The complex and systemic establishment of interactions in the ecological communities

El complejo y sistémico establecimiento de interacciones en las comunidades ecológicas

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Abstract—The central question in community ecology is explaining how species coexist in a ecological community. In this tradition, individuals belonging to species constitute the biological unit on which observations are concentrated. Individuals produce interactions, and the interactions depend on the individuals. Thus, the individual/population duality and the resulting interactions between these entities are the structuring forces, and the abiotic environment is the conditioning space that, by affecting individuals, becomes another structuring factor. Thus, ecological interactions among individuals in a community emerge as secondary entities resulting as the mere consequence of the properties of individuals (e.g., feeding, fighting, reproduction), and the set of key interactions are candidates for primary causes of community structuring. The modeling of ecological communities is done either by describing their interactions as terms of a dynamical system, links of a network, or rules in agent-based model. However, none of these frameworks can simultaneously i) handle large size systems, while ii) describing interaction mechanisms in detail, and iii) providing ways to compare different models not only based on dynamical results. Here we review the features of these modeling frameworks and introduce the language of reaction networks, native to systems biology, as an alternative method where these three features can be simultaneously achieved. Reaction networks require a paradigm shift as features of species and abiotic environment have the same importance, and the focus is not on the species interactions themselves, but on more general processes of exchange of conditions for the persistence of the whole community.

Keywords—Ecological interactions, Mathematical Biology, Mathematical Ecology, Reaction networks

Resumen— La pregunta central de la ecología de comunidades es cómo coexisten las especies en una comunidad ecológica. En esta tradición, los individuos pertenecientes a especies constituyen la unidad biológica en la que se concentran las observaciones. Los individuos producen interacciones, y las interacciones dependen de los individuos. Así, la dualidad individuo/población y las interacciones resultantes entre estas entidades estructuran su coexistencia, y el medio abiótico es el espacio condicionante que, al afectar a los individuos, se convierte en otro factor estructurante. Así, las interacciones ecológicas entre los individuos de una comunidad corresponden a entidades conceptualmente secundarias, resultantes como mera consecuencia de las propiedades de los individuos (por ejemplo, alimentación, lucha, reproducción), y entonces se busca generalmente hallar la mínima cantidad de interaciones primarias para determinar la estructuración de una comunidad. Dichas interacciones se describen como términos de un sistema dinámico, enlaces de una red o reglas en un modelo basado en agentes. Sin embargo, ninguno de estos marcos puede simultáneamente i) estudiar sistemas de gran tamaño, ii) describir en detalle los mecanismos de interacción, y iii) proporcionar métodos analíticos de comparación entre modelos. Aquí revisamos las características de estos marcos de modelización e introducimos el lenguaje de las redes de reacción, nativo de la biología de sistemas, como un método alternativo en el que se pueden conseguir simultáneamente estas tres características. Las redes de reacción requieren un cambio de paradigma, ya que las características de las especies y del entorno abiótico tienen la misma importancia, y el foco no está en las interacciones de las especies en sí, sino en procesos más generales de intercambio de condiciones para la persistencia de toda la comunidad.

Palabras clave— Biomatemática, Biología Matemática, Ecología Matemática, Redes de reaccion, Autopoiesis

INTRODUCTION

Th e central question that has guided research in community ecology is related to the coexistence of species in communities (Chesson, 2000; McPeek, 2022; Vellend, 2010). The main questions that have inaugurated research programs are: What are the processes that determine the coexistence of species in the community? How stable is this coexistence? How do these coexistence patterns vary in time and space? In a community, individuals are part of populations of different species, whose individuals interact in different contexts and give rise to patterns of diversity and species richness in a community (Hairston et al., 1960). In this tradition, individuals belonging to species constitute the biological unit on which observations are concentrated. Individuals produce interactions, and the interactions depend on the individuals. Thus, the individual/population duality and the resulting interactions between these entities are the structuring forces, and the abiotic environment is the conditioning space that, by affecting individuals, becomes another structuring factor (McGill et al., 2006).

