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.

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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

the number of species already present in the environment at time t, with available niches that increase in an exponential way. Systems with a different initial number of species, even if they have the same physico-chemical basic (abiotic) conditions, will show a different number of species after a discrete interval of time Δt, directly proportional to the number of potential niches developed, which depends on the initial number of species. Running, instead, the model towards a longer or infinite time ($t \to \infty$), every ecosystem with identical physico-chemical conditions tends to reach a similar number of species that is maximum at the succession climax and at the carrying capacity level (Cazzolla Gatti, 2011).

The BNDT can explain, for instance, why tropical ecosystems are the richest in biodiversity and why ecosystems that receive more energy account for more species (i.e., the latitudinal gradient of biodiversity and the species-energy theory). Based on the predictions of the BNDT, tropical ecosystems, receiving a greater amount of light energy (and thus having higher mean temperatures) and rainfall, possess a larger basal hypervolume than temperate ones (Cazzolla Gatti, 2016a). Without taking the effects of the BNDT into account, we might mistakenly conclude that the high amount of productivity and available food sources in regions with more energy does not explain the high biodiversity in these areas. In fact, there should only be a high quantity of available resources, and not a greater variety of these, so as to justify the higher abundances and not the higher richness of species (Sherratt and Wilkinson, 2009). Instead, the larger basal hypervolume and the biodiversity-related niches differentiation could be the reasons why some ecosystems contain more species (Cazzolla Gatti, 2016b).

3. Autocatalytic sets and RAF theory

Next, we consider the concept of autocatalytic sets, which was first introduced and studied by Kauffman (1971, 1986, 1993) in the context of the origin of life (Hordijk et al., 2010). It was later formalized mathematically and further developed as RAF theory (Steel, 2000; Hordijk and Steel, 2004; Hordijk, 2013). Here, we briefly review the basics of RAF theory and its main results.

First, we define a *chemical reaction system* (CRS) as a tuple $Q = \{X, \mathcal{R}, C\}$ consisting of a set X of molecule types, a set $\mathcal{R}$ of chemical reactions, and a catalysis set C indicating which molecule types catalyze which reactions. We also consider the notion of a food set $F \subset X$, which is a subset of molecule types that are assumed to be directly available from the environment (i.e., they do not necessarily have to be produced by any of the reactions in the system).

The notion of catalysis plays a central role here. A *catalyst* is a molecule that significantly speeds up the rate at which a chemical reaction happens, without being "used up" in that reaction. Catalysis is ubiquitous in life (van Santen and Neurock, 2006). Almost all organic reactions are catalyzed, and catalysts are essential in determining and regulating the functionality of the chemical networks that support life.

An autocatalytic set is now defined as a subset $\mathcal{R}' \subseteq \mathcal{R}$ of reactions (and associated molecule types) which is:

1 *Reflexively Autocatalytic* (RA): each reaction $r \in \mathcal{R}'$ is catalyzed by at least one molecule type involved in $\mathcal{R}'$, and
2 *Food-generated* (F): all molecules involved in $\mathcal{R}'$ can be created from the food set F by using a series of reactions only from $\mathcal{R}'$ itself.

A simple example of such a Reflexively Autocatalytic and Food-generated (RAF) set consisting of three reactions is presented in Fig. 1, but a RAF set can of course be of any size. A mathematically more formal definition of RAF sets was provided in
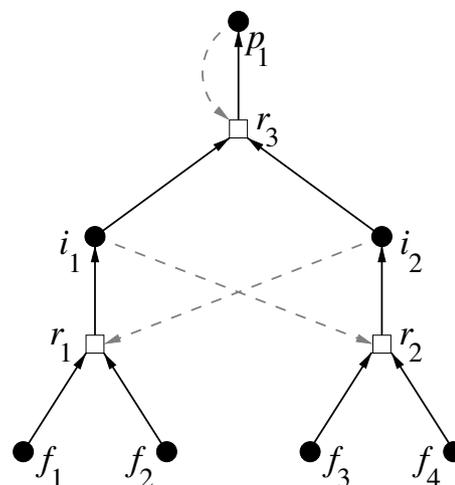

Fig. 1. An example of a simple RAF set with three reactions $\{r_1, r_2, r_3\}$. Black dots represent molecule types and white boxes represent reactions. Solid (black) arrows are reactants going into and products coming out of a reaction. Dashed (grey) arrows indicate catalysis. The food set consists of the four molecule types $\{f_1, f_2, f_3, f_4\}$.

