

Community Structure and the Niche

PAUL S. GILLER

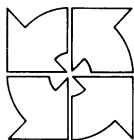


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Editors' Foreword

Both in its theoretical and applied aspects, ecology is developing rapidly. This is partly because it offers a relatively new and fresh approach to biological enquiry; it also stems from the revolution in public attitudes towards the quality of the human environment and the conservation of nature. There are today more professional ecologists than ever before, and the number of students seeking courses in ecology remains high. In schools as well as universities the teaching of ecology is now widely accepted as an essential component of biological education, but it is only within the past quarter of a century that this has come about. In the same period, the journals devoted to publication of ecological research have expanded in number and size, and books on aspects of ecology appear in ever-increasing numbers.

These are indications of a healthy and vigorous condition, which is satisfactory not only in regard to the progress of biological science but also because of the vital importance of ecological understanding to the well-being of man. However, such rapid advances bring their problems. The subject develops so rapidly in scope, depth and relevance that text-books, or parts of them, soon become out-of-date or inappropriate for particular courses. The very width of the front across which the ecological approach is being applied to biological and environmental questions introduces difficulties: every teacher handles his subject in a different way and no two courses are identical in content.

This diversity, though stimulating and profitable, has the effect that no single text-book is likely to satisfy fully the needs of the student attending a course in ecology. Very often extracts from a wide range of books must be consulted, and while this may do no harm it is time-consuming and expensive. The present series has been designed to offer quite a large number of relatively small booklets, each on a restricted topic of fundamental importance which is likely to constitute a self-contained component of more comprehensive courses. A selection can then be made, at reasonable cost, of texts appropriate to particular courses or the interests of the reader. Each is written by an acknowledged expert in the subject, and is intended to offer an up-to-date, concise summary which will be of value to those engaged in teaching, research or applied ecology as well as to students.

Community Structure and the Niche

Paul S. Giller

*Department of Zoology,
University College, Cork,
National University of Ireland*

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Preface

During the past two decades, there has been a gradual change of emphasis in ecological studies directed at unravelling the complexity of natural communities. Initially, the population approach was used, where interest lay in the way individual populations change and in the identification of factors affecting these changes. A good understanding of the dynamics of single populations is now emerging, but this has not been a very fruitful approach at the community level. In the natural world, few species can be treated as isolated populations, as most single species are the interacting parts of multispecies systems. This has led to a community approach, involving the study of interrelationships between species within communities and investigation of the actual organization of natural communities as a whole. The formalization of a number of new concepts and ideas has evolved from this approach, including niche theory, resource allocation, guild structure, limiting similarity, niche width and overlap etc., which, until fairly recently, have been examined mainly from a theoretical point of view. However, a wealth of field data is gradually being added to the literature, especially from the general areas of island biogeography and resource partitioning amongst closely related species.

Community structure embodies patterns of resource allocation and spatial and temporal abundance of species of the community, as well as community level properties such as trophic levels, succession, nutrient cycling etc. It would be difficult to approach all aspects of this complex and wide-ranging concept in a book of this size. However, by concentrating on two important indices of community

organization, namely the number of species and their relative abundance, one can begin to explore the design and functioning of natural communities and also begin to identify the patterns and ground rules of their structure.

An understanding of how communities function has practical implications in such diverse areas as land and water management, management of crop pests, design of conservation regions, controls of vectors of tropical disease and management of world fish stocks. There is thus a clear need to provide answers to questions about the nature of the structure and dynamics of natural communities.

This book is intended to give an introduction to the current theories and ideas on community structure and to provide an opening into the vast and detailed literature now available. The study of community ecology is in a state of flux, and will continue to be so until sufficient field data are available to test thoroughly the current theories and indicate in which direction new theories should go. There is thus huge scope for further work in this rapidly expanding field of ecology.

Chapter 1

Introduction and definitions

1.1 The community

At its simplest, the term community describes a group of species populations occurring together, as in a pond or woodland. However, many workers will refer to communities of birds, insects or plants for example, which causes confusion over the scale and true ecological meaning of the community. The term assemblage is a more appropriate description for such a group of similar species populations occurring together (i.e. an assemblage of birds, insects or plants). A community of organisms should be viewed more as an organized whole, and any definition should encompass interactions among constituent populations, i.e. an association of interacting populations of all trophic levels occurring in a given habitat [1]. Species do adapt to the presence of other species, so, just as populations have properties over and above those of the individuals comprising them, the community is more than the sum of the individual populations and their interactions [2]. Whittaker's definition [3] is the most precise to date, describing a community as a combination of plant, animal, and bacterial populations, interacting with one another within an environment, thus forming a distinctive living system with its own composition, structure, environmental relations, development and function. Despite this precision, it is difficult to say what a natural community is and how one recognizes it, so the concept of a community is often an abstraction. Communities are, in reality, open, generally intergrading continuously along environmental gradients rather than forming clearly separated zones as

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envisaged by early thinkers [2, 4]. Similar difficulties in identification have been faced by population biologists. Sometimes environmental heterogeneity and topographical barriers delimit a natural population; sometimes judgement, arbitrary selection or experimental demands are applied. The same criteria are used by the community ecologist. For example, some theoreticians simply specify an arbitrary set of species [5]. Another technique delimits communities objectively, using what is known as a species—area curve. By recording cumulative numbers of species in an expanding area, a characteristic curve results (Fig. 1.1). The minimal area that includes the community's representative species combination is given where the curve reaches its asymptote. Lake and woodland communities are somewhat easier to delimit, although one often arbitrarily considers only a part of such systems. Despite difficulties of definition, the study of the community is an important step in our study of the natural world as a whole.

