Advances in Environmental Microbiology 1

Christon J. Hurst *Editor*

Their World: A Diversity of Microbial Environments

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Advances in Environmental Microbiology

Volume 1

Series Editor
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The frontispiece for this volume is titled "The Blue Marble" by the National Aeronautics and Space Administration. Globe west appears above and globe east below. Their accrediting is NASA Goddard Space Flight Center Image by Reto Stöckli (land surface, shallow water, clouds). Enhancements by Robert Simmon (ocean color, compositing, 3D globes, animation). Data and technical support: MODIS Land Group; MODIS Science Data Support Team; MODIS Atmosphere Group; MODIS Ocean Group Additional data: USGS EROS Data Center (topography); USGS Terrestrial Remote Sensing Flagstaff Field Center (Antarctica); Defense Meteorological Satellite Program (city lights)

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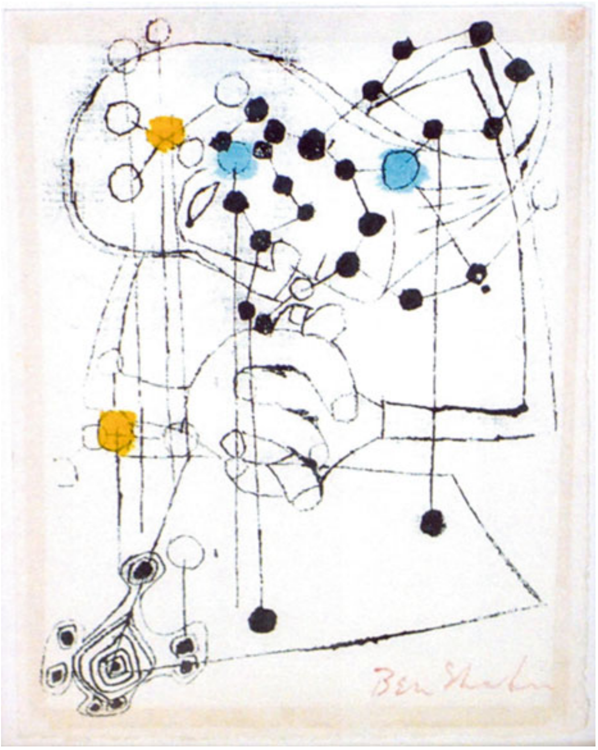
Dedication

There are many people whom I should thank for their having encouraged me towards my career as a scientist. When I was 9 years old I was accepted a year early into the Junior Naturalist program instructed by Edith Blincoe at the Dayton Museum of Natural History in Dayton, Ohio. That was about the time when I received a chemistry set from my parents. I set up my laboratory on a folding aluminum picnic table and for years everyone around me suffered the strange and often sulfurous odors of experiments which I was restricted to doing outdoors. The only remains of that chemistry set are the two test tube racks which sit in my office, and a metal stand which I have used as a support for ceramic modeling. Both of my parents had been chemists, my mother worked at a drinking water treatment facility and my father studied air quality. Perhaps it was little surprise to them when eventually I too headed into environmental science. The microbiology aspect of my studies began a year later, after my family had moved to Cincinnati, Ohio. In fifth grade, when I was 10 years old, at Bond Hill Elementary School I first saw a microscope and was one of the few students whom the teacher trusted to use that amazing tool without her supervision. The teacher arranged for me to spend every morning for 2 weeks during the following summer, when I was still 10 years old, in the bacteriology laboratory of Cincinnati General Hospital in Cincinnati, Ohio. There, the bacteriologist taught me how to culture throat swabs, identify the cultured bacteria using multiple tube fermentation tests, plus stain and microscopically examine the cultured bacteria. My mother faithfully dropped me off at the hospital every morning, and then returned to take me back home at noon. My father eventually left his old college parasitology textbook in a place where I could find it, and my fate in science continued to unfold.

My efforts at learning microbiology continued when J. Robie Vestal became my undergraduate research advisor and subsequently also my post-doctoral advisor at the University of Cincinnati. Robie shared with me his enthusiasm about environmental microbiology. My enthusiasm about sailing eventually resulted in Robie buying his first sailboat, and I remember the day when I helped him learn how to ride across the waters surface by harnessing the wind. He became a very dear friend of mine and together we shared some heartfelt conversations. We even shared a common name, because the initial J represented the same name for him as it does for me, James. I am delighted to think about Robie and my fond memories of him. It has been nearly 25 years since Robie passed away and yet I almost can feel him beside me as I write this, he would be smiling and proudly say that I had become a big mucky-muck. It is with tremendous appreciation that I proudly dedicate this volume and my work on this book series in memory of Robie. By having accepted me into his laboratory, Robie also merits a commendation for bravery.

