

Appendix A from T. Koffel et al., “Plant Strategies along Resource Gradients” (Am. Nat., vol. 192, no. 3, p. 360)

Analytical Study of Ecological Equilibria and Their Stability

In this appendix, we present the rigorous calculations underlying the graphical analyses presented in “Ecological Analysis” in the main text. More precisely, we compute the different equilibria of equation (1) and analyze their stability for both the food chain (one plant species) and the diamond food web module (two plant species). We choose to use the herbivore attack rate $a_i = a_0(1 - \rho_i)$ instead of resistance ρ_i —the latter being implicitly included in the former—to simplify both notations and calculations. Also note that the framework presented in this appendix is slightly more general, as the two plant species differ in their death rates m_1 and m_2 , plant-herbivore conversion efficiencies e_1 and e_2 , and plant-resource conversion efficiencies q_1 and q_2 . The situation of the main text is simply recovered by setting $m_1 = m_2 = m$, $e_1 = e_2 = e$, and $q_1 = q_2 = q$.

The Food Chain

Let us first compute the analytical expressions of the different equilibria in the case of the R - P_1 - Z food chain. There are two equilibria to consider with a single plant species 1: equilibrium 0, where plants are absent, and equilibrium 1, where plant 1 is present. We use the notation \hat{R} , \hat{P}_1 , and \hat{Z} for equilibrium densities to distinguish them from R_i^* and Z_i^* , defined in the main text.

Equilibrium 0. This corresponds to $\hat{P}_1 = 0$. It follows from equation (1a) and (1c) that $\hat{R} = I_R/\ell_R \equiv S_R$ and $\hat{Z} = I_Z/m_Z \equiv S_Z$.

Equilibrium 1. Here, $\hat{P}_1 \neq 0$ and thus $g_1(\hat{R}) - a_1\hat{Z} - m_1 = 0$ from equation (1b), meaning that the possible values taken by the regulating factors (\hat{R} , \hat{Z}) at equilibrium by definition belong to the zero net growth isocline (ZNGI) of species 1, denoted ZNGI_1 . We consider two cases when the plant is present: no herbivore population ($\hat{Z} = 0$) and with herbivore population ($\hat{Z} > 0$).

No herbivore population. The solution $\hat{Z} = 0$ happens only when there is no herbivore immigration, that is, $S_Z = 0$, as can be seen from equation (1a). If $\hat{Z} = 0$, it is easy to deduce from the ZNGI_1 equation that $\hat{R} = R_1^*$, with $R_1^* = g_1^{-1}(m_1)$. Then, setting equation (1c) equal to 0 leads to

$$\hat{P}_1 = \frac{\ell_R S_R - R_1^*}{q_1 m_1}. \quad (\text{A1})$$

Herbivore population. Any positive immigration rate ($S_Z > 0$) leads to an always-positive herbivore population ($\hat{Z} > 0$). From the ZNGI_1 equation, this also implies that $\hat{R} > R_1^*$. We have seen that \hat{R} and \hat{Z} have to belong to ZNGI_1 at equilibrium, which sets a first constraint. Setting equation (1a) and (1c) equal to 0 can add a second constraint. Indeed, eliminating \hat{P}_1 between the last two equations leads to

$$S_Z - \hat{Z} = \gamma_1(\hat{R}, \hat{Z})(S_R - \hat{R}), \quad (\text{A2})$$

where γ_1 is the relative impact of plant 1 on the regulating factors:

$$\gamma_1(\hat{R}, \hat{Z}) = -\frac{e_1 \ell_R a_1 \hat{Z}}{m_Z q_1 g_1(\hat{R})}. \quad (\text{A3})$$

Note that $\gamma_1(\hat{R}, \hat{Z}) < 0$. For a given supply point (S_R, S_Z) , solving for the intersection of ZNGI_1 and equation (A2) gives the values of the regulating factors (\hat{R} , \hat{Z}) at equilibrium. There is generally no analytical solution to this, but it can be represented using the graphical approach.

Using the fact that $g_1(\hat{R}) = a_1\hat{Z} + m_1$, we can deduce from equation (A3) that γ_1 is proportional to $a_1\hat{Z}/(a_1\hat{Z} + m_1)$ along the envelope. This explains why the slopes of the impact vectors are variable in the ecological section of the main text (fig. 3): when $\hat{Z} = 0$, $\gamma_1 = 0$ and the impact vectors are initially totally flat; as we move along the ZNGI, \hat{Z} becomes positive and so does the absolute value of the slope; finally, when $a_1\hat{Z}$ becomes large compared to m_1 , the ratio $a_1\hat{Z}/(a_1\hat{Z} + m_1)$ tends toward 1 and the slope reaches a constant value, as can be seen in figure 3 where the impact vectors under high supplies all look parallel.

After (\hat{R}, \hat{Z}) have been obtained, the corresponding expression of \hat{P}_1 , the density of plant 1, is deduced from equation (1a) or (1c):

$$\hat{P}_1 = \frac{\ell_R S_R - \hat{R}}{q_1 g_1(\hat{R})}. \quad (\text{A4})$$

This solution is positive only when $S_R > \hat{R}$, which also implies that $S_Z < \hat{Z}$ because of equation (A2). Geometrically, this means that the supply point (S_R, S_Z) has to be located under ZNGI₁ for this equilibrium to be valid.

To investigate the stability of equilibria 0 and 1, we first compute the Jacobian matrix of the model,

$$J(R, P_1, Z) = \begin{pmatrix} -m_Z + e_1 a_1 P_1 & e_1 a_1 Z & 0 \\ -a_1 P_1 & g_1(R) - a_1 Z - m_1 & \frac{dg_1}{dR} P_1 \\ 0 & -q_1 g_1(R) & -\ell_R - q_1 \frac{dg_1}{dR} P_1 \end{pmatrix}, \quad (\text{A5})$$

and then evaluate it at the various equilibria.

Equilibrium 0. The Jacobian matrix can be rewritten as

$$J(S_R, 0, S_Z) = \begin{pmatrix} -m_Z & e_1 a_1 S_Z & 0 \\ 0 & g_1(S_R) - a_1 S_Z - m_1 & 0 \\ 0 & -q_1 g_1(S_R) & -\ell_R \end{pmatrix}. \quad (\text{A6})$$

Due to the specific locations of the zero entries in this matrix, its eigenvalues are given by its diagonal entries. The stability criterion (all the eigenvalues being negative) is then equivalent to

$$g_1(S_R) - a_1 S_Z - m_1 < 0. \quad (\text{A7})$$

Recognizing the ZNGI₁ equation, this condition can be interpreted geometrically: the trivial equilibrium is stable if and only if the supply point is located above ZNGI₁, so the plant cannot invade the system.

Equilibrium 1. In this case, the Jacobian matrix reads

$$J(\hat{R}, \hat{P}_1, \hat{Z}) = \begin{pmatrix} -m_Z + e_1 a_1 \hat{P}_1 & e_1 a_1 \hat{Z} & 0 \\ -a_1 \hat{P}_1 & 0 & \frac{dg_1}{dR} \hat{P}_1 \\ 0 & -q_1 g_1(\hat{R}) - \ell_R - q_1 \frac{dg_1}{dR} \hat{P}_1 \end{pmatrix}. \quad (\text{A8})$$

We consider two cases: no herbivore population ($\hat{Z} = 0$) and with herbivore population ($\hat{Z} > 0$).

No herbivore population. The solution $\hat{Z} = 0$ is a possibility only when there is no herbivore immigration, so $S_Z = 0$. If $\hat{Z} = 0$, it is easy to deduce relationships involving the three eigenvalues λ_1 , λ_+ , and λ_- :

$$\lambda_1 = -m_Z + e_1 a_1 \hat{P}_1, \quad (\text{A9})$$

$$\lambda_+ \lambda_- = q_1 g_1(\hat{R}) \frac{dg_1}{dR} \hat{P}_1, \quad (\text{A10})$$

$$\lambda_+ + \lambda_- = -\ell_R - q_1 \frac{dg_1}{dR} \hat{P}_1. \quad (\text{A11})$$

Because the functional response g_1 is monotonically increasing, $dg_1/dR > 0$ and therefore $\lambda_+ < 0$ and $\lambda_- < 0$. The stability criteria reduces to $\lambda_1 < 0$, which reads $\hat{P}_1 < m_z/e_1a_1$. Using equation (A4) and the fact that $g_1(\hat{R}) = m_1$, this stability criteria can be written

$$S_R < R_1^* + R_{z,1}^*, \quad (\text{A12})$$

with $R_{z,1}^* = m_1m_zq_1/(\ell_R e_1a_1)$ and remembering that $R_1^* = g_1^{-1}(m_1)$.

