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Dynamics of ecosystem services along ecological network seascapes

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Abstract

Human societies depend on services provided by ecosystems, from local needs such as clean water and pest control to global services like the ozone layer and the ocean biological pump. Ecosystem services are linked to the states of the ecosystem, which are, in turn, governed by a web of ecological interactions. These interactions, along with the services they support, are under threat from environmental changes driven by human activities. Therefore, safeguarding these vital services requires 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 a theoretical framework that can elucidate how ecosystem services are sustained or impaired by interactions within ecosystems in fluctuating environments. Recent years have seen progress in characterizing the organization and dynamics of ecological networks. However, linking temporally varying network structure in fluctuating environments, the seascapes of ecological networks, and their impact on services remains a challenge. We propose an approach based on merging ecological network analysis with Boolean functions and modeling of fluctuating environments to address how services are affected by environmental change. We review aspects of Boolean Network models and illustrate the approach using biologically inspired Boolean rules that involve predator-prey cycles, trophic cascades, and mutualisms formed by plants and their frugivores. This 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 provide new insights into how environmental change affects the relationship between ecological networks and ecosystem services. The combination of information on the natural history of species interactions and ecosystem services, Boolean networks, and models for fluctuating environments may contribute to conservation strategies for preserving biodiversity and ecosystem services in the face of ongoing environmental change.

1. 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 and 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). 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 into how ecosystem services are maintained. This requires strategies for aggregating and simplifying the patterns and dynamics of these systems (Levin 1992). A critical step toward achieving this goal is the development of an integrative theoretical framework that can inform us about 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 (Pascual and Dunne 2006, Guimaraes 2020). 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 from 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 (Lotka 1925, Volterra 1926, Grilli *et al* 2017, May 2019, 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 qualitatively i.e. systems experience sudden changes in their 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 on 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 the presence of ecosystem services directly 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, creating a 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 their application to species-rich systems to infer the persistence of ecosystem services. Subsequently, drawing inspiration from statistical mechanics thinking, we review 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.

2. Boolean networks and ecological services

2.1. 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, their applications in ecology are 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 of mutualistic networks (Fath and Grant 2004), the assembly of plant-pollinator interactions (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. A detailed description of the approach can be found elsewhere (Kauffman 1969, Valverde *et al* 2020, Ross *et al* 2021).

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 associated with a Boolean function (but the same Boolean function involves 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 Boolean functions are described in figure 1.

Boolean networks share similarities with an increasingly used approach in ecology: individual-based models (IBMs) (DeAngelis and Grimm 2014). As in Boolean networks, IBMs are based upon a set of qualitative rules of interaction. However, in IBMs the set of rules of interaction describing how agents act and the links between agents are often stochastic, whereas in Boolean networks the rules are often deterministic and the potential links are fixed (but see the next sections of this manuscript). Indeed, a IBM describing the update of binary states of agents through deterministic rules and predetermined links between agents is a typical Boolean network. By explicitly considering the underlying network structure, regardless of whether it is fixed or changing across time, Boolean networks allow one to explore the interplay between qualitative rules of interaction and network organization.

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 an 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 (Hanski and Simberloff 1997, Leibold *et al* 2004) and the 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

