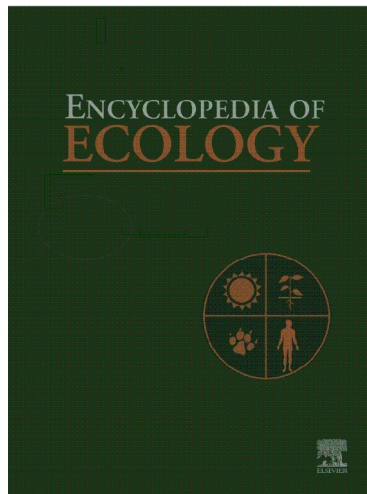


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Summary

A practical objective of ENA in general, and environ analysis in particular, is to trace material and energy flow–storage through the complex network of system interactions. The network environ approach has been a fruitful way of holistically investigating ecological systems. In particular, a series of ‘network properties’ such as indirect effects ratio, homogenization, and mutualism have been observed using this analysis, which consider the role of each entity embedded in a larger system.

See also: Cycling and Cycling Indices; Ecological Network Analysis, Ascendency; Ecological Network Analysis, Energy Analysis; Emergent Properties; Energy and Network Analysis; Indirect Effects in Ecology; Systems Ecology.

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Ecological Niche

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Introduction

Ecological niche is a term for the position of a species within an ecosystem, describing both the range of conditions necessary for persistence of the species, and its ecological role in the ecosystem. Ecological niche subsumes all of the interactions between a species and the biotic and abiotic environment, and thus represents a very basic and fundamental ecological concept. The tentative

definition presented above indicates that the concept of niche has two sides which are not so tightly related: one concerns the effects environment has on a species, the other the effects a species has on the environment. In most of ecological thinking, however, both meanings are implicitly or explicitly mixed. The reason is that ecology is about interactions between organisms, and if persistence of a species is determined by the presence of other species (food sources, competitors, predators, etc.), all species are

naturally both affected by environment, and at the same time affect the environment for other species.

If we want to treat both of these aspects of ecological niche within one framework, we can define it more formally as the part of ecological space (defined by all combinations of biotic and abiotic environmental conditions) where the species population can persist and thus utilize resources and impact on its environment. It is useful, however, to distinguish three main approaches to the niche. The first approach emphasizes environmental conditions necessary for a species presence and maintenance of its population, the second approach stresses the functional role of species within ecosystems, and the third one a dynamic position of species within a local community, shaped by species' biotic and abiotic requirements and by coexistence with other species.

Concepts of Niche

Niche as the Description of a Species' Habitat Requirements

The first formulations of the concept of ecological niche were close to the general meaning of the term: the ecological niche was defined by the place a species can take in nature, determined by its abiotic requirements, food preferences, microhabitat characteristics (e.g., a foliage layer), diurnal and seasonal specialization, or predation avoidance. This concept is associated mostly with Joseph Grinnell, who first introduced the term. He was especially interested in factors determining where we can find a given species and how niches, generated by the environment, are filled. The knowledge of a species niche determined by its habitat requirements is essential for understanding and even predicting its geographic distribution; this concept of the niche is thus more relevant in biogeography and macroecology than in community or ecosystem ecology.

Niche as Ecological Function of the Species

In this concept of niche, each species has a particular role in an ecosystem and its dynamics, and one such role can be fulfilled by different species in different places. The observation of distant species adapted to equivalent ecological roles (the resemblance between jerboa and kangaroo rat, between many eutherian and marsupial species, or the Galapagos finches diversifying to highly specialized roles including those normally taken by woodpeckers) was clearly influential to Charles Elton, who emphasized the functional roles of species. According to Elton, there is the niche of burrowing detritivores, the niche of animals specializing in cleaning ticks or other parasites, or the pollination niche. Elton's niche can apply to several species, for example, "the niche filled by birds of prey which eat

small mammals." This 'functional niche' therefore refers to a species position in food webs and trophic chains, and the concept is thus especially relevant for ecosystem ecology.

Niche as a Species Position in a Community – Formalization of Ecological Niche Concept

The emphasis on the diversity of ecological communities and interspecific competition among them in the second half of the twentieth century has led to the formalization of the niche concept, and an emphasis on the properties of the niches which enable species coexistence within a habitat. George Evelyn Hutchinson postulated that niche is a 'hypervolume' in multidimensional ecological space, determined by a species' requirements to reproduce and survive. Each dimension in the niche space represents an environmental variable potentially or actually important for a species persistence. These variables are both abiotic and biotic, and can be represented by simple physical quantities as temperature, light intensity, or humidity, but also more sophisticated quantities such as soil texture, ruggedness of the terrain, vegetation complexity, or various measures of resource characteristics. This could be viewed simply as a formalization of original Grinnellian niche, that is, the exact descriptions of a species habitat requirements. However, in the Hutchinsonian view, ecological niches are dynamic, as the presence of one species constrains the presence of another species by interspecific competition, modifying the position of species' niches within the multidimensional space. This concept therefore combines the ecological requirements of the species with its functional role in the local community.

