SYNCHRONIZATION IN ECOLOGICAL NETWORKS: A BYPRODUCT OF DARWINIAN EVOLUTION?

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The paper considers the evolution of a particular class of networks of identical chaotic oscillators, namely that of ecological networks. In these networks, nodes represent patches where a certain number of plant and animal populations interact on ecological timescale, arcs represent migration flows due to dispersal, and Darwinian evolution is responsible for variations, on a longer evolutionary timescale, of the demographic parameters characterizing the populations. Up to now, this problem has been mainly studied with reference to single-population patches described by one-dimensional discrete-time models and by considering only the dispersal rates of migrating populations as an evolving trait. Here, we propose a method of investigation which allows to study multipopulation patches described by continuous-time models with evolving traits influencing various demographic parameters (including or not dispersal). The method is casted within the frame of the so-called master stability function approach for the analysis of synchronization of coupled systems, and the results obtained in a first and very simple application support the conjecture that evolution drives ecological networks toward weak forms of synchronization.

Keywords: Chaotic dynamics; Darwinian evolution; ecological networks; synchronization.

1. Introduction

Evolution of complex networks is an important scientific problem which has already received a great deal of attention. Topological characteristics of the networks can often be interpreted, and hence predicted, as consequences of specific mechanisms governing technological and/or social evolution (see [Boccaletti *et al.*, 2006] and references therein). A weaker form of evolution occurs when the dynamical systems associated to the nodes of the network evolve, while the structure of the network remains unchanged. This is often the case in biology, the typical example being the islands of an archipelago coupled through bird migration and populated by many species, whose characteristic traits slowly change over time in accordance with Darwinian evolution principles. In this paper, we explore this class of networks and show that evolution can facilitate the emergence of collective dynamics. As for the style of the paper, we have taken the liberty of being somehow naive in the presentation of the model and in the biological interpretation of the results, as well as in the description of the mathematical technicalities. We hope that this will make the paper accessible to a broader class of readers, ranging from theoretical biologists to applied mathematicians.

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Plant and animal population assemblies are rarely present in a single homogeneous area since landscapes are often spatially fragmented in various patches. Migrations between patches is often possible, in particular when they are not too far. Thus, one can properly speak of ecological networks where nodes correspond to patches and arcs to migration flows. The species associated to each node are many and each one of them is composed of one or more populations with individuals characterized by the same values of species-specific traits. Most traits are genetically determined and called adaptive. They slowly evolve through rare and small trait variations (mutations) followed by the natural selection of the best performing variants, thus allowing the species to adapt to their environments. Species composed of one [more] population[s] are said monomorphic [polymorphic]. If the various patches of the network have similar geological and climatological characteristics, also the structure of the population assemblies associated to each node are similar.

In a great number of networks with highly diversified geographical extent and taxa, the change over time of the abundances of distant populations are highly correlated. This property, known in ecology as population synchrony, has been documented for many populations like aphids and butterflies [Hanski & Woiwod, 1993; Sutcliffe *et al.*, 1996], moths [Myers, 1998], fish [Ranta *et al.*, 1995a], crabs [Higgins *et al.*, 1997], birds [Ranta *et al.*, 1995b; Cattadori *et al.*, 1999], voles and mice [Ims & Steen, 1990; Bjørnstad *et al.*, 1999], hares [Ranta *et al.*, 1995a], squirrels [Ranta *et al.*, 1995a; Ranta *et al.*, 1997], lynx [Elton & Nicholson, 1942], sheep [Grenfell *et al.*, 1998], and others [Liebhold *et al.*,
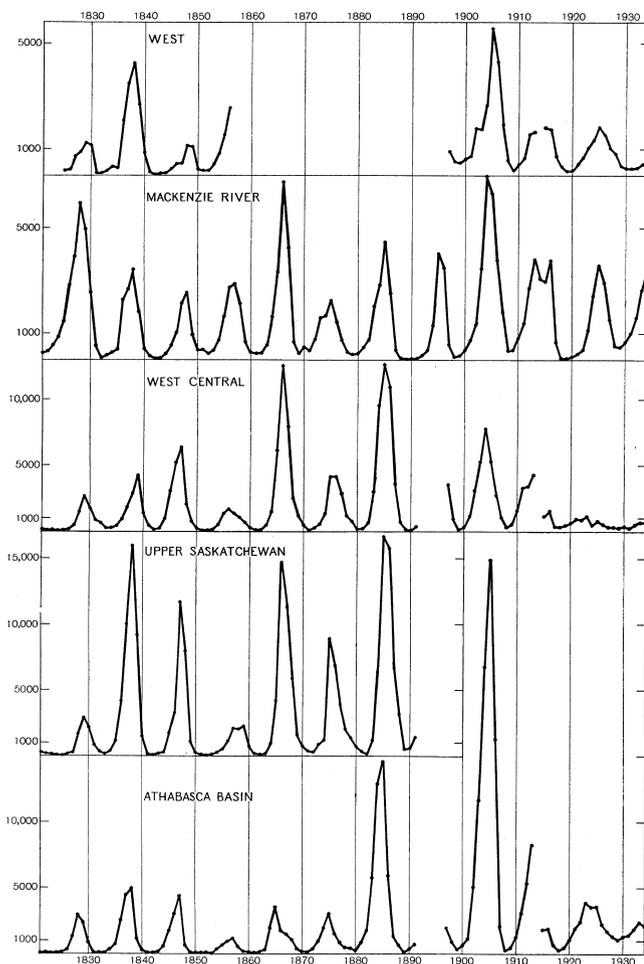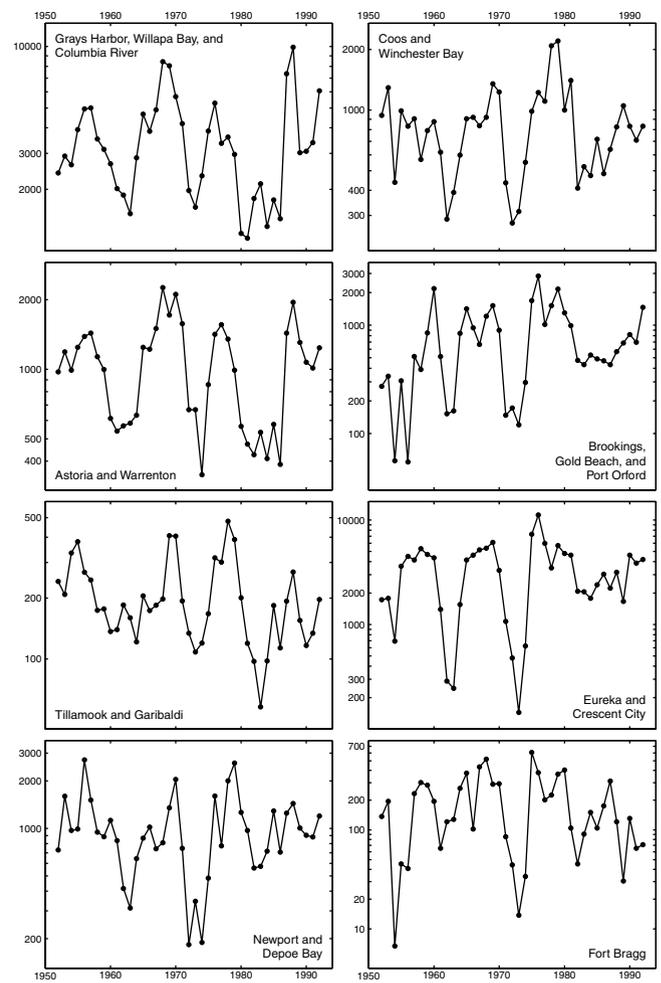
(a)   (b)

