

Boolean networks as a way to explore dynamics in ecological assemblages under environmental change

1 Current state of research in the field

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 shaped by the organization of 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)). Furthermore, the structure of these ecological networks, together with the interactions created by the constituent species, can significantly affect how ecosystems respond to environmental changes brought about by human activities (Hughes et al. (2024)). Conversely, environmental changes can threaten ecosystem services by altering ecological interactions (Alberti (2024); Wernberg et al. (2024)). Therefore, protecting these crucial services requires a profound understanding of how the structure of ecological interactions impacts ecosystem services (Windsor et al. (2022)). These services are inherently connected to specific states of the ecosystem, which are themselves determined by a complex network of ecological interactions (Margalef (1968); Estes et al. (2011); Ripple et al. (2014)).

Traditionally, our understanding of the relationship between ecological interactions and ecosystem services has been derived from studies focused on simple ecosystems (Gregn et al. (2020); Estes et al. (2011)). The challenge now lies in extending this understanding to more complex, species-rich ecosystems, such as coral reefs, large lakes, and tropical rainforests. The staggering diversity of species within these ecosystems, along with their intricate interactions (Thompson (2005)), means that gaining insights on how ecosystem services are maintained requires strategies for aggregating and simplifying the patterns and dynamics of these systems (Levin (1992)). Specifically, innovative approaches that seek to identify qualitative changes in species-rich ecosystems could facilitate an understanding of how human activities impact the preservation of ecosystem services.

A critical step towards achieving this goal is the development of an integrative theoretical framework that can elucidate how ecological services are generated, 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)). In contrast, while it is recognized that ecosystem services often depend directly on ecological interactions (such as the pollination of crop plants) or indirectly (such as the maintenance of foundational species through trophic cascades), much of our current understanding of how environmental changes impact ecosystem services is focused on abiotic drivers (Scholes (2016); Roces-Díaz et al. (2022)).

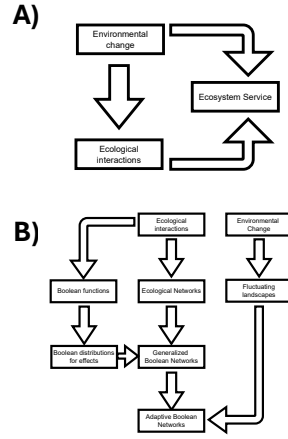


Figure 1. (A) Environmental change may directly affect ecosystem services. Alternatively, environmental change may indirectly affect ecosystem services by promoting changes in the network of ecological interactions; B) The project employs a combination of approaches, with ecological interactions serving as the foundation. These interactions are utilized to depict the organization of ecological assemblages (ecological networks) and the influence of one species on another (Boolean functions). Boolean functions are defined as distributions of positive and negative effects. The amalgamation of ecological networks and Boolean effect distributions results in Generalized Boolean Networks. Environmental change, modeled as fluctuating landscapes, is then incorporated to generate Adaptive Boolean networks.

2 Goals and Research questions

This research project aims to develop a theoretical framework for understanding how ecological networks influence the robustness and vulnerability of ecosystem services under environmental change. To achieve this goal, we propose integrating ecological network analysis with Boolean networks (Kauffman (1969)), modeling techniques for fluctuating environmental landscapes, and tools derived from statistical mechanics thinking. This innovative approach seeks to investigate how the organization of ecological interactions contributes to the robustness or vulnerability of ecosystem services. The project will specifically address the following questions: (1) How does the structure of ecological networks impact ecosystem services?; (2) How are ecosystem states associated with ecosystem services?; and (3) How do fluctuating environmental changes affect the relationship between network structure and ecosystem services?

3 Methods

Environmental change may affect directly the presence of ecosystem services or, indirectly, by reorganizing the organization of ecological interactions (Figure 1A). To address this dynamics, we will combine multiple approaches (Figure 1B).

3.1 Ecological interactions to Generalized Boolean Networks

Boolean networks are models developed to describe the dynamics of complex systems (Kauffman (1969)). Boolean networks have found applications in biology (such as gene regulatory networks), 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 still incipient. For example, recently, Boolean networks were used to explore the fragility of eusocial insect colonies to perturbations (Gaucherel et al. (2017)), evolution in mutualistic networks (Fath and Grant (2004)), and the assembling of plant-pollinator communities (Campbell et al. (2011)).

