sition, for instance) and its position in environmental gradients of temperature, moisture, pH, soil, and other conditions of existence. These three aspects of the ecological niche can be conveniently designated as the *spatial* or *habitat niche*, the *trophic niche*, and the *multidimensional* or *hypervolume niche*. Consequently, the ecological niche of an organism not only depends on where it lives but also includes the sum total of its environmental requirements. The concept of niche is most useful, and quantitatively most applicable, in terms of *differences* between species (or the same species at two or more locations or times) in one or a few major (operationally significant) features. The dimensions most often quantified are *niche breadth* and *niche overlap* with neighbors. Groups of species with comparable roles and niche dimensions within a community are termed **guilds.** Species that occupy the same niche in different geographical regions (continents and major oceans) are termed *ecological equivalents*.

Explanation and Examples

The term *habitat* is used widely, not only in ecology but elsewhere. Thus, the habitat of the water backswimmer (*Notonecta*) and the water boatman (*Corixa*) is the shallow, vegetation-choked area (*littoral region*) of ponds and lakes; one would go there to collect these particular water bugs. However, the two species occupy very different *trophic niches*, as the backswimmer is an active predator, whereas the water boatman feeds largely on decaying vegetation. The ecological literature is replete with examples of coexisting species that use different energy sources.

If the habitat is the "address" of the organism, *niche* is its "profession," its trophic position in food webs, how it lives and interacts with the physical environment and with other organisms in its community. *Habitat* may also refer to the place occupied by an entire community. For example, the habitat of the sand sage grassland community is the series of ridges of sandy soil occurring along the north sides of rivers in the southern Great Plains of the United States. Habitat in this case consists mostly of physical or abiotic complexes, whereas habitat for the water bugs mentioned previously includes living and nonliving objects. Thus, the habitat of an organism or group of organisms (population) includes other organisms and the abiotic environment.

The concept of ecological niche is not so generally understood outside the field of ecology. Terms such as niche are difficult to define and quantify; the best approach is to consider the component concepts historically. Joseph Grinnell (1917, 1928) used the word *niche* "to stand for the concept of the ultimate distributional unit, within which each species is held by its structural and instinctive limitations . . . no two species in the same general territory can occupy for long identically the same ecological niche." (Incidentally, the latter statement predates Gause's experimental demonstration of the competitive exclusion principle; see Fig. 7-2.) Thus, Grinnell thought of the niche mostly in terms of the microhabitat, or what is now called the **spatial niche.** Charles Elton (1927) was one of the first to begin using the term *niche* in the sense of the "functional status of an organism in its community." Because of Elton's great influence on ecological thinking, it has become generally accepted that niche is by no means a synonym for habitat. Because Elton emphasized the importance of energy relations, his version of the concept is designated the **trophic niche.**

G. E. Hutchinson (1957) suggested that the niche could be visualized as a *multidimensional space* or *hypervolume* within which the environment permits an individ-

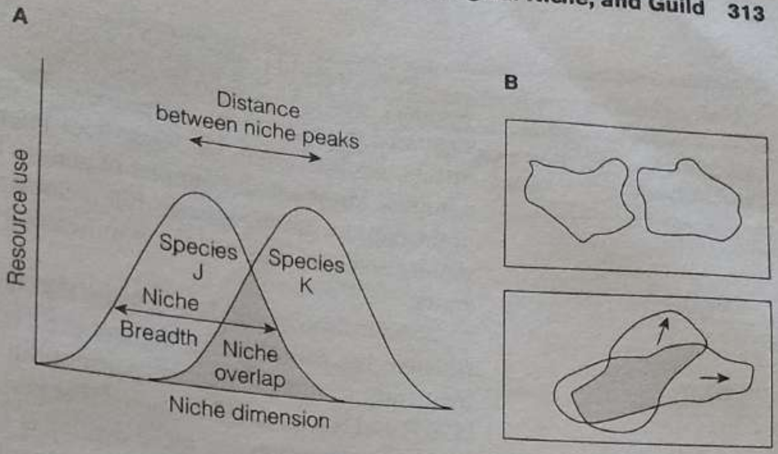

Figure 7-13. Schematic representations of the niche concept. (A) Activity curves for two species along a single resource dimension illustrate the concepts of niche breadth and niche overlap. (B) In the upper diagram, two species occupy nonoverlapping niches, whereas in the lower diagram, niches overlap so much that severe competition results in divergence, as indicated by the arrows.

