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Abstract

Coevolution between two antagonistic species follow the so-called ‘Red Queen dynamics’ when reciprocal selection results in an endless series of adaptation by one species and counter-adaptation by the other. Red Queen dynamics are ‘genetically-driven’ when selective sweeps involving new beneficial mutations result in perpetual oscillations of the coevolving traits on the slow evolutionary timescale. Mathematical models have shown that a prey and a predator can coevolve along a genetically-driven Red Queen cycle. We found that embedding the prey-predator interaction into a three-species food chain that includes a coevolving superpredator often turns the genetically-driven Red Queen cycle into chaos. A key condition is that the prey evolves fast enough. Red Queen chaos implies that the direction and strength of selection are intrinsically unpredictable beyond a short evolutionary time, with greatest evolutionary unpredictability in the superpredator. We hypothesize that genetically-driven Red Queen chaos could explain why many natural populations are poised at the edge of ecological chaos. Over space, genetically-driven chaos is expected to cause the evolutionary divergence of local populations, even under homogenizing environmental fluctuations, and thus to promote genetic diversity among ecological communities over long evolutionary time.

Introduction

Antagonistic coevolution describes the reciprocal evolutionary interactions between populations belonging to an ‘exploiter’ such as a predator or a parasite, and a ‘victim’ such as a prey or a host. It is a change in the genetic make-up of a population in response to a genetic change in the antagonistic population (Thompson, 1994). Antagonistic interactions have the potential to drive coevolutionary dynamics of adaptive traits: an evolutionary advantage gained by one antagonist is often associated with a disadvantage for the other antagonist, and may therefore prompt a counter adaptation. This may drive stabilizing selection and evolutionary specialization with extreme refinement of the coevolving traits (convergence to an evolutionary equilibrium); or runaway selection and evolutionary escalation with the exaggeration of traits (with the possible extinction of some or all coevolving populations, Matsuda & Abrams, 1994, Ferrière, 2000); or fluctuating selection and the so-called ‘Red Queen dynamics’ of perpetual reciprocal changes in the coevolving traits (convergence to a nonequilibrium evolutionary attractor, Van Valen, 1973, Stenseth & Maynard Smith, 1984, Vermeij, 1994). It has been suggested that Red Queen dynamics underlie a large number of important biological processes, some of which are still poorly understood, such as genetic recombination and sexual reproduction (Hamilton, 1980; Bell, 1982; Hamilton *et al.*, 1990), the extraordinary diversity of genes related to immune function, resistance and virulence (Salathe *et al.*, 2008), and the spatial diversity and local adaptation of exploiter-victim systems (Gandon, 2002).

An important dichotomy exists between two main types of Red Queen dynamics (Khibnik & Kondrashov, 1997; Ebert, 2008; Gaba & Ebert, 2009): ecologically-driven by negative frequency-dependent selection, and genetically-driven by beneficial mutations. This distinction is significant because the two types strongly differ in their mechanism, their underlying genetic architecture, their ecological and evolutionary consequences and the timescales on which they develop (Ebert, 2008). With ecologically-driven Red Queen dynamics, extant variants of the exploiter genotype that benefit the most from the numerically dominant victim genotypes are favored, and, similarly, victim genotypes that best resist the numerically dominant exploiter genotypes are favored. This pattern results in selection against common exploiter and victim genotypes in a time lagged negative frequency-dependent fashion (ecological instability). A consequence of this form of fluctuating selection on extant genetic variation is that genetic polymorphism is maintained in the population for long periods (balanced selection) and that allele frequencies can oscillate considerably over time periods of a few generations.

In contrast, genetically-driven Red Queen dynamics involve the repeated incidence, spread, and fixation of new beneficial mutants in populations that stabilize at ecological equilibria. Mutants are driven to fixation by directional selection (selective sweeps). Thus, genetic polymorphism is transient only, and the evolutionary dynamics are slow—for two reasons. First, new mutations causing variation in the adaptive traits involved are rare events. Second, a new mutant starts with a very low frequency ($1/N$, where N is the number of wild-type alleles in the population); thus empirically it can take hundreds of generations until the mutant becomes recognizable (e.g., 1%) at the population level (Elena *et al.*, 1996). Therefore, genetically-driven Red Queen dynamics develop on an evolutionary timescale that is several orders of magnitude slower than the timescale of ecological processes.

The slow timescale involved hampers the empirical investigation of genetically-driven Red Queen dynamics, and mathematical models have been useful to seek conditions that could favor the Red Queen over specialization or escalation. So far the majority of these models focussed on the two coevolving species and ignored the community context in which coevolution takes place. In this setting, genetically-driven Red Queen dynamics develop as regular, predictable cycles in the adaptive trait space. However, pairs of coevolving species are inevitably embedded in community-level interactions of varying degrees of complexity. It is because most species interact with suites of other species that vary dynamically across geographical landscapes, that coevolutionary processes can be important in shaping the structure and maintaining variability within specific pairwise interactions, such as predator-prey or host-parasite systems (Abrams, 1991, 1996; Strauss *et al.*, 2005; Thompson, 2005; Thrall *et al.*, 2007). For example, some trematode parasites have strong effects on the evolutionary dynamics of their snail hosts, but themselves are dependent upon waterflow for completion of their life cycle (Lively, 1999). How the community context of coevolution affects the occurrence and manifestation of genetically-driven Red Queen dynamics remains poorly known.

