Asymmetric ecological conditions favor Red-Queen type of continued evolution over stasis

Jan Martin Nordbotten[a,b] and Nils C. Stenseth[c,1]

[a]Department of Mathematics, University of Bergen, N-5020 Bergen, Norway; [b]Department of Civil and Environmental Engineering, Princeton University, Princeton, NJ 08544; and [c]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, N-0316 Oslo, Norway

Four decades ago, Leigh Van Valen presented the Red Queen's hypothesis to account for evolution of species within a multispecies ecological community [Van Valen L (1973) Evol Theory 1(1):1–30]. The overall conclusion of Van Valen's analysis was that evolution would continue even in the absence of abiotic perturbations. Stenseth and Maynard Smith presented in 1984 [Stenseth NC, Maynard Smith J (1984) Evolution 38(4):870–880] a model for the Red Queen's hypothesis showing that both Red-Queen type of continuous evolution and stasis could result from a model with biotically driven evolution. However, although that contribution demonstrated that both evolutionary outcomes were possible, it did not identify which ecological conditions would lead to each of these evolutionary outcomes. Here, we provide, using a simple, yet general population-biologically founded eco-evolutionary model, such analytically derived conditions: Stasis will predominantly emerge whenever the ecological system contains only symmetric ecological interactions, whereas both Red-Queen and stasis type of evolution may result if the ecological interactions are asymmetrical, and more likely so with increasing degree of asymmetry in the ecological system (i.e., the more trophic interactions, host–pathogen interactions, and the like there are [i.e., +/− type of ecological interactions as well as asymmetric competitive (−/−) and mutualistic (+/+) ecological interactions]). In the special case of no between-generational genetic variance, our results also predict dynamics within these types of purely ecological systems.

coevolution | evolution within ecological communities | ecosystem structure | mathematical modeling | mathematical analysis

The major part of any species' environment is represented by the other (interacting) species in the ecosystem; hence, any evolutionary change made by any species within the ecosystem will, in general, be experienced as an environmental change by the coexisting species. This is the basis for the Red Queen's hypothesis as presented by Van Valen (1)—a proposition that is very similar to an idea suggested several decades earlier by Fisher (1930) (ref. 2, pp. 44–45) as well as Darwin (3). The Red Queen's hypothesis continues to attract much attention (3–10). However, within a multispecies ecological system it remains unclear whether evolution will cease or continue in the absence of external abiotic perturbations. Although the Darwinian theory of evolution provides a satisfactory explanation of the mechanisms for evolutionary changes and can be tested against short-term events, it does not in itself provide any predictions regarding large-scale and long-term features of the evolutionary dynamics. Essentially, we do not understand to what extent biotic factors (such as between-species interactions) are important determinants of macroevolution, or rather, what is the relative importance of biotic and abiotic processes in macroevolution (cf. ref. 11). To achieve such an understanding, we need to bring ecological and evolutionary dynamics together into a common model framework.

Here, we address how evolution will proceed within a multispecies ecological system in the absence of external abiotic perturbations. This question was asked by John Maynard Smith[†] in 1980 in a plenary talk on the rate of extinction (and evolution) at the Second International Congress of Systematic and Evolutionary Biology (ICSEB II).[‡] To an audience of several hundred

evolutionary biologists, he asked: "How many think evolution will cease if all abiotic perturbations cease?". The audience was split into two fairly equal parts (see ref. 12, a paper which essentially contains his talk). Our aim is to address this unsolved issue by analyzing a general eco-evolutionary model of a multispecies ecosystem containing all types of ecological interactions (i.e., competitive interactions, trophic interactions, etc.), thereby bringing ecological and evolutionary dynamics together in a common model framework. Much previous work has been done on this topic (see, e.g., refs. 13–17; for a recent review, see ref. 8). Our main methodological contribution is to provide a general analytical framework for addressing this basic question that does not rely on numerical simulations. With this new model framework, we provide new results regarding the conditions for evolutionary stasis and Red-Queen dynamics.

The Model

Definition of the Model. Define the abundance density function of individuals, $n(x, t)$ (abbreviated simply as n when no confusion can arise), taking values at points x in phenotype space ($x \in \Omega$), and in time t for positive times ($t \in \mathbb{R}^+$). The phenotype space is in general multidimensional, representing different phenotypical attributes. Thus, if we consider a model with d traits, then $\Omega \subset \mathbb{R}^d$. The domain Ω (bounded or unbounded) corresponds to admissible phenotype states.

We have chosen to develop a purely deterministic model formulation, of which one important reason is to be able to analyze specific model outcomes (rather than their probability density functions). Our choice is to some extent also influenced

Significance

The work presented here demonstrates analytically for the very first time (to our knowledge) that, within a very general theoretical framework, both Red-Queen type of continuous evolution and evolutionary stasis may be the outcomes of ecological interactions within a multispecies ecological community. Whether or not evolution will cease or continue in an abiotically stable environment (i.e., where there are only biotic forces) has been an unsettled problem within evolutionary biology. Our contribution specifies the ecological conditions for which Red-Queen type of continuous evolution and stasis will result. The new and general eco-evolutionary model provides a profoundly new basis for further theoretical and empirical work within the field of co-evolution within multispecies ecological systems.

[†]It is worth noticing that Maynard Smith (signed as "A Correspondent") highlighted the importance of the Van Valen paper in *Nature* (58) soon after its publication.

[‡]Maynard Smith J, Second International Congress of Systematic and Evolutionary Biology (ICSEB II), July 17–24, 1980, University of British Columbia, Vancouver, BC, Canada.

by our overall question about whether or not evolution will continue should all abiotic perturbations cease (cf. refs. 18 and 19).