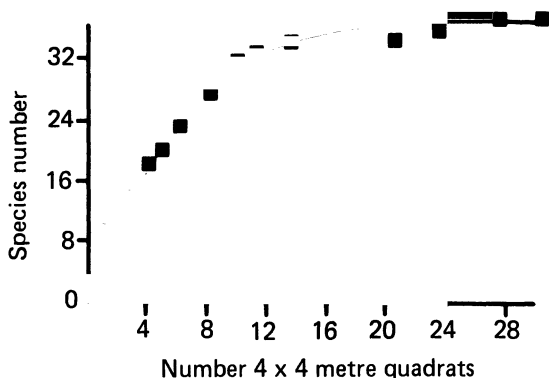


Fig. 1.1 Mainland species—area curve from a forest understory plant assemblage in North Carolina. (After McNaughton and Wolf [6]).

1.2 Community structure

It is generally believed that communities, as living systems of interacting species populations, are organized in some way, and that the role of the community ecologist is to unravel and explain that organization. One theme of this book is to identify and discuss the patterns which do seem to confer some degree of organization on to communities.

1.2.1 Levels of study

A possible method of investigating community organization

is at the individualistic level, where the behaviour and population dynamics of individual species are examined in terms of interactions between and within the populations. Such a method, originated for population studies of single species or species pairs, is difficult to extend to multispecies situations [7], so an alternative, holistic, approach tends to be used, focusing on the overall aspects of community structure. This type of investigation is helped by the concept of a guild; an assemblage of species utilizing a particular resource or group of resources in a functionally similar manner [8]. Members of such guilds interact strongly with one another and weakly with the remainder of the community. One could thus speak of an insectivorous bird guild or a habitat guild of lizards. This level of study is important, as guilds presumably represent the arenas of most intense interspecies interactions [9].

1.2.2 A definition

Plant and animal ecologists may appear to differ in their interpretation of the term community structure, but fundamentally, they both refer to the same phenomenon. Community structure embodies (a) all the various ways individual members of communities relate to and interact with one another (i.e. patterns of resource allocation and spatial and temporal abundance of species of the community); (b) the community level properties arising from these relations (such as trophic levels, succession, rates and efficiencies of energy fixation and flow, nutrient cycling etc.). It would be difficult to approach all aspects of this complex and wide-ranging concept in a book of this size. However one can examine the structure of communities by concentrating on two important indices of community organization, namely the number of species and their relative abundance [10]. Using these indices one can then try to answer the following questions:

- (i) How do species fit together to form a community?
- (ii) What determines the numbers of species making up different communities?
- (iii) How might the interactions between species populations set an upper limit to this number?
- (iv) What are the implications of differences in relative abundances of species in a community?

With this information, the ecologist may then investigate

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the similarity of community patterns from different geographical areas, validate the structured nature of natural communities, and begin to identify some of the 'ground rules' of this organization. In simple terms, ecologists observe that biotic communities differ dramatically in the numbers of plant and animal species they support (i.e. species richness), and that, given this species richness, communities show differences in the relative abundance of constituent species. We are eager to discover why!

1.3 Species diversity

In addition to simple species number indices, species diversity is often used as a more representative measure of community richness, as it incorporates both species number and relative abundance. The choice of index, from the bewildering variety available, depends on such factors as the difficulty in appraisal of species abundance and success in sampling and identifying all species present. The derivation, theory and use of such diversity indices can be found in several reviews [11, 12]. For many purposes, the number of species present is the simplest and most useful measure of local or regional diversity.

1.4 Trends in species richness

1.4.1 *Latitudinal gradients*

One method of estimating the number of species occurring within different regions is to partition maps of large land areas into equal sized quadrats, on which range maps of individual species are superimposed [13, 14]. These and other studies have revealed the well-known latitudinal gradients of species richness, where, in most groups of organisms, the number of species increases markedly towards the equator. An obvious example is a comparison of the variety of trees in most tropical rain forests with the solid stands of timber in boreal regions. Nesting birds show a typical latitudinal gradient (Fig. 1.2) and Fischer describes similar gradients for ants, corals, tunicates, amphipods, nudibranchs and gastropod molluscs [15]. More recent examples include American insectivorous birds [14, 16], lizards (Fig. 1.3) and Australian endemic *Drosophila* [17]. One of the drawbacks to such studies lies in the fact that the number of habitats in a given quadrat or area relates to topographical relief. Another is that there is a greater diversity of habitats in low latitudes (e.g. ranging from tropical to boreal with altitude) than in higher