Seminal steps in the theoretical study of coevolutionary dynamics in the community context have been taken recently (Caldarelli *et al.*, 1998; Loeuille *et al.*, 2002; Gandon, 2004; Nuismer & Doebeli, 2004; Loeuille & Loreau, 2005; Kisdi & Liu, 2006; Bell, 2007; Ferrière *et al.*, 2007; Shores *et al.*, 2008; Jones *et al.*, 2009; Stegen *et al.*, 2009), but models of genetically-driven coevolutionary dynamics in which more than two species coevolve in a multidimensional trait space are still lacking. Here we extend a simple two-species predator-prey coevolutionary system (Dieckmann *et al.*, 1995, where genetically-driven Red Queen cycles were first documented) to model coevolution in a three-dimensional trait space among three species forming a food chain. The function of each species in the food chain is determined by a continuous character

subject to rare and small genetic mutations. One may expect that the addition of a coevolving species to a coevolving pair could stabilize the evolutionary process at an evolutionary equilibrium, thereby suppressing the Red Queen dynamics (Vermeij, 1982; Futuyma, 1983); or that the addition could destabilize the periodic evolutionary oscillation and drive the genetically-driven Red Queen into chaos (Gavrilets, 1997). Here we show that conditions leading to genetically-driven periodic cycles in the two traits of coevolving predator and prey, favor chaotic dynamics in the three coevolving traits of the three-species food chain.

Model Construction

We focus on a single adaptive trait per species that characterizes the function of the species in the food chain. The trait determines competitive ability in the prey, and foraging success in the predator and super-predator. On the evolutionary timescale, *de novo* trait variation is caused by rare genetic mutation. The current phenotypes determine the ecological equilibrium of the food chain, hence the selective pressures acting on variants of the traits. Under the assumption that mutations have very small effects, the long-term coevolutionary process can be modeled as a trait substitution sequence in each species (Metz *et al.*, 1992, 1996), the dynamics of which are captured by a set of three deterministic differential equations, one per trait (Dieckmann & Law, 1996). When reduced to the classical two-trait, predator-prey coevolutionary model, the system is known to drive trait evolution toward a stable equilibrium or toward a Red Queen cycle (if not toward extinction) (Dieckmann *et al.*, 1995; Dercole *et al.*, 2003, 2006).

As in Dieckmann *et al.* (1995), Lotka-Volterra equations are used to describe the ecological dynamics of the food chain:

$$\frac{dn_1}{dt} = n_1 (r - cn_1 - a_2 n_2) \quad (1a)$$

$$\frac{dn_2}{dt} = n_2 (e_2 a_2 n_1 - d_2 - a_3 n_3) \quad (1b)$$

$$\frac{dn_3}{dt} = n_3 (e_3 a_3 n_2 - d_3) \quad (1c)$$

where n_1 , n_2 , and n_3 are prey, predator, and superpredator densities, r and c are prey intrinsic per capita growth rate and sensitivity to intraspecific competition, and a_i , e_i , and d_i are the attack rate, efficiency, and intrinsic death rate in the predator ($i = 2$) and superpredator ($i = 3$). Each species is characterized by one genetic trait x_i ($i = 1-3$), the genetic system is one-locus haploid, the genetic traits can influence the

prey competition function c and the attack rates a_2 and a_3 , and trait-dependencies are modeled by using the following functional forms:

$$c = c_0 + c_2(x_1 - c_1)^2 \quad (2a)$$

$$a_2 = \exp\left(-\left(\frac{x_1 - a_{24}}{a_{21}}\right)^2 + 2a_{23}\frac{x_1 - a_{24}}{a_{21}}\frac{x_2 - a_{25}}{a_{22}} - \left(\frac{x_2 - a_{25}}{a_{22}}\right)^2\right) \quad (2b)$$

$$a_3 = \exp\left(-\left(\frac{x_2 - a_{34}}{a_{31}}\right)^2 + 2a_{33}\frac{x_2 - a_{34}}{a_{31}}\frac{x_3 - a_{35}}{a_{32}} - \left(\frac{x_3 - a_{35}}{a_{32}}\right)^2\right) \quad (2c)$$

(with $0 < a_{23}, a_{33} < 1$ and $c_0, c_2, a_{21}, a_{22}, a_{31}, a_{32}$ all positive). Prey competition is minimum at $x_1 = c_1$, where prey are best adapted to their environment, while the attack rates a_2 and a_3 are bidimensional Gaussian functions with elliptic contour-lines centered at (a_{24}, a_{25}) (respectively (a_{34}, a_{35})) and controlled in amplitude and orientation by parameters $a_{21}-a_{23}$ ($a_{31}-a_{33}$). Differences $(x_1 - a_{24})$ and $(x_2 - a_{25})$ ($(x_2 - a_{34})$ and $(x_3 - a_{35})$) measure the degree to which the predator (superpredator) ‘matches’ the prey (predator), i.e., the attack rate is maximum when $x_1 = a_{24}$ and $x_2 = a_{25}$ ($x_2 = a_{34}, x_3 = a_{35}$), while parameters $a_{21}-a_{23}$ ($a_{31}-a_{33}$) control the sensitivity of the attack rate to the mismatch.

