

Evolution and synchronization in ecological networks

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Goal

To investigate how evolution affects synchronization in ecological networks.

Background and motivation

Plant and animal populations seldom live in a single homogeneous area, since landscapes are often spatially fragmented into various patches. Migration between different patches may be considerable, especially when patches are not too distant from one another. Such spatially structured populations are described as metapopulations or as ecological networks, where the nodes of the network graph correspond to patches and the graph's arcs to migration flows. Each node may harbor many species and/or various morphs of the same species. If patches have similar geological and climatic characteristics, also the structure of the populations associated with each node are intrinsically similar.

In a great number of ecological networks with highly diversified geographical extent and taxa, changes in the abundances of the same population in different patches are highly correlated over time. This property, often called population synchrony, has been documented with reference to many taxa, including aphids and butterflies (Hanski and Woiwod 1993, Sutcliffe et al. 1996), moths (Myers 1998), fishes (Ranta et al. 1995a), crabs (Higgins et al. 1997), birds (Ranta et al. 1995b, Cattadori et al. 1995a), voles and mice (Ims and Steen 1990, Bjornstad et al. 1999), hares (Ranta et al. 1995a), squirrels (Ranta et al. 1995a, 1997), lynx (Moran 1953, Elton and Nicholson 1942), sheep (Grenfell et al. 1998) and others (Liebhold et al. 2004).

Synchrony may arise from two independent mechanisms: (a) migration (dispersal) of populations among patches and (b) dependence of all population dynamics on some common environmental noise (rainfall, water temperature, etc.). The latter mechanism is known as the Moran effect (Moran 1953). (A third mechanism that has been sometimes been mentioned under the notion of entrained synchrony, is based on trophic interactions with populations of other species that are themselves synchronous. This, however, implies the operation of one of the two aforementioned mechanisms and therefore appears to be of lesser interest.) Both mechanisms are almost always present together, and this has generated a large debate about their relative importance. For example, with regard to Canadian lynx, only a few authors believe that the Moran effect is the main one responsible for synchronization (Sinclair et al. 1993, Cazelles and Stone 2003), particularly after the discovery (Shwartz et al. 2002) of high gene flow across distances of 3000 km. By contrast, for Dungeness crabs, even though pelagic dispersal of larvae has been ascertained, Higgins et al. (1997) showed based on a stage-structured model that the Moran effect may lead to large fluctuations with multi-year cycles that seem to be locked.

Ecological networks with wild but synchronized local dynamics are so ubiquitous worldwide that one is naturally brought to question whether this might be due to Darwinian evolution. Since this question, introduced in (Rinaldi 2006), is at the moment

addressed only indirectly, and only based on empirical evidence, it is of great interest to analyze it from a theoretical perspective.

Research questions

The main purpose of this project is to examine the role of evolution in synchronizing ecological dynamics, by studying various versions of a simple but generic eco-evolutionary model. More precisely, the target is to show that, in the absence of the Moran effect, adaptive traits evolve in such a way that the ecological network tends toward the edge of synchronization. A first step in this direction has already been taken in (Dercole et al. 2006), addressing a particular case.

Methods and work plan

Ecological dynamics

We consider a network with N patches and assume that all local populations are described on the ecological time scale by the same model,

$$\dot{n}(t) = f(n(t), x) \quad (1)$$

where $n(t) = (n_1(t), \dots, n_m(t))^T$ is an m -dimensional vector of population abundances and x is an adaptive trait that can evolve on the evolutionary time scale. Thus, in the presence of migration, the ecological model of the entire network is a set of mN ordinary differential equations,

$$\dot{n}^{(i)}(t) = f(n^{(i)}(t), x) - \sum_{j=1}^N g_{ij} D(x) n^{(j)}(t) \quad (2)$$

where $n^{(i)}$ is the population vector in patch i , the $N \times N$ matrix $G = (g_{ij})$ characterizes the network's topology (specifically, g_{ii} is the number of patches connected with patch i , while g_{ij} for $i \neq j$ is 0 if i and j are not connected and -1 otherwise), and the $m \times m$ matrix $D(x)$ is a diagonal matrix with diagonal elements $D_k(x)$ equal to zero if the k th population does not disperse, and positive otherwise. For example, in the case of two patches ($N = 2$), three populations ($m = 3$), no migration in the first population, constant dispersal D_2 in the second population and with dispersal D_3 in the third population depending upon the adaptive trait x , we have

$$G = \begin{pmatrix} 1 & -1 \\ -1 & 1 \end{pmatrix} \quad \text{and} \quad D(x) = \begin{pmatrix} 0 & 0 & 0 \\ 0 & D_2 & 0 \\ 0 & 0 & D_3(x) \end{pmatrix}. \quad (3)$$