We begin by describing the underlying network of interactions, in which nodes depict species and interactions between species are portrayed as links. Each node is linked to a binary variable, indicating one of two states: "off" or "on". Links are affiliated with Boolean functions, which dictate the state of each node based on the states of the interacting nodes. One can associate "off" with extinct species and "on" with extant species. Alternatively, "off" could also represent "low abundance", while "on" indicates high abundance. Obtaining reliable estimates of abundances for multiple species over time is consistently difficult, and therefore a solution is characterizing the system in a coarse but reliable manner, using binary descriptors such as "absence" and "presence" or "low" and "high." Similar approaches are commonly employed in ecology, including metapopulation/metacommunity dynamics (Leibold et al. (2004); Hanski and Simberloff (1997)).

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 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." 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". 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. The truth table comprehensively enumerates all possible combinations of binary states for the input species and displays the resulting states for the output species. While Boolean networks offer a natural way to describe qualitative changes in the system, the challenge lies in parameterizing the model. Specifically, it is 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. Thus, the classical Boolean network framework has a large number of parameters that one needs to specify for simulations with species-rich systems. One possible alternative is to shift to statistical descriptions of the truth tables and outcomes at the community level of the Boolean dynamics. To do so, we used the statistical mechanics thinking. Classically, 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 . In statistical mechanics jargon, \mathbf{V}^t depicts the microstate in which the system exists at time step t . These microstates may exhibit various patterns that are potentially equivalent and their consequences. To circumvent this challenge, we will summarize microstates that share similar features (i.e., macrostate). For example, we define N^t as the number of species in the "on" state at time step t . Another macroscopic descriptor is δ^t as:

$$\delta^t = \sum_{i=1}^S v_i^t v_i^{t+1}, \quad (1)$$

in which v_i^t and v_i^{t+1} are the states of the species i at the time t or $t+1$. Therefore, δ^t measures changes in species composition. We will correlate these macrostate descriptors with the presence of ecosystem services to investigate how network structure and Boolean functions shape ecosystem dynamics.

We now turn our attention to the issue of truth tables. Rather than defining a single truth table for each species, we categorize species into ensembles, creating Generalized Boolean Networks (GBNs). The GBNs, an approach introduced in this project, describe Boolean networks using simplified statistical distributions. First, we initially establish two types of links:

(1) **Positive links:** if species j is "on" favors species i to be "on" and if species j is "off" favors species i to be "off", e.g., j is a resource or facilitate the presence of species i .

(2) **Negative links:** if species j is "on" favors species i to be "off", e.g., j is a natural enemy of species i , and if species j is "off" favors species i to be "on", e.g., j is 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 interactions, we 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^- :

$$M_i^+ = \sum_{j=1}^S a_{ij}^+ v_j^t; M_i^- = \sum_{j=1}^S a_{ij}^- v_j^t \quad (2)$$

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 :

$$M_i^+ \geq c_i^+ \Rightarrow M_i^{+'} = 1; M_i^+ < c_i^+ \Rightarrow M_i^{+'} = 0; M_i^- \geq c_i^- \Rightarrow M_i^{-'} = 0; M_i^- < c_i^- \Rightarrow M_i^{-'} = 1 \quad (3)$$

Finally, we define that:

$$M_i^{+'} M_i^{-'} = 1 \Rightarrow v_i^t = 1; M_i^{+'} M_i^{-'} = 0 \Rightarrow v_i^t = 0 \quad (4)$$

Thus, the $S \times 1$ vectors \vec{C}^+ and \vec{C}^- , which describe the cut-offs values for each species for the positive and negative effects, control the species responses. 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 of 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.

3.2 Dynamic Interaction Landscapes and Adaptive Boolean Networks

To account for environmental dynamics in Boolean networks, we determine the probability of an interaction between two species to be on/off by introducing a distance threshold governed by the environmental state. This way, we use the environmental threshold to represent the environmental state and compare the threshold with the species distance. If the distance threshold from the two species is larger than from the environment, then environmental conditions prevent species to interact in the system, $d_{ij} > d(e_t)$. Otherwise, if the distance threshold from the two species is equal or smaller than from the environment, then the two species are interacting and potentially affecting to each other, $d_{ij} \leq d(e_t)$. For a given environmental threshold we compare it with a $S_e \times S_e$ matrix where elements d_{ij} describe the difference in response between species i and j to environmental state, i.e., this matrix can be parametrized from empirical data.