When a mutation occurs in trait x_1 and generates a new value x'_1 , the ecological system becomes

$$\frac{dn_1}{dt} = n_1 (r - c(x_1)n_1 - c(x_1)n'_1 - a_2(x_1, x_2)n_2) \quad (3a)$$

$$\frac{dn'_1}{dt} = n'_1 (r - c(x'_1)n_1 - c(x'_1)n'_1 - a_2(x'_1, x_2)n_2) \quad (3b)$$

$$\frac{dn_2}{dt} = n_2 (e_2 a_2(x_1, x_2)n_1 + e_2 a_2(x'_1, x_2)n'_1 - d_2 - a_3(x_2, x_3)n_3) \quad (3c)$$

$$\frac{dn_3}{dt} = n_3 (e_3 a_3(x_2, x_3)n_2 - d_3), \quad (3d)$$

so that the fitness function of mutant x'_1 is given by

$$\begin{aligned} f_1(x_1, x_2, x_3, x'_1) &= \frac{1}{n'_1} \frac{dn'_1}{dt} \Big|_{\substack{n=\bar{n} \\ n'_1=0}} \\ &= r - c(x'_1)\bar{n}_1(x_1, x_2, x_3) - a_2(x'_1, x_2)\bar{n}_2(x_1, x_2, x_3), \end{aligned} \quad (4)$$

where $n = (n_1, n_2, n_3)$ and \bar{n} denotes the ecological equilibrium of model (1) at which the food chain stabilizes in the absence of mutants (see Model Analysis and Results).

Similar equations can be written when a mutation arises in the predator (trait x_2) or superpredator (trait

x_3) (see Appendix S1 in Supplementary Material) and yield the fitness functions of mutants x'_2 and x'_3 :

$$\begin{aligned} f_2(x_1, x_2, x_3, x'_2) &= \frac{1}{n'_2} \frac{dn'_2}{dt} \Big|_{\substack{n=\bar{n} \\ n'_2=0}} \\ &= e_2 a_2(x_1, x'_2) \bar{n}_1(x_1, x_2, x_3) - d_2 - a_3(x'_2, x_3) \bar{n}_3(x_1, x_2, x_3) \end{aligned} \quad (5)$$

$$\begin{aligned} f_3(x_1, x_2, x_3, x'_3) &= \frac{1}{n'_3} \frac{dn'_3}{dt} \Big|_{\substack{n=\bar{n} \\ n'_3=0}} \\ &= e_3 a_3(x_2, x'_3) \bar{n}_2(x_1, x_2, x_3) - d_3. \end{aligned} \quad (6)$$

The long-term coevolution of traits x_1 , x_2 , and x_3 on the evolutionary timescale obey the so-called canonical equation of adaptive dynamics (Dieckmann & Law, 1996), i.e., the three-dimensional system of ODEs,

$$\frac{dx_1}{dt} = \frac{1}{2} \mu_1 \sigma_1^2 \bar{n}_1 \frac{\partial f_1}{\partial x'_1} \Big|_{x'_1=x_1} \quad (7a)$$

$$\frac{dx_2}{dt} = \frac{1}{2} \mu_2 \sigma_2^2 \bar{n}_2 \frac{\partial f_2}{\partial x'_2} \Big|_{x'_2=x_2} \quad (7b)$$

$$\frac{dx_3}{dt} = \frac{1}{2} \mu_3 \sigma_3^2 \bar{n}_3 \frac{\partial f_3}{\partial x'_3} \Big|_{x'_3=x_3}. \quad (7c)$$

The right-hand sides are the product of mutation rates (μ_i , $i = 1-3$), mutational steps variances (σ_i^2), equilibrium densities (\bar{n}_i), and selection gradients (fitness derivatives). The latter explicit expressions are cumbersome and were always generated and handled by means of symbolic computation.

Model Analysis and Results

The ecological model (1) has a unique non-trivial equilibrium

$$\bar{n}_1 = \frac{r}{c} - \frac{a_2 d_3}{c e_3 a_3} \quad (8a)$$

$$\bar{n}_2 = \frac{d_3}{e_3 a_3} \quad (8b)$$

$$\bar{n}_3 = \frac{e_2 a_2}{a_3} \left(\frac{r}{c} - \frac{a_2 d_3}{c e_3 a_3} \right) - \frac{d_2}{a_3}, \quad (8c)$$

which is positive if and only if $\bar{n}_3 > 0$. When positive, the equilibrium \bar{n} is globally stable (in the positive orthant). Thus, the ecological model (1) is only viable within the region of the trait space defined by the condition $\bar{n}_3 > 0$.

If the superpredator and the predator are able to simultaneously match the predator and the prey, respectively (i.e., $a_{25} = a_{34}$) and if, at the same time, the prey is able to minimize its sensitivity to intraspecific competition (i.e., $c_1 = a_{24}$), then $\bar{x}_1 = c_1$, $\bar{x}_2 = a_{25}$, $\bar{x}_3 = a_{35}$ is an equilibrium of the evolutionary model (7). Starting from these conditions, and fixing parameters at values corresponding to evolutionary cycles in the ditrophic model (Dieckmann *et al.*, 1995), we performed the numerical continuation of the equilibrium \bar{x} with respect to several parameters.

As expected, evolutionary stability was sensitive to the mutation rate μ_1 of the prey. As μ_1 increases, the evolutionary equilibrium loses stability through a supercritical Hopf bifurcation which yields a small-amplitude stable evolutionary cycle (see Appendix S3 in Supplementary Material). Starting from the Hopf bifurcation, we numerically continued the cycle, while monitoring its stability through the computation of the associated Floquet multipliers (i.e., the three eigenvalues of the linearized Poincaré map associated with the cycle; one of them is structurally equal to 1, and therefore its estimated value is a measure of computation accuracy; the other two determine the stability of the cycle). Again by increasing μ_1 , evolutionary stability was easily lost through a series of period-doubling bifurcations (a negative Floquet multiplier passing through -1 , see Appendix S3 in Supplementary Material). At each period-doubling bifurcation the cycle becomes unstable, and a new stable cycle (which traces twice the bifurcating cycle) appears. Switching to the continuation of the new stable cycle allowed us to find the next period-doubling bifurcation. Because the sequence of bifurcation parameter values μ_1^i , $i = 1, 2, \dots$, accumulates geometrically at the frontier μ_1^∞ of the chaotic region of the Feigenbaum period-doubling cascade, only a limited number of bifurcations in the sequence could be detected (μ_1^i , $i = 1, 2, 3$, are reported in Fig. 1). The robustness of the cascade has been checked through the continuation of the period-doubling bifurcations with respect to various pairs of parameters (details will be published elsewhere).

