Short communication

Low dimensional homeochaos in coevolving host–parasitoid dimorphic populations: Extinction thresholds under local noise

Josep Sardanyés

Instituto de Biología Molecular y Celular de Plantas, Consejo Superior de Investigaciones Científicas-UPV, Ingeniero Fausto Elio s/n, 46022 València, Spain

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ABSTRACT

A discrete time model describing the population dynamics of coevolution between host and parasitoid haploid populations with a dimorphic matching allele coupling is investigated under both determinism and stochastic population disturbances. The role of the properties of the attractors governing the survival of both populations is analyzed considering equal mutation rates and focusing on host and parasitoid growth rates involving chaos. The purely deterministic model reveals a wide range of ordered and chaotic Red Queen dynamics causing cyclic and aperiodic fluctuations of haplotypes within each species. A Ruelle–Takens–Newhouse route to chaos is identified by increasing both host and parasitoid growth rates. From the bifurcation diagram structure and from numerical stability analysis, two different types of chaotic sets are roughly differentiated according to their size in phase space and to their largest Lyapunov exponent: the Confined and Expanded attractors. Under the presence of local population noise, these two types of attractors have a crucial role in the survival of both coevolving populations. The chaotic confined attractors, which have a lower positive Lyapunov exponent, are shown to involve a very low extinction probability under the influence of local population noise. On the contrary, the expanded chaotic sets (with a higher positive Lyapunov exponent) involve higher host and parasitoid extinction probabilities under the presence of noise. The asynchronies between haplotypes in the chaotic regime combined with low dimensional homeochaos tied to the confined attractors is suggested to reinforce the long-term persistence of these coevolving populations under the influence of stochastic disturbances. These ideas are also discussed in the framework of spatially-distributed host–parasitoid populations.

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1. Introduction

The population dynamics of coevolution and the conditions promoting coexistence among competitors, mutualists or victim-exploiter type systems have become one of the most important questions to explore in evolutionary biology [1,2]. Understanding the conditions for coexistence may involve the analysis of mechanisms such as environmental noise, spatial population structure, density dependence, and genetic variation [2]. In this sense, the Red Queen (RQ) hypothesis of dynamical evolution [3–5] has provided an excellent framework to approach to microevolutionary processes in biological systems with genetic systems involved in the interactions among antagonistic species. According to the RQ hypothesis, biotic interactions among species might be the engine driving evolution. This theory emphasizes the importance of frequency-dependent selection arising from interspecific interactions [4,6], making coexisting species to continuously evolve, even in a constant physical environment [4]. The RQ provides an evolutionary scenario where the “effective environment”
comprises primarily the biota and coevolving species can achieve a steady state of change instead of long-term evolutionary stasis [4] (see [7] for a review). Several works have explored the dynamics among interacting species in experimental molecular systems [8–10] as well as in several molecular [11–16] and ecological [4,5,17–23] theoretical systems. Empirical evidences indicate that some parasite genotypes are better at infecting particular host genotypes [24,19]. The so-called gene-for-gene (GFG) and matching-allele (MA) models have been developed to charaterize this empirical phenomena. More precisely, MA models were inspired by the notion of self–nonself recognition systems that underlie animal immune systems [17]. On this framework, each parasite genotype is better than other parasite genotypes at infecting some subset of host genotypes, but is worse at infecting other host genotypes [17]. Both GFG and MA models describe coevolutionary traits between exploiter-victim dynamics, being able to produce RQ dynamics [17–21,23]. The dynamical outcomes associated to coevolutionary processes have been widely studied using non linear dynamical systems theory [4,5,25,20,21,18,22,17,23].

