

# Appendix B: Analyzing the effects of evolution on stability

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## 1 Effects of evolution under allocation costs

### 1.1 Evolution affecting intraspecific competition (Scenario 1)

As introduced in the main text, the fitness of a mutant  $\alpha_{11}^m$  in the resident population  $\alpha_{11}$  is then defined by its intraspecific growth rate:

$$W(\alpha_{11}^m, \alpha_{11}) = r_1(\alpha_{11}^m) + \alpha_{11}^m N_1^*(\alpha_{11}) + \alpha_{12} N_2^*(\alpha_{11}) \quad (1)$$

the fitness gradient may then be written:

$$\left( \frac{\partial W(\alpha_{11}^m, \alpha_{11})}{\partial \alpha_{11}^m} \right)_{\alpha_{11}^m \rightarrow \alpha_{11}} = b_1 + N_1^* \quad (2)$$

In equation (2),  $b_1$  quantifies the cost of evolution, as  $b_1 = r_1'(\alpha_{11})$ . Note that because  $r_1$  is a decreasing function of the trait,  $b_1$  is negative.

Variations of the real part of the leading eigenvalue then become:

$$\frac{dRe_\lambda}{dt} \propto \frac{\partial Re_\lambda}{\partial \alpha_{11}} \left( \frac{\partial W(\alpha_{11}^m, \alpha_{11})}{\partial \alpha_{11}^m} \right)_{\alpha_{11}^m \rightarrow \alpha_{11}} \quad (3)$$

#### 1.1.1 Stable Spiral case

This stable spiral case is only possible when interaction between species 1 and 2 is a trophic interaction and  $N_1^* \in \left[ \frac{N_2^*(\alpha_{11}\alpha_{22} - 2\alpha_{12}\alpha_{21}) - 2\sqrt{N_2^{*2}\alpha_{12}\alpha_{21}(\alpha_{12}\alpha_{21} - \alpha_{22}\alpha_{11})}}{\alpha_{11}^2}, \frac{N_2^*(\alpha_{11}\alpha_{22} - 2\alpha_{12}\alpha_{21}) + 2\sqrt{N_2^{*2}\alpha_{12}\alpha_{21}(\alpha_{12}\alpha_{21} - \alpha_{22}\alpha_{11})}}{\alpha_{11}^2} \right]$  (appendix A). In the case of stable spiral, the real part of the leading eigenvalue is half of the trace of the jacobian matrix. Equation (3) then becomes:

$$\frac{dRe_\lambda}{dt} \propto \frac{1}{2} \frac{\partial Tr(J^*)}{\partial \alpha_{11}} \left( \frac{\partial W(\alpha_{11}^m, \alpha_{11})}{\partial \alpha_{11}^m} \right)_{\alpha_{11}^m \rightarrow \alpha_{11}} \quad (4)$$

Using the equation of the equilibrium and the expression of the jacobian matrix (appendix A), it is possible to

determine the variations of the trace of the jacobian matrix with variations of the trait  $\alpha_{11}$ :

$$\frac{\partial Tr(J^*)}{\partial \alpha_{11}} = \frac{\alpha_{21}(\alpha_{22} - \alpha_{12})}{\alpha_{22}\alpha_{11} - \alpha_{12}\alpha_{21}} N_1^* + \frac{\alpha_{22}(\alpha_{21} - \alpha_{11})}{\alpha_{22}\alpha_{11} - \alpha_{12}\alpha_{21}} b_1 \quad (5)$$

Replacing equations (2), (5) in (4), one gets that evolution increases stability provided

$$(b_1 + N_1^*) \left( \frac{\alpha_{21}(\alpha_{22} - \alpha_{12})}{\alpha_{22}\alpha_{11} - \alpha_{12}\alpha_{21}} N_1^* + \frac{\alpha_{22}(\alpha_{21} - \alpha_{11})}{\alpha_{22}\alpha_{11} - \alpha_{12}\alpha_{21}} b_1 \right) < 0 \quad (6)$$

This expression is a second degree polynomial in terms of cost  $b_1$  whose roots are:

$$\begin{aligned} R_1 &= -N_1^* \\ R_2 &= \frac{\alpha_{21}(\alpha_{22} - \alpha_{12})}{\alpha_{22}(\alpha_{11} - \alpha_{21})} N_1^* \end{aligned} \quad (7)$$

If the evolving species is a prey,  $R_2 > R_1$ . Evolution then stabilizes the interaction when  $b_1 < R_1$  or  $b_1 > R_2$ . Note that the latter case is not always possible, as  $b_1$  is negative by definition while  $R_2$  may be positive (when  $\alpha_{22} > \alpha_{12}$ ).