Fig. 1.   (a) Lynx fur returns in five regions of Northern Canada (reproduced from [Elton & Nicholson, 1942]). (b) Dungeness crabs catches ($\times 10^3$ Kg) at eight locations of the Pacific coast (reproduced from [Higgins *et al.*, 1997]).

2004]. Figure 1(a) reports the most famous example, namely the yearly fur returns of Canadian lynx in five regions of Northern Canada for more than one century [Elton & Nicholson, 1942], while Fig. 1(b) reports the yearly catches of male Dungeness crabs at eight locations ranging over 1000 km of the Pacific coastline for forty years [Higgins *et al.*, 1997]. Both figures indicate that populations of the same species fluctuate more or less synchronously, even when they are very far.

Synchrony may arise from two independent mechanisms: (a) migration (dispersal) of populations among patches; (b) dependence of populations upon a common fluctuating environmental factor (rainfall, water temperature,...), a mechanism known as Moran effect [Moran, 1953]. These two mechanisms are almost always present, and this has generated a large debate on their relative importance. For example, in the Canadian lynx case, only a few authors [Sinclair *et al.*, 1993; Cazelles & Stone, 2003] believe that the Moran effect is mainly responsible of synchronization, in particular after the discovery of a high gene flow over distances of 3000 km [Schwartz *et al.*, 2002]. By contrast, in the Dungeness crab case, despite pelagic dispersal of larvae has been ascertained, Higgins *et al.* [1997] showed by means of a stage-structured model that the Moran effect alone may lead to large fluctuations with multiyear cycles that seem to be locked.

Ecological networks with wild but synchronized local dynamics, like those shown in Fig. 1, are so many around the world that one is naturally brought to conjecture that this might be a consequence of species evolution. Since this conjecture [Rinaldi, 2006] is at the moment supported more by empirical evidence than by theoretical arguments, it is of great interest to reinforce it through modeling studies. This is exactly what we do in this paper by studying a prototypical eco-evolutionary model which shows that in the absence of the Moran effect the adaptive traits characterizing the populations evolve in such a way that the network tends toward the edge of synchronization. The analysis is carried out by assuming that local dynamics are chaotic in the absence of migration and that offspring inherit parental values of their characteristic adaptive traits, with possible rare and small mutations. Previous modeling studies on the evolution of ecological networks are focused on the evolution of the dispersal rates of migrating populations and often describe the local

communities with simple one-dimensional discrete-time models or through individual-based simulations [Levin *et al.*, 1984; McPeek & Holt, 1996; Holt & McPeek, 1996; Doebeli & Ruxton, 1997; Holt, 1997; Travis & Dytham, 1998; Johst *et al.*, 1999; Parvinen, 1999; Harrison *et al.*, 2001; Mathias *et al.*, 2001; Kisdi, 2002; Murrell *et al.*, 2002; Parvinen, 2006] (see [Parvinen, 2002; Parvinen *et al.*, 2003] for continuous-time models). Discrete-time models easily yield asynchronous stationary dynamics (under which evolution disfavors dispersal [Hastings, 1983]) and alternative asynchronous non-stationary (cyclic or chaotic) attractors (see in particular [Holt & McPeek, 1996; Doebeli & Ruxton, 1997] for cases of nonstationary dynamics in the absence of Moran effect). Here, we propose a general framework for the study of evolution of any adaptive trait, with possible effects on dispersal as well as on other demographic parameters, by considering a biologically more credible continuous-time model (a tritrophic food chain model) and by analyzing synchronization in detail by means of the so-called master stability function approach [Pecora & Carrol, 1998; Boccaletti *et al.*, 2006]. Our findings are particularly in line with [Holt & McPeek, 1996].

The paper is organized as follows. In the next section we describe a general eco-evolutionary network model and outline a method of analysis. Then, in the third section we apply the method to a particularly simple network (two patches, three populations, only one dispersing population) and show that the obtained results indeed support the conjecture that evolution simplifies global behavior by enhancing the emergence of collective population dynamics. Finally, in the last section, we focus on the value as well as on the limitations of our findings and suggest studies which could further support the conjecture.

2. Model and Methods

2.1. *Ecological dynamics*

Consider an ecological network with N patches and assume that m populations with densities $n_1, n_2, \ldots, n_m$ characterized by various adaptive traits are present in each patch. A typical example is that of plants-herbivores-carnivores food chains leaving in well identified and homogeneous regions separated by natural or artificial barriers (e.g. rivers, mountains, motorways,...).

