

Link between Population Dynamics and Dynamics of Darwinian Evolution

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We provide the link between population dynamics and the dynamics of Darwinian evolution via studying the joint population dynamics of *similar* populations. Similarity implies that the *relative* dynamics of the populations is slow compared to, and decoupled from, their *aggregated* dynamics. The relative dynamics is simple, and captured by a Taylor expansion in the difference between the populations. The emerging evolution is directional, except at the singular points of the evolutionary state space. Here “evolutionary branching” may occur. The diversification of life forms thus is demonstrated to be a natural consequence of the Darwinian process.

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Modeling evolution while assuming a predefined and fixed fitness function essentially precludes understanding biological diversity: The fittest wins and excludes all other contestants. While the traditional “allopatric” theory of speciation [1,2] circumvents the problem by assuming strict spatial segregation between the old and the new species, understanding the *coexistence* of species requires unrealistic parameter fine-tuning.

The mechanism-based concept of fitness [3] allows a more consistent and more natural picture. Interactions between the contestants lead to a fitness function that depends on their relative abundances, a phenomenon referred to as “frequency dependence” [4,5]. The evolutionary process itself modifies the adaptive landscape. As evolution is not a pure gradient dynamics, its path may converge to a point where it is overtaken by a fitness minimum [6], which it leaves by branching [7–9]. This “evolutionary branching” was suggested to be the basis for “adaptive speciation” [10,11].

We restrict our analysis to evolution of asexual organisms via small steps in a continuous evolutionary state space. In this context, the fixed point analysis of the “adaptive dynamics” driven by frequency-dependent fitness landscapes was developed [7–9]. The theory was based on the concept of “invasion fitness” $s_{x_1, x_2, \dots, x_L}(y)$ representing the growth rate of an exceedingly rare y invader in a background of coestablished populations of x_1, \dots, x_L . To ensure that evolution is fully constrained by invasion fitness, it was assumed that (a) mutations are sufficiently rare that new mutants arrive only after equilibration of the already existing populations, i.e., at most one mutant substitutes at a time; (b) a mutant’s fate is determined by its and its progenitor’s mutual invasion fitnesses. Here, our goal is to remove these rather questionable

conditions by carrying out the original Darwinian program of stepping from population dynamics to evolutionary dynamics using only first principles and mild assumptions.

To build a rigorous underlying theory of evolution, we consider the joint population dynamics of *similar* populations. The mutation process is not explicitly represented in our treatment: We discuss the joint population dynamics of the mutants and their ancestors once the mutants have been generated. We suppose that population abundance (number of individuals) is large enough to consider it as a continuous variable and to neglect demographic stochasticity. Abundance is considered as a complete description of the population state; i.e., we neglect population structure with respect to age, body size, location, etc. (In many cases, population structure can be regarded as already relaxed on the slow time scale we consider [12].)

We collect the inherited properties of the individuals into a continuous “strategy” variable y (or x), which is an element of the “strategy space” $\mathcal{X} \subset \mathbb{R}^k$. Let ν denote the (Schwartz) distribution of the populations in the strategy space \mathcal{X} . Population dynamics is defined by the non-linear equation

$$\frac{d\nu(y)}{dt} = r(y, \nu)\nu(y) \quad y \in \mathcal{X}. \quad (1)$$

Here, $r(y, \nu)$ denotes the growth rate (difference between the birth and death rates) of strategy $y \in \mathcal{X}$, conditional on the background distribution ν . r plays the role of mechanism-based fitness. Its argument ν represents frequency dependence.

The “generalized competition function”

$$a_\nu(y, x) = -\frac{\delta r(y, \nu)}{\delta \nu(x)} \quad (2)$$

measures the (often detrimental) effect of strategy x on strategy y . (See the appendix for the proper definition of the functional derivative with respect to a distribution.)

We restrict our attention to the discrete strategy distribution

$$\nu = \sum_{i=1}^L n_i \delta_{x_i} \quad (3)$$

for L populations present with strategies x_i and abundances n_i ($i = 1, 2, \dots, L$). Then the following two differentiation rules apply:

$$\frac{\partial r(y, \nu)}{\partial n_i} = \int \frac{\delta r(y, \nu)}{\delta \nu(x)} \frac{\partial \nu(x)}{\partial n_i} dx = - \int a_\nu(y, x) \delta_{x_i}(x) dx = -a_\nu(y, x_i), \quad (4)$$

and

$$\frac{\partial r(y, \nu)}{\partial x_i} = \int \frac{\delta r(y, \nu)}{\delta \nu(x)} \frac{\partial \nu(x)}{\partial x_i} dx = - \int a_\nu(y, x) (-n_i \delta'_{x_i}(x)) dx = -n_i \partial_2 a_\nu(y, x_i). \quad (5)$$

Note the multiplier n_i in (5): the effect of changing the strategy of one of the populations is proportional to the number of individuals following this strategy.