If the evolving species is a predator, two sets of conditions are to be considered.

1. If  $\alpha_{11} > \alpha_{21}$  (negative effect on the other species more important than intraspecific competition), it is possible to show that  $R_2 < 0$  and  $R_1 > R_2$ . Evolution then stabilizes population dynamics when  $b_1 \in ]R_2, R_1[$
2. If  $\alpha_{11} < \alpha_{21}$  then it is possible to show that  $R_2 > 0$  and  $R_1 < R_2$ . Evolution then stabilizes population dynamics when  $b_1 < R_1$ .

### 1.1.2 Equilibrium is a stable node

This always happens when the interaction between the two species is either mutualism or competition (appendix A). If the interaction is trophic, the equilibrium is a stable node provided

$$N_1^* \in \left[ 0, \frac{N_2^*(\alpha_{11}\alpha_{22} - 2\alpha_{12}\alpha_{21}) - 2\sqrt{N_2^{*2}\alpha_{12}\alpha_{21}(\alpha_{12}\alpha_{21} - \alpha_{22}\alpha_{11})}}{\alpha_{11}^2} \right] \cup \left[ \frac{N_2^*(\alpha_{11}\alpha_{22} - 2\alpha_{12}\alpha_{21}) + 2\sqrt{N_2^{*2}\alpha_{12}\alpha_{21}(\alpha_{12}\alpha_{21} - \alpha_{22}\alpha_{11})}}{\alpha_{11}^2}, +\infty \right[.$$

The leading eigenvalue is then real:  $\lambda = Re_\lambda = \frac{Tr(J^*) + \sqrt{Tr(J^*)^2 - 4Det(J^*)}}{2}$  and it is necessary to compute its variations with trait  $\alpha_{11}$ . Differentiating this expression regarding variations in  $\alpha_{11}$ :

$$\frac{\partial \lambda}{\partial \alpha_{11}} = \frac{1}{2} \left( \frac{\partial Tr(J^*)}{\partial \alpha_{11}} + \frac{Tr(J^*) \frac{\partial Tr(J^*)}{\partial \alpha_{11}} - 2 \frac{\partial Det(J^*)}{\partial \alpha_{11}}}{\sqrt{Tr(J^*)^2 - 4Det(J^*)}} \right) \quad (8)$$

Noting that  $\sqrt{Tr(J^*)^2 - 4Det(J^*)} = 2\lambda - Tr(J^*)$  is positive in node cases, equation (8) may be transformed in:

$$\frac{\partial \lambda}{\partial \alpha_{11}} = \frac{1}{2\lambda - Tr(J^*)} \left( \lambda \frac{\partial Tr(J^*)}{\partial \alpha_{11}} - \frac{\partial Det(J^*)}{\partial \alpha_{11}} \right) \quad (9)$$

Assessing equation (9) requires to determine the variations of the trace (equation (5)) and the determinant of the jacobian matrix with variations of  $\alpha_{11}$ . Using the expression of the determinant (appendix A), the expression of the equilibrium and differentiating, one gets:

$$\frac{\partial Det(J^*)}{\partial \alpha_{11}} = N_1^{*2} \alpha_{21} + b_1 (r_2 + 2\alpha_{21} N_1^*) \quad (10)$$

The effects of evolution on the leading eigenvalues may then be determined by replacing equations (9) and (2) in equation (3):

$$\frac{d\lambda}{dt} \propto \frac{1}{2\lambda - Tr(J^*)} \left( \lambda \frac{\partial Tr(J^*)}{\partial \alpha_{11}} - \frac{\partial Det(J^*)}{\partial \alpha_{11}} \right) \left( \frac{\partial W(\alpha_{11}^m, \alpha_{11})}{\partial \alpha_{11}^m} \right)_{\alpha_{11}^m \rightarrow \alpha_{11}} \quad (11)$$

