FONDECYT REGULAR COMPETITION 2012 - 2015

Life cycles, phenology, and the dynamics of ecological networks

Rodrigo Ramos Jiliberto. Centro Nacional del Medio Ambiente. Universidad de Chile.
Pablo Moisset de Espanés. Instituto de Dinámica Celular y Biotecnología. Universidad de Chile.

Abstract

Network ecology has developed actively in recent years. This has been mainly promoted by theoretical advances in complex system theory as well as by the availability of high-quality field records of multispecies assemblages.
The network approach to the study of ecological systems has emerged as a fundamental tool to gain better insights into community functioning and population dynamics, and as a simple way of dealing with complex, many-species systems. A number of fundamental and applied questions have been and are being addressed nowadays with new impetus, inducing a steep progress of the ecological knowledge. A fundamental question, also of direct relevance to environmental management, is what are the structural and functional properties of living systems that allow species persistence through time. Most studies dealing with complex ecological networks (mutualistic networks and food webs mainly) have represented communities by means of static models, and their dynamic properties are derived in an implicit way. More recent studies have incorporated population dynamics and topological dynamics into network models. This has opened new avenues for research. Nevertheless, one of the issues that raise doubts about the biological plausibility of current dynamic models of ecological networks is that such models assume that the species in the network interact uninterruptedly over time. This implies that interacting species have organisms in active states throughout the year, which is most often not the case.
Addressing phenology and life cycles of interacting populations imply considering that interactions among species are turned on and off during the seasonal cycle. Under these considerations, only a subset of interactions are taking place at each time, thus the structure of the network at a given time can be radically different from the abstract, aggregated structure resulting from adding temporary interactions. As a consequence, the effects of incorporating phenological dynamics into the functioning of ecological networks and resulting species persistence could be profound.
In this proposal our goal is to analyze the effects of phenological dynamics associated to life cycle transitions on the long-term species persistence within the two most common classes of ecological networks: mutualistic and trophic networks. We will develop new dynamical models that suit our needs. They will consider stage-structure of populations and time-dependent functions for key biological processes, and we will use numerical methods to analyze their behavior. The topological structure of the networks will be gathered from available field records, and the key time-dependent functions will be parameterized from available empirical data when possible.
Roughly speaking, we expect the long-term dynamics of ecological networks, measured as species persistence, being dependent on the phenological dynamics operating on a seasonal time scale. In mutualistic plant-pollinator networks, we expect that phenological decoupling between flowering and emergence of pollinators

will decrease species persistence. In food webs, we hypothesize that biological cues triggering life cycle transition will lead to an increase in species persistence. Overall, this investigation constitute a step forward in the study of dynamic ecological networks and will allow a deeper understanding of the interplay between environmental forcing in a changing world and of the collective functioning of communities.

Fundamentals

One of the fundamental questions in ecology today is what are the structural and functional properties of living systems that allow species persistence through time. This knowledge could permit projecting the consequences of environmental disruption -either natural or human driven- for biodiversity on earth, mediated by the alteration of those properties. The performance of organisms to the set of physical and chemical conditions to which they are exposed, and the set of resources they have access to are undoubtedly critical for explaining persistence in a given place and time. Likewise, population-level properties such as density-dependent regulation; age, sex or genetic structure together and space occupancy also play a fundamental role in determining the fate of a given species in its habitat. Nevertheless, the nature, magnitude, distribution and dynamics of interactions among the many species that compose an ecological community constitute a source of variation that is being considered more actively than ever due to the recent advent of network thinking into ecology (Ings et al. 2009).

Network ecology, as a branch of community ecology, has exhibited a vigorous development in recent years. This has been promoted by remarkable advances in complex system theory, mainly acquired from the fields of physics and computer science (Albert and Barabási, 2002; Newman, 2003; Guimerà and Amaral, 2005), together with the availability of high quality field records of multispecies assemblages.

Network ecologists see a natural community as a large ensemble of interconnected populations of organisms that have their own impulses, but whose fates are nonetheless strongly dependent on the **collective** functioning of the whole network.

