Dynamics of ecosystem services along ecological network seascapes

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Dynamics of ecosystem services along ecological network seascapes

Paulo R. Guimarães Jr[1] **and Carlos J. Melián**[2]

1 Abstract

Human societies depend on services provided by ecosystems, from local needs as clean water and pest control to global services like ozone layer and the ocean biological pump. Ecosystem services are intrinsically linked to the states of the ecosystem, which are, in turn, governed by a complex web of ecological interactions. These interactions and, consequently, the services they support, are increasingly under threat from environmental changes driven by human activities. Therefore, safeguarding these vital services require an understanding of how the structure and dynamics of ecological interactions are affected by environmental change. A critical step towards this goal is the development of an integrative theoretical framework that can elucidate how ecosystem services are sustained or impaired by interactions within these complex ecosystems in fluctuating environments. Recent years have seen significant progress in quantitatively characterizing the organization and the dynamics of ecological interactions through the study of ecological networks. However, linking temporally varying network structure in fluctuating environments, the seascapes of ecological networks, and their impact on ecosystem services remains a challenge. We propose an approach based upon merging empirical ecological network analysis with Boolean functions and modeling techniques accounting for fluctuating environments to tackle how ecosystem services are affected by the changing structure and dynamics of ecological networks. The approach aims to contribute to the study of how the organization of ecological interactions affects the persistence of ecosystem services. Specifically, we discuss how this approach can be used provide new insights into how environmental change affect the relationship between ecological networks and ecosystem services. The combination of information on ecosystem services, Boolean networks and fluctuating environments might allow to enhance the research around conservation strategies for preserving biodiversity and ecosystem services in the face of ongoing environmental change.

keywords: Boolean functions, Boolean networks, effective ecological network, fluctuating environments, trophic cascades.

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2 Introduction

"Every system is a set of different elements or compartments or units, any one of which can exist in many different states, such that the selection of a state is influenced by the states of the other components of the system". Ramón Margalef (1968)

A key challenge in ecology lies in understanding the vulnerability of ecosystem services upon which human societies depend for their existence (Cimon-Morin et al., 2013). Ecosystem services, in turn, are partially shaped by the underlying processes in ecological assemblages (Bullock et al., 2011). A defining characteristic of ecological assemblages is that species are interconnected through ecological interactions, creating complex ecological networks (Cohen and Stephens, 2020). As a consequence, the configuration and behavior of these ecological networks can either support or jeopardize the ecological services provided by these assemblages (Windsor et al., 2022). There is indeed a connection between ecosystem services to specific states of the ecosystem, which are themselves determined by the complex network of ecological interactions (Margalef, 1968; Estes et al., 2011; Ripple et al., 2014). Furthermore, the structure of these ecological networks, a consequence of the interactions created by the constituent species, can significantly affect how ecosystems respond to environmental changes driven by human activities (Hughes et al., 2024). Conversely, environmental changes can threaten ecosystem services by altering ecological interactions (Alberti, 2024; Wernberg et al., 2024) (Figure 1). Consequently, environmental fluctuations and ecological interactions emerge as pivotal factors for comprehending the maintenance of services in ecosystems.

The diversity of species within ecosystems, along with their intricate interactions (Thompson, 2005), can help us to gain insights on how ecosystem services are maintained requires strategies for aggregating and simplifying the patterns and dynamics of these systems (Levin, 1992). A critical step towards achieving this goal is the development of an integrative theoretical framework that can inform on how ecological services are sustained or impaired by interactions within these complex ecosystems. Recent years have seen significant progress in quantitatively characterizing the organization of ecological interactions through the study of ecological networks (Guimaraes, 2020; Pascual and Dunne, 2006). However, linking the structure of these networks to the dynamics within species-rich ecosystems remains a formidable task (Bastolla et al., 2009; Allesina and Tang, 2015; Ross et al., 2021). In contrast, while it is recognized that ecosystem services often depend directly on ecological interactions, such as the pollination of crop plants (Porto et al., 2020) or indirectly, such as the maintenance of foundational species through trophic cascades (Hughes et al., 2024), much of our current understanding of how environmental changes impact ecosystem services is focused on abiotic drivers (Scholes, 2016; Roces-Díaz et al., 2022).

From a theoretical point of view, the established approach for investigating the dynamics of ecological assemblages involves the utilization of sets of deterministic or stochastic differential equations. In the examination of ecological systems, the standard state variables used to portray these assemblages are the abundances (or biomass) of each species (Lotka, 1925; Volterra, 1926). The set of equations describes how the abundances of co-occurring species evolve over time, influenced by both the environment, the intrinsic features of each species, and the ecological interactions among species. The study of differential equations has benefited since last century of robust theoretical development, making substantial contributions to our understanding of ecological systems (May, 2019). This approach facilitates the characterization of trajectories, outcomes, feasibility, and stability of ecological systems (May, 2019; Lotka, 1925; Volterra, 1926; Grilli et al., 2017; Medeiros et al., 2021).

Nevertheless, three challenges arise when employing differential equations to explore the dynamics of ecosystem services in species-rich ecological systems. Firstly, monitoring the abundances of each species in a species-rich ecological assemblage in nature proves to be an impractical task. Obtaining a one-time estimate of the abundances for a single species is already challenging and requires an extensive amount of fieldwork. This difficulty amplifies considerably when dealing with dozens of species, but see Ushio et al. (2018). Secondly, many observed responses in ecological systems, driven by ecological interactions, occur qualitative in nature, i.e., systems experience sudden changes in its macroscopic features, such as the supply of ecosystem services (Estes et al., 2011). Finally, the number of parameters involved in the set of equations describing the ecological system rapidly escalates with the number of species (S). The total number of parameters in the set of equations increases as a function of PS+cQS^2, where P represents the parameters controlling the environmental and intrinsic effects on each species (e.g., parameters governing intrinsic population growth), Q denotes the number of parameters controlling the effects of one species on a single focus species, c is the connectance, and Sc=$\langle$k$\rangle$, in which $\langle$k$\rangle$is the mean number of interactions per species. The daunting task of estimating these parameters complicates the characterization of species-rich empirical systems. In this sense, approaches based upon a smaller set of parameters that seek to identify qualitative changes in species-rich ecosystems could facilitate an understanding of how environmental change promoted by human activities impact the preservation of ecosystem services.

Environmental change may affect directly the presence of ecosystem services or, indirectly, by reorganizing ecological interactions. In this paper, we combine Boolean networks with environmental fluctuations to study their impact on the persistence of ecosystem services. This might provide insights into how qualitative shifts in ecological services are promoted by a combination of intrinsic effects of ecological interactions and extrinsic effects of environmental fluctuations, the seascape of ecological networks. While Boolean networks are widely used in other scientific disciplines (Valverde et al., 2020), their application in ecology is still in its early stages (Ross et al., 2021). We start by describing Boolean networks, along with the associated challenges in its application to species-rich systems to infer the persistence of ecosystem services. Subsequently, drawing inspiration from statistical mechanics thinking, we propose alternatives to tackle two specific challenges inherent in applying Boolean network approaches to species-rich ecological assemblages, specifically: the characterization of system states and the formulation of Boolean rules for each species. Finally, we integrate Boolean networks with environmental fluctuations to investigate how various forms of environmental changes may reorganize ecological assemblages (Figure 1).