Hordijk and Steel (2004), Hordijk et al. (2011), including an efficient (polynomial-time) algorithm for finding such sets in any given CRS.

The example RAF set in Fig. 1 requires the food set $F = \{f_1, f_2, f_3, f_4\}$, from which it produces two "intermediate" products i_1 and i_2, which are then transformed into a "final" product p_1. The intermediate products i_1 and i_2 mutually catalyze each other's production, and the final product p_1 catalyzes its own production.

Note that this RAF set requires at least two "spontaneous" (i.e., uncatalyzed) reaction events before it can be instantiated. At least one of $\{r_1, r_2\}$, and then r_3 need to happen spontaneously before all catalysts are present, when starting with only the food set. This is of course always possible, but at a much lower rate compared to when these same reactions are catalyzed. As a consequence, there may be a (random) "waiting time" before this RAF set is realized in a dynamical sense. However, once it is realized, it can in principle grow in concentration at an exponential rate, due to its (collectively) autocatalytic nature.

As argued elsewhere, this requirement for (rare) spontaneous reactions is actually a useful property for the potential evolvability of autocatalytic sets (Hordijk and Steel, 2014). Furthermore, it is the main reason why catalysts are treated separately in RAF theory, instead of including them in a reaction as both a reactant and a product, which is often done in alternative chemical reaction network representations.

RAF theory has been applied extensively to simple polymer-based models of chemical reaction networks, showing that autocatalytic sets are highly likely to exist in such models, also for chemically realistic levels of catalysis (Hordijk and Steel, 2004; Mossel and Steel, 2005) and under a wide variety of model assumptions (Hordijk et al., 2011, 2014a,b; Smith et al., 2014). However, autocatalytic sets are not just a theoretical construct, as they have also been created and studied in real chemical networks under controlled laboratory conditions (Sievers and von Kiedrowski, 1994; Ashkenasy et al., 2004; Lincoln and Joyce, 2009; Vaidya et al., 2012).

In fact, the formal RAF framework was used to analyze in detail one of these real autocatalytic networks (Hordijk and Steel, 2013), one consisting of 16 catalytic RNA molecules, or ribozymes (Vaidya et al., 2012). Moreover, it was recently shown using the RAF algorithm that the metabolic network of *Escherichia coli* forms a large autocatalytic set of close to 1800 reactions (Sousa et al., 2015). As far as we know, this is the first formal proof that living organisms (or at least essential parts thereof) are indeed autocatalytic sets.

Finally, we have shown that "higher levels" of autocatalytic sets can emerge (Hordijk et al., 2012; Hordijk and Steel, 2015). For example, a boundary (such as a lipid layer) can be considered an additional catalyst: it increases the rate at which reactions happen inside it, by keeping the relevant molecules in close proximity rather than having them diffuse away, but the boundary itself is not used up in those reactions. This way, an "autocatalytic set of autocatalytic sets" emerges, which can form a simple (proto)cell-like structure (Hordijk and Steel, 2015). This line of reasoning can, of course, be extended to then get the next emergent level of autocatalytic sets forming multicellular organisms, and so on, all the way up to the species level.

With this RAF formalism and the possibility for higher-level (emergent) autocatalytic sets in place, we now show how RAFs, niches, and biodiversity can be related to each other.

4. RAF sets, niche creation, and autocatalytic biodiversity

In Cazzolla Gatti (2011) we argued that:

"...species themselves, creating favorable conditions for the colonization of other species, allow their concurrent presence, [...] and the fundamental mechanism that supports the coexistence of species is the creation of diversity-related niches."

Furthermore, in Hordijk et al. (2012) we speculated:

"...why not consider any ecology of mutually dependent organisms as an emergent autocatalytic set, with one (group of) species enabling the evolution of (i.e., *creating niches for*) other, new, species."