J. Robie Vestal (1942–1992)

A piece of artwork which has inspired me for many decades is titled Scientist, by Ben Shahn. The title of scientist is something towards which one optimistically strives during the course of their career. That is not a title which you can presume for yourself, but instead it must be awarded to you by others. Robie was one of the people in my life who clearly were scientists and they formatively encouraged me onward. Hopefully, someday I too could be considered to merit the title.



“Scientist” by Ben Shahn, used with permission

Series Preface

The light of natural philosophy illuminates many subject areas including an understanding that microorganisms represent the foundation stone of our biosphere by having been the origin of life on Earth. Microbes therefore comprise the basis of our biological legacy. Comprehending the role of microbes in this world which together all species must share, studying not only the survival of microorganisms but as well their involvement in environmental processes, and defining their role in the ecology of other species, does represent for many of us the Mount Everest of science. Research in this area of biology dates to the original discovery of microorganisms by Antonie van Leeuwenhoek, when in 1675 and 1676 he used a microscope of his own creation to view what he termed "animalcula," or the "little animals" which lived and replicated in environmental samples of rainwater, well water, seawater, and water from snow melt. van Leeuwenhoek maintained those environmental samples in his house and observed that the types and relative concentrations of organisms present in his samples changed and fluctuated with respect to time. During the intervening centuries we have expanded our collective knowledge of these subjects which we now term to be environmental microbiology, but easily still recognize that many of the individual topics we have come to better understand and characterize initially were described by van Leeuwenhoek. van Leeuwenhoek was a draper by profession and fortunately for us his academic interests as a hobbyist went far beyond his professional challenges.

It is the goal of this series to present a broadly encompassing perspective regarding the principles of environmental microbiology and general microbial ecology. I am not sure whether Antonie van Leeuwenhoek could have foreseen where his discoveries have led, to the diversity of environmental microbiology subjects that we now study and the wealth of knowledge that we have accumulated. However, just as I always have enjoyed reading his account of environmental microorganisms, I feel that he would enjoy our efforts through this series to summarize what we have learned. I wonder, too, what the microbiologists of still future centuries would think of our efforts in comparison with those now unimaginable discoveries which they will have achieved. While we study the many

Christon J. Hurst in Heidelberg

wonders of microbiology, we also further our recognition that the microbes are our biological critics, and in the end they undoubtedly will have the final word regarding life on this planet.

Indebted with gratitude, I wish to thank the numerous scientists whose collaborative efforts will be creating this series and those giants in microbiology upon whose shoulders we have stood, for we could not accomplish this goal without the advantage that those giants have afforded us. The confidence and very positive encouragement of the editorial staff at Springer DE has been appreciated tremendously and it is through their help that my colleagues and I are able to present this book series to you, our audience.

Cincinnati, OH Christon J. Hurst

Foreword

The terms "Environmental Microbiology" and "Microbial Ecology" are often used interchangeably. In fact, a Wikipedia search for the former redirects to the latter. However, I always felt they were distinct disciplines.

To me, microbial ecology is the basic science whereas environmental microbiology focuses on specific environments, generally with a more "applied" focus. In fact, almost 50 years ago, when I published my book (*Principles of Microbial Ecology*, 1966, Prentice-Hall, Inc) I was motivated by the fact that microbial ecology had become fragmented into subfields such as soil, food, marine, aquatic, and medical microbiology. This fragmentation is now no longer the case, as the table of contents in the present series shows.

In *Principles* I wrote: "There are two groups of people who study ecological problems: those who are habitat-oriented and those who are organisms-oriented . . .. Microbial ecology embraces both approaches to ecology. Because microbes are so closely coupled to their environments, the habitat must always be taken into

Tom Brock in Yellowstone National Park, July 2002 account. And because of the peculiar experimental difficulties of microbiology, requiring the use of pure cultures for almost any study, the organism must always be reckoned with . . .. Thus I visualize microbial ecology not as a peripheral but as a central aspect of ecology . . .. Microbes play far more important roles in nature than their small sizes would suggest."