3 Boolean Networks and ecological services

3.1 Basic features of Boolean Networks

Boolean networks are models developed to describe the dynamics of complex systems (Kauffman, 1969). Boolean networks have found applications in various fields, including gene regulatory networks in biology, computer science, physics, and social sciences, providing a simplified yet effective representation of dynamic processes in complex systems (Valverde et al., 2020). However, its applications in ecology is still incipient. For example, recently, Boolean networks were used to explore the fragility of eusocial insect colonies to perturbations (Gaucherel et al., 2017), the evolution in mutualistic networks (Fath and Grant, 2004), the assembling of plant-pollinator communities (Campbell et al., 2011) and ecological communities (Yeakel et al., 2020), and the fragility of ecosystem services (Ross et al., 2021). In this section, we describe some basic features of Boolean networks. Detailed description of the approach can be found elsewhere (Valverde et al., 2020; Ross et al., 2021; Kauffman, 1969).

Similar to other modeling approaches for ecosystem level processes (Odum, 1983; May, 2019), we begin by describing the underlying network of interactions. In this context, the elements of a system are nodes, and the pairwise interactions between these elements are portrayed as links, constituting a network. In ecological systems, nodes may depict species, but see (Guimaraes, 2020), and interactions between species are portrayed as links. Each node is linked to a binary variable, indicating that it can exist in one of two states: either 0 or 1 (off or on). Each link is a directed link describing the impact of a species j on the state of a species i. To do so, each link is

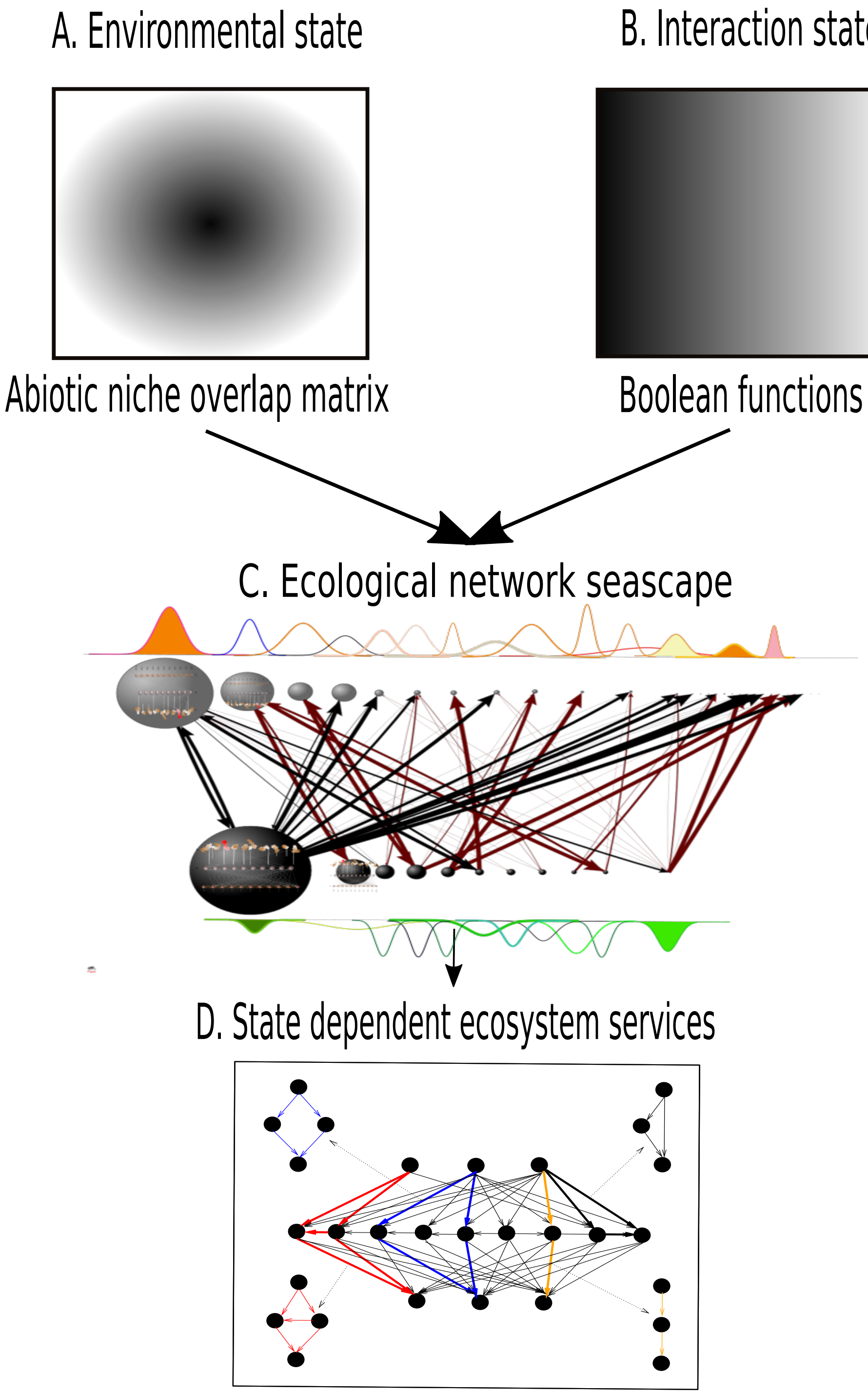

Figure 1. Ecological networks in seascapes integrate abiotic and biotic states: A) The abiotic niche overlap of each two species determines their probability of occurrence in a given environmental state. Darker areas in the center represent higher similarity in the niche overlap between two species. B) The interaction state of the two species is determined by the boolean network. Classical Boolean rules are deterministic, but because its effects may depend on non-trivial combinations of the state of other species in the system, one can think on interaction effects (positive, neutral or negative), even in a Boolean approach, as probabilistic outcomes. In B, black, grey and white represent positive, neutral and negative interaction probabilities, respectively. C) Environmental and interaction states determine the effective ecological network seascape, i.e., the effective number of species and interactions at a given state. Resource-consumer network showing their interaction patterns and their relative abundance, green (bottom) and orange (top) for resource and consumers, respectively. In a Boolean network approach, abundances may be simplified in two states (on -high; off-low), circumventing the challenge for accurately estimate species abundances. D) Ecosystem services depend on the effective ecological network seascape. The network can be decomposed into subsets, the four small modules in the four corners, each supporting specific ecosystem services. For example, carbon storage (top left), pollination (top right), nutrient cycling (bottom left), and pathogen control (bottom right). In a Boolean network approach, species in a given module will determine the state of a node describing each ecosystem service, therefore the service is under an on-off dynamics.