ual or species to survive indefinitely. Hutchinson's niche, which can be designated the **multidimensional** or **hypervolume niche**, can be measured and mathematically manipulated. For example, two-dimensional climographs, which depict *x*- and *y*-axes of a particular species of bird and a fruit fly, could be expanded as a series of coordinates (*x*-, *y*-, and *z*-axes) to include other environmental dimensions. Hutchinson (1965) also distinguished between the **fundamental niche**—the maximum "abstractly inhabited hypervolume" when the species is not constrained by competition or other limiting biotic interactions—and the **realized niche**—a smaller hypervolume occupied under particular biotic constraints. The concepts of niche breadth and niche overlap are illustrated in two dimensions in Figures 7-13A and B.

Perhaps a simple analogy from everyday human affairs will help to clarify these overlapping and sometimes confusing ecological uses of the term *niche*. To become acquainted with a person in the human community, one would need to know, first of all, his or her address, (where she or he could be found). "Address" would represent *habitat*. To "know" the person, however, one would want to know something about his or her occupation, interests, associates, and role in community life. All this information would be analogous to that person's niche. Thus, in the study of organisms, learning the habitat is just the beginning. To determine the status of the organism within the natural community, one would need to know something of its activities, especially its nutrition; energy sources and resource partitioning; relevant population attributes, such as intrinsic rate of increase and fitness; and finally, the organism's effect on other organisms with which it comes into contact, and the extent to which it modifies or can modify important operations in the ecosystem.

In a classic investigation in the history of ecology, MacArthur (1958) compared the niches of four species of American warblers (Parulidae) that all breed in the same macrohabitat (a spruce forest) and all feed on insects but forage and nest in different parts of the spruce tree. MacArthur constructed a mathematical model, which consisted of a set of competition equations in a matrix from which competition coefficients were calculated for the interaction between each species and any of the other three. Thus, niches of similar species associated together in the same habitat can be precisely compared when only a few operationally significant measurements are involved. Two species proved especially competitive, so that if either were absent, the other might be expected to move into the vacated niche space. The general tendency for niches to narrow with interspecific competition has already been illustrated in Figure 7-5.

The term **guild** is often used for groups or clusters of species, such as MacArthur's warblers, that have similar or comparable roles in the community; Root (1967) first suggested this definition. Wasps parasitizing a herbivore population, nectar-feeding insects, snails living in the forest floor litter, and vines climbing into the canopy of a tropical forest are all examples of guilds. The guild is a convenient unit for studies of interactions among species, but it can also be treated as a functional unit in community analysis, thus making it unnecessary to consider every species as a separate entity.

Examination of guilds or species that fail to coexist can illustrate what aspects of resource use contribute to the competitive exclusion principle. Niche partitioning frequently relates to resource partitioning or resource use. MacArthur and Levins (1967) and Schoener (1983) noted that perhaps the most operational approach to the study of competition and niche overlap is to focus on consumable resources, or factors that serve as surrogates for those resources, such as differences in microhabitats. Winemiller and Pianka (1990) have used this approach to identify nonrandom patterns and clusters regarding the way that species use resources in a guild.

Measurements of morphological features of larger plants and animals can often be used as indices in the comparison of niches. Van Valen (1965), for example, found that variations in the length and breadth of a bird's bill (the bill, of course, reflects the type of food eaten) provide an index of niche width; the coefficient of variation in bill width was found to be greater in island populations of six species of birds than in mainland populations, corresponding with the greater niche width (wider variety of habitat occupied and food eaten) on islands, where competing species are fewer.

