Review Article

The Fluctuation Niche in Plants

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Classical approaches to niche in coexisting plants have undervalued temporal fluctuations. We propose that fluctuation niche is an important dimension of the total niche and interacts with habitat and life-history niches to provide a better understanding of the multidimensional niche space where ecological interactions occur. To scale a fluctuation niche, it is necessary to relate environmental constrictions or species performance not only to the absolute values of the usual environmental and ecophysiological variables but also to their variances or other measures of variability. We use Mediterranean plant communities as examples, because they present characteristic large seasonal and interannual fluctuations in water and nutrient availabilities, along an episodic-constant gradient, and because the plant responses include a number of syndromes coupled to this gradient.

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1. Introduction

Ecologists have often wondered how so many plant species can coexist in a same site defying the competitive exclusion principle. Although there are a wide range of equilibrium and non equilibrium theories and mechanisms that have been invoked to explain local diversity and species coexistence [1–7], the classical resource partitioning paradigm remains as a reliable explanation. Following this idea, plants use different resources or different ratio of resources in space and time because there is local scale environmental heterogeneity. In any case, coexistence by niche separation is an unfeasible hypothesis. The theory of stable coexistence seems to have undervalued or even ignored an evident niche-multiplying factor. It is not only the average value of environmental variables and of resource availability that matters, but the range (i.e., the variance) of the spatial and temporal heterogeneity. Here we analyze the advantages of considering the variability of resource availability as a way to improve our understanding of plant coexistence. More particularly, we consider the fluctuations of the conditions and the availability of resources for plants through time and along the vertical dimension of space.

2. The “Habitat Niche”

All plants use and compete for the same resources (light, water, nutrients, and space for growth). If one species has competitive advantage, it will use those resources minimizing coexistence with other species. However, if species sufficiently partition the abiotic and biotic environments, or if there are tradeoffs in resource allocation (some species may allocate more resources to increase reproduction while others might allocate more to survival or growth), then different species can coexist by using different ranges and proportions of resources [8]. Niches may be defined as a spatial and temporal function of water, light, nutrient and temperature ranges, and competition with neighbours. This definition may be made within gradients of availability for each resource: arid-humid (water), oligotrophic-eutrophic (nutrients), shade-sun (light), cold-hot (temperature). Microsite heterogeneity, climatic variability, and disturbance have also been considered to constitute habitat gradients or patches contributing to generate local diversity. We can call it the most evident “habitat niche.” However, it is still difficult to imagine how so many species manage to divide essential resources to coexist through space and time. Other factors

must be considered and further understanding of heterogeneity is warranted.

3. The “Life History Niche”

Species could coexist even in temporally and spatially homogeneous environments, because the mechanisms of coexistence differ throughout the developing stages of the species life history (seedling, sapling, juvenile, adult, senescent). Thus, if one species has traits that are more advantageous than those exhibited by another species, but the reverse is true at different life stages, they can coexist. The set of characteristics in the early stages of plant life cycle, including crucial interactions with other organisms, is referred in literature as the “regeneration niche” [9] and has been highly influential in literature of the plant niche. Therefore, the whole life history and demography of coexisting species of the community must be considered [10] to understand plant species coexistence. The so-called “life history niche” considers the different developing stages of a species and the different life-spans and sizes of diverse species as well.

4. The Measure of Spatial and Temporal Heterogeneity

Habitat niche and, usually, life-history niche are consequences of the plant responses to environmental heterogeneity. However, a lot of confusion exists about what heterogeneity means, because geophysical constrictions, organism responses, and feedbacks between abiotic and biotic components of the system occur in time and space at different scales. As a result, although heterogeneity is present in all modern discussions on plant communities, there have been relatively few attempts to measure it and to use this measure in explaining patterns and processes. We will indicate here just some examples (see also [11]). Schlesinger et al. [12] have measured spatial heterogeneity by using the coefficient of variation (CV) of the average concentrations of nutrients analysed in the soil. In that way, they compared grasslands and desert shrublands and settled that shrubs increase the scale of heterogeneity by their coarse root systems and by creating “fertility islands.” Kleb and Wilson [13] have analysed heterogeneity for light and soil resources availability and biomass, comparing a prairie and a forest. They used autocorrelation techniques and coefficients of variation to conclude that the forest increased heterogeneity (coarser root systems, stem flow, interception and evaporation patterns, etc.).

