ELECTRONIC APPENDIX

This is the Electronic Appendix to the article

Speciation: more likely through a genetic or through a learned habitat preference?

by

J. B. Beltman and J. A. J. Metz


Electronic appendices are refereed with the text; however, no attempt is made to impose a uniform editorial style on the electronic appendices.
The selection gradient

In the following we provide the details of the adaptive-dynamical analysis. The course of evolution of the specialization coefficient \(a\), the genetic habitat preference \(g\), and the learning ability \(l\) depends in part on the intensity of selection on these traits, and in part on the mutation process. To calculate the intensity of selection on each of the traits, we need to take into account that a mutant in one of the traits \(g\), \(l\), or \(a\) can produce offspring in both habitats. Therefore it is necessary to calculate the expected density of offspring in both habitats in the next generation for a mutant. This is represented in the “reproduction matrix” \(R\), which has elements \(r_{ij}\) \((i, j \in \{A, B\})\) denoting the expected density of offspring in habitat \(i\) produced by an individual born itself in habitat \(j\). For example, a mutant that is born in habitat \(A\) will produce the following density of young in habitat \(A\) (after viability selection but before density regulation):

\[
w_A(a_m)E(1 - c_l_m)f_{AA}(g_m, l_m) ,
\]

where \(a_m\), \(g_m\) and \(l_m\) denote the trait values of the mutant. Competition with young produced by residents results in a per capita reproduction of

\[
\frac{w_A(a_m)E(1 - c_l_m)f_{AA}(g_m, l_m)}{1 + K w_A(a_r)E(1 - c_l_r)(f_{AA}(g_r, l_r)\hat{N}_A(g_r, l_r, a_r) + f_{BA}(g_r, l_r)\hat{N}_B(g_r, l_r, a_r))} ,
\]

where \(a_r\), \(g_r\) and \(l_r\) denote the trait values of residents, and \(\hat{N}_A\) and \(\hat{N}_B\) denote the population densities at equilibrium. The remaining elements of the reproduction matrix are derived analogously:

\[
\begin{pmatrix}
\frac{w_A(a_m)E(1 - c_l_m)f_{AA}(g_m, l_m)}{1 + K \hat{Y}_A(g_r, l_r, a_r)} & \frac{w_A(a_m)E(1 - c_l_m)f_{BA}(g_m, l_m)}{1 + K \hat{Y}_B(g_r, l_r, a_r)} \\
\frac{w_B(a_m)E(1 - c_l_m)f_{AB}(g_m, l_m)}{1 + K \hat{Y}_A(g_r, l_r, a_r)} & \frac{w_B(a_m)E(1 - c_l_m)f_{BB}(g_m, l_m)}{1 + K \hat{Y}_B(g_r, l_r, a_r)}
\end{pmatrix},
\]

where \(\hat{Y}_x\) denotes the density of young produced in habitat \(x\) by residents at population dynamical equilibrium. When the dominant eigenvalue of the
reproduction matrix is larger than unity, a mutant in one of the traits has a nonzero probability to invade the population of residents. The dominant eigenvalue $\lambda$ of our reproduction matrix equals

$$\frac{w_A f_{AA} K_B + w_B f_{BB} K_A + \sqrt{(w_A f_{AA} K_B - w_B f_{BB} K_A)^2 + 4 w_A w_B f_{BA} f_{AB} K_A K_B}}{2 K_A K_B}, \quad (7)$$

where for brevity in the notation it is omitted that $w_A$, $w_B$, $f_{AA}$, $f_{AB}$, $f_{BA}$ and $f_{BB}$ are here functions of the mutant traits, and that $K_A$ and $K_B$ are functions of the resident traits:

$$K_x = \frac{(1 + Kw_x(a_r) E(1 - cl_r) (\bar{N}_A(a_r, g_r, l_r) f_{Ax} + \bar{N}_B(a_r, g_r, l_r) f_{Bx}))}{E(1 - cl_r)}. \quad (8)$$

The partial derivatives of the dominant eigenvalue $\partial \lambda / \partial a_m$, $\partial \lambda / \partial g_m$, and $\partial \lambda / \partial l_m$ give the three components of the selection gradient. The sign and magnitude of these components result in directional evolution until each of the components become zero (Dieckmann & Law 1996). The trait values at which the selection gradients become zero are the equilibria of directional evolution, the so-called evolutionarily singular points. Although we could not solve the equilibrium equation in full generality, for some special points it can be shown that they are (under some circumstances) evolutionary singularities. In particular this is true when (i) the population consists of generalists without a habitat preference ($a = (a_A + a_B)/2$, $g = 0.5$ and $l = 0$), or when (ii) the population consists of specialists with a genetic preference for the habitat they are specialized on (either $a = a_A$, $g = 0$ and $l = 0$, or $a = a_B$, $g = 1$ and $l = 0$). Evolutionarily singular points have two properties that determine how evolution will proceed (Geritz et al. 1998, Metz et al. 1996). First, the convergence stability property determines whether the singular point will be approached or not. Second, the evolutionary stability property determines whether nearby mutants can invade or not when the singular point has been attained. In the following we study these two types of stability for the special points mentioned above.

