

# THE USEFULNESS OF ECOLOGICAL NICHE CONCEPTS IN UNDERSTANDING PLANT COMMUNITIES

## Kegunaan Konsep Relung Ekologis Dalam Memahami Komunitas Tumbuhan

Iyan Robiansyah

Centre for Plant Conservation Bogor Botanic Garden, Indonesian Institute of Sciences

Jl.Ir.H. Juanda 13 Bogor 16003 Indonesia

Email: iyanrobiansyah@yahoo.com

### Abstract

Plant communities have been attracting many scientists due to their complexity and unclear underlying mechanisms that support it. How large numbers of competing plant species manage to coexist, for instance, is one of the major unresolved questions in plant community ecology. Ecological niche concept is a classical theory which tries to address this question. The development of this concept will be presented in this paper. Recent studies, although few in number and incomplete in many ways, do suggest that plants segregate along various environmental niche axes. 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 ecological niche concept plays a more significant role than has been previously appreciated.

**Keywords:** Ecological niche, plant community, coexistence

### Abstrak

Komunitas tumbuhan merupakan salah satu topik ekologi yang telah menarik banyak peneliti terutama karena tingkat kompleksitasnya yang tinggi dan ketidakjelasan mekanisme yang menopangnya. Mengapa begitu banyak spesies berkompetisi tetapi dapat hidup berdampingan (*coexistence*) merupakan salah satu contoh pertanyaan yang belum dapat dijawab secara jelas dalam bidang ekologi komunitas. Konsep relung ekologis (*ecological niche concept*) adalah teori klasik yang dilontarkan dalam rangka usaha menjawab dan menjelaskan pertanyaan ini. Perkembangan konsep ini dalam usahanya menjelaskan koeksistensi spesies tumbuhan dibahas dalam paper ini. Penelitian-penelitian terkini, walaupun masih sedikit dalam jumlah dan tidak lengkap dalam beberapa segi, telah menunjukkan bahwa tumbuhan bersegregasi menurut berbagai macam sumbu relung lingkungan (*environmental niche axes*). Walaupun segregasi relung menurut sumbu lingkungan bukan merupakan satu-satunya mekanisme yang mendasari koeksistensi dalam komunitas tumbuhan, bukti-bukti hasil penelitian menunjukkan bahwa konsep relung ekologis kini telah memainkan peran yang lebih signifikan dibandingkan dengan masa-masa sebelumnya dalam studi ekologi komunitas.

**Kata Kunci:** relung ekologi, komunitas tumbuhan, koeksistensi ,

## Introduction

The scientific meaning of *niche* word starts to be gained when Elton (1933) stated that the niche of an organism was like trades or jobs or professions in a human community. It begins to be utilized to describe how, rather than just where, an organism lives. In 1957, Hutchinson proposed a new concept which became the basis of modern concept of niche. He argued that niche was the way of an individual or species practises its way of life in which tolerances and requirements interacted to define the condition and resources needed. For instance, temperature limits the growth and reproduction of all organisms, but there is great variation of temperature's ranges that can be tolerated by every organism. This range of temperature is one dimension of ecological niche of an organism. Since a species tolerates different ranges of various conditions (temperature, relative humidity, water flow, wind speed, Ph and so on) and needs various resources, the real niche of a species thus must be multidimensional (Begon *et al.*, 2006).

## Ecological niche and plant communities

The basic assumption of ecological niche concept is the differential utilisation of resources among species so that they can avoid competition and be able to coexist (MacArthur & Wilson, 1967; MacArthur, 1972; Schoener, 1986; Chesson, 2000). If there is no such differentiation, then it will follow the Competitive Exclusion Principle or 'Gause's Principle' where one competing species will exclude the other (Begon *et al.*, 2006). Applying this concept in order to understand plant communities is not as easy as that in animal since most plants need the same basic resources: nitrogen, phosphorus, potassium, micronutrients, light, water, CO<sub>2</sub> and space for growth. Moreover, plant communities often show very high richness of species – in which up to 300 tree species per ha can be found in some tropical forests and yet up to 40 herbaceous plant species per m<sup>2</sup> occur in certain temperate grasslands. Such situation leads species in the same communities experiencing similar environmental conditions (Silvertown, 2004; Silvertown and Law, 1987). Thus, it is difficult to explain how all occurring species coexist

and share available essential resources and habitat niche space adequately.

## Tilman's resource-ratio hypothesis

Tilman (1985) through his resource-ratio hypothesis tried to explain this phenomenon by dividing up the existing niche. He argued that although plants required the same resources, they might coexist through the utilisation of different limited resources, indicating that one species was limited by a certain resource and the other species by another. He pointed out that even a few resources could create a wide range of resource ratios which might account for the structure of plant communities. Although this theory has been criticized by several authors (see Thompson, 1987; Thompson and Grime, 1988), it has generated great attention and has considerably stimulated the study of the coexistence mechanism that determines the structure and dynamics of plant communities (Grace, 1991; Miller *et al.*, 2005).