Herbivore population. If $\hat{Z} > 0$, it follows from equation (1a) that $-m_z + e_1a_1\hat{P}_1$, the first diagonal term of $J(\hat{R}, \hat{P}_1, \hat{Z})$, is equal to $-m_zS_z/\hat{Z}$ and thus negative. From there, the sign structure of $J(\hat{R}, \hat{P}_1, \hat{Z})$ is such that this equilibrium is always stable when it exists (i.e., when the supply point is under the isocline, as shown in the previous section), as can be checked using the Routh-Hurwitz stability criterion.

To conclude, this stability analysis shows that equilibrium 1 is always stable when valid, except when $\hat{Z} = 0$ (a possible solution when $S_z = 0$). In this case, resource supply has to satisfy the supplementary condition $S_R < R_1^* + R_{z,1}^*$. Otherwise, the $\hat{Z} = 0$ solution is destabilized by the existence of another equilibrium with $\hat{Z} > 0$.

The Diamond Food Web Module

Again, let us first compute the analytical expressions of the different equilibria of the system. There are now four cases to consider with the diamond food web module: equilibrium 0, where plants are absent; equilibrium 1, where only plant 1 is present; equilibrium 2, where only plant 2 is present; and equilibrium 1&2, where plants 1 and 2 coexist.

Equilibrium 0. This now consists of $\hat{P}_1 = \hat{P}_2 = 0$. It follows from equation (1a) and (1c) that $\hat{R} = S_R$ and $\hat{Z} = S_z$.

Equilibrium 1. This consists of $\hat{P}_1 \neq 0$ and $\hat{P}_2 = 0$. Similarly to the food chain, \hat{R} and \hat{Z} are obtained by combining ZNGI_1 and the impact vector map, that is, $g_1(\hat{R}) - a_1\hat{Z} - m_1 = 0$ and $S_z - \hat{Z} = \gamma_1(\hat{R}, \hat{Z})(S_R - \hat{R})$. The value \hat{P}_1 is then deduced from equation (1a) and is positive when the supply point (S_R, S_z) is located under ZNGI_1 .

Equilibrium 2. This is identical to equilibrium 1 after swapping indices 1 and 2.

Equilibrium 1&2. This consists of $\hat{P}_1 \neq 0$ and $\hat{P}_2 \neq 0$. This means that $g_i(\hat{R}) - a_i\hat{Z} - m_i = 0$ for $i = 1, 2$: \hat{R} and \hat{Z} are located at the intersection of ZNGI_1 and ZNGI_2 , giving a necessary condition for this coexistence equilibrium to be valid (in the positive quadrant). The equilibrium values \hat{P}_1 and \hat{P}_2 are deduced after inversion of the system made of equation (1a) and (1c) set equal to 0. Indeed, this system is linear in \hat{P}_i and can be inverted if $\gamma_1(\hat{R}, \hat{Z}) \neq \gamma_2(\hat{R}, \hat{Z})$, that is, if the impact vectors of the two species at equilibrium are not colinear. The positivity condition $\hat{P}_1 > 0$ and $\hat{P}_2 > 0$ adds a further constraint: $(S_z - \hat{Z})/(S_R - \hat{R})$ must be between $\gamma_1(\hat{R}, \hat{Z})$ and $\gamma_2(\hat{R}, \hat{Z})$. As a geometrical interpretation, this means that the supply point has to be located inside the cone made by species 1 and 2 impact vectors and passing through the intersection of the two ZNGIs (Leibold 1996).

To investigate the stability of these equilibria, we compute the Jacobian matrix of the model:

$$J(R, Z, P_1, P_2) = \begin{pmatrix} -m_z + e_1a_1P_1 + e_2a_2P_2 & e_1a_1Z & e_2a_2Z & 0 \\ -a_1P_1 & g_1(R) - a_1Z - m_1 & 0 & \frac{dg_1}{dR}P_1 \\ -a_2P_2 & 0 & g_2(R) - a_2Z - m_2 & \frac{dg_2}{dR}P_2 \\ 0 & -q_1g_1(R) & -q_2g_2(R) & -\ell_R - q_1\frac{dg_1}{dR}P_1 - q_2\frac{dg_2}{dR}P_2 \end{pmatrix}.$$

Equilibrium 0. As for the case of the food chain, $J(S_R, S_z, 0, 0)$ can be diagonalized, leading to the stability criteria:

$$\begin{cases} g_1(S_R) - a_1S_z - m_1 < 0 \\ g_2(S_R) - a_2S_z - m_2 < 0 \end{cases}. \quad (\text{A13})$$

This means that equilibrium 0 is stable if and only if the supply point is simultaneously located above ZNGI_1 and ZNGI_2 .

Equilibrium 1. In this case, the Jacobian matrix reads

$$J(\hat{R}, \hat{Z}, \hat{P}_1, 0) = \begin{pmatrix} -m_Z + e_1 a_1 \hat{P}_1 & e_1 a_1 \hat{Z} & e_2 a_2 \hat{Z} & 0 \\ -a_1 \hat{P}_1 & 0 & 0 & \frac{dg_1}{dR} \hat{P}_1 \\ 0 & 0 & g_2(\hat{R}) - a_2 \hat{Z} - m_2 & 0 \\ 0 & -q_1 g_1(\hat{R}) & -q_2 g_2(\hat{R}) & -\ell_R - q_1 \frac{dg_1}{dR} \hat{P}_1 \end{pmatrix}. \quad (\text{A14})$$

By expanding $\det(J - \lambda I_4)$ along the third row, it is easy to see that the eigenvalues of J are the same as those of equilibrium 1 in the food chain case plus a fourth one equal to $\lambda_4 = g_2(\hat{R}) - a_2 \hat{Z} - m_2$, which is the invasion criterion for species 2. Thus, when it exists, equilibrium 1 is stable only if the regulating factor point (\hat{R}, \hat{Z}) is located above ZNGI_2 . If $\hat{Z} \neq 0$, this condition is sufficient. Otherwise, it is also necessary to check that $S_R < R_1^* + R_{Z,1}^*$ (see food chain).

Equilibrium 2. By symmetry, the same conclusions hold in this case after swapping indices 1 and 2.

Equilibrium 1&2. Noting from equation (1a) set equal to 0 that $-m_Z + e_1 a_1 \hat{P}_1 + e_2 a_2 \hat{P}_2 = -m_Z s_Z / \hat{Z}$, we have

$$J(\hat{R}, \hat{Z}, \hat{P}_1, \hat{P}_2) = \begin{pmatrix} -\frac{m_Z s_Z}{\hat{Z}} & e_1 a_1 \hat{Z} & e_2 a_2 \hat{Z} & 0 \\ -a_1 \hat{P}_1 & 0 & 0 & \frac{dg_1}{dR} \hat{P}_1 \\ -a_2 \hat{P}_2 & 0 & 0 & \frac{dg_2}{dR} \hat{P}_2 \\ 0 & -q_1 g_1(\hat{R}) & -q_2 g_2(\hat{R}) & -\ell_R - q_1 \frac{dg_1}{dR} \hat{P}_1 - q_2 \frac{dg_2}{dR} \hat{P}_2 \end{pmatrix}. \quad (\text{A15})$$

From this sign structure, it follows that the Routh-Hurwitz criteria can be reduced to $\det J > 0$, a condition that can be rewritten as

$$[e_1 a_1 q_2 g_2(\hat{R}) - e_2 a_2 q_1 g_1(\hat{R})] \left(a_1 \frac{dg_2}{dR} - a_2 \frac{dg_1}{dR} \right) > 0, \quad (\text{A16})$$

$$\Leftrightarrow (\gamma_2 - \gamma_1) \left(\frac{dZ}{dR} \Big|_2 - \frac{dZ}{dR} \Big|_1 \right) > 0, \quad (\text{A17})$$

where $dZ/dR|_i$ denotes the slope of the tangent line to the ZNGI_i . This local stability condition can be interpreted geometrically in terms of relative position of crossing ZNGI s and impact vectors at the coexistence point (León and Tumpson 1975; Leibold 1996; Meszéna et al. 2006; Koffel et al. 2016).

Appendix B from T. Koffel et al., “Plant Strategies along Resource Gradients” (Am. Nat., vol. 192, no. 3, p. 360)

Analytical Results on Adaptive Dynamics with Two-Way Allocation Problems

In this appendix, we mathematically demonstrate the results presented in table 2, that is, we determine the sign of the response of the plant convergence stable strategy (CSS) traits along the resource gradient for the three possible partial two-way allocation problems. To do so, we first build on a previous study (Koffel et al. 2016) to derive general relationships linking the response of an evolutionarily stable strategy (ESS) and a CSS to a change in resource supply and then apply these relationships to the three particular two-way allocation problems.

We choose here to use the herbivore attack rate $a = a_0(1 - \rho)$ instead of resistance ρ —the latter being implicitly included in the former—to simplify both notations and calculations. After inversion, this relationship gives $\rho = 1 - a/a_0$. Note that ρ and a vary in opposite directions, as $\partial\rho/\partial a < 0$.

All the cases treated here concern two-way trade-offs, which means that they can be reduced to one-dimensional strategy spaces described by a single focal trait— α , μ , or a —that we will call x in the generic results of the next subsection (the other varying trait seen as a function of this focal trait x).

