



Niche emergence as an autocatalytic process in the evolution of ecosystems

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ABSTRACT

The utilisation of the ecospace and the change in diversity through time has been suggested to be due to the effect of niche partitioning, as a global long-term pattern in the fossil record. However, niche partitioning, as a way to coexist, could be a limited means to share the environmental resources and condition during evolutionary time. In fact, a physical limit impedes a high partitioning without a high restriction of the niche's variables. Here, we propose that niche emergence, rather than niche partitioning, is what mostly drives ecological diversity. In particular, we view ecosystems in terms of autocatalytic sets: catalytically closed and self-sustaining reaction (or interaction) networks. We provide some examples of such ecological autocatalytic networks, how this can give rise to an expanding process of niche emergence (both in time and space), and how these networks have evolved over time (so-called evoRAFs). Furthermore, we use the autocatalytic set formalism to show that it can be expected to observe a power-law in the size distribution of extinction events in ecosystems. In short, we elaborate on our earlier argument that new species create new niches, and that biodiversity is therefore an autocatalytic process.

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1. Introduction

It is now well-accepted that all objects in ecological networks interact with and influence the others in the web and that there are no null community-level relations (Fath, 2007; Cazzolla Gatti 2016a). Moreover, the idea that species diversity can drive speciation was proposed (Emerson and Kolm, 2005) and tested (Gruner et al., 2008; Bailey et al., 2013). With the “Biodiversity-related Niches Differentiation Theory” (BNDT; Cazzolla Gatti, 2011), it was suggested that mutualistic networks of the ecosystem allow, through circular and feedback mechanisms, the enhancement of the number of species, generating a non-linear self-sustaining (or autopoietic) system. The BNDD stressed that species tend—directly, through interactions, or even 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 hyper-volume, until they reach the carrying capacity of the ecosystem. In this manner, the presence of the species expands the environmental openings for other species: i.e., diversity begets diversity.

Ulanowicz et al. (2014), analysing the behaviour of self-sustaining systems, considered three actors interacting in an autocatalytic cycle, 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, whereby internal selection pulls progressively more resources into the orbit of the autocatalytic cycle (usually at the expense of non-participating elements). The *Uricularia* communities, which dominated the oligotrophic interior of the Florida Everglades, but which disappeared when new resources (mostly phosphorus) became available, provide a good example. The *Uricularia* reappeared, however, in the eutrophic canals where the species could grow fast enough to stay ahead of the choke-off (Ulanowicz, 1995). It was proposed (Levin, 1998) that aggregation and hierarchical assembly are not imposed

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on complex adaptive systems (CAS), but emerge from local interactions through endogenous pattern formation. These patterns of aggregation constrain interactions between individuals and thereby profoundly influence the system's further development.

More generally, the existence of so-called ecological autocatalytic sets (EcoRAFs: species, or "guilds" of species that exploit the same set of resources in similar but slightly different ways), producing intermediate and final products/conditions that enable the appearance and existence of other EcoRAFs, was recently advanced (Cazzolla Gatti et al., 2017a). The simple conclusion coming from combining the BNDT and the EcoRAF hypothesis was that "new species create new niches". Thus, biodiversity is autocatalytic, and increasingly diverse ecosystems are its emergent properties (Cazzolla Gatti et al., 2017a).

Here we explore the long-term effects of the idea that "biodiversity is autocatalytic": at evolutionary time scales new species, simply by coming into existence, create ever new niches into which further new species can emerge, creating yet more new niches, and so on (Cazzolla Gatti, 2011; Kauffman, 2016).

2. Ecosystems and autocatalytic sets

Previously, we argued that an ecosystem can be viewed as a collection of autocatalytic sets representing species, or species guilds (Cazzolla Gatti et al., 2017a). An *autocatalytic set* is a (chemical) reaction network where each reaction is catalysed by at least one molecule from the set, and each molecule can be built up from a basic food set by a sequence of reactions from the set itself. The food set consists of those elements that are assumed to be available from the environment (although not necessarily in an unlimited supply). In other words, elements from the food set do not need to be produced by any of the reactions from the autocatalytic set itself (although they could be by-products of other autocatalytic sets). Thus, an autocatalytic set forms a catalytically (or *functionally*) closed and self-sustaining reaction network. The concept of autocatalytic sets was formalized mathematically as RAF sets: reflexively autocatalytic and food-generated sets (Hordijk and Steel, 2014, 2017).