Many studies support this hypothesis, especially those on soil-water resources. The study of European wet meadows by Silvertown *et al.* (1999) demonstrated that many species occurred in wet meadows communities were able to coexist due to segregation of hydrological gradients. Each species became specialized and occupied distinct niches as a result of a trade-off between aeration stress tolerance and drying stress tolerance. The next example comes from the study by Nippert and Knapp (2007) conducted in Konza prairie, Kansas, which clearly supports the Tilman's resource-ratio hypothesis. The study showed that when water resource was limited, the grass species in the community could coexist as a result of soil water partitioning. A recent study on fynbos plant communities (Araya *et al.*, 2010) also found niche segregation along fine-scale hydrological gradients, which was identical to the study conducted by Silvertown *et al.* (1999) in wet meadows communities. Many studies show that soil moisture partitioning can be found among competing species in almost all ecosystems: littoral species (Grace & Wetzel, 1981), fen species (Kotowski *et al.*, 2006),

European grassland (Verheyen et al., 2008), desert plants (Manning & Barbour, 1988; Nobel, 1997), Mediterranean shrublands (Filella & Penuelas, 2003) and woodlands (Groom, 2004), savannah (Weltzin & McPherson, 1997; Jackson et al., 1999) as well as temperate (Dawson, 1996) and tropical forests (Jackson et al., 1995; Meinzer et al., 1999; Stratton et al., 2000).

### New dimensions of plant's niche

Another way to understand coexistence phenomena in plant communities is to elaborate a new dimension to the niche shape of plant. Grubb (1977) proposed some other components of plant niche, including habitat niche, life form niche, phenological niche, and regeneration niche. The habitat niche describes chemical and physical limit tolerated by mature plants. A more detailed definition was given by Terradas et al. (2009) who defined habitat niche as a spatial and temporal function of water, light, nutrient and temperature ranges, and competition with neighbors. This niche dimension involves micro-site heterogeneity, climatic variability, and disturbance to constitute habitat gradients contributing to generate local diversity.

The life form niche relates to plant size and annual productivity. This niche variation can be clearly observed in a species-poor community where very few dominant species are able to utilize the available resources in a given area (Grubb, 1977). In such community it is very likely that epiphytes, shade-tolerant herbs, or a tolerant species of climber can coexist with the dominant.

The phenological niche represents the pattern of seasonal development variation within community. A simple example of this niche variation comes from the persistence of certain weeds in crops (Aspinall and Milthorpe, 1959; Aspinall, 1960). In such situation the weeds are not excluded and can even coexist due to their ability to persist in a suppressed state with an ability to develop rapidly to the stage of ripe seed production before harvest. In natural plant communities, phenological niche can be observed in the flowering time variation in savanna (Silva and

Ataroff, 1985), the germination timing variation in grassland (Fargione and Tilman, 2005) and the non-coincidence of flushing in trees of tropical rain forest (Frankie et al., 1974).

The regeneration niche describes that species within a community differ from one another during the regeneration phase of the life cycle which potentially contribute to coexistence (Grubb, 1977). In broader view, Terradas et al. (2009) called this niche with a 'life history niche' which described the whole life history and demography of coexisting species and considered the different developing stages of a species and the different life-spans and sizes of diverse species. One of the evidences of this niche can be found in Lamont and Bergi (1991) study who examined the three co-occurring shrubs of *Banksia* species in Western Australia. They found that the adult shrubs could coexist without niche differentiation. Davis (1991) suggested that niche differentiation in these shrubs might occur in the early regeneration stage after fire indicating the importance of the regeneration niche. Recent studies suggest that regeneration niche changes over the life cycle of individuals, known as ontogenic niche shifts (Miriti, 2006). Quero et al. (2007) had observed these ontogenic shifts in the endangered Mediterranean tree species *Acer opalus* ssp. *granatense*.

By elaborating those new dimensions, there are many niche spaces available in community so that many species can coexist. The limitation of the search for more niche dimension is that the significant niche axes and appropriate measurements may be rather hard to find since the number of niche dimensions is potentially infinite (Silvertown and Law, 1987; Polechova and Storch, 2007). Yet, there is an uncertainty whether the observed niche differentiation among coexisting species is the cause or effect of their coexistence (Fitter, 1987).

### Temporal aspect of niche

All those explanations above assume that the environment in which the coexisting species occurred changes only in space but not in time. Terradas et al. (2009) proposed a 'fluctuating niche' concept which

incorporated temporal fluctuation of resources availability. The two rational bases of this theory are, firstly, if resource availability fluctuates, the temporal advantages of one species become balanced by the advantages of the other species at another time. Secondly, coexistence may be ensured by the ability of species to tolerate scarcity of resource periods. Facing this fluctuating resource, 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 favorable periods. The interaction of the 'fluctuating niche' with those niches proposed by Grubb (1977) increases the number of possible occurring niches in community.

#### Future development of the concept

This paper has shown that many studies have been done in order to prove the concept of ecological niche. The results of those studies do suggest that plants segregate along various environmental niche axes. However, this concept has been challenged by the neutral theory (see Bell (2000; 2001) and Hubbell (2001) for more discussion on the theory), which counters the idea that coexistence is primary due to differentiation in resource use. Instead, the later theory suggests that a wide variety of ecological patterns, including coexistence, can be explained by pervasive dispersal limitation, ecological drift and a balance between random extinction and speciation. Although these two concepts occupy the two extreme ends of a continuum (Adler et al., 2007; Gravel et al., 2006), Chase and Myers (2011) had shown that both concepts actually occurred simultaneously. Thus in the future, the ecological niche concept will be still important in studying plant communities. Indeed, Chase and Myers (2011) had suggested that in order to understand the ecological community, a more general theory elaborating ecological niches concept at its core was needed in the future studies.

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