For the discrete distribution the population dynamics can be written as

$$\frac{d}{dt} (\ln n_i) = r(x_i, \nu). \quad (6)$$

We rewrite this dynamics using the aggregated abundance $N = \sum_i n_i$ and the relative frequencies $p_i = n_i/N$ as new dynamical variables:

$$\frac{d}{dt} (\ln N) = \bar{r} \quad (7)$$

with $\bar{r} = \sum_i p_i r(x_i, \nu)$ the averaged growth rate and

$$\frac{d}{dt} \left(\ln \frac{p_i}{p_j} \right) = r(x_i, \nu) - r(x_j, \nu). \quad (8)$$

(As $\sum_i p_i = 1$, it is enough to specify the dynamics of the ratios of the p_i .)

We suppose that the strategies x_1, \dots, x_L are similar; i.e., let

$$x_i = x_0 + \varepsilon \xi_i, \quad (9)$$

where $\varepsilon \rightarrow 0$. Without loss of generality we set $x_0 = 0$. As the difference on the right-hand side of (8) is proportional to ε , the (relative) dynamics of the p_i 's is slow compared to the (aggregated) dynamics of N . That is, on the slow time scale, (8) can be approximated as

$$\frac{d}{dt} \left(\ln \frac{p_i}{p_j} \right) = \langle r(x_i, \nu) - r(x_j, \nu) \rangle, \quad (10)$$

where $\langle \dots \rangle$ denotes the ergodic average over the fast time scale.

After writing the distribution ν as a function of the aggregated and the relative abundances

$$\nu(N, \mathbf{p}, \varepsilon) = N \sum_{i=1}^L p_i \delta_{\varepsilon \xi_i}, \quad (11)$$

we Taylor expand the fitness function in the small parameter ε :

$$\begin{aligned} r(y, \nu(N, \mathbf{p}, \varepsilon)) &= r(y, N \delta_0) - \varepsilon N \sum_{i=1}^L p_i \partial_2 a_\nu(y, 0) [\xi_i] \\ &+ \frac{\varepsilon^2}{2} (\text{quadratic in } p_i) + \dots \end{aligned} \quad (12)$$

(Expressions like $\partial_2 a_\nu(y, 0) [\xi_i]$ mean that the derivative $\partial_2 a_\nu(y, 0)$, as a linear operator, is applied to the vector ξ_i .) The nontrivial feature of this expansion is that in each term the order of ε equals the order of \mathbf{p} . This is a consequence of the differentiation rule (5).

The linear term of expansion (12) can be rearranged as

$$r(y, \nu(N, \mathbf{p}, \varepsilon)) = r(y, N \delta_0) - \varepsilon N \partial_2 a_\nu(y, 0) [\bar{\xi}] + \text{h.o.t.}, \quad (13)$$

where $\bar{\xi} = \sum_{i=1}^L p_i \xi_i$ is the ‘‘average’’ of the ξ_i 's.

Consequently,

$$r(y, \nu(N, \mathbf{p}, \varepsilon)) = r(y, N \delta_{\varepsilon \bar{\xi}}) + o(\varepsilon), \quad (14)$$

where $\varepsilon \bar{\xi}$ is the average of the L strategies, weighted by the abundances. That is, up to order ε the L -morphic strategy distribution $\nu(\varepsilon)$ is equivalent to the *monomorphic* population with the same aggregated abundance and averaged strategy.

At a fixed value of the slow variable \mathbf{p} , the fast aggregated dynamics (7) can be written as

$$\begin{aligned} \frac{d}{dt} (\ln N) &= \sum_{j=1}^L p_j r(\varepsilon \xi_j, \nu(N, \mathbf{p}, \varepsilon)) \\ &= r(\varepsilon \bar{\xi}, N \delta_{\varepsilon \bar{\xi}}) + o(\varepsilon). \end{aligned} \quad (15)$$

Here we used (14) and applied a similar trick in the first variable.

We conclude that, up to order ε , the aggregated dynamics of the L populations is equivalent to the dynamics of a single population with the strategy $\varepsilon \bar{\xi}$. We assume that the ergodic averages inherit this equivalence; i.e., the averages over attractors are the same for the two kinds of fast dynamics up to ε order. This assumption certainly holds for simple attractors, [like point attractors, (quasi)cyclic attractors] away from bifurcation points.

In our context the invasion fitness function is defined as

$$s_{x_1, x_2, \dots, x_L}(y) = \left\langle r \left(y, \sum_{i=1}^L n_i \delta_{x_i} \right) \right\rangle. \quad (16)$$

This is the long-term growth rate of a rare newcomer y in the ergodic environment created by the long-term coexistence of the “resident” strategies x_1, \dots, x_L .