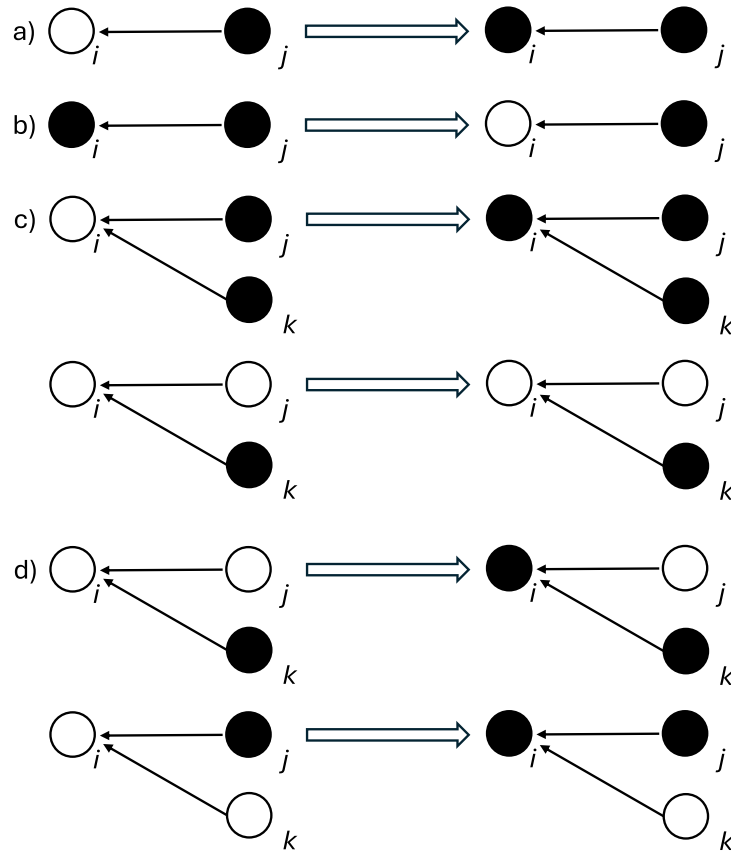


Figure 1. Examples of Boolean functions applied to networks. Black circles are 'on' states, white circles are 'off' states. The arrow indicates that a node (the base of the arrow) affects the state of the other node (the tip of the arrow). Graphs on the left describe the system at time step t and the graphs on the right describe the system at the time step $t+1$. (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'.

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 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 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 in overcoming the challenges of modeling 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 1). 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 1). 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 1). In the next section, we illustrate the Boolean networks approach using two classical empirical ecological examples, the latter including the description of an ecosystem service supply.

