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Dynamics of Similar Populations: The Link between Population Dynamics and Evolution

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Dynamics of similar populations: the link between population dynamics and 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, where "evolutionary branching" may happen.

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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 *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]. 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 [5] which it leaves by branching [6–8]. This “evolutionary branching” was suggested to be the basis for “adaptive speciation” [9, 10].

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 [6–8]. 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 co-established 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 a new mutant arrive only after equilibration of the already existing populations, i.e., at most one mutant substituting 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 unrealistic conditions by carrying out the original Darwinian program [11] 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. Moreover, we consider population abundance (number of individuals) as a complete description of the population state, using a time scale separation argument to get rid of age or spatial structure.

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 nonlinear equation

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

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"

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

measures the (often detrimental) effect of strategy x on strategy y. (See Appendix for the proper definition of the functional derivative with respect to a distribution. The ν dependence of a will be suppressed.)

We restrict our attention to the discrete strategy distribution

$$\nu = \sum_{i=1}^{L} n_i \delta_{x_i} \tag{2}$$

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

$$\begin{aligned} \frac{\partial r\,(y,\nu)}{\partial n_i} &= \int \frac{\partial r(y,\nu)}{\partial \nu(x)} \cdot \frac{\partial \nu(x)}{\partial n_i} dx = \\ &= -\int a(y,x)\delta_{x_i}(x) dx = -a(y,x_i), \end{aligned} \tag{R1}$$

and

$$\begin{aligned} \frac{\partial r\,(y,\nu)}{\partial x_i} &= \int \frac{\partial r(y,\nu)}{\partial \nu(x)} \cdot \frac{\partial \nu(x)}{\partial x_i} dx = \\ &= -\int a(y,x)\left(-n_i \delta'_{x_i}(x)\right) dx = -n_i \partial_2 a(y,x_i). \end{aligned} \tag{R2}$$

Note the multiplier n_i in (R2): 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

$$\frac{d}{dt}\left(\ln n_i\right) = r(x_i,\nu). \tag{3}$$

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:

$$\frac{d}{dt}(\ln N) = \bar{r} \tag{4}$$

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

$$\frac{d}{dt}\left(\ln \frac{p_i}{p_j}\right) = r(x_i,\nu) - r(x_j,\nu). \tag{5}$$

(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

$$x_i = x_0 + \varepsilon \xi_i, \tag{6}$$

where $\varepsilon \to 0$. Without loss of generality we set $x_0 = 0$. As the difference on the r.h.s. of (5) 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, (5) can be approximated as

$$\frac{d}{dt}\left(\ln \frac{p_i}{p_j}\right) = \left\langle r(x_i,\nu) - r(x_j,\nu)\right\rangle, \tag{7}$$

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

$$\nu(N,\boldsymbol{p},\varepsilon) = N \sum_{i=1}^{L} p_i \delta_{\varepsilon\xi_i}, \tag{8}$$

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

$$\begin{aligned} r\left(y,\nu(N,\boldsymbol{p},\varepsilon)\right) = r\left(y, N\delta_0\right) - \varepsilon N \sum_{i=1}^{L} p_i \partial_2 a(y,0)\left[\xi_i\right] \\ + \frac{\varepsilon^2}{2}\left(\text{quadratic in } p_i\right) + \dots \end{aligned} \tag{9}$$

(Expressions like $\partial_2 a(y,0)\left[\xi_i\right]$ mean that the derivative $\partial_2 a(y,0)$, as a linear operator, is applied to the vector ξ_i.) The non-trivial feature of this expansion is that in each term the order of ε equals the order of $\boldsymbol{p}$. This is a consequence of the differentiation rule (R2).

The linear term of expansion (9) can be rearranged as

$$r\left(y,\nu(N,\boldsymbol{p},\varepsilon)\right) = r\left(y,N\delta_0\right) - \varepsilon N \partial_2 a(y,0)\left[\bar{\xi}\right] + \text{h.o.t.} \tag{10}$$

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

Consequently,

$$r\left(y,\nu(N,\boldsymbol{p},\varepsilon)\right) = r\left(y, N\delta_{\varepsilon\bar{\xi}}\right) + o(\varepsilon), \tag{11}$$

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 *monomorpic* population with the same aggregated abundance and averaged strategy.

At a fixed value of the slow variable $\boldsymbol{p}$, the fast aggregated dynamics (4) can be written as

$$\frac{d}{dt}\left(\ln N\right) = \sum_{j=1}^{L} p_j r\left(\varepsilon\xi_j, \nu(N,\boldsymbol{p},\varepsilon)\right) = r\left(\varepsilon\bar{\xi}, N\delta_{\varepsilon\bar{\xi}}\right) + o(\varepsilon). \tag{12}$$

Here we used (11) 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

$$s_{x_1,x_2,\dots,x_L}(y) = \left\langle r\left(y, \sum_{i=1}^{L} n_i \delta_{x_i}\right)\right\rangle. \tag{13}$$

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 $x_1,\ldots,x_L$.