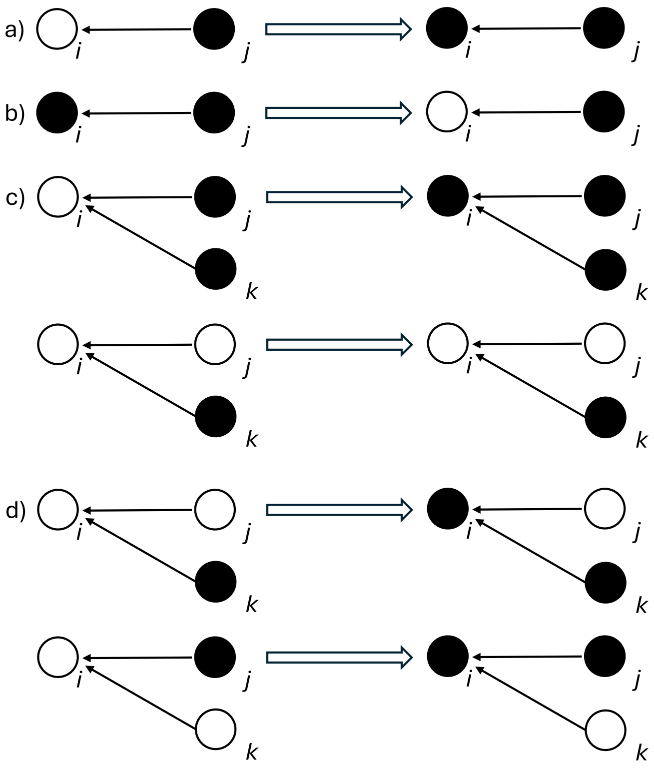

Figure 2. Examples of Boolean functions applied to networks. Black circles are on states, white circles are off states. (a) the species *i* is on only if species *j* is on; (b) the species *i* is only on if species *j* is NOT on; (c) the species *i* is on if species *j* AND *k* are on, and (d) the species *i* is on if species *j* OR *k* are on.

associated with a Boolean function (but the same Boolean function involve the combination of the effects of all links affecting that particular species). The Boolean function describes how the state of the node *i* is affected by the states of the nodes interacting with it. Examples of of Boolean functions are described in Figure 2. The Boolean rules can be organized into tables for each species. The set comprising all possible combinations of input states and the corresponding output states, based on the Boolean functions associated with each species, is referred to as the truth table for that species. This truth table enumerates all possible combinations of binary states for the input nodes and displays the resulting states for the output nodes.

The most fundamental interpretation of the two states, "off" and "on", for ecological assemblages is to associate "off" with locally extinct species and "on" with extant species. However, this is not the only possible use of the "on/off" description. "Off" can also represent "low abundance/biomass", while "on" can indicate "high abundance/biomass". In this context, Boolean networks offer a way to circumvent the challenge of tracking species abundances when studying the ecological dynamics of species-rich systems. Given the difficulty of obtaining reliable estimates of abundances for multiple species over time in a single site, particularly in species-rich systems, a potential solution is to adjust the scale of description, embracing the fact the system cannot be characterized in a extremely accurate way. This entails characterizing the system in a coarse but reliable manner, using binary descriptors such as "absence" and "presence" or "low" and "high." The concept of changing the scale of description from continuous abundances to coarse-but-reliable, binary descriptors is commonly employed in ecology for various problems, including the study of metapopulation/metacommunity dynamics (Leibold et al., 2004; Hanski and Simberloff, 1997) and description of patterns of species occurrence and richness at broader scales (Brown, 1995). Alternatively, "off" and "on" can also describe a number of distinct features of the system, such as two distinct prevalent phenotypes or two distinct behavioral responses of a given species depending on the states of their resources, mutualistic partners, or natural enemies.

As in the study of ecological networks such as food webs (Guimaraes, 2020), the nodes of the Boolean network description of the system can depict non-species features of the system. In this sense, we can describe a special node in the network that describe an ecosystem service (Ross et al., 2021). A node describing an ecosystem service is "on" if the ecosystem provides the service and "off" if it is not providing the service (Ross et al., 2021). Because the update of the state of a ecosystem service node depends on the the state of the other nodes (e.g., species) in the network, the Boolean network approach allows one to describe the presence and absence of ecosystem services as a direct function of the status of the underlying ecological network.

The Boolean Network approach also allows for overcoming the challenges of modeling abrupt transitions and the seemingly qualitative changes driven by ecological interactions. This circumvention is achieved through partially due to a coarse-but-reliable description of the state of each species ("on"/"off") rather than a quantitative state variable such as abundance. Another crucial aspect of Boolean networks that may be useful to overcoming the challenges of modelling abrupt transitions is the use of logical rules that streamline the description of non-linear effects of ecological interactions. For instance, if the presence of species j is sufficient for the presence of species i, regardless of other species interacting with i, a Boolean rule can be coded stating that if species j is "on," then species i is "on" no matter the state of the other species interacting with i (Figure 2). Moreover, if the species i is only present if a predator j is absent, a Boolean rule can be coded stating that if species j is "on," then species i is "off" (Figure 2). Alternatively, if the presence of a species is shaped by compensatory effects of its partners, a Boolean rule can be coded indicating that species i is "on" if the interacting species j AND/OR species k are "on" (Figure 2). In the next section, we illustrate the Boolean networks approach using two classical empirical ecological examples, including the description of an ecosystem service supply.

3.2 Illustrating Boolean network to ecosystem service approach using empirical examples

Let us consider the pairwise dynamics of the Canada Lynx (*Lynx canadensis*) and the Snowshoe Hare (*Lepus americanus*) (Elton and Nicholson, 1942). Empirical evidence reveals rise-and-fall cycles in the abundances of both species, but see (Stenseth et al., 1997). These rise-and-fall cycles were first detected by tracking the numbers of animal pelts of both species. This system can be modeled as a Boolean network, where the Canada Lynx is "on" if the Snowshoe Hare is "on," and the Canada Lynx is "off" if the Snowshoe Hare is "off". Conversely, the Snowshoe Hare is "on" if the Canada Lynx is "off," and the Snowshoe Hare is "off" if the Canada Lynx is "on" (Figure 3A). These Boolean rules allow for the qualitative capture of the rise-and-fall cycles, described here as sequential on-off cycles (see Figure 3B-C).

Now, let us incorporate ecosystem services (Ross et al., 2021) using a more complex example: the dependence of ecosystem services on cascading effects within Pacific North Coast kelp forests of Americas (Estes and Palmisano, 1974). Within some kelp forest ecosystems, sea otters (*Enhydra lutris*) mediate cascading effects that control ecosystem services (Figure 4). Sea otters prey on sea urchin species, such as *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*, creating a top-down effect. Similarly, when sea urchins graze in large numbers, it results in the destruction of kelps (Laminariales). Therefore, the presence of sea otters, by regulating the population of sea urchins, favor the maintenance of the kelp forest. The destruction of kelps, in turn, lead to the collapse of ecosystem services such as carbon storage (Figure 4).

One can model these systems in its simplified form as a network comprising four nodes describing the elements of the system: hunters, sea otters, sea urchins, and kelps. In addition to those nodes, we can add special nodes describing ecosystem services (e.g.,

