Although Graham Bell has suggested that "niche" is "a term perhaps best left undefined" (Bell, 1982, p. 510), the niche concept has been an important organizing idea in ecology ever since its introduction by Joseph Grinnell and Charles Elton early in this century. Some have heralded the niche as a foundational concept and one of the most important theoretical developments of modern ecology (Hutchinson and Deevey, 1949, quoted in Krebs, 1978, p. 231). Others have criticized it as tautological (Peters, 1976), or speculated that the concept would "probably turn out to be unnecessary, allowing an always welcome simplification of ecological jargon" (Margalef, 1968, p. 7). Differing insights rest, in part, on the heterogeneity of uses to which the niche concept has been put during its "curious" history (see Cox, 1980).

The common meaning of the term "niche," according to the Concise Oxford English Dictionary, is a "vertical recess in wall to contain statue, vase, etc.; (fig.) place destined for person's occupation"; it is probable that early ecological meanings derive from the sense of a special place suited to its occupant. The history of the meanings and uses of the niche concept trace to nineteenth-century ideas of the balance of nature, design, and the superorganism. 1

Over the last century there have been three major shifts in the meaning of “niche”: (1) from the nineteenth-century focus on a species’ place in the balance of nature to concepts of the specific place or role of a population or species in an environment or community, (2) from the concept of place or role to a formal, geometric definition of the occupant of a place in terms of idealized environmental dimensions, and (3) from the formal definition to an operationalized description in terms of actual resource utilization (Schoener, 1989). In addition, uses of the niche concept have shifted as interests of animal ecologists changed from the geographical basis of speciation and evolution to problems in community structure, to the ecological dynamics of laboratory populations, and to the evolutionary dynamics of communities. More recently, some biologists have argued for a return to some of the earliest conceptions of the niche (James et al., 1984). Others have questioned some of the perceived consequences of early conceptions of the niche, particularly the heavy emphasis on the role of competition in structuring niches (Simberloff, 1982, 1984) as well as the concept of a vacant niche (Herbold and Moyle, 1986; Colwell on Niche).

Roswell Johnson (1910) is probably the first biologist to use the word “niche” to mean the place of an organism in nature (Gaffney, 1975; cf. Cox, 1980, and Schoener, 1989). Joseph Grinnell, however, was the first to develop a full account of the niche concept and to incorporate it into a broad program of biological research. Grinnell and Charles Elton introduced the niche concept independently to designate a place or role in an environment or community (Grinnell and Swarth, 1913; Grinnell, 1914, 1917a, 1924, 1928, excerpts reprinted in 1943; Elton, 1924, 1927, 1946). Grinnell's focus on environment and Elton's on community reflect their differing theoretical programs.

Their ideas about niches—extended Darwin's metaphor of a world so filled with species that the improvement of one by natural selection often implied the “wedging” out of another (see Egerton, 1977). Grinnell's focus on problems of distribution and evolution led him to think of the niche as a unit whose limits are set by factors of food supply, shelter (including refugia from enemies and safe breeding places), competition, parasitism, temperature, humidity, rainfall, insolation, nature of the soil, and others (Grinnell, 1917b, 1928). Elton's focus on food relations as the fundamental structure underlying all animal communities led him to think of niches in terms of roles in food chains, such as herbivore and carnivore, although he was aware of many factors influencing these roles.

Grinnell: Geography, evolution, and the niche. Joseph Grinnell was interested in how the evolution of the environment brings populations of animals into changing association with other plant and animal species and thus drives organic evolution and speciation (Grinnell, 1924). He used “ecologic niche” and “environmental niche” as equivalent terms (Grinnell, 1924, p. 227).

Grinnell's approach to natural history was based on late nineteenth-century traditions of biogeography, systematics, and Darwinian evolution (Mayr, 1973; Star and Griesemer, 1989; Griesemer, 1990). In considering the physical and biotic environment of a species, he developed an ecologic hierarchy of world realms, regions, life zones, faunal areas, (plant) associations, and niches to parallel the systematic hierarchy from kingdoms to subspecies (see Grinnell, 1928). Each level of the hierarchy picked out relevant environmental factors that might serve as causes of speciation through effects on the distribution and abundance of species and subspecies. Abiotic factors were mostly associated with higher levels, for example, temperature with life zones and humidity with faunal areas. At the lowest level niches were associated with a complex of biotic and abiotic factors and were unique; each species occupied one niche, that is, one set of hierarchically characterized abiotic factors plus plant and animal species that served a variety of roles as elements of each species’ environment. It is Grinnell's hierarchical concept of environmental determinants of distribution that led him to characterize the niche as the ultimate distributional unit (Grinnell, 1928).