2.2. Illustrating the Boolean network to ecosystem services 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'.

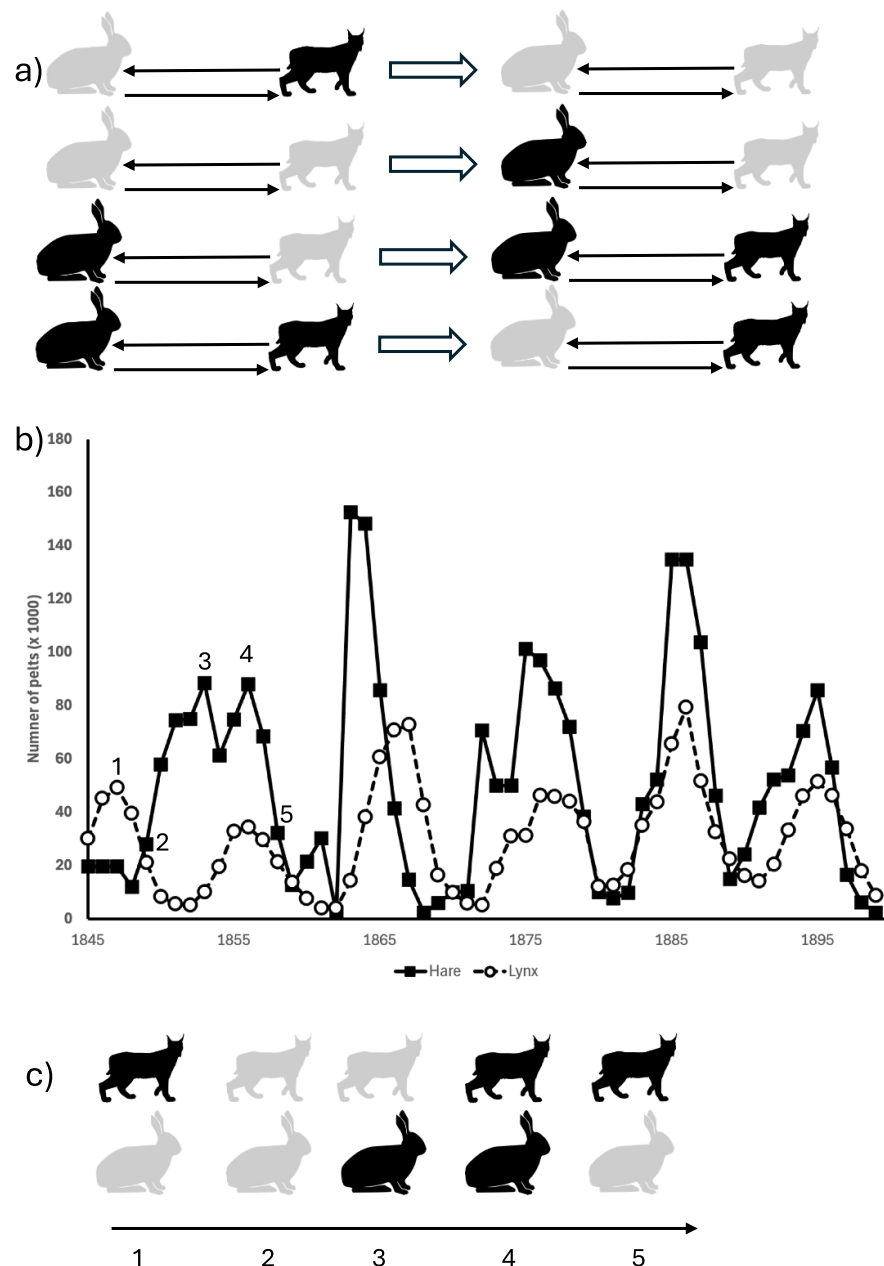
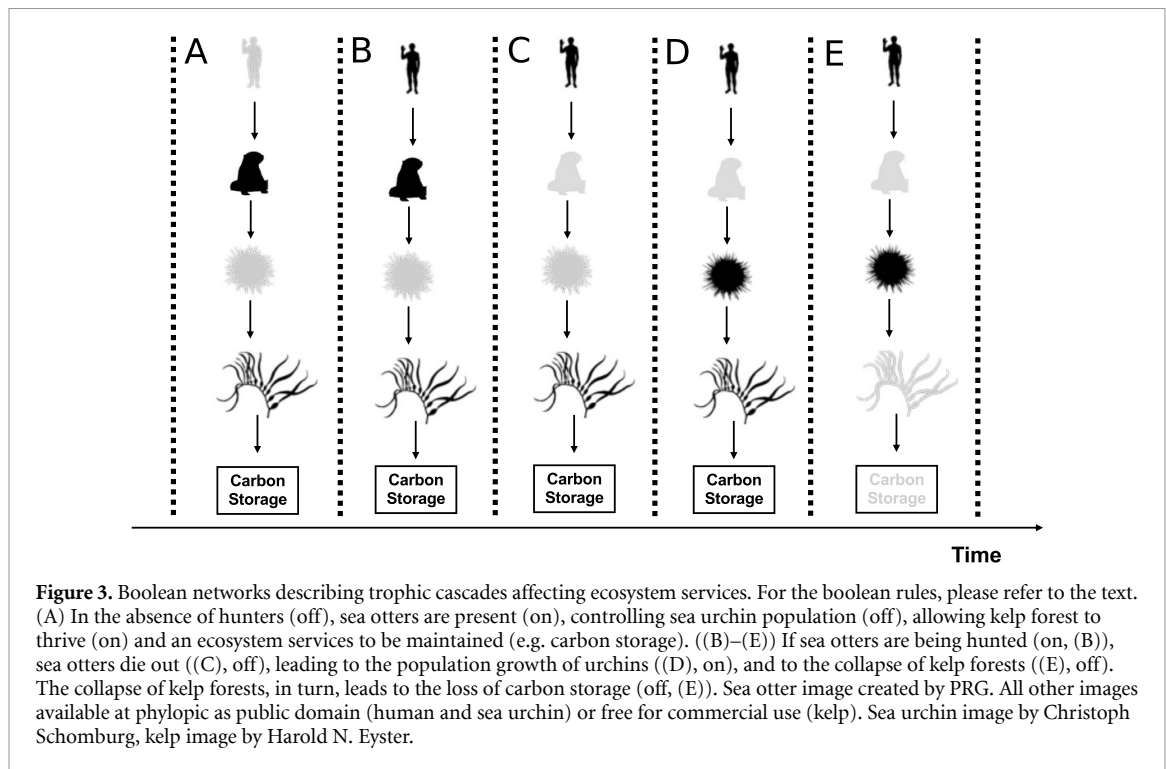


Figure 2. Examples of Boolean functions applied to ecological dynamics. (a) Boolean rules for a predator (Canada Lynx *Lynx canadensis*) and prey (Snowshoe Hare *Lepus americanus*) dynamics. Grey symbols are 'off', black symbols are 'on'. The two arrows connecting symbols indicate that the state of the lynx is affected by the hare and the state of the hare is affected by the lynx, in such a way that the lynx is 'off' if the hare is 'off', the hare is 'on' if the lynx is 'off', the lynx is 'on' if the hare is 'on', and the hare is 'off' if the lynx is '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 deterministic Boolean simulation qualitatively reproduces the empirical dynamics (cut-off values for the state 'on' used were 70 000 pelts of hares and 20 000 pelts of lynxes). Lynx-hare dataset: <http://people.whitman.edu/~hundredr/courses/M250F03/M250.html>. Lynx and hare images available at phylopic as public domain. Lynx image was created by Margot Michaud.