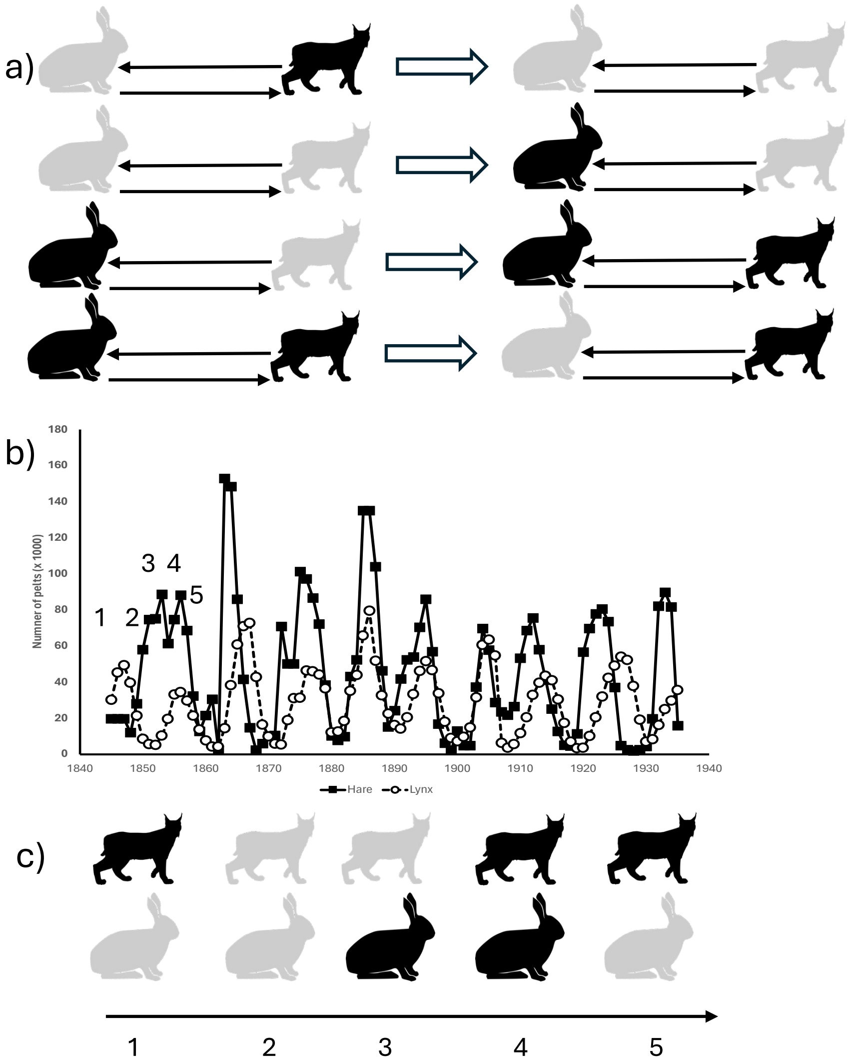

Figure 3. Examples of Boolean functions applied to ecological dynamics. A) Boolean rules for a predator (Canada Lynx *Lynx canadensis*) and prey (Snowshoe Hare *Lepus americanus*) dynamics. Grey symbols are off, black symbols are on. B) the classical data on oscillation of lynx and hare populations estimated by the number of pelts of each species obtained by hunters. C) the Boolean description of the dynamics on B generated by the rules on A. (B-C) Numbers indicate the timesteps in which the simulation reproduces the empirical dynamics. Lynx-hare dataset: `http://people.whitman.edu/~hundledr/courses/M250F03/M250.html`. Lynx and hare images available at phylopic as public domain. Lynx image was created by Margot Michaud.

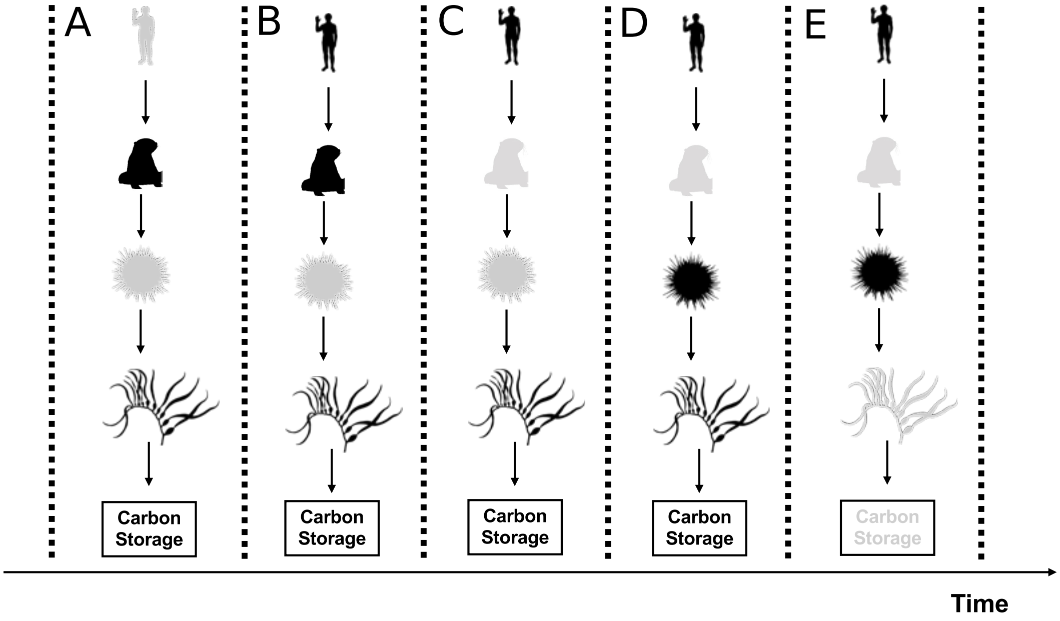

Figure 4. Boolean networks describing trophic cascades affecting ecosystem services. For the boolean rules, please refer to the text. A) in the absence of hunters (off), sea otters are present (on), controlling sea urchin population (off), allowing kelp forest to thrive (on) and an ecosystem services to be maintained (e.g., carbon storage). B-E) if sea otters are being hunted (on, B), sea otters die out (C, off), leading to the population growth of urchins (D, on), and to the collapse of kelp forests (E, off). The collapse of kelp forests, in turn, lead to the loss of carbon storage (off, E). Sea otter image created by PRG. All other images available at phylopic as public domain (human and sea urchin) or free for commercial use (kelp). Sea urchin image by Christoph Schomburg, kelp image by Harold N. Eyster.

carbon storage). The system's dynamics can be represented with the following rules: (1) sea otters are "on" only if hunters are "off" - assuming (i) other resources are supporting sea otter population, (ii) that these resources are not affected by the dynamics of interest, and therefore that (iii) sea otters does not depend on sea urchins to persist; (2) sea urchins are "on" only if sea otters are "off" - "off" meaning the sea urchin population is under control; (3) kelps are "on" only if sea urchins are "off"; (4) the carbon storage by kelps (an ecosystem service) is "on" only if the kelps are "on". In this system, activating hunters "on" generates a trophic cascade, qualitatively reproducing the collapse of kelp forests and leading to the alternative state of the system: a barren seabed with a high density of sea urchins in which important ecosystem services, such as carbon storage, are lost (Figure 4).

Recently, it was shown that sea otters mediate another cascade effect in salt marsh habitats (Hughes et al., 2024). By preying upon shore crab *Pachygrapsus crassipes*, the sea otter release the dominant salt marsh plant, the pickleweed (*Salicornia pacifica*), from the consumption by the crabs. The salt marsh vegetation that emerge under the control of crabs by sea otters, in turn, provide a number of ecosystem services, such as shoreline protection (Hughes et al., 2024). This system can be modeled in similar ways that sea otter-sea urchin-kelp-ecosystem service system and using similar set of Boolean rules.

3.3 Challenges and possible solutions to use Boolean networks to model ecosystems

Creating logical rules associated with the states of interacting species allows to model various ecological effects in Boolean networks. The state of a Boolean network is represented by a vector $\mathbf{V^t}$ that describes the state of each node at time step *t*. Therefore, $\mathbf{V^t}$ depicts, in a statistical mechanics metaphor, the microstate in which the system exists at time step *t*. In Boolean networks aiming to model ecosystem services, one of the nodes, and consequently its associated state, describe the ecosystem service supply (Ross et al., 2021). While Boolean networks offer a natural way to describe qualitative changes in the system, a challenge lies in analyze the patterns generated by the model. Boolean networks are known to generate very complex dynamics, exhibiting various patterns that are often challenging to describe in detail, especially for species-rich systems (Figure 5A). This complexity emerges even for low S and k and simple network structures (e.g., regular networks in which all species have the same number of partners shaping its state). These patterns are often more challenging to characterize than steady states of sets of deterministic or stochastic differential equations. For example, the number of possible microstates rapidly increases with the number of the nodes of the system, S, 2^S, making difficult to characterize particular patterns. The microstates of a Boolean network simulation, however, may exhibit various patterns that are potentially equivalent in their consequences to the system behavior (Figure 5A). Thus, in the same way that in statistical mechanics one can describe a macrostate of the system by lumping microstates with similar properties, i.e., it is possible to circumvent the problem of characterizing the dynamics of the system by moving to the description of macroscopic dynamical patterns.