In real ecological networks the demographic parameters of the various populations slightly differ

from patch to patch, due to small differences in geological and climatological conditions. This spatial dependence precludes complete synchronization of the network, a property which is very important for developing simple theories and to obtain transparent results [Boccaletti *et al.*, 2006]. For this reason, we assume that local population dynamics are the same in all patches, i.e. that all demographic parameters are spatially independent. In other words, we assume that in the absence of migration all local population assemblies are described, on ecological time t, by the same m differential equations (ODE's)

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

where x is the vector of adaptive traits, which is constant on ecological timescale, but varies on a longer evolutionary timescale, as specified below.

In the presence of migration the ecological model of the entire network is a set of mN ODE's

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

where $n^{(i)}$ is the vector of population densities in patch i, the $N \times N$ matrix $G = [g_{ij}]$ identifies the network topology (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), the $m \times m$ diagonal matrix $D = [D_k]$ specifies the migration flows (D_k is the dispersal rate of population k, which is zero if population k does not migrate, while it is positive and possibly trait-dependent otherwise), and ϵ is a positive control parameter that scales dispersal in all migrating populations (when the discussion with respect to this factor is not of interest ϵ can be simply set to one). For example, in the case of two patches ($N = 2$), three populations ($m = 3$) and migration only in the third population, we have

$$G = \begin{bmatrix} 1 & -1 \\ -1 & 1 \end{bmatrix}, \quad D(x) = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & D_3(x) \end{bmatrix}. \quad (3)$$

In the following model (2) is called resident model because it describes the ecological dynamics of all populations in the absence of mutations.

The conditions under which the network is synchronized, i.e. the conditions under which complete synchronization ($n^{(i)}(t) = n^{(j)}(t)$ for all i, j and t) is stable, are rather complex because they depend upon local dynamics (f), dispersal (ϵD),

and network topology (G). Using the master stability function approach [Pecora & Carrol, 1998; Boccaletti *et al.*, 2006] the problem of synchronization can be effectively discussed by separating the information concerning network topology from the rest. More precisely, consider the largest Lyapunov exponent $L(p, x)$ of the m-dimensional linear time-varying system

$$\dot{z}(t) = \left[\left. \frac{\partial}{\partial n} f(n, x) \right|_{n=n(t)} - pD(x) \right] z(t), \qquad (4)$$

where $n(t)$ is a solution of (1) for a generic initial condition and p is a non-negative control parameter, and define the region

$$S = \{(p, x) : L(p, x) \leq 0\} \qquad (5)$$

in the two-dimensional space (p, x). Notice that $L(0, x)$ is the largest Lyapunov exponent of system (1) which is assumed to be chaotic. Hence, $L(0, x) > 0$ so that $L(p, x)$ can become negative for suitably large values of p (this is guaranteed if $D(x) = I$ because in this case $L(p, x) = L(0, x) - p$). Then, the master stability function approach implies that the network is synchronized if

$$(\epsilon \lambda_i, x) \in S, \quad i = 2, \ldots, m, \qquad (6)$$

where the λ_i's are the positive eigenvalues of G (notice that $\lambda_1 = 0$ because G is zero-row-sum and that, if the network is connected, $\lambda_i > 0$, $i = 2, \ldots, m$, because G is symmetric and with non-positive off-diagonal entries). For this reason region S is called synchronization region. If the network cannot be desynchronized by increasing dispersal (i.e. by increasing ϵ), then the synchronization condition (6), which involves the $(m-1)$ points $(\epsilon \lambda_i, x)$, $i = 2, \ldots, m$, reduces to

$$(\epsilon \lambda, x) \in S, \qquad (7)$$

where λ is the smallest positive eigenvalue of G (for example, $\lambda = 2$ in case (3)).

If condition (7) is satisfied with $(\epsilon \lambda, x)$ on the boundary of S, we say that the network is on the edge of synchronization. By contrast, if point $(\epsilon \lambda, x)$ lies slightly outside S, there are only symptoms of synchronization which for special network topologies are revealed by interesting spatio-temporal patterns. Such phenomena, detectable through a thorough bifurcation analysis of model (2) in the presynchronization region ($(\epsilon \lambda, x)$ outside but close to the boundary of S), will not be presented here.

2.2. *Evolutionary dynamics*

From time to time, a mutation occurs in one of the populations, say in population m, i.e. a few individuals of population m with different characteristic trait (x' instead of x) appear in one of the patches, say in patch i. Thus, from that point on there are $(m + 1)$ populations in patch i: the $(m - 1)$ resident populations $n_1^{(i)}, \ldots, n_{m-1}^{(i)}$, the resident population $n_m^{(i)}$ with trait x, and the mutant population $n_m'^{(i)}$ (initially very scarce) with trait x'. If mutant populations migrate and the network is connected, after a short time mutant individuals are present in all patches where they interact with local resident individuals. In other words, after the appearance of a small amount of mutants somewhere in the network the ecological dynamics of all populations are described by a so-called resident-mutant model composed of $(m + 1)N$ ODE's (an example of this type of models is discussed in the next section).

In agreement with general results of competition theory [Geritz *et al.*, 2002; Geritz, 2005; Dercole & Rinaldi, 2007], if the mutant and resident populations are very similar (i.e. if x and x' are very close), then generically only one of the two populations $n_m^{(i)}$ and $n_m'^{(i)}$ persists while the other goes extinct (of course this is true if no new mutations occur in the meantime, i.e. if mutations are rare on ecological timescale). If the mutant population goes extinct, then nothing changes in the end, since the trait value characterizing the mth population is still x. By contrast, if the mutant population is competitively superior, it remains in the game and the resident population is ruled out. In such a case, the final consequence is the substitution of the trait value x with x'. In other words, the trait evolves through very small steps ($x \to x'$) which are taken very rarely on the ecological timescale and thus trace an evolutionary trajectory on a longer evolutionary timescale.

