come securely established in the place thus made free for them. Space and food are necessary as the first requisites of every social community, even in the great seas. Oyster-beds are formed only upon firm ground which is free from mud, and if upon such ground the young swarming oysters become attached in great numbers close together, as happened upon the artificial receptacles in the Bay of Saint Brieux, their growth is very much impeded, since the shell of one soon comes in contact with that of another, and they are thus unable to grow with perfect freedom. Not only are they impeded in growth in this manner, but each oyster can obtain less nourishment when placed close together than when lying far apart.

CHAPTER 7

On the Reasons for Distinguishing *Niche, Habitat,* and *Ecotope*

Robert H. Whittaker, Simon A. Levin, and Richard B. Root

In response to George Kulesza's (1975) comment [on Whittaker et al. 1973], we first restate the concepts and their relations to one another. The ecotope "describes the species' response to the full range of environmental variables to which it is exposed" and "is the ultimate evolutionary context of a species. . . . Species' distributions over ranges of habitats and migrations between communities . . . are to be understood in terms of the ecotope. The niche may moreover be regarded as the restriction of the ecotope to a particular community, however that community is defined" (Whittaker et al. 1973: 334). Niche refers to the functional relationships of a species within a community (ibid.: 332), and habitat to its distributional response to environmental factors at different points in the landscape (ibid.: 328).

Many investigations focus on the species within a community (it is in this connection that the term *niche* is most often used). Therefore, it is useful to identify the factors within a community to which species respond as "niche variables." Similarly, another tradition emphasizes the distributions of species over the landscape. When the points in the landscape are arranged along gradients of environmental factors, the distribution of a species can be analyzed in terms of "habitat variables." Clearly niche and habitat variables intergrade; distinction between them depends largely on the investigator's scale of consideration. We agree with Kulesza's point that temperature, for example, is not simply a niche or habitat factor. If one takes a forest stand as the unit of study, the temperature differences in the different strata of the community, and the daily and seasonal temperature changes to which species respond, are niche variables. Conversely, if the scale of study is larger than a community (e.g., an elevation gradient within mountains), temperature changes that characterize different environments are habitat variables.

There is indeed no discontinuity between the two groups of variables, as we

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have sought to indicate (Whittaker et al. 1973: 327, 334). However, the fact that niche and habitat factors sometimes overlap does not in itself argue against distinguishing the concepts. A great many of the concepts of science and other human discourse are based on useful distinctions recognized within (or at the poles of) continua. Clarity in both field research and ecological and evolutionary theory is served by distinguishing niche and habitat as concepts. Kulesza observes, for example, that competitive displacement can occur in different ways. When two species that are closely related, and that are closely similar in ecological relationships when allopatric, also occur sympatrically, their sizes or other characteristics may diverge in the area where they occur together. This divergence, which implies difference in niche by which the species can coexist in the sympatric area, is character displacement in the usual sense (Brown and Wilson 1956). Two closely similar species can also occur sympatrically, however, if their habitats diverge in the area of overlap, so that in this area they occur primarily in different communities. This habitat divergence can occur without morphological divergence. It is worthwhile to recognize the latter as a "habitat shift" and as an adaptive tactic permitting sympatry that is rather different from morphological divergence expressing niche difference (Schoener 1975). More broadly, it is difference in ecotope that makes sympatry possible.

We agree with Kulesza that microhabitat factors should be treated as part of the niche hypervolume. Microhabitat factors vary, in connection with the internal structure and patterning of what we reasonably interpret as a given community; these are niche variables. Species can maintain themselves within individual communities by utilizing resource patches, such as those formed by local disturbance (Levin 1974; Levin and Paine 1974; Root and Chaplin 1976). This exploitation of patchiness, which is a natural feature of most environments, is a fundamental aspect of *niche.* (Macro)habitat factors, in contrast, vary in space and relate to one another different communities in different biotopes. The distinction is not pointless because it is a matter of scale, and it is part of Hutchinson's (1958b, 1967) formulation.