Preliminary Results

In adaptive dynamics involving a single trait x , a singular point is a local ESS if and only if $\partial^2 w/\partial x^2 < 0$, where $\partial^2 w/\partial x^2$ is the second derivative of the invasion fitness with respect to the invader trait, evaluated at the resident trait. In a previous article (Koffel et al. 2016), we established the following relationship:

$$\frac{\partial w}{\partial Z} \left(\frac{d^2 Z}{dR^2} \Big|_E - \frac{d^2 Z}{dR^2} \Big|_Z \right) = \left(\frac{d\hat{x}}{dR} \Big|_E \right)^2 \cdot \frac{\partial^2 w}{\partial x^2}, \quad (\text{B1})$$

where $d^2 Z/dR^2|_E$ and $d^2 Z/dR^2|_Z$ are the second derivatives of the envelope and the tangent ZNGI, respectively, and thus quantify their curvature. The value $\partial w/\partial Z$ quantifies how plant fitness responds to a variation in herbivore density, and $d\hat{x}/dR|_E$ is the total variation of the ESS trait \hat{x} (either $\hat{\alpha}$, $\hat{\mu}$, or \hat{a} depending on the two-way allocation problem considered) as R varies along the envelope. Expanding on the calculations of a previous study (Koffel et al. 2016), it is actually possible to show the following general result:

$$\frac{d^2 Z}{dR^2} \Big|_E - \frac{d^2 Z}{dR^2} \Big|_Z = \frac{d\hat{x}}{dR} \Big|_E \cdot \frac{\partial}{\partial x} \left(\frac{\partial Z}{\partial R} \Big|_Z \right). \quad (\text{B2})$$

Combining equations (B1) and (B2), we obtain the following useful relationship, linking the variation of the trait along the envelope and the ESS criteria:

$$\frac{d\hat{x}}{dR} \Big|_E \cdot \frac{\partial^2 w}{\partial x^2} = \frac{\partial w}{\partial Z} \cdot \frac{\partial}{\partial x} \left(\frac{\partial Z}{\partial R} \Big|_Z \right), \quad (\text{B3})$$

where $\partial Z/\partial R|_Z$ is obtained after differentiating the ZNGI equation given by setting equation (1b) equal to 0. In the case of the diamond food web module, this is equal to

$$\frac{\partial Z}{\partial R} \Big|_Z = \frac{1}{a} \frac{\mu^2 \alpha}{(\mu + \alpha R)^2}. \quad (\text{B4})$$

We will need to compute the right-hand side of equation (B3) to conclude. This will be done for the three different two-way trade-offs in the next subsections.

A second result from our previous study (Koffel et al. 2016) can help make the link between the properties of the singular points and trait variation:

$$\frac{\partial \hat{R}}{\partial S_R} \cdot \mathcal{J}(x) = \delta(x) \frac{\partial^2 w}{\partial x^2}, \quad (\text{B5})$$

where δ is a strictly positive function of the trait x in the particular case of the diamond food web module and

$$\mathcal{J}(x) = \frac{d}{dx} \left(\frac{\partial w}{\partial x} \right) = \frac{\partial^2 w}{\partial x^2} + \frac{\partial \hat{R}}{\partial x} \frac{\partial^2 w}{\partial R \partial x} + \frac{\partial \hat{Z}}{\partial x} \frac{\partial^2 w}{\partial Z \partial x} \quad (\text{B6})$$

is the Jacobian of the fitness gradient. In adaptive dynamics, a singular point is said to be convergence stable if and only if $\mathcal{J}(x) < 0$. This link between ESS and convergence stability properties on one side and eco-evolutionary response of the resource level to an increase of its supply on the other side is striking. It leads to the following result for a singular point \hat{x} :

$$\hat{x} \text{ is a CSS} \Rightarrow \frac{\partial \hat{R}}{\partial S_R} > 0. \quad (\text{B7})$$

This relationship will be particularly useful in the examples of the different two-way trade-offs of the next subsections.

Case α versus μ

Having $x = \mu$ in mind for this subsection, let us rewrite the trade-off as a general relationship $\alpha(u)$, with $\alpha' < 0$ and a kept constant. Calling $\hat{\mu}$ the focal trait of the ESS, we introduce the simplifying notation $\hat{\alpha} \equiv \alpha(\hat{\mu})$, $\hat{\alpha}' \equiv \alpha'(\hat{\mu})$, and $\hat{R} \equiv R(\hat{\mu})$ for the equilibrium resource level at the ESS. Setting the fitness gradient equal to 0, it is then possible to show that singular points satisfy

$$\hat{R} = -\hat{\alpha}' \left(\frac{\hat{\mu}}{\hat{\alpha}} \right)^2. \quad (\text{B8})$$

This gives the parametric equation of the envelope as a function of the trait $\hat{\mu}$. Using $x = \mu$, we can differentiate the expression of $\partial Z / \partial R|_Z$ obtained in equation (B4) to compute the right-hand side of equation (B3):

$$\frac{\partial w}{\partial Z} \frac{\partial}{\partial \mu} \left(\frac{\partial Z}{\partial R} \Big|_Z \right) = - \frac{\hat{\alpha}^2 \hat{R}}{(\hat{\mu} + \hat{\alpha} \hat{R})^2}, \quad (\text{B9})$$

where we used equation (B8) to get rid of $\hat{\alpha}'$. From equation (B3), we conclude that for any trade-off between α and μ ,

$$\frac{d\hat{\mu}}{dR} \Big|_E \frac{\partial^2 w}{\partial \mu^2} = - \frac{\hat{\alpha}^2 \hat{R}}{(\hat{\mu} + \hat{\alpha} \hat{R})^2} < 0. \quad (\text{B10})$$

Thus, a singular trait $\hat{\mu}$ corresponding to an ESS (i.e., satisfying $\partial^2 w / \partial \mu^2 < 0$) has to increase when moving along the envelope with increasing \hat{R} . Because of the trade-off, this means that $\hat{\alpha}$ conversely decreases. These results are intuitive: plant growth is a balance between resource acquisition at rate αR and biomass synthesis at rate μ . When R increases, resource acquisition gets faster, and it is thus optimal to reallocate from α to μ to keep the two processes balanced. Remember that a is constant in this case; thus, the only way to cope with herbivory is to grow faster.

This can be further investigated through the environmental feedback loop. First, let us note that

$$\frac{\partial \hat{\mu}}{\partial S_R} = \frac{d\hat{\mu}}{dR} \Big|_E \cdot \frac{\partial \hat{R}}{\partial S_R}. \quad (\text{B11})$$

Combining equations (B7) and (B10) leads to the central result:

$$\hat{\mu} \text{ is a CSS} \Rightarrow \frac{\partial \hat{\mu}}{\partial S_R} > 0. \quad (\text{B12})$$

This is a general result true for any trade-off between μ and α satisfying $\partial\alpha/\partial\mu < 0$. This result also does not depend on the details of the plant impact on R and Z (e.g., with e and q functions of μ) as long as the overall impact of the plant on the herbivore remains positive.

Case α versus ρ

Having $x = \alpha$ in mind for this subsection, let us rewrite the trade-off as a general relationship $a(\alpha)$ with $a' > 0$ and μ kept constant. Calling $\hat{\alpha}$ the focal trait of the ESS, we introduce the simplifying notation $\hat{a} \equiv a(\hat{\alpha})$, $\hat{a}' \equiv a'(\hat{\alpha})$, and $\hat{R} \equiv R(\hat{\alpha})$ for the equilibrium resource level at the ESS. Setting the fitness gradient equal to 0, it is then possible to show that singular points satisfy

$$\frac{\hat{a}'}{\hat{a}} = \frac{\mu^2 \hat{R}}{\mu + \hat{\alpha} \hat{R}} \cdot \frac{1}{\mu \hat{\alpha} \hat{R} - m(\mu + \hat{\alpha} \hat{R})}. \quad (\text{B13})$$

Applying equation (B3) with $x = \alpha$ and using the relationship (B13) leads to

$$\left. \frac{d\hat{\alpha}}{dR} \right|_E \frac{\partial^2 w}{\partial \mu^2} = \frac{\hat{a}' m \mu^2 + (\mu - m)(\hat{\alpha} \hat{R})^2}{\hat{a} \hat{R}(\mu + \hat{\alpha} \hat{R})^2} > 0. \quad (\text{B14})$$

As a conclusion, for any trade-off between α and a ,

$$\hat{\alpha} \text{ is an ESS} \Rightarrow \left. \frac{d\hat{\alpha}}{dR} \right|_E < 0, \quad (\text{B15})$$

$$\hat{\alpha} \text{ is a CSS} \Rightarrow \frac{\partial \hat{\alpha}}{\partial S_R} < 0. \quad (\text{B16})$$

Thus, a singular trait $\hat{\alpha}$ corresponding to a CSS has to decrease when moving along the envelope with increasing S_R . Because α and a are traded off, this means that resistance $\rho = 1 - a/a_0$ conversely increases. Again, this is a general result, true for any trade-off between α and ρ and fairly insensitive to the details of the plant impact on R and Z .