Wilson [11] differentiated two aspects of the relation between heterogeneity and species richness. One is the partition of niche between species, that he describes as “more heterogeneity is equivalent to more niches,” following Rosenzweig [14]. This corresponds to the habitat niche. The other one is what he calls heterogeneity partition, because “some species might be favoured by relatively uniform habitats, whereas others might be favoured by heterogeneous habitats” [15, 16]. Wilson considers that we need to quantify heterogeneity to understand the relationship between heterogeneity and species richness, because he argues that

whereas niche partition is well documented, heterogeneity partition requires much more comparative measurements. In fact, spatial heterogeneity measures could be quite simple: he recommends the use of CV at plant significant scales, instead of semivariograms, that require much more sampling effort.

Although a number of possible measures of spatial heterogeneity have been proposed, such as CV, Moran's I and β -diversity [17], the concept of heterogeneity itself remains complex. Organisms can produce heterogeneity by themselves [12, 13], and in some cases they can produce self-organized patterns that are likely to be scale-dependent [17]. So, we can conclude that different scales and variables, and a more specific conceptual approach, are needed to gain understanding of Wilson's “heterogeneity partition.”

In this paper we focus on one component of this “heterogeneity partition,” that is, related to the fluctuations of resources availability through time at the same site and along the vertical axis (mainly, light above ground and water and nutrients below ground). Goldberg and Novoplaski [18] proposed to analyse the relationship between temporal heterogeneity and competition in poor habitats under the perspective of two-phased resource dynamics: the idea is that resource availability is not continuous, instead there are a number of pulses and interpulses. Plants compete for resources during the pulses, and try to survive during interpulses. The number of pulses and the duration of interpulses of water or nutrients availability change from wet to dry habitats, for instance. They conclude that competition exists at any level of productivity, but it is limited to pulses. In the less productive habitats, the winners will be not the best competitors but the plants able to resist long interpulses. A similar emphasis in pulse-interpulse dynamics was used by one of us to introduce energetic considerations in explaining the distribution of Mediterranean woody plant growth-forms along a mesic-xeric gradient [19].

5. The “Fluctuation Niche”

At any point of the land surface, many components in the plant environment vary through time in amplitude, frequency, and predictability, but there is a scarcity of evaluations of the role of time fluctuations on plant coexistence. We propose to approach this specific kind of heterogeneity by including the different responses to fluctuations and the control of fluctuations by plants. The heterogeneity resulting from temporal fluctuations can be considered another dimension of the niche, and can be estimated by the variance in the environmental and plant variables. We propose to call this niche dimension “fluctuation niche.” Similarly to other niche dimensions, it is expected to correspond to plant attributes variability.

The ecological rationale for enhanced coexistence with increasing fluctuations is based first on the different growth response of species to resources availability (Figure 1). If resources availability fluctuates, the temporal advantage of one species become balanced by the advantage of the other species at another time, but if resources availability remains constant, one of the species is likely to competitively exclude the other. Secondly, coexistence is ensured by the ability of

species to tolerate interpulse periods. That may be reached by adjusting life-cycle traits, like ephemeral species do, or by physiological, morphological, or anatomical attributes. However, long-term scarcity of resources will result in the inability of most species to persist. So, the differences among species on their limits of tolerance to prolonged interpulses are also a key element to understand species coexistence in fluctuating environments.

Testing the reliability of the fluctuation niche shows similar methodological shortcomings than the rest of other niche dimensions. Our preliminary prediction should be that increasing fluctuation would allow the coexistence of species able to tolerate interpulse periods by life-cycle or physiological mechanisms. A simple guide should include the building of models of species performance in relation to resource availability that should be applied to different scenarios of fluctuation, from constant resource availability to high variance (pulse-interpulse pattern). Of course these models should be referred to existing communities where empirical data on environmental fluctuation and species behaviour are known. Another approach would include experiments modifying the temporal pattern of resource availability and surveying physiological and population response of coexisting species. Finally, field observations of higher numbers of coexisting species or functional groups in environments with higher temporal variability will also support the relevance of the fluctuation niche.