The first element is positive, and the product of the two lasts can be written as a second degree polynomial of  $b_1$ . It has two roots:

$$\begin{aligned} R_1 &= -N_1^* \\ R_2 &= - \frac{N_1^* \alpha_{21} (N_1^* P + \lambda (\alpha_{12} - \alpha_{22}))}{P (r_2 + 2N_1^* \alpha_{21}) + \lambda (\alpha_{11} - \alpha_{21}) \alpha_{22}} \end{aligned} \quad (12)$$

where  $P = \alpha_{11}\alpha_{22} - \alpha_{21}\alpha_{12}$  is positive to ensure that the equilibrium before mutation is stable (see appendix A). The first root is always negative while the sign of the second root can be either negative or positive. Resilience is increased by evolution whenever the polynomial is negative. Studying the higher coefficient of this polynomial it is possible to show that this happens if  $b_1$  lies between the two roots provided:

$$N_2^* < \frac{\lambda (\alpha_{11} - \alpha_{21})}{P} + \frac{\alpha_{21} N_1^*}{\alpha_{22}} \quad (13)$$

Note that condition (13) does not provide a simple boundary in terms of population  $N_2^*$ , as the right hand side depends on  $N_2^*$  through  $N_1^*$  and  $\lambda$ . If condition (13) is not true, evolution increases the resilience of the system provided  $b_1 \in ]-\infty, \min(R_1, R_2)[ \cup ]\max(R_1, R_2), 0]$ , else evolution increases the resilience of the system provided  $b_1 \in [R_1, R_2]$ .

### 1.1.3 Special cases

Computations above lead to general conditions that may not be independent one from the other. For instance, it is possible that some interactions types always lead to positive values of  $R_2$ , so that  $b_1 > R_2$  is no longer possible. Similarly, it is possible that for some interactions we always have  $R_2 > R_1$  (or vice versa) which would simplify the conditions expressed above. Finally, note that some situations could lead to always negative values of the right hand side of equation (13), which would make the condition trivially false. Finally, note that the conditions under which we have a spiral or a node are not obviously independent of condition (13). Because of all these interactions

between the conditions I introduced, some simplifications emerge depending on the type of interaction.

**Interaction is mutualistic** Then we have  $R_2 > R_1$  plus condition (13) is always false. Therefore evolution increases the resilience of the system when  $b_1 \in ]-\infty, R_1[ \cup ]R_2, 0]$

**Interaction is competitive** If condition (13) is true, then  $R_2 < R_1$ , so that evolution increases resilience when  $b_1 \in ]R_2, R_1[$ . If the condition is not true, then  $R_2$  is positive and evolution increases resilience provided  $b < R_1$ .

**Trophic interaction, evolving species is the prey** If condition (13) is true,  $R_2 > R_1$ , so that evolution then increases resilience provided  $b_1 \in ]R_1, R_2[$ ; else condition is as in the general case.

**Trophic interaction, evolving species is the predator**  $R_2 > R_1$ , so if condition (13) is true, evolution increases resilience provided  $b_1 \in ]R_1, R_2[$ ; else  $b_1 \in ]-\infty, R_1[ \cup ]R_2, 0]$ .

## 1.2 Evolution of interspecific interaction (scenario 2)

It is similarly possible to study the effects of the evolution of  $\alpha_{12}$  on the resilience of the system. The fitness of a mutant  $\alpha_{12}^m$  in the resident population  $\alpha_{12}$  is then defined by its intraspecific growth rate:

$$W(\alpha_{12}^m, \alpha_{12}) = r_1(\alpha_{12}^m) + \alpha_{11}N_1^*(\alpha_{12}) + \alpha_{12}^m N_2^*(\alpha_{12}) \quad (14)$$

the fitness gradient is equation (15).

$$\left( \frac{\partial W(\alpha_{12}^m, \alpha_{12})}{\partial \alpha_{12}^m} \right)_{\alpha_{12}^m \rightarrow \alpha_{12}} = b_2 + N_2^* \quad (15)$$

In equation (15),  $b_2$  quantifies the cost of evolution, as  $b_2 = r_1'(\alpha_{12})$ . Note that because  $r_1$  is a decreasing function of the trait,  $b_2$  is negative (allocation cost).

