Ecological Niche

Article · December 2008

2 authors:

Jitka Polechová
University of Vienna
20 PUBLICATIONS   **521** CITATIONS

SEE PROFILE

David Storch
Charles University in Prague
129 PUBLICATIONS   **3,239** CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Project   GrassPlot - Scale-dependent phytodiversity patterns of Palaearctic grasslands (a project of the EDGG) View project

Project   Carnivores in habitats of current landscape: a comparison based on camera trap recordings View project

Ecological niche

Jitka Polechová[1,2,5] **& David Storch**[3,4]

[1] *Department of Ecology and Evolutionary Biology, University of Tennessee, 37996 Knoxville, Tennessee*

[2] *BIOSS, King's Buildings, EH93JZ Edinburgh, Scotland, UK (email: jitka@bioss.ac.uk)*

[3] *Center for Theoretical Study, Charles University, Jilská 1, 110 00-CZ Praha 1, Czech Republic (e-mail: storch@cts.cuni.cz)*

[4] *Department of Ecology. Faculty of Science, Charles University, Viničná 7, 128 44-CZ Praha 2, Czech Republic*

[5] *Department of Mathematics. University of Vienna, Oskar-Morgenstern Platz 1, 1090-AT Vienna, Austria*

Synopsis

An ecological niche characterizes the position of a species within an ecosystem, comprising both the habitat requirements and the functional role of a species. Despite undergoing several substantial transformations, this century-old concept still represents a major heuristic tool for our understanding of nature. The niches of distinct, even closely related, species tend to differ in at least some aspects, as interspecific competition minimizes their overlap. In general, interspecific differences in abundance and distribution can be explained by different niche width and position. However, due to spatiotemporal population dynamics, partitioning of the niche space is never perfect, and in some part of their habitat, species will coexist in the absence of a substantial niche separation. Species' evolution always implies the evolution of species' niche. To some extent, we can predict niche evolution based on knowledge of the environment and of the trade-offs that affect the potential resource utilization of individual species. In the course of evolution, species have a tendency to narrow their niches due to interspecific competition and intraspecific optimization. Consequently, niche widening often occurs when a species is released from interspecific competition. Furthermore, species do not passively adapt to their niches but rather actively modify them. This feedback leads to the coevolution of species with their environments and to the evolution of whole ecological communities.

Keywords

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 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 an ecological niche were close to the general meaning of the term: the ecological niche was defined by a place a species can take in nature, determined by its abiotic requirements, food preferences, microhabitat characteristics (for example 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 a 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 trophic chains and food webs, 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 within them in the second half of 20th century has lead to the formalization of 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 attributes as temperature, light intensity or humidity, but also more sophisticated attributes 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, i.e. 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 favourable 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. Thus, a realized niche 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 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, analysed by Robert MacArthur, showed significant (though incomplete) separation along only three niche axes (feeding behaviour, 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 (for example, a prey size).

Competitive exclusion

Historical development of the niche theory is very closely related to one of the most important topics of ecology, i.e. 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, whilst 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 utilises 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 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 due to environmental or demographic stochasticity: over time, one of the species would ultimately become extinct by chance.

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, i.e. 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; 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 – under negative frequency-dependence. Also, coexistence between species can be facilitated by nonlinear responses of the competitors to common fluctuations in the environment. 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 sexually reproducing populations, recombination generates all possible combinations from the common gene pool, although some of these may be maladaptive. Trade-offs in utilizing the resource spectrum may – or may not – generate disruptive selection strong enough to drive evolution of reproductive isolation and evolution of distinct species, thus eliminating maladapted recombinant genotypes. In contrast, in asexual species, clones bearing favourable combinations do not recombine, and therefore those adapted to the various resource combinations can be arbitrarily spaced in the niche space. 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, favouring in each species phenotypes differing from the phenotype of the competitor. Current niche segregation can be due to the processes that took place in distant evolutionary past – sometimes emphasized by the term "the **ghost of competition past**". When phenotypic differences arose due to divergent evolution of sympatric competitors, we speak of **character displacement**. Typically, sympatric populations of competing species evolve towards more different sizes of characters associated with food consumption (beaks, teeth) than allopatric populations – if there is an island with only one species of Galapagos finches, it has an intermediate beak size enabling it to utilize a wide spectrum of seed sizes, whereas if there is an island with two species, one has a bigger and the other a 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 always has an option to thrive outside of the range of conditions preferred by the 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 rates of spreading and growth, which enable them to quickly occupy empty places before arrival and eventual overgrowth of competitively superior species. In this case, we speak about the **regenerative niche**, representing a time window for the success of 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, i.e. 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 tree species on the basis of their niche differences – the dispersal assembly and coexistence without significant niche differentiation seems 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 rare 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 non-equilibrium 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 the distribution 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, i.e. that 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 other. 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 **trade-offs** in resource utilization: resources can always potentially be utilized in many ways, but a species which utilizes many resources typically does so with a lower efficiency compared to a specialist. 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. Some strategies in resource utilization are mutually exclusive: 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 slower growth. Whilst natural selection supports phenotypes that are better at utilizing available resources, it can only explore the vicinity of the current strategy, selecting from the available phenotypes. Consequently, evolution leads to utilization of only a restricted spectrum of resources.