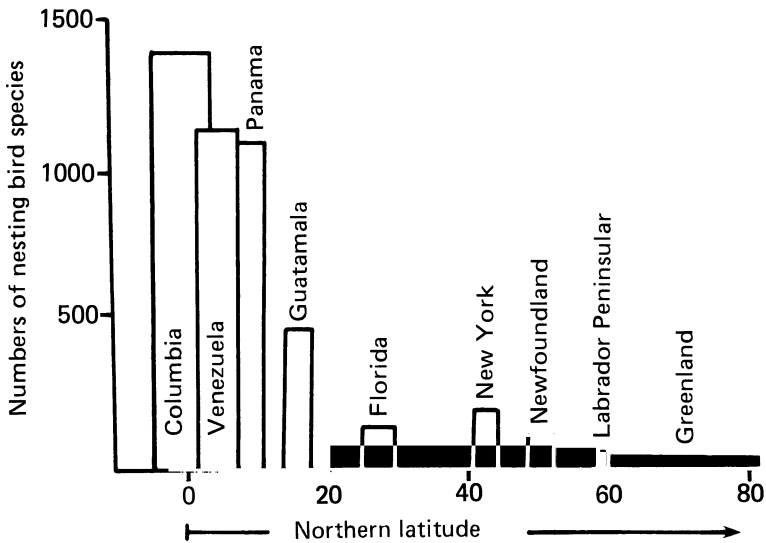


Fig. 1.2 Latitudinal diversity gradient in nesting birds. (From Fischer [15].)

latitudes (which progressively lose this range), so it is not surprising that on this gross scale, more species are found in the tropics. Nevertheless, a comparison of similar habitats, for example at high altitude, still reveals greater species richness in the tropics [9].

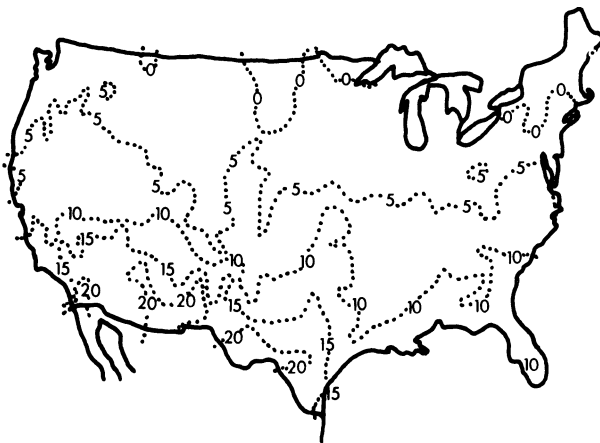


Fig. 1.3 Geographic patterns in species densities of lizards in the United States. (After Schall and Pianka [14].)

1.4.2 *Habitat gradients*

Smaller scale studies compare species richness across many different habitats within latitudinal belts. These usually reveal differences between adjacent habitats, even though there are no physical barriers preventing species from one habitat invading another (Fig. 1.4). In addition, consistent trends in species numbers involving altitude, topographic relief, island size and location, peninsular effects and proximity to oceans have been documented [15].

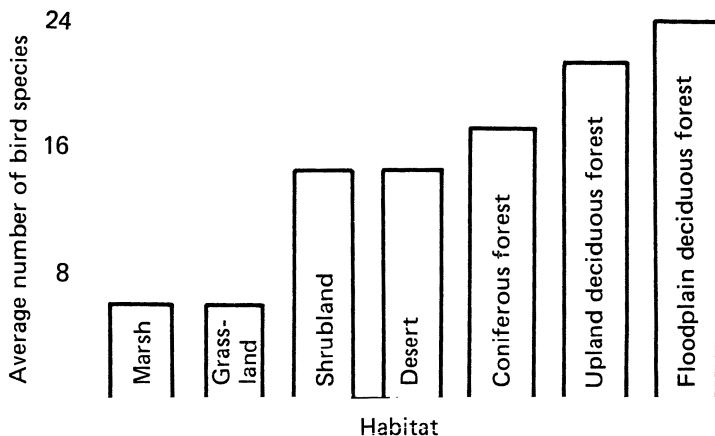


Fig. 1.4 Species richness of birds in representative temperate zone habitats. (After Tramer, E. (1969), *Ecology*, 50, 927–29.)

1.4.3 *Exceptions to the rule*

Latitudinal trends are not universal. The gradients are not shown by burrowing marine invertebrate groups like Ophiuroids and Holothuroids which show little diversity anywhere. Similarly, the prosobranch mollusc family Naticidae, a soft bottom dweller, shows no trends, whereas the epifaunal prosobranchs show good latitudinal gradients [15]. Latitudinal trends are virtually non-existent among Australian vertebrate taxa [14], and are often not very clear in plant assemblages apart from forests [18]. The prevalent trend is also occasionally reversed, often by small specialized taxonomic groups. For example, sandpipers and plovers are more diverse in the Arctic [10], a greater diversity of breeding birds is found at higher latitudes in Eastern deciduous forests of the USA [16], and marsupials appear to be more diverse

in temperate regions than the tropics [14]. Red algae and kelps also show greater diversity in temperate regions [15]. These exceptions to the rule are, nevertheless, worthy of further investigation. Elucidation of their controlling factors is as important to our understanding of community structure as is success in explaining the general trends described earlier.