The function n denotes the abundance of individuals, which can be characterized by the phenotype vector x at a given time, t. Because the phenotypes are given as a continuous parameter space, we might think of n as a density measured as [individuals]/[phenotype in phenotype space]. When $n(x,t) = 0$, this corresponds to no individuals of phenotype x. Conversely, when $n(x,t)$ has a local and isolated maximum at x, this intuitively corresponds to a monomorphic species with traits x, whereas having several clustered peaks might be seen as a polymorphic species.

Here, we include no spatial dimension; however, it is straightforward to consider n as a function also of spatial position $y \in \mathbb{R}^3$, such that $n = n(x,y,t)$. Thus, let us consider the following nonlocal and nonlinear partial differential equation describing the population growth rate, governing the dynamics of the abundance function, $n = n(x,t)$:

$$\frac{\partial n}{\partial t} = rn - bn^2 + n \int_\Omega \alpha(x,x')n(x')dx' + \nabla \cdot (g\nabla n). \qquad [1]$$

This equation is valid for $n > 0$ and is constrained such that $\partial n/\partial t \geq 0$ when $n = 0$. The parameter functions r, b, and g are all functions of x, as described below. Eq. **1** may be seen either as a generalization of an ecological population growth model to include evolution (through the last term), or conversely, as a reaction-diffusion–type Fisher–Kolmogorov equation with a nonlocal interaction (the second-last term) (20). The following processes are incorporated (see *Methods* for justification):

i) Linear birth and mortality rates are given by $r(x)n(x,t)$. The function $r(x)$ may take positive and negative values ($r(x) < 0$); however, for present phenotypes (and species) it cannot be negative for all x.

ii) Quadratic self-interaction corresponding to self-limitation and is given by $b(x)n(x,t)^2$.

iii) Bilinear interaction between species are given by the integral interaction operator $n(x,t)\int_\Omega \alpha(x,x')n(x',t)dx'$. The function $\alpha(x,x')$ represents the impact of individuals with phenotype x' on individuals with phenotype x. We choose the sign convention such that competition is characterized by negative values of α and symbiotic interaction by positive values.

iv) Generational genetic mutations are included in the model as a diffusion process, given by $\nabla \cdot (g(x)\nabla n(x,t))$; the function $g(x)$ represents the genetically based variability in phenotype between generations, and as usual $\nabla \cdot$ is the divergence operator, whereas ∇ is the gradient, both with respect to x. If $g = 0$, the model will correspond to an ecological model as no new genotypes (and resulting phenotypes) will occur. [Notice that g might be seen as a measure of evolvability (cf. refs. 21 and 22).]

We consider the processes included above as archetypical for the kind of interactions occurring in an eco-evolutionary system (23).

The Parameters. The time-independent parameter functions r, b, α, and g represent the reproductive and competitive traits of individuals possessing the phenotype vector x and are considered intrinsic properties of the multispecies ecological system. This imposed time independence rests on the underlying fundamental assumption that the phenotype space is sufficiently large so that all relevant traits of individuals are included. The arguments of the terms will be suppressed as long as possible to avoid cluttering the equations.

All of our biological conclusions reported below apply for any nonnegative value of b, including $b = 0$. The explicit inclusion of the self-limiting term, b, may seem redundant, as it could be subsumed by the bilinear interaction term by defining a modified interaction term as $\bar{\alpha}(x,x') = \alpha(x,x') - b(x)\delta(x,x')$, where δ is the Dirac measure. However, in this case, the modified interaction term $\bar{\alpha}$ is infinite at $x = x'$, whereas it is reasonable to assume that the original term α is finite. For simplicity, we therefore keep the two terms separate. Nevertheless, we will allow for $b(x) = 0$ (i.e., no local self-regulation). In this case, mutualistic interaction risks enabling a pair of "runaway" species with exponential growth (*Methods*, *Lemma 2*), and the structure of α becomes essential. The presence of a positive self-limitation term, b, allows for simplified criteria on admissible symbiotic interaction without species pairs (or groups) growing exponentially. We further note that the presence of the diffusive term g (i.e., the between-generation genetic variation) ensures that the solution n is continuous; therefore, a purely local self-limiting term b is a reasonable approximation of self-limitation also due to individuals of neighboring traits. It should be noted that if, for instance, $\alpha(x,x')$ is constant in x', then the integral $\int_\Omega \alpha(x,x')n(x')dx'$ represents the global density; that is, the integral value of $\alpha(x,x')$, defined below as $A(x)$, defines the limitation due to the global density of species x.

Clustering of Phenotypes into Species. Our model has no a priori defined species, and the notion of a species can only be considered a posteriori. This implies that we need not consider specific measures by which a new species appear or existing species branch into two separate species—these concepts emerge naturally from Eq. **1**. Indeed, due to the structure of Eq. **1** as a nonlocal Fisher–Kolmogorov equation, the solution $n(x)$ will for many parameter functions tend to involve highly nontrivial "clustering" (see ref. 20 for a thorough review). The clustering in the solution corresponds to separate species, similar to the morphological species concept widely used when delimiting species out in nature and in the fossil record. In real ecological systems, species with low abundance may, due to stochasticity, become extinct; this is, however, beyond the scope of this paper.

The Ecological Structure of the Evolutionary Model. The ecological interactions are defined by the α functions. The ecological interactions can be decomposed into symmetric and asymmetric components. The "symmetric" component of interactions is defined by $\alpha(x,x') + \alpha(x',x)$, and measures competitive $(-/-)$ or mutualistic $(+/+)$ interaction. "Asymmetric" interactions are defined by the remaining component $\alpha(x,x') - \alpha(x',x)$, and measure the degree of trophic interactions, host–pathogen interactions, and the like (i.e., $+/-$ type). Note that asymmetric competitive $(-/-)$ and mutualistic $(+/+)$ ecological interactions with different reciprocal strengths have both symmetric and asymmetric components. When we refer to a symmetric system, this is one where asymmetric interactions are zero, and thus, $\alpha(x,x') = \alpha(x',x)$.