I also noted in *Principles* that microbial ecology was developing more slowly than the other branches of ecology, . . . "because it . . . has been out of fashion with microbiologists. Yet, microbial ecology has the potential of becoming the most sophisticated branch of ecology . . ."

To a great extent, this prediction has been fulfilled, as this series illustrates and I am glad to see it published.

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Volume Preface

This book introduces the series *Advances in Environmental Microbiology* by presenting a broad perspective regarding the diversity of microbial life that exists on our planet. Although we often identify Earth as the planet of humans, this planet does not belong to just ourselves, and the planets metabolic balance mostly is ruled by its microorganisms. And so, I use the word our in reference to all of the world's species. Humans are only one part of the biofilm that has developed on our wet, rocky world. The first two chapters of this book present theoretical perspectives that help to understand a species niche and habitat. Chapter three addresses the fossil record of microorganisms. The subsequent chapters in this volume then introduce microbial life that currently exists within various terrestrial and aquatic ecosystems.

I wish to thank the following people who very graciously served as reviewers for this volume: Teckla G. Akinyi, David A. Batigelli, Alexa J. Hojczyk, Karrisa M. Martino, and Lord Robert M. May of Oxford. I am tremendously grateful to Hanna Hensler-Fritton, Andrea Schlitzberger, and Isabel Ullmann at Springer DE, for their help and constant encouragement which has enabled myself and the other authors to achieve publication of this collaborative project.

Cincinnati, OH Christon J. Hurst

Contents

Chapter 1
Towards a Unified Understanding of Evolution, Habitat and Niche

Christon J. Hurst

Abstract Evolution, the compartmentalization of habitats, and delineation of a species niche, function in a coordinated way and have unifying commonality in that each generally can be perceived as a balance of forces acting in opposition against one another. We intrinsically think of habitats as occupying a volume of space, but it also is possible to similarly imagine a niche in that way. This chapter suggests the depiction of a niche as having some theoretical volume, termed niche space. The concept of niche space can be assessed as pertaining either to an individual species or a larger taxonomic grouping as a whole, and can be envisioned as a multidimensional surface. Each biological group will attempt to occupy the greatest possible amount of niche space, and its competitive efforts will include speciation as either necessary or possible so as to achieve expansion into additional niche space while successfully defending that space which it already holds. Images of sculptures are used to help visualize the processes of how creating new niches and movement into existing but otherwise occupied niche space results from an outward evolutionary pressure acting against resistive exclusion. The niche determines the form of species which occupy it. If a niche closes then those species which occupy that niche will be doomed to extinction. Examples are presented which illustrate that if the same niche reopens at another time in either the same or a different location, then a new species with similar anatomical characteristics will evolve to occupy that reopened niche.

1.1 Introduction

The concepts of evolution, habitat, and niche, unite as three aspects of an interactive process. Evolution is the development of species through a process of sequential selections based upon the adequacy and comparative fitness of individuals metabolic and physiologic traits, driven by the search to find and utilize potential energy resources. The ecology of a species has two components, a habitat that is physically

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defined, and a niche that is biologically defined. If I could give you a phrase to ponder as we begin our journey together in an effort to mutually understanding these concepts, it would be that "a species inhabits its niche while dwelling within its habitat." More basically worded, the habitat is where members of a species live, and the niche is what members of the species do within that habitat. Without a potentially habitable location, there can be no evolution to develop and occupy the niches which exist within that habitat. If given the existence of a habitat, then evolution will produce species capable of using the energy resources available in that habitat, and utilization of those resources is done through interaction with other species which occupy connecting niches. Accomplishing that usage of resources will change the habitat and may include competition between species. Those changes and competitions can in turn help to drive additional evolution. Trying to comprehend how these three concepts of evolution, habitat and niche interrelate thus requires a unified understanding.

The potential habitat of a species may be very broad, and that potential habitat will have been defined by the evolutionary path which produced the species. However, the species will be restricted to residing within a more limited operational habitat which is defined by abiotic and biotic considerations. Those restrictions most notably are imposed by availability of resources and competition from other species. The potential niche of a species also will have been defined by evolution and that potential niche may be very broad, although the species will be restricted to a more limited operational niche as similarly defined by biotic and abiotic considerations. It is possible to understand the concepts of habitat and niche, both at the potential and operational levels, on a larger scale pertinent to the biological lineage of those taxonomic groupings which represent the evolutionary origin of a given species. Thus, each biological phylum, class, order, and family generally can be understood to have its collective habitat and niche.