Variations of the real part of the leading eigenvalue then become:

$$\frac{dRe_\lambda}{dt} \propto \frac{\partial Re_\lambda}{\partial \alpha_{12}} \left( \frac{\partial W(\alpha_{12}^m, \alpha_{12})}{\partial \alpha_{12}^m} \right)_{\alpha_{12}^m \rightarrow \alpha_{12}} \quad (16)$$

### 1.2.1 Stable Spiral

As before, the real part of the eigenvalue is simply proportional to the trace of the jacobian matrix so that:

$$\frac{dRe_\lambda}{dt} \propto \frac{1}{2} \frac{\partial Tr(J^*)}{\partial \alpha_{12}} \left( \frac{\partial W(\alpha_{12}^m, \alpha_{12})}{\partial \alpha_{12}^m} \right)_{\alpha_{12}^m \rightarrow \alpha_{12}} \quad (17)$$

Using the position of the equilibrium (main text, equation 1) and the expression of the jacobian matrix (appendix A), it is possible to determine the variations of the trace of the jacobian matrix with  $\alpha_{12}$ :

$$\frac{\partial Tr(J^*)}{\partial \alpha_{12}} = \frac{(b_2 + N_2^*)(\alpha_{21} - \alpha_{11})\alpha_{22}}{P} \quad (18)$$

Assessing the effects of evolution on resilience requires the product of equations (15) and (18) (see equation (3)), it is easy to see that resilience increases through time provided  $\alpha_{21} > \alpha_{11}$ .

This condition is trivially true whenever the evolving species is a prey. If the evolving species is a predator, evolution still increases the resilience whenever the effect of an individual predator on its prey is less negative than the competitive effect it has on conspecifics (“weak predator”), else evolution decreases the resilience.

### 1.2.2 Stable node

As before, note that variations in the real part of the leading eigenvalue may then be written:

$$\frac{\partial \lambda}{\partial \alpha_{12}} = \frac{1}{2\lambda - Tr(J^*)} \left( \lambda \frac{\partial Tr(J^*)}{\partial \alpha_{12}} - \frac{\partial Det(J^*)}{\partial \alpha_{12}} \right) \quad (19)$$

After computing the variations of the determinant of with  $\alpha_{12}$ , it is possible to show that:

$$\frac{\partial \lambda}{\partial \alpha_{12}} = \frac{\alpha_{21}N_1^*(P(N_2^* - b_2) + \alpha_{21}\alpha_{12}(N_2^* + b_2)) - \alpha_{22}(N_2^* + b_2)(-PN_2^* + 2\lambda(\alpha_{11} - \alpha_{21}) - r_1\alpha_{21} - N_2^*\alpha_{11}\alpha_{22})}{2P(2\lambda - \alpha_{11}N_1^* - \alpha_{22}N_2^*)} \quad (20)$$

The product of equations (20) and (15) allows the determination of the effects of evolution on the resilience of the system (see equation (3)). This product may be written as a second degree polynomial of  $b_2$  whose two real roots are:

$$\begin{aligned} R_1 &= -N_2^* \\ R_2 &= N_2^* \left( -1 + \frac{\alpha_{21}N_1^*P}{P(\alpha_{21}N_1^* - \alpha_{22}N_2^*) + \alpha_{22}\lambda(\alpha_{11} - \alpha_{21})} \right) \end{aligned} \quad (21)$$

The first root is always negative while the sign of the second root can be either negative or positive. Resilience is increased by evolution whenever the polynomial is positive. Studying the higher coefficient of this polynomial it is possible to show that this positivity happens between the two roots provided:

$$N_2^* < \frac{\lambda(\alpha_{11} - \alpha_{21})}{P} + \frac{\alpha_{21}N_1^*}{\alpha_{22}} \quad (22)$$

, outside the two roots else.