Here, we make these arguments and speculations more concrete by showing a simple but formal example of how this could work. This then also immediately provides formal support for the BNDT, as we will discuss below.

Recall that an autocatalytic (RAF) set depends on a given food set F, i.e., molecules that are directly available from the environment. However, an autocatalytic set itself produces additional molecules which could now also become available to other (potential) autocatalytic sets. In other words, each autocatalytic set generates an "extended food set" (Hordijk and Steel, 2015). For example, the simple RAF set in Fig. 1 generates the final product p_1 from the food set $F = \{f_1, f_2, f_3, f_4\}$, and thus an "extended food set" $F' = F \cup \{p_1\}$. Consequently, once this RAF set is realized (in a dynamical sense), other autocatalytic sets that otherwise would not be realizable (given only F) could now potentially also come into existence (using F').

An example of such a situation is shown in Fig. 2. At the bottom of this figure the original example RAF set of Fig. 1 is shown. We have labelled it $\mathcal{R}_1$ and enclosed it in a blue dashed ellipse. This is simply to distinguish it from other reactions that may exist in the overall reaction network, and does not necessarily represent a physical boundary or membrane. Two other RAF sets ($\mathcal{R}_2$ and $\mathcal{R}_3$) are also shown, which partially depend on the product p_1 generated by $\mathcal{R}_1$. For example, $\mathcal{R}_2$ uses several of the molecules in the original food set F, but one of its required reactants is p_1. Similarly, $\mathcal{R}_3$ uses all the molecules in the original food set F (although in different combinations), but needs p_1 as one of its catalysts.

Strictly speaking, for the original food set F, $\mathcal{R}_2$ and $\mathcal{R}_3$ are not proper RAF sets. Elsewhere, we have called such sets a *co-RAF*, i.e., a subset of reactions that combined with a proper RAF set forms a larger RAF set (Steel et al., 2013). However, for the extended food
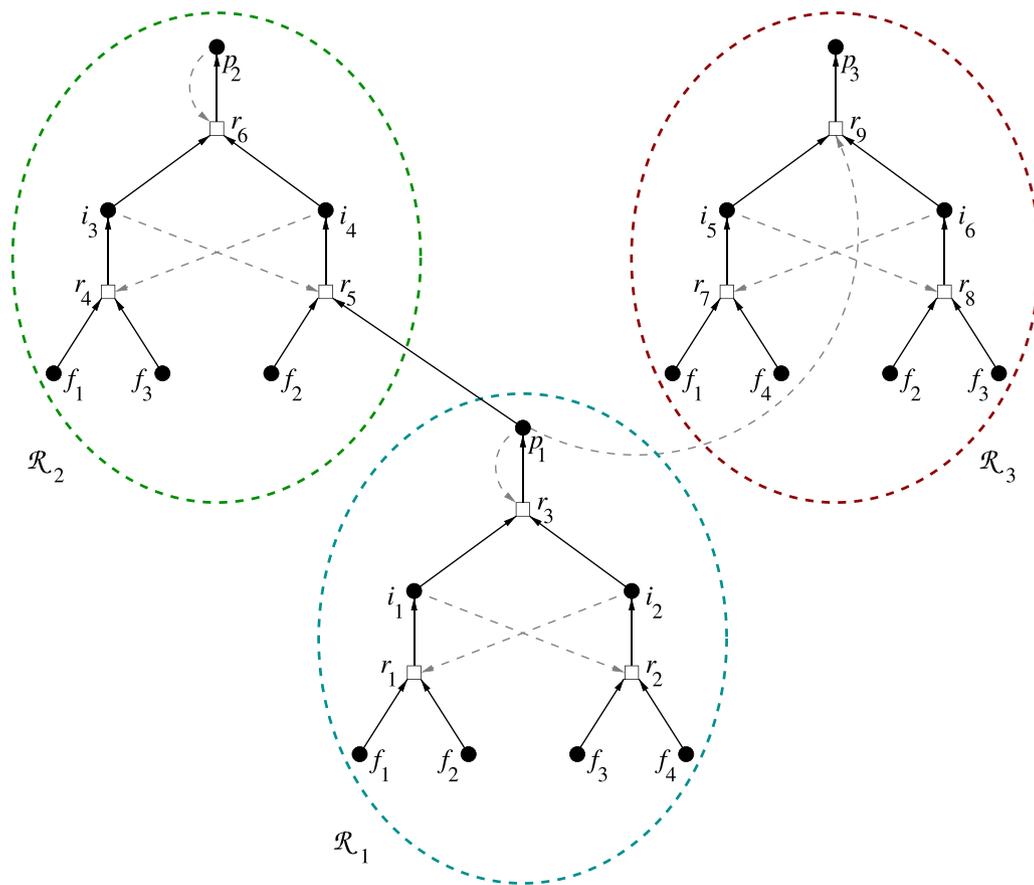