Having prefaced this chapter with those statements, then it is important to add mention that once a species has evolved to occupy some given niche which exists within a specified habitat, the species becomes constrained by that evolutionary outcome. Those constraints include the necessity of surviving within a definable combination and range of environmental conditions that can be described mathematically in the form of vital boundaries (see Chap. 2, Hurst 2016) which are operationally defined by the physiological and metabolic limitations of a species.

1.2 Evolution

Evolution is a process of custom tailoring and its specificity is evidenced by the characteristic nature of the communities that are present within individual habitats. Thusly, many of the bacteria, fungi, and protozoa present in surface waters are not characteristic of soils. The types of autotrophic organisms, those which derive their operating energy either from photosynthesis (photoautotrophic) or chemosynthesis (chemoautotrophic) that are found in soils are often quite different from organisms found on the surfaces of leaves. These contrast with the often equally specific heterotrophs, organisms which derive their operating energy from organic compounds found in their surrounding environment. The forces of selection often are based upon nonbiological environmental characteristics that require a community able to cope with restraints or limitations such as a low pH, exposure to high radiation intensity, and absence of available oxygen. Such abiotic (not biological in origin) factors are often reasonably easy to demonstrate. However, more difficult to establish and often scientifically more interesting are the biotic (of biological origin) stresses such as the types and concentrations of readily available carbon sources that are available in environments. Biotic stresses can dominate the composition of communities in which major abiotic stresses do not make those determinations.

1.3 Habitat

Habitat is a term which could be defined as the place where everything must occur, and that definition requires understanding a complex combination of characteristics including not just the physical location but also the suitability of environmental conditions. Both habitat and niche exist not only in space but also in time. A location which represents a comfortable habitat, and accommodates the niche requirements for a species, may change to conditions that are less suitable and those changes may be cyclic. The result can be some requirement for a species either to enter hibernation until more favorable conditions hopefully resume, or for that species to move from one place to another. Examples of such movement include migrations of various distances, and we require an understanding that endosymbiont transference between hosts also represents migration.

Habitats are defined by gradients representable as mathematical variables with the physical and chemical conditions, abiotic and as well as biotic, combining to create locations that can be detailed either broadly or narrowly. Habitats can be considered from the perspective of zones, a concept that Grinnell (1917) termed as being “life zones.” We can define such habitational zones in many ways, they are generally representative physical areas which include the more specified habitats occupied by individual species. Perhaps the most obvious approach would be to organize habitational zones by climate classification. That concept includes physical traits among which are the temperature of a particular location, whether that location is terrestrial versus aquatic, and altitude versus depth relative to oceanic surface level. One climate classification approach which includes both altitude and aquatic depth information yields the following list: alpine, subalpine, highland, lowland, riverine, estuarine, littoral, continental shelf, continental slope, and abyssal. Another approach is classification using latitude, which divides the earths geographical zones into frigid versus either temperate or torrid.

A large terrestrial surface area, for example, can be divided into zones on many different size scales by using increasingly selective criteria. A few of those criteria could be grouped into categories with a required understanding that the categories strongly overlap and interrelate. The category of climate is abiotic and comprised of such factors as insolation, temperature including the way in which temperature is impacted by altitude, plus atmospheric humidity which is related both to temperature and level of precipitation. Chemistry of the ground or surface matrix will be another abiotic component, in addition to whether that matrix is of either consolidated rock, loosely deposited material, or a developed soil. The physical aspects of valleys and either hilltops or mountain tops versus their slopes is a major abiotic consideration, along with a consideration of which parts of that terrestrial area are cultivated versus those which are not. Cultivation, including the application of agricultural chemicals and irrigation, will of course impact both the abiotic chemistry and biotic factors pertinent to a location. The consideration of ground surface is accompanied by additional abiotic factors including its porosity, which is a measure of how much of that matrix is open space, and its permeability which in this case would be a measure of the ease with which water as a vital fluid can move through those pores. The root zone and deep subsurface will have their own sets of abiotic and biotic factors and of these, at least the root zone will be chemically impacted by the plants and animals residing there. The living components of an ecosystem are, of course, its biotic factors. Typically the living components are sorted into two groups with regard to whether they are either autotrophs or heterotrophs as mentioned above. Autotrophs can satisfy their nutritional requirements from substances in their surroundings by using either radiant energy or chemical energy to obtain usable carbon from inorganic sources. Heterotrophs get their reduced carbon from other organisms. Biotic considerations include competitive exclusions, plus an understanding of which other predator or prey species may be present, and the possibility of beneficial symbioses and commensal interactions. When considering the biotic aspects affecting microorganisms that are endosymbiotic, we would need to address as distinguishing environmental characteristics a variety of factors relating to the hosts' individual cells, tissues and organs. In the microbial world, a life zone might be only a few millimeters thick and scarcely larger than that in circumference.