In order to estimate μ_1^∞ , we computed the full spectrum of the attractor's Lyapunov exponents $L_1 \geq L_2 \geq L_3$ for finely incremented values of μ_1 (step 10^{-5}) (see Appendix S2 in Supplementary Material). $L_1 > 0$ implies that μ_1 is in the chaotic region, whereas $L_1 = 0$ in periodic windows (see Fig. 1); in the chaotic region L_2 is structurally equal to 0 (its estimated value measures computation accuracy), while L_3 is negative. The attractor's fractal dimension then follows from Kaplan-Yorke formula (see Fig. 2).

In this example the dominant Lyapunov exponent equals $+0.0081321$ and the fractal dimension of the attractor is 2.0176 (the attractor lies roughly on a two-dimensional Möbius strip). Typically, the prey and predator characters oscillate with small irregular fluctuations in amplitude and frequency, while variation in the amplitude of the oscillations in the superpredator trait is more pronounced.

Our analysis shows that the genetically-driven Red Queen turns chaotic under conditions similar to those leading to genetically-driven Red Queen cycles, provided that the mutation timescale of the prey is short enough compared with the mutation timescales of predator and superpredator. That is (Dieckmann *et al.*, 1995; Dercole *et al.*, 2003), the predator efficiency should be great enough to drive the prey away from its genetic optimum; and there should be sufficient need for the predator to track the prey's character change. As the prey departs from its optimum, its population density drops, which causes a reversal of selection on the predator's trait, followed by a reversal of selection on the prey's character. If the prey evolves fast enough it will not be 'caught up' by the predator and permanent trait oscillations will evolve; the system ends up in chaos because the predator is also engaged in a coevolutionary chase with the superpredator. Broad comparative analyses (e.g., Martin & Palumbi, 1993) have established a strong relationship between nucleotide substitution rate and body size. For instance, rates of nuclear and mtDNA evolution are slow in whales, intermediate in primates, and fast in rodents, and a similar effect of body size also exists in poikilothermic vertebrates. Thus, trophic chains with smaller prey, hence faster mutagenesis, may be more prone to coevolutionary chaos.

Discussion

Even though quantitative data on long-term predator-prey coevolutionary dynamics remain elusive (Barnosky, 2001), the fossil record supports the view that predation is an important driver of evolutionary change (Kelley *et al.*, 2003). Moreover, paleontological and phylogenetic analyses gather increasing evidence for the role of three-level chain interactions in coevolution (Currie *et al.*, 2003; Kelley *et al.*, 2003). These empirical findings have been paralleled by extensions of coevolutionary theory beyond pairwise interactions (Abrams, 1996; Caldarelli *et al.*, 1998; Loeuille *et al.*, 2002; Gandon, 2004; Nuismer & Doebeli, 2004; Loeuille & Loreau, 2005; Kisdi & Liu, 2006; Bell, 2007; Ferrière *et al.*, 2007; Shores *et al.*, 2008; Jones *et al.*, 2009; Stegen *et al.*, 2009), but so far the complexity of evolutionary dynamics among more than two species coevolving in a multidimensional trait space has been little explored. As a step forward in that direction, we

added a superpredator as a third, coevolving species, to coevolution between a prey and a predator.

Prey-predator-superpredator trophic chains have long attracted the attention of ecologists as they occur by diverse mechanisms, can cross ecosystem boundaries, and have practical importance, for example in management of fisheries or biological control of crop pests (Cohen *et al.*, 2009). Our model descends from the lineage of two-species models that addressed genetically-driven predator-prey coevolution (Stenseth & Maynard Smith, 1984; Rosenzweig *et al.*, 1987; Rand & Wilson, 1991; Marrow *et al.*, 1992; Dieckmann *et al.*, 1995; Doebeli, 1997; Gavrillets, 1997; Khibnik & Kondrashov, 1997; Dercole *et al.*, 2003, 2006) and specifically extends the analysis of Dieckmann *et al.* (1995), where stable cycles in adaptive dynamics were first documented.

We searched for strange attractors in the three-trait, three-species coevolutionary model by weaving intuition and theory. Theory was telling us that in third-order dynamical systems the most common route to chaos is the Feigenbaum period-doubling cascade (see Appendix S3 in Supplementary Material), and we knew that evolutionary stability in predator-prey models was especially sensitive to the mutation rate of the prey (Dieckmann *et al.*, 1995; Dercole *et al.*, 2003). Thus, our analysis of the tritrophic evolutionary dynamics was organized by looking for parameters that caused evolutionary cycles in the lower ditrophic model, and such that increasing the prey mutation rate could trigger doubling of the cycle period; and then, tracking the period-doubling cascade. The strategy was successful at detecting transitions toward evolutionary chaos in the three-species system.