Linking our Approach to Earlier Model Approaches. Our basic model considering continuous variation in traits thus represents a generalization of a standard multispecies community model (e.g., ref. 24) with the addition of a term, $\nabla \cdot (g\nabla n)$, for new genetic variation occurring continuously and randomly (with respect to whatever the local fitness optimum should be) across generations. A diffusion process, similar to the adaptive dynamics approach (see, e.g., ref. 25), is used in the model to represent evolution. With this contribution of ours, we are able to provide analytically derived results, rather than relying on numerical simulation, thus being able to reach more general conclusions.

The main novelty of this new model formulation is to bring together ecological and evolutionary dynamics within a common analytical model framework:

i) If there is no between-generation genetic variation ($g = 0$), the model will be a generalization of fairly standard ecological models (e.g., ref. 24) both by making it continuous as well as reducing the emphasis on individual species as we consider the distribution of phenotypes directly; in this case, there will be no evolution.

ii) If we allow for between-generation genetic variation ($g > 0$), the ecological model becomes an eco-evolutionary model. When the between-generation variation is significant relative to the intrinsic growth rate of the ecological system, evolution might occur.

Common with many similar earlier models within the field of ecology and evolution (including the adaptive dynamics approach), our model assumes asexual reproduction.

Our Objectives. We address the following three specific questions:

i) Under what conditions are evolution of n bounded, such that the number of individuals $n(x)$ never grows uncontrollably for any trait x?

ii) Under what conditions are the stationary solutions of Eq. **1** stable, such that an evolutionarily stable state without any change in the species composition $n(x)$ may arise?

iii) Under what conditions, and in what sense, will the species modeled by Eq. **1** continue to evolve (i.e., Red-Queen type of evolution[§]) and under what conditions will evolution cease (i.e., achieving stasis[¶])?

Our results will fully settle question *i*, but more importantly provide several new results regarding questions *ii* and *iii*.

Results

Our results regarding Eq. **1** are collected in *Lemma 1*, *Lemma 2.1*, and *Lemma 2.2* (*Methods*), and *Lemma 3.1* and *Lemma 3.2* (*Supporting Information*). Together, they characterize the temporal (ecological and evolutionary) dynamics. We summarize the results here, using the notation that the integral of the positive part of the interaction kernel [i.e., the sum of all positive interactions acting on a species with phenotype x, is defined as $A_2^+(x) = \int_\Omega \max[\alpha(x,x'), 0]\, dx'$]. In this summary, the x-dependent parameters are implicitly treated as constants.

i) If the level of self-regulation in the system is such that $b < A_2^+$, the system is subjected to blowup, which we denote the "unbounded state." We consider the blowup of the system as unreasonable; this inequality thus imposes a restriction on admissible parameters. From this, we conclude that there must be sufficient self-limiting competition to dominate over synergetic/mutualistic interaction. Sufficient self-limitation can also be achieved by the structure of α (thus allowing for $b = 0$; *Lemma 2.1* and *Lemma 2.2*).

ii) If the system is stable as defined in *Lemma 1*, this implies that a constant (with respect to x) and stable (with respect to time) evolutionary state exists wherein species cannot be identified (i.e., without any peaks in the phenotype space). We denote this as the "constant state." The structure of α [describing the nature of and strength of the between-species interactions (trophic interaction, competition, and the like)] that allows this to happen would be where there is very little synergetic/mutualistic interaction. We note that because it is the real part of the Fourier transform of α that determines stability, it is only the symmetric interactions that affect stability. Asymmetry in $\alpha(x,x')$ may thus impact the time evolution, but not the stability of constant state.

iii) The case where the system does not blow up (see *i* above), although unstable in the constant state, is the most biologically interesting. We call this the "species state." This is the case where the system provides solutions where species may be identified and seen to coexist in a reasonably well-behaved state. For particular parameter regimes, *Lemma 3.1* and *Lemma 3.2* show that, in the case of only symmetric interactions, stationary solutions corresponding to stasis (defined as a stationary steady state) will arise. It should be noticed that when $+/-$ ecological interactions are absent/missing, the

conditions do not correspond to real ecological systems, but might correspond to artificial laboratory systems restricted to only competitive pairs or mutualistic pairs.

iv) Our next step is to characterize characterize systems in the species state where the interaction α is nonsymmetric. For homogeneous systems, *Lemma 1* shows that, in the linear regime, the solution tends to settle in a continuously evolving state (i.e., Red-Queen type of evolution) depending on the extent and character of asymmetry in the system. It should be noted that asymmetry may exist in mutualistic and competitive ecological interactions as well as the (obvious) trophic and host–parasite type of ecological interactions, because for any two traits x and x', there may be an asymmetric component of the interaction, even if both $\alpha(x,x')$ and $\alpha(x',x)$ are positive (or negative). On this basis, we conclude that asymmetric ecological interactions favor Red-Queen type of evolution.

v) Finally, we show, as a corollary to *Lemma 2.1* and *Lemma 2.2*, that for any stable system with a finite trait space Ω, there must exist a state $n_0(x)$ for the time evolution of the solution $n(x,t)$, which the time-dependent solution essentially returns to infinitely many times. This state n_0 can thus either represent stasis or be interpreted as a limiting factor on the Red-Queen type of evolution.

Altogether, our biological conclusions are as follows:

i) An ecological system with only symmetric interactions, such that $\alpha(x,x') = \alpha(x',x)$ (each pair of species is affected by the other symmetrically), will, in the absence of external abiotic perturbations, favor stasis. This may be understood intuitively in the sense that, without asymmetric interaction, there is no notion of a preferred direction for continued evolution of the system.

ii) An ecological system with asymmetric interactions (such as predator–prey interactions) may lead to both stasis and Red-Queen type of continued evolution: The stronger (or more dominant) the asymmetric ecological interactions (such as $+/-$ interactions and asymmetric $-/-$ and $+/+$ interactions in the ecological system) are, the more likely Red-Queen type of evolution will be—fully independent of the between-generation genetic variation (quantified by g).[#]

iii) As a corollary, *i* and *ii* imply that ecological continued temporal changes (i.e., only temporal variation in the abundances of the interacting phenotypes/species) and evolutionary dynamics (with both temporal variation in the abundance of the interacting phenotypes/species as well as evolution of new phenotypes and extinction of existing phenotypes) are particularly likely if there is asymmetric ecological interactions, including, for instance, asymmetric competitive interaction between species. For evolution to occur, $g > 0$ is required.