Elton (1927) did a good job of distinguishing potential terrestrial habitats in the state of California, United States of America, based upon the plants which lived in a particular area. For uncultivated land, he considered such distinct main zones as grassland, bracken with scattered trees potentially forming a sort of bracken savannah, and woodland. If considering only the woodland, then the biotic factors would include the types of trees. Zonations in the tree-tops would include leaves versus twigs and branches, plus the under bark and rotten wood of branches. For tree trunks, we would need to consider the upper part with lichens as being somewhat drier, versus the lower part with mosses and liverworts as being damper owing to run-off from the trunk. The undergrowth includes a litter containing dead leaves, underlain in some places by a moss carpet, beneath which is the surface soil, and finally the underground.

Ricketts and Calvin (1948) described that the general area between high and low tides on the ocean shore can be divided into zones based upon the periodicity of immersion, depth within the deposited shore materials, presence of other biotic materials such as plants or invertebrates, and abiotic conditions such as the presence of either rocks or anthropogenic structures. The invertebrates present, and correspondingly of course the microbial populations present, would be different in each zone. An overlapping range of abiotic and biotic factors would similarly divide aquatic environments into zones, with each zone definably having its own suitability for the species found there (Hutchinson 1957). Each of these three authors, (Elton 1927; Ricketts and Calvin 1948; Hutchinson 1957) addressed their subject from the perspective of studying macroorganisms, and their concepts of zones often were defined from the relative perspective of which macroorganism species are found in any particular place. However, their insights directly apply to the study of microorganisms.

Each habitat contains its own characteristic set of niches along with the species which correspond to those niches. The groups of species, which are termed communities, and the location of their individual component species down to the level of each individual member of a species within a habitat, relates to abiotic factors as well as biotic factors. This seems like a circular path of understanding, and indeed it truly is! The biotic considerations and to some extent the abiotic considerations, including the important way in which both relate to the availability of nutrients, vary as a result of non-equilibrium conditions as explained by Hutchinson (1961). The result of an increasingly detailed zonation is subdivision of a physical habitat into increasingly smaller spaces. Presence of the individual species found within any given place relates both to the suitability of that place, as expressed in terms of whether the corresponding needs for the niche of a particular species are satisfied, along with the possible existence of exclusionary pressure exerted by other species which are competing for similar space and resources. The questions of suitability and exclusion produce minute distinctions resulting in a three dimensional patchwork of niche spaces within a habitat and this corresponds to an arrangement of how various species are located within a biotope (in German, *biotop*) as illustrated by Hutchinson (1957).

The habitat of a species can be defined on two levels. Its potential habitat would consist of all locations where the abiotic and biotic conditions are suitable for permanent settlement. The operational habitat will be smaller, reflecting a truth that the location in which members of any one species can live often will be limited by competitive pressure from other species. Figure 1.1 is a presentation of how mutually exclusive forms appear in a three dimensional space, and is being used at this point in the chapter to visualize the subdivision of a habitat. In this case, each color represents a different species. The species represented by orange presumably could occupy this entire volume as its potential habitat, but instead this species is being restricted to occupying a smaller volume as its operational habitat due to competitive pressure from its neighboring species. This same illustration also could serve as a visualization of competition between species for niche space, and to that end I again will refer to this same figure later in the chapter.