Our analysis of three-species coevolution was intended as an extension of Dieckmann *et al.*'s (1995) two-species model. This is the technical motivation for our choice of the type I functional response to describe trophic interactions, hence the Lotka-Volterra structure of the ecological model. This has the important consequence of ensuring that the food chain always stabilizes at an equilibrium on the ecological timescale. Therefore, oscillations predicted by the evolutionary model could only be due to nonlinear interactions between selective pressures acting on genetic variation in the adaptive traits—not to trait variation induced by instabilities in the ecological dynamics (as in Abrams & Matsuda, 1997b). More realistic food chain models with, for example, saturating (type II) functional responses or self-limitation at higher trophic levels, can also stabilize at ecological equilibria, though ecological cycles and ecological chaos are also expected in viable regions of the trait space. This opens the possibility of Red Queen chaotic dynamics that would be ‘ecogenetically-driven’, *sensu* Khibnik & Kondrashov (1997) (see Dercole *et al.*, 2003, and Dercole *et al.*, 2006, for the two-species case).

Another fundamental feature of the model is the definition of the adaptive traits. We keep the ‘matching model’ used in Dieckmann *et al.* (1995), which has long been popular in the theory of predator-prey coevolution (Cohen *et al.*, 1993; Abrams, 2000; Loeuille & Loreau, 2005; Stegen *et al.*, 2009). The matching model assumes that the traits of a species and its prey jointly determine the attack (and capture) rate of the latter by the former, and that the attack rate is maximized when the two traits match. Scaled body size is a commonly used surrogate measure for such traits (Williams & Martinez, 2000). Defining the adaptive traits according to the matching model is known to promote genetically-driven Red Queen cycles in two-species predator-prey coevolutionary model (Marrow *et al.*, 1992, 1996; Dieckmann *et al.*, 1995; Abrams & Matsuda, 1997a; Doebeli, 1997; Gavrillets, 1997), and thus provided us with the appropriate framework to answer our main question—‘how are two-species Red Queen cycles affected by the coevolution of a third species?’

Several well-studied antagonistic pairwise interactions seem to conform to the matching model. This includes parasitic cuckoo and their hosts, in which the probability that a parasitic egg be rejected depends on the similarity of host and parasite egg morphologies (Robert & Sorci, 1999); crossbills and lodgepole pines, for which fitnesses are influenced by matching between bill size and cone structure (Benkman, 1999); feather lice and dove hosts, in which louse fitness at least is influenced by matching size with host size (and host size correlates with parasite size across species) (Clayton *et al.*, 2003). Other equally well-studied systems, however, better fit an alternate model in which the strength of between-species interactions is a monotonic function of the difference between the predator and prey’s traits. This is the case of parsnip web-worms and wild parsnips, in which feeding efficiency of defended plants increases with higher production of detoxifying enzymes (Berenbaum & Zangerl, 1992). Likewise, the rate of successful attack in the Japanese camelia-camelia-weevil system is a monotonic function of the difference between camelia fruit wall thickness and weevil mouthpart size (Toju & Sota, 2006, 2009). The ‘difference model’ so defined also fits the trophic interaction between toxic newts (prey) and potentially toxin-resistant garter snakes (predators) (Brodie *et al.*, 2002; Hanifin *et al.*, 2008).

Nuismer *et al.* (2007) theoretical analysis of antagonistic coevolution under the difference model of attack rate shows that coevolutionary cycles are still possible with this model, provided that selection is strong enough and stabilizing selection acts on the traits. Thus, genetically-driven coevolutionary cycles in pairwise antagonistic interactions appear to be at least possible under relatively broad conditions when the attack rate is described by the difference model. The question of whether coevolutionary cycles turn

into chaos in the three-species food chain is open to investigation. Future models should also examine the coevolution of alternate or additional traits besides the attack rate. Dercole *et al.* (2003) and Kisdi & Liu (2006), for example, considered the evolution of handling time, a key factor of the functional response. As an extension of our model, it would be interesting to account for genetic variation in predator and superpredator handling times, track the evolution of the functional responses themselves as a by-product, and monitor the potential bifurcations experienced by the coevolutionary dynamics as a consequence.

The possibility that natural selection acting on extant genetic variation drives community dynamics into chaos has been known since early analyses of host-pathogen models (May & Anderson, 1983), and is not unexpected given that competition between multiple species or genotypes can easily destabilize population dynamics (Hofbauer & Sigmund, 1998; Turchin, 2003). This type of chaotic evolutionary dynamics has been found in theoretical studies of genetic polymorphisms under frequency-dependent selection (e.g., May & Anderson, 1983; Seger, 1992; Ferrière & Fox, 1995; Solé & Sardanyés, 2007), strategy frequencies in evolutionary games (Nowak & Sigmund, 2003), and rapid evolution of a continuous trait in interaction with population dynamics (Abrams & Matsuda, 1997b). All these are instances of evolutionary chaos on the ecological timescale. The system considered here is different since the timescales of ecology and evolution are separated: the population dynamics of different alleles stabilize on a monomorphic state over a timescale which is fast compared to the slow evolutionary timescale over which the dynamics of the adaptive traits develop. Thus, our analysis uncovers the first example of genetically-driven chaotic Red Queen.