Detecting synchronization

The conditions under which the network synchronizes, i.e., under which complete synchronization (defined by $n^{(i)}(t) = n^{(j)}(t) \forall (i, j, t)$) is stable, are rather complex because they depend on local dynamics (f), dispersal (D), and topology (G). Using the master function approach (Pecora and Carrol 1998), the problem of synchronization can be analyzed by separating the information concerning network topology (G) from the rest. Through the computation of a suitable Lyapunov exponent depending upon f and D , a region S in the space (p, x) , where p is a positive real number, can be determined and the condition of synchronization becomes

$$(\lambda, x) \in S, \quad (4)$$

where λ is the smallest positive eigenvalue of the matrix G . (For example, in case (3), $\lambda = 2$.) If the point (λ, x) lies on the boundary of S , we say that the network is on the edge of synchronization.

Evolutionary dynamics

Assuming that mutations are small and rare we can, in principle, derive the canonical equation of adaptive dynamics, which is of the form

$$\frac{dx}{d\tau} = F(x) \quad (5)$$

and describes changes of the adaptive trait x over evolutionary time τ . Equation (5) has to be derived from the $(m+1)N$ dimensional resident-mutant model obtained by adding to the mN -dimensional model (2) N mutant equations (one for each patch i) characterized by a trait x' very close to x . However, the full analytical derivation of (5) is practically impossible if the resident-mutant model is chaotic. Thus the evolutionary problem will be addressed through repeated simulations of the resident-mutant model for many pairs (x, x') of the resident and mutant traits. Each simulation will reveal whether or not the mutant population x' replaces the resident population x , thus defining, step by step, the evolutionary trajectory in x , and thus also the evolution of the point (λ, x) in the space (p, x) . It will therefore be possible to see whether or not evolution tends toward the edge of synchronization.

Previous work

The first numerical experiment of this kind (Dercole et al. 2006) has shown that starting from ancestral conditions in the set S (i.e., starting from a synchronized network) the evolutionary trajectory reaches the boundary of S and crosses it just before stopping at an evolutionary equilibrium. Conversely, starting from a definitely asynchronous network (i.e., far from S), evolution drives the network toward synchronization and stops at the same evolutionary equilibrium outside the region S . This first experiment has thus indicated that evolution may lead to synchronization.

Similar issues have been addressed in two previous studies, by Holt and McPeck (1996) and by Doebeli and Ruxton (1997), by considering a simple one-dimensional discrete-time model. These studies concluded that dispersal of asynchronous populations always increases up to the edge of synchronization, while, more realistically, if a cost is associated with an increase in dispersal, evolution stops before the edge of synchronisation is reached (as shown in (Dercole et al. 2006)). A comparison of our approach with (Doebeli and Ruxton 1997) is more difficult, as those authors considered a model that, although looking simple, has a complex bifurcation structure involving multiple attractors.

Work plan

The work plan for this project is to analyze a number of interesting networks using the method of investigation described above. The ecological model will always describe a tritrophic food chain composed of resource (n_1), consumer (n_2), and predator (n_3). The basic model (as characterized by the function f) will be the Rosenzweig-MacArthur model (Rosenzweig and MacArthur 1963), but variants of interest, like tritrophic food chain models with intraspecific competition among consumers, anti-predator behavior, cooperative behavior among predators, will also be considered. As for the adaptive traits, various assumptions will be made, not excluding the case in which the trait impacts dispersal (as in (Holt and McPeck 1996) and (Parvinen 1999)).

Finally, it will also be checked whether or not evolution's synchronization capacity is influenced by unequal dispersal among the considered populations. Other interesting questions concerning, for example, the role played by network dimension and topology, will be considered if time will be available.

Relevance and link to EEP's research plan

Population synchrony is a classical problem in ecology. Understanding whether, and if so how, evolution drives ecological networks toward synchronization is therefore an important problem that targets a topic in the area of interest of EEP. Apart from providing another fundamental application of adaptive dynamics theory, results from this project might eventually also have implications for biological conservation.

Expected output and publications

The results of this study will hopefully give rise to one or more co-authored publications in international scientific journals.

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