The use of macroscopic descriptions of Boolean network dynamics is a tool to explore the underlying factors shaping the dynamics. The definition of a macrostate will depend of the questions asked and the dynamics studied. For example, Ross et al. (2021) explored the robustness of ecosystem services to species extinctions using a Boolean network approach. In this case, a natural description of the macroscopic dynamics was the distinct extinction sequences and then explore how these extinction sequences are prone to promote the collapse of an ecosystem service (Ross et al. (2021)). A complementary system macrostate that could be defined is N^t, the number of species in the "on" state at time step t. This number can be averaged across all time steps:

$$\langle N \rangle = \sum_{t=0}^{T} N^t, \tag{1}$$

in which T is the number of timesteps in the simulation. Another description can be how variable is the number of species in the "on" state across time:

$$\sigma_N^2 = \frac{1}{T}\sum_{t=0}^{T}(N^t - \langle N \rangle)^2. \tag{2}$$

Similarly, we can describe how consistent is an ecosystem service i by measuring two descriptors, s_i, which is the proportion of time steps in which the ecosystem service is "on", and $\sigma_{s_i^2}$ measures how variable is the state of the ecosystem services across time:

$$s_i = \frac{1}{T}\sum_{t=0}^{T} v_i^t, \tag{3}$$

$$\sigma_{s_i}^2 = \frac{1}{T}\sum_{t=0}^{T}(v_i^t - s_i)^2. \tag{4}$$

in which v_i^t is the state of the species i at the time t. One could correlate the descriptors of the state of species networks in equations (1) and (2) with the descriptors of ecosystem services in equations (3) e (4) to investigate how network structure and dynamics and Boolean functions shape the provisioning of ecosystem services (Figure 5B).

We now turn our attention to the problem of parametrization of Boolean networks. It is especially difficult to specify the state of a given species i based on the combination of the states of each of its interacting partners. For instance, if species i interacts with k other species in the community, one needs to specify the outcomes of 2^k combinations for species i in its truth table. Assuming all S species have k interactions, we will have $S2^k$ outcomes, which increases rapidly with both S and, particularly, with k. Thus, the classical Boolean network framework, as frameworks using set of stochastic and deterministic differential equations, has a large number of parameters that one needs to specify for simulations with species-rich systems.

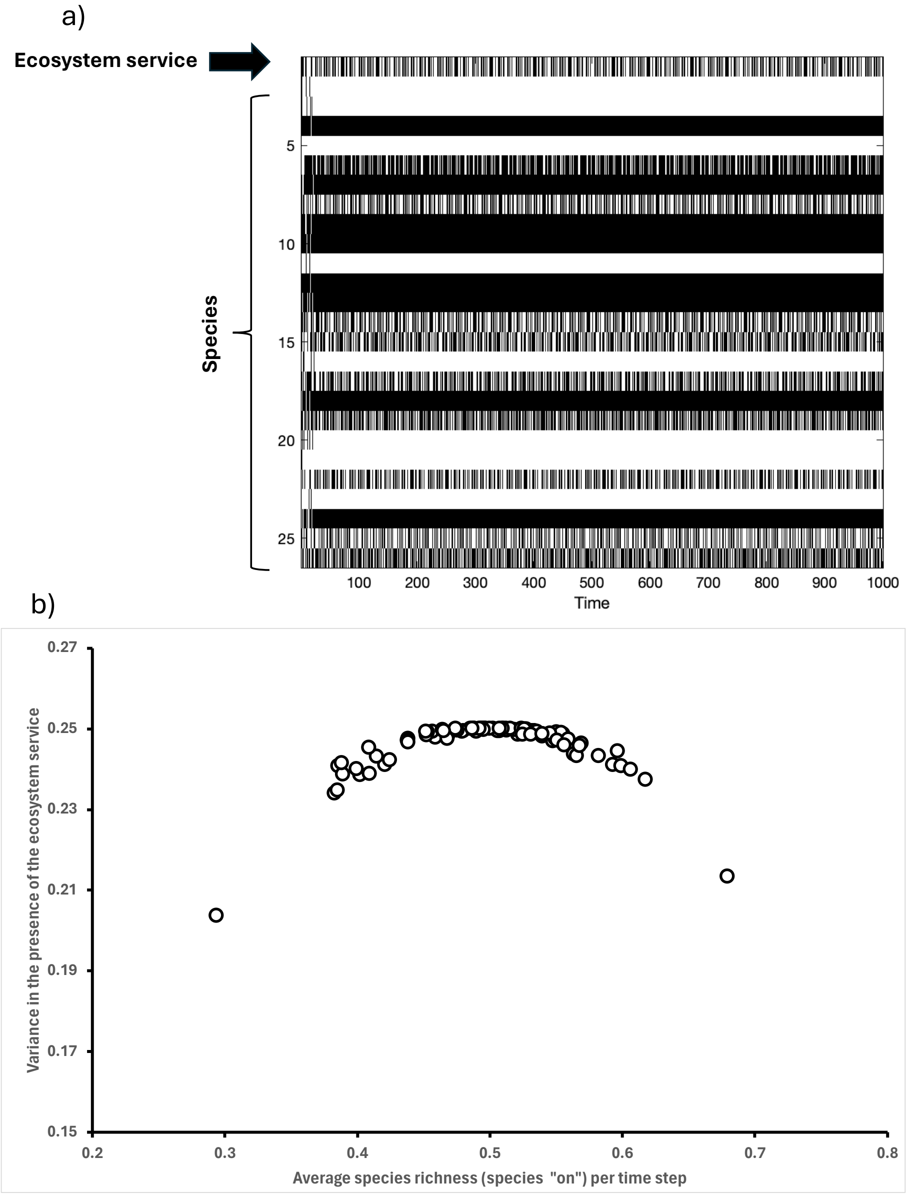

Figure 5. Boolean networks, complex dynamics and ecosystem services. A) The plot describes the on (black) off (white) dynamics of 25 species and one ecosystem service. Even simple Boolean networks may can generate very complex dynamics. B) Describing the macroscopic state of the system may provide information on the reliability of ecosystem services proving by ecological networks. In this example, the variance of the presence of an ecosystem service across time, $\sigma_{s_i^2}$, varies in non-linear ways with the average species richness across time $\langle N \rangle$ in 100 numerical simulations. Both plots were generated using theoretical networks in which the states of each node is randomly determined by the state of three nodes randomly assigned (i.e., a regular random network associated with random truth tables to each species).