The genetically-driven chaotic Red Queen implies that non-linear interactions of selective pressures can drive phenotypic changes that are unpredictable over the slow timescale of long-term evolution, even in a perfectly constant abiotic environment. (Note that with chaos in allele, or strategy, frequencies driven by negative frequency-dependence there is unpredictability in the dynamics of frequencies, but the identity of alleles, or strategies, never changes.) This has implications for our understanding of the role of ‘chance’ in evolution (Travisano *et al.*, 1995; Beatty, 2006). Chance manifests itself when the evolutionary trajectories of adaptive traits diverge between replicated populations that were initiated in similar phenotypic and genotypic states. Experimental tests on bacterial systems have provided some of the best evaluation of the role that chance may play in evolution. Although founded by the same clone, and evolving in identical conditions, replicate populations often diverge from one another in their relative growth rate, demographic traits, morphological features, and performance in other environments (Elena & Lenski, 2003, and references therein). The conventional explanation for evolutionary divergence ‘by chance’ involves genetic stochastic-

ity (the randomness of mutation and drift due to demographic stochasticity) and environmental stochasticity (random changes in environmental conditions) (Lenormand *et al.*, 2008). However, models of adaptive trait dynamics derived from individual-level ‘first principles’ have shown that the effect of genetic stochasticity is often ‘smoothed out’ in the long term, with traits converging towards the attractor of a deterministic dynamical system, provided that there is some minimal separation between the timescales of mutation and selection (Champagnat *et al.*, 2006). The present study shows that even if the randomness of genetic stochasticity is smoothed out, uncertainty can arise from the selection component of the evolutionary process: adaptive trait trajectories converge towards a deterministic attractor, yet the chaotic nature of the attractor renders the trait dynamics unpredictable beyond a short evolutionary time horizon. Thus, the nonlinearity of the selection gradient offers an alternative to genetic or environmental stochasticity to explain the ‘chance’ component of evolutionary trajectories in real populations.

Further examples of genetically-driven chaotic Red Queen dynamics are likely to be discovered in models of long-term evolution in which the adaptive process operates in a three- (or more) dimensional trait space—even if all traits, e.g., behavioral or life-history traits, pertain to the same, single species. Genetically-driven chaos might also arise in two-trait adaptive dynamics models, or even in one-trait systems showing ecological multistability (Dercole *et al.*, 2002), that are subject to externally-driven periodic fluctuations in mutation or selection. Besides its conceptual value, the genetically-driven chaotic Red Queen suggests three new hypotheses (discussed below) about coevolutionary dynamics. Each hypothesis opens an avenue for future theoretical work.

The intrinsic unpredictability of coevolutionary dynamics is widespread

In view of the general theory of dynamical systems, the existence of chaotic evolutionary attractors over some parameter region can affect the coevolutionary dynamics broadly outside that region. Even when the coevolutionary attractor of the food chain is an equilibrium or a cycle, the ‘shadow’ of evolutionary chaos will be seen in the form of long erratic transients (Hastings, 2004). Genetic noise, due, e.g., to random drift or stochastic gene flow, or stochastic environmental fluctuations on the slow evolutionary time scale, may actually maintain these transients for arbitrarily long evolutionary times. Such ‘noise-induced chaos’ illustrates the general fact that small amounts of exogenous noise can have disproportionate qualitative impacts on the long-term dynamics of a nonlinear system in which chaotic structures exist for some parameter values (Tel, 1990; Rand & Wilson, 1991; Lai *et al.*, 2003; Ellner & Turchin, 2005).

Coevolution can drive population dynamics to the edge of chaos

Looking at evolution on a slow timescale in contrast with or even completely separated from the fast timescale of ecology does not mean that the coevolutionary process has no effect on the ecological state of the system. In fact, the genetically-driven chaotic Red Queen implies that the population size of each species also fluctuates chaotically, but these fluctuations develop on the slow, evolutionary timescale, because at each point in evolutionary time the food chain model analyzed here is at ecological equilibrium. In other food chain models, ecological cycles and chaos occur readily (Hastings & Powell, 1991; Gross *et al.*, 2005). In the light of this and other studies (Khibnik & Kondrashov, 1997; Dercole *et al.*, 2006), the trait domain corresponding to ecological chaos may contain part or all of the coevolutionary attractor (ecogenetically-driven Red Queen). A sharp change in the selective regime at the boundary between chaotic and non-chaotic ecological dynamics is expected in general (Ferrière & Gatto, 1995; Dercole *et al.*, 2006), and may poise the food chain near that boundary for long evolutionary times, in a process called ‘evolutionary sliding’ (Dercole *et al.*, 2006). This would provide an evolutionary explanation for the standing puzzle that the abundance of many natural populations seemingly fluctuates ‘at the edge of chaos’ (Turchin, 2003; Ellner & Turchin, 1995).

The chaotic Red Queen promotes genetic divergence in metacommunities

There is considerable interest in better understanding how coevolutionary processes work in geographically structured habitats (Thompson, 2005). The arising of genetically-driven chaos has direct implications for the origin and maintenance of genetic diversity in spatially extended communities. Let us consider the metaphor of a fragmented landscape in which all patches are identical and isolated. Genetically-driven chaotic Red Queen dynamics imply that each local trophic chain evolves along the same strange attractor, but small ancestral differences in the genetic make-up of local communities will result in permanent genetic differences between patches. The magnitude of these differences will vary over time, and be sometimes as large as the coevolutionary attractor. In contrast, small ancestral differences remain small in the case of periodic Red Queen dynamics (and the same would be true if the Red Queen were ecologically driven). In other words, local genetically-driven coevolutionary chaos promotes spatial genetic divergence, even in the absence of environmental differences between patches. Red Queen dynamics in general can explain phenotypic mismatches between coevolving species even in the absence of spatial structure, gene flow or

genetic drift (Berenbaum *et al.*, 1986; Hanifin *et al.*, 2008); the chaotic Red Queen, in particular, predicts the persistence of different degrees of mismatches between local communities, even if environmental conditions are spatially uniform.