Perhaps the most important paradigm sustaining this approach is the Hutchinson´s Niche Theory (Hutchinson, 1959; Slack, 2010). A set of models based on this paradigm has been successful developing experimental and/or correlational research protocols that require determining the composition, distribution, and abundance of species in specific temporal and spatial contexts. The Niche Theory focuses on environmental conditions resources and how individuals use that context, and therefore the models are validated by measuring individual survival and reproductive performance as well as the summation of this at the population level. Thus, ecological interactions among individuals (entities) in a community emerge as secondary and subordinated concepts, resulting as the mere consequence of the properties of individuals (e.g., feeding, fighting, reproduction), and the set of key interactions are candidates for primary causes of community structuring. Modeling interactions from this perspective has resulted in valuable contributions to community ecology. The Lotka-Volterra models of ecological interactions, the theory of island biogeography, are successful examples. A first problem with this approach is that by focusing on the individuals, ecological interactions are treated one after the other (e.g., competition, predation, mutualism, etc.). Because of that, the analytics of community dynamic turns highly complex and computationally demanding, but not impossible. The multiplicity of direct and indirect interactions involving organisms is a challenge when this approach is based on the attributes of individuals, modeled mostly by differential equations. However, even complex numerical modeling and statistical techniques make it possible to estimate the relative importance of each interaction and, in some way, to distinguish the core set of interactions that structure communities. Even small dynamical systems generate extremely complicated equations that are virtually impossible to solve analytically, and very expensive to simulate computationally, and asymptotic methods are hard to analyze due to the large number of parameters involved. Thus, despite the elegance and precision of this framework, it is often inadequate to study complex ecosystems that involve large groups of diverse species. Indeed, modern community ecology has come a long way in creating models for the complexity of interactions. Only recently models of multilayered networks of interactions have been developed, which incorporate the simultaneous effect of interactions of different types (e.g., antagonistic, competitive, or mutualistic interactions) (Hutchinson, 1959; Pilosof et al., 2017). Communities need to be understood as complex systems and, as such, must consider all possible ecological interactions and from that allow predicting the trajectory of the whole. But this individual-based approach lacks shedding some light on the imminent outcomes of the full set of interactions and the dynamic of the community, and the trajectory of the community as an emergent organized structure. This is the second problem of the individual-based approach, the weakness on accounting for the stability and persistence of the entities and the interactions in the community. By establishing the structuring factors requires identifying self-maintaining forces of the whole which are determined by the conforming entities. More importantly, even in the highly complex system of equation describing the dynamic of populations in a community, it does not identify the organizing processes keeping the structure or protecting the trajectory of transformation of the community. Deciphering this is crucial to predict the consequence of perturbations on a community and how evolves.

THE PARADIGM CRISIS IN ECOLOGICAL MODELING

While the traditional interactions-based ecological modeling has produced interesting advances in our understanding of ecological communities, current approaches have not been able to provide a sound conceptualization of the complexity of the full set of interactions in ecological communities. In this context, there is less room for progress connecting science and policy making. An important example is the Complexity Stability Debate (CSD) in ecology, which seeks to resolve how ecological complex features such as resilience, resistance, robustness or, in wider terms, stability respond to changes in species diversity, richness, connectivity or, in wider terms, complexity. From the traditional perspective in ecology, an ecological community consists of a large and diverse group of species interacting in a common space in different ways. The dynamics of these interactions describe the evolution and stability of the community (Pimm, 1984). Whereas the fathers of ecology regarded as obvious the fact that more entangled communities would be more stable, early mathematical models proved that diversity and stability could be anticorrelated in large systems (Robert, 1972). Multiple studies focused on modeling, management, and policy making have supported each of the two opposite views (Dunne et al., 2002; Kondoh, 2003; May, 2001; McCann, 2000; Thébault and Fontaine, 2010), inducing an atomization of the debate and a subsequent disconnection between the three perspectives. Recently, prominent figures around the CSD have suggested that the problem is deeper, and that radically novel approaches are required to describe the fact that different ecological systems require multiperspective representations. For example, in (Donohue et al., 2016) they claim:

"We assess the scientific and policy literature and show that

this disconnect is one consequence of an inconsistent and the usual one-dimensional approach that ecologists have taken to both disturbances and stability. This has led to confused communication of the nature of stability and the level of our insight into it. Disturbances and stability are multidimensional. Our understanding of them is not".