Case μ versus ρ

Having $x = \mu$ in mind for this subsection, let us rewrite the trade-off as a general relationship $a(\mu)$ with $a' > 0$ and α kept constant. Calling $\hat{\mu}$ the focal trait of the ESS, we introduce the simplifying notation $\hat{a} \equiv a(\hat{\mu})$, $\hat{a}' \equiv a'(\hat{\mu})$, and $\hat{R} \equiv R(\hat{\mu})$ for the equilibrium resource level at the ESS. To establish a result similar to that of the previous section, we need to get an explicit expression of \hat{R} as a function of $\hat{\mu}$. Setting the fitness gradient equal to 0, we get

$$\left[\frac{\hat{a}}{\hat{a}'} - (\hat{\mu} - m) \right] \left(\frac{\alpha \hat{R}}{\hat{\mu}} \right)^2 - (\hat{\mu} - 2m) \frac{\alpha \hat{R}}{\hat{\mu}} + m = 0. \quad (\text{B17})$$

This equation has solutions if and only if $\Delta = \hat{\mu}^2 - 4m\hat{a}/\hat{a}'$ is positive. Then, there are two solutions:

$$\hat{R}_{\pm} = \frac{\hat{\mu}}{2\alpha \hat{a}/\hat{a}' - (\hat{\mu} - m)} \frac{\hat{\mu} - 2m \pm \sqrt{\Delta}}{\hat{\mu}}. \quad (\text{B18})$$

We have the following results on their signs:

$$\hat{R}_+ > \hat{R}_- > 0 \iff \frac{\hat{a}}{\hat{a}'} > \hat{\mu} - m > m, \quad (\text{B19})$$

$$\hat{R}_- > 0 > \hat{R}_+ \iff \hat{\mu} - m > \frac{\hat{a}}{\hat{a}'}. \quad (\text{B20})$$

When there are singular solutions, positive \hat{R}_- always exists, while positive \hat{R}_+ exists only under the condition $\hat{a}/\hat{a}' > \hat{\mu} - m > m$. Applying equation (B3) with $x = \mu$ and substituting the solution (B18) leads to

$$\left. \frac{d\hat{\mu}}{dR_{\pm}} \right|_E \frac{\partial^2 w}{\partial \mu^2} = \mp \frac{\hat{a}'}{\hat{a}} \frac{\hat{\mu} \alpha}{(\hat{\mu} + \alpha \hat{R})^2} \sqrt{\Delta}. \quad (\text{B21})$$

As a conclusion, for any trade-off between μ and α ,

$$\hat{\mu} \text{ is an ESS} \Rightarrow \left. \frac{d\hat{\mu}}{dR_+} \right|_E > 0 \text{ and } \left. \frac{d\hat{\mu}}{dR_-} \right|_E < 0, \quad (\text{B22})$$

$$\hat{\mu} \text{ is a CSS} \Rightarrow \left. \frac{\partial \hat{\mu}}{\partial S_R} \right|_+ > 0 \text{ and } \left. \frac{\partial \hat{\mu}}{\partial S_R} \right|_- < 0. \quad (\text{B23})$$

As the smaller R_- portion always exists, $\hat{\mu}$ of a CSS starts by decreasing along increasing S_R . However, if the larger R_+ portion also exists, $\hat{\mu}$ hits a minimum and then increases with S_R . In this case, the nonmonotonic behavior of $\hat{\mu}$ leads some strategies to be CSS twice along the resource gradient (for both low and high S_R).

Appendix C from T. Koffel et al., “Plant Strategies along Resource Gradients” (Am. Nat., vol. 192, no. 3, p. 360)

Analytical Results for the Fitness Optimization Approach with Two-Way Allocation Problems

In this appendix, we mathematically demonstrate the results presented in table 3, that is, we determine the sign of the response of the plant optimal traits along the resource gradient in the absence of the environmental feedback loop for the three possible partial two-way allocation problems. To do so, we first derive general relationships linking the response of an optimal strategy (OS) to a change in resource supply and then apply these relationships to the three particular two-way allocation problems.

We choose to use herbivore attack rate $a = a_0(1 - \rho)$ instead of resistance ρ —the latter being implicitly included in the former—to simplify both notations and calculations. After inversion, this relationship gives $\rho = 1 - a/a_0$. Note that ρ and a vary in opposite directions, as $\partial\rho/\partial a < 0$.

All the cases treated here concern two-way trade-offs, which means that they can be reduced to one-dimensional strategy spaces described by a single focal trait— α , μ , or a —that we will call x in the generic results of the next subsection (the other varying trait seen as a function of this focal trait x).

Preliminary Results

Contrary to the adaptive dynamics approach, the fitness optimization approach consists in maximizing plant net growth rate $w = g(R) - aZ - m$ without taking into account any environmental feedback loop (i.e., with R and Z fixed). This means in the case of the two-way trade-offs that a local OS with trait \hat{x} has to satisfy

$$\frac{\partial w}{\partial x} = 0 \quad \text{with} \quad \frac{\partial^2 w}{\partial x^2} < 0. \quad (\text{C1})$$

Solving the previous equation theoretically gives an expression of \hat{x} as a function of R . Differentiating $\partial w/\partial x = 0$ leads to the useful result,

$$\frac{\partial \hat{x}}{\partial R} \frac{\partial^2 w}{\partial x^2} = - \frac{\partial^2 w}{\partial x \partial R}. \quad (\text{C2})$$

This relationship is equivalent to equation (B3) from appendix B, the difference arising from the absence of feedback of the plant on its environment imposed by a zero net growth constraint $w(R, Z) = 0$. Indeed, Z does not vary along the resource gradient here because the plant does not feed the herbivores back. As previously, applying equation (C2) allows us to conclude on the direction of variation of an OS with trait \hat{x} along the resource gradient.

Note that in the optimization approach, R directly plays the role of S_R , as it is the parameter that is determined externally and controls resource availability in the system. To allow more direct comparison with the adaptive dynamics case, let us simply define here that $S_R \equiv R$.

Case α versus μ

Having $x = \mu$ in mind for this subsection, let us write the trade-off as a general relationship $\alpha(\mu)$ with $\alpha' < 0$, with a kept constant. With $\hat{\mu}$ the ESS solution, we introduce the simplifying notation $\hat{\alpha} \equiv \alpha(\mu)$ and $\hat{\alpha}' \equiv \alpha'(\hat{\mu})$. Setting the fitness gradient equal to 0, it is then possible to show that a local OS satisfies

$$\frac{\hat{\alpha} R}{\hat{\mu}} = - \frac{\hat{\alpha}'}{\hat{\alpha}} \hat{\mu}. \quad (\text{C3})$$

Applying equation (C2) with $x = \mu$ and substituting the expression (C3) to get rid of $\hat{\alpha}'$ leads to

$$\frac{\partial^2 w}{\partial \mu \partial R} = \frac{\hat{\alpha}^2 R}{(\hat{\mu} + \hat{\alpha} R)^2} > 0. \quad (C4)$$

Because of equation (C2), this means that

$$\hat{\mu} \text{ is an OS} \Rightarrow \frac{\partial \hat{\mu}}{\partial S_R} > 0. \quad (C5)$$

Thus, a trait $\hat{\mu}$ corresponding to an OS has to increase with increasing S_R . Conversely, the trait α decreases. This is a general result true for any trade-off between α and μ . It is actually possible to show that this result still holds with $a(\mu)$ and $m(\mu)$ satisfying $a' > 0$ and $m' > 0$.