1.5 The problem restated

These repeated patterns in species richness suggest that general explanations may be possible. If we accept the premise that a community is a structured assemblage of organisms, then it is the interactions between these organisms that should provide the structure. The ecological niche is a reflection of the organism's or species' place in the community, incorporating not only tolerances to physical factors, but also interactions with other organisms. The obvious question posed by patterns in species richness is 'What are the main factors controlling the number of species in an area?' This can be more precisely stated as 'What factors control the number of niches in a given area?', given that individual species utilize different niches. Terms such as species packing, niche overlap and niche width have arisen as a direct result of theoretical attempts at solving this problem, and have become incorporated into an almost separate discipline, Niche Theory.

Chapter 2

Niche theory

The concept of the niche pervades all of ecology, yet it has become somewhat confused through popularization and attempts to make objective sense out of an originally subjective idea (e.g. use of a systems approach [19] or mathematical integration of related concepts [5]). It arose as an attempt to describe the total role of a species in a community, defining all the bonds between populations, community and the ecosystem. As such, the niche relates the concepts of the population and community, describing how ecological objects fit together to form enduring and functioning wholes, and enabling us to see how very different communities may resemble each other in the essentials of their organization. It is this role that has led to its rise in importance over the last 30 years.

2.1 Development of the niche concept

This has been discussed in detail elsewhere [5, 20], but a brief review would be useful.

Grinnell [21] introduced the term niche as a habitat concept, defining the ultimate distributional unit of a species. He implied that niches of species do not overlap, and thus identified the potential nature of a species' distribution in the absence of interactions with other species. Elton's independent definition of the niche encompassed mainly a functional concept, describing an organism's place in the biotic environment in terms of its relations to food and

enemies [22]. He was, in effect, referring to a species' actual rather than potential place in nature.

2.1.1 The competitive exclusion principle

At the same time, the associated concept of competitive exclusion was developing. This suggests that two species with identical ecologies cannot survive simultaneously in the same place. This idea was implicit in Darwin's writings [23], and qualitatively stated by Grinnell, but apparently excited little interest at the time. However, between 1920 and 1940 mathematical demonstrations (Lotka—Volterra equations) and controlled laboratory experiments (the famous studies of Gause and Park), showed that competitive exclusion will often occur in the establishment of a two species population equilibrium. Since then, the principle of competitive exclusion, stated in the form 'complete competitors cannot coexist indefinitely', has become one of the central tenets of theoretical ecology [20]. In the present context, the corollary of this principle is important. If two species do coexist, then there should be some ecological difference between them, implying such species each have their own unique niche.

The Competitive Exclusion hypothesis could be considered of little scientific worth, as it is untestable (e.g. [9, 20]). However, it has been of immense value, both in the development of the niche concept and in prompting ecologists to answer such questions as: how do similar species coexist? how much difference between species allows coexistence? and how is competitive exclusion avoided? These questions have directed research in a way that provides a better understanding of community organization.

2.1.2 The multidimensional approach

The niche of the 1940s and 1950s took on the vague definition of an organisms 'profession' within the community (e.g. [24]), but thereafter achieved a formal and potentially quantitative definition through the work of Hutchinson [25]. He considered the niche to be defined by the total range of environmental variables to which a species must be adapted (physical, chemical and biotic), and under which a species population lives and replaces itself indefinitely. Ideally, every pertinent environmental variable can be considered as a gradient along which the species has an activity

or tolerance range. An example is light intensity, which suffers a logarithmic extinction from the forest canopy downwards as light is intercepted by plants [11]. The species evolve to relate themselves to this gradient, each adapting to a different range of light intensities. In some boreal forests this leads to an ideal, size related structure containing 5–7 species, including canopy and smaller trees, tall and low shrubs and herbs, and a ground level moss [11].

Each environmental gradient can be thought of as a dimension in space. If there are n pertinent dimensions, the niche can be described in terms of an n -dimensional space, or hypervolume. Potentially, this can be built up one dimension at a time. Fig. 2.1 shows a species response to one environmental gradient, where some measure of fitness is normally distributed about a preferred point on the gradient. Simultaneous response patterns to two and three resources can be depicted graphically (Fig. 2.2) and this procedure can be extended to any number of axes using n -dimensional geometry [9], producing a very complex hypervolume representing the responses of the species population to all environmental factors. (This assumes all relevant variables are included and are independent of each other.) Hutchinson further defines two states of a species niche. The *fundamental niche* describes the entire set of optimum conditions

