

Plant coexistence and the niche

Jonathan Silvertown

Department of Biological Sciences, The Open University, Walton Hall, Milton Keynes, UK, MK7 6AA

How large numbers of competing plant species manage to coexist is a major unresolved question in community ecology. The classical explanation, that each species occupies its own niche, seems at first unlikely because most plants require the same set of resources and acquire these in a limited number of ways. However, recent studies, although few in number and incomplete in many ways, do suggest that plants segregate along various environmental niche axes, including gradients of light, soil moisture and root depth, and that partitioning of soil nutrients occurs, possibly through the mediation of microbial symbionts, some of which are more species specific than was previously thought. Although it is unlikely that niche separation along environmental axes is the only mechanism of coexistence in any large community, the evidence now suggests that it plays a more significant role than has been previously appreciated. More research into the consequences of various known tradeoffs is likely to uncover further cases of niche separation facilitating coexistence.

Research in plant community ecology is overshadowed by a fundamental question to which we still have no definitive answer: how do plant species, which can reach densities of 40 m^{-2} in grassland or nearly 300 tree species ha^{-1} in tropical forest, stably coexist? The answer offered by classical ecological theory based upon the Lotka-Volterra competition model is Gause's principle, which states that stable coexistence between competing species requires them to occupy different NICHES (see Glossary) [1]. The niche concept, as initially conceived by zoologists Joseph Grinnell and Charles Elton, emphasized the role of habitat and food in defining the niche of an animal [2] and the best examples of Gause's principle in operation are found in animal communities, where coexisting species often exhibit differences in diet or foraging patterns [3]. Because plants furnish animals with food and shelter, plants are frequently the source of niche separation in animal communities, through the structural complexity of habitat that they create or the variety of foods that they provide. Therefore, even understanding animal diversity ultimately depends upon understanding plant coexistence.

However, the TROPHIC NICHE, which is so easily observed in animals, offers no obvious explanation of coexistence among plants, even if we interpret 'food' to mean the resources that plants consume. All plants require water, CO_2 , light, nitrogen, phosphorus, potassium and a common set of minor mineral nutrients. Different species acquire these resources in similar ways, even to the point

of sharing the mycorrhizal fungi that are essential to the nutrition of most wild plants. Among the 420 000 extant species of seed plants that have been described [4], there are only three biochemical pathways for carbon acquisition, two of which have evolved repeatedly [5,6]. Contrast this with the $>30\,000$ defensive compounds that plants have evolved [7] and it is apparent that there must be severe constraints on the evolutionary scope for diversification in plant nutrition. Nitrogen fixation by symbionts is an example of one escape from a nutritional constraint but, in this case, it is remarkable that, even though the ability to fix nitrogen has evolved several times and with several different symbionts, all nitrogen-fixing angiosperm groups belong to a single lineage [8]. This implies the necessary existence of some (as yet unidentified) precursor to the evolution of this trait.

Not only do most plants require the same resources and acquire them in similar ways, but it is also now clear from field experiments that interspecific competition for these resources is the norm in plant communities [9–11]. In habitats where rainfall is too scarce to support the closed canopy that normally forces plants to compete with each other for light, plants still compete with one another below

Glossary

α Diversity: the number of species found in a local community.

α Niche: the region of the realized niche of a species corresponding to species diversity at the local community (or α -diversity) scale at which interactions among species occur. Niche differences at this scale should facilitate coexistence.

Character displacement: the evolutionary accentuation of trait differences between sympatric species caused by competition for resources.

Community structure: regularity in the membership (presence or absence) or abundance of species in a community with respect to random expectation based upon an appropriate null model of trait or taxonomic distribution.

Fundamental niche: the region of its niche that a species is able to occupy in the absence of interspecific competition and natural enemies.

Guild: a group of functionally similar or taxonomically related species that exploit a common resource and, hence, are expected to experience greater interspecific competition among guild members.

Niche: an n -dimensional hypervolume [74] defined by axes of resource use and/or environmental conditions and within which populations of a species are able to maintain a long-term average net reproductive rate that is ≥ 1 .

Niche axis: a dimension in n -dimensional niche space along which species can show segregated distributions.

Niche dimension: used interchangeably with niche axis.