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 1(A)). These Boolean rules allow for the qualitative capture of the rise-and-fall cycles, described here as sequential on-off cycles (see figures 2(B) and (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 the Pacific North Coast kelp forests of the Americas (Estes and Palmisano 1974). Within some kelp forest ecosystems, sea otters (*Enhydra lutris*) mediate cascading effects that control ecosystem services. 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, favors the maintenance of the kelp forest. Hunting



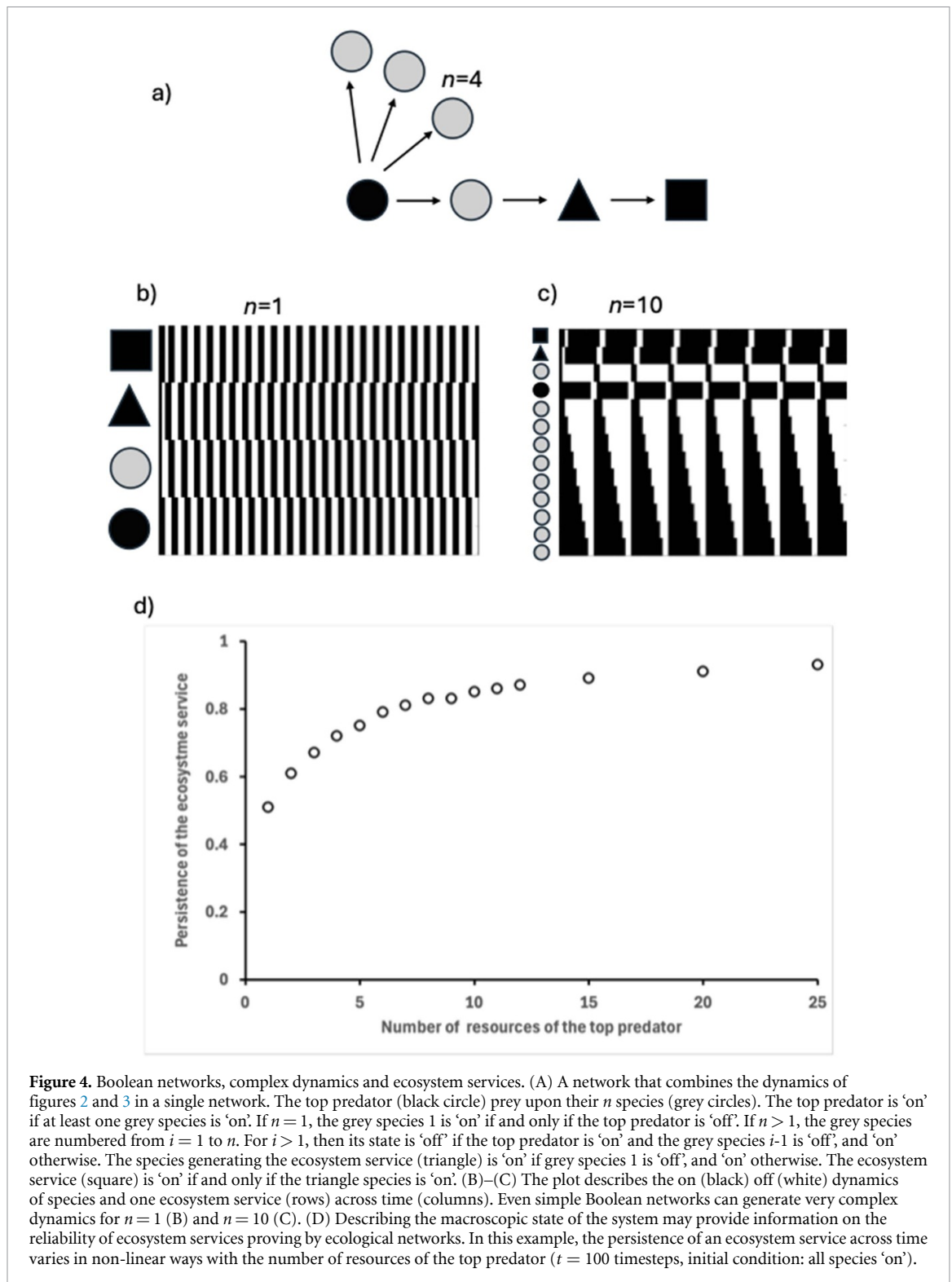
of sea otters by humans, in turn, indirectly leads to the destruction of kelps, promoting the collapse of ecosystem services, such as carbon storage (figure 3).