The lack of a sound conceptualization in ecology is largely because the different formal modeling frameworks available encompass only some of the necessary features, while no framework encompasses all the needs for a sound conceptualization at once. There are three central modeling frameworks in SCD: Dynamical systems, Networks and Agent-based models. Dynamical systems are based on a specification of the time evolution of the relevant variables of the system by means of equations (Strogatz, 2018), and these provide a suitable framework to accurately model the interactions of a small group of interactants. However, even moderately small dynamical systems generate extremely complicated equations that are impossible to solve from an analytic perspective and can only be approximated using simulations. Thus, and despite the elegance and precision of this framework, it is inadequate to study systems involving a changing environment, as there are no methods to compare and learn from dynamical systems whose equations are subject to change. An alternative approach is to focus on the interactions between the different kinds of agents in the system (by agent we mean a general notion which can be a species, a resource etc.), and to describe such interactions as links between the agents, implying that the system is represented as a network. Typically, two ecological species are connected by a link if one species predates the other (Thébault and Fontaine, 2010). While new entities and interactions can be easily accommodated here by adding new nodes, and graph theory handles well the concepts related to the evolution of changing networks, network models do not appropriately incorporate the fact that in real systems multiple interaction types operate simultaneously (Fontaine et al., 2011). In ecology for example, most network applications represent depredation interactions only (foodwebs), neglecting important interactions such as symbiosis, amensalism and others (see Table 2). Network theory has not a principled way to integrate different kinds of links. The latter implies that, when modeling ecological systems with networks, systemic notions can be represented from a narrow perspective, restricted to the kind of interaction considered in the network only. Alternatively, Multi-layered networks and Agent-Based Models are the most recent approaches to ecological modeling and provide a detailed description of all the interactions happening in the system (Donohue et al., 2016). These models are very interesting because they arrive at the bottom of reductionism by representing every single detail of the entities and their interactions by means of a large collection of behavioral rules, making possible to compute the dynamical evolution of the rule-system over space and time with reasonable computational resources. However, conceptual reasoning in these frameworks is done based on the simulation results only, while no underlying and model-independent community conceptualization exists in these frameworks. Therefore, different models can hardly be compared, making these approaches increasingly less conceptually transparent and more

Model	Entities	Interacts.	Mechs.	Analytic	Contrast
Dynamic Eqs.	Small	Few	Yes	Yes	Hard
Network	Large	One	No	Yes	Easy
Multi-layer Network	Large	Many	No	Yes	Hard
Agent	Large	Many	Yes	No	Hard

TABLE 1: COMPARISON OF MODELING METHODS APPLIED IN COMMUNITY MODELING. FIRST COLUMN DESCRIBES THE MODELING APPROACH, SECOND COLUMN DESCRIBES THE SIZE OF THE SYSTEM THE MODEL IS USEFUL FOR, THIRD COLUMN DESCRIBES THE NUMBER OF DIFFERENT INTERACTIONS THE APPROACH CAN HANDLE, THE FOURTH COLUMN DESCRIBES WHETHER INTERACTION MECHANISMS CAN BE REPRESENTED, THE FIFTH COLUMN DESCRIBES WHETHER ANALYTIC METHODS CAN SUPPORT SIMULATIONS, AND THE SIXTH COLUMN DESCRIBES WHETHER MODELS CAN BE CONTRASTED.

simulation-dependent for larger systems (Gotts et al., 2019; Preiser et al., 2018). The latter is evidenced by the growth of models in different areas that cannot be compared, and by the absence of theoretical advances relating structural properties with stable configurations (An et al., 2021; Kahlen et al., 2017; Pourbohloul and Kieny, 2011). We summarize the modeling features of these different approaches in Table 1.