Fundamental and Realized Niche

Hutchinson recognizes a species' 'fundamental niche', a multidimensional 'cloud' of favorable conditions determined by all environmental (abiotic and biotic) variables where the species can reproduce and survive, and the 'realized niche', which is a subset of the abstract fundamental niche, where the species can persist given the presence of other species competing for the same resources. Realized niche thus always has a narrower extent along respective dimensions; a species which could potentially live in a broad range of humidity conditions, for instance, may occupy a much narrower range of these conditions in an environment with competing species, since its population growth rate decreases to negative values in some conditions. To a good approximation, if we ignore stochastic sampling from a heterogeneous species' population, species does fill its realized niche.

According to Hutchinson's formalization, niches of different species can be separated along any of these dimensions or by a combination of them (i.e., their

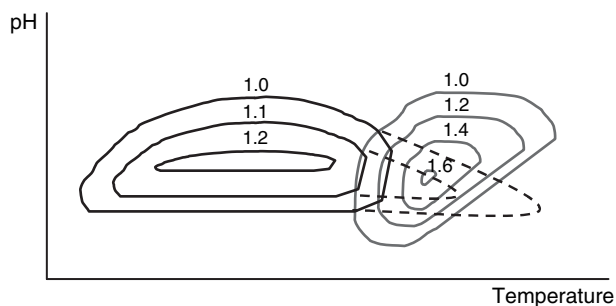


Figure 1 A hypothetical example of species niches and their interaction. Two niche axes are shown, pH and temperature. The two species of hypothetical protists have different optima, and one (left) is adapted to wider range of conditions and has overall lower growth rate (measured at a given low density). When the niches of the two species overlap, the growth rates are expected to decrease, potentially to the point where the population cannot be sustained. If one of the species is fully dominant in its niche, the other species can sustain its population only on a part of its fundamental niche, and its growth rate decreases at the overlapping areas. The growth rate isoclines are shown, with the dashed lines depicting the growth rate isoclines of the fundamental niche (i.e., had the other species been absent).

interaction) (Figure 1). Although this formal model of the niche has quite straightforward theoretical consequences, in practice it can be quite difficult to describe properly the ecological niches of real species, because the number of niche dimensions is potentially infinite, and the significant niche axes (and appropriate measurements) may be rather hard to find: a niche overlap among species may mean we did not succeed in determining the crucial niche axes of separation. However, often a few variables are sufficient to separate species' realized niches, and they or their correlates can be inferred assuming we understand the species' biology reasonably well. For example, five species of warblers, analyzed by Robert MacArthur, showed significant (though not complete) separation along only three niche axes (feeding behavior, feeding height, and nesting time).

The difficulties in determining appropriate niche axes, however, still considerably limit the usefulness of the concept in empirical research. Even if we know the important resources, it is still problematic to decide which characteristics to measure. A further problem, albeit rather technical, is posed by including discrete categories: the width of the cloud in the respective dimension would be reduced to zero, and its position can be arbitrary. More importantly, although species can often potentially live in a much broader range of environmental conditions than where they do actually live, the distinction between the 'fundamental' and 'realized' niche is slightly arbitrary, driven purely by the interest in coexistence of species sharing resources. As the dimensions of the fundamental niche are both abiotic and biotic, there is

no *a priori* reason to exclude presence of competitors from the dimensions characterizing fundamental niche. The distinction between the fundamental and realized niche may also be blurred, as species' interactions need not fit to our discrete categories – for example, competitors may act also as predators.

Due to the difficulties with the concept, and for tractability, a considerable part of the theory actually dealing with species coexistence works with a one-dimensional approximation of the 'trophic niche', a 'resource utilization function' – given by the frequency distribution of an important characteristic of utilized resource (e.g., a prey size).