The parts of a species' habitat either may be contiguous or separated by barriers, with some examples of barriers being listed in Table 1.1. Many barriers can be

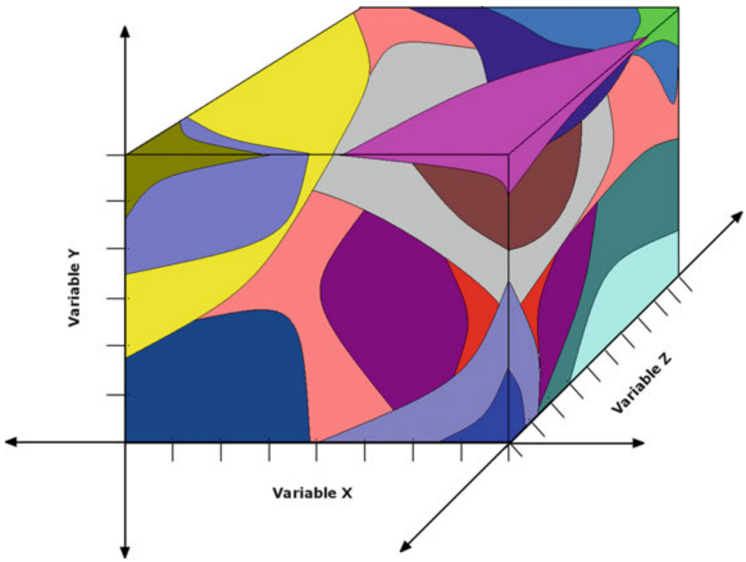

Fig. 1.1 Mutually exclusive forms in a three dimensional space. This figure is being used to represent the result of competition between different species, depicted here as different colors, for living space described as habitat within a three-dimensionally defined location. This figure also could be used more basically as a representation of competition for niche space, although that type of usage needs to be accompanied by an understanding that truly depicting niche space would require incorporating a far greater number of dimensions as variables. The factor of time has not been included here for the sake of simplicity. However, the importance of time cannot be considered negligible because the competition for niche space and its accompanying partitioning of habitat space results in three-dimensionally defined spatial arrangements or patterns of species appearance that consequently change with time. The term biotope often is used to describe the location pattern which results when species partition available living space

physically defined and are determinable by physical measurements. Such barriers also may be tangible. For example, a species' oxygen requirements may turn geographical features into barriers. Barriers are not fixed with regard to either location or time. Barriers can appear, disappear, and move, with examples being the fact that mountain ranges rise and fall, glaciers advance and retreat, continents shift, and competing species evolve or become extinct. Species tend to evolve survival mechanisms that allow their individual members to successfully move as the conditions of a habitat change and as their pertinent barriers move. Cyclical migrations are a particularly noticeable example of species movement, in which the continuing survival of a species depends upon periodic relocation between parts of their habitat. For example, seasonal migrations occur among many species of bats, birds, butterflies, caribou, salmon, and whales. Even trees migrate, albeit on a longer time scale, as evidenced by their having advanced and retreated in correspondence with cyclical patterns of glaciation (Pitelka and Plant Migration Workshop Group 1997). In the cases of monarch butterflies and maple trees, no individual member of the species completes the full migration. The populations

Table 1.1 Barriers to species movement as generally considered from the perspective of preventing infectious diseases

Categories of Chemical Barriers
Ionic (includes pH and salinity)
Surfactant
Oxidant
Alkylant
Desiccant
Denaturant
Categories of Physical Barriers
Thermal
Acoustic (usually ultrasonic)
Pressure
Barometric
Hydrostatic
Osmotic
Radiation
Electronic
Neutronic
Photonic
Protonic
Impaction (includes gravitational)
Adhesion (adsorption)
Electrostatic
van der Waals
Filtration (size exclusion)
Geographic features
Atmospheric factors
(Includes such meteorological aspects as humidity, precipitation, and prevailing winds)
Categories of Biological Barriers
Immunological
(Includes specific as well as nonspecific)
Naturally induced
(Intrinsic response)
Naturally transferred
(Lacteal, transovarian, transplacental, etc.)
Artificially induced
(Includes cytokine injection and vaccination)
Artificially transferred
(Includes injection with antiserum and tissue transfers such as transfusion and grafting)
Biomolecular resistance
(Not immune-related)
Lack of receptor molecules
Molecular attack mechanisms

(continued)

Table 1.1 (continued)

(Includes nucleotide-based restrictions)
Antibiotic compounds
(Metabolic inhibitors, either intrinsic or artificially supplied)
Competitive
(Other species in ecological competition with either the microbe, its vectors, or its hosts)

of microbial species whose lives are either dependent upon or interdependent with migrating macrobial hosts must successfully comigrate in conjunction with their hosts, because a failure of successful comigration could well result in extinction of the microbial species. Many other species choose metabolic hibernation rather than migration as a way of surviving periodically unfavorably habitat conditions, and similarly their microbial symbionts must survive that period of hibernation.