An important point in evolutionary biology is the coupling between biological processes occurring at different time scales. For instance, the dependence of the long-term stability and possible evolution of the populations with their population dynamics arising from the biological interactions [26–29]. In this context, several models indicate that chaos might be a likely outcome in population dynamics [30–37,27,38–40] (for reviews see also [41–44]), or in catalytic replicator networks [45,14]. The importance of the attractor’s structure was emphasized by Hastings and co-workers [42]. It was argued that the presence of an strange attractor might not necessary involve an asymptotically unstable population with a higher extinction probability, as supported by Berryman et al. [26]. However, population levels on the attractor (even with chaos) can remain sufficiently far from zero [42]. Several theoretical studies have also shown that in interacting multispecies systems, chaos might not involve strong fluctuations in population numbers [28,29]. Actually, several works suggest the presence of chaotic dynamics in real ecosystems’ dynamics [46,42,47,48,44,49]. Recently, laboratory experiments conducted with a whole natural food-web suggest that chaos might be a likely outcome in the population dynamics for real systems [50]. Moreover, it has been shown theoretically that the underlying instabilities of local host–parasitoid dynamics can disappear in patchy eco-systems with a constant immigration flow of hosts and parasitoid from neighboring sites, allowing both populations to persist together [35]. Furthermore, Allen and co-workers [27] demonstrated that weakly coupled metapopulations can avoid global extinctions (driven by the synchronization of subpopulations due to regional weather patterns) under the presence of noise by means of chaotic dynamics involving asynchronies in local population dynamics. As stated by Allen et al. [27], some potentially interesting points to adress would be the search for circumstances in which chaos reduces extinction rates at both the subpopulations and global populations of species, as well as the examination of the effect of chaos on extinction in spatially distributed systems of interacting species. In this sense, the study of extinctions coupling noise with models describing antagonistic interactions and exhibiting chaos would combine both deterministic and stochastic population fluctuations, and would provide a better approach to real systems dynamics of single or interacting species. The study of stochastic population dynamics in time and space is fundamental in ecology and conservation biology for describing and predicting the time variation of population’s sizes, especially regarding to extinction processes. For instance, stochastic fluctuations can cause the extinction of a population that deterministically would persist indefinitely [51]. Obviously, this may have important implications for conservation of small single populations and of metapopulations composed of multiple subpopulations subject to local extinction and colonization. Stochasticity can also interact with human exploitation to cause the collapse or extinction [51].

In this work I study the discrete time dynamics between host and parasitoid populations with an interaction determined by a pair of haploid diallelic loci. The model is given by a discrete map and two scenarios are considered: (i) purely deterministic dynamics, and (ii) stochastic dynamics simulating population disturbances. Both approaches are compared assuming that stochasticity, included with low levels of noise, does not qualitatively change the deterministic chaotic dynamics. The model can be extended to study a single host and parasitoid population where the individuals con occupy two geographically separated regions (labeled 0 and 1, according to Fig. 1) interconnected by means of a migration flow. Hence, the effect of the population dynamics on the stability of coupled subpopulations can be studied considering antagonistic interactions. The main goal of this work is to explore the relation between the size and the dynamical properties of the attractors with the long-term stability of both populations, especially focusing in the dynamics governed by strange attractors and considering noise in the population dynamics. Several questions naturally arise for this particular system: which is the effect of increasing the intrinsic growth rates of both populations in the attractor’s characteristics? Are the location of the attractor in phase space as well as its shape and dynamical properties important in the survival of both populations? Which is the effect of the noise in the dynamics of coevolution of antagonistic populations with matching allele interactions or with spatially-distributed subpopulations?

2. Host–parasitoid discrete model

An extension of the well-known Nicholson and Bailey model [52,53,35] describing the discrete dynamics of host and parasitoid populations is used by introducing a minimal allelic interaction network between both populations (see Fig. 1). Hence, host and parasitoid individuals have two available alleles at a single locus responsible of the host–pathogen interaction. In a homogeneous environment, assuming non-overlapping generations in each population and parasitoid individuals searching randomly and independently, the matching allele dynamics between these two species can be described by the next set of difference equations:
Local noise is used to model disturbances affecting individual genotypic populations, and are included by means of the additive differential sensitivities to disturbances. Hence, the disturbances (labeled local noise) can be defined as in [27]. Such a local global population dynamics of the purely deterministic model under study are shown by increasing host’s self-replicating rate with $\alpha = 0.5$, $\mu_H = \mu_P = 10^{-3}$, $l' = 1.5$ and: (a) $\gamma = 7.4$, (b) $\gamma = 8.46$, (c) $\gamma = 9$, (d) $\gamma = 10.4$, (e) $\gamma = 11.3$, (f) $\gamma = 12.2$, (g) $\gamma = 15$, and (h) $\gamma = 19.4$ (the attractors are represented in the $(H(s),P(s))$ phase space). Note that from (a) to (h) the attractor changes its shape. Two types of attractors can be roughly differentiated: the Confined (e.g., (d) and (e)) and the Expanded (e.g., (g) and (h)) sets (all the attractors contain $4 \times 10^4$ points). On the left and on the right sides, we show, respectively, the overlapped time dynamics of the host’s (upper) and parasitoid’s (lower) haplotypes with $\gamma = 10.4$ and $\gamma = 19.4$ (corresponding to letters d and h of the displayed attractors). For both cases: haplotypes 0 (black) and haplotypes 1 (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