### 1.2.3 Special cases

**Mutualistic interactions** Condition (22) is never possible and  $R_2 > R_1$ , so that evolution increases resilience whenever  $b_2 \in ]-\infty, R_1[ \cup ]R_2, 0]$ .

**Competitive interaction** If condition (22) is true, then it is possible to show that  $R_1 < R_2$ , evolution increases the resilience when  $b_2 \in ]R_1, R_2[$ , else  $R_1 > R_2$  and evolution increases resilience when  $b_2 \in ]-\infty, R_2[ \cup ]R_1, 0]$ .

**Trophic interaction, evolving species is a prey** If condition (22) is true then it is possible to show that  $R_2 < R_1$ , evolution increases resilience when  $b_2 \in ]R_2, R_1[$ , else  $R_2 > R_1$  and evolution stabilizes the system when  $b_2 \in ]-\infty, R_1[ \cup ]R_2, 0]$ .

**Trophic interaction, evolving species is a predator** If condition (22) is true, then  $R_2 > R_1$  and evolution increases resilience when  $b_2 \in ]R_1, R_2[$ , else  $R_2 < R_1$  and evolution stabilizes the system when  $b_2 \in ]-\infty, R_2[ \cup ]R_1, 0]$ .

## 2 Effects of evolution under ecological costs (scenario 3)

When trait has an ecological cost, if a mutation affects an interaction positively, it incurs a cost in terms of another interaction. In the instance of the simple model presented here, evolution that affects intraspecific competition also affects the interspecific interaction. Fitness may then be written:

$$W(\alpha_{11}^m, \alpha_{11}) = r_1 + \alpha_{11}^m N_1^*(\alpha_{11}) + \alpha_{12}(\alpha_{11}^m) N_2^*(\alpha_{11}) \quad (23)$$

The gradient of fitness may then be written:

$$\left( \frac{\partial W(\alpha_{11}^m, \alpha_{11})}{\partial \alpha_{11}^m} \right)_{\alpha_{11}^m \rightarrow \alpha_{11}} = N_1^* + b_3 N_2^* \quad (24)$$

where  $b_3$  corresponds to the curvature of the trade-off function at  $\alpha_{11}$ , that is  $b_3 = \alpha'_{12}(\alpha_{11})$ , is negative, and quantifies the ecological cost incurred by a mutation affecting  $\alpha_{11}$ .

### 2.1 Ecological equilibrium is a stable spiral

Effects of evolution on the resilience of system are still described by the equation (4), with fitness  $W(\alpha_{11}^m, \alpha_{11})$  defined as in equation (23) and variations of the trace of the jacobian matrix described by:

$$\frac{\partial Tr(J^*)}{\partial \alpha_{11}} = N_1^* - \frac{\alpha_{22}(\alpha_{11} - \alpha_{21})(N_1^* + b_3 N_2^*)}{P} \quad (25)$$

Replacing equations (24) and (25) in equation (4) yields a second degree polynomial in terms of cost  $b_3$ , whose roots may be written:

$$\begin{aligned} R_1 &= -\frac{N_1^*}{N_2^*} \\ R_2 &= -\frac{N_1^*}{N_2^*} \left( \frac{-P - \alpha_{22}(\alpha_{11} - \alpha_{21})}{\alpha_{22}(\alpha_{11} - \alpha_{21})} \right) \end{aligned} \quad (26)$$

Two cases are then possible:

1. If  $\alpha_{11} > \alpha_{21}$ , evolution increases the resilience of the system provided  $b_3$  is between the two roots ( $b_3 \in ]\min(R_1, R_2), \max(R_1, R_2)[$  )
2. Else, evolution stabilizes the system provided  $b_3 \in ]-\infty, \min(R_1, R_2)[ \cup ]\max(R_1, R_2), 0]$ .

### 2.1.1 Special cases

**Evolving species is a prey** Then only the second point above is possible. Note also that  $R_1 < R_2$ , so that evolution increases the resilience of the system whenever  $b_3 \in ]-\infty, R_1[ \cup ]R_2, 0]$ .