Case α versus ρ

Having $x = \alpha$ in mind for this subsection, let us write the trade-off as a general relationship $a(\alpha)$ with $a' > 0$, with μ kept constant. With $\hat{\alpha}$ the OS solution, we introduce the simplifying notation $\hat{a} \equiv a(\hat{\alpha})$ and $\hat{a}' \equiv a'(\hat{\alpha})$. To establish a result similar to that of the previous section, we can solve the inverse problem by getting an explicit expression of R as a function of $\hat{\alpha}$ for the OS. Setting the fitness gradient equal to 0, we obtain

$$\left(\frac{\hat{\alpha} R}{\mu}\right)^2 + \left(2 - \frac{\mu}{\hat{\alpha} \hat{a}' Z}\right) \frac{\hat{\alpha} R}{\mu} + 1 = 0. \quad (C6)$$

This equation has solutions if and only if $\Delta = b(b - 2)$ is positive, with $b = \mu/(2\hat{\alpha}\hat{a}'Z)$. Then, there are two of them and they read

$$R_{\pm} = \frac{\mu}{\hat{\alpha}} \left(b - 1 \pm \sqrt{b(b - 2)}\right). \quad (C7)$$

It is moreover easy to show that when they exist, they satisfy

$$\hat{\alpha} R_+ \geq \mu \geq \hat{\alpha} R_- > 0. \quad (C8)$$

Computing the right-hand side of equation (C2),

$$\frac{\partial^2 w}{\partial \alpha \partial R} = \mu^2 \frac{\mu - \hat{\alpha} R}{(\mu + \hat{\alpha} R)^3}. \quad (C9)$$

Thus, substituting inequality (C8) in equation (C9), we obtain

$$\frac{\partial^2 w}{\partial \alpha \partial R_-} > 0 \quad \text{and} \quad \frac{\partial^2 w}{\partial \alpha \partial R_+} < 0, \quad (C10)$$

leading to

$$\hat{\alpha} \text{ is an OS} \Rightarrow \begin{cases} \frac{\partial \hat{\alpha}}{\partial S_R} > 0 & \text{if } \hat{\alpha} < \frac{\mu}{S_R}, \\ \frac{\partial \hat{\alpha}}{\partial S_R} < 0 & \text{otherwise.} \end{cases} \quad (C11)$$

The situation can get complicated for a generic trade-off, potentially with multiple local optima. However, the idea from these general results is always the following: if increasing S_R makes a local OS appear, the trait $\hat{\alpha}$ where this maximum is attained will first increase as S_R keeps increasing. At one point, $\hat{\alpha}$ will hit the value $\alpha_c = \mu/S_R$ for which it stops increasing. Continuing to increase S_R then leads to a decrease of $\hat{\alpha}$ either toward 0 or until the OS is destabilized.

This result can be understood by the fact that both αS_R and μ limit plant growth. When both $\hat{\alpha}$ and S_R are small, resource acquisition is strongly limiting, leading to significant benefits to allocate to α rather than a . However, as S_R becomes large, plant growth saturates to μ and the benefits of a large α vanish, making allocation to ρ more useful again.

Case μ versus ρ

Having $x = \mu$ in mind for this subsection, let us write the trade-off as a general relationship $a(\mu)$ with $a' > 0$ and α kept constant. With $\hat{\mu}$ the OS solution, we introduce the simplifying notation $\hat{a} \equiv a(\hat{\mu})$ and $\hat{a}' \equiv a'(\hat{\mu})$. Then, computing the right-hand side of equation (C2) reads

$$\frac{\partial^2 w}{\partial \mu \partial R} = 2 \frac{\hat{\mu} \alpha^2 R}{(\hat{\mu} + \alpha R)^3} > 0. \quad (\text{C12})$$

This directly gives the result

$$\hat{\mu} \text{ is an OS} \Rightarrow \frac{\partial \hat{\mu}}{\partial R} > 0. \quad (\text{C13})$$

Thus, a trait $\hat{\mu}$ corresponding to an OS has to increase when moving along the envelope with increasing S_R . Conversely, the trait $\hat{\rho}$ decreases. This is a general result true for any trade-off between μ and ρ .

Appendix D from T. Koffel et al., “Plant Strategies along Resource Gradients” (Am. Nat., vol. 192, no. 3, p. 360)

Scenario 3: Hump-Shaped Resistance along the Resource Gradient

In this appendix, we present a scenario where a combination of accelerating and diminishing returns can lead to a hump-shaped pattern in resistance allocation and plant density along the resource supply gradient. For this third scenario, we assume that $\varepsilon_\alpha < 1$, $\varepsilon_\mu = 1$, and $\varepsilon_\rho > 1$. The strategy turnover along the resource gradient is at first similar to scenario 2: reallocation from an acquisition specialist to a more tolerant strategy and then allocation to resistance. However, this allocation to resistance does not tend toward complete resistance at high supply. Instead, it reaches a maximum along increasing resource supply before decreasing toward a completely nonresistant strategy again (fig. D1C). This complete removal of allocation to resistance leads to reallocation to both acquisition and tolerance. This hump-shaped resistance allocation pattern along the resource gradient translates into plant biomass also being hump-shaped (fig. D1D). Finally, the completely resistant strategy invades at one point and brings us back to the same evolutionarily stable coexistence pattern described in scenario 1. The hump shape of plant density P is reminiscent of one of the tolerance scenarios in “Analytical Results for the Two-Way Allocation Problems.”

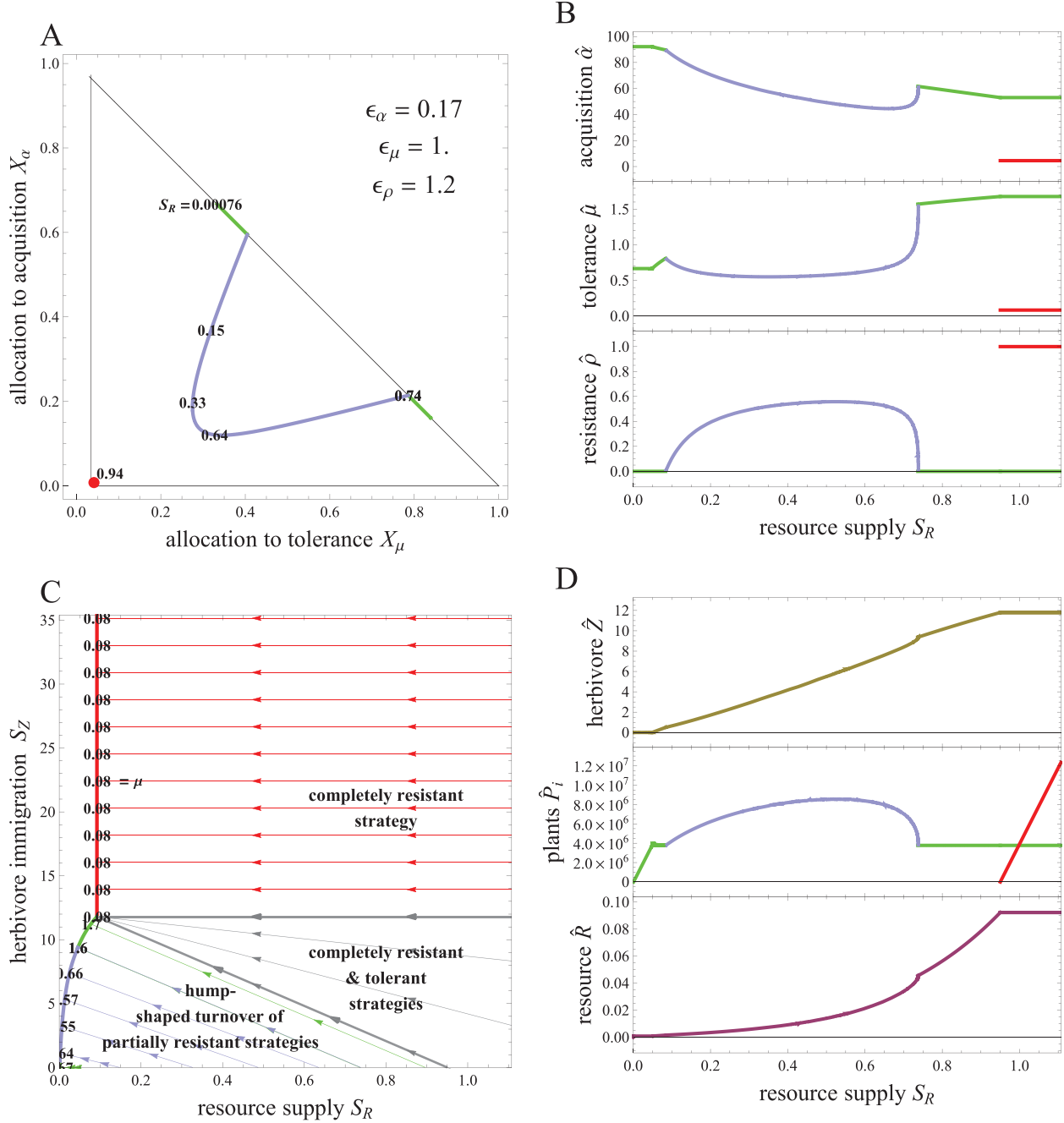


Figure D1: Scenario 3: eco-evolutionary results under diminishing, linear, and accelerating returns on allocation to affinity, maximal growth rate, and resistance, respectively ($\epsilon_\alpha < 1$, $\epsilon_\mu = 1$, and $\epsilon_\rho > 1$). *A*, Adaptive strategy turnover between nonresistant (green), partially resistant (blue), and completely resistant (red) strategies in the allocation space (X_μ, X_α) along increasing resource supply S_R (numbers in black) in the absence of herbivore immigration ($S_Z = 0$). *C*, Bifurcation diagram along the supply gradient. *B*, *D*, Plant adaptive trait turnover (*B*) and equilibrium densities (*D*) along the resource gradient in the absence of herbivore immigration. Parameters are from table 1.