Fig. 2. An example of one RAF set ($\mathcal{R}_1$) generating an "extended food set" $F' = F \cup \{p_1\}$, which allows other RAF sets ($\mathcal{R}_2$ and $\mathcal{R}_3$) to come into existence as well. $\mathcal{R}_2$ needs p_1 (produced by $\mathcal{R}_1$) as one of its reactants, and $\mathcal{R}_3$ needs p_1 as one of its catalysts. Neither $\mathcal{R}_2$ nor $\mathcal{R}_3$ are RAF sets (but are co-RAFs) for the original food set $F = \{f_1, f_2, f_3, f_4\}$. However, both are proper RAF sets for the extended food set F'.

set F, as generated by $\mathcal{R}_1$, both $\mathcal{R}_2$ and $\mathcal{R}_3$ *are* proper RAF sets by themselves.

Taking the "species as higher-level (emergent) autocatalytic sets" view, as described above, we can now consider a so-called *Eco-RAF* as a "guild" of species that exploit the same set of resources in similar but slightly different ways, producing intermediate and final products/conditions that are able to facilitate other Eco-RAFs (i.e., other guilds of species).

Thus, an *ecological autocatalytic set* (Eco-RAF) is a RAF set $\mathcal{R}$, where the resources (f) available from the resource (or "food") set F are required to allow interactions ("reactions") r between species and their own environment (biotic-abiotic reactions). These interactions realize (in Hutchinsonian terms) a species' niche and produce intermediate (i) and final (p) products/conditions that can catalyze interactions within and among the Eco-RAFs (i.e., the guilds), facilitating the realization of other species' niches and the development of other guilds ($\mathcal{R}_2$, $\mathcal{R}_3$, etc.) through an extended resource ("food") set.

In an Eco-RAF the primary "reactions" (r) are the biotic-abiotic interactions, while the secondary reactions are intra-inter-specific interactions, which are included in the Eco-RAFs (guilds) but derive from the primary ones between each species and its environment. Therefore, the intra-inter-specific interactions are those arising within and among each Eco-RAF set, between the species that interact with their own environment and with each other. For example, r_1 (species 1 interacting with environment 1) interacts with r_2 (species 2 interacting with environment 2) through the intermediate (i) and final (p) products/conditions they produce (represented by "reaction" r_3). These products and conditions can also include non-material elements and behaviours, such as mating calls, warning signals, threat displays, allopatic substances, or chemical exchanges, which, in turn, can "catalyze" (facilitate) other "reactions" (interactions).

As a simple but realistic example, the autocatalytic set $\mathcal{R}_1$ could represent trees, which provide food, as leaves, for monkeys (represented by autocatalytic set $\mathcal{R}_2$) and act as catalysts, by providing nesting space, for birds (autocatalytic set $\mathcal{R}_3$). In such an ecological context, $\mathcal{R}_1$ can be considered an autotrophic guild of species, and $\mathcal{R}_2$ and $\mathcal{R}_3$ heterotrophic guilds (being partly dependent on $\mathcal{R}_1$). Of course this line of reasoning can easily be extended to higher trophic levels, as illustrated in Fig. 3, where species guilds (Eco-RAFs) in each next level depend in various ways on already existing guilds in lower levels (which provide "reactants" and "catalysts" in an extended resource set).