In the following section we present an approach based on reaction networks that we believe places processes leading to interactions at the center of the analysis (Veloz and Razeto-Barry, 2017a). This is an approach that focuses on transformative processes, in which entities are understood as reactants generating products that are, in turn, reactants participating in a system of reactions. A reaction network ontologically differs from a traditional ecological network (i.e. foodwebs) because it does not understand interactions as encounters between individuals with effects on individual fitness, but as concatenated and juxtapositioned transformative encounters between entities.

REACTION NETWORKS AND ECOLOGICAL MODELING

Reaction Networks

Reaction networks entail a way to represent transformations of entities into other entities. The language is utilized under different names in different areas such as nuclear reactions in particle physics, chemical reactions in chemistry, metabolic networks in biology and Petri nets in computer science (Maldonado, 2022; Feinberg, 2019; Koch, 2010), and has been additionally proposed as a language for the modeling of complex adaptive systems from a process-based perspective (Veloz and Razeto-Barry, 2017a; Veloz et al., 2022).

A reaction network consists of a set $M = \{s_1, s_2, \dots s_m\}$ of molecular species, simply called species, and a set $R \subseteq \mathscr{P}(M) \times \mathscr{P}(M)$ of reactions, where $\mathscr{P}(M)$ denotes the set of multisets of M. For example, in figure 1 it is depicted a reaction network where $r_1 = a \to 2a$ represents a self-reproduction process of species a, reaction $r_2 = a + c \to c$ represents the destruction of species a as a consequence of

the interaction between a and c, and $r_3 = b + c \rightarrow b + 2c$ represents the production of c catalyzed by b. Reaction networks are widely applied and analyzed in mathematical modeling (Wilkinson, 2018; Fell, 1992; Dittrich and Di Fenizio, 2007) specially in biochemistry, and its dynamics can be built upon difference, stochastic or differential equations (Angeli, 2009).
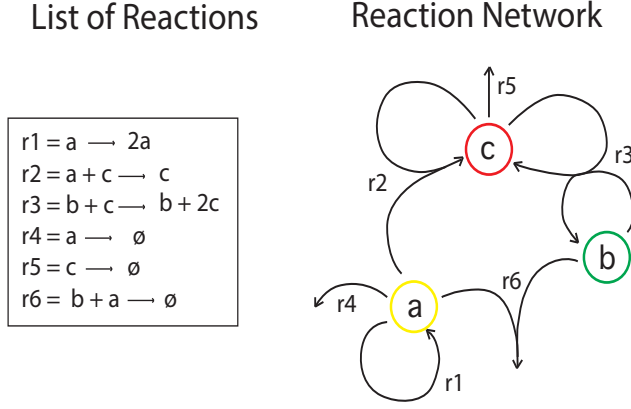
List of Reactions   Reaction Network

r1 = a ⟶ 2a
r2 = a + c ⟶ c
r3 = b + c ⟶ b + 2c
r4 = a ⟶ ø
r5 = c ⟶ ø
r6 = b + a ⟶ ø

Figure 1: a) A reaction network, b) Graphical representation of a reaction network.

Recently, reaction networks have been proposed to represent ecological interactions and ecosystems (Veloz, 2020a; Veloz and Flores, 2021; Veloz et al., 2022). In Table 2 we show ecological interactions represented using the simple possible reaction networks.

Ecological Interaction	Reaction
Amensalism	$s_1 + s_2 \rightarrow s_1$
Antagonism	$s_1 + s_2 \rightarrow 2s_1$
Mutualism	$s_1 + s_2 \rightarrow 2s_1 + 2s_2$
Commensalism	$s_1 + s_2 \rightarrow s_1 + 2s_2$
Competition	$s_1 + s_2 \rightarrow s_1$, and $s_1 + s_2 \rightarrow s_2$

TABLE 2: A SIMPLE MODEL OF THE FUNDAMENTAL ECOLOGICAL INTERACTIONS USING REACTIONS.

Topology, process, and dynamics

Reaction networks can be used to model an ecological system at three different levels. At each level it is possible to obtain more details about the dynamics of the system, at the cost of requiring more complex methods. For a thorough review we point the reader to (Veloz and Razeto-Barry, 2017a).