Discussion

General. Our answer to "Will evolution cease if all abiotic perturbations cease?" is that, if all ecological interactions are symmetric (implying no trophic interactions), evolution will cease in an abiotically stable environment. If, however, there are asymmetric interactions, we have shown that the more asymmetry in the ecological system (in the sense of asymmetry with the same frequency in Fourier space as the interspecies distance) the more likely is evolution to continue in a Red-Queen type of fashion, even in the absence of abiotic perturbations, a conclusion profoundly extending the earlier conclusion reached by Stenseth and Maynard Smith (26).

It is worth noting that, in our analysis, the evolutionary pattern (stasis vs. Red Queen) is primarily a property of the ecological system within which a species finds itself [i.e., $\int_{\Omega} \alpha(x,x')n(x)dx'$]. This is explicitly the case for the linearized analysis and holds in the general case, both when there is no between-generation variation (i.e., $g = 0$; no evolution), as well as when there is much between-generation variation (i.e., $g \gg 0$). This is a theoretical conclusion of profound importance—to our knowledge, no one before has been able to reach a similarly general conclusion within a generalized eco-evolutionary model. Here, it suffices to point out that our analysis links the Red-Queen evolutionary literature profoundly to the food web literature (27, 28). Indeed, this brings ecology and evolution closer together: the evolutionary dynamics being a direct result of the property of the ecological system the species finds itself in, just as with the adaptive dynamics perspective (see, e.g., refs. 13–16 and 25).

We might assume either $g = 0$ (to make it a purely ecological model), or consider $g \gg 0$ (to include evolution in the ecological model). It is, however, the combination of both ecological and evolutionary dynamics that applies in nature. Much of the literature on the Red-Queen hypothesis focuses on (+/−) type of ecological interactions, especially trophic and parasite–host interactions (e.g., refs. 9 and 29–32), which is consistent with our results showing that this is indeed the type of asymmetric ecological interactions that would yield Red-Queen type of evolution. The importance of asymmetry has earlier been pointed out by, e.g., refs. 16 and 33.

Interpretation. The interpretation of the solution $n(x,t)$ in terms of species, lag, and mean and variance in traits (*Supporting Information*) allows our model framework to be directly linked to the lag–load concept of Maynard Smith (34). Maynard Smith suggested that genetic evolution of a species i will reduce the evolutionary lag L_i in proportion to the current lag—that is to say that the following equation holds with a time-independent coefficient β_i, a coefficient being equivalent to the coefficient β_{ii} in Stenseth and Maynard Smith (26):

$$\frac{dL_i}{dt} = -\beta_i L_i(t). \qquad [2]$$

Furthermore, Fisher (2) assumed that fitness of a species i is proportional to the genetic variance Σ_i^2. For our model, it is reasonable to assume that, near equilibrium, fitness may be linearly approximated by the evolutionary lag; thus the following equation holds with a time-independent coefficient γ_i:

$$\frac{dL_i}{dt} = -\gamma_i \Sigma_i^2(t). \qquad [3]$$

It is worth noting that the lag–load model and Fisher's fundamental theorem can hold simultaneously, if and only if $\Sigma_i^2(t) = (\beta_i/\gamma_i)L_i(t)$. This will only be the case if there is no genetic variance in the optimal state [for which by definition $L_i(t) = 0$]. In our model, it is impossible for all individuals of a species to converge to a single trait, because the presence of the g term (i.e., between-generation genetic variation) will ensure that, for every generation, a slight variability in traits remains.

This leads us to the observation that Fisher's model is applicable at early stages of evolution, which in practice implies the initial response to external environmental forcing. In contrast, the lag–load model is applicable to the later stages of evolution within an environment with fixed external forcing.

Another key concept within the evolutionary literature should be mentioned—the concept of evolutionarily stable strategies (ESS), originally contributed by Maynard Smith and Price (35); see also Maynard Smith (36, 37); for a mathematical definition of this concept for differential-equation population models, see ref. 38. This concept will only apply to the case of stasis or close to stasis—not Red Queen. Furthermore, our results contradict the results given within the context of ESS, where Rosenzweig et al. (39) conclude that Red-Queen–type evolution can only be

supported for unbounded traits (see, e.g., refs. 15, 25, and 30 for earlier work on this topic). Their conclusion is obtained within the context of a lag–load formalism, where the species are a priori defined. A complete analysis of the emergence of ESS within our new model remains to be done. We note, however, an important distinction from our framework: in traditional discussions of ESS, one considers a species with an optimized trait, common for all individuals of that species. As discussed after Eq. **3**, this is impossible, thus in our model framework an ESS must be considered within the context where the trait variability is the minimum variability permitted by the between-generation genetic variation, evolvability, g.

Further Challenges. The biological challenges emerging from our study are as follows: (*i*) interpreting previously published models for the Red Queen within our new model framework; (*ii*) interpreting the literature on food web coupled with evolution (see, e.g., refs. 40 and 41), determining whether we can understand the different modes of evolution as a consequence of the food web stature; (*iii*) interpreting paleontological records in light of our current results (see, e.g., refs. 42–44); (*iv*) linking our model structure to the ecometrics literature within the field of evolutionary biology (see, e.g., refs. 45–47; and (*v*) undertaking experimental studies using microorganisms to test the conclusion of our analysis—and beyond.