Niche shift: a change in the mode and/or a reduction in the variance of the distribution of a species (or of its resource use) along a niche axis caused by the presence of competitors.

Niche space: the n -dimensional envelope containing all the niches present in a community of species.

Realized niche: the region of its niche that a species is able to occupy in the presence of interspecific competition and natural enemies.

Regeneration niche: the component of the niche of a plant that is concerned with processes such as seed production and germination and by which one mature individual is replaced by another [69].

Trophic niche: the place of an organism in the environment in relation to its food and the consumers that prey upon it.

Corresponding author: Jonathan Silvertown (j.silvertown@open.ac.uk).

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Box 1. Theories of coexistence relevant to the α niche

The theories of coexistence listed here either require the existence of α niches of a particular kind or, in the case of the neutral theory, would be refuted if plant communities are found to be structured by interspecific competition. All except the neutral theory involve some form of tradeoff [28].

Lotka–Volterra competition model

This is the classical model upon which Gause's principle is based. It predicts that stable coexistence will occur between a pair of species if each inhibits its own population growth (through intraspecific competition) more than it inhibits that of the other species (through interspecific competition). This situation is most likely to arise if the species occupy different niches.

Competition–colonization tradeoff

A negative correlation between the interspecific competitive ability of species in a community and their ability to colonize recruitment sites can enable coexistence to occur if competitive asymmetry is strong enough ('winner-takes-all'). However, in nature competition tends to be less asymmetric, weakening the ability of this mechanism to produce stable coexistence, which will not occur unless there are also niche differences between competing species [37,67].

Forest architecture hypothesis

A tradeoff between maximum tree size and recruitment rate into canopy gaps enables the stable coexistence of trees to occur if they differ in the typical height that they reach in the canopy [68].

Regeneration niche

This is a multi-faceted hypothesis that highlights the many ways in which species within a community differ from one another during the regeneration phase of the life cycle, potentially contributing to coexistence [69]. The storage effect is one example and niche separation by gap size requirements for recruitment is another [70] (Table 1, main text).

Resource ratio model

More than two species can coexist on just two limiting soil resources (e.g. nitrogen and phosphorus) if the ratio of concentration of these resources varies within the habitat and species switch from being limited by one to being limited by the other, depending upon the local ratio of the resources [17].

Microbial mediation

Soil nutrients occur in a variety of chemical forms, creating the possibility that plants specialize on particular pools, such as nitrate, ammonium or amino-acid sources of nitrogen [43]. Microorganisms associated with plant roots might help species access different pools, thereby dividing nutrient resources into trophic niches. This will promote coexistence among plants if there is sufficient specificity in microbial–plant interactions and negative feedback between the abundance of a plant and the abundance of its microbial partner [48,49].

Storage effect

When species have different environmental requirements for successful recruitment and the environment varies from year-to-year, species will recruit in different years. So long as species are perennial (or have a dormant seed bank) and established recruits can resist competition, those produced in the good years are stored through the unfavourable ones. In effect, species have temporal niches that enable them privileged access to shared resources for limited periods of time during which interspecific competition is reduced relative to intraspecific competition [28].

Unified neutral theory

This theory assumes that the long-term fitnesses of different species are equal and that the relative abundance of species in a community is determined by a random-walk process [19]. The model successfully predicts patterns of relative species abundance in communities; however, the same patterns are also predicted by non-neutral models [71,72]. If plant communities have niche structure, the core assumption of the neutral theory is violated.

ground for water and nutrients [12–15]. The conundrum, then, is how can competing species coexist as they do in nature, apparently without the niche differences that classical ecological theory predicts to be necessary? Or to put it another way, how do we reconcile the high level of α DIVERSITY (*sensu* [16]) that is found in many plant communities with competition for resources? Only two answers are possible. Either the classical theory is wrong or incomplete, or there are niche differences between plants that have been overlooked. The first of these has been addressed by numerous theoretical models, many of which start with similar assumptions to those of the Lotka–Volterra model but emphasize particular NICHE AXES, such as the REGENERATION NICHE or add on additional conditions, such as temporal or spatial heterogeneity (Box 1). An important refinement of this kind of model is the resource ratio model, according to which spatial [17] or temporal [18] heterogeneity in just two resources can enable more than two competitors to coexist (Box 1).