The first level, so-called relational or topological level, simply focuses on what species are needed to produce other species, without specifying their quantities involved in the reactions. The topological level provides a structural description of the reaction network, and properties such as generativity, i.e. what species are needed to generate others, and closure, i.e. what sets of species do not produce novel species, can be determined. Note that if we consider that the species of our community model can be ecological species or resources, the question of generativity translates to identifying what collections of ecological species and resources

are needed for other species to survive, and the question of closure considers identifying the groups of ecological species and interactions whose interactions form a bounded system.

The relational level provides information about the type of species transformed only, but not about how many species of each type are transformed by the reaction. A second level, so-called stoichiometric level, provides information on how reactions and processes can be triggered and what quantitative outcomes are obtained. In particular, we represent the state of a reaction network by a vector $\mathbf{x}$ of non-negative coordinates such that $\mathbf{x}[j]$ corresponds to the number of species of type $s_j \in M$. Since each reaction r_i is represented by

$$r_i = a_{i1}s_1 + ...a_{im}s_m \rightarrow b_{i1}s_1 + ...b_{im}s_m \qquad (1)$$

with a_{ij}, and $b_{ij} \in \mathbb{N}_0$, and $i = 1, ..., n$.

The number $a_{ij} \in \mathbb{N}_0$ denotes the number of reactants of type s_j of the i-th reaction. Together, these numbers form a *reactant matrix* $\mathbf{A} \in \mathbb{N}_0^{n \times m}$. Analogously, the number b_{ij} denominates the number of products of type s_j of the i-th reaction. Together, these numbers form a *product matrix* $\mathbf{B} \in \mathbb{N}_0^{n \times m}$. From here, we can encode the way in which species are consumed and produced by the reactions in the stoichiometric matrix $\mathbf{S} = \mathbf{B} - \mathbf{A}$.

Since the stoichiometric analysis considers the amount of each type of species involved in the reactions, processes can be extended to specify the number $v_i \in \mathbb{N}_0$ of times that each reaction $r_i \in R$ occurs. Thus, a process corresponds to a vector $\mathbf{v} = (\mathbf{v}[1] = v_1, ..., \mathbf{v}[n] = v_n)$.

From here we can compute the arrival state $\mathbf{x_v}$ of the reaction network once process $\mathbf{v}$ is applied to the system in state $\mathbf{x}$ by the following equation:

$$\mathbf{x_v} = \mathbf{x} + \mathbf{Sv}. \qquad (2)$$

For simplicity, we assume here that the coordinates of $\mathbf{x}$ are large enough for the reactions in $\mathbf{v}$ to take place in any order. The study of processes where the number of species in the state $\mathbf{x}$ might forbid the occurrence of certain processes has been profoundly studied in the context of Petri Nets using the notion of deadlock state (Murata, 1989). See (Kreyssig et al., 2014) for more details.

From here, we can define some relevant processes. In particular, if we consider the equation

$$\mathbf{x_v} \geq \mathbf{x}, \quad \text{i.e.} \quad \mathbf{Sv} \geq 0,$$

we identify processes which ensure that none of the species of our reaction network decrease by the happening of the process $\mathbf{v}$. In particular, if such process triggers all possible reactions of the reaction network, we would encounter a way in which all interactions are active and none of the species system decrease. This implies that under such form of operation, the species and resources will self-maintain through their own operation, implying co-existence and autopoiesis (Veloz, 2020b).

Further, the third level of analysis involves modeling the process $\mathbf{v}$ as function of the state vector and time, and implies building a dynamical system. In this case the state is represented by $\mathbf{x}(t) = (\mathbf{x}[1](t), ..., \mathbf{x}[m](t))$, where $\mathbf{x}[j](t)$ encodes the number of species s_j at time t, and by defining the

process $\mathbf{v}(\mathbf{x}, t)$ we obtain the differential equation

$$\dot{\mathbf{x}}(\mathbf{t}) = \mathbf{S}\mathbf{v}(\mathbf{x}, \mathbf{t}), \qquad (3)$$

with initial conditions specified by $\mathbf{x}(t_0)$. For (continuous, discrete or stochastic) dynamics, the process vector $\mathbf{v}(\mathbf{x}, \mathbf{t})$ describes the (rate, number of, probability of) occurrence of the reactions in the network.