First applications of network theory to ecological systems dealt with the statistical characterization of the structure of such systems, in relation to that of appropriate null models. Since the nineties, network theory has been applied to the analysis of complex ecological interaction networks, both as a testing ground for topological patterns found in other complex networks and as a tool to gain understanding on their structure and functioning. Thus, the analysis of the network structure of ecological systems has emerged as a fundamental approach to gain better insights into community function and population dynamics, and as a simple way of dealing with complex, many-species systems (see Pascual and Dunne, 2006). These applications have dealt primarily with the analysis of food webs, or networks of who-eats-whom (Martinez, 1992; Williams and Martinez, 2000; Montoya and Solé, 2003; Pascual and Dunne, 2006) and later on the analysis of mutualistic plant–pollinator or plant-disperser systems (Jordano, 1987; Memmott, 1999; Bascompte et al., 2003; Jordano et al., 2003; Bascompte and Jordano, 2007) and less significantly spatial dispersion webs (Fortuna et al., 2006). See **Fig. 1** for a graphical representation of the two major types of ecological networks. This approach has allowed addressing basic and applied questions such as the relationship between community complexity and stability (Kondoh 2003, Uchida & Drossel 2007) and the response of whole communities to environmental disturbances such as species loss (Dunne et al., 2002; Memmott et al., 2004; Brose et al., 2005) or habitat deterioration (Fortuna et al., 2006).

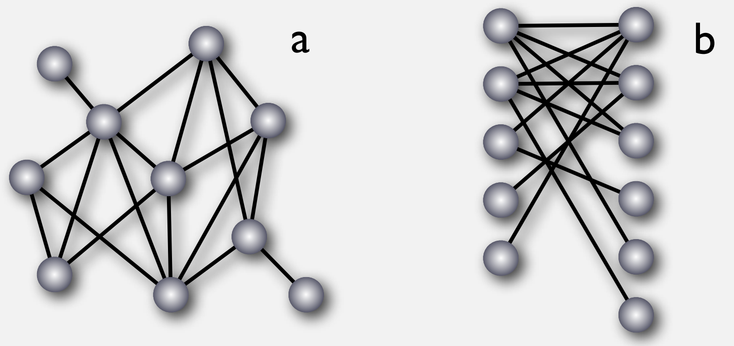

Figure 1: Main types of ecological networks analyzed in the scientific literature. **a)** Unipartite graph representing species interconnected by means of trophic relationships (food web), and **b)** bipartite graph representing a mutualistic web composed by plants connected with their pollinators or seed dispersers.

Static versus dynamic ecological networks

Early studies addressing the community responses to perturbations utilized static models of species interaction networks (Dunne et al., 2002). Static models are simple, require only empirical topological information, and have proved to be useful tools for identifying structural properties associated with the tolerance of trophic (Dunne et al. 2002) and mutualistic (Memmott et al., 2004) networks to community disruption. This research found that the number of interactions in the networks (more specifically their *connectance*) related positively with network robustness (Dunne et al., 2002) and suggested that certain architectural patterns of species interactions such as nestedness (Memmott et al., 2004) and modularity (Olesen et al., 2007) likely confer robustness to primary loss of species.

Nevertheless, dynamic models are an inescapable tool for uncovering processes and outcomes that are impossible to anticipate without their application, mainly due to the many cause-effects relationships (i.e. sign of direct effects between species), the intricate organization of such cause-effects fundamental unities, and the nonlinearities that are manifest in many biological functional relationships. Therefore, a major effort is currently underway to incorporate realistic dynamics into ecological network models (Drossel et al., 2001; Williams and Martinez, 2004; Fortuna and Bascompte, 2006). This approach, nowadays based primarily on the use of dynamic rules for the change in species abundance and the change of trait values related to the magnitude of interspecific interactions, should allow obtaining more accurate projections of population and community dynamics and a better assessment of the risk of species extinctions in front of actual biodiversity threats.

The incorporation of dynamic modeling into ecological networks has revealed that the robustness of communities to external perturbations (i.e. their stability) is enhanced by a variety of biological mechanisms such as implicit (Williams, 2008;

Berlow et al., 2009) or explicit (Kondoh, 2003) adaptiveness of consumption efforts of organisms, by adaptive prey behavior (Kondoh, 2007), larger predator-prey body mass ratios (Brose. et al., 2006), and spatial coupling by large predators (McCann and Rooney, 2009). In addition, the study of dynamic ecological network has shown evidence that the eradication of a few definite species exerts a disproportionate effect on the structure of the community (Ramos-Jiliberto et al., 2009), and particularly that the eradication of exotic plants could impair species coexistence more strongly that the eradication of native species (Valdovinos et al., 2009). More recently, Thébault and Fontaine (2010) using population dynamics into ecological networks found that in mutualistic webs nestedness exerted a stabilizing effect while modularity exerted a destabilizing effect. Surprisingly, the effects were the opposite in food webs of comparable features. These results were partially confirmed by Stouffer and Bascompte (2011) in a recent study that shows a stabilizing effect of compartmentalization in food webs. Overall, network structure and network dynamics emerge as two interdependent factors whose interaction defines the functioning of communities. Dynamics of the populations will produce different outcomes under different structural substrates. Conversely, the structure of an ecological network will depend on which species and interactions persist, features that are themselves an outcome of the dynamics (Gross and Blasius, 2008).

