

Dynamical networks in agroecology: the milpa as a model system

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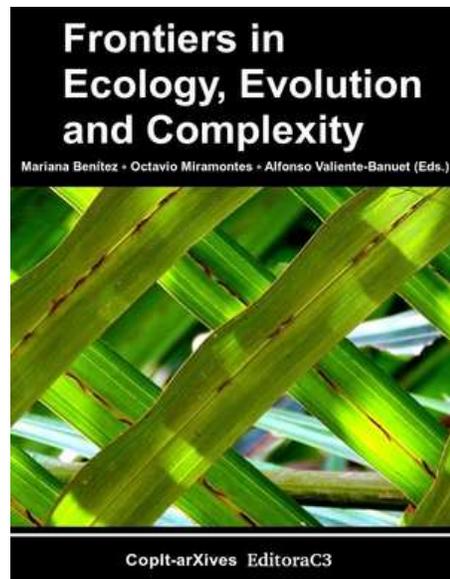
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Networks in agroecology

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1 Abstract

In the context of biodiversity and alimentary crises, it is necessary to develop and promote agricultural practices that both contribute to food security and biodiversity conservation. The Mesoamerican polycrop known as milpa is a diverse and complex agroecosystem that, given its ample diversification and adaptation to local conditions, provides an excellent model system for Agroecology. In this chapter we argue that such a system can be studied with the conceptual and technical tools of Theoretical Ecology and Complex Systems Sciences —dynamical network models in particular— in order to advance in the understanding and design of sustainable agricultural practices, and to render analytical tools that can inform farmers and other social actors by enabling the assessment of contrasting scenarios and management schemes.

2 Resumen

En el contexto de las crisis alimentarias y de biodiversidad, es necesario desarrollar y promover prácticas agrícolas que al mismo tiempo contribuyan a garantizar la seguridad alimentaria y a conservar la biodiversidad. El policultivo mesoamericano conocido como milpa es un agroecosistema diverso y complejo que, dada su amplia diversificación y adaptación a ambientes locales, provee de un excelente sistema modelo para la agroecología. En este capítulo, argumentamos que dicho sistema puede ser estudiado con las herramientas técnicas y conceptuales de la ecología teórica y las ciencias de la complejidad —los modelos dinámicos de redes en particular— para avanzar en la comprensión y diseño de prácticas agrícolas sustentables, así como para generar herramientas analíticas que permitan a los campesinos y a otros actores sociales evaluar distintos escenarios y esquemas de manejo.

3 Agroecological communities: multiscale nonlinear interactions

Agroecological systems are inherently complex, as they comprise non-additive or non-linear interactions established among cultivated plants, associated native species of plants and animals, soil micro- and meso- communities, and the human agency. The prevalence of non-linear interactions among and within populations often give rise to unpredictable or non-proportional effects in the face of community alterations. Moreover, species in these ensembles are tightly intertwined, which makes them an ecological unit that, due to the human management, are subjected to natural and artificial processes of selection and evolution at the species and the community level. For example, artificial selection driven by Mesoamerican peasants has led to the domestication and semi-domestication of thousands of maize, bean, squash and other plant races and varieties, many of them generated and locally adapted in close association with each other. The study of agrocommunities could thus help address the question of how selection on species and community traits shapes ecosystem structure and services; for instance, how selection on species and community traits shapes ecosystem structure, and how this translates to enhancement of farmers life quality.

With this integrative view, the growing field of Agroecology postulates that agricultural systems may be studied and modeled by using tools and concepts similar to those that have proven useful in the study of “natural” communities and ecosystems. For instance, agricultural production can be seen from the perspective of population and community ecology; then, yield and other properties become a consequence of the growth and survival rates of each plant population and the effect of species interactions. Similarly, the transit from one community state to another (e.g. from high to low biodiversity) is also largely due to the collective plant-plant and animal-plant interactions [1, 2]. Hence we revise the use of particular ecological and mathematical tools to study agroecosystems. There are, however, some specific aspects of agroecological systems that should be taken in consideration when being studied as ecological units, such as the forcing of the system by producers (farmers), which establishes initial conditions of the system and may change ecological interactions between crops and the associated biota. Indeed, research of simple agroecosystems such as monocrops and two-crop mixtures pioneered the study of intra and interspecific plant competition, in man-made and natural communities [3, 4], and it is likely that the study of well-characterized and relatively controlled ecological communities such as diversified agroecosystems may lead to a better understanding of ecological systems in general. For example, the study of agrocommunities could help address the question of how selection on species and community traits shapes ecosystem structure.