Appendix E from T. Koffel et al., “Plant Strategies along Resource Gradients” (Am. Nat., vol. 192, no. 3, p. 360)

Scenarios 1', 2', and 3'

In this appendix, we present the three alternative scenarios 1', 2', and 3' that replace scenarios 1, 2, and 3, respectively, when complete resistance cannot be attained. This happens within our model when ε_μ is large (see fig. F2 in app. F), because the minimal allocation $X_{\mu,\min}$ needed to be viable ($\mu > m$) and the allocation needed for complete resistance $X_{\rho,\max}$ together exceed the available allocation (i.e., $X_{\mu,\min} + X_{\rho,\max} > 1$).

In scenario 1', resistance is never adaptive and no resistant strategy invades, even under high resource supply, so plants progressively switch from good competitive ability under low resource availability to tolerance to herbivory only under high resource availability (fig. E1). Scenario 2' consists of allocation to resistance under high supply, but this is coupled with a persisting finite allocation to tolerance, so that the asymptotic strategy is truly a mixed resistant/tolerant strategy (fig. E2). In scenario 3', there is a single tolerant strategy dominating high supplies similarly to scenario 1', while medium supplies show the characteristic hump-shaped allocation to resistance of scenario 3 (fig. E3).

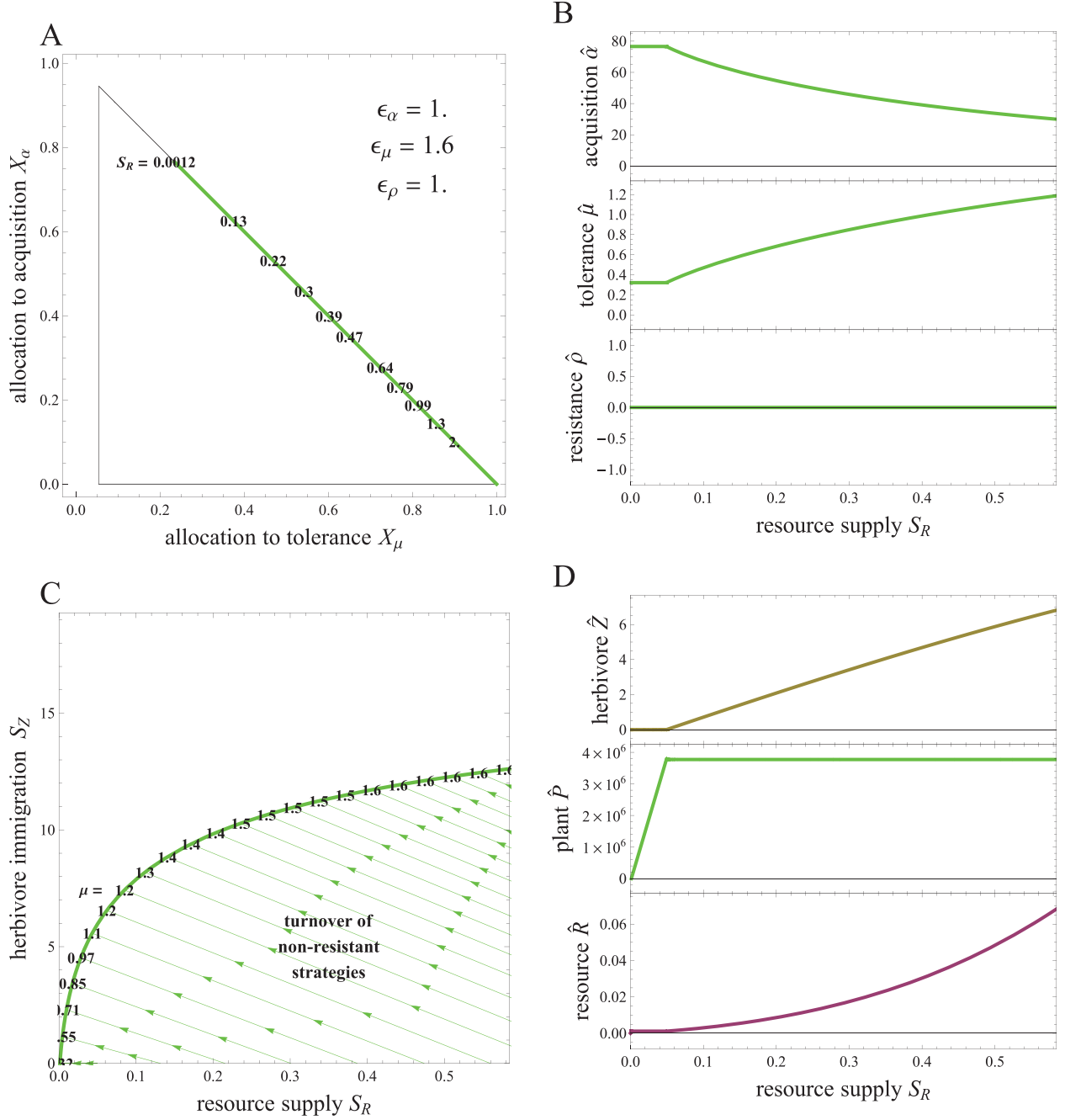


Figure E1: Scenario 1': eco-evolutionary results under accelerating returns on allocation to maximal growth rate and linear allocation to affinity and resistance ($\epsilon_\alpha = 1$, $\epsilon_\mu > 1$, and $\epsilon_\rho = 1$). *A*, Adaptive strategy turnover between nonresistant (green) strategies in the allocation space (X_μ , X_α) along increasing resource supply S_R (numbers in black) in the absence of herbivore immigration ($S_Z = 0$). *C*, Bifurcation diagram along the supply gradients. *B*, *D*, Plant adaptive trait turnover (*B*) and equilibrium densities (*D*) along the resource gradient in the absence of herbivore immigration. Parameters are from table 1.

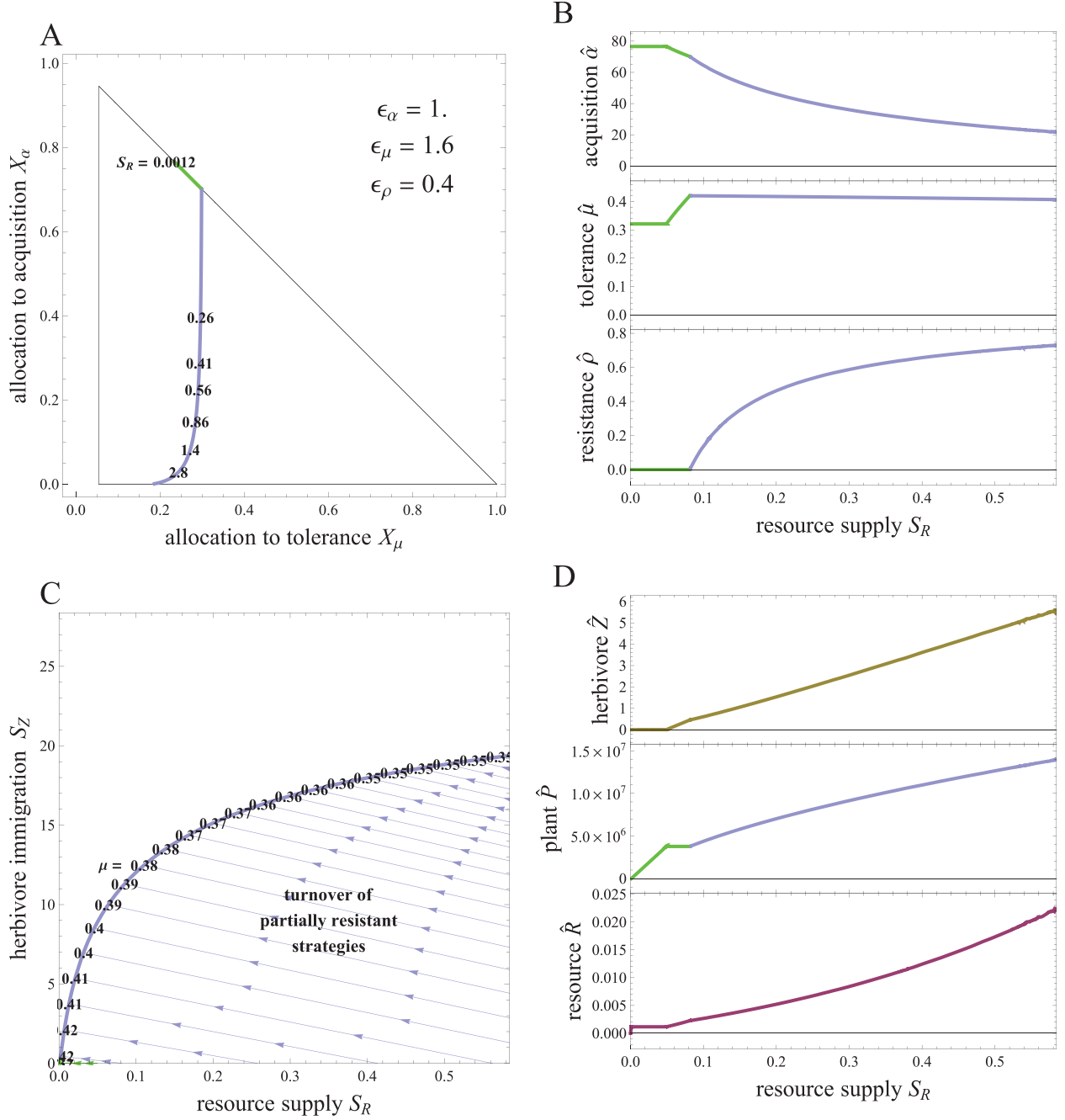


Figure E2: Scenario 2: eco-evolutionary results under linear, accelerating, and diminishing returns on allocation to affinity, maximal growth rate, and resistance, respectively ($\epsilon_\alpha = 1$, $\epsilon_\mu > 1$, and $\epsilon_\rho < 1$). *A*, Adaptive strategy turnover between nonresistant (green) and partially resistant (blue) strategies in the allocation space (X_μ , X_α) along increasing resource supply S_R (numbers in black) in the absence of herbivore immigration ($S_Z = 0$). *C*, Bifurcation diagram along the supply gradients. *B*, *D*, Plant adaptive trait turnover (*B*) and equilibrium densities (*D*) along the resource gradient in the absence of herbivore immigration. Parameters are from table 1.