The novelty: Phenology and life cycle transitions

One of the issues that raise doubts about the biological plausibility of current dynamic models of ecological networks is that such models assume that the species in the network interact uninterruptedly over time. This implies that interacting species have organisms in active states throughout the year. Nevertheless, in many instances this is not the case. In seasonally fluctuating environments, ecological interactions usually are realized during a discrete, vegetative, season. During non-vegetative seasons, organisms rest in life cycle stages that are inactive for the interactions of interest. These states can be considered as latent states. Therefore, seasonal succession (phenology) and life cycles are intimately related in many real cases. For example, many aquatic invertebrates exhibit diapause or resting eggs during winter or when the environment turns harsh (Alekseev et al., 2007), while microorganisms such as bacteria and algae form resting stages under similar conditions (Lennon and Jones 2011). These life history strategies could prevent organism, for example, being consumed by predators and thus some trophic interactions are temporary suppressed at these phases. On the other hand, the mutualistic interactions between terrestrial plants and their insect pollinators only take place when plants are flowered and pollinators are in adult phase.

Addressing phenology and life cycles of interacting populations imply considering that interactions among species are turned on and off during the seasonal cycle and not, as usually assumed, that species maintain their interactions continuously through time. As only a subset of interactions are taking place at each time, **the actual structure of the network at any time can be radically different to the abstract, aggregated structure resulting from adding temporary interactions**. See **Fig. 2** for an illustration of this issue. As structure determines dynamics and vice versa (see previous section), introducing externally forced phenological succession into ecological networks will generate a sequence of instantaneous networks with different structure, with their corresponding particular pressures on the dynamics of populations. If phenological phases are relatively brief, then the community system is likely to never reach equilibrium and the dynamics will be constrained to successive transient phases. Thus, the effects of incorporating phenological dynamics on the functioning of ecological networks and resulting species persistence could be profound.

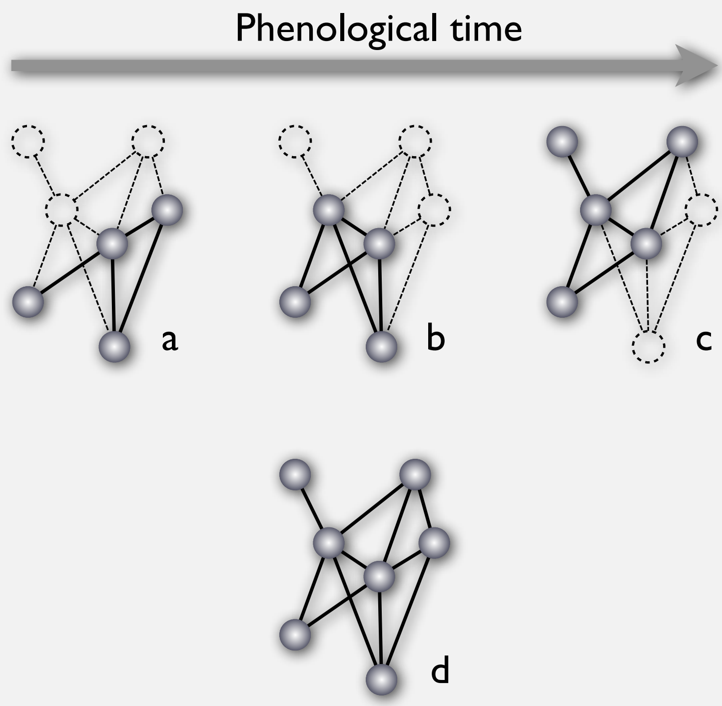

Figure 2: Representation of phenological changes in the structure of an idealized ecological network. Nodes are species and links are interactions. The network states in successive times (snapshots) are depicted in **(a-c)**, where dotted nodes represent latent states present in a given phenological phase and dotted links represent temporary suppressed interactions. Graph **(d)** shows the aggregated annual data, as usually worked out. Note that species richness varies from 4 to 4 and 5 through time **(a, b, c)**, while connectance (interactions/richness^2) is 0.08, 0.10 and 0.12 from **(a)** to **(c)**. In contrast, the aggregated network **(d)** exhibits richness and connectance values of 7 and 0.22 respectively.