**Evolving species is a predator** If  $\alpha_{11} > \alpha_{21}$  (strong predator), then  $R_1 > R_2$  and resilience is increased when  $b_3 \in ]R_2, R_1[$ , else (weak predator),  $R_1 < R_2$ , so that evolution increases the resilience of the system whenever  $b_3 \in ]-\infty, R_1[ \cup ]R_2, 0]$ .

## 2.2 Ecological equilibrium is a stable node

Effects of evolution on resilience may then be studied by solving equation 11, with  $W(\alpha_{11}^m, \alpha_{11})$  defined by equation 23. This expression may be written as a second degree polynomial of  $b_3$  whose roots are:

$$\begin{aligned} R_1 &= \frac{-N_1^*}{N_2^*} \\ R_2 &= \frac{-N_1^*}{N_2^*} \left( \frac{\alpha_{21} \lambda (\alpha_{22} - \alpha_{12}) - P N_1^*}{\alpha_{22} \lambda (\alpha_{21} - \alpha_{11}) + P N_2^*} \right) \end{aligned} \quad (27)$$

Evolution stabilizes the ecological dynamics provided  $b_3$  lies between the two roots when:

$$N_2^* < \frac{\lambda(\alpha_{11} - \alpha_{21})}{P} \quad (28)$$

Else, evolution increases the resilience when  $b_3$  lies outside of the roots.

### 2.2.1 Special cases

**Mutualistic interaction** If condition (28) is true, then  $R_1 < R_2$  and evolution increases resilience when  $b_3 \in ]R_1, R_2[$ . If it is false then conditions for increased stability are the same as in the general case.

**Competitive interaction** Then condition (28) is always false. Furthermore,  $R_2 > 0$ , so that evolution increases resilience provided  $b_3 < R_1$ .

**Trophic interaction, evolving species is a prey** In this instance  $R_1 < R_2$ . If condition (28) is true, evolution stabilizes the system provided  $b_3 \in ]R_1, R_2[$ . Else, if  $b_3 \in ]-\infty, R_1[ \cup ]R_2, 0[$ .

**Trophic interaction, evolving species is a predator** If condition (28) is true, then  $R_2 > 0$  and evolution stabilizes the system when  $b_3 > R_1$ . If it is false, then  $R_1 < R_2$  and evolution increases the resilience of the system provided  $b_3 \in ]-\infty, R_1[ \cup ]R_2, 0[$ .

Scenario	Mutualism	Competition
(1) Allocation cost Intraspecific competition		
(2) Allocation cost Interspecific interaction		
(3) Ecological cost		
Scenario	Trophic interaction (as prey)	Trophic interaction (as predator)
(1) Allocation cost Intraspecific competition		
(2) Allocation cost Interspecific interaction		
(3) Ecological cost		

Table 1: Effects of evolution on the resilience for the two-species model for the three scenarios listed in the main text and above. In each case, an axis is drawn corresponding to the values of cost  $b < 0$ . As shown in appendix B, the issue is reducible to the computation of two roots,  $R_1$  (white circle) that corresponds to the value below which the trait is counter-selected, and  $R_2$  (black circle) that corresponds to the value for which the effect of variation in the trait on resilience changes sign. When relative position of  $R_1$  and  $R_2$  is not fixed, the two are figured in grey. Costs for which evolution increases resilience are hatched. WP (resp SP) corresponds to spiral cases where the evolving species is a weak predator ( $\alpha_{21} > \alpha_{11}$ ) (resp strong predator:  $\alpha_{21} < \alpha_{11}$ ). For nodes, effects of evolution depend on a condition  $N_2^* < f(\lambda, N_1^*)$ , where function  $f$  depends on the type of cost but not on the type of interaction (appendix B). If the condition is respected, the case is named “low  $N_2^*$ ”, else “high  $N_2^*$ ”, though these names are somewhat misleading, as  $\lambda$  is linked to  $N_2^*$  so that the condition above may not be easily translated in terms of  $N_2^*$  populations. Details and mathematical expressions of the conditions in Appendix B.