of a niche to be limited to the food resources consumed. However developments in the field of ecology through the 1900s have made it clear that an expanded definition of the niche that encompasses all the interactions of a species within a community is most appropriate. A broad definition of the niche includes all potential interactions that ultimately have the effect of changing the population density of another species in the community.

Mutualistic interactions are somewhat different from food resources in that they are often not literally consumed, nor are they occupied as in a nesting or sheltering place. However in niche descriptions, mutualistic interactions are treated much the same as other resources in that they may be limiting and therefore may even be competed for. For instance, pollinators interact mutualistically with angiosperms, yet from the point of view of a plant, they may be regarded as any other resource.

C. Indirect Interactions

Competition for resources has historically played a central role in niche descriptions. More recently, studies have uncovered processes where two or more species coexist because of factors that have little to do with resource niche axes. For example, predation can act to promote coexistence of potentially competing species in the following way: The presence of a predator may reduce the numbers of one prey species and thereby allow other species that have similar resource requirements to coexist. If two or more species are all harvested by a predator that does not show preferences for any specific prey type, then the most common prey will experience a disproportionate amount of predation. In this way, the presence of a predator can actually promote coexistence of species and an increase in biodiversity. Predators that have this effect have been referred to as keystone species because of their disproportional affect on community diversity.

An excellent example of this process can be found in the rocky intertidal communities of the eastern Pacific. Paine (1980) and colleagues conducted a unique set of experiments demonstrating that the presence of a starfish predator (*Pisaster*) enabled the coexistence of a number of species, whereas in the absence of the starfish, the community was dominated by the California mussel. The niche description for a barnacle in this community would therefore be incomplete without incorporating information about not only the presence of the California mussel, but also the relative vulnerability of each of these species to starfish predation. This implies that the niche characterization may change depending on the presence of potential predators and prey and their specific traits.

Predation certainly can be seen as a direct interaction, but the example above falls into the class of indirect interactions. A keystone predator can enhance the abundance of a species by interacting with a third species. Many interactions may cause ripple effects through a community in indirect ways. Elephants change the physical structure of their habitats, and many species excavate holes and nests that are used by other species. Parasites and pathogens can also have indirect effects on entire communities.

Viruses and other pathogens may initially appear to occupy a very simple niche, especially those that are confined to live entirely inside the body of a host species. How can such an organism play an important role in the community through indirect interactions? Pathogens can significantly impact the population size of the host species. This change in abundance may have consequences for other species, such as predators and prey of the infected species.

Some pathogens have complex life cycles that depend on more than one host species, and sometimes these hosts are very different. For instance, in using humans and snails at different stages of its life cycle, Schistosomiasis provides a clear link between humans and some snail species that are used as hosts for different stages of the life cycle.

Another interaction involving pathogens provides an example of apparent competition. One host species may be relatively unaffected by a pathogen, whereas other species may be severely impacted. In this case, the unaffected species can act as a carrier, spreading the pathogen to other species in the community that are more susceptible, causing their decline. On the surface, this pattern may resemble competition.

Community ecologists have used various methods to incorporate these indirect interactions into model representations of communities. It is certainly not as straightforward as simple resource utilization graphs. Mathematical matrices have been applied to study the dynamics of communities. In this format, all pairwise interactions can be explicitly considered, and broad concepts such as the relationship between community stability and complexity have been studied within this framework. Recently, web theory has been applied to this task because complex interactions within communities can be more explicitly constructed. All of these theoretical constructs of communities are based on the niche concept, thus the utility of the niche concept

has grown even as the field of ecology has undergone dramatic changes.

IV. EVOLUTION OF THE NICHE

Ecological studies can help us to understand *why* species occupy unique niches, but *how* did the great diversity of species arise in the first place? The processes underlying the evolution, adaptation, and coexistence of species that have unique niches is a fundamental aspect of understanding biodiversity.

For many organisms the primary mode of species formation, and therefore the primary generating force for biodiversity, is thought to involve differentiation of isolated populations. A terrestrial species may have populations separated by water, or coastal marine populations may be isolated by unsuitable open ocean. Over time, these populations undergo changes and begin to accumulate different characteristics. Some of these differences are due to chance events such as mutation and genetic drift. Traits change over time as the organisms adapt to the unique features of their respective habitats. Subtle environmental differences may result in the evolution of thicker shells in a population of crabs, or a preference for fish over mammals in a population of killer whales.