As complex systems, agroecological systems exhibit global properties that arise from the interactions among their components, this is, among species and abiotic factors. These properties, often referred to as emergent properties, are thus defined for the whole web

of interactions and cannot be understood only from the isolated study of species or pairs of species. Among them are resilience, productivity and diversity, which in turn appear to affect each other in non-trivial ways [5, 6]. A property that has been less studied as an emergent and community-level feature is tolerance. At the population level tolerance has been defined in a broad sense as the capacity to buffer individual fitness consequences of physical and biotic stresses [7]. Tolerance is usually estimated as the relationship between fitness and a gradient of damage (intensity of stressful conditions) for individual genotypes [8]. The rationale behind this concept could be easily escalated at the community level to better understand the connection between complexity and stability. Communities are also known to be negatively affected by natural and human induced perturbations [9]. However, attributes like species composition and diversity can increase the speed of recovery (resilience) of communities after disturbance [10] (a component of community tolerance). Further examination of emergent properties of communities is required to focus management efforts to warrant community stability in agroecosystems. In this sense, identification of population and community attributes that increase tolerance, for example, to disturbance pressures can help to design better management programs.

The milpa as a model system in agroecology

The milpa is a polyculture originated and still practiced in Mexico and the rest of Mesoamerica (see Figure 1). In this system maize, common beans and squash are typically grown in association, sometimes along with tomatoes, multiple varieties of chilies, semi-domesticated herbs (*quelites*), etc. This method of polyculture has been improved over thousands of years, and is now adapted to a variety of climatic, edaphic and cultural conditions and, despite the current tendency towards its extreme simplification, it has been the foundation of food security in many Latin American rural communities for centuries [11]. The milpa's value extends far-beyond the calories it provides or the simple combination of species; being based on locally adapted and diversified plant varieties, the system provides a reliable source of diverse and complementary foodstuffs that meet nutritional needs and local cultural preferences [11, 12]. In addition, domesticated species used in the milpa were selected in the presence of natural consumers (in the absence of agrochemicals), thus human selection has favored crop varieties, genotypes and species associations that are tolerant and resilient in an ecological scenario where pests, competition, and resource limitation were the most frequent conditions. The milpa thus represents a valuable source of genetic and ecological resources to face the negative effect of diverse factors affecting plant performance and productivity. For example, theoretical and empirical studies support the expectation that because plant tolerance does not affect negatively natural consumers, it reduces the coevolutionary response usually observed between resistant traits of plant and their natural enemies [13]. Thus, studying crop tolerance in agroecosystems can help reduce the need of artificially defending plants through agrochemicals while reducing the opportunities for pest adaptation to the plant resistance.



Figure 1: The milpa as a complex agroecosystem. A) The milpa is a polyculture based on maize that usually also includes bean, squash, semidomesticated herbs, and other plant and animal species. Picture taken at the milpa plots located at Vicente Guerrero, Tlaxcala, Mexico. B) Schematic network representation of some of components and interactions comprised in the milpa agroecosystem: 1. *Zea mays* L. (corn), 2. *Cucurbita* ssp (squash), 3. *Phaseolus vulgaris* (bean), 4. *Spodoptera frugiperda* (army worm), 5. *Baculovirus SfVPN*, 6. *Homo sapiens* (farmer).

Moreover, it has been suggested that biodiverse agroecological systems such as the milpa play a key role in the maintenance and regeneration of biological diversity. In contrast to conventional –species poor– agricultural systems, the milpa constitutes a heterogeneous system based on combinations of locally adapted species, often using little or no agrochemicals, which enables the coexistence of the cultured plants with numerous associated species, which frequently includes shrubs, columnar cacti, and trees in the borders or dispersed within the plot [14]. Agro- and biodiversity sustained in systems like the milpa make it a matrix permeable to native animal and plant species, thus facilitating migration, dispersal and, in consequence, the conservation of primary vegetation [15, 16]. Then, the milpa offers a valuable resource to meet ecological and socioeconomic challenges, such as climate change, changes in water availability, disease and pest incidence, and the alimentary crisis currently faced by Mexico and other countries.