It should be pointed out that there are two different time scales involved in this view of ecosystems as a network of mutually dependent autocatalytic sets. First, there is the (faster) time scale within one Eco-RAF (species guild). At this time scale, the stability and rate of reproduction of components of one particular Eco-RAF is determined, and phenomena like centripetality play a role. Next, there is the (slower) time scale at which new Eco-RAFs come into existence, depending on which others are already present in the ecosystem. This is the time scale at which mutual "enablement" of RAF sets relates directly to the BNDT, and provides a mechanistic explanation for how biodiversity can increase proportionally. Of course the dynamics at the slower time scale, with new Eco-RAFs coming into existence over time, then also reciprocally influences the dynamics at the faster time scale, within individual Eco-RAFs.

Finally, additional similarities between RAF sets and ecological niches become immediately evident from the Eco-RAF point of view as well. For example, as was mentioned earlier, sometimes there is a (random) waiting time for one or more spontaneous reactions to happen before a RAF set can be fully realized in a dynamical sense. The equivalent of this in an ecosystem is the concept of *pioneer species*, which are fundamental to start the colonization process and to create the fundamental niche conditions. For example, they increase humidity and mineral content of soils, reduce insolation, protect against erosion and weathering, etc. And, as was also already mentioned, the largest part of the whole colonization process is taken by this niche expansion and realization phase (the "waiting time"), after which new niches are filled up (and created) more quickly.

In conclusion, an ecological niche is clearly not only defined by the abiotic environment (in this case the original food/resource set F), but also by other species guilds (Eco-RAFs) that are already present in an ecosystem, and which generate an extended food/resources set. Thus, the existence of one or more species enables the evolution and/or establishment of other species in the same ecosystem. In short, new species create new niches. In this way we can say that biodiversity is autocatalytic and that increasingly diverse ecosystems are its emergent properties. Development, whether in nature or in economies, is thus best viewed as an open-ended process by which differentiation emerges from generality, which then become other generalities from which further differentiation emerges (Jacobs, 2000). Thus, diversity of species expands in a rich environment, which is created by the diverse use and reuse of received energy.

5. Discussion

We have argued that biodiversity can be viewed as a system of autocatalytic sets, and that this view offers a possible answer to
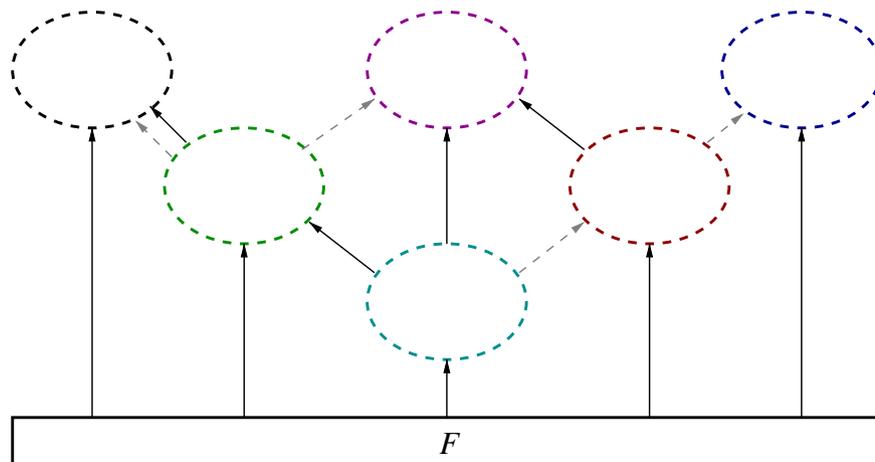

Fig. 3. An ecosystem of several trophic levels of species guilds (Eco-RAFs), where guilds in each next level depend in various ways on products (extended resource sets) of guilds in previous levels, rather than just the original resource set (the rectangle labelled *F*).

the fundamental question of why so many species can coexist in the same ecosystem. The idea that species themselves are essential in generating biodiversity, by proportionally (possibly even exponentially) increasing the number of potentially available niches in a given ecosystem, was already suggested with the BNDT, for which initial experimental support exists (Cazzolla Gatti, 2011). Here, we have combined this theory with that of autocatalytic sets (RAF theory), which can provide a mechanistic explanation of how this process of increasing biodiversity would work, as we have illustrated with a simple but formal example.