One can model these systems in their 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. 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 do 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 3). It is interesting to note that the dynamics of the two Boolean networks, the hare-lynx system and the kelp forest system, lead to very distinct dynamics. The hare-lynx system reaches a never-ending oscillatory behavior characterized by the sequential rise-and-fall of hare and lynx populations, whereas the kelp forest dynamics reach one of the two alternative steady states: the presence or the destruction of kelp forest, depending on whether hunters are 'off' or 'on', respectively.

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 releases the dominant salt marsh plant, the pickleweed (*Salicornia pacifica*), from the consumption by the crabs. The salt marsh vegetation that emerges under the control of crabs by sea otters, in turn, provides a number of ecosystem services, such as shoreline protection (Hughes *et al* 2024). This system can be modeled in similar ways to the sea otter-sea urchin-kelp system using a similar set of Boolean rules.

2.3. Challenges and possible solutions to using 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, describes 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 analyzing 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. This complexity emerges even for low species richness, S and simple network structures (e.g. regular networks in which all species have the same number of partners, k , 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 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. Thus, in the same way that in statistical mechanics one can describe a macrostate of the system by lumping microstates with similar properties, it is possible to circumvent the problem of characterizing the dynamics of the system by moving to the description of macroscopic dynamical patterns (figure 4).

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 the study explored 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:

$$\langle N \rangle = \frac{1}{T} \sum_{t=0}^T N^t, \quad (1)$$

in which T is the number of timesteps in the simulation. Another description can be how variable the number of species in the ‘on’ state is across time:

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

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:

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

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

in which v_i^t is the state of the service i at the time t , and v_i^t assumes values 1 or 0 if the state of the species is ‘on’ or ‘off’ respectively. 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) and (4) to investigate how network structure and dynamics and Boolean functions shape the provisioning of ecosystem services.

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 well as frameworks using sets of stochastic and deterministic differential equations, has a large number of parameters that one needs to specify for simulations with species-rich systems.

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 a species-rich community. One possible solution is the use of random Boolean networks (RBNs) in which the random truth tables are assigned to all nodes in the system (Kauffman 1969). RBNs are extremely useful for exploring the role of connectivity and architecture of networks in shaping dynamics and patterns of a system (Kauffman 1969), but they might not be suitable for exploring how particular forms of Boolean functions shape the dynamics of a given ecological network. Specifically, in RBNs, there are 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, specially if randomly generated, since no correlations are expected across truth tables.

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^- in a given timestep:

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

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

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

$$M_i^+ \geq c_i^+ \Rightarrow M_i^{+'} = 1 \quad (7)$$

$$M_i^+ < c_i^+ \Rightarrow M_i^{+'} = 0 \quad (8)$$

$$M_i^- \geq c_i^- \Rightarrow M_i^{-'} = 0 \quad (9)$$

$$M_i^- < c_i^- \Rightarrow M_i^{-'} = 1. \quad (10)$$

Finally, we define that:

$$M_i^{+'} M_i^{-'} = v_i^t. \quad (11)$$

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 $S \times S$ matrices \mathbf{A}^+ and \mathbf{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 $S \times 1$ vectors \vec{C}^+ and \vec{C}^- , which describe the cut-off 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 service. 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 supply an ecosystem service, then $c_i^+ = k_i$. More importantly, one can use similar approaches to reduce the complexity of describing truth tables for all species in the system when modeling species-rich Boolean networks.

3. 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 (including hunting by humans) 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 present or not will depend on the environmental and the interaction states. In nature, ecosystem services and also non beneficial impacts (‘ecosystem disservices’) are the product of ecological and evolutionary processes shaping populations and interacting communities. In our approach the diversification of services, e.g. the diversification of ecosystem services and the origin of the ozone layer or the ocean biological pump, is not

possible at this stage. Right now, we focus on the persistence of already-existing services. In this sense, the details of the services provided by an ecosystem will depend greatly on the dynamics of the abiotic and biotic ecosystem contexts and we should look for an statistical understanding of their occurrence and fluctuations once the abiotic and biotic environments are represented. As a first approach, we have implemented 1D and 2D environmental fluctuations scenarios into the Boolean networks and ecosystem services framework (Guimaraes and Melian 2024).