We agree also that competition and other species interactions are important in determining habitat distribution. Evolutionary responses to niche and habitat factors are not separate, but there are often differences in the kinds of adaptations from which result differences in niche, in contrast to differences in habitat (Whittaker et al. 1973: 324). Niche differentiation can permit coexistence of species within a biotope. Species with nonoverlapping habitats occur in different biotopes; they do not coexist and need not evolve adaptation to one another, but they have evolved differences in response to some spatially extensive environmental factor(s). As Kulesza observes, there is a connecting case—species populations that are centered in different biotopes but meet with possible competition or other interaction where they are in contact. Furthermore, the relationships between species occupying different habitats may be subject to continued testing as propagules or immigrants of one species are wafted by passive dispersal or driven by intraspecific contest into the habitat of the other species, where they attempt to establish themselves. These types of encounter, especially where competition is involved, strengthen the interest of distinction between niche and habitat. Competition between species can lead to evolution toward: different niches that are contiguous in the niche hyperspace, with competition reduced by resource use or other difference where the species occur together; different habitats that are contiguous along extensive environmental gradients, with competition reduced by occurrence in different biotopes; or different ecotopes, with competition reduced by simultaneous divergence in niche and habitat.

The ultimate arena for consideration of species relations to environment is, of course, the ecotope. The ecotope concept is independent of the notion of community and is thus a useful concept even when niche and habitat factors intergrade. Therefore it may have most utility to ecologists dealing with motile animal populations. Thus Root (1967), while studying gnatcatcher niches within a California woodland, showed that the ability of the gnatcatcher *Polioptila caerulea* to utilize different plant formations was a critical adaptation permitting the population to ride out local fluctuation in food supply. Kulesza's citations of Grinnell (1904) and Caccamise (1974) provide other examples. The ecotope concept also offers a framework for dealing with the fact that, although species persistence in a community is often discussed in terms of niche difference, species can maintain themselves in suboptimal habitats if they are superior elsewhere and have sufficient dispersal ability (Levin 1974).

On the other hand, even for higher animals, many interesting questions concern niche relationships within particular communities, such as the birds of an oak woodland or a spruce-fir forest, the rodents or lizards of a desert, or the insects and their trophic structure on a mangrove island. The study of niches in communities is not made less important by the fact that a "community" is in many cases an arbitrarily bounded segment of a continuum. The ecotope is the true evolutionary context, but the niche is the appropriate focus of many investigations. We feel that understanding will be much advanced if biologists use *ecotope* in discussing the broader evolutionary context and restrict *niche* to the role of species within a community. In restricting *niche* to one meaning, we seek to emphasize the importance of all three concepts (niche, habitat, ecotope) by providing each with its own name.

Our article was written because of our feeling that confused usage threatened the useful life of the term *niche.* We do not seek the enshrinement of particular definitions, but we feel that science would be poorly served if individual users simply chose whatever definitions suited them; such a practice would only compound confusion. Scientific concepts develop by interaction between (a) applications that indicate directions of greatest usefulness and (b) periodic efforts at formal statement and systematic interrelation of concepts. Our effort had as its purpose strengthening the usefulness of the concepts discussed by clarifying their relations to one another and stating them in ways appropriate for research using measurements of population variables. The best test of what we have written will be its usefulness in application. We hope that application may show that our formulation of three valuable concepts—niche, habitat, and ecotope—will in practice serve well both the field researcher and the ecological and evolutionary theorist.

CHAPTER 8

Biological Diversity in Ecology

Ruth Patrick

In the field of ecology the term *diversity* is commonly used to describe the assemblage of species that interact . . . and form . . . a community. Species in the complex do not merely respond to a particular environment but create new conditions through their interactions with each other. For example, one species may modify an environmental factor such as light so that another species, or group of species, can live more successfully, or one species may be the food source for another or produce oxygen by photosynthesis, which is necessary for respiration of both. Through such interactions the community develops its identity and carries out its characteristic functions.

Diversity is a generalized term that refers to the structure of the community. In a sense, it expresses the genetic variability existing in the taxa that occur together and, therefore, the adaptive capacity of the assemblage. Thus, the measure of diversity is not merely a count of presence but rather it is a measure of the structural and functional interactions of the community.

When one considers the structure of communities of organisms, the first question that arises after one has the list of species in hand is why are there so many species with such different characteristics? Reasoning from our human experience, we might think that a single-species community structure might be more efficient. However, this is not the case. For example, at the herbivore level of an aquatic community we might find insects and fish of a variety of species, genera, and families feeding upon the plants. In another comparable community we might find protozoa, as well as insects and fish, serving as herbivores. Intuitively one would say that the gene pool present in these herbivore taxa was greater in the second case than in the first. Furthermore, the second set might consume a greater variety in size and taste preference. Its tolerance to natural products produced by various plants also might be broader; therefore, nutrient transfer from the primary production level might be more, not less, efficient (Freeland and Jansen 1974).

In general we find that species seem to prefer a variety of food rather than a

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