The approximation of L similar strategies with a single population with an averaged strategy immediately extends

$$\frac{d}{dt} \left(\ln \frac{p_i}{p_j} \right) = \varepsilon \frac{\partial s_x(y)}{\partial y} [\xi_i - \xi_j] + \frac{\varepsilon^2}{2} \left\{ \frac{\partial^2 s_x(y)}{\partial y^2} [\xi_i][\xi_i] - \frac{\partial^2 s_x(y)}{\partial y^2} [\xi_j][\xi_j] + 2 \frac{\partial^2 s_x(y)}{\partial y \partial x} [\xi_i - \xi_j][\xi_i] \right\} + \text{h.o.t.} \quad (18)$$

(All partials are evaluated at $x = y = 0$.) The linear and the first two quadratic terms come from Taylor expanding (17) in the y variable. The last quadratic term is a consequence of displacing the averaged strategy from 0 to $\varepsilon \bar{\xi}$. Note that this term depends on \mathbf{p} linearly through $\bar{\xi}$.

Observe the simplicity of this expression: The relative dynamics is decoupled from the possible complicatedness of the fast dynamics and fully constrained by the derivatives of the single-resident invasion fitness.

As only the second order terms depends on the p_i , frequency dependence becomes relevant only when the fitness gradient $\partial s_x(y)/\partial y$ vanishes in all $(\xi_i - \bar{\xi})$ directions. Generically, this happens at the “singular” points characterized by $\partial s_x(y)/\partial y = 0$. As under the dominance of the linear term the fittest wins, generically the coexistence of similar strategies (i.e., a stable internal fixed point of the relative dynamics) is possible only in the vicinity of the singular points.

Frequency dependence is linear even at the singular points. As the nonboundary ($p_i \neq 0$) fixed point of the relative dynamics is determined by a linear set of equations [the bracketed terms of (18) equated to zero], it generically exists and is unique. This fixed point represents a biologically realistic coexistence state if it corresponds to positive p_i s and is stable.

As frequency dependence is restricted to the neighborhood of the singular points, so is the possibility of evolutionary branching. With mutation generation, away from the singular points lack of frequency dependence would lead to Eigen’s quasispecies picture [13]: a cloud of mutants evolves into the direction jointly determined by the fitness gradient and the mutation distribution. At a singular point, the possibly coexisting subpopulations evolve either towards or away from each other, depending on the second order terms.

If the dynamics of a single population has multiple attractors, this analysis is valid for each attractor separately. That is, coexistence of L similar populations, if possible, is unique for each monomorphic attractor. Evolutionary replacements, which are matters of the relative dynamics, do not lead to a switch between the population dynamical attractors until a bifurcation point is reached (cf. [14]).

The evolutionary implications of our results are demonstrated for a 1D strategy space in Fig. 1 with the simple

to the s functions. For small ε , the L -resident invasion fitness can be approximated by the s function corresponding to a single resident:

$$s_{x_1, \dots, x_L}(y) = \langle r(y, \nu(N, \mathbf{p}, \varepsilon)) \rangle = \langle r(y, N \delta_{\varepsilon \bar{\xi}}) \rangle + o(\varepsilon) = s_{\varepsilon \bar{\xi}}(y) + o(\varepsilon). \quad (17)$$

Then the slow dynamics (10) can be expanded as

$$\frac{d}{dt} \left(\ln \frac{p_i}{p_j} \right) = \varepsilon \frac{\partial s_x(y)}{\partial y} [\xi_i - \xi_j] + \frac{\varepsilon^2}{2} \left\{ \frac{\partial^2 s_x(y)}{\partial y^2} [\xi_i][\xi_i] - \frac{\partial^2 s_x(y)}{\partial y^2} [\xi_j][\xi_j] + 2 \frac{\partial^2 s_x(y)}{\partial y \partial x} [\xi_i - \xi_j][\xi_i] \right\} + \text{h.o.t.} \quad (18)$$

“Lotka-Volterra” choice

$$r(y, \nu) = K(1 - y^2) - \int \exp \left[-\frac{(y-x)^2}{2\sigma^2} \right] \nu(x) dx. \quad (19)$$

The first term is the frequency-independent part of the fitness. An easy analysis shows that its maximum at $y = 0$ is the only singular strategy of the model. The second term represents a simple kind of frequency dependence: it is advantageous to be different from the other individuals. Note that the exponential expression corresponds to the competition function $a(y, x)$, which in this case is independent of ν .