In table 3 we describe the levels of representation, as well as methods and computational cost associated to the use of each level for understanding the dynamics of a model built using reaction networks.

Level	Methods	Comp. cost
Relational	Graphs, Logic	Low
Stoichiometric	Linear Algebra	Moderate
Kinetic	Dynamical Systems Theory	High

Table 3: Comparison of mathematical and algorithmic techniques, and computational cost to perform analysis at the distinct levels of description.

Why reaction networks is a better modeling tool?

In the following we explain how reaction networks provide the right modeling tool in all the dimensions covered in table 1.
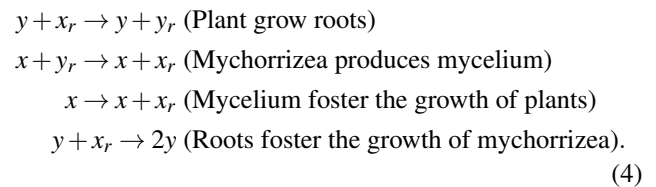
Many entities:

Technically speaking, a reaction network is a bipartite graph (**?**). Therefore, the model does not become intractable, at least at a relational and stoichiometric levels (see table 3), by incorporating a large number of entities. Additionally, it is interesting that species of a reaction network can be not only ecological species, but also resources, or any other kind of constrains or affordances, implying that the modeling can upgrade to socio-ecological and other interdisciplinary dimensions (Veloz et al., 2022).

Many kinds of interactions:

Contrary to network approaches, which represent different ecological interactions by different types of links, reaction networks characterize types of ecological interactions by the way in which combinations of inputs produce combinations of outputs, i.e. as reaction pathways. This opens up an exponentially wider range of interacting processes. Namely, typical ecological interactions such as depredation, cooperation, and parasitism are easily expressed by means of reaction networks. For example, reaction $r_3 = a + c \rightarrow c$ of the reaction network in figure 1 corresponds to an amensalistic interaction, since a is destroyed in the presence of c without altering c. Likewise, $r_4 = b + c \rightarrow b + 2c$ is a commensalistic relation, because c benefits from its interaction with b without altering b. Thus, reaction networks allow the integration of different kinds of interactions in the model by default.

Encoding interaction mechanisms:

The previous examples provide a very simple description of how reaction networks can represent interactions. If we are interested in representing a more detailed form of ecological interaction, where the interaction mechanism is broke down into steps, we can upgrade and enrich the description without having to change the model methods drastically. For example, consider the mutualistic relation between mychorrizae and plants (Marschner and Dell, 1994). Let x and y represent the mycorrhizae and the plant respectively. We could in a simplistic manner represent their interaction by the reaction $x + y \rightarrow 2x + 2y$. However, we can also represent an enriched form of interaction, by assuming that mycorrhizae x feeds from the roots y_r of the plant y, and contributes to the production of mycelium x_r, which in turn increments the absorption capacities of y. Thus, our interaction mechanism is now described by the following set of reactions

$$y + x_r \rightarrow y + y_r \text{ (Plant grow roots)}$$
$$x + y_r \rightarrow x + x_r \text{ (Mychorrizea produces mycelium)}$$
$$x \rightarrow x + x_r \text{ (Mycelium foster the growth of plants)}$$
$$y + x_r \rightarrow 2y \text{ (Roots foster the growth of mychorrizea).}$$
$$\qquad (4)$$

Thus, in this approach ecological interactions are represented by pathways represented as sequences of reactions, and an ecological community corresponds thus to a large reaction network composed by the coupling of these multiple sub-networks.

Plenty of analytic tools:

When systems become too large, the use of dynamical system theoretical notions is not applicable because they rely on high-dimensional structures that are hard to visualize and mentally picture. Therefore, it becomes very hard to understand the actual behavior and crucial features that entail the coexistence of communities by these methods. For the case of reaction networks however, large systems is the norm in biochemistry, so various methodologies have been developed to deal with large systems and produce relevant and precise information about their long-term behavior. Of particular interest is combining the information that can be obtained at the different levels of description, and for example use topological information to target specific processes at the stoichiometric level, and further analyze spaces of processes to target dynamical analysis and simulations. In this respect, the notions introduced by chemical organization theory (Dittrich and Di Fenizio, 2007; Peter et al., 2021), reaction network theory (Feinberg, 2019), metabolic pathways (Schilling et al., 1999) can be used to understand the dynamical evolution of the system at a computationally tractable cost and complement the use of dynamical simulations.