![Graph showing population dynamics](image)

$$H_{t+1}(s_i) = (1 - \mu_p)H'_t(s_i) + \frac{\mu_H}{V} \sum_{s_k \in \Omega'} H'_{t+1}(s_k),$$  

$$P_{t+1}(s_i) = (1 - \mu_p)P'_t(s_i) + \frac{\mu_P}{V} \sum_{s_k \in \Omega'} P'_{t+1}(s_k),$$

with

$$H'_t(s_i) = \gamma_1 H_t(s_i) e^{-\alpha H_t(s_i) - 2P_t(s_i)} + \xi_H(t),$$

$$P'_t(s_i) = \Gamma_1 H_t(s_i) [1 - e^{-2P_t(s_i)}] + \xi_P(t),$$

where $i = 0,1$ (the number of haplotypes of each of the species is $2^i$, being $v = 1$ the length of the sequence for the corresponding genotypes (i.e., 1-bit alleles)). Here $H_t(s_i)$ and $P_t(s_i)$ denote, respectively, the population numbers of host and parasitoid individuals with allele $i$ at generation $t$. Parameter $\gamma_1$ is the average number of offspring produced by an unparasitized host (note that it is assumed a density-dependence in host’s reproduction, being $\rho$ a constant parametrizing the exponential density-dependent growth factor). Parameter $\Gamma_1$ is the average number of parasitoid individuals with genotype $i$ emerging from each host with allele $i$ parasitized, and $\alpha$ corresponds to the searching efficiency of the parasitoid. Note that the population numbers of individuals with allele $i$ can be represented by considering that each allele lives in a vertex of a sequence space (see Fig. 1). For the sake of simplicity, the neutral fitness landscape is analyzed, with $\gamma_1 = \gamma$ and $\Gamma_1 = \Gamma$, $\forall i$.

The number of hosts and parasitoids emerging at every time generation at each vertex of sequence space is computed from Eqs. (3) and (4), respectively. Then, mutation (migration) from the neighboring orthants, $s_k$, is allowed to take place according to Eqs. (1) and (2), giving the final population numbers for each individual with allele $i$. Mutation rates for host and parasitoid genotypes are given by $\mu_H$ and $\mu_P$, respectively. It is assumed that all the alleles of each population have equal mutation rates. As previously mentioned, the model can be extended to a simple model of spatially-distributed host and parasitoid populations assuming that each genotype corresponds to a subpopulation placed in a neighboring geographic region (with two patches, labeled 0 or 1). Thus, host and parasitoid individuals can emigrate to the neighboring zone proportionally to the emigration rate, $\mu_H$, (mutation in the MA model).

To study the dynamics of Eqs. (1) and (2) considering noise, it is assumed that the genotypes of both populations have differential sensitivities to disturbances. Hence, the disturbances (labeled local noise) can be defined as in [27]. Such a local noise is used to model disturbances affecting individual genotypic populations, and are included by means of the additive noise terms $\xi_H(t)$ (for host’s genotypes) and $\xi_P(t)$ (for parasitoid’s genotypes) in Eqs. (3) and (4). Local noise is assumed to occur at every generation and the perturbations affecting different genotypes are independent. Moreover, these disturbances are assumed to be uniformly distributed in $U(-\eta,\eta)$ (considering small local noise (e.g., $\eta < 0.1$) according to [27]). In all the analyses, initial conditions are: $H_{t=0}(s_0) = 0.85$, $H_{t=0}(s_1) = 0.8$, $P_{t=0}(s_0) = 0.15$ and $P_{t=0}(s_1) = 0.25$. Finally, local (i.e., genotypic) populations’ extinctions are assumed to occur with densities below $10^{-4}$. For simplicity we hereafter use $\rho = 0.35$ and $\alpha = 0.5$. 