At this point it is necessary to introduce an additional concept. In network theory, the temporal evolution of networks involves two different processes: local dynamics, generating dynamics *on* networks, and topological dynamics, (generating dynamics *of* networks (Gross and Blasius, 2008; Newman, 2010). Local dynamics refers to temporal changes in the values associated with network components (nodes and links); in the case of ecological networks normally represented by changes in population abundance (either in numbers or biomass) over time, as well as by changes in the strength of interactions. On the other hand, topological dynamics refers to the temporal variation in node composition and changes in the distribution of connections among nodes. In topological dynamics, the network architecture itself is regarded as a dynamical system whose temporal evolution is governed by specific rules. For ecological networks, topological dynamics consists of changes in species composition and the rewiring of interactions among species. Remarkably, in ecological systems both topological and local dynamics are interdependent processes. Local dynamics may promote topological dynamics through generating extinctions of both species and interactions, and by triggering interaction rewiring when organisms adjust their behavior in response to changes in their trophic environment. Conversely, topological dynamics may influence local dynamics since the variation of species composition and shifts in the pattern of interactions among species may produce changes in population sizes and interaction strengths.

Recent studies have greatly improved our understanding of the functioning of complex ecological networks through incorporating local dynamics, in the form of population dynamics (Williams and Martinez, 2004) and interaction strength flexibility based on adaptive behavior (Kondoh, 2003; 2007). Conversely, little is known about the effects of topological dynamics on the stability and robustness of ecological network. Phenological dynamics produced by environmentally driven life cycle transitions are a widespread mechanisms leading to topological dynamics (or dynamics *of* networks) in nature. To our knowledge, only one single study has considered topological dynamics in mutualistic networks (Kayser-Bunbury et al., (2010) and one more did it for food webs (Staniczenko et al., 2010). Nevertheless, those studies did not include population dynamics but are static in a local sense, which largely restricts their analyses and applicability to different questions. This is the state-of-the-art up to date, which reveals how much research is needed in the field of network dynamics for gaining a comprehensive understanding of the functioning of natural ecological communities.

In this proposal, we will analyze the effect of phenological dynamics, coupled with life-cycle transitions in the species forming part of ecological interaction networks, on the long-term dynamics of complex communities. More specifically, we will address the role of phenological timing of life-cycle transitions on the species persistence in the two most-studied types of ecological networks: mutualistic and food webs. This investigation is a step forward in the study of dynamic ecological networks and will allow a deeper understanding of the interplay between environmental forcing in a changing world and of the collective functioning of communities. We will consider both mutualistic (bipartite) networks and trophic (unipartite) networks (i.e. food webs). We will develop new dynamical models that suit our needs. They will consider stage-structure of populations and time-dependent functions for key biological processes. We developed an approach that avoids the use of delay differential equations, and instead we use systems of non-autonomous integro-differential equations including partial derivatives, and we will use numerical methods to analyze their behavior. The models will be parameterized from empirical data as much as possible. Thus, the topological structure of the networks will be gathered from available field records, and the key time-related functions (flowering, maturation, dormancy transition) will be taken from empirical information, subjected to availability.

Literature cited

Albert, R., Barabási, A.-L., 2002. Statistical mechanics of complex networks. Rev. Mod. Phys. 74, 47-97.

Alekseev, V.R., Destasio, B.T., Gilbert, J., 2007. Diapause in Aquatic Invertebrates. Springer, New York, NY, USA

Bascompte, J., Jordano, P., 2007. Plant-animal mutualistic networks: the architecture of biodiversity. Annu. Rev. Ecol. Evol. Syst. 38, 567–593.

Bascompte, J., Jordano, P., Melian, C.J., Olesen, J.M., 2003. The nested assembly of plant–animal mutualistic networks. PNAS 100, 9383–9387.

Berlow, E.L., Dunne, J.A., Martinez, N.D., Stark, P.B., Williams, R.J. & Brose, U., 2009. Simple prediction of interaction strengths in complex food webs. PNAS 106, 187–191.

Brose, U., Berlow, E.L., Martinez, N.D., 2005. Scaling up keystone effects from simple to complex ecological networks. Ecology Letters 8, 1317–1325.

Brose, U., Williams, R.J. & Martinez, N.D., 2006. Allometric scaling enhances stability in complex food webs. Ecology Letters 9, 1228–1236.