The most radical theory is Hubbell's Unified Neutral Theory [19] which proposes that: (i) species are competitively equivalent, (ii) niche differences are irrelevant; and (iii) species diversity is governed by a process of drift, akin to that which determines genetic diversity among neutral loci in population genetics (Box 1). Hubbell's theory has given new impetus to the hunt for evidence of plant niches [20,21]. So too has the recent interest in plant

mixtures that yield disproportionately more biomass than do monocultures of the component species (i.e. overyielding). In many instances overyielding appears to be caused by niche differentiation between species [22,23], although the precise niche axes involved are usually unknown. Studies of plant COMMUNITY STRUCTURE [24] and CHARACTER DISPLACEMENT in flower traits [25,26] also provide circumstantial evidence of niche separation in some habitats, but are outside the scope of this review.

There have been several reviews of the theoretical alternatives to classical coexistence theory [27–29], but no comprehensive, recent review of progress made in the search for empirical evidence of niche separation in plants. A peculiarity of the concept of the niche makes a review of the evidence particularly necessary; that is, there is no *a priori* method of identifying the right niche axes to study [30]. Therefore, if a study finds that species do not partition one particular niche axis, it does not mean that partitioning does not occur along some other axis that has not yet been identified, or that differences accumulated across many axes do not explain coexistence. It is impractical and unparsimonious to go on looking indefinitely for niche differences, but when should one stop? If positive evidence of niche separation is being discovered, we need to know on which axes it is being found. If there is no apparent progress, then we need to ask whether niche separation in plants has been examined with sufficient

rigour by enough studies for us to reach a firm conclusion about its role in the organization of plant communities.

Scope of the review: what are we looking for?

Definitions of the term 'niche' vary notoriously between authors and are a continuing source of confusion [2]. To make it clear that the kind of niche that is relevant here must potentially enable segregation of resources within habitats at the local scale of α diversity, I follow Pickett and Bazzaz [31] in using the term α NICHE. (Although, for readability, I often use the unqualified term 'niche', which should be understood to mean α niche). Innumerable studies describe physiological, morphological, phenological or ecological differences among species and tradeoffs between traits, many of which are potentially relevant to plant community structure. However, these studies are of limited use as evidence of niche separation unless they also demonstrate that the observed differences or tradeoffs facilitate coexistence. Therefore, I focus here on empirical studies that have conducted at least two of four critical tests of whether segregation on putative α niche axes facilitates coexistence in accordance with classical competition theory.

I derive the four tests from competition theory as follows. Although the refinements of classical theory can be quite complex [28,32], a sufficient condition for stable coexistence to occur is that a species always increases once it has become rare [33]. This can occur by a variety of mechanisms, but, in classical competition theory, the condition for it to happen is [34]:

- Test 1: intraspecific competition is greater than interspecific competition.

This can occur when each species specializes on one particular region of NICHE SPACE in which it is superior to its competitors. Competition between specialists causes species to displace one another from their regions of specialism and, hence, we expect:

- Test 2: segregation on a resource or environmental axis.

This should be tested against a null model [35]. Species are forced to specialize by tradeoffs, which prevent any species being a superior competitor under all resource conditions, so there should be:

- Test 3: tradeoffs between traits or in performance on different niche axes

Finally, the acid test of niche separation is that manipulating the densities of individual competitors should alter the distribution of other species in niche space. Therefore, there should be:

- Test 4: NICHE SHIFTS in response to experimental manipulation of competitors.

This test is essentially a comparison between FUNDAMENTAL and REALIZED NICHES, and comparisons between *ex situ* (e.g. glasshouse) and field responses to niche axes are one way to establish whether a niche shift occurs in response to interspecific competition. In selecting studies, I relaxed the conditions of test 4 to accept evidence from 'natural experiments' where natural variation in the occurrence of competing species has been used in place of experimental manipulation.

Although the storage effect (Box 1) operates through temporal niches for recruitment it requires different diagnostic tests [36], which I do not consider here. The

role of competition-colonization tradeoffs (Box 1) in plant coexistence has been the subject of a recent review [37].