Fig. 1. (Middle, upper-left) Host–pathogen interactions considering a perfect allele matching (dashed arrows). The same system can be used to model host and parasitoid dynamics in geographically separated regions (patch 0 and 1), interconnected with a migration flow. Several of the attractors governing the global population dynamics of the purely deterministic model under study are shown by increasing host’s self-replicating rate with $\alpha = 0.5$. To illustrate, we considered different scenarios, with $\gamma = 7.4$ and $\gamma = 8.46$, $H_{t=0}(s_0) = 0.85$, $H_{t=0}(s_1) = 0.8$, $P_{t=0}(s_0) = 0.15$ and $P_{t=0}(s_1) = 0.25$. For simplicity we hereafter use $\rho = 0.35$ and $\alpha = 0.5$. 

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2.1. Deterministic versus stochastic dynamics

In this section, the dynamical behaviors of the discrete model are firstly studied without considering local population noise (i.e., with $n_{Ht}(s_i)\equiv 0$ and $n_{Pt}(s_i)\equiv 0$). Then the system is explored considering a small level of noise in the population dynamics (using $g=0.1$ and $g=0.25$). As the main interest of this work is to explore the effect of the interplay between noise and chaos in the long-term persistence of both species, a single scenario considering same mutation rates for both populations (i.e., $l_H=l_P=1/3$) will be analyzed.

In order to analyze the effect of increasing host’s growth rate, $\gamma$, on the population dynamics, the bifurcation diagram corresponding to the global population of hosts (considering both haplotypes) is shown in Fig. 2A (using $\Gamma=1.5$). Note that as $\gamma$ increases a Ruelle–Takens–Newhouse route to chaos [54] occurs and the boundaries of the strange attractor grow. Hence our model shows a wide parametric range of cyclic and quasiperiodic fluctuations of haplotypes within each species. Moreover, the asynchrony between the haplotypes of each of the species in the chaotic regime is also shown in Fig. 1. Here, the population numbers of both haplotypes are represented overlapped (black for the host’s haplotypes and red for the parasitoid’s haplotypes). As Fig. 1 shows, both haplotypes show time asynchronies in the population numbers. As shown in Figs. 1 and 2C, the increase of $\gamma$ gives raise to different types of strange attractors, which tend to expand in phase space as this parameter increases. The characterization of the values of $\gamma$ involving chaotic dynamics is done by means of numerical stability analysis computing the Lyapunov spectrum from the long-time average of the product of Jacobi matrices with Gram-Schmidt orthogonalization [55]. The largest Lyapunov exponent, $\lambda_1$, is shown for the same parameter values as in Fig. 1 (indicated with the same letters). The largest Lyapunov exponent for each case is: (d) $\lambda_1^*=0.061$; (e) $\lambda_1^*=0.076$; (g) $\lambda_1^*=0.19$; and (h) $\lambda_1^*=0.2735$.

![Fig. 2. (A) Bifurcation diagram (in linear-log plot) for the global host population dynamics, and the largest Lyapunov exponent (B), $\lambda_1$, for the deterministic model using $\gamma$ as control parameter with $\Gamma=1.5$ and $\mu_H=\mu_P=10^{-4}$. (C) The same bifurcation diagram for the global population of hosts is represented considering local population noise distributed as $U(-\eta,\eta)$, with $\eta=0.1$. Here, the red lines indicate host and parasitoid extinction probabilities as a function of $\gamma$, using two intensities of noise: $\eta=0.1$ (right) and $\eta=0.25$ (left). Below, the chaotic attractors (projected on the $(H_t(s_0),P_t(s_0))$ phase space) unfolding confined chaos ((d) and (e)) and expanded chaos ((g) and (h)) in the deterministic model are shown for the same parameter values as in Fig. 1 (indicated with the same letters). The largest Lyapunov exponent for each case is: (d) $\lambda_1^*=0.061$; (e) $\lambda_1^*=0.076$; (g) $\lambda_1^*=0.19$; and (h) $\lambda_1^*=0.2735$.](image-url)
to zero. On the contrary, the largest Lyapunov exponent for the Expanded sets (ES) (e.g., with $\gamma = 19.4$ and $\lambda^* = 0.2735$), see Fig. 1(h)), has a higher positive value.