To incorporate environmental fluctuations we explored a problem inspired by ecosystem services provided by frugivores and the plants they disperse. In tropical forests, the vast majority of plants rely on fruit-eating animals to disperse their seeds. Some of the plants dispersed have economical interests, such as *Euterpe edulis*, which is harvested by their palm hearts (Galetti and Aleixo 1998, Galetti and Fernandez 1998), fruits, and fibers. *Euterpe edulis* rely upon a variety of frugivores for seed dispersal (Galetti *et al* 2013). To explore this problem, we built up a theoretical ecological network in which we assume there are four sets of species, plants, fruit-eating birds, insect herbivores, and predators (figure 5). Each node represents a species and links depict interspecific ecological interactions. We assumed the network structure of plants and frugivores is nested (Bascompte *et al* 2003) and that the ecosystem service is provided by the plant species with the largest coterie of seed dispersers, emulating the fact that *E. edulis* is dispersed by a variety of vertebrate species. We then set up that the main fruiting-eating bird (e.g. a toucan or a fruitcrow) is consumed by a predator (e.g. the forest falcon *Micrastur semitorquatus*) (figure 1(a)). We then defined rules of interaction in which the predator-frugivores and insect herbivores-plants interactions will enter, if in isolation, in a cycle dynamics similar to lynx and hare (figure 2). Also, we assume that, if in isolation, the three-species chain palm-toucan-falcon will enter in a cascading effect that, however, will not generate alternate effects as in the kelp-sea otter system (figure 3), but rather a coextinction cascade due to disruption of a mutualistic interaction by the presence of the predator. We emphasize here that the ecological interactions are only providing a biological motivation for the Boolean rules. It is not our aim, at this point, to generate a ‘realistic’ Boolean description of a tropical ecological network. For instance, although predators may generate top-down effects in tropical systems (Terborgh 1992), it is unlikely that simple top-down effects may regulate entire species-rich tropical forests (Brewer *et al* 1997). Moreover, although birds may generate trophic cascades (Mäntylä *et al* 2011) and falcons of other species may create fear landscapes for frugivorous birds, disrupting fruit consumption (Shave *et al* 2018), it is unknown if and how tropical birds of prey may regulate fruiting-eating birds. The aim of this theoretical exercise is to illustrate the potential of Boolean networks in exploring the dynamics of ecosystem services under environmental seascapes.

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’). In this scenario, we assumed that θ is fixed for the entire simulation. 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:

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

in which $b = 0.2$ controls the importance of trait matching with the environment for species persistence, and both θ and z_i are sampled from Gaussian distribution with $\mu = 0$ and $\sigma = 1$. In the fluctuating scenario, we assumed that environmental filtering changes across time following:

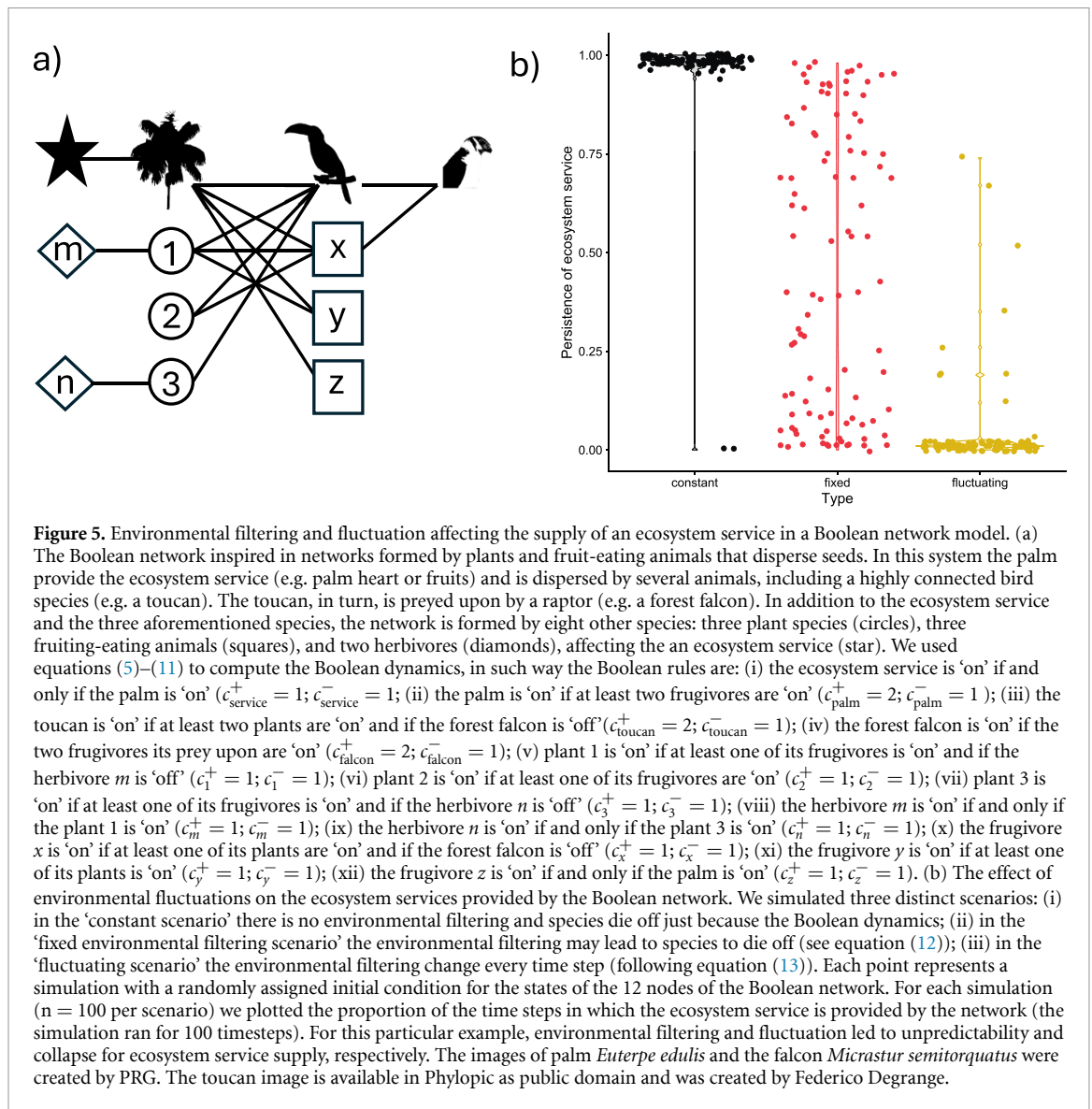
$$\theta^{t+1} = \theta^t + \epsilon^t \quad (13)$$