Drossel, B., P. G. Higgs, and A. J. McKane. 2001. The influence of predator-prey population dynamics on the long-term evolution of food web structure. Journal of Theoretical Biology 208, 91-107.

Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecology Letters 5, 558-567.

Fortuna, M. A., and J. Bascompte. 2006. Habitat loss and the structure of plant–animal mutualistic networks. Ecology Letters 9, 281-286.

Fortuna, M.A., Gómez-Rodríguez, C., Bascompte, J., 2006. Spatial network structure and amphibian persistence in stochastic environments. Proc. R. Soc. Lond. B: Biol. Sci. 273, 1429–1434.

Gross, T., and B. Blasius. 2008. Adaptive coevolutionary networks: a review. Journal of the Royal Society Interface 5, 259-271.

Guimerà, R., Amaral, L.A.N., 2005. Cartography of complex networks: modules and universal roles. J. Stat. Mech.-Theory Exp. (art. no. P02001).

Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., van Veen, F.J., Warren, P.H., Woodward, G., 2009. Ecological networks - beyond food webs. J. Anim. Ecol. 78, 253-69.

Jordano, P., 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. American Naturalist 129, 657–677.

Jordano, P., Bascompte, J., Olesen, J.M., 2003. Invariant properties in coevolutionary networks of plant–animal interactions. Ecology Letters 6, 69–81.

Kaiser-Bunbury, C. N., S. Muff, J. Memmott, C. B. Müller, and A. Caflisch. 2010. The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. Ecology Letters 13, 442-452.

Kondoh, M. 2003. Foraging adaptation and the relationship between food-web complexity and stability. Science 299, 1388-1391.

Kondoh, M. 2007. Anti-predator defence and the complexity stability relationship of food webs. Proceedings of the Royal Society B 274, 1617-1624.

Lennon, J.T., Jones, S.E., 2011. Microbial seed banks: the ecological and evolutionary implications of dormancy. Nature Reviews Microbiology 9, 119-130.

Martinez, N.D., 1992. Constant connectance in community food webs. American Naturalist 139, 1208–1218.

McCann, K.S., Rooney, N., 2009. The more food webs change, the more they stay the same. Phil. Trans. R. Soc. B 364, 1789-1801.

Memmott, J., 1999. The structure of a plant–pollinator food web. Ecology Letters 2, 276–280.

Memmott, J., N. Waser, and M. Price. 2004. Tolerance of pollination networks to species extinctions, Proceedings of the Royal Society B 271, 2605-2611.

Montoya, J.M., Solé, R.V., 2003. Topological properties of food webs: from real data to community assembly models. Oikos 102, 614–622

Newman, M.E.J., 2003. The structure and function of complex networks. SIAM Rev. Soc. Ind. Appl. Math. 45, 167-256.

Newman, M.E.J., 2010. Networks. An introduction. Oxford University Press, New York.

Olesen, J.M, Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. PNAS104, 19891–19896.

Pascual, M., Dunne, J.A., 2006. Ecological Networks: Linking Structure to Dynamics *in* Food Webs. Oxford University Press, UK.

Ramos-Jiliberto, R., Albornoz, A.A., Valdovinos, F.S., Smith-Ramírez, C., Arim, M, Armesto, J.J., Marquet P.A., 2009. A network analysis of plant-pollinator interactions in temperate rain forests of Chiloé Island, Chile. Oecologia 160: 697-706.

Staniczenko, P. P. A., O. T. Lewis, N. S. Jones, and F. Reed-Tsochas. 2010. Structural dynamics and robustness of food webs. Ecology Letters 13, 891-899.

Stouffer, D.B., Bascompte, J., 2011. Compartmentalization increases food-web persistence. PNAS 108, 3648-3652.

Thébault E., and C. Fontaine. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. Science 329, 853-856.

Uchida, S., Drossel, B., Brose, U., 2007. The structure of food webs with adaptive behavior. Ecological Modelling 206, 263–276.

Valdovinos F.S., Ramos-Jiliberto, R., Flores, J.D., López, G., Espinoza, C., 2009. Structure and dynamics of pollination networks: the role of alien plants. Oikos 118: 1190-1200.

Williams, R. J., and N. D. Martinez. 2004. Stabilization of chaotic and non-permanent food-web dynamics. European Physical Journal B 38, 297-303

Williams, R.J., 2008. Effects of network and dynamical model structure on species persistence in large model food webs. Theoretical Ecology 1, 1874–1746.

Williams, R.J., Martinez, N.D., 2000. Simple rules yield complex food webs. Nature 404, 180–183