Empirical evidence for the existence of α niches

I found only 13 studies published since 1990 that applied at least two of the tests to plant communities in the field and none that applied all four (Table 1). This appears to reflect the general decline in interest in the niche detected by Chase and Leibold [2], who found that the percentage of articles published in *Ecology* during the 1990s containing the search term 'niche' was less than it had been at any time since the 1960s. All 13 studies showed segregation of species along one or more niche axes, eight demonstrated a tradeoff that could explain why species specialize and six showed a niche shift. Only two studies compared the relative strengths of intraspecific and interspecific competition.

The studies selected are listed in Table 1, divided into two broad categories: studies of belowground niche axes (nutrients, soil moisture, microtopography and rooting depth) and studies of aboveground niche axes (canopy height, light intensity, size of canopy light gap and aspects of regeneration niche). The reason for using such broad categories is that often a NICHE DIMENSION will represent a complex of resources and conditions. For example, soil moisture is an important variable that might simultaneously measure the availability of a resource (water) and soil conditions that regulate oxygen concentration and nutrient availability; canopy gap size in a forest correlates with the availability of light and water resources, and with conditions such as temperature and humidity. Even the distinction between above- and belowground niches is not an absolute one given that canopy gaps alter soil as well as light conditions [15,38].

Below ground

There is evidence of niche segregation by rooting depth among temperate grassland herbs (Table 1, [39]) and between shrubs and herbs in arid environments [40,41]. Meadow plants [42] segregate along hydrological gradients (Box 2), whereas tundra communities utilize different nitrogen sources and also show some temporal partitioning of these resources [43,44]. Partitioning of soil resources can also involve microbial mediation (Box 1). Arbuscular mycorrhizal fungi (AMF) have higher diversity and can be more specific in their relationships with plants than was once thought [45,46], which explains experimental evidence that plant diversity can depend upon AMF diversity [47], and also lends support to the hypothesis that soil nutrients are partitioned through microbial mediation [48,49] (Box 1) (reviewed in [50,51]).

Reviewing mechanisms of coexistence in tropical forests [52], Wright considered niche separation on small-scale topographical gradients to be a real, although minor factor in explaining α diversity. Several recent studies [53–57] that apply only one test, and so are omitted from Table 1, bear out the view that topographical segregation occurs to some degree in most tropical forest communities, but that it is insufficiently fine grained to account for much diversity at the α scale.

Table 1. Recent studies applying at least two of four tests of niche separation in plant communities

Taxa	Species no.	Growth form	Habitat	Tests ^a				Hypothesis supported ^b	Refs
				Competition	Segregation	Tradeoff	Niche shift		
Below ground									
<i>Opuntia, Hilaria, Larrea</i>	3	Succulent, grass, shrub	Desert	Correlation of size & distance to nearest neighbour suggests intraspecific competition > interspecific competition	By rooting depth	–	–	CNS	[40]
<i>Agave, Encelia, Pleuraphis</i>	3	Succulent shrub, grass	Desert	–	By rooting depth	–	Rooting depths diverged when species were near each other	CNS	[41]
<i>Laguncularia, Avicennia</i>	2	Tree	Mangrove	–	On nutrient & salinity gradients	Photosynthetic N use efficiency vs photosynthetic water use efficiency	Coexistence where only one of the two species was N limited	CNS	[75,76]
Monocots & eudicots	82	Herb	Meadow	–	On hydrological gradients in the field	Drought tolerance vs water-logging tolerance	Shifts in distribution along a water table gradient in a lysimeter experiment	CNS	[42] ^c
<i>Carex, Betula, Eriophorum, Vaccinium, Ledum</i>	5	Graminoids & shrubs	Tundra	–	N resource segregated by timing, depth & chemical form of uptake	–	Uptake preferences for amino acid N over N from NH ₄ differed in field vs solution cultures of individual species; probable niche shifts between fundamental & realized niches	CNS (involving microbial mediation?)	[43,44]
Angiosperms	8	Herb	Grassland	–	By rooting depth	–	Changes in rooting depth when nutrients applied	CNS	[39]
<i>Poa, Hordeum, Puccinellia</i>	3	Herb	Marsh	–	On salinity gradient	–	Grasses showed niche shifts along experimental salinity gradient when grown in glasshouse mixtures, mimicking field distributions	CNS	[77]
Above ground									
Angiosperms	27	Tree	Tropical forest	–	By maximum height attained	Height vs recruitment	–	FAH	[65]
Angiosperms	14	Tree	Warm temperate forest	–	By canopy height among larger species & growth response to canopy gaps among smaller ones	Canopy height vs shade-tolerance & growth response to canopy gaps vs shade-tolerance	–	FAH	[66]
Angiosperms	4	Tree	Tropical forest	–	On light gradient	Growth rate in high light vs survival rate in shade (shade tolerance)	–	CNS	[61]
Angiosperms & gymnosperms	9	Tree	Temperate forest	Conspecific aggregation	On light gradient	Growth rate in high light (correlated with good seed dispersal) vs survival rate in shade (shade tolerance)	–	CNS; CCT	[58–60]
<i>Macaranga</i>	11	Tree	Tropical forest	–	On light & soil texture gradients	Maximum height vs shade tolerance	–	CNS	[78]
Pioneer trees	3–6	Tree	Tropical forest	–	Seedling performance varied according to gap size	Wet season growth vs dry season survival in small gaps	–	RN	[79,80]