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 reduces the persistence and increases the unpredictability 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 5(b)).

We use the same Boolean functions (equations (1)–(11)) as in the 1D environmental scenario to explore a 2D fluctuating environment accounting for the amplitude and the frequency of an environmental variable. We remark 1D fluctuating environment uses equations (12) and (13) while 2D environment uses equation (14):

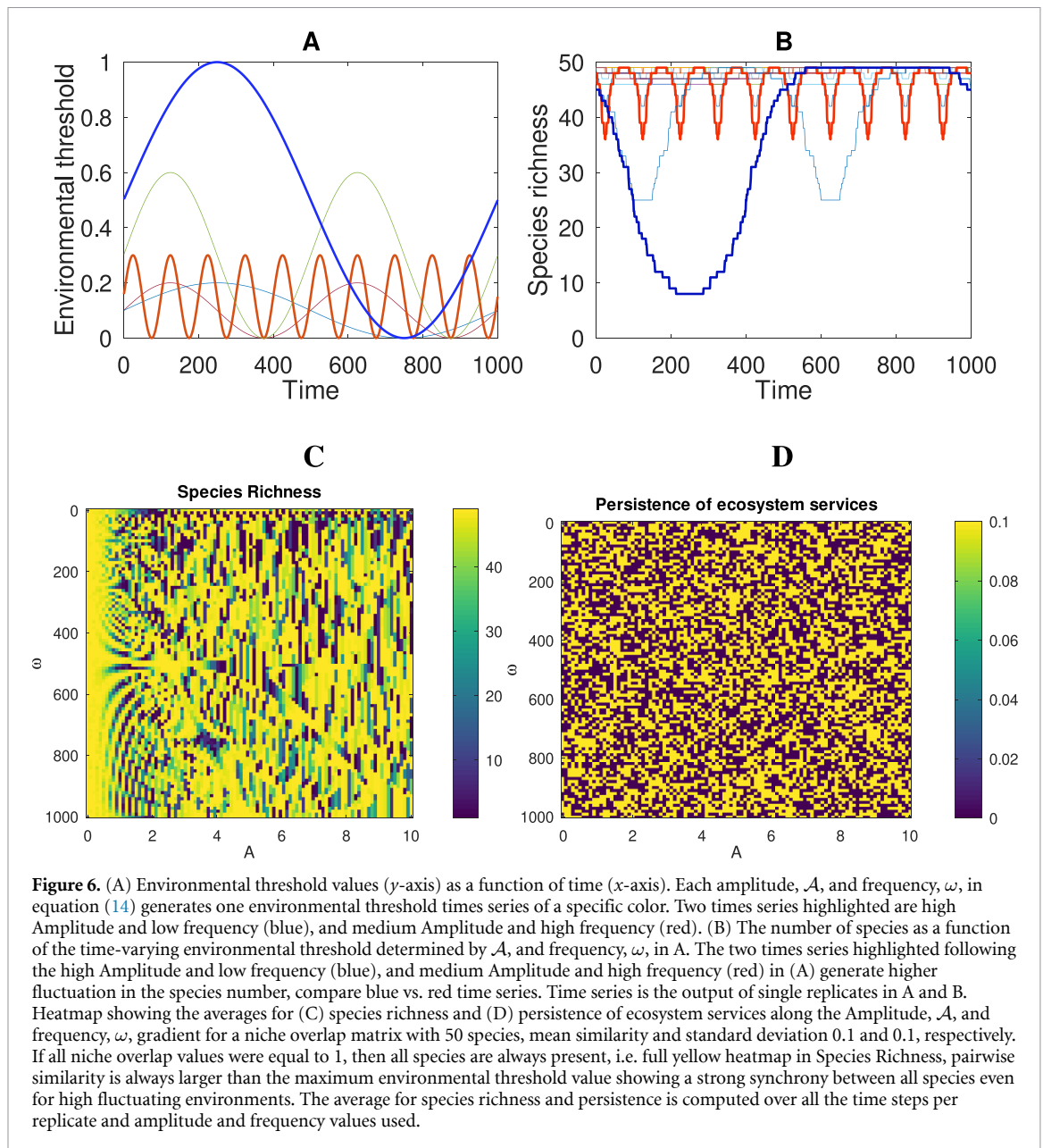
$$\mathcal{E}_t = \frac{\mathcal{A}}{2} (1 + \sin(2\pi\omega t)), \quad (14)$$