Competitive Exclusion

Historical development of the niche theory is very closely related to one of the most important topics of ecology, that is, the problem of species competition and coexistence. Since the beginning of the ecological niche concept, it has been assumed that no two species sharing a single niche could locally coexist. Originally, the later Volterra–Gause principle states that “under constant conditions, no two species utilizing, and limited by, a single resource can coexist in a limited system” and was formulated and proved by Vito Volterra, while Alfred Gause showed experimental evidence of competitive exclusion in an undiversified environment. The explanation of the competitive exclusion lies in the fact that utilization of a limited resource leads to its depletion, and the population growth, therefore, necessarily leads to a moment when the resource level is insufficient for further growth. If only one population utilizes the resource, this situation leads to simple negative feedback, causing the decrease of population growth rate and thus a release of resource consumption, stabilizing the population size. However, in the case of two species sharing the resource, there will likely exist a resource level when the first species population can still grow up even if the second cannot, leading to further decrease of population growth rate of the second species, and eventually to its extinction. Even if two species sharing several resources have exactly the same requirements and ability to utilize them, the coexistence of such species is not stable in a stochastic environment (if their total population density is limited): one of the species would ultimately become extinct by chance over infinite time (unless there is an advantage for the less abundant species).

The 'competitive exclusion principle' is the core principle in community ecology, and much of this field has been devoted to study how species with similar ecological requirements can coexist. This question has transformed into the problem of 'limiting similarity': how similar can ecological niches be to still ensure local coexistence.

Limiting Similarity, Species Packing – How Close Can Species Be to Each Other?

Hutchinson states that a species' realized niche is exclusive, that is, no two species can share a single niche and no overlap in the realized niches is possible in a stable environment. In other words, were there to be an overlap in, say, the trophic 'dimension' of the niche, species would differ in other dimensions, for example in their tolerance to abiotic factors, or avoidance of predators. Now, the (rather vague) consensus is that a little overlap between niches is consistent with coexistence, whereas somewhat larger overlap is not. The theory of 'limiting similarity', formalized by Robert MacArthur and Richard Levins, predicts the minimum permissible degree of overlap in the resource utilization curve. They showed that coexistence between species utilizing a continuous resource is possible when the ratio between the niche width (see **Box 1**) and the distance between species' optima is approximately unity or smaller. (This has been derived using the Lotka–Volterra equations describing the growth rates and hence stability of populations of competing species, where the competition coefficients were determined by the proximity of species' bell-shaped utilization curves.) However, the result is sensitive to the assumptions about the form of the resource utilization function and population growth rate:

Box 1 Niche width

Niche width describes the dispersion of population resource use along a niche dimension. As such, it is very laborious to measure: more often, we get estimates of niche width from the morphological traits related to the resource use: for example beak dimensions, jaws or teeth size. However, this measure delivers only a part of the information: both phenotypic variation in the traits important for food gathering and the ability of an individual to exploit a range of resources generally contribute to the niche width. For example, the niche breadth of *Anolis* lizards, studied by Joan Roughgarden, is mostly determined by variation in jaw size within species, but any individual still contributes to the total niche width, having its own range of prey sizes. Importantly, Roughgarden shows that a measure of the total niche width can be calculated as a sum of a 'within-phenotype component', the average variance of the individual's utilization function, and a 'between-phenotype component', the variance in population resource utilization function. Often, the range of two standard deviations (twice the square root of the sum), comprising about 95% of resource used, is denoted as the niche width.

The related term 'niche breadth' is originally due to Richard Levins. Levins' measures of niche breadth reflect the diversity of species' use of available resources: niche breadth is determined by the Shannon index (i.e., information entropy), or Simpson's index (i.e., the inverse of the sum of squared frequencies of the focal species over all resources). Although niche breadth intuitively captures differences between generalists and specialists, the measure is very sensitive to the categorization of resources and their frequency distribution.

notably, highly peaked resource utilization functions show actually almost no limits to coexistence (as their overlap is always minute) and niches can overlap broadly when fitness increases as the frequency of individuals carrying the respective trait decreases (negative frequency dependence). Also, coexistence between species can be facilitated by fluctuations in the environment generating frequency or density-dependent selection, or when the response of competitors to the common fluctuations is nonlinear. Note that the predictions of the theory of limiting similarity cannot be directly corroborated by observation: by definition, the population density of one of the species is close to zero if the species pair is close to limiting similarity, and thus the utilization functions are not observable in such a situation. On the other hand, finding a similarity higher than predicted would clearly indicate that some of the assumptions of the model are violated.

The spacing between species in niche space, resulting from partitioning the available resources ('species packing'), differs considerably between sexually and asexually reproducing species. In asexual species, clones bearing favorable combinations do not recombine, and therefore those adapted to the various resource combinations can be arbitrarily spaced in the niche space. In sexual populations, individuals share common gene pool which does not allow divergence in adaptive response to varying resource combination. (Over time, of course, tradeoffs in utilizing the resource spectrum can lead to disruptive selection strong enough to drive evolution of reproductive isolation and evolution of distinct species.) Due to the necessity of finding a mating partner, population growth rate of sexual populations can sharply decrease at low densities ('Allee effect'), limiting both adaptation to marginal conditions and invasion to a new area. Both these effects contribute to discontinuities in distribution of resource use of sexually reproducing species.