^a– indicates the test was not applied.

^bAbbreviations: CNS, classical niche separation; CCT, competition–colonization tradeoff; FAH, forest architecture hypothesis; RN, regeneration niche.

^cSee Box 2.

Box 2. Case study: the hydrological niches of meadow plant communities

No single study listed in Table 1 (main text) satisfies all four tests of niche separation, but plants in English meadow communities do demonstrate three of them [42].

An example of segregation in niche space is found between *Heracleum sphondylium* (Figure 1a grey shading) and *Silaum silaus* (Figure 1a black shading) both of which belong to the Apiaceae. Segregation is based upon hydrologically defined niche axes. In Figure 1a, poor soil aeration caused by waterlogging is measured on the vertical axis and drought stress caused by soil dryness on the horizontal axis. The scale on each axis is a Sum Exceedance Value (SEV), which measures, in units of metre weeks, the exposure of plants to aeration of drought stress when the water table falls below (causing drought) or rises above (causing aeration stress) a physiologically determined threshold value for each axis. Pie diameter is proportional

to total abundance of the two species. The niches of the two species overlap less than is expected from a null model ($P < 0.001$). The figure is reproduced, with permission, from [73].

A tradeoff between species' tolerances on two niche axes is detailed in Figure 1b, between waterlogging tolerance and drought tolerance for 60 species of meadow plants. The figure is reproduced, with permission, from [29]. An example of niche shifts under experimental conditions is detailed in Figure 1c and 1d, which show the distribution of plant biomass for six meadow grasses (each line is a separate species) grown on an experimental water table gradient in monocultures (Figure 1c; mean pairwise niche overlap=94%) and in a mixture of all species (Figure 1d; mean pairwise niche overlap=72%) [42]. The figures are reproduced, with permission, from [29].