**Specialists with a genetic preference for their optimal habitat**

At the point where the population consists of specialists with a genetic preference for the habitat they are specialized on (due to the symmetry this means either $a = a_A$,
$g = 0$ and $l = 0$ or $a = a_B$, $g = 1$ and $l = 0$), the three components of the selection gradient are $\partial \lambda / \partial a_m = 0$, $\partial \lambda / \partial g_m = -1 + E \exp((- (a_A - a_B)^2)/(2\sigma^2))$, and $\partial \lambda / \partial l_m = -c$. Hence, the component of the selection gradient in the direction of $a$ is zero. Although the $g$ and $l$ components of the selection gradient are not zero, the point can still be an evolutionary singularity. This is because for $g$ and $l$ we are at the border of the biologically meaningful trait space (both should be between 0 and 1). This means that when the selection gradient points away from the biologically relevant part of the trait space, evolution of these traits will come to a halt. This is always true for $l$, and for $g$ when

$$\sigma^2 \leq \frac{-(a_A - a_B)^2}{2 \ln (1/E)}.$$ (9)

In conclusion, the points $a = a_A$, $g = 0$, $l = 0$ and $a = a_B$, $g = 1$, $l = 0$ are evolutionarily singular points when inequality (9) holds. To determine the convergence and evolutionary stability of these two singular points, we need to study the components along and perpendicular to the border of the biologically relevant trait space separately. The border is formed by either the $g = 0$ and $l = 0$ or the $g = 1$ and $l = 0$ planes. To assure convergence toward the border, the selection gradient in the singular point should be exactly perpendicular to the border. A slight deviation from this direction would, for certain mutational processes, allow an evolutionary escape away from the border and thus away from the singular point (see below for a further explanation of the influence of the mutational process on the course of evolution). Here, the two planes that form the border are perpendicular to each other, and the selection gradient is indeed exactly perpendicular to the border (the $a$ component of the selection gradient is zero). Hence, when in addition the selection gradient points toward the singular point, which is true when condition (9) is fulfilled, convergence toward the border is guaranteed. We also need to study the convergence and evolutionary stability along the border (the $a$ direction). These can be determined from the partial second derivatives with respect to the mutant and resident. These derivatives are:

$$\frac{\partial^2 \lambda}{\partial a_m^2} = -\frac{\partial^2 \lambda}{\partial a_r^2} = -\frac{1}{\sigma^2}.$$ (10)

Hence, because $\partial^2 \lambda / \partial a_r^2 > \partial^2 \lambda / \partial a_m^2$, the singular points are convergence stable, and because $\partial^2 \lambda / \partial a_m^2 < 0$ they are also evolutionary stable (for these conditions see e.g. Geritz et al. 1998).
Generalists without a habitat preference

When the population consists of generalists without a genetic habitat preference, that is, at $a = (a_A + a_B)/2$, $g = 0.5$, the three components of the selection gradient are $\partial \lambda/\partial a_m = 0$, $\partial \lambda/\partial g_m = 0$, and $\partial \lambda/\partial l_m = -c/(1 - cl)$. Hence, when in addition $l = 0$ there is an evolutionarily singular point because the $g$ and $a$ components of the selection gradient are zero, and because the component in the $l$ direction of the selection gradient points away from the biologically relevant trait space. Alternatively, when there is no cost of learning ($c = 0$), there exists a whole line of singular points for all values of $l$ (selection is then neutral in the $l$ direction). The analysis of both cases is similar but slightly different. For the singular point at $l = 0$ (with $c > 0$), we again need to consider separately the components along and perpendicular to the border, which is formed by the $l = 0$ plane. Convergence toward the border is guaranteed because the selection gradient in the singular point is exactly perpendicular to the border (the $a$ and $g$ components of the gradient are zero), and points toward the singularity. Determining the convergence stability in the $g$ and $a$ direction (as well as the $l$ direction when $c = 0$) is more complicated than in the case of evolution of a single trait, because in multidimensional trait spaces not only the selection gradient but also the mutation process can influence convergence stability of a singular point (Leimar 2001, 2005, Matessi & Di Pasquale 1996). In multidimensional adaptive dynamics, the mutation process is modelled by means of a mutational variance-covariance matrix, which contains information about genetic correlations between traits and about mutation probabilities of genes that underly the traits. We study when the singular point is strongly convergence stable (Leimar 2001, 2005), i.e., for all mutational matrices convergence is guaranteed for all solutions of the canonical equation of adaptive dynamics (Dieckmann & Law 1996, Durinx & Metz 2004) that start sufficiently near to the singular point. A singular point is strongly convergence stable if and only if the matrix