Modes of Species Coexistence

Species coexistence is often ensured by niche separation. The 'niche shift' can follow from the competitive exclusion of one species from the part of ecological space where the niches overlap, or from coevolution of competing species, favoring in each species phenotypes differing from the phenotype of the competitor. The latter case is often referred to as the 'ghost of competition past', emphasizing that current niche segregation can be due to the processes that took place in distant evolutionary past. If morphological differences arose due to divergent evolution of sympatric competitors, we speak of 'character displacement'. Typically, sympatric populations of competing species evolve toward more different sizes of characters associated with food consumption (beaks,

teeth) than allopatric populations – if there is only one species of Galapagos finches on an island, it has an intermediate beak size enabling to utilize wide spectrum of seed sizes, whereas if there are two species, one has bigger and the other has smaller beak than the species occurring without competitors. If there are more than two locally coexisting species, we often observe regularly spaced sizes of morphological characters, again indicating past competition leading to maximum niche separation.

Simple separation of niche optima is not, however, the only way that stable local coexistence of species is attained. Many species pairs, for instance, consist of one species which is competitively dominant, and the other species which is less specialized and can thrive in a broader range of ecological conditions. An example is the pair of two closely related species of redstarts, where the black redstart *Phoenicurus ochruros* is bigger and more aggressive, but the common redstart *Phoenicurus phoenicurus* can utilize a wider spectrum of habitats, such that it has always an option to thrive out of the range of conditions preferred by black redstart. Such niche division between dominant aggressive specialist and subordinate generalist has also been observed in many mammal species, and is apparently stable. In plants, competitively inferior species are often those with higher rate of spreading and growth, which enables them to quickly occupy empty places before arrival and eventual overgrowth of competitively superior species. In this case we speak about 'regenerative niche', representing a time window for competitively inferior, but fast-spreading and fast-growing species, thus ensuring long-term coexistence of competitors in the same habitat.

If species are very similar to each other, such that they do not differ substantially in their utilization of resources, the competitive exclusion can take a very long time. If the replacement of old individuals by young ones is basically a random process, that is, all individuals regardless of species identity have equal chances to give birth to their descendants within an environment, populations of all involved species will fluctuate randomly and the prevalence of a particular species is just a matter of chance. However, due to these stochastic fluctuations and due to the fact that the species which incidentally prevails in a time step will have higher probability to further increase its abundance, this process will finally lead to apparent competitive exclusion. This process, called 'community drift', can be relatively slow and may be further slowed down by dispersal limitations (leading to random prevalence of different species in different local communities isolated by migration barriers) and balanced by the emergence of new species (i.e., speciation or migration from elsewhere).

Communities where dispersal limitation and community drift play a major role are called 'dispersal-assembled communities', in contrast to 'niche-assembled communities'

where niche differences play a major role in determining species distributions and abundances. Trees in tropical forests represent a very good candidate for dispersal-assembled communities. Most tropical tree species are very similar in terms of their ecology and growth characteristics, and it has been documented that for their recruitment the proportion of parent individuals in a given locality (i.e., dispersal limitation of more distant individuals) is much more important than any habitat characteristics. Still, an incredible number of species can coexist locally. It is hardly believable that there are several hundreds of different narrow ecological niches (i.e., combinations of environmental characteristics) on a hectare of tropical forest to enable coexistence of several hundreds of tree species on the basis of their niche differences – the dispersal assembly and coexistence without significant niche differentiation seem more likely. However, an unusual aspect of niche differences can still be involved in this classical case of species coexistence. It has been demonstrated that coexistence of tropical trees is facilitated by frequency dependence, where relatively rarer species have an advantage of not being so severely attacked by natural enemies which strongly limit recruitment of more common species on which they specialize. In a sense, all species compete for 'enemy-free space', and this 'niche' for a given species is open only if the species is not too abundant to allow population growth of specialized natural enemies. Separation of 'niches' of tropical trees seems thus to be determined by the community of species-specific pathogens.

In conclusion, coexistence among species can be certainly maintained both by niche differences and – at least in a nonequilibrium world – by niche similarity. Coexistence of species with similar niches maintained by dispersal-assembly processes could be a reason why we often observe that species are not regularly distributed in a niche space, but form clumps of species whose niches are closer to each other than to other species.

How Many Ecological Niches Are There?

The notion that ecological niches cannot be infinitely similar to each other, and the knowledge that ecological space is heterogeneous and that total number of resources available to a community is always limited, has led to an idea that for a given environment there is a limited number of available niches which could be potentially occupied. An environment then could be seen as a set of empty niches, which could – but may not – be filled with species. Consequently, we might ask whether in a particular case the niche space is or is not saturated with species.