The best solution would undoubtedly be to incorporate information about the natural history of the system. However, even decades of detailed study of natural history may not fully elucidate the potential of ecological interactions to control the presence/absence of interacting partners in species-rich community. One possible alternative is to shift to statistical descriptions of the truth tables and outcomes at the community level of the Boolean dynamics. One example of such approach are Random Boolean Networks (RBNs) in which the random truth tables are assigned to all nodes in the system (Kauffman, 1969). Please refer to Figure 5 for one example of Boolean network dynamics generated using RBNs. RBNs are extremely useful to explore the role of the connectivity and architecture of networks in shaping dynamics and patterns of a system (Kauffman, 1969), but it might not be suitable to explore how particular forms of Boolean functions shape the dynamics of a given ecological network. Specifically, in RBNs, there is no correlations between truth tables outcomes. Moreover, the amount of information that needs to be stored for systems with large species richness (*S*) and a large number of interactions per species (*k*) is prohibitive even if randomly generated.

One possible alternative is to shift to statistical descriptions of the truth tables at the community level of the Boolean dynamics. These statistical descriptions of truth tables may be based upon some fundamental principles that could summarize rules of response to the state of different species. For example, instead of defining a single truth table for each species, we can categorize species into classes. To achieve this, we first establish two types of links:

(1) Positive links: if species *j* is "on" favors species *i* to be "on", e.g., species *j* is a resource or facilitate the presence of species *i*. If species *i* and species *j* have positive links to each other, then their interaction is a mutualism.

(2) Negative links: if species *j* is "on" favors species *i* to be "off", e.g.,a natural enemy of species *i*, such as a competitor, parasite or predator.

Then, instead of computing the truth table with all 2^{k_i} combinations for every species *i* with k_i interactions, one could chose to describe two macroscopic quantities for each species: the total positive impact of the interacting partners of species *i*, M_i^+, and the total negative impact of the partners of species *i*, M_i^-:

$$M_i^+ = \sum_{j=1}^{S} a_{ij}^+ v_j^t, \tag{5}$$

$$M_i^- = \sum_{j=1}^{S} a_{ij}^- v_j^t, \tag{6}$$

where a_{ij}^+ is 1 if the species *j* has a positive impact on species *i*, and zero otherwise. Similarly, a_{ij}^- is 1 if the species *j* has a negative impact on species *i*, and zero otherwise. We then define thresholds at which positive and negative impacts are strong enough to potentially affect the state of species *i*:

$$M_i^+ \geq c_i^+ \Rightarrow M_i^{+'} = 1 \tag{7}$$

$$M_i^+ < c_i^+ \Rightarrow M_i^{+'} = 0 \tag{8}$$

$$M_i^- \geq c_i^- \Rightarrow M_i^{-'} = 0 \tag{9}$$

$$M_i^- < c_i^- \Rightarrow M_i^{-'} = 1 \tag{10}$$

Finally, we define that:

$$M_i^{+'} M_i^{-'} = v_i^t \tag{11}$$

Thus, each species in the network is associated with the same rule described by the set of equations and inequalities above. However, a species can respond differently to the state of its partners. In this context, four sets of parameters control the response of a species to its interacting partners. Firstly, the *S* x *S* matrices **A+** and **A-** where elements a^+_{ij} (a^-_{ij}) describe both the network structure and the positive (negative) effects of species *j* on the state of species *i*. Secondly, the *S* x 1 vectors $\vec{C^+}$ and $\vec{C^-}$, which describe the cut-offs values for each species for the positive and negative effects.

We now illustrate some limiting cases for the values of $\vec{C^+}$ and $\vec{C^-}$. For example one can model a producer as a species in which $c^+_i = 0$, i.e., the species is potentially "on" without the need for other species as resources. For species that are only controlled by bottom-up effects, one could set $c^-_i = k_i + 1$, i.e., even if all natural enemies of species *i* are "on", the presence of species *i* only depends on the presence of resources. In contrast, top-down control by any natural enemy of a given species will occur if species *i* has $c^-_i = 1$. These are only examples, as by using distributions of values for $\vec{C^+}$ and $\vec{C^-}$, one can explore the continuum of cases in between these extreme examples. Accordingly, one could model the presence of an ecosystem services. For example, if one assume that ecosystem services are supported by the presence of at least one species with a given particular functional trait (Ross et al., 2021) or from a given functional group (Fonseca and Ganade, 2001), then this kind of rule can be modeled assuming that $c^+_i = 1$ for the ecosystem service. In contrast, if all the supporting species are needed to make an ecosystem service supply, then $c^+_i = k_i$. More importantly, one can use similar approaches to reduce the complexity of describing truth tables to all species in the system when modelling species-rich Boolean networks.

4 Dynamics of ecological networks in seascapes and their effect on ecosystem services

We have been exploring how to use Boolean networks to model the maintenance of ecosystem services under the assumption that ecological interactions are the only driver of the presence or absence of ecosystem services. However, in trying to model the strength and maintenance of ecosystem services, an important observation is that, generally, whether a service is beneficial or not ("ecosystem disservices"), and by how much, will depend of the environmental and the interaction states, and hence the ecological and evolutionary history of the ecosystem: any service that is beneficial would have already occurred and fixed, but also non beneficial services can be existing in the ecosystem. In our approach the diversification of services, i.e., the speciation and extinction of positive and negative services are not possible at this stage. An extension accounting for diversification of ecosystem services, for example, the origin and maintenance of the ozone layer, the ocean biological pump, etc, might make the approach useful to quantify ecosystem services at local, regional and global spatiotemporal scales. The details of the services provided by an ecosystem will depend greatly on the dynamics of the abiotic and biotic ecosystem context and we should look for an statistical understanding of their occurrence and fluctuations once the abiotic and biotic environments are fully represented.

We have implemented 1D and 2D environmental fluctuations scenarios into the Boolean networks and ecosystem services framework. We built up a theoretical ecological network in which we assume there are two sets of species, resources and consumers. This bipartite structure can be observed in plant-herbivore interactions, the most common form of ecological interactions among plants and animals. Each node represent a species and links interspecific interactions. The links were distributed between consumers and resources randomly with probability p (i.e., the underlying network is a bipartite version of a Erdös-Rényi graph). To each link there is a positive effect from the resource to the consumer and a negative effect from the consumer to the resource. We used equations 5 to 11 to circumvent the need of computing the truth tables. For all resources we assumed that $c^+_i = 0$, e.g., all resources are producers, whereas for consumers, c^+_i were sampled from an uniform distribution in such way that $1 \leq c^+_i \leq k_i$. For both resources, c^-_i were sampled from an uniform distribution in such way that $1 \leq c^-_i \leq k_i + 1$, in which the upper limit, $k_i + 1$ means that the species is not regulated by top-down effects. For consumers in our simulation, c^-_i is meaningless since $M^-_i = 0$ for all consumers by definition due to the perfect two trophic