2.3. *Methods of analysis*

In principle one could pretend to obtain the evolutionary trajectory by solving the so-called Adaptive Dynamics canonical equation [Dieckmann & Law, 1996], which in the present case is a first-order ODE of the form

$$\frac{d}{d\tau}x(\tau) = F(x(\tau)), \qquad (8)$$

where τ spans the evolutionary timescale. However, the analytical derivation of function F in (8), is

practically impossible when the dynamics over ecological time t (i.e. for frozen values of the adaptive trait) of the resident model (2) are chaotic. We are therefore forced to solve the problem through repeated simulations of the resident-mutant model which reveal the sign of $F(x)$. In practice, we can proceed as follows.

(i) *Simulation of the resident populations before the mutation.* Fix x and simulate the resident model (2). Then, when system (2) is on its strange attractor, stop the simulation at a random time t_{mut}, called time of mutation.

(ii) *Simulation of mutation.* Maintaining the resident populations at the previously established values, simulate a small mutation by selecting at random a patch i and a value x' close to x and by assigning to the mutant population in patch i a randomly generated small positive value $n_m'^{(i)}(t_{\text{mut}})$.

(iii) *Simulation of resident-mutant competition.* Simulate the resident-mutant model for a long time starting at $t = t_{\text{mut}}$ with the above established parameters and initial conditions.

With the exception of pathological cases, step (iii) has two possible outcomes:

1. all populations but the resident populations $n_m^{(j)}$, $j = 1, \ldots, N$, persist;
2. all populations but the mutant populations $n_m'^{(j)}$, $j = 1, \ldots, N$, persist.

If the above outcomes are robust with respect to the (randomly selected) time and amplitude of mutation, then one can say that in case n.1 [2] the mutation $x \to x'$ is at evolutionary advantage [disadvantage]. In other words, the process of mutation and the resident-mutant competition (i.e. Darwin's natural selection), fix unambiguously the sign of function F in (8), namely the direction of evolution (for example, if $x' > x$ and the outcome of (iii) is n.1, then $F(x) > 0$ and x increases).

In conclusion, through a huge number of well organized simulations one can detect the sign of F in (8) and hence obtain an evolutionary trajectory. Plotted in space (p, x), evolutionary trajectories are represented by straight vertical lines with $p = \epsilon\lambda$, so that one can easily check if evolution is driving the network toward synchronization or not. The typical result of this analysis (confirmed by the particular application described in the next section) is that the

trait converges toward a particular value $\overline{x}$ because

$$F(x) \begin{cases} > 0, & \text{for } x < \overline{x}, \\ < 0, & \text{for } x > \overline{x}. \end{cases}$$

For this reason, the value $\overline{x}$ of the adaptive trait is called evolutionary equilibrium and the conjecture is supported if point $(\epsilon\lambda, \overline{x})$ is close to the boundary of S.

Finally, it is worth mentioning that for pairs (x, x') very close to $(\overline{x}, \overline{x})$ one could obtain simulation scenarios where all populations persist. This means that two very similar populations can coexist close to the equilibrium $\overline{x}$. This is a necessary (but not sufficient) condition for a monomorphic species to turn polymorphic (so-called evolutionary branching [Geritz *et al.*, 1997, 1998]), a phenomenon which is very important in view of explaining the emergence of population diversity in ecological networks. Evolutionary branching in the evolution of dispersal has been observed in some of the above mentioned studies performed on discrete-time models [McPeek & Holt, 1996; Holt & McPeek, 1996; Doebeli & Ruxton, 1997; Parvinen, 1999], but will not be investigated here.

3. Application

We now apply the method described in the previous section to an ecological network in which each patch is populated by a tritrophic food chain composed of resource (n_1), consumer (n_2), and predator (n_3). The model we consider (see Eq. (1)) is the most commonly used tritrophic food chain model [Rosenzweig & MacArthur, 1963], namely

$$\dot{n}_1 = rn_1 \left(1 - \frac{n_1}{K} \right) - \frac{a_2 n_1}{b_2 + n_1} n_2, \tag{9a}$$

$$\dot{n}_2 = e_2 \frac{a_2 n_1}{b_2 + n_1} n_2 - d_2 n_2 - \frac{a_3 n_2}{b_3 + n_2} n_3, \tag{9b}$$

$$\dot{n}_3 = e_3 \frac{a_3 n_2}{b_3 + n_2} n_3 - d_3 n_3, \tag{9c}$$

where r and K are the net growth rate (per-capita) and carrying capacity of the resource and a_2, b_2, e_2, d_2 [a_3, b_3, e_3, d_3] are maximum predation rate, half saturation constant, efficiency and death rate (per-capita) of consumer [predator]. This model fits our purposes because it can be chaotic in wide regions of parameter space [Hastings & Powell, 1991; Kuznetsov *et al.*, 2001]. We assume that mutations can occur only in the predator population and that the adaptive trait impacts on efficiency e_3 and dispersal D_3 (i.e. $e_3 = e_3(x)$ and

$D_3 = D_3(x)$). Since an increase in dispersal is a potential advantage for the mutant [Holt & McPeek, 1996], in order to avoid biologically trivial cases we assume that D_3 increases with x, while e_3 decreases. More precisely, we identify D with the trait x and fix the trait-dependence of e_3 as follows

$$e_3(x) = \frac{e_{30} + e_3^\infty e_{31} x}{1 + e_{31} x}, \tag{10}$$

where e_{30} is the value of e_3 in the absence of migration ($x = 0$), $e_3^\infty < e_{30}$ is the asymptotic value of e_3 corresponding to very high dispersal (for given values of all other parameters, we set e_3^∞ to the value of e_3 at which model (9) ceases to be chaotic), while e_{31} controls the slope of function (10).