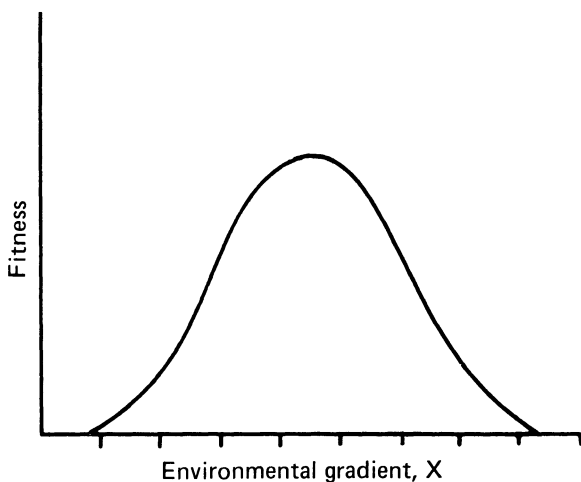


Fig. 2.1 A species response to a single environmental gradient. Measures of fitness include reproductive success, population size and survivorship.

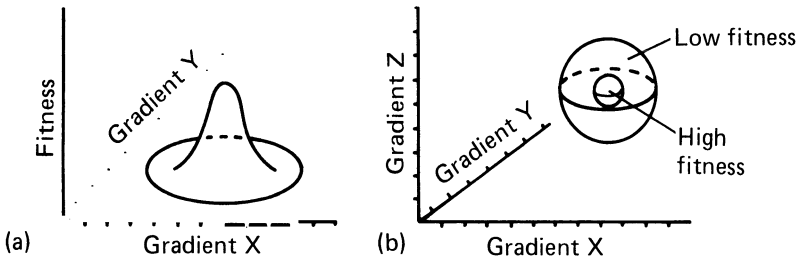


Fig. 2.2 Simultaneous species response to two environmental gradients (a), and to three environmental gradients incorporating species fitness (b). (After Pianka [9].)

which a species can occupy in the absence of enemies. The *realized niche* is the actual set of conditions in which the species normally exists. This is less than or equal to the fundamental niche.

This multidimensional approach provides a means of conceiving how species relate to one another and has thus enhanced our interpretation of community organization. In crude terms, one can think of total niche space of a habitat as an '*n*-sided' box, into which the niches of all species of the community fit, just like '*n*-sided' balls. If niches are always discrete (i.e. no overlap of fundamental niches), then the species richness of a community depends on the total amount of niche space (a habitat variable) and the average size of each niche (a species variable). Wide niches should lead to a lower species richness than narrow ones for a given variety of resources.

2.1.3 *The niche as a resource utilization spectrum*

Niche width (the size of a niche) is of central importance in niche theory, as an understanding of its controlling forces will lead to a greater understanding of the causes of species diversity. Under the multidimensional approach, niche width is defined as the sum total of the variety of different resources exploited by a species population. Its measurement at this level requires a description of all relevant parameters, and a continual estimation of simultaneous proportional utilization of resources, which is clearly an impossible task. Thus the ecological niche has become identified increasingly with the distribution of species activity (resource utilization spectra) along just one or a few of the most important (or most easily measured) niche dimensions [5, 26–28]. The

niche of each species is then defined by a utilization function (the distribution of species' activity) along a resource gradient (Fig. 2.1). Provided the niche dimensions examined are truly independent, overall multidimensional utilization may be thought of as a product of the individual, unidimensional utilization functions.

The most important characteristics of a niche described in this way are the height (maximum rate of resource utilization or level of activity) and the breadth of the utilization curve, the latter providing some limited but attainable measure of niche width.

2.2 Niche width

Two separate components combine to form the niche width of a species [26]. The within-phenotype component (WPC) describes the level of variation in resource use by individuals, and the between-phenotype component (BPC) describes variation amongst individuals of the species population. Total niche width (B) is given by $WPC + BPC$. If B is 100% BPC, the species will be polymorphic with specialists, whereas if B is 100% WPC, the species will be monomorphic with generalists. Obviously real populations will lie somewhere in between (Fig. 2.3).

Two basic procedures for the measurement of resource utilization have been identified [29]. The first involves a simple description of the species utilization of a continuous resource in terms of the mean (d) and width (w , as 1 standard deviation) of the utilization curve on the resource gradient. A large w indicates a wide niche. Adjustments are possible when w is different on either side of the mean [29]. This

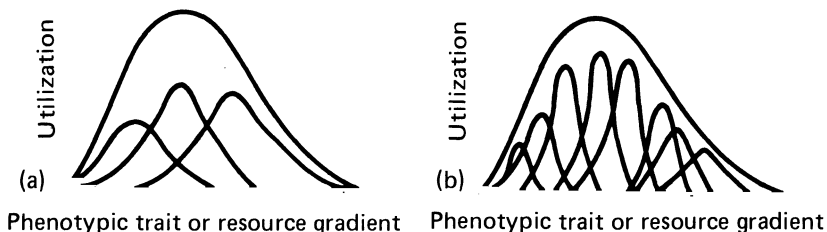


Fig. 2.3 Idealized representation of populations differing in the components of niche width. (a) High within-phenotype component; (b) high between-phenotype component. (After Pianka [9].)

measure of niche width is commonly used to assess resource utilization on the basis of morphological variation in a trait related to resource use, e.g. feeding structures [26, 30]. The second method does not require resources to be ordered along a continuum, but is based on proportional utilization of various resource states (e.g. prey species). Broad niche species tend to use resources in proportion to their availability, whereas narrow niche species will tend to concentrate on items in only some resource states. A number of different indices of niche width have been formulated (e.g. [31, 32]) and a comparison of those most commonly used is provided in a recent review [33].

