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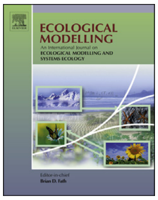

Biodiversity is autocatalytic

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ABSTRACT

A central question about biodiversity is how so many species can coexist within the same ecosystem. The idea that ecological niches are critical for the maintenance of species diversity has received increasing support recently. However, a niche is often considered as something static, preconditioned, and unchanging. With the "Biodiversity-related Niches Differentiation Theory" (BNDT), we recently proposed that species themselves are the architects of biodiversity, by proportionally increasing the number of potentially available niches in a given ecosystem.

Along similar lines, but independently, the idea of viewing an ecosystem of interdependent species as an emergent autocatalytic set (a self-sustaining network of mutually "catalytic" entities) was suggested, where one (group of) species enables the existence of (i.e., creates niches for) other species.

Here, we show that biodiversity can indeed be considered a system of autocatalytic sets, and that this view offers a possible answer to the fundamental question of why so many species can coexist in the same ecosystem. In particular, we combine the two theories (BNDT and autocatalytic sets), and provide some simple but formal examples of how this would work.

1. Introduction

The variability among living organisms in terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which they are a part, have been defined with the term "*biodiversity*" (CBD Secretariat, 1992). Apart from the formal definitions and the different ways to measure it, the central question about biological diversity on Earth is how so many species can coexist within the same ecosystem (Sherratt and Wilkinson, 2009).

In an attempt to explain this issue, some authors formalized neutral theories of biodiversity (MacArthur and Wilson, 1967; Hubbell, 2001), which assume that all species belonging to the same trophic level of an ecological community are "neutral" in relation to their fitness. This implies that there are no real differences between the niches of each species and that their success is dictated by the randomness of the moment (Rosindell et al., 2011).

In contrast, the idea that niches are critical for the maintenance of species diversity, challenging the neutral theory of biodiversity, has received increasing support recently (McGill, 2003). An *ecological niche* is the role and the position a species has in its environment (its food and shelter needs, its survival and reproduction strategies, etc.). The concept of a niche as the set of ecological requirements, from the reproductive to the alimentary ones, developed by Elton (1927) and improved by Hutchinson (1957) with the definition of hyper-volume, is a powerful tool for understanding the role of each species in its environment.

These multidimensional spaces or hypervolumes that include all of a species' interactions with the biotic and abiotic factors of its environment, led to the consideration of niches as fundamental ecological variables able to regulate species composition and relations within an ecosystem. For example, it has been suggested that niche differences stabilize competitor dynamics by giving species higher per-capita population growth rates when rare than when common, and that coexistence occurs when these stabilizing effects of niche differences overcome species in overall competitive ability (Levine and HilleRisLambers, 2009). Moreover, it seems that nestedness of niches reduces interspecific competition and enhances the number of coexisting species (Bastolla et al., 2009).

Some authors suggested a relationship between the utilization of ecospace and change in diversity of, for example, marine shelf faunas through time (Bambach, 1983). However, most of these previous studies emphasized the effect of niche *partitioning* as a global long-term pattern in the fossil record to explain the exponential diversification of life (Benton and Emerson, 2007). The main

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explanation for a pattern of exponential diversification is that as diversity increases, the world becomes increasingly divided into finer niche spaces. This explanation could be a result of the fact that nearly all studies of the impact of species interactions on diversification have concentrated on competition and predation, leaving out the importance of other types of interactions (Joy, 2013).

However, the idea that interactions between species are important catalysts of the evolutionary processes that generate the remarkable diversity of life is gaining interest among ecologists. For instance, it has been shown that symbiosis between gall-inducing insects and fungi catalyzed both the expansion in resource use (niche expansion) and diversification (Joy, 2013). Indeed, facilitation (a process that allows the colonization and presence of new species taking advantage of the presence of other ones by expanding the ecosystem hypervolume) plays a major role in species coexistence, strongly increasing the biodiversity of an area. With the "Biodiversity-related Niches Differentiation Theory" (BNDT), we recently proposed that species themselves are the architects of biodiversity, by proportionally (possibly even exponentially) increasing the number of potentially available niches in a given ecosystem (Cazzolla Gatti, 2011).

Fath (2007) suggested that all objects in ecological networks interact with and influence the others in the web and that there are no null community-level relations. Moreover, network mutualism is made by community-level relations that usually have a greater occurrence of mutualism than competition, making them more positive than the direct relations that produced them. Fath (2014) also proposed that there are no individual species as such, but only historically contingent constructs that emerge from the structural couplings of physical and environmental systems. Species themselves, within an ecosystem, appear and disappear over time, as the environmental conditions allow and construct. A species emerges from this environment and is an expression, in fact a historically contingent expression, of those interactions. In other words, species are expressed and maintained by a complex interacting ecological network.