$$\frac{\partial^2 \lambda}{\partial x_r^2} + \frac{\partial^2 \lambda}{\partial x_m \partial x_r}, \quad (11)$$

where $x_r$ and $x_m$ are the resident and mutant components respectively, is negative definite in the singular point (Leimar 2001, 2005). This matrix is called the Jacobian of the selection gradient (Leimar 2005). When $l = 0$, it is a two-dimensional matrix (for the $l$ direction the convergence stability follows from the $l$ component of the selection gradient):
This matrix is negative definite when

\[ E > e \frac{(a_A - a_B)^2}{4\sigma^2} \left( \frac{(a_A - a_B)^2}{4\sigma^2} + 1 \right). \]

From condition (13) it can be seen that the singular point is strongly convergent stable when \( \sigma^2 \) is above a certain threshold. At high \( E \) the threshold is lower than at low \( E \). The Jacobian of the selection gradient could not be determined analytically for the case that \( l > 0 \) and \( c = 0 \). Therefore, we determined when the conditions for strong convergence stability are fulfilled numerically. Again, this occurs when \( \sigma^2 \) is above a certain threshold. The position of the threshold is higher at high \( l \) than at low \( l \).

Although strong convergence stability is biologically the most relevant characteristic determining whether an evolutionary singularity will be approached, sometimes such a point has the even stronger property of absolute convergence stability. When a singular point is absolutely convergence stable, this guarantees that in a certain area around the point no evolutionary escape is possible from evolution toward the singularity, independent of whatever mutations are produced, even when these are produced by a "Darwinian demon" keen on tipping the balance toward escaping (Leimar 2001). A singular point is absolutely convergence stable when condition (11) is fulfilled, and when in addition the Jacobian of the selection gradient is symmetric (Leimar 2001, 2005). In the case we study, this is always true when \( a = (a_A + a_B)/2, \ g = 0.5 \) and \( l = 0 \) (see matrix (12)). Hence, strong convergence stability then implies absolute convergence stability. In contrast, numerical analysis showed that the Jacobian of the selection gradient is not symmetric in the singular points with \( l > 0 \) and \( c = 0 \). Hence, these singular points are only strongly convergence stable, but not absolutely convergence stable.

For multidimensional adaptive dynamics, the evolutionary stability of a singular point (whether mutants can invade the resident population when the system has attained the point) is determined by the matrix \( \partial^2 \lambda/\partial x_m^2 \) at the singular point. When this matrix, which in our case is

\[
\begin{pmatrix}
    \frac{(a_A - a_B)^2 - 4\sigma^2}{4\sigma^2} & \frac{a_B - a_A}{\sigma^2} & 0 \\
    \frac{a_B - a_A}{\sigma^2} & \frac{a_B - a_A}{\sigma^2} & 0 \\
    0 & 0 & 0
\end{pmatrix},
\]

(14)
is negative definite, the singular point is evolutionarily stable. Because the dominant
eigenvalue of this matrix,

\[
\frac{(1 + l)(a_A - a_B)^2 - 4\sigma^2(1 - l) + \sqrt{((1 + l)(a_A - a_B)^2 - 4\sigma^2(1 - l))^2 + (8(1 - l)(a_A - a_B)\sigma^2)^2}}{8\sigma^4(1 - l)}
\]

(15)
is always positive, the singular point is always evolutionarily unstable. There is thus
disruptive selection at this singular point, with intensity approaching infinity when
\(\sigma^2 \to 0\), and zero when \(\sigma^2 \to \infty\). Disruptive selection is present in both \(g\) and \(a\)
direction (the exact direction depends on \(\sigma^2\), \(a_A\) and \(a_B\) as can be concluded from the
accompanying eigenvector). The learning ability may be larger than zero at the
singular point, because selection on \(l\) is neutral at \(c = 0\), or because there may be
selection pressures in favor of learning for reasons other than studied in this model
(see discussion of main article). In that case, the intensity of disruptive selection is
higher at high learning abilities than at low learning abilities. Hence, because
speciation is more likely for strong disruptive selection than for weak disruptive
selection, the presence of learning promotes speciation.

References


Durinx, M. & Metz, J. A. J. 2004 Multi-type branching processes and adaptive
dynamics of structured populations. In *Branching processes: variation, growth and

Ecol.* 12, 35–57.


Leimar, O. 2005 Multidimensional convergence stability and the canonical adaptive

Math. Biol.* 34, 613–653.