

Do Plants Need Niches?

Some Recent Developments in Plant Community Ecology

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Species-rich plant communities appear to defy the competitive exclusion principle, showing relatively few obvious niche differences between coexisting species. Here we explore alternatives to the potentially endless search for new niche axes. Spatial aggregation in populations, non-transitive competition, episodes of density-independent mortality and various non-equilibrium theories allow trophically similar species to coexist for extended periods. In perennial plants or annuals with a seed pool, asynchrony between species in recruitment permits coexistence by the 'storage effect'. There is increasing evidence that species-specific herbivores and pathogens regulate populations of tropical trees to low levels at which competitive exclusion does not occur. The wide variety of alternatives to niche differentiation lead us to question whether plants need occupy different niches to coexist.

Plant communities often display a remarkable richness of species – up to 180 tree species ha^{-1} can be found in some tropical forests and up to 40 herbaceous plant species m^{-2} in certain temperate grasslands. Classical competition theory leads us to expect that niche differentiation among species competing for a limited resource is a prerequisite for their coexistence¹. Most green plants need much the same basic resources: nitrogen, phosphorus, potassium, several micronutrients, light, water, CO_2 and space for growth. Moreover, plants which live together in the same community obviously tend to experience similar environmental conditions. It is difficult to imagine how so many species manage to divide essential resources and 'habitat' niche space sufficiently to coexist. This dilemma has recently led to some creative arguments about the mechanisms that enable plant species to coexist – arguments stimulated in part by the major reevaluation that is in prog-

ress of the forces structuring animal communities². In the comments below, the niche of a species is defined as the trophic, habitat and microsite conditions in which it occurs, although it should be understood that different authors have used the term niche in different ways.

The most obvious way round the coexistence problem is to look for new dimensions in niche space. Some of these new dimensions suggest themselves by virtue of the fact that plants are sessile and that to acquire resources they must first capture some physical space. For example, the idea that plants have a 'regeneration niche' – a set of conditions that a plant species needs, to reproduce and establish the next generation – has been particularly influential in the last few years^{3,4}. Alternatively, the existing niche space may be divided up in new ways. Tilman⁵ has suggested that it is more appropriate to consider the ratios of limiting nutrients than their absolute amounts; this is a promising suggestion because there are many more ratios of limiting nutrients than nutrients themselves. This idea too is predicated upon the fact that plants are sessile and it assumes that the environment (local ratios of essential resources) is heterogeneous. Given enough heterogeneity in the ratios over the area occupied by the community, many species could, in principle, coexist.

A drawback to the search for more niche dimensions is that, unless there are *a priori* reasons for testing a particular dimension, coexistence by niche separation is an unfalsifiable hypothesis. If there appears to be insufficient separation between species on one niche axis, we can never rule out the possibility that there are other unsuspected dimensions in which niche differentiation has taken place. Moreover, even if there is demonstrable niche differentiation among coexisting species, we may be uncertain as to whether it is the cause or effect of their coexistence⁶. It is also by no means straightforward to translate overlaps in niche space, measured by nutrient use for example, to the competitive interactions among species on which their coexistence ultimately depends. Alternative mechanisms for coexistence of competing

species that do not require niche differentiation are, therefore, well worth considering, especially for plants and other sessile organisms.

The influence of spatial structure

Classical competition theory was developed for mobile organisms and, in its simplest form, it assumes no age, size or spatial structure in populations and no density-independent mortality. The prediction of the classical theory that species must occupy different niches in order to coexist turns out to be sensitive to changes in any of these assumptions. Since plants interact primarily with their immediate neighbours, the spatial layout of plants will determine the scope for competition between species⁷ and the outcome of competition between adjacent individuals may be determined by their relative size (e.g. seedling versus adult) rather than by which species are involved⁸. Clearly, the tendency towards spatial aggregations of conspecifics – which occurs widely in terrestrial plants – should enhance intraspecific relative to interspecific competition, increasing the likelihood of coexistence. There is some support for this from modelling competition in animals living on discrete, ephemeral resources, such as *Drosophila* flies that feed on the fruiting bodies of fungi^{9,10}; given enough aggregation within species, coexistence between species can be achieved in the absence of any niche differentiation.

Plant ecologists are becoming particularly interested in this theory because gaps in vegetation can be envisaged as ephemeral resources. How far the analogy can reasonably be taken remains to be seen. The fact that plant communities occupy continuous space (rather than discrete, isolated patches) suggests that approaches based on diffusion may prove more productive than discrete models¹¹.

Yodzis¹² takes local competition within gaps a step further. He argues that, in communities of sessile organisms, competition for space is all-important: an individual can monopolize the resources in the space it occupies. His modelling of such communities leads to the prediction that coexistence is quite possible in the absence of niche differentiation and that the community structure eventually obtained depends on the dominance relations of the species or, if functional dominants are not present, on properties of the initial colonization.