In the presence of trade-offs, 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 trade-offs between adaptations, and since all the trade-offs 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 trade-offs 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 trade-offs - 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 other 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 a given habitat and for a 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 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, i.e. where it finds its niche. However, the "presence of the niche" is not a sufficient condition for the presence of a species, and in special cases 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 fulfills 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, hindering 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 neighbouring 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 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 non-linearity of the dynamics of metapopulations). Moreover, the statistical relationship between niche breadth and abundance can actually have a reversed

12

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 lognormal, though other models may fit the observed species-abundance distribution better in particular situations). This distribution has been modelled 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 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 – 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 the 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.

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 favoured 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: when the niche becomes narrower, the species' range and hence total population size decreases. 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 ever changing world.

Evolution of niche width

Progressive specialization, i.e. narrowing of niche width in the course of evolution, is forced by interspecific competition (when the niches overlap) and intraspecific optimization, and thus represents an expected evolutionary trend. The opposite process, i.e. an extension of niche width, is observed mostly after entering a new environment without competitors, allowing utilizaton 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 behaviourally, as an immediate response to an altered resource or species structure.

Although sometimes there is an obvious constraint on expanding a species' niche - e.g. 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. However, even a gradual change in the environment can lead to a sharp range margin, as "swamping" by gene flow from central to marginal areas can create a positive feedback between the reduction in fitness, where population size decreases due to maladaptation, and the erosion of genetic variance by genetic drift. When local genetic variance is too low, continuous adaptation to a spatially variable environment fails. Moreover, when there is a large asymmetry in the carrying capacity across the habitats, even alleles which

neutral or nearly neutral in the main population and deleterious in the marginal populations, can sweep through the small marginal population, thus preventing the adaptation.

Asexual reproduction or self-fertilization can hence 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 favourable 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 coworkers on Caribbean birds. In the first stage, an immigrant, which is mostly a species with a high dispersal 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 the resource space generated by an emerging tree or of successive colonization of an island, where first colonizers modify the environment for their successors.

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 to adapt to it, 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 can 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 spatiotemporally 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 trade-offs: 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, i.e. particular ecological roles, can be rather stable even if species evolve, go extinct and new species emerge - 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.

Further reading

Abrams, P. (1983). The theory of limiting similarity. Ann.Rev.Ecol. & Syst. **14**, 359-376.

Chase, J. M., and Leibold, M. A. (2003). Ecological niches: Linking classical and contemporary approaches. University of Chicago Press.

Elton, C. (1927). Animal Ecology. London: Sidgwick & Jackson.

Grinnell, J. (1917). The niche-relationships of the california thrasher. Auk **34**, 427-433.

Hutchinson, G. E. (1958). Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. **22**, 415-427.

Hutchinson, G. E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? American Naturalist **93**, 45-159.

Leibold, M. (2003). Ecological niches: linking classical and contemporary approaches. Chicago: University of Chicago Press.

Losos, J. (1992). The evolution of convergent community structure in Caribbean Anolis communities. Systematic Biology **41**, 403-420.

MacArthur, R. (1958). Population ecology of some warblers of northeastern coniferous forests. Ecology **39**, 599-619.

MacArthur, R. and R. Levins (1967). The Limiting similarity, convergence, and divergence of coexisting species. American Naturalist **101**, 377-385.

Odling-Smee, F.J., K.N. Laland and M.W. Feldman (2003): Niche construction: the neglected process in evolution. Princeton: Princeton University Press.