Furthermore, general results on the synchronization of dynamical systems subject to common fluctuating exogenous forces warn that the genetic divergence between local populations can be lost in the presence of long-term environmental fluctuations (this is known in ecology as Moran effect; see Royama, 1992, for a review). However, recent results (Colombo *et al.*, 2008) show in great generality that this is possible only if environmental fluctuations are large and tuned specifically to the endogenous dynamics of the system. Genetically-driven coevolutionary chaos could therefore play an important role in promoting genetic diversity in ecological communities threatened by environmental homogenization (Olden *et al.*, 2004). We conclude that genetically-driven Red Queen chaos might explain genetic differentiation of local communities without invoking local adaptation to different habitat conditions or to multiple steady states of local populations in the metacommunity. This points to the possibility that, in sexual species, the genetic divergence of local populations induced by complex adaptive dynamics might favor the evolution of reproductive isolation and hence parapatric speciation—even across relatively uniform habitats, as in marine species (Palumbi, 1994; Kirkpatrick & Ravigne, 2002). Extension of speciation models along ecological gradients (Doebeli & Dieckmann, 2003) will help examine this hypothesis further.

Concluding Remarks

Here we have extended Dieckmann *et al.*'s (1995) model of predator-prey genetically-driven coevolution by adding a coevolving superpredator to the system. When Red Queen periodic cycles develop in the two-species model, the adaptive dynamics of the three coevolving species are often chaotic. A general condition for this to happen is that the evolutionary rate of the prey be large enough. The greatest irregularity is then predicted in the dynamics of the superpredator trait. Because the ecological model of the food chain is always at equilibrium throughout the trait space, instability in the ecological dynamics plays no role in generating this chaotic Red Queen, which is thus entirely driven by nonlinear interactions between the selective pressures acting on rare genetic variation of the traits.

The specificities of the model and the new hypotheses arising from the results call for continued theoretical investigation of chaotic dynamics in genetically-driven coevolutionary processes. This theoretical

endeavor should be paralleled by an empirical effort focusing on the patterns of temporal unpredictability and spatial heterogeneity of antagonistic coevolution; and the consequences for population dynamics, genetic differentiation in metacommunities, and macroevolutionary processes including speciation.

A key difference between coevolutionary cycles and coevolutionary chaos lies in the expectation that geographically distinct communities subject to homogenizing factors of their environment (e.g., large scale climatic fluctuations) should exhibit similar degrees of phenotype mismatching when coevolving cyclically, and persistently dissimilar degrees of mismatching when coevolving chaotically. Spatially heterogeneous mismatches have been documented recently in the camelia-weevil (Toju, 2009) and newt-garter snake (Hanifin *et al.*, 2008) systems. In the light of our results, the fine-scale divergence of coevolution in the former may not require geographic variation of environmental factors (Toju, 2009). Molecular data supporting the role of beneficial mutations, rather than standing genetic variation, as fueling coevolution between newts and their snake predators (Feldman *et al.*, 2009) offers promising evidence for the relevance of genetically-driven Red Queen models to deepen our understanding of geographic patterns of coevolution in nature.

Besides trophic interactions, the Red Queen is expected to reign in many exploiter-victim systems (Lythgoe & Read, 1998). Biomedical science has already revealed the potential ubiquity of the Red Queen in parasitic and pathogenic interactions (Moya *et al.*, 2004). Experimental coevolution in host-pathogen systems is being used successfully to evidence the patterns and dissect the processes of ecologically-driven Red Queen dynamics in laboratory systems (e.g., Koskella & Lively, 2007, 2009) and in nature (Decaestecker *et al.*, 2007). On the evolutionary timescale, antagonistic coevolutionary dynamics fueled by *de novo* genetic variation have been studied experimentally using bacterial systems (Lenski & Levin, 1985; Bohannan & Lenski, 2000; Buckling & Rainey, 2002; Mizoguchi *et al.*, 2003; Forde *et al.*, 2004; Lopez-Pascua & Buckling, 2008; Gallet *et al.*, 2009). The time-shift experimental design (Gaba & Ebert, 2009) implemented to study ecologically-driven Red Queen dynamics could be applied to measure how predictable genetically-driven coevolutionary trajectories are under different experimental treatments, and thus to search for the essential property of chaotic dynamics—exponentially declining predictability of trajectories. Combining experiments with sufficiently detailed mathematical models of the study systems will be instrumental to identify relevant experimental treatments, to design data collection and analysis, and to interpret the results (Decaestecker *et al.*, 2007). If it were supported by such experiments on microbial systems, the genetically-driven chaotic Red Queen might contribute to our understanding of the rapid and indeterminate evolution of viral pathogens (Kirkwood & Bangham, 1994; Moya *et al.*, 2004), and perhaps influence the study and

control of emergent pathogens on large temporal and spatial scales.

Ultimately the important question raised by the genetically-driven chaotic Red Queen is unlikely to be whether or not long-term evolution in any specific ecological system is chaotic—a question that makes sense only in the realm of mathematical models. Population ecologists have long gone beyond that question—chaos versus nonchaos—to draw stunning insights from nonlinear dynamics theory into how environmental forces and internal dynamics shape species abundance and distribution in nature (Allen *et al.*, 1993; Dixon *et al.*, 1999; Turchin, 2003; Ellner & Turchin, 1995). The same move could take place in evolutionary biology, as genetically-driven Red Queen chaos challenges our ability to measure, compare, and interpret coevolutionary patterns and processes in the real world.