Paraphrasing von Uexküll (1926), the output of one species, through a series of direct linkages, indirectly connects back again as input to the original "generating" species. In this manner, the species affects its own input operating in closed function circles. Luhmann states that "function systems are operationally closed and function autopoietically" (quoted in Moeller (2006, p. 101)). Autopoiesis is a concept that was introduced by Maturana and Varela (1980, 1987) to describe a system that uses itself to create more of itself, such as a biological cell.

At the ecological scale a similar concept, that of autocatalysis, was promoted by Ulanowicz (1995, 2008). Autocatalysis is considered to be "a necessary condition for maintaining structured gradients that allow for the continuation of system function at high levels of organization" (Fath, 2014). Ulanowicz (2014) considered three actors, related in cyclical fashion, each receiving benefit from its upstream partner and providing benefit to its downstream counterpart. Implicit in this configuration resides a positive form of selection. The end result is the phenomenon called *centripetality* (Ulanowicz, 1997), whereby internal selection pulls progressively more resources into the orbit of autocatalysis (usually at the expense of non-participating elements).

Kauffman (1993) argued that the complexity of biological systems and organisms might result as much from self-organization and far-from-equilibrium dynamics as from Darwinian natural selection. He also proposed the self-organized emergence of collectively autocatalytic sets of polymers to explain the origin of molecular reproduction (Kauffman, 1971, 1986, 1993). An autocatalytic set is a group of entities (e.g. molecules and the chemical reactions between them), each of which can be produced catalytically, i.e., triggered by other entities within the set, such that the entire set is able to sustain and reproduce itself from a basic food source. In other words, the set as a whole is self-sustaining and collectively autocatalytic. This concept is intimately related to those of Ulanowicz (2008) and Maturana and Varela (1980), but worked out in more mathematical detail (Hordijk, 2013).

Autocatalytic sets were originally defined in the context of chemistry (in particular polymer systems; see below), but have more recently been extended to study systems in biology (Sousa et al., 2015) and possibly economics (Hordijk, 2013). Here, we show that biodiversity can also be considered a system of autocatalytic sets, and that this view offers a possible answer to the fundamental question of why so many species can coexist in the same environment.

In the following sections, we briefly review the Biodiversity-related Niches Differentiation Theory (BNDT) and the theory of autocatalytic sets. The BNDT describes how the number of species in an ecosystems changes over time, depending on the number currently present, and autocatalytic sets can provide a mechanistic explanation for this process. This idea is illustrated with a simple but formal example.

2. The biodiversity-related niches differentiation theory

With the *Biodiversity-related Niches Differentiation Theory* (BNDT) (Cazzolla Gatti, 2011), we recently proposed that species themselves are the architects of the greatest biodiversity of a given environment, because through the realization of their fundamental niche they allow for an expansion of available niches for other species. The BNDT states that (Cazzolla Gatti, 2011):

> "...in natural conditions of immigration and emigration, with every environmental condition, species tend – directly or indirectly, thanks to their simple presence and life roles – to increase the number of potentially available niches for the colonization of other species, enhancing the limit imposed by the basal hypervolume, until they reach the carrying capacity of the ecosystem. At the same time, niches and mutualistic networks of the ecosystem allow, through circular and feedback mechanisms, the rise of the number of species, generating a non-linear autopoietic system."

According to the BNDT, generalist species (e.g. pioneers) expand the basal ecosystem hypervolume (with a limited number of niches available). Once created, the new niches are filled (through colonization/immigration) by specialist species. The largest part (in terms of time) of the whole process is taken by the "niche expansion and realization" of the first stages. When one or more species are able to fill the basal niche's space, and because most species are strict for some ecological condition but tolerant for other variables, the basal ecosystem hypervolume (considered as the sum of every species' range of variables) enhances its dimensions, allowing other species to colonize the environment. In this way a niche that was originally forbidden to some species for some ecological characteristics becomes available, simply because of the presence of another species that can tolerate those initial conditions.

The BNDT was formalized through the differential equation

$$\frac{dN(t)}{dt} = \rho N_e \left(1 - \frac{N_e}{K}\right)$$

where $N(t)$ is the number of niches at time t, N_e is the net number of available niches in the ecosystem, i.e., the difference between the number of niches at time t and that at time 0 ($N_e = N(t) - N(0)$), K is the carrying capacity of the ecosystem, and ρ is the coefficient of niche facilitation, with $\rho = S_t + i_{\Delta t} - e_{\Delta t}$, where S_t is the number of species at time t, $i_{\Delta t}$ is the rate of immigration/speciation, and $e_{\Delta t}$ the rate of emigration/extinction. Over time, the ecosystem is subjected to an increase in the number of species proportional to