The mathematical challenges emerging from our study are as follows: (*i*) a further analysis of the case of symmetric ecological interaction, to settle the question as to whether symmetric interaction can preclude Red-Queen type of evolutionary dynamics also for moderate g; (*ii*) a more complete treatment of the long-term dynamics for the nonlinear evolutionary regime, including the categorization of stationary solutions and limit cycles; (*iii*) a rigorous understanding of the link between the continuous solution and the identification of individual species; (*iv*) incorporation of spatial heterogeneity and stochastic environmental forcing (see, e.g., ref. 48) in the model framework; (*v*) incorporation of sexual reproduction and age/size-structured populations in the model framework; and (*vi*) efficient computational tools allowing for high-dimensional numerical simulation.

Essentially, our paper contributes to the further development of a theory for understanding large-scale features of the evolutionary dynamics (see also refs. 49–52).

Methods

Justification for the Mathematical Model. Consider the following multispecies ecological model:

$$\frac{\partial n}{\partial t} = f_b(n) - f_d(n). \qquad [4]$$

The functional $f_b(n)$ describes the rate of birth of individuals with trait x, and similarly the functional $f_d(n)$ describes the rate of death. We consider death as proportional to the number of individuals n, and furthermore dependent on interaction and competition, justifying the form:

$$f_d(n) = \left(r_d + bn - \int_{\Omega} \alpha(x,x')n(x')dx'\right)n. \qquad [5]$$

We consider the number of births from trait x as proportional to $n(x)$ but recognize that the actual newborns may have slightly different traits. If we assume that the traits of the next generation are spread according to a multidimensional Gaussian distribution $N_d(x,x')$ with covariance matrix d, this leads to the following:

$$f_b(n) = r_b \int_{\Omega} N_d(x,x')n(x')dx. \qquad [6]$$

However, Gaussian spreading is the solution operator of the diffusion equation; thus, for small variability between generations, we can use a Taylor expansion to obtain the following:

$$f_b(n) = r_b \exp(\nabla \cdot (d\nabla))n \approx r_b(n + \nabla \cdot (d\nabla n)). \qquad [7]$$

By letting $g = r_b d$, and $r = r_b - r_d$, we obtain Eq. **1**. Note that a generalization to nonlocal, "innovative," genetic mutations can be incorporated by using a

non-Gaussian spreading with fatter tails; in this case, the diffusive term would take the form of a fractal derivative operator, e.g., $\nabla \cdot (d\nabla^\nu n)$, for some exponent $0 < \nu \leq 1$.

We may distinguish two types of phenotypes (represented as dimensions in phenotype space): linear and circular. The linear phenotype is the most intuitive and represents any quantity that is strictly ordered (such as size). Linear phenotypes may be either bounded or infinite. The circular phenotype represents quantities that contain no ends, such as relative hues of color in the red–green–blue scheme, stripe orientation on a zebra, plant growth orientation relative to external factors, or phases of growth relative to the seasons (20).

Due to the presence of a second-order differential term, we assign to the boundary of Ω either Dirichlet or Neumann boundary conditions (53). A Dirichlet boundary condition is equivalent to specifying the species density n at the boundary (typically 0), whereas a Neumann boundary condition is equivalent to specifying the normal component of $g(n)\nabla n$ (and hence the evolutionary drift, also typically 0) across the boundary. Note that, in the dimensions associated with circular phenotypes, the domain is periodic, and thus the domain does not contain a boundary.

We refer to the ecological system given in Eq. 1 with general parameter functions $r(x)$, $b(x)$, $g(x)$, and $\alpha(x, x')$ as "heterogeneous"; most of our results hold in this setting. However, to facilitate the presentation and to obtain results in *Lemma 1*, which rely on the Fourier transform, we will sometimes work with the instructive case of constant coefficients, which we refer to as "homogeneous." This implies the simplifications $r(x) = r$, $b(x) = b$, and $g(x) = g$. Furthermore, in the homogeneous setting, we assume the function describing the ecological interactions to depend only on signed distance in phenotype space [i.e., $\alpha(x, x') = \alpha(x - x')$]. The assumption of homogeneity implies that we study the interspecies interaction, rather than the impact of the competitive advantages of various locations in the phenotype space Ω.

Stability of Constant Stationary States. Stationary states for Eq. 1 are obtained by solving for $\partial n/\partial t = 0$. These stationary states can be divided into three types: zero, constant, and variable. Here, we define the (negative) integral of the kernel as $A(x) = -\int_\Omega \alpha(x, x') dx'$.

Constant steady-state solutions (with respect to x) are available for homogeneous systems. Then the differential term vanishes, and furthermore the integral term simplifies. We are then left with $0 = rn - (b + A)n^2$. This equation has two solutions, the zero solution, which is of no interest, and the nonzero constant solution, which we denote $n_C = r/(b + A)$.

Variable Steady-States Solutions. Variable steady-states solutions are in general defined as any nontrivial solutions to the nonlinear equation obtained from Eq. 1 by setting $\partial n/\partial t = 0$. In general, this equation must be solved numerically.

The zero stationary state will always be unstable, because we assume that $r > 0$ for some x. However, the nonzero constant state n_C is less obvious. Indeed, the system has some similarities with the Turing equations (54), and the stability depends on the balance between the nonlocal interaction and diffusion.