There are two facets of the problem, which are sometimes confused. First, there is no doubt that the limited

amount of resources in an ecosystem can sustain only limited total number of individuals (assuming a given body size distribution). Therefore, there is always a limited potential for the whole community size determined by total amount of resources, and thus also for a limited number of species (given that each species needs some viable population size). If this potential is fully utilized, we speak about biotic saturation of the community. However, biotic saturation does not imply that the number of ecological niches is fixed and that all possible niches are occupied. Such a statement would be much stronger and would require at least some level of discreteness of ecological niches, that is, ecological space cannot be divided into an infinite number of subtly different niches with arbitrary positions. Is there any reason to believe that niches are discrete and their number within an environment is limited?

Apparently, there is a considerable level of environmental heterogeneity in resource distribution and abundance; resources are more abundant for some combinations of parameters than for others. Environmental heterogeneity would not be, however, a sufficient condition for discreteness of ecological niches if species could utilize equally easily several different resources. The discreteness of ecological niches comes out from the existence of 'tradeoffs' in resource utilization: resources can be always potentially utilized by many ways, but some ways are mutually exclusive. A Galapagos finch from the genus *Geospiza* can have either a big beak appropriate for cracking big seeds, but then it can crack small seeds with much more difficulty, and vice versa. A plant can either invest to its rapid growth and so quickly utilize resources, or it can invest into woody trunk which enables it to grow higher and sustain longer – but at a cost associated with a slower growth. Moreover, some methods of resource utilization are less effective than others and natural selection supports phenotypes better utilizing available resources, some phenotypes being suboptimal. Consequently, evolution leads to utilization of only a restricted spectrum of resources.

In the presence of tradeoffs, there is only a limited number of mutually exclusive ways to utilize resources, and thus a limited number of available niches. However, as the discreteness of niches follows from the tradeoffs between adaptations, and since all the tradeoffs are determined by unique properties and constraints of given organisms, it makes sense to speak about available niches only in relation to organisms which already inhabit the environment. A habitat without its inhabitants can provide a potentially infinite number of opportunities for existence, and this landscape of opportunities changes with each new inhabitant. For the organism in an environment, the number of possible niches is determined by the number of possible ways to utilize the resource – with all constraints and tradeoffs of the given organism.

Therefore, it is likely that there are always more niches than the current number of species, because each species has several mutually exclusive possibilities of future adaptive evolution arising from the tradeoffs – unless all niche changes require a corresponding niche change in other species.

In some cases, the number of available niches can be predicted from the knowledge of resource heterogeneity and the possibilities of resource utilization for given taxon. The number of Galapagos finches occurring on each island is reasonably well predicted by the number of peaks of the 'landscape' constructed using the knowledge of frequency distribution of seed size, the general relation between finch and seed biomass, and the relation between preferred seed size and beak depth (Figure 2). Similarly, using the knowledge of the relationship between beak shape of crossbills (*Loxia curvirostra*) and their foraging efficiency in obtaining cone seeds from cones of various coniferous tree species, it is possible to construct a resource utilization function related to different morphologies, and find out how many optimal shapes do exist. And again, it has been found that there are several ecomorphs of crossbills, each of them occupying one adaptive peak (optimum) in the morphological space.

There is another evidence that ecological niches are partially predictable – the phenomenon of community convergence. Animal or plant communities occurring on different continents or biotic provinces often comprise similar morphological types utilizing similar types of resources. *Anolis* lizards, for instance, have evolved independently into several well-recognizable ecomorphs on each Caribbean island, with known sequence of this evolution, repeated on every island. However, there can be more than one species within each ecomorph, and thus this convergence does not imply that the number of species-specific niches is predictable. This is quite typical for most cases of community convergences: they provide a clue to our understanding of how many possibilities are there for utilizing resources within given habitat and for given taxon, but not to the prediction of how many species can actually coexist there. The total potential number of species within an environment is given by the total amount of resources determining the total number of all individuals, regardless of the level of discreteness of ecological niches.