Away from the singular point, the essentially frequency-independent selection promotes directional evolution towards $y = 0$. There, frequency dependence expresses itself in the counterintuitive phenomenon that uphill evolution

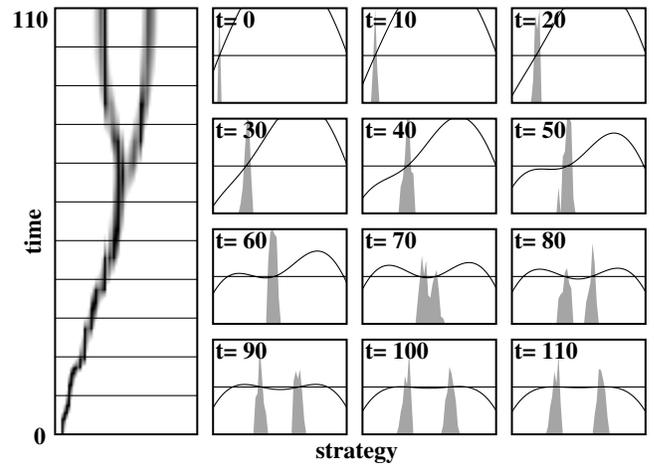


FIG. 1. Course of evolution in the Lotka-Volterra model (19). Horizontal axes represent the strategy interval $[-1, 1]$. Left pane: time dependence. Small panes: Instantaneous fitness function (curve, horizontal line represents zero) superimposed on the population distribution (gray). Each small pane corresponds to an instant of time represented by a horizontal line on the left pane. Observe that uphill evolution ends up in arriving at the *minimum* of the fitness function, where evolutionary branching occurs. After the branching, the two subpopulations evolve away. $K = 10000$, $\sigma = 0.5$; mutation probability: 0.002. See [18] for the details of the stochastic modeling of the mutations, which are not rare, and for the multidimensional results.

ends up in a *minimum* of the fitness function. [The second term of (19) makes the singular strategy $y = 0$ pessimal when all individuals have a strategy around 0.] As a consequence, evolutionary branching occurs: two subpopulations evolve away following their respective fitness gradients.

Note that the advantage of being different from the rest of the population diminishes with increasing σ . When $\sigma > 1/\sqrt{2}$, $y = 0$ remains a fitness maximum when the population converges there. No branching occurs in this case.

The complete classification of the possible local configurations of the $s_x(y)$ function was provided earlier for a 1D strategy space [8,9]. With assumptions (a) and (b) this analysis showed that the directional evolution and the possible branching at the singularities exhaust the possibilities. Our results establish the same picture without these restrictions. Assumption (a) is superfluous because the evolution of an arbitrary cloud of mutants is controlled by the one-resident invasion fitness $s_y(x)$. Assumption (b) becomes a *consequence* of the small fitness difference between the strategies, a conclusion reached also in [15].

We conclude that the only important assumption, leading to the adaptive dynamics picture, is that evolution proceeds in small steps.

The picture of the small-step evolution in a continuous state space is an approximation of the real process taking place in an underlying high-dimensional discrete sequence space (cf.[16]). Mutations with a large effect on the phenotype of a higher organism are generally expected to be detrimental, as they destroy the consistency of the genetic plan. Evolution via *small* modifications is an integral part of the Darwinian picture. We developed the consistent and parsimonious mathematical theory of this picture and demonstrated that it leads to a *diverse* life in a natural way, in accordance with Darwin's own views, without needing to relegate speciation to extraneous mechanisms, as has been the custom since the neo-Darwinian synthesis of the middle 1900s.

The entertaining aspect of this study is the deep connection between essential biological and mathematical issues. The simple evolutionary picture emerges from an arbitrarily complicated population dynamics because of the coupling between the order of ε and the order of \mathbf{p} in the ε expansion. In turn, this coupling is a consequence of the differentiation rule (5), which was derived from a functional analytic underpinning. To unify the population dynamical and the evolutionary state spaces in a properly continuous manner, we had to work in the space of distributions and invent a chain-rule-preserving definition of the functional derivative in this space (see the appendix).

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Appendix.—As there is no norm in the space of distributions, the functional derivative (2) cannot be defined in

the Banach-space manner. Instead, the derivative of the map $f:\mathcal{E}\mapsto\mathcal{F}$ (where \mathcal{E} and \mathcal{F} are topological vector spaces) is defined as a linear operator $L:\mathcal{E}\mapsto\mathcal{F}$ such that, for any curve $c:\mathbb{R}\mapsto\mathcal{E}$, the derivative of $f\circ c$ is $L\circ c'$. This definition ensures validity of the chain rule, which was used in deriving the rules (4) and (5). In our case, \mathcal{E} is the space of distributions, so the derivative L is an element of the dual of this space, i.e., of the “test function” space \mathcal{D} of infinitely many times differentiable functions with compact support [17]. Consequently, for any $y, a_\nu(y, \cdot) \in \mathcal{D}$. So, the differentiability of the generalized competition function in its second argument is guaranteed by the here-defined differentiability of $r(y, \nu)$ with respect to ν .

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