In order to keep the computational burden under control, we limit the analysis to networks composed of two patches ($N = 2$), so that the matrices G and D appearing in the resident model (2) are given by (3). The resident-mutant model, written for $\epsilon = 1$, is therefore given by the following eight ODE's

$$\dot{n}_1^{(1)} = rn_1^{(1)} \left(1 - \frac{n_1^{(1)}}{K} \right) - \frac{a_2 n_1^{(1)}}{b_2 + n_1^{(1)}} n_2^{(1)}, \tag{11a}$$

$$\dot{n}_2^{(1)} = e_2 \frac{a_2 n_1^{(1)}}{b_2 + n_1^{(1)}} n_2^{(1)} - d_2 n_2^{(1)}$$
$$- \frac{a_3 n_2^{(1)}}{b_3 + n_2^{(1)}} (n_3^{(1)} + n_3'^{(1)}), \tag{11b}$$

$$\dot{n}_3^{(1)} = e_3(x) \frac{a_3 n_2^{(1)}}{b_3 + n_2^{(1)}} n_3^{(1)} - d_3 n_3^{(1)}$$
$$- x(n_3^{(1)} - n_3^{(2)}), \tag{11c}$$

$$\dot{n}_3'^{(1)} = e_3(x') \frac{a_3 n_2^{(1)}}{b_3 + n_2^{(1)}} n_3'^{(1)} - d_3 n_3'^{(1)}$$
$$- x'(n_3'^{(1)} - n_3'^{(2)}), \tag{11d}$$

$$\dot{n}_1^{(2)} = rn_1^{(2)} \left(1 - \frac{n_1^{(2)}}{K} \right) - \frac{a_2 n_1^{(2)}}{b_2 + n_1^{(2)}} n_2^{(2)}, \tag{11e}$$

$$\dot{n}_2^{(2)} = e_2 \frac{a_2 n_1^{(2)}}{b_2 + n_1^{(2)}} n_2^{(2)} - d_2 n_2^{(2)}$$
$$- \frac{a_3 n_2^{(2)}}{b_3 + n_2^{(2)}} (n_3^{(2)} + n_3'^{(2)}), \tag{11f}$$

$$\dot{n}_3^{(2)} = e_3(x)\frac{a_3 n_2^{(2)}}{b_3 + n_2^{(2)}}n_3^{(2)} - d_3 n_3^{(2)}$$

$$- x(n_3^{(2)} - n_3^{(1)}), \tag{11g}$$

$$\dot{n}_3'^{(2)} = e_3(x')\frac{a_3 n_2^{(2)}}{b_3 + n_2^{(2)}}n_3'^{(2)} - d_3 n_3'^{(2)}$$

$$- x'(n_3'^{(2)} - n_3'^{(1)}), \tag{11h}$$

where the trait values x and x' are the dispersals of the resident and mutant populations, respectively. The resident model (see Eq. (2)) can be immediately obtained from (11) by disregarding the two mutant equations and by annihilating the densities $n_3'^{(1)}$ and $n_3'^{(2)}$ of the mutant populations. Thus, the Lyapunov exponent $L(p,x)$ of system (4) can be computed on a grid of the space (p,x) and the synchronization region S (see Eq. (5)) can be obtained numerically (all computations of Lyapunov exponents have been performed with the so-called standard algorithm based on Gram–Schmidt orthonormalization [Ramasubramanian & Sriram, 2000] with adaptive time steps and convergence criterion).

The result is shown in Fig. 2 for the parameter values indicated in the caption. The most interesting property of region S (shaded region in the figure) is that it is unbounded in the p direction, so that Eq. (7) can be used to test if the network is synchronized. Reading Fig. 2 at $p = 2$ (recall that $\lambda = 2$ and $\epsilon = 1$ in (7)) we obtain the synchronization threshold x^*, which turns out to be $x^* = 0.01002\ldots$ The correlation between the predators of the two patches in the presynchronization region ($x < x^*$) is shown in Figs. 3(a)–3(c) for different values of x, while Fig. 3(d) shows a case of complete synchronization ($x > x^*$). As expected, the correlation increases with x and tends to one for x approaching x^*. Of course, different parameter settings give rise to different values of the threshold x^* and different correlations in the presynchronization region, which however are always increasing with x.

Now we apply the three-steps procedure outlined in the previous section. The typical simulation scenario obtained with

$$x^* < x' < x, \tag{12}$$

is shown in Fig. 4. Before the time t_{mut} at which the mutants are injected into the system, the two predator resident populations are equally abundant because the system is synchronized (x being larger
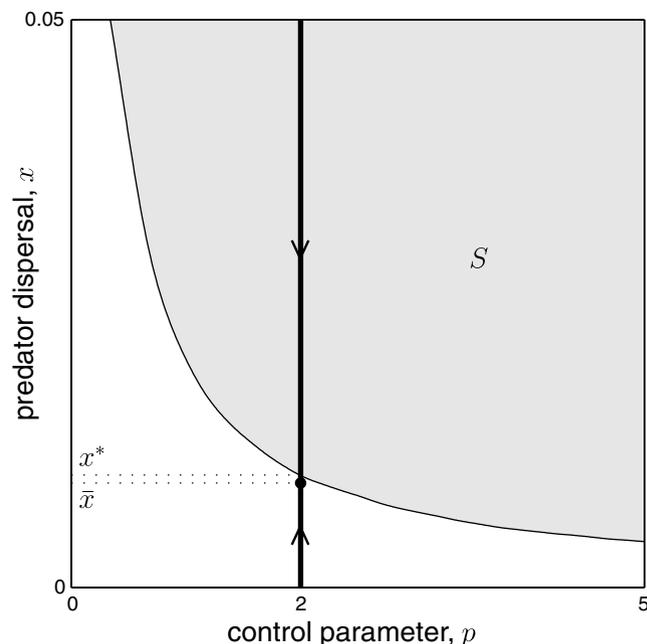

Fig. 2. The synchronization region S (shaded region) and the evolutionary trajectory (thick line with $p = 2$). Evolutionary equilibrium: $\overline{x} = 0.00961\ldots$ (see Fig. 3(c) for the corresponding predator correlation in the two patches); synchronization threshold $x^* = 0.01002\ldots$ Parameter values: $r = 1.2$, $K = 1.1$, $a_2 = 5$, $a_3 = 0.1$, $h_2 = 0.6$, $h_3 = 20$, $d_2 = 0.4$, $d_3 = 0.01$, $e_2 = 1$, $e_{30} = 1$, $e_{31} = 0.1$, $e_3^\infty = 0.8118$.