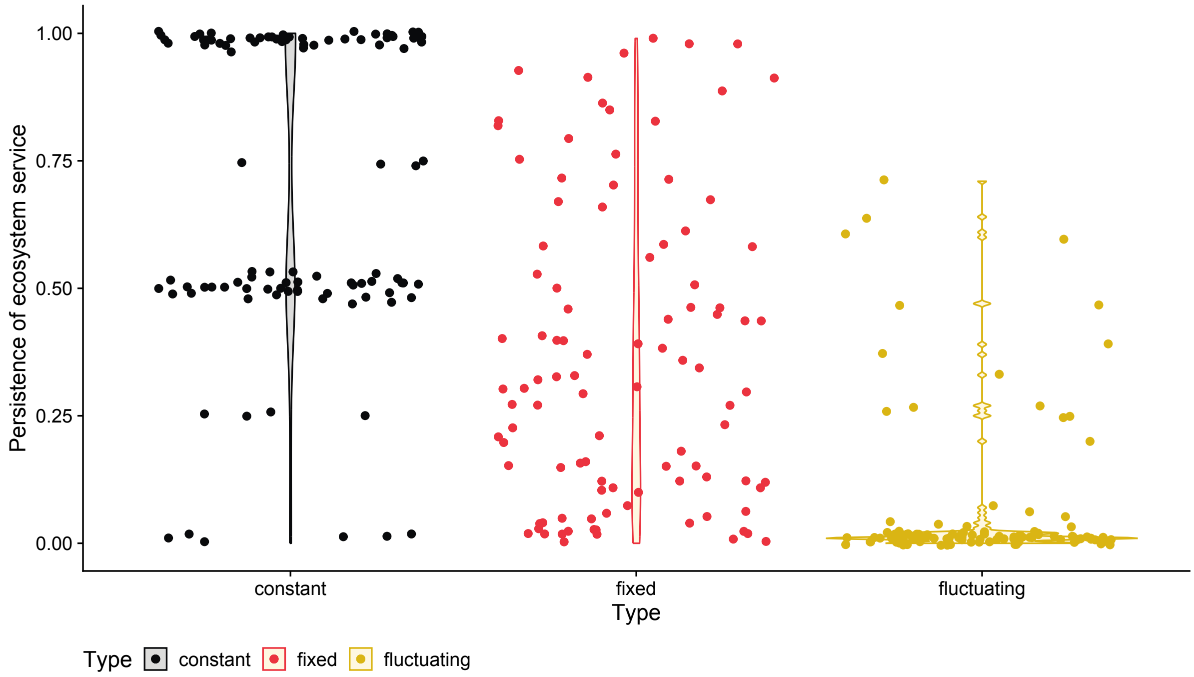

Figure 6. The outcome of environmental filtering and fluctuation to the supply of an ecosystem service in a Boolean network model. In the three sets of simulations an ecosystem service is provided by three resource species (e.g., carbon storage). These species are part of a network with 29 species, 14 resources and 15 consumers. In the "constant scenario" there is no environmental filtering and species die off just because the Boolean dynamics. In the "fixed scenario" the environmental filtering may lead to species to die off (see equation 13). Finally, in the "fluctuating scenario" the environmental filtering change every time step (following equation 14). For this particular set of simulations (n = 100 for each scenario), environmental filtering and fluctuation led to the inconstancy for ecosystem service supply. See text for further details on the simulations, including the Boolean rules.

level organization of the system. We then added a special node describing the ecosystem service assuming that it is provided by three randomly assigned resources (e.g., carbon storage). We assume that the ecosystem service is "on" if at least two of three species that support it are "on" ($c_i^+ = 2$, $k_i = 3$). We start simulating environmental fluctuation as an one-dimension effect on the species presence ("on"). Each species is associated with a trait value, z_i sampled from a normal distribution. We assumed that if the z_i is far from a given trait value favored by the environment, θ, then the species may die off ("off"). Specifically, in the environmental filtering scenario, we assume the following probability P_i^t of a species die off (go "off") due to environmental effects:

$$P_i^t = 1 - e^{-b(\theta^t - z_i)^2} \tag{12}$$

in which $b = 2$ controls the importance of trait matching with the environment for species persistence, and both θ and z_i are sampled from normal distribution with $\mu = 0$ and $\sigma = 1$. In the fluctuating scenario, we assumed that environmental filtering change across time following:

$$\theta^{t+1} = \theta^t + \epsilon^t \tag{13}$$

in which ϵ^t is a random variable sampled from a gaussian distribution with $\mu = 0$ and $\sigma = 0.1$. The introduction of environmental filtering reduce the persistence of the ecosystem service supply, but fluctuating environmental seascape led to a scenario in which most of the time the system was not able to supply the service (Figure 6).

We use the same Boolean functions than in the 1D environmental scenario to explore a 2D fluctuating environment accounting for the amplitude and the frequency of an environmental variable. This will allow us to test how the size of the ecological network limits the persistence of the ecosystem service. Now, the probability two species co-occur depends on a threshold governed by the environmental state. If two species have a high niche overlap, the expectation is that they synchronize with the environmental state, i.e., they will co-occur frequently because they are responding similarly to the abiotic environment, even if the environment fluctuates severely. Therefore, if the abiotic similarity between two species i and j, s_{ij}, is larger than a temporally-varying threshold from the environment, $\mathcal{E}_t$, then the two species are responding synchronously to the environment and they are potentially active in the system, s_{ij} $> \mathcal{E}_t$. This activation is potential because Boolean functions associated with the ecological interactions may lead to species to die out ("off"). Otherwise, if the similarity between the two species i and j, s_{ij}, is smaller or equal than the threshold from the environment, $\mathcal{E}$, then the two species are not active in the system, $s_{ij} \leq \mathcal{E}_t$. The temporally-dependent environmental threshold depends on two parameters, the amplitude, $\mathcal{A}$, and the frequency, ω, of a sinusoidal function. We compare this threshold with the niche overlap matrix, S_e x S_e, with elements $S_e[s_{ij}]$ describing the niche similarity between species i and j to the environmental state (Figure 7).

Let us consider a periodic environment as the starting point. In this scenario, the environmental state is governed by a sinusoidal function representing a seasonal periodic environment. The larger the niche overlap between two species, the larger the time these two species are on in the ecosystem for a broad set of frequency and amplitude fluctuations of the environment. On the other side, the lower the niche overlap between two species, the shorter the time these two species are on in the ecosystem. The dynamics of the environment can be explored by varying the similarity threshold from low- to high- fluctuating environments (de Filho and Metzger, 2006). This means the environment can have low, medium and high frequency and amplitude fluctuations. The quantification of the environmental fluctuations taking into account periodic environmental dynamics for species i and j with a temporally-varying environmental threshold has a form given by

$$\mathcal{E}_(t) = \frac{\mathcal{A}}{2}(1 + \sin(2\pi\omega t)), \tag{14}$$

where t is time, $\mathcal{A}$ and ω are the amplitude and the frequency of environmental dynamics determining the temporal fluctuations of the environmental threshold, $\mathcal{E}_(t)$. We can compute the number of species in the network by joining the niche overlap matrix to the environmental threshold using equation 14. Figures 7a-b show the time-varying environmental threshold and species richness and 7c-d show the species richness and the persistence of the ecosystem service along an amplitude and frequency gradient, i.e., heatmap using 100 values in the range, $\mathcal{A}$ = [0.0001,10] and ω = [0.001,20000] starting with 50 species and 1 ecosystem service.