Grinnell's most cited paper on the concept of niche is “The Niche-Relationships of the California Thrasher” (Grinnell, 1917a), although he first used the term “niche” in his 1913 Ph.D. dissertation (see Grinnell, 1914). (The 1917 paper is the first of Grinnell’s in which “niche” appears in the title, probably explaining why some authors claim 1917 as the year of Grinnell's introduction of the term—e.g., Udvardy, 1959.) It seems probable that the term emerged from discussions among the active group of faculty and students at Stanford University attracted by the evolutionist David Starr Jordan and inspired by the western biogeographic work of C. Hart Merriam, whose life-zone concept provided a starting point for much of Grinnell's work.

The term “niche” first appears in Grinnell's published work in a paper coauthored with Harry Swarth, whose later work at the California Academy of Science on speciation in Galapagos finches predates Lack's (Grinnell and Swarth, 1913; see Cox, 1980, and Kingsland, 1985). Grinnell and Swarth characterized the niche as a subdivision of association: “As with zones and faunas, associations are often capable of subdivision; in
fact such splitting may be carried logically to the point where but one species occupies each its own niche" (1913, p. 218).

Grinnell’s idea of the niche as an ultimate distributional unit flows from his conception of “competitive exclusion,” usually attributed to G. F. Gause (e.g., Hutchinson, 1957, calls it the Volterra-Gause principle; Udvardy, 1959, and Hutchinson, 1965, acknowledge Grinnell). Darwin had articulated the core idea in On the Origin of Species and Grinnell presented a similar view: “It is only by adaptations to different sorts of food, or modes of food getting, that more than one species can occupy the same locality. Two species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region. One will crowd out the other; the one longest exposed to local conditions, and hence best fitted, though ever so slightly, will survive, to the exclusion of any less favored would-be invader” (1904, pp. 375–377).

Elton: Food chains, animal communities, and the niche. Charles Elton’s widely read book, Animal Ecology, introduced a generation of scientists to a modern conception of animal community (Kingsland, 1985). The core of Elton’s theoretical outlook was that ecology is the study of what organisms are doing in their environments. By studying the circumstances and limiting factors under which animals do what they do, Elton thought it would be possible to discern “the reasons for the distribution and numbers of different animals in nature” (Elton, 1927, p. 34).

Elton’s focus on the overriding importance of food relations led him to characterize the niche primarily in terms of populations’ functional roles in a community as eaters and eaten: “Animals have all manner of external factors acting upon them—chemical, physical, and biotic—and the ‘niche’ of an animal means its place in the biotic environment, its relations to food and enemies. The ecologist should cultivate the habit of looking at animals from this point of view as well as from the ordinary standpoints of appearance, names, affinities, and past history. When an ecologist says ‘there goes a badger’ he should include in his thoughts some definite idea of the animal’s place in the community to which it belongs, just as if he had said ‘there goes the vicar’ “ (1927, pp. 63–64).

Elton’s interest in functional roles stemmed from his concern to develop a coherent account of food chains and cycles and to explain his new concept of the “pyramid of numbers,” which relates the relative sizes and numbers of organisms to their position in a food chain (1927, chap. 5). As such, he was less interested in species per se than in comparisons among local community structures that would support generalizations about food chains, size, and relative abundance. Nevertheless, Elton was aware of a wide variety of factors influencing niches, and he often mentioned microhabitat factors such as suitable soil types for nesting birds and places in which different species feed.

Despite the fact that Elton and Grinnell both considered biotic and abiotic factors, many textbooks distinguish the two by calling Grinnell’s concept the “habitat” niche and Elton’s the “functional” niche, as if to suggest that Grinnell’s concept was primarily abiotic and Elton’s biotic (Krebs, 1978; Ricklefs, 1979; cf. Schoener, 1989, for a counterargument). Whittaker et al. (1973, p. 322), following Dice (1952) and Clarke (1954), attempt to distinguish “place” and “functional” concepts of niche, arguing that the functional concept is the more fundamental and that part of the confusion of the two stems from the mixture of habitat and niche dimensions of Grinnell’s (and Hutchinson’s) views (see also Pianka, 1974, pp. 185–187). Grinnell’s and Elton’s niche concepts are better distinguished against the backdrop of their differing theoretical aims of explaining speciation versus community structure, however, rather than focusing on a few aspects of their explicit definitions of “niche” (see also Community).