There are certain limitations involved in the use of such indices. For example, because the width of niches only relates to the available width of the resource spectrum, one cannot readily compare the width of one species' niche with that of another using a different and unequal resource spectrum. Also, the accuracy of the measure of niche width depends on how objectively the ecologist defines the available resources [33]. Niches are not smooth curves along a few, simple, dimensions of the environment, and our ability to measure niches may fall far short of reality.

2.3 Niche overlap

Most organisms do not inhabit their potential, fundamental niche, but, due to interactions with other organisms, occupy a reduced, realized niche. The major interactions are normally considered to be predation and competition, and the latter has become involved in niche theory through the concept of niche overlap. Rather than niches in a community appearing as discrete, non-interacting units, species tend to share parts of each others fundamental niches, resulting in simultaneous demands upon some resource by two or more species populations. In Hutchinson's terminology, the niche hypervolumes of species include parts of others, thus overlap.

2.3.1 *Possible outcome of niche overlap*

If the overlap is very small, or the resources superabundant, then these species can coexist in essentially separate and almost fundamental niches. If niches overlap to a greater extent and resource availability in the overlap zone cannot meet demand, then the abundance of the less-efficient species will be limited by interactions with the more efficient. Ultimately, competitive exclusion may occur in the over-

lapping parts of any two niches. Making this an assumption, one can consider the hypothetical outcome of different degrees of niche overlap between two species [9].

- (i) Under the improbable situation of the two fundamental niches being identical, the competitively superior species would totally exclude the other.
- (ii) One fundamental niche might be totally included within a second, larger one. Here, an inferior included species would be eliminated, but a superior included species would eliminate the other species from the contested space (Fig. 2.4(a)).
- (iii) With partial overlap of fundamental niches, the competitively superior species occupies the shared niche space, and each species has an exclusive, uncontested refuge (Fig. 2.4(b)). Coexistence is thus theoretically possible, but will depend on the amount of overlap which can be tolerated by the inferior species.
- (iv) Niches may abut against each other (Fig. 2.4(c)). No direct competitive exclusion can occur, but such niche relations might reflect the avoidance of competition.
- (v) Niches are entirely disjunct, so both species occupy their fundamental niche (Fig. 2.4(d)).

For example, most forests contain many more than the 5–7 plant species described in an earlier example (Section 2.1.2). The additional species will also utilize the gradient

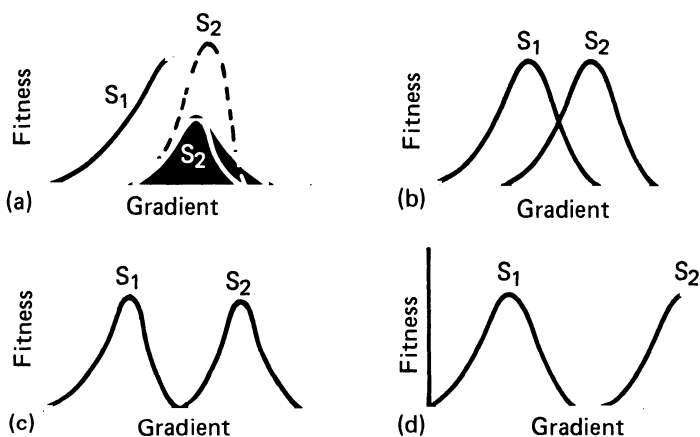


Fig. 2.4 Possible niche relationships between two species on a single environmental gradient. (a) An included niche; (b) overlapping niches; (c) abutting niches; (d) disjunct niches. (After Pianka [9].)

of light intensity, fitting in between the centres of population of other species. On the basis of the above exercise, the inclusion of extra species along the gradient should decrease the niche width of species already present, and lead to the packing of increasing numbers of plant species along the same gradient of light intensity.

2.3.2 *Measurements of niche overlap*

It has often been suggested that the key to understanding species interactions in a community is to measure the degree that niches of two species overlap, rather than trying to describe the niches of all species [10]. Such overlap is usually measured in terms of utilization data of resources such as food and microhabitat (a combination of the important and easy to measure factors). Niche overlap is thus described as overlap of utilization between two adjacent species on a resource gradient.