This differentiation by adaptation to different habitats with different food resouces is in itself one engine for generating biodiversity, however it cannot explain the vast diversity of species that occur within a single habitat. Eventually, populations that have been isolated for a while may reestablish contact, and individuals will attempt to coexist within the same community. It is at this stage of speciation, referred to as secondary contact, that one can see how the concept of the niche is fundamentally related to species diversity.

When secondary contact occurs, one of three outcomes is possible. First, populations may interbreed, and speciation is not completed. Second, if populations do not interbreed, they may either coexist, or, third, one may outcompete the other. Which of these two latter outcomes is realized will depend on the amount of niche overlap between these species. If overlap is high, then one species is likely to outcompete the other. If overlap is low enough, the species may coexist.

In situations where coexistence is possible (or at least extinction is not very rapid), and the species involved still possess similar traits, we would expect evolutionary changes to occur over time. Individuals that consume limiting resources that are shared with another species will experience more competition and may survive or reproduce less than individuals that do not overlap as much. If there is natural variation in resource consumption among individuals in each population, and if the traits that cause this variation are genetically passed to offspring, then the species are expected to diverge over time to minimize niche overlap. This process is called ecological character displacement, and it is a logical extension of the competitive exclusion principle into evolutionary time. Figure 6 illustrates the process of character displacement. It is the change in a trait of a species, such as body size, that leads to a shift along a niche axis and reduction of overlap.

The empirical evidence for character displacement lies mostly in descriptive, snapshot-like comparisons of species. Typically, closely related communities are compared and character displacement is inferred if the presence or absence of one species is correlated with a change in the traits of another species. These studies infer that it is niche overlap in the use of a single limiting resource that has led to the observed species differences. Lack (1947) was one of the first to infer character displacement in this way in his study of Darwin's finches Figure 7.

Static character differences constitute indirect evidence for competitive processes and have therefore received criticism. To document evolution directly in natural populations is a difficult task because even rapid

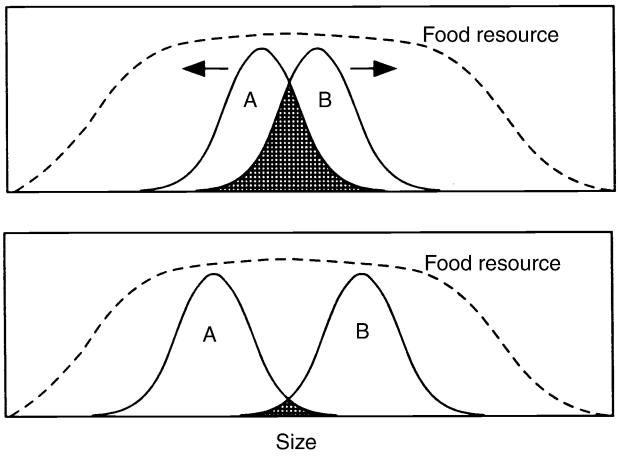

FIGURE 6 A graphical representation of ecological character displacement. Initially upon secondary contact, species have highly overlapping resource utilization. Over time (b) resource overlap and competition is reduced through evolutionary changes that result in a shifting of the niche.

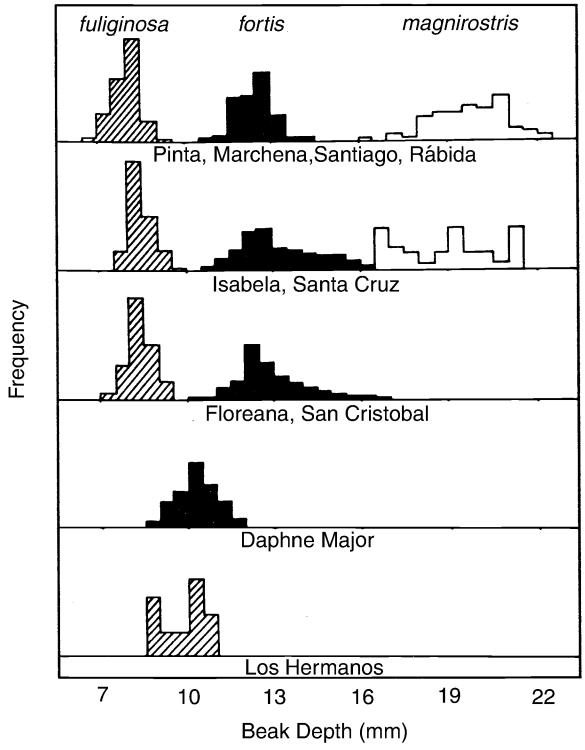

FIGURE 7 Size variation among three species of Darwin's finches (genus *Geospiza*) that specialize on seeds. Individuals are pooled among islands (given) to generate the histograms of beak depth. Populations on islands with fewer species (lower two panels) are intermediate in size compared to islands with the complete complement of species (upper panels). This is indirect evidence for ecological character displacement caused by competition for seeds; Pennsylvania in the United States. From Grant and Schluter, Ecological Communities. Copyright © 1984 by Princeton University Press. Reprinted by permission of Princeton University Press.