Grinnell and Elton both identified the niche as the place/role a species happens to occupy in an environment, not a property of the occupying species as in the Hutchinsonian and modern resource utilization conceptions of the niche. Grinnell wrote, “if a new ecological niche arises, or if a niche is vacated, nature hastens to supply an occupant, from whatever material may be available. Nature abhors a vacuum in the animate world as well as in the inanimate world” (1924, p. 227).

The principal point on which Grinnell and Elton appear to differ is whether more than one species can occupy a single niche, but this stems from Elton’s less precise characterization of the niche; a comparison of their examples shows the two concepts to be rather similar (Schoener, 1989). Grinnell concluded that niches are unique because his taxonomical approach took all important environmental factors into account. Elton identified functional food relations in a community loosely enough to suggest that niches “are only smaller subdivisions of the old conceptions of carnivore, herbivore, insectivore, etc., and that we are only attempting to give more accurate and detailed definitions of the food habits of animals” (1927, p. 64). As functional roles, niches could be filled by distinct (but often closely related) species in different communities. Elton suggested a concept of ecological “equivalents,” arguing, for example, that an arctic niche filled by foxes that eat guillemot eggs and remains of seals left by polar bears is filled in tropical Africa by hyenas that eat ostrich eggs and remains of zebras killed by lions (1927, p. 65).

However, just as Elton recognized that factors other than food were often important in determining the species in a community, Grinnell fully recognized the functional nature of niches in his version of ecological equivalents, calling attention to “the great number of similar ecologic types of animals which are developed in widely separated regions and which are derived from unrelated stocks. The Kangaroo Rat of our deserts
corresponds ecologically to the Jerboa of the Sahara; but it is derived from squirrel ancestry, while the Jerboa is more nearly related to house mice" (Grinnell, 1924, p. 227). Grinnell's conclusion that the niches of distinct species could be ecologically similar, but not identical, probably followed from his greater attention to the vast number of determining environmental factors.

Grinnell tended to focus on the distribution of species into niches because he was an evolutionary biologist whose first concerns were speciation and the relationship between the evolution of the environment and organic evolution (Grinnell, 1924; cf. Griesemer, 1989). Populations of the same species may be distributed among a number of local communities of the sort that interested Elton. Grinnell placed great emphasis on subspecies because these are of greatest interest to evolutionists. Elton's interest in evolution appears to have had more to do with population numbers and the possible role of ecologists in solving the problem of how nonadaptive traits might spread. Elton suggested that release from competition after a population crash might allow nonadaptive traits to spread before they are scrutinized by selection (1927, chap. 12).

Early empirical studies of the niche. Empirical studies of competition in the laboratory and the field were essential to development of the niche concept (Hutchinson, 1978; Kingsland, 1985; McIntosh, 1985). G. F. Gause (1934) brought together Elton's concept of the niche and V. Volterra's mathematical descriptions of two-species interactions in predator-prey systems to found an important branch of the experimental investigation of competition. Gause's approach was to construct simple laboratory systems based on Volterra's equations in order to see whether the predicted oscillations of predators and prey could be realized. A related but different approach was pioneered by Thomas Park in experimental studies of competition among species of the flour beetle genus Tribolium (e.g., Park, 1948, 1954b; for reviews, see Neyman et al., 1956, and Park, 1962; see Park, 1939, for a contrast between Gause's and Park's approach).

Experimental studies of competition had two important consequences for the concept of the niche. First, they focused attention squarely on central theoretical problems such as the dynamics of competition and held out hope for an ecological theory based on general principles. Second, they reinvigorated the competitive exclusion principle, which stated that "complete competitors cannot coexist" (Hardin, 1960, p. 1292). Complete competitors are usually understood to be species that have identical ecological niches. Prior to the experimental studies, competitive exclusion was perceived to be a qualitative principle so obvious as to seem uninteresting (Hutchinson, 1975; Kingsland, 1985). Also, Grinnell's earlier use of competitive exclusion in an integrated evolutionary view had virtually disap-peared as geneticists took over the development of evolutionary theory and systematists developed the new speciation theory. Gause's and Park's experiments showed that the concept of niche, in the guise of determinants of relations of competitive exclusion, was central to an understanding of population dynamics and the evolutionary structuring of communities.