The concept of autocatalytic sets was originally developed in the context of chemistry and the origin of life. The theory has been successfully applied to study real chemical reaction networks created in the laboratory (Hordijk and Steel, 2013), and also actual living organisms (Sousa et al., 2015). We have even argued that economic systems could possibly be viewed as autocatalytic sets (Hordijk, 2013). If the views expressed here are valid, then the theory can be extended to the field of ecology as well.

Ecologists have long questioned how biological diversity is maintained. However, after recently being challenged by the neutral theory of biodiversity, which explains coexistence with the equivalence of competitors, the importance of niches for the maintenance of species diversity has been restored (Levine and HilleRisLambers, 2009). Moreover, many past theories of biodiversity that either neglected species interactions (Alonso et al., 2006; Volkov et al., 2007) or assumed that species interact randomly with each other (May, 1974; Chesson, 2000), have recently been refuted by empirical work that revealed that ecological networks are highly structured (Bascompte et al., 2003; Montoya et al., 2006; Pascual and Dunne, 2006).

Some authors (Bastolla et al., 2009) suggested that the lack of a theory that takes into account the structure of interactions precludes further assessment of the implications of such network patterns for biodiversity, and proposed that the architecture of mutualistic networks minimizes competition and increases biodiversity. In this way, the autocatalytic nature of biodiversity (as proposed here) could represent an explanatory process for the above mechanism, and seems to be able to unify the patterns proposed by different authors in a formal and general framework.

In terms of systems theory, Luhmann refers to this self-reinforcing inter-mingling as structural coupling as "a state in which two systems shape the environment of the other in such a way that both depend on the other for continuing their autopoiesis and increasing their structural complexity" Moeller (2006, p. 19). Changes in an ecosystem, besides being structure-preserving, must also be wholeness-extending transformations (Alexander, 2012, p. 428). This is because a species must not only preserve itself, but also engage in autocatalytic feedback cycles (e.g. reward loops, function circles, autopoiesis, etc.) that contribute to the overall function of the local environment (Wicken and Ulanowicz, 1988; Fath, 2014). The phenomenon of autocatalysis could, therefore, be considered a process of internal and external selection (Ulanowicz, 2014). Ulanowicz (2009a,b) argued that as the autocatalytic configuration matures, it binds its participants ever more tightly to one another, increasing constraints.

These ideas open up many new and interesting research questions and directions relating to niches, ecosystems, and biodiversity. For instance, we could ask if there is a limit to the growth in number of Eco-RAFs, and if so, as we suspect, does this limit coincide with the ecosystem carrying capacity? Furthermore, what defines this capacity? For example, is it simply determined by the amount of available resources, or are other factors involved as well? Finally, what implications does all this have for RAF sets and ecology?

Another open question which derives from the Eco-RAF ideas is: if biodiversity is indeed autocatalytic, does it follow a sigmoidal growth over time (as every autocatalytic reaction)? Consider, for

example, the trends of number of genera during the Phanerozoic (Rohde and Muller, 2005), which follows an exponential growth curve. We argue that, if the answer to the above question is positive, this curve should – in absence of catastrophic events – eventually reach a plateau and show a sigmoidal curve (as predicted by the differential equation of the BNDT).

A more practical and empirically interesting question, which could be answered by the "autocatalytic biodiversity hypothesis", is whether we can estimate the (possible or existing) number of species of a particular group from ecological variables (mainly influencing the autocatalysis of that group), such as biomass. For example, Kauffman (1993) calculated the number of cell types as the square-root of the number of genes of an organism. Similarly, we attempted to calculate the number of vascular plants by taking the square-root of the estimated total live plant biomass of 550 bTC (billion tonnes of carbon) (Groombridge and Jenkins, 2000). The result we obtain is 741,620 vascular plant species. As of 2013, approximately 350,000 are accepted species names and over 240,000 names remain to be resolved into 'accepted name' or 'synonym' (see http://www.theplantlist.org/). Considering that an unknown number of plant species have yet to be discovered, and summing the number of accepted species to a mean number of unresolved names, the final sum is surprisingly close to our estimate. Is this result just a coincidence or is it truly a consequence of the theory? Hopefully we will be able, at some point, to perform a similar calculation for animal groups and resolve this question.

Acknowledgements

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