A rather esoteric alternative to niche separation is that competition

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could be non-transitive. By 'non-transitive', we mean competitive relationships of the form $A > B$, $B > C$, but $C > A$ ¹³; although there is no pairwise combination of species which can coexist in this case, the competitive relationships are organized in such a way that a large set of species may still be able to live together. It is not yet known whether such competitive interactions play a significant role in maintaining species diversity within plant communities, and the existence of such interactions is not, in itself, sufficient to ensure coexistence in an ecologically meaningful sense¹⁴. However, a case has been made for coexistence through non-transitivity in communities of certain sessile organisms in marine systems¹⁵. More generally, the addition of further competing species to plant communities is thought to promote coexistence of species that would otherwise exclude one another¹⁶.

Non-equilibrium alternatives

Huston¹⁷ has shown that the introduction of occasional episodes of density-independent mortality into classical (Lotka-Volterra) models of interspecific competition can delay the effects of competitive exclusion which would otherwise rapidly reduce the number of species in a community. Pickett¹⁸ argues that many plant communities are not at equilibrium and that disturbances such as windthrow in forests create situations which promote coexistence without the need to invoke niche differences between plants. So-called 'non-equilibrium' theories of coexistence are rapidly gaining favour with community ecologists studying sessile organisms (see Ref. 19 for a review). Scale is all-important in non-equilibrium communities. Local disturbances may perturb a community which, at the scale of an entire forest, maintains its community structure. There is no contradiction between non-equilibrium dynamics at the population level and coexistence at the level of the community.

The non-equilibrium 'community-drift model' of Hubbell and Foster²⁰ explicitly assumes that competing species do not occupy different niches (i.e. they are ecologically identical to, though reproductively isolated from, each other) and allows the abundance of competitors to follow a random walk. Hubbell and Foster find that when communities are very large, competitive exclusion occurs at a slower rate than expected rates of speciation. They believe that

their model fits the situation of species-rich tropical forests.

The 'lottery for living space' model, originally suggested as the mechanism underlying the coexistence of territorial fish species on coral reefs^{21,22} is a potentially attractive non-equilibrium theory for plants. Here, the gaps needed for regeneration arise unpredictably through time and space, and are filled on a 'first come first served' basis from the pool of dispersed propagules. Since the first propagule to arrive holds the gap against later arrivals, it is a lottery as to which species will fill the gap: no one species consistently wins. However, coexistence here depends very much on interactions at other stages in life²³, and the model is probably too simple to apply to plant communities without modification. Nonetheless, Shmida and Ellner²⁴ have incorporated it into a more realistic model for competition between two plant species, in which some propagules remain in the parental microsite while others disperse. They show that the two species can coexist without niche differentiation if they have different life histories: one being more prolific in reproduction and the other having greater adult survival.

Warner and Chesson²⁵ attribute the power of the lottery model, and others like it, to promote coexistence among similar species to what they call the 'storage effect'. In essence, species are able to persist in a community offering them no immediate chances for recruitment because of the presence of strong cohorts of recruits established in occasional good recruitment years in the past. This does require, though, that the species should differ in which are their good years for recruitment. In a sense this is niche differentiation. In these models, coexistence is the result of non-equilibrium conditions (recruitment possibilities vary from year to year) and age structure. Both are realistic features for models of communities of perennials or of annuals with a dormant seed pool.

Interactions with other trophic levels

Rather than looking for mechanisms internal to the plant community, such as those above, we may appeal to interactions with other trophic levels. It has long been recognized that predators can reduce the intensity of interspecific competition sufficiently to prevent one prey species from excluding another²⁶. Nonetheless, this is by no means the only kind of effect that herbivores may have on plant communities²⁷. For example, a negative interaction

between two plant species could be intensified by a shared herbivore if, together, the plant species support a larger herbivore population. Indirect interactions of this kind have been called 'apparent competition' by Holt²⁸ and, in a curious way, they take us right back to where we began, with the need for niche differentiation as a prerequisite for coexistence; the niche space now consists of herbivores, and niche differentiation takes the form of not sharing herbivores with other species of plant – the 'enemy-free space' of Jeffries and Lawton²⁹.

Another alternative, which combines host-specific herbivory and plant dispersal, is the Janzen-Connell hypothesis for coexistence of tropical tree species^{30,31}. This theory argues that herbivores will be concentrated where their food plants are most abundant and will bring about disproportionate mortality in the clusters of offspring in the immediate vicinity of their parents. Clearly, dominance by a small group of species can be prevented as long as they have specific herbivores. Despite criticism³² and some negative tests of the idea³³, it has recently gained new support and popularity³⁴⁻³⁹.

The arguments sketched above give no more than a flavour of the rich mixture of ideas currently exercising the minds of those interested in coexistence of plant species. It is too early to tell what will emerge from this, but it is already clear that a wealth of possibilities awaits us when our thoughts are no longer channelled into an unending search for different niches. The great challenge, like so many in biology, is to show what blend of the possible mechanisms best accounts for the observed properties of plant communities.

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