Ecological Niches and Patterns in Species Abundance and Distribution

Species spatial distributions as well as their abundances are often attributed to the breadth and position of their niches. A species occurs in places where its requirements are fulfilled, that is, where it finds its niche. However, the 'presence of the niche' is not a sufficient condition for the

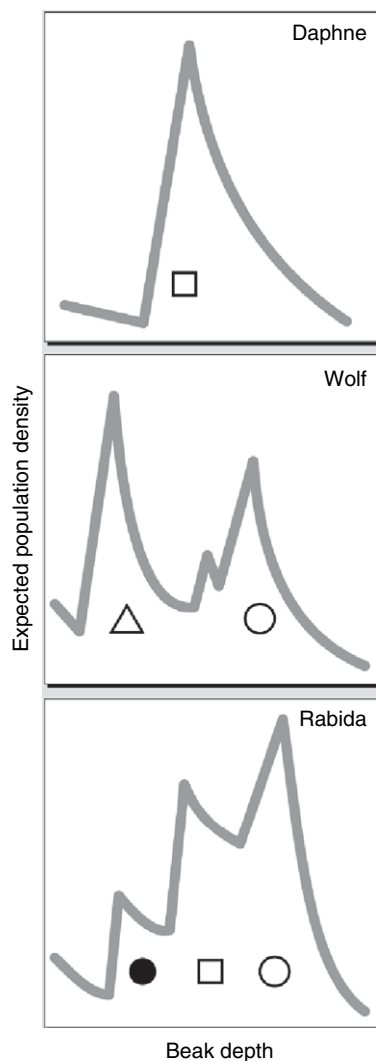


Figure 2 In this example of Galapagos finches on three different islands, the number of niches can be predicted from the peaks in the expected finch density. The expected finch density is calculated from distribution of seed biomass converted to finch numbers, using preferred seed size estimated from the mean size of the beak. The beak depth of the finches occurring on each island corresponds well to the maxima of the curve. Position of the symbols mean beak depth of male ground finch on each of the three islands: *Geospiza fortis* (squares), *G. difficilis* (triangles), *G. magnirostris* (open circles), and *G. fuliginosa* (closed circles). The beak depth scale is kept the same for the three pictures; the population density is scaled to the maximum. Modified from Schluter D and Grant PR (1984) Ecological correlates of morphological evolution in a Darwin's finch, *Geospiza difficilis*. *Evolution* 38: 856–869.

presence of a species, and in a special case it may not be even the necessary condition. Spatial population dynamics driven by dispersal and spatial distribution of available habitat patches is equally important. Consequently, species may be absent even in sites containing habitat that fulfils its niche requirements if the site is far away from

other occupied sites and the dispersal distance of the organism in concern is relatively small for the immigration into the site. On the other hand, a species may be present even in a site where its niche requirements are not fulfilled and population growth is negative if the population is maintained by a continuous supply of individuals from neighboring sites with positive population growth (so-called source–sink population dynamics). Therefore, species spatial distributions are determined by species niches and available habitat distributions, as well as by spatial population dynamics and dispersal limitation.

In a similar line, it has been argued that a significant proportion of the variation of species' abundances can be explained by the breadth of species' niches (**Box 1**). It is reasonable to assume that species which are able to utilize wider spectrum of resources can attain higher population abundances and also can occupy more sites. Local population densities are mostly positively correlated with species range sizes, which can be taken as an evidence of such niche differences. However, patterns in species abundances can be often well explained by spatial population dynamics – for instance species which were incidentally able to spread to more sites have higher chance to colonize further sites and to further increase local population densities by immigration (this is the nonlinearity of the dynamics of metapopulations). Moreover, the statistical relationship between niche breadth and abundance can have actually a reversed causality, as abundant species are forced to utilize a wider range of resources due to intraspecific competition. More abundant species can also be those that do not utilize a broader range of resources, but are specialized on resources which are relatively more abundant, or may simply have higher population growth and/or dispersal rate (although these features can be understood as niche properties).

One of the most prominent ecological patterns is the frequency distribution of abundance of individual species within local communities or regional species assemblages – the so-called species-abundance distribution. It is always highly unequal, the majority of species having low abundance and only a few being common (the frequency distribution is often close to log–normal, though other models may fit the observed species-abundance distribution better in particular situations). This distribution has been modeled as a stepwise division of niche space, where each newly arriving species obtains some (random) proportion of niche space previously utilized by other species. One of these models, based on sequential resource partitioning, predicts observed species-abundance distribution quite well (**Box 2**). However, models based on spatial dynamics and dispersal limitations – especially those involving 'community drift' (see above) – can provide equally good predictions of species-abundance distribution. This again indicates the complementarity between niche-based and

Box 2 Sequential resource partitioning

It appears that relative species abundances within taxa can be reasonably well explained by a simple null model of resource partitioning between species, proposed by Mutsunori Tokeshi. A common resource, represented by a 'stick', is divided once at a random location chosen uniformly along its length, and for further partitioning one part is chosen with a probability proportional to its length raised to a power of K , where K is a parameter between 0 and 1 (e.g., 0.05), and the division and selection process continue to distribute the 'niche' among all the species within the taxon. The model seems to describe well the relative abundances of species within taxa, across a large range of their species richness.

dispersal-based explanation of ecological patterns, and supports our consideration of both niche differences and spatial population dynamics as essential drivers of species distribution and abundance.