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 . Adding a 2D environment allows us to test how the size of the ecological network limits the persistence of the ecosystem service. Now, the probability that



two species co-occur depends on a threshold governed by the environmental state. If two species have a high abiotic niche overlap in tolerance, the expectation is that they synchronize with the environmental state, i.e. they will co-occur frequently because they are responding similarly to the state of the abiotic environment, even if the environment fluctuates severely. Therefore, if the overlap between two species i and j , s_{ij} , is larger than a temporally-varying threshold determining the state of the environment, \mathcal{E}_t , then the two species are responding synchronously to the environment and they are 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 have low tolerance to that environmental state and are not active in the system, $s_{ij} \leq \mathcal{E}_t$. Therefore they cannot enter in the Boolean function in that time step. A species must be at least in one $s_{ij} \leq \mathcal{E}_t$ to be off the system at time t , otherwise, the species is active and enters in the Boolean functions at that time step.

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 equation (14).



The temporally-dependent environmental threshold depends on two parameters, the amplitude, \mathcal{A} , and the frequency, ω , of a sinusoidal function (equation (14)). We compare this threshold with the niche overlap tolerance matrix, $S_e \times S_e$, with elements $S_e[s_{ij}]$ describing the niche similarity between species i and j responding to the environmental state (figure 6). We can compute the number of species in the network by joining the niche overlap matrix to the environmental threshold using equation (14). Figures 6(a)–(b) show the time-varying environmental threshold and species richness and 6c–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, $\mathcal{A} = [0.000 \ 110]$ for amplitude and $\omega = [0.001 \ 20 \ 000]$ for frequency starting with 50 species and 1 ecosystem service.

4. 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. 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 how ecological 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 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 compared to the static environment (figures 5 and 6).

Increasing amplitude and frequency in the 2D fluctuating environment is independent of the persistence of ecosystem services and therefore the decreasing number of species present in the system (figure 6(B)) does not alter the persistence of the service (figure 1(D)). These results are consequence of our assumptions of ecosystems services. They are provided with the same probability by a randomly generated subset of the total 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, for example the palmito *Euterpe edulis* case study for different specialization degrees of the frugivores, might bring evidence about the persistence of ecosystem services along ecological network seascapes with varying fluctuating environments with different frequencies and amplitudes (figure 6).

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 hand, 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 hand, 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 avenues 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 response to biotic and abiotic environments are decoupled.
- Stimulating 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 seed dispersal and 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.

5. Authors contribution

PRG developed the main idea and drafted the first version of the manuscript around Boolean networks and ecosystem services. CJM developed the idea of incorporating the environmental seascapes. PRG and CJM designed the flow of the analysis, performed the simulations, and wrote the manuscript.

Data availability statement

No new data were created or analysed in this study.

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Conflicts of interest

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

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