We proceed considering the homogeneous system, after which by linearizing [Eq. 1] around n_C, we obtain the following equation for the deviation $m = n - n_C$. Here, it is assumed that m is infinitesimal and periodic:

$$\frac{\partial m}{\partial t} = -bn_C m + n_C(\alpha * m) + g\Delta m. \tag{8}$$

The linear coefficient evaluates to zero, since $r - (b + A)n_C = 0$; furthermore, we denote the convolution integral by an asterisk (*). Considering the case where we take Neumann boundary conditions, a Fourier transform of Eq. 8 now leads to the following:

$$\frac{\partial \hat{m}(\mathbf{k})}{\partial t} = f(\mathbf{k})\hat{m}(\mathbf{k}). \tag{9}$$

Here, we have denoted the transformed functions by a hat (i.e., $\hat{m}$ is the Fourier transform of m), and the transform variable is denoted by $\mathbf{k}$. The function f is defined as follows:

$$f(\mathbf{k}) \equiv -bn_C\delta(\mathbf{k}) + n_C\hat{\alpha}(\mathbf{k}) - g|2\pi\mathbf{k}|^2. \tag{10}$$

Based on Eqs. 8 and 9, we now deduce the following stability modes:

i) By setting $\mathbf{k} = 0$, we see that the system is "locally" unstable if $n_C(b + A) > 0$ (i.e., any constant perturbation will grow exponentially).
ii) The system is "nonlocally" unstable if there exists a $\mathbf{k} > 0$ such that $f(\mathbf{k}) > 0$. This implies that patterns of frequency $\mathbf{k}$ will be unstable, even though the system may be locally stable according to i).
iii) The system is "globally" stable if $n_C \operatorname{Re}\{\hat{\alpha}(\mathbf{k})\} - g|2\pi\mathbf{k}|^2 < 0$ for all $\mathbf{k} > 0$.

Note that i is just a special case of ii, where $\mathbf{k} = 0$. Furthermore, for convenience, we denote the frequency where $f(\mathbf{k})$ attains its maximum as $\mathbf{k}_*$, which we refer to as the "most unstable mode."

We can deduce more from the linearized analysis. Indeed, the linear structure of Eq. 10 allows us to write the time evolution of the perturbation explicitly as follows:

$$\hat{m}(\mathbf{k}, t) = \hat{m}(\mathbf{k}, 0)e^{f(\mathbf{k})} \tag{11}$$

In particular, this expression shows that perturbations decay (and grow) in a stationary way (with respect to motion in the Ω domain) if and only if $\operatorname{Im}\{f(\mathbf{k})\} = n_C\operatorname{Im}\{\hat{\alpha}(\mathbf{k})\} = 0$. In particular, if $\operatorname{Im}\{\hat{\alpha}(\mathbf{k})\} \neq 0$, the most unstable (and thus dominant) perturbation will be non-stationary. The following lemma summarizes the situation.

Lemma 1. *The constant stationary state n_C is stable if and only if $f(\mathbf{k}) < 0$ for all $\mathbf{k}$. Moreover, nonlocally unstable growth is stationary in Ω if and only if $\operatorname{Im}\{\hat{\alpha}(\mathbf{k})\} = 0$ for all $\mathbf{k}$ where $f(\mathbf{k}) > 0$.*

The homogenous setting needed for the Fourier transform analysis leads to results where the presence of the evolution term g is strictly stabilizing. However, for heterogeneous parameters, the opposite case may arise, due to the existence of Turing-like instabilities in the system (54) (see *Supporting Information* for an example).

Boundedness of time evolution: We now consider the evolution given by equation (1). In particular, we will ascertain under what conditions we can guarantee that a "blow-up" of the solution n cannot occur. This is a prerequisite for the mathematical well-posedness (existence and uniqueness of solutions, etc.) of the model. Indeed, we define the standard L^q norms by the notation $\|n\|_q = (\int_\Omega n^q)^{1/q}$. Here it is understood that in the present setting, we simplify the notation since it is known that $n \geq 0$. Now, by integrating equation (1), we obtain

$$\frac{d}{dt}\|n\|_1 \leq r^+\|n\|_1 - b^-\|n\|_2^2 + \int_\Omega n(y) \int_\Omega \alpha(x, x')n(x')dx' \, dy + \int_\Omega \nabla \cdot (g\nabla n)dx. \tag{12}$$

Here, we define $r^+ = \max_x r(x)$ and $b^- = \min_x b$. The third term can be bounded from above by using that $n(x) \geq 0$ and the triangle inequality, to obtain

$$\int_\Omega n(x) \int_\Omega \alpha(x, x')n(x')dx' \, dx \leq A_1^+\|n\|_2^2. \tag{13}$$

In order to allow for $b = 0$ we denote

$$A_1^+ \equiv \max_{n(x) > 0} \frac{\int_\Omega n(x)\int_\Omega \alpha(x - x')n(x')dx' \, dx}{\|n\|_2^2} \leq \max_x \int_\Omega \max[0, \alpha(x, x')]dx' \equiv \max_x A_2^+(x). \tag{14}$$

Furthermore, the differential term can be integrated by parts, after which the boundary terms can be omitted for Neumann boundary conditions. Thus, equation (12) satisfies the inequality:

$$\frac{d}{dt}\|n\|_1 \leq r^+\|n\|_1 - b^-\|n\|_2^2 + A_1^+\|n\|_2^2. \tag{15}$$

Now, since $\|n\|_1 \leq \|n\|_2$, it holds that $\|n\|_1$ is bounded satisfying

$$\|n\|_1 \leq \frac{r^+}{b^- - A_1^+} \leq \frac{r^+}{b^- - A_2^+}. \tag{16}$$

Again, we summarize the result in a lemma:

Lemma 2.1. *The time evolution $n(x, t)$ remains bounded in the L^1 norm if $b^- > A_1^+$.*

We will, for simplicity of interpretation, typically consider the condition $b^- > A_1^+$ in Lemma 2.1 (and in similar instances below) in the two specialized cases where either:

i) The self-limitation dominates synergetic interaction pointwise, thus, $b(x) > A_2^+(x)$; or

ii) There is no self-limitation, $b = 0$, but interaction has strictly negative eigenvalues, e.g., $A_1^+ < 0$.