Niche Divergence and Resource Specialization

The diversity of ecological niches even among closely related species is enormous and demands explanation. What is the reason for such diversity? We have already mentioned one of the most important factors, the interspecific competition, which pushes ecological niches of species far away, to avoid niche overlap. More specifically, natural selection prefers such phenotypes of competing species which utilize different resources than those which share them. Competition thus leads to the increase of resource range utilized by a given taxon, and this process is faster when other taxa do not constrain this diversification. Indeed, the increase of the breadth of utilized resources in the course of evolution is fastest in such situations where other taxa with similar requirements are absent. For example, ecomorphological diversification of Galapagos finches and Hawaiian honeycreepers has been much faster than the diversification of related taxa on the mainland, where the utilization of new resources was constrained by other taxa already utilizing them. Availability of resources almost always increases diversification rate, indicating the role of interspecific competition for this process.

Interspecific competition is not, however, the only force driving niche diversification. Each species has its own evolutionary history, and thus can adapt to different resources by an independent process of evolutionary optimization, as phenotypes which are more efficient in transforming obtained energy into offspring are favored by natural selection. If there are several mutually exclusive ways to achieve this, it is likely that each species will go by a different route due to evolutionary contingency,

and niche diversification will follow without competition. Notably, optimization does not lead to an advantage of the whole species in terms of the resource utilization, but only to an individual advantage regardless of the evolutionary fate of the whole species. As evolution is opportunistic, species can evolve to extremely specialized forms in terms of either habitat utilization or food preference, which is apparently disadvantageous for future species persistence in an everchanging world.

Evolution of Niche Width

Progressive specialization, that is, narrowing of niche width in the course of evolution, is forced by interspecific competition and intraspecific optimization, and thus represents an expected evolutionary trend. The opposite process, that is, an extension of niche width, is observed mostly after entering a new environment without competitors, allowing utilization of a wider spectrum of resources. This process is called 'ecological release' and may be underlined both by the extension in within- and between-phenotype component of species ecological variation (importance of the two contributing modes vary widely among species). Species niches can widen also because of 'phenotypic plasticity' (heritable genotype–environment interactions directing the trait in the early ontogenesis), and can vary even purely behaviorally, as an immediate response to an altered resources or species structure.

Although sometimes there is an obvious constraint on expanding a species' niche – for example, physiological constraints like freezing of body fluids or presence of a competing species – we often see no apparent reason why species niches stay restricted to a fraction of a resource which continuously varies in space. One possibility is that gene flow from the central large population adapted to average conditions restricts adaptation to marginal conditions: the alleles neutral or nearly neutral in the main population which are deleterious in the marginal populations will sweep through the small marginal population, thus preventing the adaptation. The argument, however, does not extend to a population on a continuous gradient, as it requires significant asymmetry in frequency and quality of the habitats. Often we actually do not have a good understanding of why a species' realized niche (and consequently its geographic range) stays limited without adaptive response to the environmental variation. Constraints on genetic variance or genetic drift leading to a weaker response to selection represent possible causes.

On the other hand, asexual reproduction or self-fertilization can provide an advantage in adapting to marginal conditions – both because small populations are still viable (as there is no need to find a mating partner) and because gene flow does not restrict adaptation to marginal conditions. Indeed, it is found in many

plants and animals adapting to extreme, marginal habitats (classic animal examples are *Daphnia pulex* or freshwater snail *Campeloma*). However, although lack of recombination in asexuals means that locally favorable gene combinations are maintained, adaptive evolution in asexual species is significantly slowed down as beneficial combinations have to arise in each strain independently. It appears that high levels of, but not obligatory, self-fertilization or asexual reproduction (parthenogenesis and vegetative reproduction) are commonly advantageous for adaptation to marginal habitats.

In some cases, we observe an apparent regularity in the evolution of niche width and position. The classical example represents cycles of species dispersal, specialization, and local adaptation (and eventual extinction) observed on various archipelagoes, called 'taxon cycles'. They were originally described by Edward O. Wilson on Melanesian ants, but were best documented by Robert Ricklefs and his co-workers on Caribbean birds. In the first stage, an immigrant, which is mostly a species with a high dispersive ability, colonizes coastal or disturbed areas. Then the species spreads across the island, adapting to the new resources and expanding its niche (quite likely as a consequence of a release from competitors, predators, and parasites). In the next step, the species becomes more specialized, and its distribution becomes spottier. The narrowing of its niche may be driven by an immediate advantage of an adaptation to a local resource or immigration of new generalist competitor. Finally, species distribution becomes very fragmented, ending in local endemism, and ultimately extinction.