than x^*). After the mutation (i.e. for $t > t_{\mathrm{mut}}$) the mutant populations have a positive trend, while the resident populations decline. More precisely, in the long run the mutants substitute the residents. The same kind of scenario (outcome n.1) has been obtained for all close by values of x and x' satisfying inequality (12) and for all time t_{mut} and mutant initial conditions ($n_3'^{(1)}(t_{\mathrm{mut}})$ or $n_3'^{(2)}(t_{\mathrm{mut}})$). This means that above the synchronization threshold mutations decreasing the tendency to migrate of the predator are at evolutionary advantage. In other words, if for some reason an ecological network is synchronized, evolution tries to desynchronize it. As discussed in [Holt & McPeek, 1996] this result is intuitively obvious. In fact, the decrease of dispersal from x to x' does not imply any penalty for the mutants since dispersing and nondispersing individuals are in any case facing the same biological and physical environment, while the corresponding increase of efficiency from $e_3(x)$ to $e_3(x')$ gives an advantage to mutant individuals in terms of growth rate.

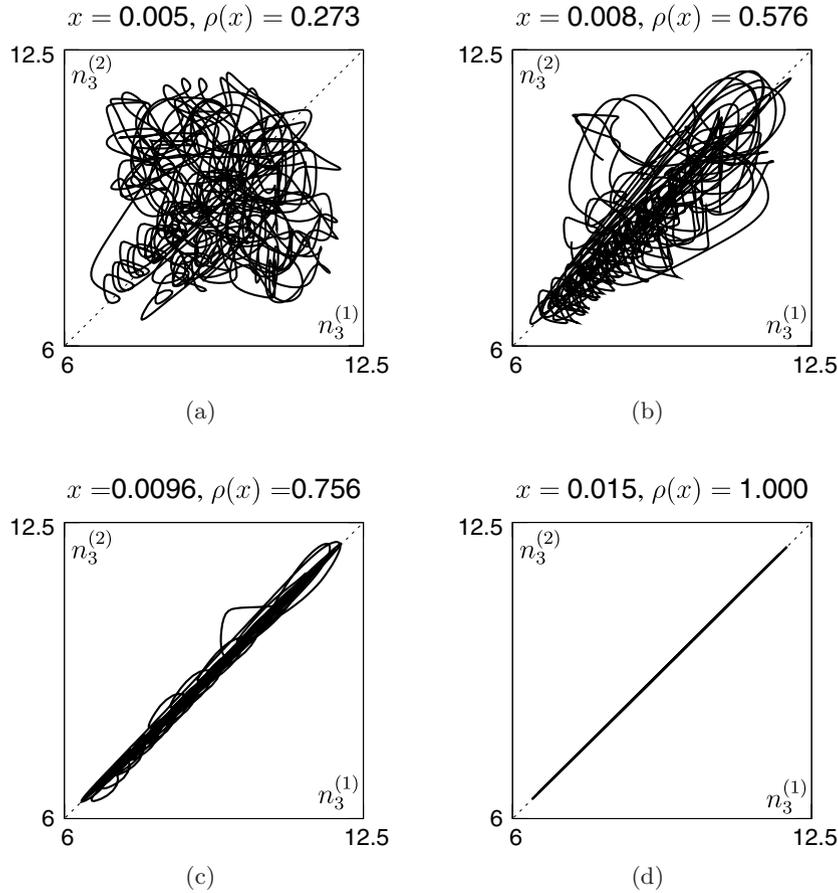The same kind of substitution is obtained for

$$x < x' < x^*, \tag{13}$$

Fig. 3. Correlation between the predator populations $n_3^{(1)}$ and $n_3^{(2)}$ in the two patches in the absence of mutants. Panels (a)–(d) show the attractor projection in the plane $(n_3^{(1)}, n_3^{(2)})$ for different values of the adaptive trait x ((a)–(c) in the presynchronization region $(x < x^*)$, (d) in the synchronization region $(x > x^*)$) and report the corresponding values of the correlation index $\rho(x)$. Complete synchronization $(\rho(x) = 1)$ is represented by the diagonal of the plane $(n_3^{(1)}, n_3^{(2)})$ (dotted line). Parameter values as in Fig. 2.
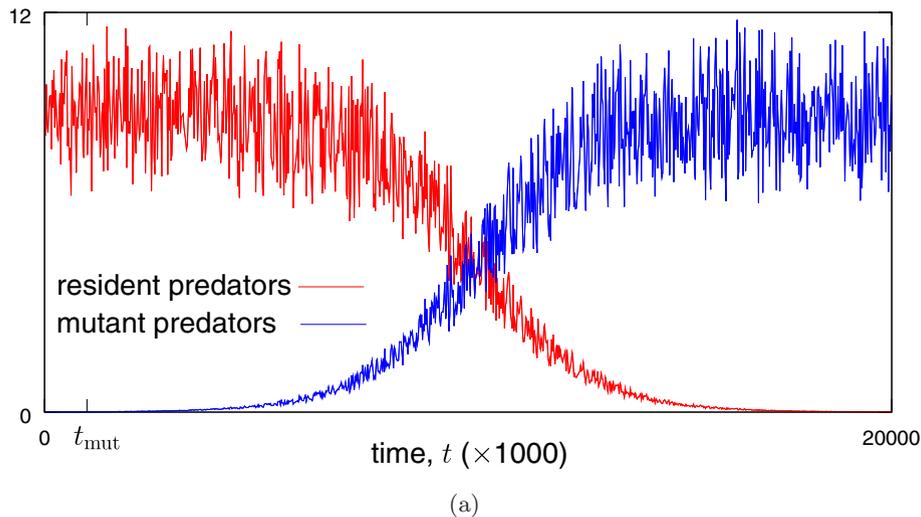