1.4 Niche

Niche is a term which could be defined as the way in which a species biologically fits into its habitat, including its total collective activities and interactions both with its surrounding physical environment and also with other species encountered in that habitat. The term niche similarly can apply to the collective actions of even larger taxonomic groups within their respective habitats.

Each species evolves to occupy a single specific niche. And, it is important to remember that when we examine the morphological characteristics and behavior of a species we actually are viewing the biological representation of its niche. Where evolution occurs so to does homeostasis, which is a collective biological force generally perceived as preferring constancy and resisting change. Homeostasis is a stabilizing mechanism that represents the interlocking biological activities of those species which occupy connecting niches. Not everything represents happiness within that interlocking community, because the activities include competition and predation in addition to cooperation. It is important to note that both biological invasions including those attributable to pathogens, as well as natural phenomenon such as cyclical fluctuations and unidirectional changes in climate, periodically throw a figurative wrench into this mixture of activities. Homeostasis is powerful but not infallable, and conceivably it needs a measure of flexibility in order to allow the community some long term potential for change in membership and activities. Unless there were at least some capability for change, having a rigid sense of homeostatic inflexibility could result in an entire community collapsing should a part of the community fail consequent to the appearance of that figurative wrench.

Extinction is the consequence of a species failure to successfully thrive in this milieu. These three forces or evolution, homeostasis and extinction metaphorically could be envisioned as the Hindu trimurti, depicted in Fig. 1.2. The trimurti consists

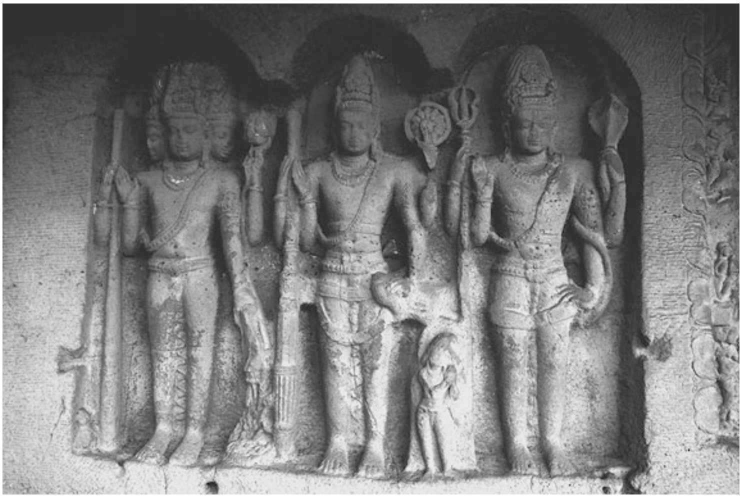

Fig. 1.2 The trimurti of Hindu Gods. This image titled "Trimurti ellora" is by Redtigerxyz and used under the Creative Commons Attribution 2.0 Generic license. It shows a sculpture depicting *from left to right* Brahma, Vishnu, and Shiva at Ellora Caves. It is being presented here with Brahma the creator philosophically representative of evolution, Vishnu the preserver of balance philosophically representing homeostasis, and Shiva the destroyer philosophically representing extinction

of three gods with Brahma representing creation, Vishnu representing the existence of a balancing force, and Shiva representing destruction.

1.4.1 Evolution and Niche

The availability of an energy resource enables evolution and for this reason we cannot completely separate the two concepts of evolution and niche. Both the characteristics of the available energy resource as well as the physical and chemical characteristics of the available habitat in which that resource is located represent some of the pressures which define a niche. In turn, the requirements of a niche determine the form, physiology and metabolic characteristics of those species which evolve to occupy that niche.

As is the case with a species habitat, the niche of a species can be defined on two levels. The species potential niche would consist of all possible conditions and interactions for which a species has become suited as a consequence of its evolutionary development. The operational niche of that species will be smaller, reflecting a truth that the conditions under which members of any one species can live often will be limited by such factors as competitive interactions with other species existing within the same habitat area. At this point I refer you again to Fig. 1.1, which can be perceived as representing how the opportunities of one