concept in ecology. Möbius was among the first to write about the community, but he gave it a unique name, the *biocönose,* to distinguish the ecological community from the human community. Thus, ecological concepts are grounded in many ways other than the evolutionary, systems, and natural history themes discussed in the earlier chapters. Each concept deserves analysis, which will lead to greater precision in thought and method.

CHAPTER 6

An Oyster Bank Is a Biocönose, or a Social Community

Karl Möbius

The history of the impoverishment of the French oyster-beds is very instructive. When the beds of Cancale had been nearly deprived of all their oysters, by reason of excessive fishing, with no protection, the cockle (*Cardium edule*) came in and occupied them in place of the oyster; and vast hordes of edible mussels (*Mytilus edulis*) under similar circumstances appeared upon the exhausted beds near Rochefort, Marennes, and the island of Oléron. The territory of an oyster-bed is not inhabited by oysters alone but also by other animals. Over the Schleswig-Holstein sea-flats, and also along the mouths of English rivers, I have observed that the oyster-beds are richer in all kinds of animal life than any other portion of the sea-bottom. As soon as the oystermen have emptied out a full dredge upon the deck of their vessel, one can see nimble pocket-crabs (*Carcinus moenas*) and slow horn-crabs (*Hyas aranea*) begin to work their way out of the heap of shells and living oysters, and try to get to the water once more. Old abandoned snail-shells begin to move about, caused by the hermit-crabs (*Pagarus bernhardus*), which have taken up their residence in them, trying to creep out of the heap with their dwelling. Spiral-shelled snails (*Buccinum undatum*) stretch their bodies as far out of the shell as they can, and twist from side to side, trying, with all their power, to roll themselves once more into the water. Red starfish (*Asteracanthion rubens*), with five broad arms, lie flat upon the deck, not moving from the place, although their hundreds of bottle-shaped feet are in constant motion. Sea-urchins (*Echinus miliaris*), of the size of a small apple, bristling with greenish spines, lie motionless in the heap. Here and there a ring-worm (*Nereis pelagica*), of a changeable bluish color, slips out of the mass of partially dead, partially living, animals. Black edible mussels (*Mytilus edulis*) and white cockles (*Cardium edule*) lie there with shells as firmly closed as are those of the oysters.

From *The Oyster and Oyster-Culture,* trans. H. J. Rice. In *Documents of the Senate of the United States for the Third Session of the Forty-sixth Congress and the Special Session of the Forty-seventh Congress (1880–1881),* pp. 721–24. Notes omitted.

Even the shells of the living oysters are inhabited. Barnacles (*Balanus crenatus*), with tent-shaped, calcareous shells and tendril-shaped feet, often cover the entire surface of one of the valves. Frequently the shells are bedecked with yellowish tassels a span or more in length, each of which is a community of thousands of small gelatinous bryozoa (*Alcyonidium gelatinosum*), or they are overgrown by a yellowish sponge (*Halichondria panicea*), whose soft tissue contains fine silicious spicules. Upon many beds the oysters are covered with thick clumps of sand which are composed of the tubes of small worms (*Sabellaria anglica*). These tubes, called "sand-rolls," resemble organ-pipes, and are formed from grains of sand cemented into shape by means of slime from the skin of the worm. The shell forms a firm support upon which the worms can thus live close together in a social community. Upon certain beds near the south point of the island of Sylt, where the finest-flavored oysters of our sea-flats are to be found, there lives upon the oyster-shells a species of tube-worm (*Pomatoceros triqueter*) whose white, calcareous, three-sided tube is very often twisted about like a great italic s. The shells of many oysters upon these beds also carry what are called "sea-hands" (*Alcyonium digitatum*), which are white or yellow communities of polyps of the size and shape of a clumsy glove. Often the oyster-shells are also covered over with a brownish, clod-like mass, which consists of branched polyps (*Eudendrium rameum* and *Sertularia pumila*), or they may be covered with tassels of yellow stems which are nearly a finger long and have at their distal ends reddish polyp-heads (*Tubularia indivisa*). Among these polyps, and extending out beyond them, are longer stems, which bear light yellow or brown polyp-cups (*Sertularia argentea*). Within the substance of the shell itself animals are also found. Very often the shells are penetrated from the outside to the innermost layer, upon which the mantle of the living oyster lies, by a boring sponge (*Clione cleata*), and in the spaces between the layers of the shell in old oysters is found a greenish-brown worm (*Dodecaceraea concharum*), armed with bristles, and bearing twelve large tentacles upon its neck. I once took off and counted, one by one, all the animals living upon two oysters. Upon one I found 104 and upon the other 221 animals of three different species. The dredge also at times brings up fish, although it is not very well adapted for catching them. Soles (*Platessa vulgaris*), which seek by jumping to get out of the vessel and once more into the water, stone-picks (*Aspidophorus cataphractus*), and sting-rays (*Raja clavata*), which strike about with their tails, are abundant upon the oyster-banks. Besides those already mentioned, there are many other larger animals which are taken less frequently in the dredge. There are also a host of smaller animals covered up by the larger ones, and which can be seen only with a magnifying glass. Very few plants grow upon the banks. Upon only a single one of the oyster-beds of the sea-flats has eel-grass (*Zostera marina*) taken root. Upon other beds reddish-brown algae (*Floridiae*)

are found, and, floating in the water which flows over the beds, occur microscopic algae (*Desmidiae* and *Diatomaceae*), which serve as nourishment to the oysters. If the dredge is thrown out and dragged over the sea-flats between the oyster-beds, fewer and also different animals will be found upon this muddy bottom than upon the sand. Every oyster-bed is thus, to a certain degree, a community of living beings, a collection of species, and a massing of individuals, which find here everything necessary for their growth and continuance, such as suitable soil, sufficient food, the requisite percentage of salt, and a temperature favorable to their development. Each species which lives here is represented by the greatest number of individuals which can grow to maturity subject to the conditions which surround them, for among all species the number of individuals which arrive at maturity at each breeding period is much smaller than the number of germs produced at that time. The total number of mature individuals of all the species living together in any region is the sum of the survivors of all the germs which have been produced at all past breeding or brood periods; and this sum of matured germs represents a certain quantum of life which enters into a certain number of individuals, and which, as does all life, gains permanence by means of transmission. Science possesses, as yet, no word by which such a community of living beings may be designated; no word for a community where the sum of species and individuals, being mutually limited and selected under the average external conditions of life, have, by means of transmission, continued in possession of a certain definite territory. I propose the word *biocœnosis* for such a community. Any change in any of the relative factors of a biocönose produces changes in other factors of the same. If, at any time, one of the external conditions of life should deviate for a long time from its ordinary mean, the entire biocönose, or community, would be transformed. It would also be transformed, if the number of individuals of a particular species increased or diminished through the instrumentality of man, or if one species entirely disappeared from, or a new species entered into, the community. When the rich beds of Cancale, Rochefort, Marennes, and Oléron were deprived of great masses of oysters, the young broods of the cockles and edible mussels which lived there had more space upon which to settle, and there was more food at their disposal than before, hence a greater number were enabled to arrive at maturity than in former times. The biocönose of those French oyster-banks was thus entirely changed by means of over fishing, and oysters cannot again cover the ground of these beds with such vast numbers as formerly until the cockles and edible mussels are again reduced in number to their former restricted limits, because the ground is already occupied and the food all appropriated. The biocönose allows itself to be transformed in favor of the oyster, by taking away the mussels mentioned above, and at the same time protecting the oysters so that the young may be-

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

From *American Naturalist* 109 (1975): 479–82.