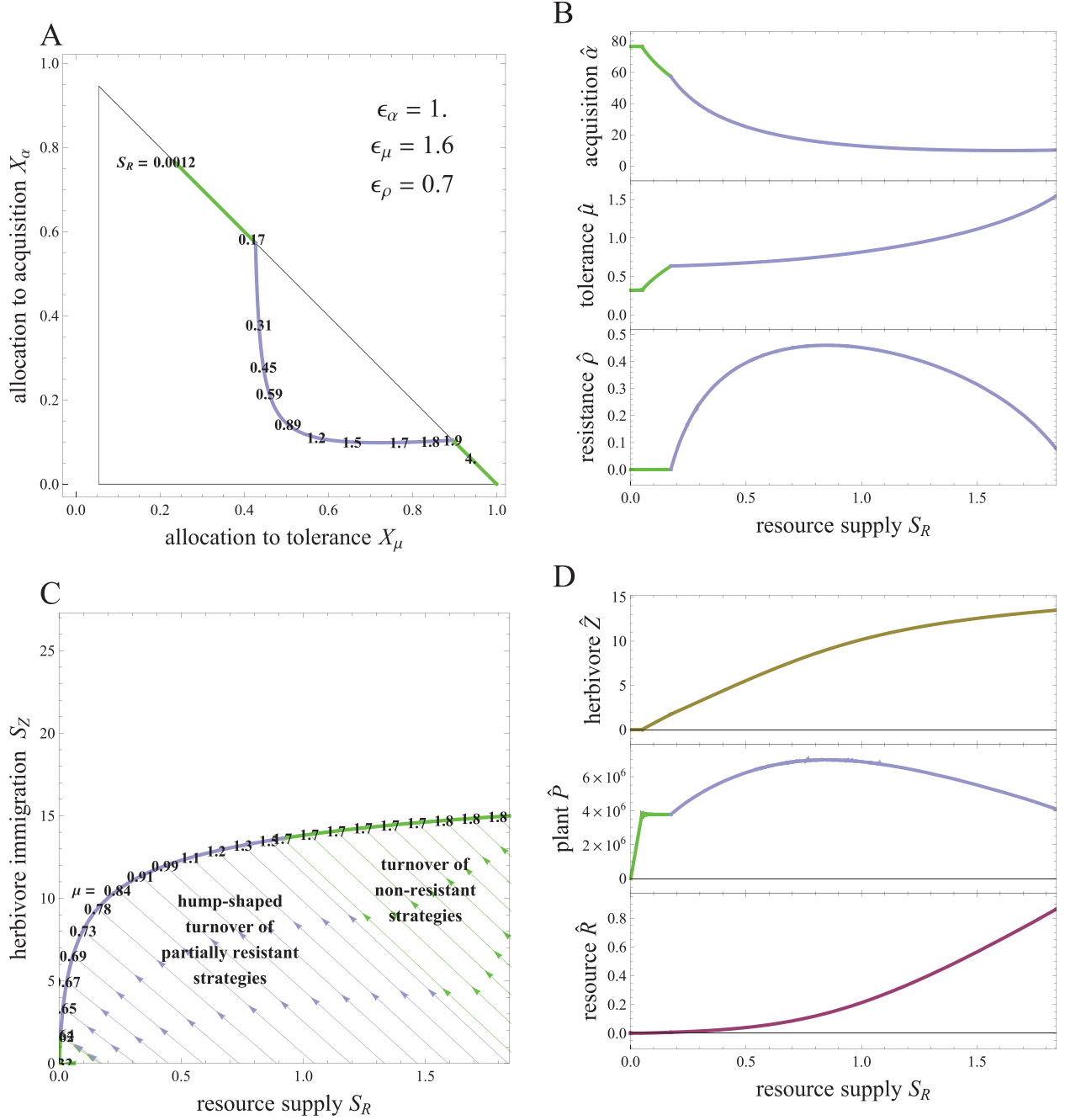


Figure E3: Scenario 3: eco-evolutionary results under linear, accelerating, and diminishing returns on allocation to affinity, maximal growth rate, and resistance, respectively ($\epsilon_\alpha = 1$, $\epsilon_\mu > 1$, and $\epsilon_\rho < 1$). *A*, Adaptive strategy turnover between nonresistant (green) and partially resistant (blue) strategies in the allocation space (X_μ , X_α) along increasing resource supply S_R (numbers in black) in the absence of herbivore immigration ($S_Z = 0$). *C*, Bifurcation diagram along the supply gradients. *B*, *D*, Plant adaptive trait turnover (*B*) and equilibrium densities (*D*) along the resource gradient in the absence of herbivore immigration. Parameters are from table 1.

Appendix F from T. Koffel et al., “Plant Strategies along Resource Gradients” (Am. Nat., vol. 192, no. 3, p. 360)

Overview of Different Scenarios

In this appendix, we present a thorough exploration of the occurrence of the six possible scenarios presented in the main text and in appendixes D and E along the three dimensions of the allocation shape parameter space. More precisely, we set one of the three allocation shape parameters equal to 1 and numerically associate a scenario to each combination of the two other parameters. This enables us to assess the range of shape parameters for which every scenario occurs.

The results in the ε_α and ε_ρ plane with $\varepsilon_\mu = 1$ are represented in figure F1. We see that scenarios 1 and 2 are separated by a decreasing curve going through the point $(\varepsilon_\alpha, \varepsilon_\rho) = (1, 1)$, with scenario 3 squeezed between them in the bottom right quadrant. The fact that this boundary goes through $(1, 1)$ means that the scenario with linear returns on allocation on the three traits is mathematically degenerate, as any slight curvature of an allocation function would have sharp consequences by tipping the situation into scenario 1 or 2. This underscores the role played by the shape parameters, a posteriori justifying their introduction. Moreover, the bottom left corner (diminishing returns on both α and ρ) corresponds to scenario 2 with only a single generalist strategy, while the top right corner (accelerating returns on both α and ρ) corresponds to scenario 1 with evolutionarily stable coexistence of two specialists. The top left quadrant, even though dominated by scenario 2, can also lead to scenario 3 when ε_ρ is close to 1. All three scenarios are possible in the bottom right quadrant.

We have seen in appendix E that completely resistant strategies are not always viable. This happens when ε_μ is large enough that there is not enough allocation to be simultaneously viable and completely resistant. Formally, this condition on ε_μ writes $\varepsilon_\mu > \varepsilon_{\mu,c}$ with

$$\varepsilon_{\mu,c} = \frac{\mu_{\max} - m}{m} \cdot \frac{1 - X_{\rho,\max}}{X_{\rho,\max}}, \quad (\text{F1})$$

where we have used the specific shape of the return-on-allocation function f_μ of equation (5). This shows how the critical value $\varepsilon_{\mu,c}$ under which completely resistant strategies are viable depends on $X_{\rho,\max}$. More precisely, $\varepsilon_{\mu,c}$ decreases as $X_{\rho,\max}$ increases. With the parameters of table 1 used to generate the figures in this article, we have $\varepsilon_{\mu,c} \approx 1.45$. Figure F2 shows how the three scenarios 1', 2', and 3' replace scenarios 1, 2, and 3, respectively, as ε_μ is greater than $\varepsilon_{\mu,c}$.