The simplest measurements are based on separation of resource utilization functions, and overlap is described by the following resource separation ratio [29]

$$\rho_{ij} = d_{ij}/w_{ij}$$

where d_{ij} is the difference between the means of resource utilization by species i and j , and w_{ij} is the common width of the utilization curve (1 standard deviation), given by

$$w_{ij} = (w_i^2 + w_j^2/2)^{\frac{1}{2}}$$

If ρ_{ij} is less than 3, there should, theoretically, be some interaction between the species. There should also be some minimum separation value below which competitive exclusion operates (see Chapter 4).

More complex measurements are based on a variety of methods including percentage similarity, chi-square goodness of fit and information theory. At least eight different indices are in current use and have been examined critically elsewhere [34–36]. A picture of niche overlap between all members of a guild or community can be built up using a niche overlap resource matrix [9]. An m by n matrix is constructed, indicating the amount of each of m resource states utilized by each of n different species, and from this an n by n matrix of overlap between all species pairs can be generated.

One can also assess the combined overlap along two or more resource dimensions to obtain some measure of total

overlap between species. For independent resources, the product of individual overlap measures is used, but if the resources are dependent ones, summation of overlap values is necessary [35]. No method has yet been devised to allow for various degrees of independence between resource dimensions.

In the measurement of niche overlap, allowances must be made for the fact that continuous resource dimensions do not provide equal ecological opportunities along their entire length. For example, small prey are likely to be more abundant than large prey. It is also possible for significant differences in resource utilization to occur between different weight, size or age classes of a species (e.g. [37]). Such intraspecific differences must be accounted for when niche overlap comparisons are made with other species. (See also Section 4.2.)

2.3.3 *Niche overlap and competition*

Niche overlap values are frequently equated with the competition coefficient (α) of the classical interspecific competition equations of Lotka and Volterra [5, 10, 36]. However, such comparisons are fraught with biological difficulties [29] and the actual relationship between niche overlap and competition is not clear.

Mere overlap in resource use does not necessarily lead to competition, as assumed in Fig. 2.4. Likewise, the intensity of competition need bear no relation to the degree of niche overlap [37].

The more abundant the resource, the less likely it is that competition will result from its common use, and no competition is expected between species sharing an unlimited resource in some habitats (oxygen is an obvious example in most terrestrial systems). Thus the ratio of demand to supply, or the degree of saturation, of the environmental resource is of vital importance in the relationship between niche overlap and competition. Few authors, however, have actually incorporated resource availability into measures of niche overlap and competition [38]. In addition, overlap on one resource gradient may indicate diversification in other ways. (See Chapter 4.)

Finally, an inverse relationship between competition and niche overlap has been suggested [9], predicting that maximum tolerable overlap should be lower in intensely competitive situations than in environments with lower demand/supply

ratios. (This Niche Overlap hypothesis will be discussed in more detail in Chapter 3.)

2.4 Diffuse competition

Consideration of niche overlap has led to another aspect of niche theory, diffuse competition. A species niche will usually only overlap with a limited number of adjacent niches on one resource gradient, but the potential number of neighbours increases as one examines more and more environmental dimensions simultaneously. Therefore, although pairwise niche overlap may be small, the cumulative effect of this diffuse competition can severely reduce the size of the realized niche, even to the point where it is too small to support a viable population (Fig. 2.5). A species can thus be 'squeezed out' by a group of other species.

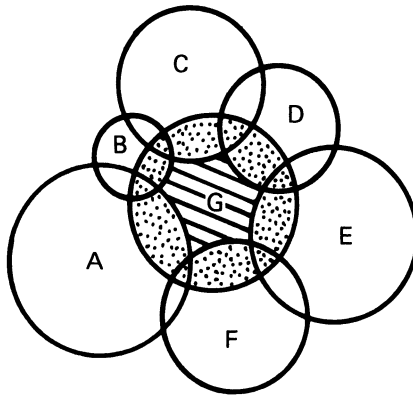


Fig. 2.5 Diffuse competition can reduce the fundamental niche of species G (stippled plus cross-hatched area) to its realized niche (cross-hatched area only).

The number of potential niches in a community can now be considered as a function of the degree to which development of the community leads to separation of partially overlapping niches under a given environmental regime [39]. In terms of the simple 'ball-and-box' model, each ball's volume can be decreased by squashing more balls into the box. The resilience or flexibility of the balls will control how many of them can then be packed into the available space.

2.5 Niche dynamics

Our ability to visualize and study an organism's niche, and its interactions with those of other organisms, is certainly curtailed by its ability to change both in time and from place to place as the physical and biotic environment varies (i.e. the niche can change position within the total niche space).

Temporal changes can be short term, i.e. within the life of an individual or over a few generations (ecological time scale). This is especially true of organisms undergoing some form of metamorphosis during development, such as holometabolous insects, planktonic and sessile crustacea, most aquatic insects, amphibians etc. Such organisms have disjunct niches at different times in their life histories [9]. Other organisms such as hemimetabolous insects, and predators utilizing different prey sizes as they grow, may show a more gradually and continuously changing niche. Niche changes over evolutionary time have undoubtedly taken place, where the opening up of new adaptive zones has allowed scope for their exploitation through evolution and adaptive radiation.