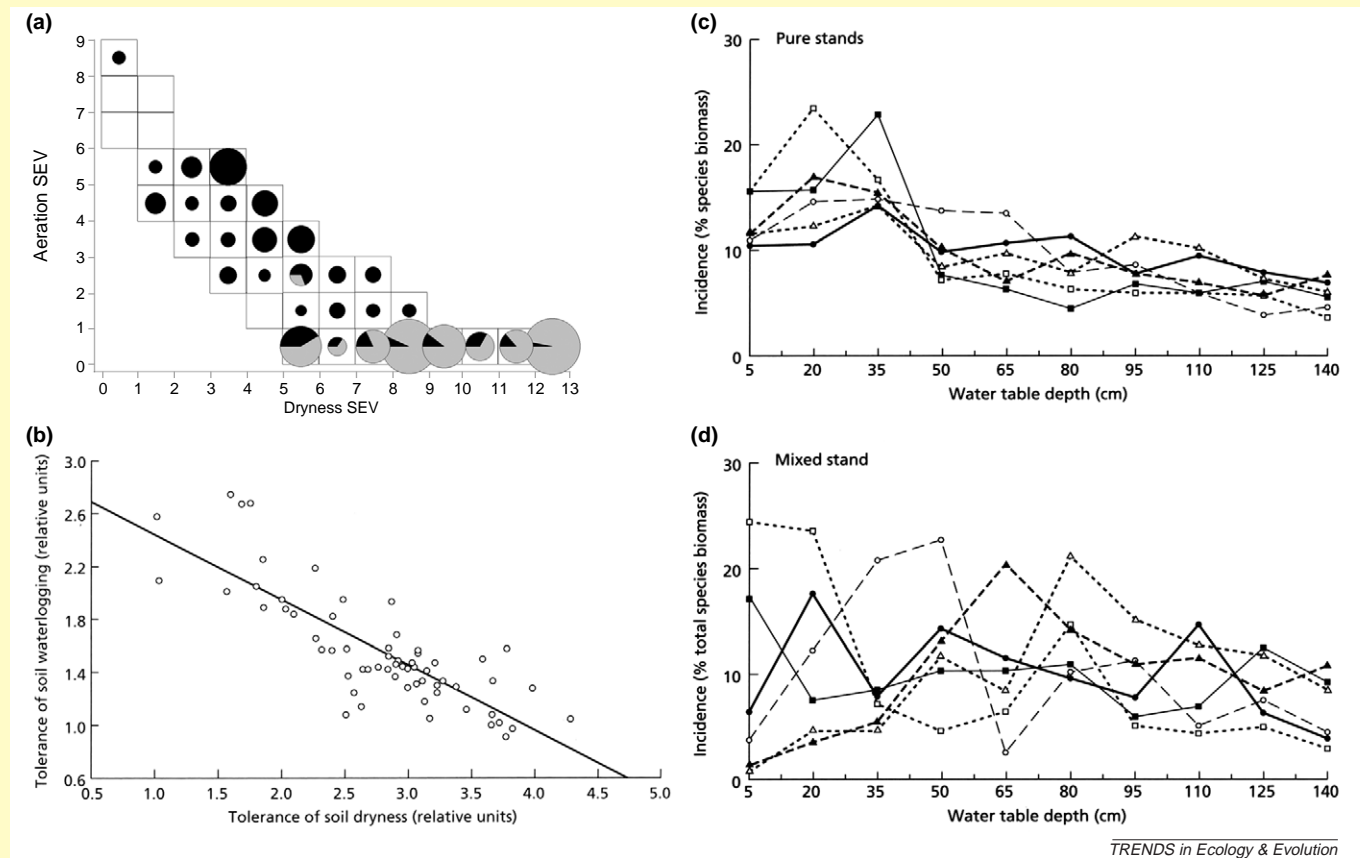


Figure 1.

Above ground

Forest studies indicate that small GUILDS of species might partition light gradients through a tradeoff between growth rate in better light conditions and survival in shade [58–61]. Partitioning of light gradients might in theory also occur if the slope of the relationship between relative growth rate (RGR) and light intensity varies between species in such a way that curves for different species intersect, causing the rank order of the RGRs of species to switch between locations with different degrees of illumination [62]. However, whether this mechanism occurs is controversial [63,64].

Studies of seedlings in gaps suggest that the regeneration niche might be particularly relevant in forests, but, in the cases in Table 1, regeneration is not the whole

story and tradeoffs between height and recruitment supporting the forest architecture hypothesis are also important [65,66].

Conclusions

The most striking feature of Table 1 is how few studies it contains and how incomplete, in terms of the four tests, those studies are. Even so, the results indicate that plants do segregate along a variety of niche axes and that this is likely to facilitate coexistence. Therefore, the paucity of research on this topic cannot be explained by the absence of niche separation in plants. Rather, it would appear that, as Chase and Leibold [2] have argued, the concept of the niche has been neglected over the past decade. Even among the 13 studies listed in Table 1, only three contain

the term 'niche' in the title of the article. We should be working towards applying all four tests in the field. Given the ubiquity of tradeoffs and their central importance to coexistence theory, examining these should be the first step towards finding the niche axes on which species can be expected to segregate in plant communities. It is time for the niche to be rehabilitated and for plant ecologists, in particular, to investigate its role in a more sophisticated fashion.

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