Some systems have been established as model ecological systems; their components and interactions have been thoroughly characterized, enabling the postulation and analysis of particular ecological networks. Among these systems are for example, some lake and grass communities [6]. The consolidation of these ecological systems as models for field, experimental and theoretical work has provided ecologists with a catalog of eco-

logical networks that can now be used to point at common structural and dynamical properties of ecological communities. Similarly, the milpa constitutes a model system in agroecology, from which the collective dynamics of cultivated plants and the associated diversity can be uncovered. Additionally, this system has been studied in detail, although not necessarily with an integrative nor an evolutionary approach, mainly by farmers – who have crystallized in traditional practices their profound ecological understanding of the milpa – and also by agronomists. There is therefore a large amount of data that can inform the evolutionary patterns and specification of a network model for the milpa (e.g. [17]).

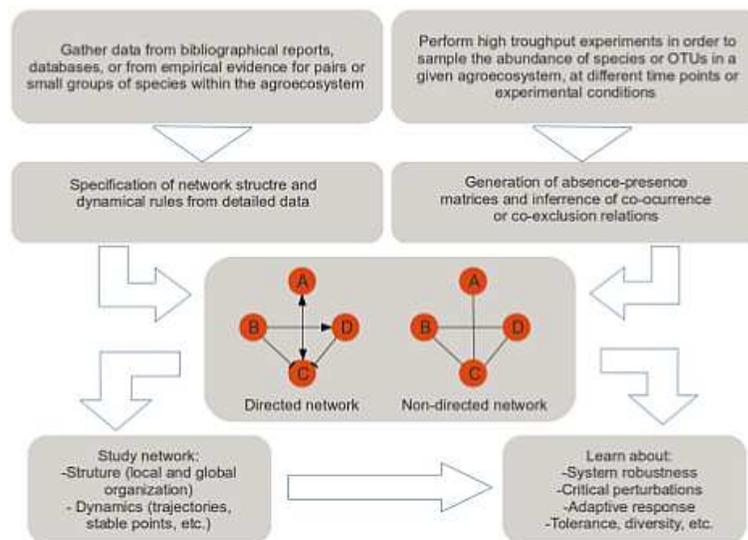


Figure 2: Diagram showing the basic steps to the inference of ecological networks from field, genetic, physiological and other types of data.

Dynamic network models in the study of agroecosystems

Networks have been widely used to represent the skeleton of complex systems, as they provide a rather natural way to integrate diverse interacting elements. Network modeling has been extensively used during the last century in the ecosystems study, initially mostly with a trophic-energy flux focus [18, 19], but it was not until Robert May's work [2] that new formal aspects about the ecological networks (e.g. topology, stability) began to be considered. Since the mid-twentieth century, theoretical ecologists posed questions regarding the chaotic dynamics that could arise in communities that involved two or more populations. For example, a long standing question in ecology concerns the relationship between the complexity of a community and its stability, and recent studies on this topic

have been motivated by conservational and ecosystem management issues [20]. In the last decades, other studies have developed analytic criteria to evaluate and compare the stability of relatively large competitive, mutualistic and predator-prey communities [21]. Indeed, the use of network models has helped address this and other central questions in ecology (e.g. [22–24]). We, as well as other authors [25], argue that agrocommunities can be modeled with the set of tools developed to study networks and that the quantitative and qualitative data generated by the agronomists and farmers will help in the model building and validation.

Network models consist of nodes that represent the elements conforming a web of interactions, and edges that correspond to such interactions. In directed networks, such interactions can be positive or negative depending on the effect that a node has on another one. These models have been used to study not only the structure but also the collective dynamics of biological systems [26]. In a dynamic network model, any given node can take a quantitative value, which is calculated for every time unit according to a function that considers the state of the nodes regulating each node. In ecological networks nodes often correspond to species (taxonomic or functional), while the edges stand for trophic, competitive, mutualistic, and other types of ecological interactions.