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Supplementary Material

The following supplementary material is available for this article:

Appendix S1: Mutant-resident ecological interaction

Appendix S2: Lyapunov exponents computation

Appendix S3: Technical references on bifurcation analysis

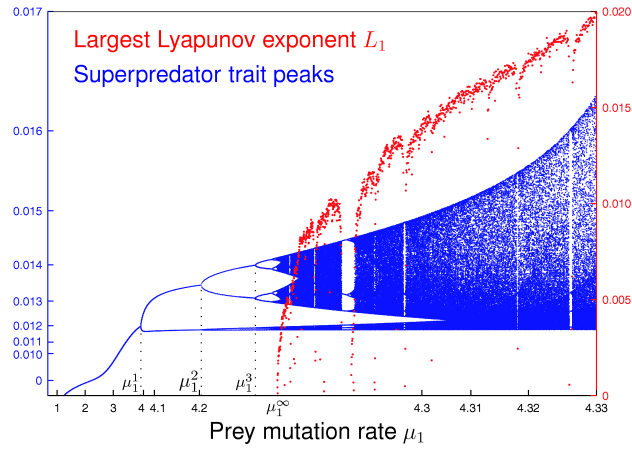


Figure 1: Period-doubling route toward genetically-driven Red Queen chaos in a three-species food chain. Peak values of the superpredator trait, x_3 (blue), in the corresponding evolutionary attractor, and the largest Lyapunov exponent, L_1 (red), as functions of the prey mutation rate, μ_1 . The value μ_1^∞ indicates the lower limit of the chaotic range. Parameter values: $\mu_2 = 1$, $\mu_3 = 1$, $\sigma_1^2 = 0.3$, $\sigma_2^2 = 2$, $\sigma_3^2 = 2$, $r = 0.5$, $d_2 = 0.05$, $d_3 = 0.02$, $e_2 = 0.14$, $e_3 = 0.14$, $a_{21} = 0.22$, $a_{22} = 0.25$, $a_{23} = 0.6$, $a_{24} = 0$, $a_{25} = 0.04$, $a_{31} = 0.22$, $a_{32} = 0.25$, $a_{33} = 0.6$, $a_{34} = 0$, $a_{35} = -0.04$, $c_0 = 0.5$, $c_1 = 0$, $c_2 = 3$.

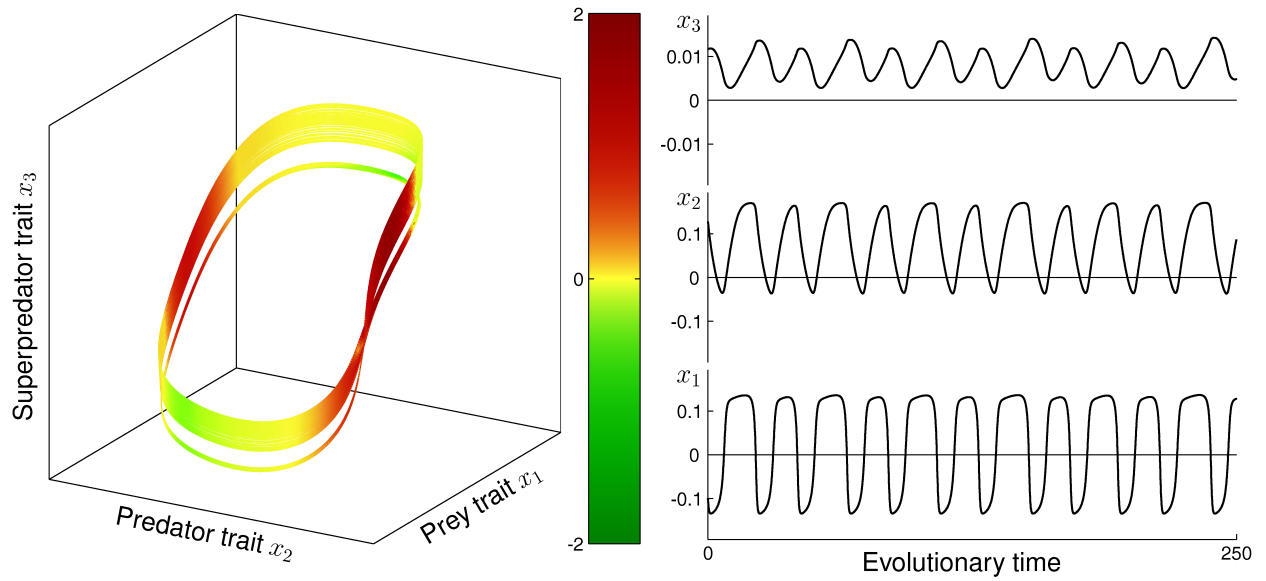


Figure 2: Genetically-driven chaotic Red Queen in a three-species food chain. Left panel: evolutionary strange attractor. The estimated Lyapunov exponents are $L_1 = 8.1321 \cdot 10^{-3}$, $L_2 = -2.3923 \cdot 10^{-6}$, $L_3 = -4.6270 \cdot 10^{-1}$, and the fractal dimension is $2 - L_1/L_3 = 2.0176$ (Kaplan-Yorke formula). Color codes the largest local Lyapunov exponent (see Appendix S2 in Supplementary Material). Chaotic time-series of prey, predator, and superpredator traits are shown on the right. Parameter values as in Fig. 1 and $\mu_1 = 4.2667$.