Some disagreement over the utility of the niche concept stems from apparent circularity of the competitive exclusion principle. If species are observed to coexist, then by the competitive exclusion principle they must have different niches to avoid competition, whether these differences are discernible or not. If species do not coexist, then they must overlap in their niches and competition prevents, or would prevent, coexistence. Such explanations appear to be "competitionist story-telling" after the fashion of adaptationist story-telling: assume that competition is ubiquitous and you will find that you can explain all community relations in terms of competition. G. E. Hutchinson (1957, p. 418) tried to rescue the competitive exclusion principle by reformulating it as an empirical claim: realized niches do not intersect.

There are still dangers of circular reasoning about niches based on studies of resource utilization, however: if species coexist and one resource dimension indicates too much overlap to permit coexistence, perhaps two resource dimensions will separate them; if two will not do, try three (see also RESOURCE). The competitive exclusion principle, and with it the niche concept, is thus reduced to triviality on the presumption that no two species will be identical in all respects, and therefore some resource dimension will explain coexistence (Hardin's "axiom of inequality"). In addition to conceptual problems, many naturalists were skeptical of the relevance of "bottle experiments" to natural populations (see, e.g., discussion by Mayr in Park, 1939, p. 254), which could only be established by attention to the problem of explaining coexistence among species in natural communities.

David Lack (1947a; see also Kingsland, 1985) studied Galapagos finch species that seemed to share niches, prompting him to give a nonadaptive explanation but then to change his interpretation in light of fine discriminations in resource utilization based on bill size. Stephen Jay Gould (1983) identifies this shift as part of a broader "hardening" of the evolutionary synthesis between the 1940s and 1960s against nonadaptive explanations.

Hutchinson and his student Robert MacArthur also raised questions about how the evolution of niches permits coexistence. Hutchinson's famous "paradox of the plankton" concerned the partitioning of an apparently homogeneous environment so as to permit coexistence of similar planktonic species (Hutchinson, 1961). His concept of limiting similarity expressed the limits of niche overlap that permit coexistence in measurable terms (Hutchinson, 1959; Abrams, 1983). MacArthur made an equally famous study of warblers that showed that careful field observation may
reveal how species avoid competition on the slenderest of niche separations (MacArthur, 1958). Equally important were the efforts by Robert MacArthur, Richard Levins, Jonathan Roughgarden, Thomas Schoener, and others to develop operational measures of niche metrics that could be applied to field studies (reviewed in Colwell and Fuentes, 1973; Schoener, 1989).

Hutchinson's geometrical abstraction of the niche. G. E. Hutchinson (1957, 1959, 1965, 1975, 1978) formalized the niche concept in terms of the occupation of a hypervolume of a phase space whose dimensions represent all the environmental factors acting on organisms. This represented a radical shift in the meaning of the niche concept from the place or role of a species or population in a community to the environment utilization properties of the occupying species (see Schoener, 1989). Although the credit for this shift is usually accorded to Hutchinson for his famous “Concluding Remarks” of 1957, Hutchinson himself credits MacArthur for the concept of fundamental niche.

The fundamental niche represented the range of environmental factors that would permit the occupying species to persist indefinitely. Points in the physical environment (biotope) map onto points in this abstract niche space. The realized niche represented that fraction of the fundamental niche in which the species actually persists, that is, the actual part of the fundamental niche that does not overlap that of other species plus that overlapping part in which the species can persist by excluding competitors. The realized niche is, therefore, defined in relation to a set of other species.

Hutchinson's conception shifted the focus away from the (possibly empty) place or role and toward the occupant of that place in a community, defined by the total multivariate range of permissive environmental conditions, including the presence of other species that may compete with the occupant for resources. Nevertheless, whether niches are environmental or populational attributions (see Colwell on NICHE) depends on how “resources” are treated. Because Grinnell and Elton emphasized other species as well as physical resources such as light and heat, “empty niches” can clearly exist in the sense that the species serving as resources might occur without the presence of a given species. Competition became of central importance in understanding the realized niche, because competitors interacted to restrict each other's occupancy of regions of overlapping niche space.

Hutchinson's definition is of the niche of a species. The region that constitutes the fundamental niche is characterized either set-theoretically or geometrically, usually in terms of the set of points (combinations of environmental factor values) at which a species persists. Hutchinson's abstraction is static, atemporal, and does not immediately suggest how to repre-
that study of their historical predecessors can provide considerable insight into modern concepts. Ecologists have not devoted the same attention to their own past, and one is tempted to speculate that some current controversies in theoretical ecology reflect a lack of attention to the historical roots of ecology’s central concepts.
KEYWORDS IN EVOLUTIONARY BIOLOGY

EDITED BY
Evelyn Fox Keller and Elisabeth A. Lloyd

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