Easily contrast different models:

If we change our model hypotheses, or when we change parameters, we will modify in general the way entities of our model interact and this might produce models that cannot be compared, except numerically, in their results. For example, if we consider an extended dynamical models including more

terms in the equations, we can hardly compare the structural properties of both equations (except for perturbative cases). For reaction networks however, a theory of structural change has been advanced (Veloz and Razeto-Barry, 2017b), in which reaction networks can be structurally perturbed, meaning species and reactions can be added or eliminated and the impact on the dynamics can be formally traced. In this respect, a major question in chemical organization theory is to determine whether a modified reaction network is going to be dynamically stable, and more generally what are the possible dynamical structures contained in a reaction network. Such structure is called organisational hierarchy, and it has been shown that such hierarchy of organisations changes when the reaction network changes its structure. This theory is incipient but has a major potential in regards to its possibilities to explain structural evolution. See (Veloz and Razeto-Barry, 2017b; Veloz et al., 2022) for details.

DISCUSSION: THE ESTABLISHMENT OF INTERACTIONS

From a representational point of view, a reaction network is a universe whose dynamics corresponds to the permanent happening of reactions, being contextual events represented by the instantiation of a collection of entities (reactants) that become another collection of entities (products). Therefore, reaction networks embody a modeling paradigm for contextual processes leading to the emergence of autopoietic structures, whose objectual nature (unity) is dynamically kept through self-production.

We would like to consider this perspective to describe how ecological communities reach stable interactions that underlie their co-existence. Namely, we propose to step back from the idea of interactions as fundamental concepts with a predefined mathematical representation (terms of an equation, or links of a network), and start from an idea of fundamental transformative processes, which reflect the basic operations that species and resources perform in a given environment.

In this way we approach the complexity of ecological interactions by modeling them as reaction pathways. So, we extend the traditional view proposing that the complete repertoire of interactions in the community is what determines the conservation of the observed regularities, to a deeper view where the repertoire of interactions is already emergent with respect to an underlying reactive basis of the entities, being ecological species, resources, constraints, etc. This concept would come to configure an ecological interactome, with certain similarities with the original concept of interactome in molecular biology (Sanchez et al., 1999) in the sense that there is a basal structure that enables a multiplicity of possible interactions. Multiplex or multilayer ecological networks observe similarities with the reaction networks presented here, despite the fact that the former do not represent the transformative process, but rather describe the networks according to the observed frequency of interactions and the capita effect on species (Hutchinson et al., 2019). In addition, the reaction networks narrate the diversity of interactions based on the natural history of the species. For example, species A pollinates species B through a specific mechanism that eliminates a resource X, species B parasites species C, and species C preys on A and also on X. Hence, the relation between A

and C is both positive and negative because on the one hand its a prey of C, but on the other hand it eliminates another potential prey of C (X) and additionally polinizes C's parasite (B). Hence, these multiple narrations are concatenated and juxtaposed, giving rise to transformation processes that result in frequency variations of the entities. Somehow, this approach does not directly consider the conservation of interacting lineages in terms of survival and reproduction, but rather in their relative change in frequency, local extinction, or transformation into new entities (e.g, symbiosis).

Once such processes are determined, interactions results of processes entailing specific mechanisms, which in principle can involve several steps transforming several entities and resources of our model, and that as the result of such collective transformation we see an observable result with either positive or negative effect on the involved entities. Such mechanisms emerge and become stable in the community not from their direct objective existence, but from the fact that these, altogether, allow for the co-existence of some species and for the extinction of all other species. Hence, this approach to community ecological modeling is compatible with an evolutionary perspective in which communities can be affected by the arrival of novel species, or by the evolution of the species in the environment.

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