The approximation of L similar strategies with a single population with an averaged strategy immediately extends to the s-functions. For small ε, the L-resident invasion fitness can be approximated by the s function corresponding to a single resident:

$$\begin{aligned} s_{x_1,\ldots,x_L}(y) &= \langle r\,(y,\nu(N,\boldsymbol{p},\varepsilon))\rangle = \\ &= \left\langle r\left(y, N\delta_{\varepsilon\bar{\xi}}\right)\right\rangle + o(\varepsilon) = s_{\varepsilon\bar{\xi}}(y) + o(\varepsilon). \qquad (14)\end{aligned}$$

Then the slow dynamics (7) can be expanded as

$$\begin{aligned} \frac{d}{dt}\left(\ln\frac{p_i}{p_j}\right) &= \varepsilon\frac{\partial s_x(y)}{\partial y}\,[\xi_i-\xi_j] + \\ &+ \frac{\varepsilon^2}{2}\left\{\frac{\partial^2 s_x(y)}{\partial y^2}\,[\xi_i]\,[\xi_i] - \frac{\partial^2 s_x(y)}{\partial y^2}\,[\xi_j]\,[\xi_j]\right. \\ &\left. + 2\,\frac{\partial^2 s_x(y)}{\partial y\partial x}\,[\xi_i-\xi_j]\,\left[\bar{\xi}\right]\right\} + \text{h.o.t.} \qquad (15)\end{aligned}$$

(All partials are evaluated at $x=y=0$.) The linear and the first two quadratic terms come from Taylor expanding (14) 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 $\boldsymbol{p}$ 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, generic coexistence (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 non-boundary ($p_i \neq 0$) fixed point of the relative dynamics is determined by a linear set of equations [the bracketed terms of (15) equated to zero], it generically exists and is unique. This fixed point represents a biologically realistic coexistence state if it is stable and corresponds to all positive p_is.

As frequency dependence is restricted to the neighborhood of the singular points, so does the possibility of evolutionary branching. With mutation generation, away from the singular points lack of frequency dependence would lead to Eigen's quasispecies picture [12]: a cloud of mutants evolves into the direction jointly determined by the fitness gradient and the mutation distribution. (See [13] for the dynamical equation in the case of rare mutations.) At a singular point, the possibly coexisting subpopulations evolve either towards or away from each other, depending on the second order terms.

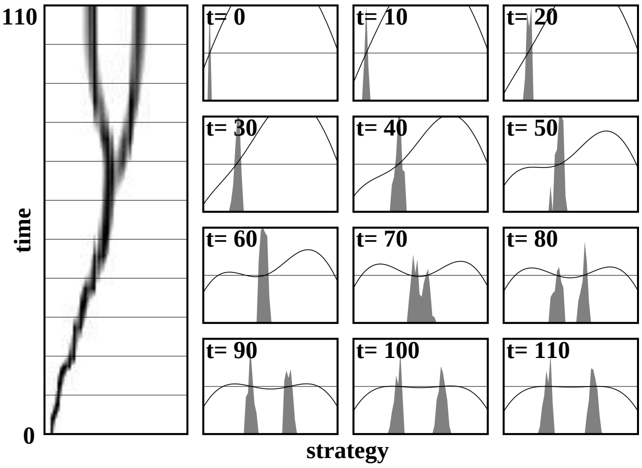

FIG. 1: Course of evolution in the Lotka-Volterra model (16). Horizontal axes represent the strategy interval $[-1,1]$. Left pane: time dependence. Small panes: Instantaneous fitness function (curve, horizontal line represents zero) superimposed on the population distribution (gray). Each small pane 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 rate: 0.002.

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. (Cf. [14]. Care should be taken at the bifurcation points of the dynamics though.)

The evolutionary implications of our results are demonstrated for a 1D strategy space in Figure 1 with the simple "Lotka-Volterra" choice

$$r(y,\nu) = K(1-y^2) - \int \exp\left[-\frac{(y-x)^2}{2\sigma^2}\right]\nu(x)dx. \qquad (16)$$

(See [15] for the details of the stochastic modeling of the mutations, which are not rare, and for the multidimensional results.) 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 $a(y,x)$.

Away from the singular point, the essentially frequency-independent selection promotes directional evolution towards $y=0$. There, frequency dependence expresses itself in the counter-intuitive phenomenon that uphill evolution ends up in a *minimum* of the fitness function. [The second term of (16) makes the singular strategy $y = 0$ pessimal when all individuals have a strategy around 0.] As a consequence, evolutionary branching occurs: two sub-populations evolve away following their respective fitness gradient.

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 [7, 8]. With the assumptions (A) and (B) this analysis showed that the directional evolution and the possible branching at the singularities exhaust the possibilities. Our results establishes 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 [14].

We conclude that the only important assumption, leading to the adaptive dynamics picture, is that evolution proceeds in small steps (cf. [16, 17]).

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 $\boldsymbol{p}$ in the ε expansion. In turn, this coupling is a consequence of the differentiation rule (R2), which was derived from a functional analytic underpinning. To unify the population dynamical and the evolutionary state spaces, we had to work in the space of distributions and invent a chain-rule-preserving definition of the functional derivative in this space (Appendix).

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APPENDIX

As the space of distributions is not normable, the functional derivative (CF) 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 (R1) and (R2). 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 [18]. Consequently, for any y, $a(y, .) \in \mathcal{D}$. So, the differentiability of the generalized competition function in its second argument is guarantied by the here-defined differentiability of $r(y, \nu)$ with respect to ν.

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