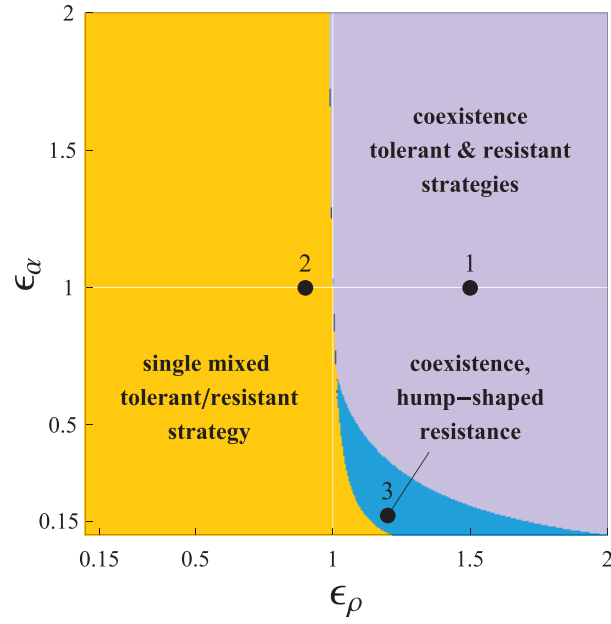


Figure F1: Overview of scenarios 1 (mauve), 2 (yellow), and 3 (blue) in the ϵ_ρ - ϵ_α shape parameter plane with $\epsilon_\mu = 1$.

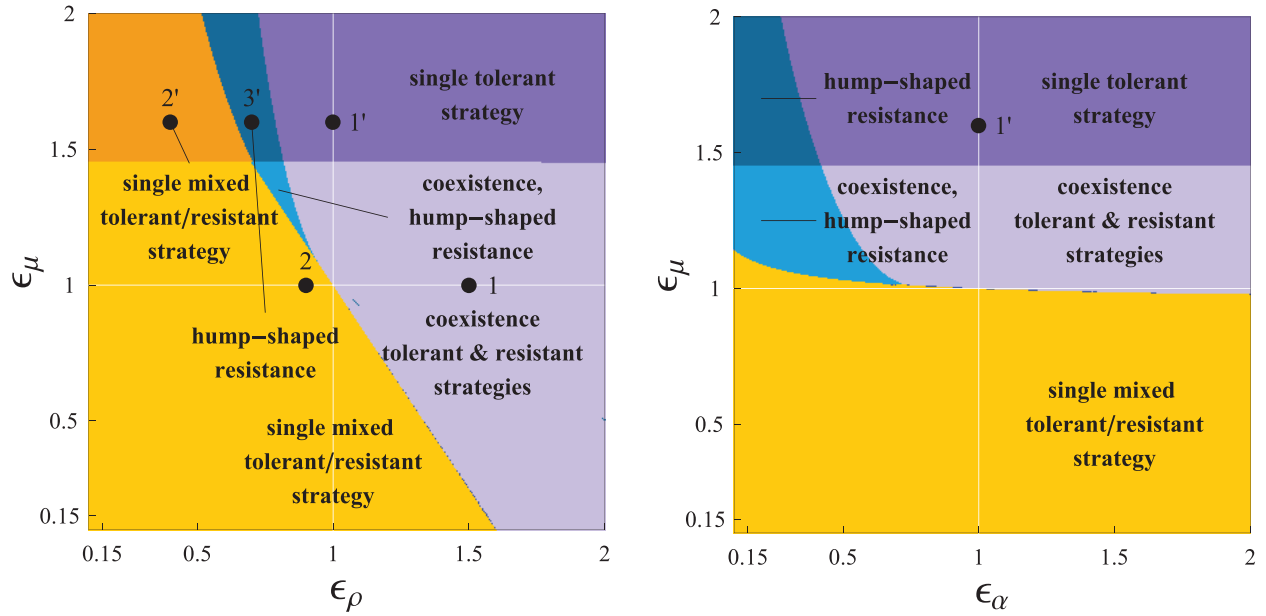


Figure F2: Overview of scenarios 1 (mauve), 2 (yellow), 3 (blue), 1' (orange), 2' (dark blue), and 3' (purple) in the ϵ_ρ - ϵ_μ and ϵ_α - ϵ_μ shape parameter planes.

Appendix G from T. Koffel et al., “Plant Strategies along Resource Gradients” (Am. Nat., vol. 192, no. 3, p. 360)

Type II Functional Response of Herbivores

In this appendix, we show how our approach can be adapted to account for a type II functional response of herbivores instead of a type I functional response and how this only quantitatively changes the results presented in the main text. More precisely, we expect the overall adaptive pattern along the resource gradient to be similar but shifted to the right as the top-down control by the herbivore is weakened by the type II functional response.

The main feature of the type II functional response is that it introduces handling times h_i , defined as the time needed for one herbivore to handle a plant from species i . The per capita mortality rate of plant i due to herbivory then takes the form

$$\frac{a_i Z}{1 + \sum_{j=1}^n a_j h_j P_j}. \quad (\text{G1})$$

Note that this generalizes the model presented in the main text, as a type I functional response is recovered when taking $h_i = 0$ for all i . The equations describing the ecological dynamics are rewritten as

$$\frac{dZ}{dt} = I_Z - m_Z Z + \sum_{i=1}^n \frac{e_i a_i P_i Z}{1 + \sum_{j=1}^n a_j h_j P_j}, \quad (\text{G2a})$$

$$\frac{dP_i}{dt} = \left[g_i(R) - \frac{a_i Z}{1 + \sum_{j=1}^n a_j h_j P_j} - m_i \right] P_i \quad \text{for all } i = 1, \dots, n, \quad (\text{G2b})$$

$$\frac{dR}{dt} = I_R - \ell_R R - \sum_{i=1}^n q_i g_i(R) P_i. \quad (\text{G2c})$$

Interestingly, the growth rates of the plants now depend directly on plant densities P_i , in the denominator of the type II functional responses in equation (G2b). Such direct density dependence shares some similarities with a general Lotka-Volterra model, suggesting that more than two strategies—possibly an unlimited number—could coexist. However, the key point to be noticed here is that this direct density dependence influences every plant strategy i in a similar fashion, thus not providing any new regulating factor. This can be seen formally through a change of variable, by introducing the density of active herbivores Z_a :

$$Z_a = \frac{Z}{1 + \sum_{j=1}^n a_j h_j P_j}. \quad (\text{G3})$$

As the name of this new limiting factor suggests, we can formally think of the herbivore population as being split between its active component Z_a and the one busy handling plant Z_h , with $Z_h + Z_a = Z$. Using this new notation, the first two equations of model (G2) can be rewritten as

$$\frac{dZ}{dt} = I_Z - m_Z Z + \sum_{i=1}^n e_i a_i P_i Z_a, \quad (\text{G4a})$$

$$\frac{dP_i}{dt} = [g_i(R) - a_i Z_a - m_i] P_i \quad \text{for all } i = 1, \dots, n. \quad (\text{G4b})$$

From the plant growth perspective, we have formally replaced the regulating factor Z by an effective regulating factor Z_a . This means that the ESS is essentially unchanged in this new regulating factor space, thus not fundamentally altering

the adaptive pattern along the resource gradient. Again, this change of variable was possible only because the handling effect on herbivores is perceived in a similar way by all the plants, indifferently of their strategies. Note that such a situation is not fundamentally different from the type I case, where the Z influencing plant invasion fitness can at equilibrium also be thought of as being a function of both the densities and the traits of the resident plant populations.

As a consequence, there are still only two regulating factors affecting plant growth in the type II case, R and Z_a , which means that no more than two strategies can coexist in the system. Yet equation (G4a) is now a function of both Z and Z_a . This can be overcome using equation (G3) to rewrite the herbivore dynamics at equilibrium using Z_a only, simply leading to

$$0 = I_Z - m_Z \hat{Z}_a + \sum_{i=1}^n (e_i - m_Z h_i) a_i \hat{P}_i \hat{Z}_a. \quad (\text{G5})$$

This is similar to equation (G2a) at equilibrium if one notes that we just replaced \hat{Z} by \hat{Z}_a and e_i by $e_i - m_Z h_i$. The main effect of increased handling times h_i is thus a reduced impact of plants on the active herbivore population Z_a by decreasing the “effective” conversion efficiency. Interestingly, high handling times satisfying $h_i > e_i/m_Z$ can totally overturn the positive feeding effect of plants on herbivores, leading to a net negative effect (i.e., mortality) per unit of plant on their growth, resulting in positive feedback loops and alternate stable states under high herbivore immigration. When $h_i < e_i/m_Z$, the feeding impact of the plant on the herbivore is still reduced, which means that the top-down control of the plant by the herbivore is reduced in favor of a bottom-up control by the resource. This means that all else equal, an increase in h_i leads to a reduction in both resource availability R and active herbivore density Z_a , while plant density P_i increases. The response of Z is less clear and would need a more detailed investigation.

To conclude, the overall adaptive pattern along the resource gradient is expected to be qualitatively similar under given, relatively low handling times but shifted to the right, as the top-down control by the herbivore is weakened by the type II functional response. This means that for a given resource supply along the gradient, the inclusion of a type II functional response of the herbivore would favor allocation toward acquisition over tolerance and resistance. Note that our analysis implicitly assumed that the ecological equilibria were stable. This ideally should be checked by a more careful analysis, as such type II functional responses are known to potentially lead to limiting cycles (Hastings and Powell 1991; Abrams and Roth 1994).