There are several theoretical approaches that have been proposed to model network dynamics, two of which are: the continuous and the discrete. Continuous network models are built as a system of coupled differential equations that quantitatively describe the change of a node state in time. In the context of ecological systems, this description is particularly suitable when the systems under study is small – or can be simplified to consider few nodes – and the interactions among species have been thoroughly characterized (e.g. [4, 32]). However, at the ecological level, tens or even hundreds of species are required for global ecological processes to occur, such as the completion of biogeochemical cycles. In that case, the continuous approach can become intractable due to the great number of variables and unknown parameters involved. The discrete approach to model ecological networks describes in a qualitative way the ecological interactions occurring in a community or ecosystem, and can be used to understand the overall regulatory logic of ecological processes. This approach focuses on the persistence of a population or species, rather than on its abundance. Thus, the state of a given node is represented by a discrete variable that usually takes the values 1 if the species is present and 0 if is not. However, there are also multivalued discrete systems in which the abundance of a species can be approximated by a set of discrete values (0,1,2,...). The use of network models in various fields, such as genetics and development, has shown that discrete models can incorporate a large number of components and interactions, and that in spite of their simplicity, they are able to capture key aspects of biological complexity [33].

When using a network approach for modeling the ecological dynamics of a particular agrocommunity, one aims at representing the taxonomical or functional groups as nodes and their ecological interactions or energy fluxes as directed edges [34, 35]. Several issues emerge from this approach. It is possible to aggregate or collapse some of the components



Figure 3: Examples of Educational Resources for Navigating the complexity of Ecological and Socio-Ecological Networks. (1) Azteca Chess [27] captures in a stylized form some of the cascading interactions that occur among a number of insects and fungi species in the Mesoamerican Shade Coffee Agroecosystem. The complexity of this network and its practical implication for autonomous pest control has been unveiled by the seminal work of a large international team of researchers and postgraduate students led by world leaders in agroecology (see for example [28]). Agrodiversity v.2 [29] is an upgrade of our previous Agent Based Model in Netlogo Language that challenges users to find the biological and management parameters with which functional biodiversity can selforganize to produce ecological and economic sustainability far from equilibrium (for details see [30]). (3) Sierra Springs [31] is a four player board game that can be played under a number of different sets of social norms, and that challenges participants to make a livelihood without collapsing critical ecological functions at the watershed level. It exposes participants to coordination, cooperation and solidarity dilemmas that emerge from the interaction of environmental constraints, social norms and public policies.

of the network by considering their ecological role, but there is a risk of oversimplification of the network if partially redundant paths are lost or disregarded, as different types of redundancy has been shown to confer robustness to networks [36]. Also, in order to simplify their study, ecological networks have often been separated into subnetworks including only trophic, mutualistic, or other types of interactions, yet it is central to keep in mind that these networks are part of larger ones and to develop integral models as data become available.

The detailed evidence to build data-based ecological networks and specify the functions that determine their dynamics can be obtained through at least two different approaches. The first one is based on gathering direct evidence for interactions between pairs or groups of species. Such data can be obtained in the field, common garden experiments, or in the laboratory, as well as from scientific reports and databases. Several ecological network models have been successfully built and analyzed following this strategy (e.g. [37–39]). Current high-throughput technology has opened a second avenue to infer interspecific interactions and ecological networks, specially in the case of microbial communities. Data generated by next-generation sequencing – for example, a microbial soil community – provides information about the abundance of the different microbial operational taxonomic units (OTUs) in different experimental conditions. The pattern of co-occurrence and co-exclusion among these OTUs has been used to predict ecological interactions among species (e.g. mutualism, competition, predation, etc.), which may then be summarized in networks where the nodes correspond to OTUs and the edges to the interactions among them (for an excellent review regarding this type of network inference see [40], see also Figure 2).