evolutionary changes may require generations to occur. Nevertheless, there is solid empirical evidence for niche evolution in nature. The Grants and their colleagues (see Grant, 1999) have shown the niche of Darwin's finches evolved over time according to the seeds that are available. In unique experimental tests of character displacement, Schluter (1994) has shown that stickleback fish populations changed over time in response to competition and niche overlap. Natural selection acted against individuals with feeding anatomies that caused them to harvest resources that were shared between species.

Ecologists may differ in opinion about the importance of character displacement in specific instances, and there are surely other very important forces that act to shape community composition and species traits. Nevertheless, few would doubt that character displacement is an important fundamental process in shaping communities of organisms.

V. THE HABITAT AND BIODIVERSITY

We have traced the habitat concept from its independent origin through its incorporation into the concept of the niche. With growing awareness of the need to conserve biodiversity, the habitat concept has emerged again as an important tool for management. Essentially, habitats contain functioning communities of organisms. If the goal is to protect a focal species, then setting aside appropriate habitat will likely result in preserving the required niche elements of the species as well.

Assessing appropriate habitat has two great advantages over attempting to define niches. First, because of the physical nature of habitats, they are easier to recognize and quantify. Second, ecological communities tend to fall along similar boundaries as habitats, thus by preserving a habitat one is more likely to preserve communities with all niche interconnections intact. This relationship among species, communities, and habitats has become the center of the more recent conservation efforts termed habitat conservation plans.

For example, in San Diego county, a number of endangered or threatened species rely on a unique type of habitat: chaparral, or coastal sage scrub. A major goal of habitat conservation plans in this region is to create contiguous regions of appropriate habitat. In this way, the needs of many species can be met at once.

Habitat fragmentation is a major concern because small refuges of habitat are essentially islands. Islands are prone to a number of processes that degrade biological diversity. Small populations on islands are prone to extinction through random fluctuations in numbers. The geometry of islands gives them a high ratio of edge to interior. Because animals may wander across this boundary, those that rely on the interior island habitat experience more competition and predation from those outside the island. More isolated islands are also less likely to be recolonized in the event that a population has gone extinct. Therefore, natural reserves and habitat conservation plans pay particularly close attention to fragmentation and try to consolidate larger parcels of unbroken natural habitat.

Once a habitat has been severely degraded, there may be ways to return it to its former natural state. Habitat restoration is a challenging field, but one that has made great strides recently. Wetlands have been restored by controlling of the water table and planting

appropriate vegetation. Foresters have been restoring habitat for decades by replanting harvested areas. Highway construction projects aim to restore natural vegetation upon completion of a project by spraying a mix of grass, flower, and shrub seeds in a fertilizing matrix onto the bare ground. Another interesting example of habitat restoration can be seen with the construction of artificial reefs. By placing physical structures on the seafloor, a reef community can take hold and flourish. This is an example of how subtle environmental features such as physical structure can have a profound effect on habitat quality and species diversity.

Two general mechanisms act to promote species diversity within structurally diverse habitats. First, biological species diversity leads to more species diversity. A monoculture such as an orchard allows for relatively little niche differentiation of the organisms within. There is little opportunity for species to adapt to specific host species, and this applies to insects, birds, mammals, and parasites. Reduced numbers of species limits the number of possible niches in an orchard when compared to a tropical rain forest.

Artificial reefs belong to a second class of mechanisms that generate biodiversity by acting over and above the biological mechanisms. These are the purely physical features of the habitat that allow for increased niche differentiation. Dead logs, snags, distinct ground, and shrub layers will provide habitat heterogeneity that allow higher trophic levels to differentiate. Just as warblers partition the physical space within a single tree species, other competitors that use different tactics to forage on similar prey can partition a structurally diverse habitat to a finer scale. Behavior plays a key role as foraging tactics and escape strategies of prey are honed to specific microhabitats within the larger forest. MacArthur and colleagues (1962) were among the first to correlate purely physical aspects of a habitat with species abundances. Since then, physical habitat structure has been shown to augment species diversity in systems as diverse as birds, lizards, stream invertebrates, fish in marine reefs, and microorganisms in beakers.