Fig. 4. Typical simulation scenario for $x^* < x' < x$. The two mutant (less dispersive) predator populations (in blue) are at evolutionary advantage and substitute the resident (more dispersive) predator populations (in red). Panels (a) and (c) show that the resident and mutant predator populations are synchronous before the mutation (panel (a)) and after the substitution (panel (c)). Panel (b) shows that the mutation occurs in patch 1 and that the mutant populations quickly synchronize. Adaptive traits: $x = 0.015$, $x' = 0.011$. Parameter values as in Fig. 2.
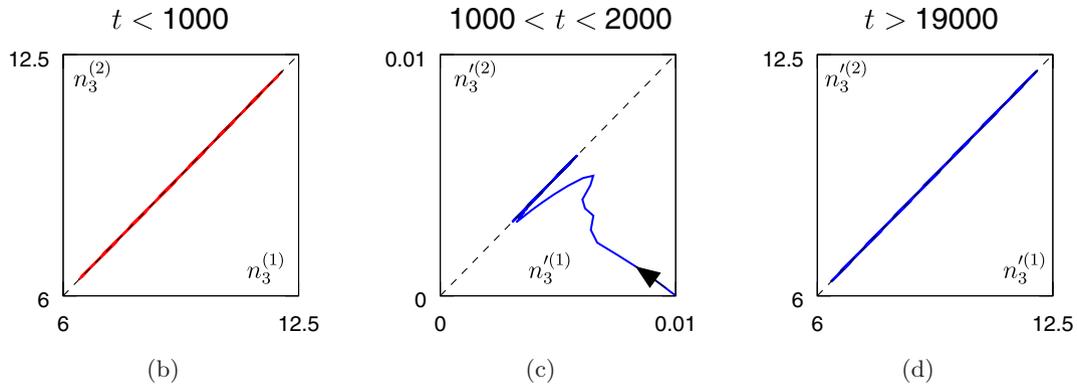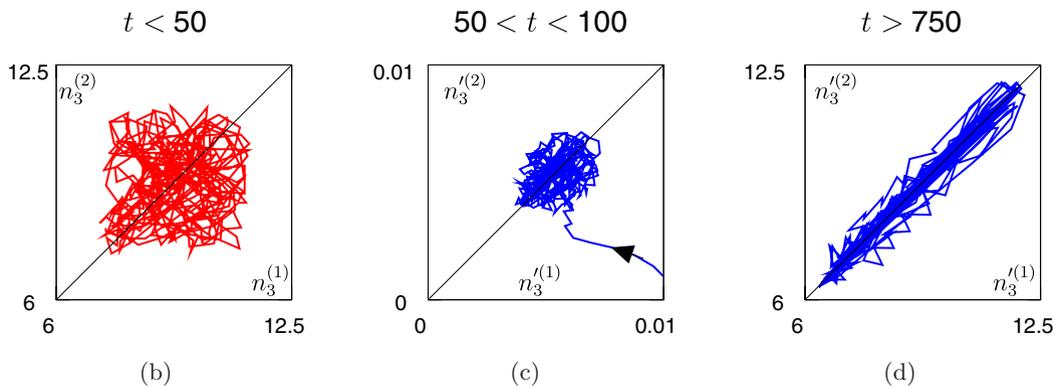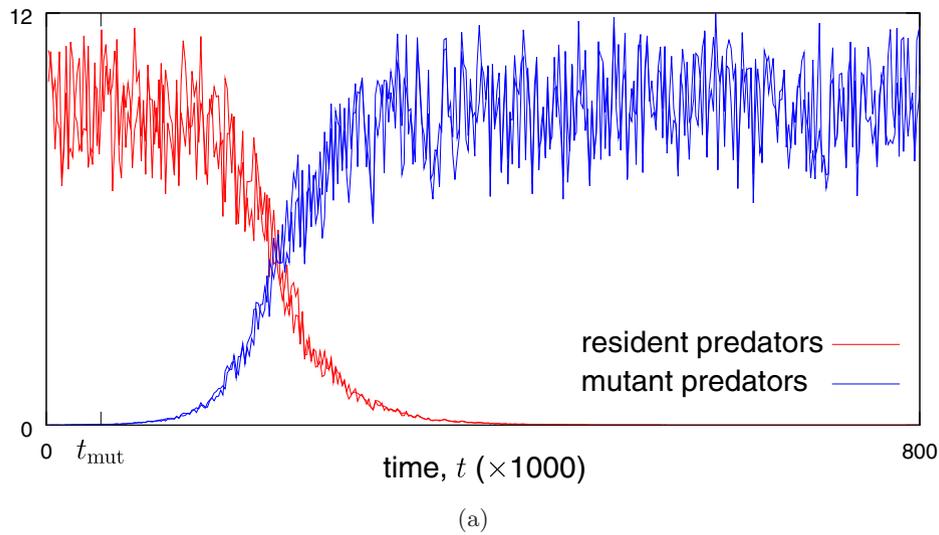
Fig. 4. (*Continued*)

Fig. 5. Typical simulation scenario for $x < x' < x^*$. The two mutant (more dispersive) predator populations (in blue) are at evolutionary advantage and substitute the resident (less dispersive) predator populations (in red). Panels (a) and (c) show that the resident and mutant predator populations are asynchronous before the mutation (panel (a)) and after the substitution (panel (c)). Panel (b) shows that the mutation occurs in patch 1 and that the mutant populations remain asynchronous. Adaptive traits $x = 0.004$, $x' = 0.008$. Parameter values as in Fig. 2.

when x and x' are not too close to x^* (see Fig. 5). Again the result is independent upon the time of mutation and initial densities of the mutant populations, provided x and x' are sufficiently close. This