Inferring ecological networks by either method allows for structural and sometimes also dynamical analysis of ecological systems, as well as for the identification of the features that are key to their resilience, tolerance and productivity, and the study of their behavior in different scenarios. For instance, structural analyses reveal how connectivity patterns affects the networks overall stability; this helps predict system responses to local extinction or species' introductions. Additionally, specifying the dynamical rules of these networks, be it with a discrete or continuous formalism, helps to identify the nodes and interactions that are sufficient and necessary for global properties such as resilience to emerge [41–43]. Importantly, network approaches to the study of agroecosystems can lead to the development of software and other tools that help farmers and other social actors in the assessment of different scenarios, as well as to attain a better understanding of complex socio-ecological systems. The complexity, relevance, challenges, and beauty of many ecological and socio-ecological processes are not easily grasped by social actors collectively involved in their (mis)management. At El Colegio de la Frontera Sur, Mexico, L.G.B and coworkers have drawn inspiration from the recent and increasing efforts world-wide to model such networks, and have developed a number of original stylized board games and interactive agent-based models that allow participants coming from the most contrasting social backgrounds to experience and understand the non-linear processes and

the surprising properties, challenges and opportunities that emerge at different scales in socio-ecological systems. Figure 3 depicts three examples of such network-inspired board games.

We have outlined a general framework that could be used to build integrative and dynamical models of the milpa agroecosystem on the basis of currently available and continuously emerging data. As in other areas of Biology, and in Ecology in particular, such models could help uncover and understand complex processes of different variants of the milpa. In turn, this analysis would provide novel insights about key elements or interactions leading to successful management in this and other agroecosystems. Recent advances in agroecology jointly with complex systems theory can learn from ancestral and more recent practices to suggest model systems of sustainable production and management. We advocate that studying the milpa in this context can represent a feasible alternative strategy to warrant food security and production in Mexico and, at the same time preserve both agrobiodiversity and biodiversity in general.

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4 Box 1. Glossary

Complex system: a set of entities interacting usually in a non-linear manner, that can become auto-organized and exhibit spatiotemporal heterogeneities or patterns [44].

Diversity: at the community level, it is the quantity of species in relation to their abundances in a location [9].

Emergent property: it is a system's property that can only be observed when its parts are interacting, and cannot be understood only from the study or observation of the isolated parts [44].

Matrix: in the context of Agroecology, it is the set of the different types of fragments from a landscape that characterizes a particular region. Even if organisms usually inhabit within one or a few of these particular fragments, populations are often maintained because of the migration dynamics generated between them. In this way, it is important to define and evaluate the quality of a matrix, as this could affect the migration rates of subpopulations and, consequently, their conservation [15].

Non-linear interaction: given a dynamical system, its dynamic is said to be non-linear if the relationship between its subsequent states is not determined by a proportional quantity that remains constant during time, that is, the rate of change is not constant [45].

Productivity: the biomass quantity per unit area that is produced by the organisms of a particular locality [9].

Redundancy: in information theory, it is the property exhibited by a system when two or more of its components are identical and have the same effects over an output of the system. In biological systems, the identity of the components is almost impossible to satisfy, mostly because of the ambiguity that emerges when distinguishing between their structure and function and also because some components may perform differently in different contexts. So degeneracy, the capability of structurally different components to affect an output in a similar way is a complementary concept that accounts for the evaluation of the redundancy in a system [46].

Resilience: the velocity in which a system returns to an equilibrium state after a perturbation, understanding an equilibrium state as in the context of dynamical systems [20].

Robustness: a type of stability that focuses on the response of certain features when a system is perturbed. In ecology, the notion of robustness is useful when thinking about the maintenance of certain properties of a system in the face of species lost [20].

Stability (local and global): local asymptotic stability is the property of a dynamical system to response to perturbations, applied around a small neighborhood of an equilibrium state, making its effect decay during time in an asymptotic way (i.e. observing long term behaviors). Qualitative global stability, is also a characteristic of the way in which a system responds to perturbations, it is qualitative in the way that its analysis is based just on the signs and not on the magnitudes of the interactions, it is global because there are no constraints about the initial conditions (i.e. no small neighborhood around an equilibrium state is required). This last one has been widely used in the ecological network analysis [20].

Tolerance: capacity of biological systems (genotype, population, community) to buffer the negative effects of natural or human induced disturbances on their functioning and performance [8].

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