Autocatalytic sets are assumed to be an essential underlying property of living systems, and to have played an important role in the origin of life. They have been shown to exist in computational models of chemical reaction networks, as well as in real chemical and biological reaction networks (Hordijk and Steel, 2017). For example, Sousa et al. (2015) showed that the metabolic network of *E. coli* forms a large autocatalytic (RAF) set, containing 98% of the reactions in that metabolic network. Assuming the same holds for most, if not all species, it seems a valid alternative to represent species by the RAF sets formed by their respective metabolic networks, as opposed to representing them by their genomes. This gives an outward framing of the species in its interactive environment, similar to the "envirogram" approach proposed by Andrewarthe and Birch (1984) and Fath (2014).

Cazzolla Gatti et al. (2017a) then argued that existing species (represented by their respective RAF sets) in an ecosystem create additional niches for new species to evolve or immigrate and occupy these new niches, in turn creating yet more additional niches, and so on. This process of niche creation happens due to each species (or rather their metabolic networks, or RAF sets) producing additional "food" elements and catalysts for other RAF sets (species) to come into existence (Cazzolla Gatti et al., 2017a). Occurrence of niche creation has been well studied and documented in ecological systems (Odling-Smee et al., 2013; Mathews et al., 2014). This is an important and related concept for the EvoRAF hypothesis, which has added focus on the process that generates the new niches. This process thus gives rise to an ever (and potentially exponentially) expanding niche space (Figs. 1 and 2), and

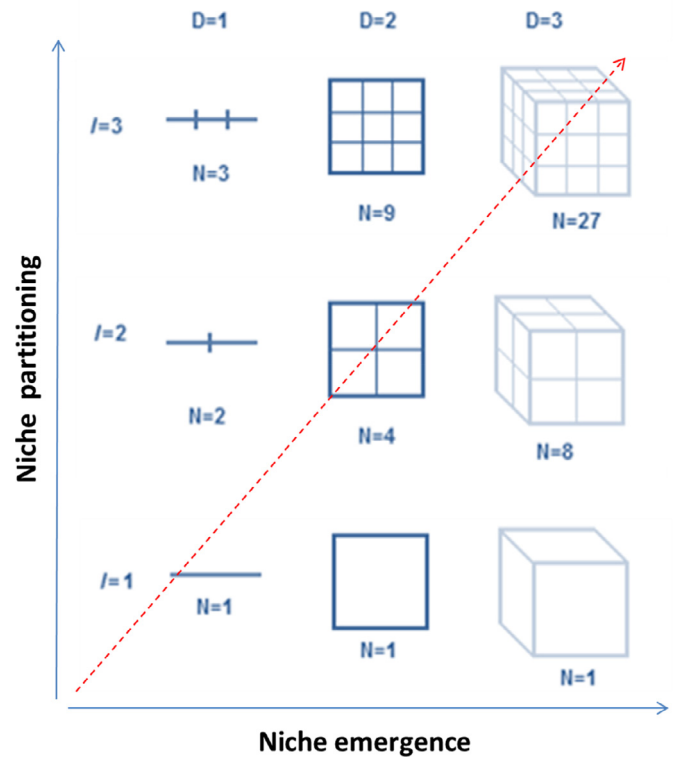


Fig. 1. Trade-off between niche partitioning and emergence. Only by niche emergence (horizontal development; increase of D = the fractal dimension from 1 to 3) it is possible to increase the number of niches of an ecosystem and, therefore, the number of coexistent species. In fact, if the niche partitioning (vertical development; I = the iteration of partitioning) were the only process, in the absence of niche emergence, the number of available niches (N) would be limited. The red-dotted arrow represents the species' trade-off between niche partitioning (iterativity) and emergence (fractality).

provides a realistic (metabolic) mechanism for how this can happen. A RAF set is based on "facilitation" processes (Bruno et al., 2003; Kikvidze and Callaway, 2009; Cazzolla Gatti, 2011; Calcagno et al., 2017), where the catalyst species is a "facilitator" in niche emergence (Cazzolla Gatti et al., 2017a).

Here we extend this line of reasoning to argue that an ecosystem itself can also be represented as an autocatalytic set. In this case, the nodes in the network are not molecules, but species. The equivalent of a chemical reaction is the transfer of biomass and energy from one or more species to another (i.e., individuals from one or more species being eaten by individuals from another species). So, the underlying "reaction network" consists of the usual food web representing a given ecosystem. However, the notion of catalysis can be added in the form of processes such as:

- one species providing safe nesting space for another species (such as trees and coral reefs do for birds and fish);
- one species helping to spread seeds or pollen for another species (such as birds and bees do for plants and trees);
- one species helping to digest food or produce essential vitamins for another species (such as gut bacteria do for humans and other animals);
- any kind of symbiosis, which would constitute "reciprocal catalysis" (such as with ants and aphids, or legumes and nitrogen fixing bacteria).

Note that in all of these examples the "catalyst" species allows or causes the other species to increase its fitness (i.e., reproduce at a higher rate than it would otherwise), without being "used up" (eaten, not in a predation process) in that process. This is simply

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