Grant (1986) was able to separate feeding niches of Galápagos finches by measuring beak morphology. He found that differences in beak size correlated to differences in diet. Within the same species, competition is often greatly reduced when different stages in the life history of the organism occupy different niches; for example, the tadpole functions as a herbivore and the adult frog as a carnivore in the same pond. Niche segregation may even occur between sexes. In woodpeckers of the genus *Picoides*, males and females differ in bill size and in foraging behavior (Ligon 1968). In hawks, some weasels, and many insects, the sexes differ markedly in size and, therefore, in the dimensions of their food niche.

Both nutrients and toxic chemicals introduced into natural ecosystems can be expected to alter the niche relations of species most severely affected by the perturbation. In a long-term (11-year) experimental study of the effect of applying N-P-K commercial fertilizer and municipal sludge to old-field vegetation, W. P. Carson and Barrett (1988) and Brewer et al. (1994) reported that niche width was significantly enhanced for summer annuals, especially *Ambrosia trifida, A. artemisiifolia*, and *Setaria faberii*, which increased their coverage at the expense of perennials such as *Solidago canadensis*.

Ecologically equivalent species, which occupy similar niches in different geographical regions, tend to be closely related taxonomically in contiguous regions, but are often not related in noncontiguous regions. The species composition of communities differs widely in different floral and faunal regions, but similar ecosystems develop equivalent functional niches wherever physical conditions are similar, regardless of geographical location. The equivalent functional niches are occupied by whatever biological groups happen to make up the flora and fauna of the region. Thus, a grassland ecosystem develops wherever there is a grassland climate, but the species of grass and grazers may be quite different, especially when the regions are widely sep-

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Table 7-3

Table 7-4

Table 7-3

Ecologically equivalent grassland birds in a Kansas field and a Chilean field

Ecologically equivalent pair of species	*Body size (mm)*	*Bill length (mm)*	*Ratio of bill depth to length*
Eastern meadowlark (*Sturnella magna*), Kansas	236	32.1	0.36
Red-breasted meadowlark (*Pezites militaris*), Chile	264	33.3	0.40
Grasshopper sparrow (*Ammodramus savannarum*), Kansas	118	6.5	0.60
Yellow grass finch (*Sicalis luteola*), Chile	125	7.1	0.73
Horned lark (*Eremophila alpestris*), Kansas	157	11.2	0.50
Chilean pipit (*Anthus correnderas*), Chile	153	13.0	0.42

Source: After Cody 1974.

Note: In each field the three species differ in feeding niches as shown by differences in body size and bill dimensions, but each pair of equivalents is very closely matched morphologically indicating very similar niches. The meadowlarks are closely related taxonomically, but the second pair are related only at the family level, and the third pair belong to different families.

Table 7-4

Ecological equivalents in three major niches of four coastal zones of North and Central America

Niche	*Tropical*	*Coast*	*Upper West Gulf Coast*	*Upper East Coast*
Grazer on intertidal rocks (periwinkles)	*Littorina ziczac*	*L. danaxis*, *L. scutulata*	*L. irrorata*	*L. littorea*
Benthic carnivore	Spiny lobster (*Palinurus*)	King crab (*Paralithodes*)	Stone crab (*Menippe*)	Lobster (*Homarus*)
Plankton-feeding fish	Anchovy	Pacific herring, sardine	Menhaden, threadfin	Atlantic herring, alewife

arated by barriers. The large kangaroos of the Australian grassland are the ecological equivalents of the bison and pronghorn of the North American grassland (both now largely replaced by domesticated grazers). Examples of bird ecological equivalents on two continents are listed in Table 7-3. Examples of ecological equivalents in aquatic habitats are shown in Table 7-4.