Keystone species have a disproportional effect on many other species in the environment, and as such are often the focus of conservation efforts. Starfish foraging in the intertidal zone have a positive effect on biodiversity. Jaguars prey on a number of small rodents and animals, and they tend to capture prey in proportion to their abundance. The net effect is to prevent any single species from becoming very common and outcompeting other prey species. The niche of the jaguar and the starfish includes this community-wide role, and they are sometimes referred to as keystone predators.

Management strategies have turned more attention toward keystone species in order to preserve communities. A similar keystone role is played by tree species such as the Guanacaste tree of Central America. In this instance the link between the niche, the habitat and biodiversity is clear. The Guanacaste tree is vital for establishing forest in grassland habitats, and it therefore plays a key role in restoring tropical dry forest. The niche of this species would include its role in developing habitat structure and therefore intersects with the niches of many other species in the community.

The habitat and the niche can interact synergistically with human activity to cause extinctions and loss of biodiversity. Niche complementarity has led to a very general pattern whereby species with similar niches are spatially segregated. Increased human movements on a global scale has had a dramatic effect in bringing these species into contact by introducing exotic species into new geographic regions. If these alien species have high niche overlap with resident species, the resident species can be driven to extinction by a successful invader. Even though there are many cases where introduced species can not establish or outcompete residents, many threatened and endangered species are at risk because of invaders. This threat also extends to introduced predators. Resident species that have adapted to a niche in one community can be driven to extinction by a predator that has evolved in a different community.

VI. CONCLUSIONS AND NEW FRONTIERS

The concepts of the habitat and the niche have grown mainly through study of the organisms most familiar to us as humans. Most conceptual advances were derived in some way from the study of larger animals and plants. Even within these groups, there has been a disproportionate amount of study of birds. Yet there have been significant contributions from other sectors of the biological world. For instance, Gause's study of *Paramecium* lies at the heart of the niche concept. It is fitting then that more attention is returning toward understanding the niches of microorganisms.

Experimental evolution using bacteria is a growing field that holds great promise. The short generation times and relatively simple ecologies of bacteria enable evolutionary experiments on the scale of the commu-

nity. This is one of the few instances where the interaction of ecological and evolutionary factors can be studied during the process of community formation.

There is an enormous number of microscopic, planktonic and meiofaunal (0.4–1 mm) organisms about which we know very little. These organisms are ubiquitous, speciose, and show an amazing amount of diversity in form. However there are significant obstacles encountered in studying these smaller organisms that even make it difficult to quantify the habitats in which they can be found. Practical problems arise while trying to observe them in nature, while on the other hand, many fail to survive the transfer to laboratory environments. Yet there are compelling reasons to learn more about their ecology.

The niche of a terrestrial vertebrate or marine invertebrate is often defined largely by how it feeds or defends itself. In turn, anatomical structures have evolved that reflect these niche differences. Similar examples can be found in the nearly invisible world of small creatures around us. For instance, ciliates and other protozoans possess anatomical structures that suggest a diversity of roles even greater than those observed in larger organisms, yet there has been comparatively little study of their niches in nature.

Some organisms stretch the concepts of the niche and habitat to their limit. Some plants display an extreme amount of what is referred to as phenotypic plasticity: different individuals develop extremely different body forms depending on the environmental circumstances. Some ciliates have the ability to radically change the form of feeding or defensive appendages even within the lifetime of an individual.

Many bacteria, and even some larger meiofauna like the bearlike tardigrades, can enter a sporelike state to withstand extreme environmental conditions. They may persist for long periods of time in this state and may be very difficult to detect. Much like the seed bank of desert plant communities, these alternative states pose difficult problems in understanding the dynamics of their communities.

The habitat and the niche have grown, developed, and been applied with great success. Observation and theory have played important roles throughout, and experimental investigation has undergone a resurgence. Yet it is intriguing to ponder that most of this development has included only a subset of the biological world. Only time will tell whether the concepts of the habitat and niche will persist as the complex interactions of these diverse communities of small creatures are revealed.

See Also the Following Articles

CONSERVATION BIOLOGY, DISCIPLINE OF • DIFFERENTIATION • DIVERSITY, COMMUNITY/REGIONAL LEVEL • ECOLOGY, CONCEPTS AND THEORIES IN • GUILDS • SPECIES DIVERSITY, OVERVIEW

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