Case i) allows us to obtain a stronger result, not available for $b = 0$: It may be of interest to distinguish the total number of individuals, captured by the L^1 norm, from the maximum density of individuals with a single trait, which is captured by the maximum norm, denoted L^∞. By considering the point x at which $n(x, t)$ attains a maximum (over x), we see that the maximum can remain bounded only if $b(x) > A_2^+(x)$ for all x. We summarize this in the second part of the lemma.

Lemma 2.2. The time evolution $n(x, t)$ remains bounded in the L^∞ norm if $b(x) > A_2^+(x)$ for all x.

Lemmas 2.1 and 2.2 have an interesting corollary. Since the solution $n(x, t)$ lives in a space of bounded functions, if furthermore Ω is finite, Eq. 1 is a nonlinear diffusion equation with bounded coefficients, and the space of solutions is compact. This implies that we may choose a sequence of sampling times $t = \{t_1, t_2, \ldots\}$, with $t_i - t_{i-1} > \Delta t$ for some time interval Δt, and corresponding solutions $n(x, t_i)$. Since $n(x, t_i)$ lies in a compact space, any sequence has a sub-sequence which is a Cauchy sequence [see e.g. (55)]. We express this statement in the sense that there exist for any small number ϵ, a sub-sequence of t_i of infinitely many sampling times $t = \{t_{j_1}, t_{j_2}, \ldots\}$ and a fixed point $n_0(x)$, such that $\|n(x, t_{j_i}) - n_0(x)\|_1 \leq \epsilon$ for all j_i. This shows that even if Red-Queen evolution occurs, the system will return to essentially the same species distribution infinitely many times (resembling convergent evolution).

Evolution Toward Stasis. In *Lemma 1*, *Lemma 2.1*, and *Lemma 2.2*, we obtain bounds on the parameter values that are required to have biologically plausible evolution. Furthermore, *Lemma 1* shows the time evolution in the linearized regime. However, the general question regarding the behavior of solutions in the fully nonlinear regime remains open. Here, we partially answer this question by showing two different cases in which it can be proved that the solution evolves toward stasis. This is achieved by showing that the governing equations have a so-called gradient flow structure when interactions are symmetric and either

i) the evolvability is negligible [e.g., $g(x) = 0$; i.e., only ecological dynamics], or

ii) the evolvability is sufficiently large [e.g., $g(x) \gtrsim r(x)$; i.e., evolutionary dynamics dominating over ecological interaction].

A gradient flow structure is based on the physical analogy where it is possible to define some "potential energy," and where the system evolves to minimize that energy; gradient flow theory has been previously used to establish stability of biological systems; see, e.g., Hopfield (56) for an early example. If, furthermore, there is dissipation in the system (e.g., friction, in the physical analogy), this implies that the solution will approach a stationary state, i.e., stasis (see, e.g., ref. 57 for an introduction). We provide the details of this approach through *Lemma 3.1* and *Lemma 3.2* in *Supporting Information*.