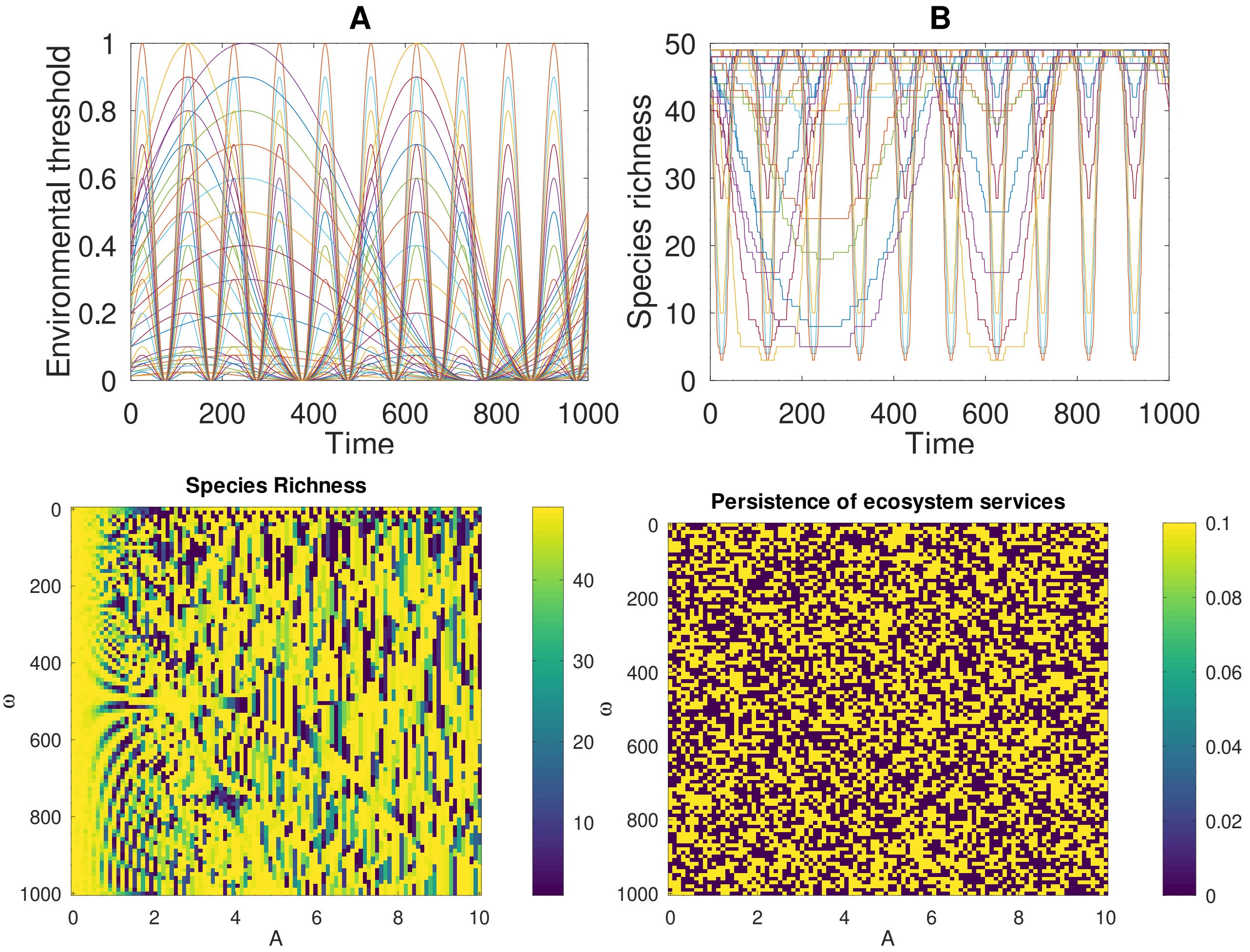

Figure 7. A) Environmental threshold (y-axis) as a function of time (x-axis) along an amplitude, $\mathcal{A}$, and frequency, ω, gradient following equation 14. B) Number of species as a function of the time-varying environmental threshold. If all niche overlap values were equal to 1, then all species are always present, i.e., full yellow heatmap in (Species Richness), pairwise similarity is always larger than the maximum fluctuation showing a strong synchrony even for high fluctuating environments. C) Species richness and D) Persistence of ecosystem services heatmap along the Amplitude, $\mathcal{A}$, and frequency, ω, gradient for a niche overlap matrix with 50 species, mean similarity and standard deviation 0.1 and 0.1, respectively.

5 Conclusions and future directions

We have introduced two complementary angles to study ecosystem services in fluctuating biotic and abiotic environments. By joining the two angles we can build seascapes in adaptive boolean ecological networks (Agarwala and Fisher, 2019) to explore the dynamics of ecosystem services (Figure 1). Boolean networks describe the presence-absence, strength and signs of interactions among species and other elements and functions of ecosystems. Fluctuating environments describe the probability of species occurrence or co-occurrence. Models accounting for only for how ecologica interactions shape ecosystem services (Ross et al., 2021), fluctuating abiotic (Palamara et al., 2023) or fluctuating biotic (Kortsch et al., 2021) interactions do exist but the connection between them and their impact on the dynamics of ecosystem services is just starting to emerge. The connection between boolean networks to ecosystem services without environmental fluctuations can have a complex dynamics with the presence of an ecosystem service responding non-linearly with species richness (Figure 5). Furthermore, the persistence of ecosystem service differs between static and fluctuating environments. The persistence decreases in 1D fluctuating environments in comparison to the static environment (Figure 6). Increasing amplitude and frequency in the fluctuating environment is independent of the persistence of ecosystem services and therefore the decreasing number of species present in the system (Figure 7B) does not alter the persistence of the service (Figure 7D). These results are consequence of our assumptions of ecosystems services. They are provided with the same probability by a randomly generated subset of species and network composition regardless the number of species and the structure of the ecological network. Future research accounting for the heterogeneous distribution of ecosystem services within a given network structure might bring evidence about the persistence of ecosystem services along ecological network seascapes with increasing frequency and amplitude in the environmental fluctuations (Figure 7).

There are at least two different trait architectures we can consider along ecological network seascapes for connecting biotic and abiotic interactions. One is when the environmental state is decoupled from interaction state. This means that the abiotic and biotic traits are not correlated at the organismal level, e.g., the traits that mediate the ability of organisms to cope with environmental factors are distinct from those mediating ecological interactions, leading to a modular trait architecture. On the other side, the environmental response and interaction state can be coupled due to correlated trait architecture. Exploring the dynamics of these two scenarios, the modular and the correlated trait architecture by decoupling or coupling biotic and abiotic response dynamics in ecological network seascapes, can have distinct consequences for ecosystem services. In our scenarios, coupling the biotic and the abiotic trait architecture can be made by joining the abiotic niche overlap matrix to the generalized Boolean networks functions, i.e., the similarity in the response to the abiotic environment between two species is coupled to a specific interaction strength and sign in the boolean network. This represents the correlated ecological network seascape scenario. On the other side, if we keep the biotic and the abiotic traits decoupled, meaning the niche overlap graph is independent of the interactions in the boolean network, then we are under the modular ecological network seascape scenario. Combining Boolean networks and fluctuating environments open at least three different venues for connecting fluctuating biotic and abiotic factors to ecosystem services:

- deciphering the principles linking the fluctuating dynamics of biotic and abiotic forces to ecosystem services
- providing new insights into how environmental changes affect the dimensionality of ecosystem services in species-rich ecosystems. Dimensionality connects to varying trait architecture, i.e., modular contains higher dimensions because the reponse to biotic and abiotic environments are decoupled.
- estimulating new research into the connection between climate change and the persistence of ecosystem services at local, regional and global spatiotemporal scales, i.e., for example from pollination services to the global ozone layer and the ocean biological pump.

We do hope the combination of information on ecosystem services, Boolean networks, and fluctuating environments might advance not only our theoretical understanding of ecosystems but also to inform practical conservation strategies for preserving biodiversity and ecosystem services in the face of ongoing environmental change.

6 Authors contribution

PRG and CJM designed the research, performed the simulations, and wrote the manuscript.

7 Conflicts of interest

We state we are not aware of any conflict of interest related to this research.

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