On a smaller scale, the size or width of a realized niche is likely to change through the responses of a species or its competitors to changes in resource levels or to activities of the resources themselves. Such changes are predicted by optimal foraging theory which is based on the idea that individual consumers should maximize individual fitness (usually through maximization of net energy gain) through their foraging behaviour (e.g. [40]). Finally, the community niche space is likely to shift in daily and seasonal rhythms, so the inter-relationships of each species in the community must also continually change. In terms of the simple model of the community, not only can the 'balls' alter in shape, size or position within the 'box', but the volume and shape of the 'box' can also change. It is these dynamic properties that make the niche so difficult to measure, so that at best one can obtain fragmentary measures which indicate the relative degrees of niche width and overlap within communities, and use these to help unravel the complexities of community organization.

2.6 The niche — a property of the species or the community?

Niches and organisms form complementary pairs, and one view, noting the role that the organism itself plays in creating and defining the environment in which it lives, suggests that

niches are generated by the occupant [19]. This is acceptable in part, when one considers the construction of artifacts such as nests, termite hills and beaver dams, as these modify the environment and contribute part but not all of the niche of an organism. An alternative view is that the niche is really a property of the community, and has no meaning except in the community context [39]. This implies that niches are generated by abiotic and biotic ecosystem components, are thus pre-existing, and are filled through species adaptation over a period of evolutionary change. One would therefore expect that communities in ecosystems characterized by similar environments should be of similar construction, and contain one or more essentially identical niches. The adaptations of populations filling such niches in these independently evolved communities should also be similar, even though the species may be totally unrelated. This is the phenomenon of ecological equivalence or convergent evolution, and its existence provides support for the community status of the niche.

The existence of habitat types that can be grouped together as biomes implies some form of community convergence. At a more specific level, succulent desert plants in the USA are cacti and these are almost identical to the plants of the spurge family (Euphorbiaceae) in South Africa [39]. Convergent evolutionary responses are also found in desert lizards. North American and Australian deserts each support a cryptically coloured, hornily armoured ant specialized species, a medium sized, lizard-eating species, and a long-legged species found in open spaces between plants. Similarly, Africa and Australia have convergent pairs, such as subterranean species [41]. Ecological equivalence is frequently documented in birds, where, for example, it is possible to match morphology and ecology of single species of Mediterranean birds on three continents [42], and similarly, nine species pairs of ecological equivalents have been found in Panama and Liberia (Fig. 2.6).

For two unrelated species to evolve to a point where they are almost identical, the niches to which they have adapted must also be almost identical. This is impossible if the niche is a property of the species population. This conclusion is further substantiated by species turnover on islands which show a stable species richness (see Chapter 7).

However, among larger guilds, or corresponding guilds of unequal species number, such exact matches appear to become obscure, and species replacement of two for three, three for

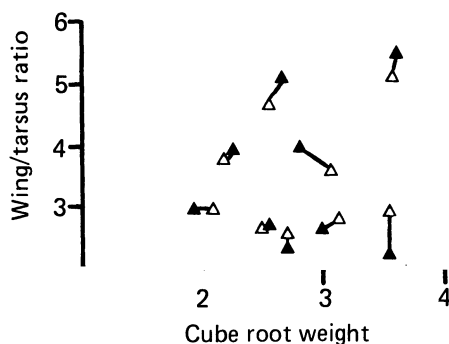


Fig. 2.6 Morphological similarities of ecological equivalent bird species in Panama (▲) and Liberia (△). (After Karr and James [43].)

five and other complex bases can occur [43]. This implies that in these situations the observed niches may be more a property of the species present.

Is the niche then a property of the species or the community? It seems that a certain ecological niche space is created by the physical and biotic components of an ecosystem, and this is a community property. The corresponding space in two similar saturated ecosystems can be divided amongst their species on a one to one basis, producing ecological equivalence, and at this level the niche appears to be a community property. Complex ratios of species replacement between two similar ecosystems may be due to historical factors, taxonomic barriers to convergence, or differences in the state of resources. These will influence the number and type of species present and the likelihood of equivalence. The observed niches in one or both communities may then be more a property of the constituent species.

2.7 Summary

The community can be thought of as a large, n -dimensional hyperspace, within which each species population evolves towards its own portion of the space. The position of the species and its response to factors of the community hyperspace defines its niche. Each species thus occupies a vaguely outlined, diffuse volume that differs from but perhaps overlaps with, those of other species in the community. The size and position of the niches are probably changing over both ecological and evolutionary time scales.

The full potential of the genotype of a species population

in all ecological matters has been termed its ecopotential [294]. However, the distribution and abundance of species is ultimately determined by tolerances to extremes of physical conditions (the fundamental niche), and species are usually further limited to some smaller range of habitats and population size by interactions with other organisms (the realized niche). Hence, if communities are organized by such interactions, then the manner and degree of organization will be reflected in differences between sizes and shapes of the realized and fundamental niche. Competition and predation are two major species interactions influencing these differences. In the following few chapters the evidence for these interactions and their effects on niche size, species packing, species richness and community organization will be examined.