means that when the network is not synchronized, mutant populations with higher dispersal can be at evolutionary advantage, even though they have a reduced efficiency. However, when inequality (13) is
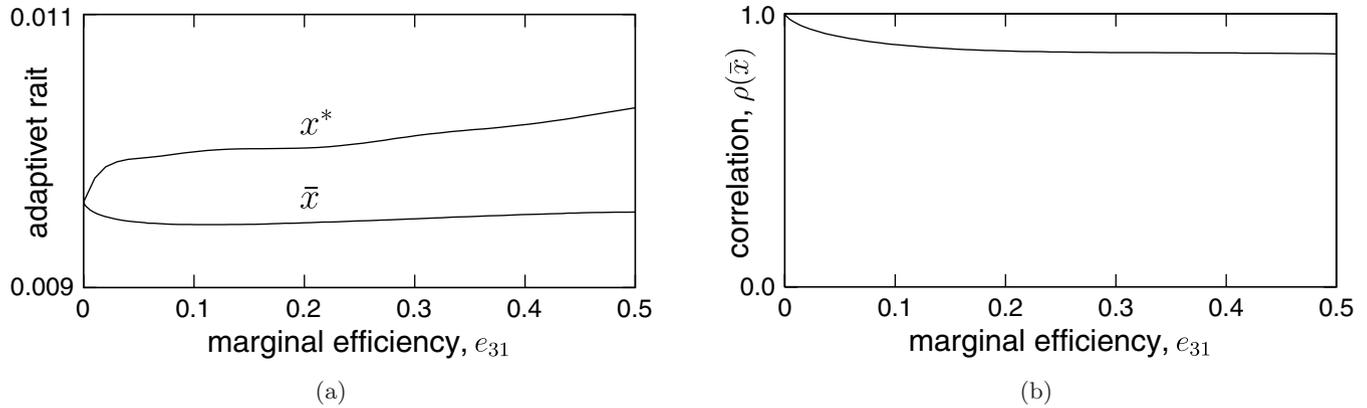
Fig. 6. Influence of marginal efficiencies e_{31} on evolutionary equilibrium $\overline{x}$ and synchronization threshold x^* (a) and on predator correlation $\rho(\overline{x})$ in the two patches at evolutionary equilibrium (b).

satisfied with x and x' close to x^*, it can also happen that the mutant populations do not survive in the long run (outcome n.2). Also this result can be justified intuitively. In fact, if x and x' in (13) are close to x^*, the populations are highly correlated, though they are not completely synchronized, so that any individual after migration is facing almost the same biological and physical environment than before migration. This implies that the advantages due to migration are modest while the disadvantages due to the drop of efficiency can be more conspicuous.

By repeating the above simulations for many different pairs (x, x') we have obtained the evolutionary trajectory (straight vertical line in Fig. 2) and an accurate estimate of the evolutionary equilibrium $\overline{x}$. Figure 2 clearly points out that the evolutionary equilibrium is close to the edge of synchronization. In other words, evolution has the power to desynchronize synchronous ecological networks (upper segment of the trajectory ending at $x = \overline{x}$), but at the same time it has the power of driving asynchronous networks toward the edge of synchronization (lower segment of the trajectory). This result, which is fully justifiable on a purely intuitive basis, is more precise than that of [Holt & McPeek, 1996] who erroneously concluded that higher dispersals are always at evolutionary advantage if local ecological dynamics are chaotic and asynchronous. At the same time, our result is also more transparent than that of [Doebeli & Ruxton, 1997] who found sophisticated evolutionary dynamics of dispersal by relying, however, on a resident model with a rather complex bifurcation structure involving coexisting synchronous and asynchronous attractors.

How close the evolutionary equilibrium $\overline{x}$ is to the synchronization threshold x^* and how correlated the predator populations are at the evolutionary equilibrium, obviously has to do with how severe is the drop in efficiency caused by increasing dispersal. This is controlled by the parameter e_{31} in Eq. (10), which measures marginal efficiency. Figure 6 summarizes the results obtained by repeating all the above numerical experiments for different marginal efficiencies.

4. Conclusions

A particular but important class of evolving networks, namely ecological networks, has been analyzed in this paper. In such networks nodes represent patches where a certain number of plant and animal populations dynamically interact and arcs represent migration flows due to dispersal. Within this context there are, in general, two separated timescales of interest dealing, respectively, with ecology (fast dynamics) and evolution (slow dynamics). Observations on ecological timescale reveal that a great number of networks around the world have rather wild local dynamics which are, however, at least weakly synchronized. It is therefore quite natural to conjecture [Rinaldi, 2006] that these two properties are a long-term byproduct of evolution.

In this paper we have given a formal support to the above conjecture by studying the evolution of a very simple network with only two nodes and a tritrophic food chain composed of resource, consumer, and predator populations associated to each node. The model is more complex and realistic than previously considered models [Holt &

McPeek, 1996; Doebeli & Ruxton, 1997]. Following a standard approach which is justified when mutations are small and rare, and restricting the analysis to the case in which only the predator population can mutate, we have shown through a huge number of suitably organized simulations that evolution is responsible for very slow trends in demographic and dispersal parameters which drive the network toward weak forms of synchronization. In other words, given that local ecological dynamics are chaotic (first part of the conjecture), it looks like evolution is indeed capable of slowly modifying the demographies in such a way that weak forms of collective dynamics emerge (second part of the conjecture).

The merit of this paper is to have shown that it is possible to support a fascinating conjecture concerning the role of Darwinian evolution through a formal approach melting together for the first time the theory of Adaptive Dynamics [Dieckmann & Law, 1996; Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998] (see also [Dercole & Rinaldi, 2007]) and the theory of network synchronization [Pecora & Carrol, 1998; Pikovsky *et al.*, 2001; Boccaletti *et al.*, 2006]. However, the specific application discussed in this paper is extremely simplified with respect to reality, so that other studies of the same kind are needed to further support the conjecture. First of all, one could check if the obtained results remain valid for more realistic models taking into account phenomena like predator cooperation, antipredator behavior, predator harvesting, as well as others. This seems to be possible by applying the same general method of analysis proposed in this paper. Conceptually more difficult would be variants concerning migration flows depending upon the abundances of prey or predators of the dispersing population (active dispersal). Also the extension to networks with physically diversified nodes would be of interest because this is always the case in real world. But this variant is far from being trivial because spatial heterogeneity gives more room to species polymorphism. Finally, it is worth noticing that in the present paper we have completely ruled out the Moran effect, which is always present in real ecological networks where close patches are characterized by very similar climatological and meteorological variabilities. This means that in order to better support the conjecture the theoretical studies we have just suggested should also be performed by substituting the dispersal mechanism with the Moran effect or by considering both of them at the same time (see e.g. [McPeek & Holt, 1996; Johst *et al.*, 1999]).

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