The environmental state is governed by a sinusoidal function representing a seasonal periodic environment. We will explore a broad range of environments by dynamically varying the distance threshold from low to high- fluctuating environments (de Filho and Metzger (2006)). To explicitly take into account periodic environmental dynamics, two species i and j are connected if their environmental distance, d_{ij} , is equal or smaller than the environmental distance radius $d(e_t)$ following a periodic, sinusoidal form given by:

$$d(e_t) = \frac{\mathcal{A}}{2}(1 + \sin(2\pi\omega t)), \quad (5)$$

where t is time, \mathcal{A} and ω are the amplitude and the frequency of environmental dynamics determining the temporal fluctuations of the environment. We define as an Adaptive Boolean Network the combination of a Generalized Boolean Network with a Dynamical Interaction Landscape. It is adaptive because describes the feedback between network structure and the state of the species in the system, under the effects of environmental change (Fricker et al. (2009); Raimundo et al. (2018)).

4 Project Assessment: Outcome, Risks, and Impact

4.1 Expected output

To understand the role of environmental fluctuations in ecological networks we combine Boolean networks and landscape dynamics to describe relationships between species to infer patterns of persistence of species and interactions. The comparison would allow us to statistically explore the relative contributions of the two scenarios, Boolean networks and dynamic landscapes. We would gain theoretical but also empirically-driven understanding of how environmental fluctuations drive the emergence of biodiversity patterns when species interactions are taken into account. Derived diversity and ecological networks metrics would include species and interaction persistence and turnover and how the type of fluctuation, i.e., periodic and non-periodic, changes network patterns. We will then compare these metrics of diversity dynamics between environmental fluctuations, white, red, and other colours, for the Boolean and the dynamic landscapes scenarios.

4.2 Risks

To predict the role of environmental changes on biodiversity we would need to develop methods to understand how species and interactions respond to changes in species-rich assemblages. Here, we introduce two complementary approaches, one coming from boolean networks and the other from dynamic landscapes, to decipher the temporal dynamics of species and interactions and to evaluate the overall role of temporal fluctuations in the persistence of species in ecological networks. The Boolean network approach has the limitation of requiring the truth table, where there is a large number of combinations when the number of species is large. There is a way of narrowing down the combinations by parameterizing the combinations using species-specific data, but this data is usually absent for large networks. A complementary approach to the parametrization is the distribution of Boolean effects we describe in this project. Moreover, it is possible to use the niche overlap graph from pairwise niche similarity to define thresholds, i.e., species-species presence is given by an environmental state. The risk associated to this approach involves obtaining sufficient data to build the niche overlapping matrix prior to the simulations. Therefore, both approximations presented here have risks in determining the temporal fluctuations of species and interactions. Nonetheless, the combination of both approximations might serve as a proof of concept to further develop data-driven methods of ecological networks in rapidly fluctuating and changing ecosystems.

4.3 Potential impact of the project

Projected predictions of climate change suggest many species are responding to increasing temperatures and the variation associated to it and related environmental variables. In this context, modeling temporal fluctuations in species-rich ecosystems to uncover network changes and species extinctions is challenging and still rare in the literature. The present proposal makes shortcuts, i.e., connect boolean networks states and dynamic landscapes to understand the temporal fluctuations of interactions and species. This will provide new insights into how environmental changes affect the relationship between network structure and ecosystem services to advance not only our theoretical understanding of ecological networks, but also to inform practical conservation strategies for preserving biodiversity and ecosystem services in the face of ongoing environmental change. There is also an impact component to develop a mechanistic approach to understand multispecies assemblages in the context of nonequilibrium dynamics under rapid environmental changes, where the limitation of phenomenological steady-state descriptions can be severe when rapid and varying fluctuations occur. We will produce open-source tools and software, i.e., jupyter notebook and open git repositories to facilitate reproducibility of all results and to allow for the replication of the whole process in different model ecosystems.