If fluctuations are important, different responses of coexisting species can be expected involving phenotypic plasticity, investment in mechanisms or structures to overcome difficult periods, or fitting of the life cycle to the favourable periods. The fluctuation niche gradient would run from episodic to constant resource availabilities [19], Goldberg and Novoplanski [18]. Obviously the “fluctuation niche” and its interactions with the “habitat niche” and the “life history niche” geometrically increase the number of possible niches. Even though these interactions do not necessarily enhance plant species richness (heterogeneity can have positive, null or negative effects on richness, [11]), they provide a better understanding of the multidimensional niche space where ecological interactions occur.

The plant traits associated to the “fluctuation niche” constitute different syndromes. A good example of the importance of the “fluctuation niche” and of the presence of these different syndromes is found in the Mediterranean environment, which shows characteristic large seasonal and interannual rain fluctuations. These fluctuations have been mostly studied in the deserts that, differently from Mediterranean ecosystems, present very scarce plant cover. In these ecosystems, a vertical gradient of fluctuations is generated in the soil: water availability strongly fluctuates within and between years in the surface layers and much less in the deep layers. A particular case is provided by “dehesas,” which are constituted by an aboveground mosaic of tree and herb-dominated patches, but with underground coexistence of roots, similarly to tropical savannahs. As a result, the depth of roots profoundly affects the variance of water availability, which in turn affects the variance of nutrient availability and the variances in the leaf water and nutrient status. In fact, the

main division in Mediterranean communities is established between species with deep roots, with more constant water and nutrient resources, and species with shallow roots, which use episodic rainwater and associated nutrient uptake. Plants develop several responses between the two extremes of this constant-episodic gradient: (1) a great development of the vertical structure, both aboveground and belowground, to ensure minimum interannual and interseasonal fluctuation in the availability of resources, versus a high capacity for high rate activity and turnover of leaves and roots in favourable periods; (2) a slow growth, to ensure space domain, versus a fast growth to take advantage of disturbances; (3) a high structural investment and low reproductive and dispersal effort versus a low investment in structure and high capacity of reproductive regeneration and dispersal. It is also the traditional distinction between stress tolerance and stress avoidance syndromes, which allows coexistence. At the sites of maximal fluctuation of resources (superficial soil layers) that can be estimated from CV, there is maximal coexistence of the roots of these biological types. Therefore, we suggest that the competition outcome in many cases would not depend on the average availabilities of an essential resource, but on the patterns of time-space fluctuations of that availability. Obviously, the variation range will become determinant only if it is larger than some threshold value, different in each case.

Fluctuations are included, most times in an implicit way, in many traditional and recent views of plant attributes. For instance, they are included in the definition of plant ecological strategies or in the classical distinction between *r*- and *K*-selected species. There is a gradient from a conservative strategy, when fluctuations are scarce (permanent space occupation, strong protective investments, and greater resource allocation to ensure seedling establishment), to an opportunistic strategy, which withstands larger fluctuations with a more discontinuous activity (fugitive use of space, lower protection from risks, and maximisation of dispersion versus growth). Thermodynamically, conservative species use more efficiently the resources with less energy dissipation, giving to them more advantage at the end of successional processes [20]. However, as disturbances always exist, all strategies are possible and complementary.

Of course, the ultimate constriction for coexistence is not imposed by the species characteristics, but by water, radiation, and nutrients. To scale and test the relevance of the fluctuation niche, it is necessary to compare the coexistence of species and its performance (i.e., ecophysiological response) not only to the mean values of the usual environmental variables which represent the classical niche approach, but also to the variances (or to the number and span) of pulses (defined over some threshold) of resources availability. There are many published data on variability of the environment and of the status of many species, but there are few experiments designed to follow the evolution along time of both environmental variables and attributes of coexisting species. Therefore, we propose the use of the environmental variance as a multidimensional descriptor of the position of each species within the fluctuation niche. To test the usefulness of this approach, further specific

FIGURE 1: Fluctuation environments (a) allow alternate dominance (considered as growth rate) of different species A and B (b), while constant environments may lead to a permanent higher growth rate of a given species, allowing competitive exclusion. In the figure, constant resource availability around 4 (logarithm scaled) represents a permanent higher growth of species B.

observations are warranted. In any case, the concept of “fluctuation niche” should be added to the existing “habitat” and “life-history” niches in order to understand species stable coexistence.

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