Changing the Niche Space, Niche Construction, and Coevolution

Both environment and species change in the course of time, and thus ecological niches are not stable and given forever. Species not only respond to environmental changes, but also actively change their biotic and abiotic environment, affecting both their own niche and the niches of other organisms. The importance of competition, predation, or mutualism has been already stressed. Moreover, organisms often make niche space for other organisms available in the environment – think of successive colonization of an island where first colonizers modify environment for their successors, internal (endobiotic) organisms, or emerging trees. Some organisms strongly directly affect abiotic environment, determining possible niches for a whole community of species – beavers building dams, earthworms altering soil structure, or, on a larger scale, plants providing oxygen are classical examples. Organisms substantially affecting abiotic environment are often called 'ecosystem engineers' and the process in which an organism systematically modifies its own niche (both biotic and abiotic components), is called

'niche construction'. Obviously, this process is most pronounced in *Homo sapiens*, which is currently the most conspicuous ecosystem engineer.

If a species can change its environment as well as adapt to it, a coevolution between a species and its niche can follow, based on the continuous feedback between a species' 'niche construction' and its adaptation. Since species continuously change the environment for themselves as well as for other species, species' niches could be very dynamic. Often, however, species' ecological requirements are quite stable over evolutionary time, so that it is even possible to reliably reconstruct an ancient environment on the basis of presence of particular species in the fossil record and the knowledge of their contemporary ecological niches. This can be attributed to the fact that it is often easier to search for appropriate habitat elsewhere if an environment within a locality is changing than to adapt to it. All species have some dispersal abilities, and are thus able to track spatio-temporally changing habitat availability by migration rather than adapt to different conditions by mutation-selection process. The other reason for the apparent niche conservatism is the existence of evolutionary constraints and consequent tradeoffs: species often cannot easily change their traits in a particular direction if these traits are associated with other traits whose change is not advantageous.

As species undertake evolutionary changes, their functional niches can change, leading to changes in the overall 'ecological space' in an ecosystem, and promoting further changes in species traits. On the other hand, some functional niches, that is, particular ecological roles, could be rather stable even if species evolve, go extinct, and new species emerge – a similar functional role can be progressively fulfilled by different species. Community evolution can be therefore viewed as a coevolution of ecological niches rather than of species themselves.

See also: Allee Effects; Biotopes; Community; Competition and Coexistence in Model Populations; Gause's Competitive Exclusion Principle; Habitat.

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Ecological Risk Assessment

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Analysis – Exposure Characterization

Analysis – Effects Characterization

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Introduction

Managers and decision makers are challenged to solve complex environmental problems associated with the increasing pressures placed on vital natural resources by human activities. These challenges are made difficult by the sheer number and diversity of human disturbances and exacerbated by the complexity of imperfectly understood natural ecological systems. The process of ecological risk assessment (ERA) addresses ecological complexity and incorporates uncertainty in characterizing the impacts of natural and man-made disturbances on ecological resources.

ERA integrates ecology, environmental chemistry, environmental toxicology, geochemistry, hydrology, and other fundamental sciences in estimating the probabilities of undesired ecological impacts. In theory, ERA can be viewed as a subset of basic disturbance ecology. In practice, ERAs derive from specific needs to assess human-induced impacts on the environment. Many ERAs conducted in the United States are motivated by legislation, including the National Environmental Policy Act (NEPA), the Toxic Substances Control Act (TSCA), and the Comprehensive Environmental Response, Compensation, and Liability Act (CERCLA or Superfund). ERAs are also undertaken by private industry to determine future risks and liabilities associated with the development, use, and disposal (i.e., life cycle) of new or existing products (e.g., herbicides, pesticides, and industrial chemicals).

Several different approaches for performing an ERA have been developed internationally. No single methodology has been officially sanctioned. However, the approach

developed by the United States Environmental Protection Agency (US EPA) guides many ERAs performed in the United States. The following discussion emphasizes this methodology.

Definition of Ecological Risk

Risk is defined as the probability that an undesired event will occur. Correspondingly, ecological risk refers to the probability of the occurrence of an undesired ecological event. Alternative definitions of risk include an evaluation of the consequences of the undesired event along with estimation of its occurrence. For the most part, risk pertains to the probability of occurrence and this definition will serve this presentation.

ERA originally focused on the undesired ecological effects of toxic chemicals. As ERA evolved, the set of stressors has expanded to include physical, geological, hydrological, and biological stressors. Examples of these kinds of stressors include physical habitat degradation, erosion of soils or sediments, drought/floods, and introductions of exotic species. One testament to the conceptual soundness of this approach to ERA has been its successful application to nonchemical stressors.

Problem Formulation

This initial and perhaps most important part of the assessment defines the nature and scope of the ERA, describes