References

- Alberti, M. (2024). Cities of the anthropocene: urban sustainability in an eco-evolutionary perspective. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 379(1893):20220264.
- Allesina, S. and Tang, S. (2015). The stability–complexity relationship at age 40: a random matrix perspective. *Popul. Ecol.*, 57(1):63–75.
- Bastolla, U., Fortuna, M. A., Pascual-García, A., Ferrera, A., Luque, B., and Bascompte, J. (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*, 458(7241):1018–1020.
- Bullock, J. M., Aronson, J., Newton, A. C., Pywell, R. F., and Rey-Benayas, J. M. (2011). Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends Ecol. Evol.*, 26(10):541–549.
- Campbell, C., Yang, S., Albert, R., and Shea, K. (2011). A network model for plant–pollinator community assembly. *Proceedings of the National Academy of Sciences*, 108(1):197–202.
- Cimon-Morin, J., Darveau, M., and Poulin, M. (2013). Fostering synergies between ecosystem services and biodiversity in conservation planning: A review. *Biol. Conserv.*, 166:144–154.
- Cohen, J. E. and Stephens, D. W. (2020). *Food Webs and Niche Space. (MPB-11), Volume 11*. Princeton University Press.
- de Filho, F. J. B. O. and Metzger, J. P. (2006). Thresholds in landscape structure for three common deforestation patterns in the Brazilian Amazon. *Landscape Ecology*, 21:1061–1073.
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., Shurin, J. B., Sinclair, A. R. E., Soulé, M. E., Virtanen, R., and Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, 333(6040):301–306.
- Fath, B. D. and Grant, W. (2004). Ecosystems as evolutionary complex systems: A synthesis of two system-theoretic approaches based on boolean networks.
- Fricker, M. D., Boddy, L., Nakagaki, T., and Bebbler, D. P. (2009). Adaptive networks: Theory, models and applications. *Understanding Complex Systems*, pages 51–70.
- Gaucherel, C., Théro, H., Puiseux, A., and Bonhomme, V. (2017). Understand ecosystem regime shifts by modelling ecosystem development using boolean networks. *Ecological Complexity*, 31:104–114.
- Gregg, E. J., Christensen, V., Nichol, L., Martone, R. G., Markel, R. W., Watson, J. C., Harley, C. D. G., Pakhomov, E. A., Shurin, J. B., and Chan, K. M. A. (2020). Cascading social-ecological costs and benefits triggered by a recovering keystone predator. *Science*, 368(6496):1243–1247.
- Guimaraes, Jr, P. R. (2020). The structure of ecological networks across levels of organization. *Annu. Rev. Ecol. Evol. Syst.*
- Hanski, I. and Simberloff, D. (1997). The metapopulation approach, its history, conceptual domain, and application to conservation. *Metapopulation biology*, pages 5–26.

- Hughes, B. B., Beheshti, K. M., Tinker, M. T., Angelini, C., Endris, C., Murai, L., Anderson, S. C., Espinosa, S., Staedler, M., Tomoleoni, J. A., Sanchez, M., and Silliman, B. R. (2024). Top-predator recovery abates geomorphic decline of a coastal ecosystem. *Nature*, 626(7997):111–118.
- Kauffman, S. (1969). Homeostasis and differentiation in random genetic control networks. *Nature*, 224(5215):177–178.
- Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology letters*, 7(7):601–613.
- Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology*, 73(6):1943–1967.
- Margalef, R. (1968). Perspectives in ecological theory. *philpapers.org*.
- Pascual, M. and Dunne, J. (2006). *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press, USA.
- Raimundo, R. L., Guimarães, P. R., and Evans, D. M. (2018). Adaptive networks for restoration ecology. *Trends in Ecology & Evolution*, 33(9):664–675.
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., and Wirsing, A. J. (2014). Status and ecological effects of the world’s largest carnivores. *Science*, 343(6167):1241484.
- Roces-Díaz, J. V., Santín, C., Martínez-Vilalta, J., and Doerr, S. H. (2022). A global synthesis of fire effects on ecosystem services of forests and woodlands. *Front. Ecol. Environ.*, 20(3):170–178.
- Scholes, R. J. (2016). Climate change and ecosystem services. *Wiley Interdiscip. Rev. Clim. Change*, 7(4):537–550.
- Thompson, J. N. (2005). The geographic mosaic of coevolution.
- Valverde, J. C., Mortveit, H. S., Gershenson, C., and Shi, Y. (2020). Boolean networks and their applications in science and engineering. *Complexity*.
- Wernberg, T., Thomsen, M. S., Baum, J. K., Bishop, M. J., Bruno, J. F., Coleman, M. A., Filbee-Dexter, K., Gagnon, K., He, Q., Murdiyarso, D., Rogers, K., Silliman, B. R., Smale, D. A., Starko, S., and Vanderklift, M. A. (2024). Impacts of climate change on marine foundation species. *Ann. Rev. Mar. Sci.*, 16:247–282.
- Windsor, F. M., Armenteras, D., Assis, A. P. A., Astegiano, J., Santana, P. C., Cagnolo, L., Carvalheiro, L. G., Emary, C., Fort, H., Gonzalez, X. I., Kitson, J. J. N., Lacerda, A. C. F., Lois, M., Márquez-Velásquez, V., Miller, K. E., Monasterolo, M., Omacini, M., Maia, K. P., Palacios, T. P., Pocock, M. J. O., Poggio, S. L., Varassin, I. G., Vázquez, D. P., Tavella, J., Rother, D. C., Devoto, M., Guimarães, Jr, P. R., and Evans, D. M. (2022). Network science: Applications for sustainable agroecosystems and food security. *Perspect. Ecol. Conserv.*, 20(2):79–90.