These types of attractors might also be found in the bifurcation diagram of the logistic map describing the discrete population dynamics for a single species (see [26]) as well as in other models for ecological dynamics. One interesting question concerning the CS is if its dynamical properties provide robustness against extinction, as opposed to the ES. This hypothesis is tested by introducing local population noise in the deterministic model. These disturbances might increase extinction probabilities because the probability for the population solutions of visiting near-zero values will increase. Hence, in the following lines, Eqs.(1) and (2) are explored considering noise in the population dynamics for the same parameter values as for the deterministic bifurcation diagram shown in Fig. 2. The extinction probability, $P_e$, is characterized with this set of parameters. Such an extinction probability is computed as the number of runs involving both host and parasitoid extinction from 500 independent replicas (from a time series with $10^5$ generations). In Fig. 2C, $P_e$ is shown at increasing $\gamma$ using a noise intensity of $\eta = 0.1$ and $\eta = 0.25$. Note that $P_e$ is zero or very low when the deterministic dynamics is governed by the point attractor, the quasiperiodic regime and the chaotic CS, while the strange ES are shown to involve higher extinction probabilities.

The time series obtained with the stochastic model are shown in Fig. 3. It is shown that local noise typically destabilizes the deterministic dynamics (as shown in Fig. 2C). The dynamics with noise for the chaotic windows in the bifurcation diagram of Fig. 2 can undergo different asymptotic dynamical regimes depending on the type of the strange attractor (i.e. CS or ES). In this sense, and for the particular runs used in Fig. 3, the more expanded chaotic attractor (i.e., the one with $\gamma = 19$, see Fig. 1(d)), involves host and parasitoid extinctions. This is not the case for the chaotic CS, for which host and parasitoid populations do not become extinct. Note that some of the attractors corresponding to the periodic or the chaotic CS with noise are able to concentrate the solutions in the regions of the deterministic attractors (see for example Fig. 3(b)–(e)). Thus the deterministic dynamics would play an important role when considering noise. From the time series and the attractors of Fig. 3, it can be seen that the strength of the oscillations is bigger as we increase $\gamma$. This might be a direct effect driven by the dynamical properties of the deterministic attractor’s, where the increase in the growth parameter involves qualitative changes in the dynamics as well as the enlargement of the attractor’s boundaries. In this sense, the chaotic ES could involve a
higher amplification of noise. Finally, the bifurcation diagram for host’s population is displayed by using $\Gamma$ as control parameter. Here, a Ruelle–Takens–Newhouse route to chaos is also shown (see Fig. 4A). The extinction probability $P_e$ is shown to be very small for the parameter values corresponding to the CS (see for example Fig. 4C(a)–(c)). On the contrary, the extinction probability increases for the ES, which have a highest largest Lyapunov exponent (see Fig. 4B).

2.2. Lyapunov exponents and extinction thresholds

In this section we focus on the relation between the Lyapunov exponents and the probability of extinction of both co-evolving populations in the chaotic regime. The largest (positive) Lyapunov exponents, $\lambda_i^+$, obtained using same parameter values as in Fig. 2B, have been ordered in an ascending way, and, for each Lyapunov exponent, the extinction probability $P_e$ has been computed as in the previous section. Moreover, the effect of increasing $\lambda_i^+$ on the amplitude of the fluctuations for both host and parasitoid global populations is also analyzed, as well as the change of both host and parasitoid local population minima. These results are shown in Fig. 5. As shown in the bifurcation diagrams of Figs. 2 and 4, the extinction probability increases when $\lambda_i^+$ increases. The extinction curve in this parameter space follows a sigmoidal function (see Fig. 5D), also shown in Fig. 2C and Fig. 4C. The critical largest Lyapunov exponent (i.e. the value of $\lambda_i^+$ beyond which $P_e$ increases) has a lower value when considering a level of noise with $\eta = 0.25$ (Fig. 5D).

The amplitude of the fluctuations in the population dynamics for both host and parasitoid populations increases with increasing $\lambda_i^+$, and the noise involves a higher amplitude range. Fig. 5A and C shows the effect of the largest Lyapunov exponents in the local population minima for both host and parasitoid populations. For the case without noise (in black), the local minima decrease for the population of hosts (squares) and for the population of parasitoids (triangles), although for low $\lambda_i^+$, the local minimum for the parasitoids does not decrease. If a noise intensity of $\eta = 0.1$ is considered (in red), host local minima (squares) follow the deterministic fashion for low values of the Lyapunov exponent. However, with increasing $\lambda_i^+$ (i.e., $\lambda_i^+ \geq 0.2$), these minima rapidly decrease thus increasing the probability of extinction. Parasitoid’s local minima (triangles) start decreasing at a lower value of $\lambda_i^+$. These results suggest that parasitoids are more sensitive to local noise. If the level of noise is increased up to $\eta = 0.25$ (Fig. 5C), the local minima for both host and parasitoid populations decreases very fast at increasing $\lambda_i^+$. Here, such local minima for the population of parasitoids drastically approaches to zero values.