Ricklefs, R.E. and Bermingham, E. (2002): The concept of the taxon cycle in biogeography. Global Ecology and Biogeography **11**, 353-361.

Roughgarden, J. (1974). Niche Width: Biogeographic patterns among anolis lizard populations. American Naturalist **108**, 429-442.

Schluter, D. (2000). The ecology of adaptive radiation. Oxford: Oxford University Press.

Schluter, D. and P. R. Grant (1984). Determinants of morphological patterns in communities of Darwin's finches. American Naturalist **123,** 175-196.

Schoener, T. (1989). The ecological niche. In Cherrett, J. (ed.) Ecological concepts. pp. 79-113. Oxford: Blackwell Scientific Publications.

Tokeshi, M. (1999). Species coexistence: ecological and evolutionary perspectives. Oxford: Blackwell Science.

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, Rougharden 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. Levin's 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.

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 continues to distribute the "niche" among all the species within the taxon. The model seems to describe well relative abundances of species within taxa, across a large range of their species richness.

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. Here, one of the species if fully dominant in its niche. Therefore, the other species can sustain its population only on a part of its fundamental niche, as 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).

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 islands corresponds well to the maxima of the curve. Position of the symbols marks mean beak depth of male ground finch on each of the three islands: *Geospiza fortis* (□)**,** *G. difficilis* (Δ), *G. magnirostris* (〇) and *G. fuliginosa* (●)**.** The beak depth scale is kept the same for the three pictures; the population density is scaled to the maximum. (Modified from Schluter & Grant 1984).

Cross-references
Biotope, habitat, microhabitat, character displacement, Shannon diversity index, Allee effect, community.
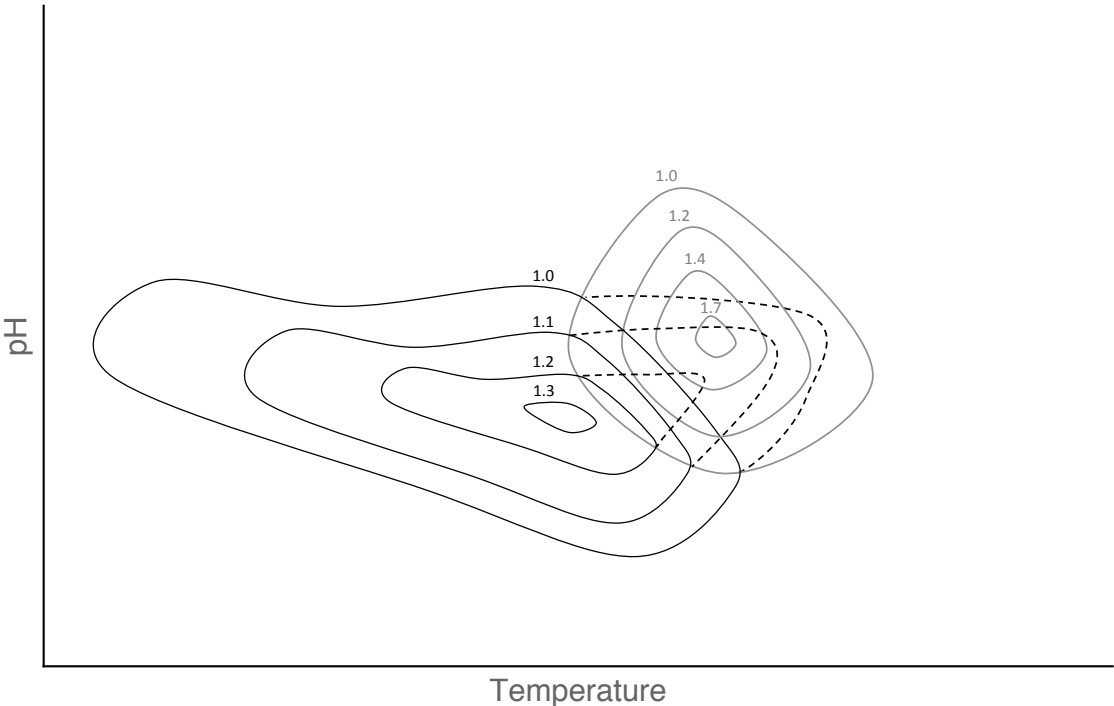
Figure 1

Figure 2