1. Van Valen L (1973) A new evolutionary law. *Evol Theory* 1:1–30.
2. Fisher RA (1930) *The Genetical Theory of Natural Selection* (Clarendon, Oxford).
3. Darwin C (1859) *On the Origin of Species* (John Murray, London).
4. Maynard Smith J (1976) A comment on the Red Queen. *Am Nat* 110(973):325–330.
5. Stenseth NC (1979) Where have all the species gone? On the nature of extinction and the Red Queen hypothesis. *Oikos* 33(2):196–227.
6. Stenseth NC (1985) Darwinian evolution in ecosystems: the Red Queen viw. Evolution. *Essays in Honour of John Maynard Smith*, eds PJ Greenwood, Harvey PH, Slatkin M (Cambridge Univ Press, Cambridge, UK), pp 55–72.
7. Salthe SN (2008) Natural selection in relation to complexity. *Artif Life* 14(3):363–374.
8. Liow LH, Van Valen L, Stenseth NC (2011) Red Queen: From populations to taxa and communities. *Trends Ecol Evol* 26(7):349–358.
9. Brockhurst MA, et al. (2014) Running with the Red Queen: The role of biotic conflicts in evolution. *Proc Roy Soc Biol Sci* 281(1797):20141382.
10. Voje KL, Holen ØH, Liow LH, Stenseth NC (2015) The role of biotic forces in driving macroevolution: Beyond the Red Queen. *Proc Roy Soc Biol Sci* 282(1808):20150186.
11. Vrba ES (1995) On the connections between paleoclimate and evolution. *Paleoclimate and Evolution with Emphasis on Human Origins*, eds Vrba ES, Denton GH, Partridge TC, Burckle LH (Yale Univ Press, New Haven, CT), pp 24–45.
12. Maynard Smith J (1989) The causes of extinction. *Philos Trans R Soc Lond B Biol Sci* 325(1228):241–252.
13. Kisdi E (1999) Evolutionary branching under asymmetric competition. *J Theor Biol* 197(2):149–162.
14. Kisdi E, Geritz SA (2001) Evolutionary disarmament in interspecific competition. *Proc Roy Soc Biol Sci* 268(1485):2589–2594.
15. Kisdi É, Jacobs FJA, Geritz SAH (2002) Red Queen evolution by cycles of evolutionary branching and extinction. *Selection* 2(1-2):161–176.
16. Law R, Marrow P, Dieckmann U (1997) On evolution under asymmetric competition. *Evol Ecol* 11(4):485–501.
17. Khibnik AI, Kondrashov AS (1979) Three mechanisms of Red Queen dynamics. *Proc Roy Soc Biol Sci* 264:1049–1056.
18. Dieckmann U, Ferrière R (2004) Adaptive dynamics and evolving biodiversity. *Evolutionary Conservation Biology*, eds Ferrière R, Dieckmann U, Couvet D (Cambridge Univ Press, Cambridge, UK), pp 188–224.
19. Parvinen K (2005) Evolutionary suicide. *Acta Biotheor* 53(3):241–264.
20. Murray JD (2003) *Mathematical Biology II: Spatial Models and Biomedical Applications* (Springer, New York), 3rd Ed.
21. Houle D (1992) Comparing evolvability and variability of quantitative traits. *Genetics* 130(1):195–204.
22. Hansen TF, Houle D (2008) Measuring and comparing evolvability and constraint in multivariate characters. *J Evol Biol* 21(5):1201–1219.
23. Roughgarden J (1979) *Theory of Population Genetics and Evolutionary Ecology: An Introduction* (Macmillan, New York).
24. May RM (1973) Stability and complexity in model ecosystems. *Monogr Popul Biol* 6:1–235.
25. Dieckmann U, Brännström Å, HilleRisLambers R, Ito H (2007) The adaptive dynamics of community structure. Mathematics for Ecology and Environmental Sciences, Biological and Medical Physics, Biomedical Engineering, eds Takeuchi Y, Iwasa Y, Sato K (Springer, Berlin), pp 145–177.
26. Stenseth NC, Maynard Smith J (1984) Coevolution in ecosystems: Red Queen evolution or stasis? *Evolution* 38(4):870–880.
27. Pimm SL, Pimm JW (1982) Resource use, competition, and resource availability in Hawaiian honeycreepers. *Ecology* 63(5):1468–1480.
28. Pimm SL (1984) The complexity and stability of ecosystems. *Nature* 307(5949):321–326.
29. Dawkins R, Krebs JR (1979) Arms races between and within species. *Proc R Soc Lond B Biol Sci* 205(1161):489–511.
30. Marrow P, Law R, Cannings C (1992) The coevolution of predator-prey interactions: ESSs and Red Queen dynamics. *Proc Roy Soc Biol Sci* 250(1328):133–141.
31. Nuismer SL, Ridenhour BJ, Oswald BP (2007) Antagonistic coevolution mediated by phenotypic differences between quantitative traits. *Evolution* 61(8):1823–1834.
32. Rabajante JF, et al. (2015) Red Queen dynamics in multi-host and multi-parasite interaction system. *Sci Rep* 5:10004.
33. Heard MJ, Sax DF (2013) Coexistence between native and exotic species is facilitated by asymmetries in competitive ability and susceptibility to herbivores. *Ecol Lett* 16(2):206–213.
34. Maynard Smith J (1976) What determines the rate of evolution? *Am Nat* 110(973):331–338.
35. Maynard Smith J, Price GR (1973) The logic of animal conflict. *Nature* 246:15–18.
36. Maynard Smith J (1982) *Evolution and the Theory of Games* (Cambridge Univ Press, Cambridge, UK).
37. Maynard Smith J (1976) Evolution and the theory of games. *Am Sci* 64(1):41–45.
38. Reed J, Stenseth NC (1984) Evolution of cannibalism in an age-structured population. *Bull Math Biol* 46(3):371–377.
39. Rosenzweig ML, Brown JS, Vincent TL (1987) Red Queens and ESS: The coevolution of evolutionary rates. *Evol Ecol* 1(1):59–94.
40. Ito H, Shimada M, Ikegami T (2009) Coevolutionary dynamics of adaptive radiation for food-web development. *Popul Ecol* 51(1):65–81.
41. Takahashi D, Brännström Å, Mazzucco R, Yamauchi A, Dieckmann U (2013) Abrupt community transitions and cyclic evolutionary dynamics in complex food webs. *J Theor Biol* 337:181–189.
42. Barnosky AD (2001) Distinguishing the effects of the Red Queen and Court Jester on Miocene mammal evolution in the northern Rocky Mountains. *J Vertebr Paleontol* 21(1):172–185.
43. Benton MJ (2009) The Red Queen and the Court Jester: Species diversity and the role of biotic and abiotic factors through time. *Science* 323(5915):728–732.
44. Benton MJ (2015) Exploring macroevolution using modern and fossil data. *Proc Roy Soc Biol Sci* 282(1810):20150569.
45. Eronen JT, et al. (2010) Ecometrics: The traits that bind the past and present together. *Integr Zool* 5(2):88–101.
46. Polly PD, et al. (2011) History matters: Ecometrics and integrative climate change biology. *Proc Roy Soc Biol Sci* 278(1709):1131–1140.
47. Fritz SA, et al. (2013) Diversity in time and space: Wanted dead and alive. *Trends Ecol Evol* 28(9):509–516.
48. Sæther BE, Engen S (2015) The concept of fitness in fluctuating environments. *Trends Ecol Evol* 30(5):273–281.
49. Pelletier F, Garant D, Hendry AP (2009) Eco-evolutionary dynamics. *Philos Trans R Soc Lond B Biol Sci* 364(1523):1483–1489.
50. Post DM, Palkovacs EP (2009) Eco-evolutionary feedbacks in community and ecosystem ecology: Interactions between the ecological theatre and the evolutionary play. *Philos Trans R Soc Lond B Biol Sci* 364(1523):1629–1640.
51. Kendall BE (2015) Some directions in ecological theory. *Ecology* 96(12):3117–3125.
52. Power DA, et al. (2015) What can ecosystems learn? Expanding evolutionary ecology with learning theory. *Biol Direct* 10(1):69.
53. Evans LC (2010) *Partial Differential Equations* (American Mathematical Society, Providence, RI), 2nd Ed.
54. Turing AM (1952) The chemical basis of morphogenesis. *Phil Trans R Soc B* 237(641):37–72.
55. Rudin W (1987) *Real and Complex Analysis* (McGraw-Hill, New York), 3rd Ed.
56. Hopfield JJ (1984) Neurons with graded response have collective computational properties like those of two-state neurons. *Proc Natl Acad Sci USA* 81(10):3088–3092.
57. Mielke A (2011) A gradient structure for reaction–diffusion systems and for energy-drift-diffusion systems. *Nonlinearity* 24(4):1329–1346.
58. A Correspondent (1973) The Red Queen. *Nature* 245:353–354.