3. Conclusions

In the present work I analyze a discrete time model describing the matching allele dynamics of coevolution between a host and a parasitoid population with an interaction determined by a pair of haploid diallelic loci. Both deterministic and
stochastic dynamics are studied considering equal mutation rates for host and parasitoid alleles, and focusing in the chaotic regime of coevolution and persistence of both populations evolving under the presence of noise. Stochasticity is included by means of uniformly distributed, additive noise in the growth function of both host and parasitoid populations, simulating local disturbances affecting independently the genotypes of both populations. The purely deterministic model shows cyclic and aperiodic Red Queen dynamics of haplotypes within each species. A Ruelle–Takens–Newhouse route to chaos is shown to happen at increasing host’s and parasitoid’s growth rate in the deterministic model. The quasiperiodic route to chaos has been described in some biological models describing antagonistic interactions among species (i.e., predator–prey dynamics) in spatially-extended systems [56] as well as in well-stirred populations of replicators [14].

From the structure of the bifurcation diagram as well as from the largest Lyapunov exponents, two different types of attracting sets are differentiated: the **Confined** and the **Expanded** sets (i.e., CS and ES). The CS is given by an attractor which is confined in some regions of phase space being able to maintain and concentrate the solutions far away from extinction. The chaotic CS has a positive, close to zero largest positive Lyapunov exponent (on the edge of chaos). Actually, empirical evidences in real systems undergoing the “on the edge of chaos” regime have been reported from data on vole populations (see [49] and references therein). On the contrary, solutions living in the strange ES explore a wider region of phase space, achieving a higher probability of visiting near-zero population values. The largest Lyapunov exponent for the chaotic ES is higher than the one of the CS. It is shown that under the presence of local population noise, the CS are more robust in maintaining both interacting populations, as opposed to the ES, which easily entails the extinction of both coevolving populations.

The model analyzed in this work can be easily extended to a minimal spatial model, where a population of a host and of a parasitoid can inhabit two different geographic regions (patches 0 and 1, see Fig. 1), which are interconnected by means of migration (for this case mutation rates might correspond to migration rates between subpopulations). According to Berryman and co-workers [26], chaos might not be found in population dynamics because would involve large fluctuations in population dynamics thus increasing the probability of extinction. Although the extinction probability increases in the chaotic regime for a single population [26,27], such a probability may depend on the type of attractor. Allen et al. [27] showed that a population with metapopulation structure could avoid global extinctions by means of local asynchronies in subpopulations under the chaotic regime. In this sense, so-called confined chaos could also involve the asynchronous effect described in weakly coupled metapopulation dynamics [27], which combined with the decrease of local population’s extinction because of the confinement of solutions (i.e., lower amplitude in population fluctuations and higher local minima in population numbers) could perhaps reinforce the survival of the species in each subpopulation under the presence of global noise such as variations in regional weather patterns, which may tend to synchronize subpopulations. The same phenomenon could also happen with global noise tending to synchronize the densities of both genotypes of each species.

The possibility of stable population dynamics with chaos has been suggested to appear in spatially-extended systems [35,27,16]. Moreover, it has also been described in dynamical systems modeling multispecies interactions, where a weak...
high-dimensional chaotic state can arise [28,29]. Such a homeodynamic state, which has been labeled homeochaos, involves a dynamic stability of a complex set of elements which are temporally updated through their interaction [28,29]. Homeochaos has been then reported in high-dimensional systems where many positive, but close to zero Lyapunov exponents are found. This work suggests that "low-dimensional homeochaos" may arise in the vicinity of the bifurcation from periodic or quasiperiodic to chaotic regimes (on the edge of chaos), where the largest Lyapunov exponent has a lower positive magnitude. Such a type of homeochaos is suggested to involve lower extinction probabilities for antagonistic populations with diallelic matching allele dynamics under the presence of random population disturbances.

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References