

# Plant Strategies along Resource Gradients

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**ABSTRACT:** Plants present a variety of defensive strategies against herbivores, broadly classified into tolerance and resistance. Since resource availability can also limit plant growth, we expect plant allocation to resource acquisition and defense to vary along resource gradients. Yet, the conditions under which one defensive strategy is favored over the other are unclear. Here, we use an eco-evolutionary model to investigate plant adaptive allocation to resource acquisition, tolerance, and resistance along a resource gradient in a simple food web module inspired by plankton communities where plants compete for a single resource and are grazed on by a shared herbivore. We show that undefended, acquisition-specialist strategies dominate under low resource supplies. Conversely, high resource supplies, which lead to high herbivore abundance because of trophic transfers, result in either the dominance of very resistant strategies or coexistence between a completely resistant strategy and a fast-growing, tolerant one. We also explore the consequences of this adaptive allocation on species biomasses. Finally, we compare our predictions to a more traditional, density-independent optimization model. We show that density dependence mediated by resources and herbivores is the cause of the increase in plant resistance along the resource gradient, as the optimization model would instead have favored tolerance.

**Keywords:** herbivory, tolerance, resistance, resource gradient, adaptive dynamics, coexistence.

## Introduction

Herbivory is a major selective pressure for plants, with dramatic consequences for their growth, survival, and reproduction. In response, plants have developed two broad classes of defensive strategies throughout their evolutionary history: resistance and tolerance. Resistance comes from adaptations that reduce the amount of herbivore damage experienced by a plant. Tolerance does not reduce herbivore damage but mitigates its impact on plant fitness through compensatory growth (Tiffin 2000; Stowe 2013). While dealing with her-

bivory, plants must also acquire resources such as light, water, and nutrients. As availabilities of these resources vary along environmental gradients, so do selective pressures on plants, in turn influencing their defense allocation patterns (Coley et al. 1985; Wise and Abrahamson 2007; Endara and Coley 2011; Hahn and Maron 2016). In this context, a major question is what determines plant optimal allocation to resource acquisition, tolerance, and resistance.

A diversity of hypotheses and models have been proposed to investigate the evolution of plant defenses (Stamp 2003). Early theoretical approaches consisted of fitness optimization under given, fixed herbivore densities (Coley et al. 1985; Simms and Rausher 1987). However, some evolutionary biologists emphasized the dynamical nature of herbivore density, which results in density- and frequency-dependent selection with significant impacts on the evolution of plant defense (Augner et al. 1991; Tiffin 2000). Such density- and frequency-dependent selection arises through the environmental feedback loop (Dieckmann and Metz 2006), defined hereafter by the way plants' impact on resource availability and herbivore density feeds back on plant growth, and is naturally accounted for within ecological models of food chains and food web modules (Armstrong 1979; Leibold 1996; Loreau and de Mazancourt 1999; Chase et al. 2000). Combined with game-theoretical thinking (McNickle and Dybzinski 2013; Brown 2016), such models have given rise to eco-evolutionary approaches that have been used over the last decades to investigate plant adaptation and community assembly under joint resource competition and herbivore selective pressure (de Mazancourt et al. 2001; Abrams and Chen 2002; Loeuille and Loreau 2004; Våge et al. 2014). Similar approaches have clarified the conditions, such as trade-off or allocation shapes, that allow plants with differing defense allocation to coexist on evolutionary timescales (Abrams 2003; Jones and Ellner 2004; Zu et al. 2015).

Yet, all these models to date have concentrated on the trade-off between resource acquisition and herbivore resistance. Empirical evidence suggests that in some scenarios,

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nonresistant species can survive under intense herbivory and high resource availabilities by having a high growth rate, a strategy called tolerance (Moen et al. 1993; Agrawal 1998; Oksanen and Oksanen 2000). To study the evolution of tolerance, we must also take into account a third trait, intrinsic growth rate. This leads to a CRT triangle, a three-way allocation problem between resource acquisition (competition), resistance to herbivory (resistance), and maximal growth rate (tolerance). Such three-way strategic models have been influential in ecology (Grime 1974, 1977) and are characterized by an overarching three-way trade-off, which can mask two-way trade-offs when the third trait is not controlled for (van Noordwijk and de Jong 1986; Mole 1994). There is evidence in the empirical literature supporting such trade-offs, involving tolerance and resistance (Fineblum and Rausher 1995), resource acquisition and resistance (Yoshida et al. 2004; Edwards et al. 2011), or resource acquisition and maximal growth rate (Edwards et al. 2013).

In this article, we investigate plant adaptive allocation to competitive ability, tolerance, and resistance along a resource gradient within a simple food web module closely inspired by phytoplankton systems. We use a recently developed extension of contemporary niche theory's graphical approach (Tilman 1982; Leibold 1996; Chase and Leibold 2003) that uses geometrical envelopes of requirement niches to graphically solve for the best-adapted strategies along the environmental gradients (Koffel et al. 2016). We first describe the ecological model and show how the addition of a third trait dimension, tolerance, influences the environmental feedback loop through variation in resource level and herbivore density along the resource gradient. These ecological results are critical to understanding what drives selective pressures on the plant in the eco-evolutionary analysis. Second, we describe the three-way allocation problem and the evolutionary approaches to answer the following questions: at the functional trait level, which environmental conditions select for tolerance, resistance, or both? At the community level, when is evolutionarily stable coexistence of a tolerant and a resistant species favored over the dominance of a single intermediate one? At the ecosystem level, what are the consequences in terms of resource availability and plant and herbivore densities of the evolution of plant defense? Finally, what role does the environmental feedback loop, which leads to density- and frequency-dependent selection, play in these predictions?

### Ecological Analysis

#### Mathematical Model

We first introduce the ecological model describing the dynamics of the ecosystem in the absence of evolution. This three-level diamond food web is a classic model of theo-

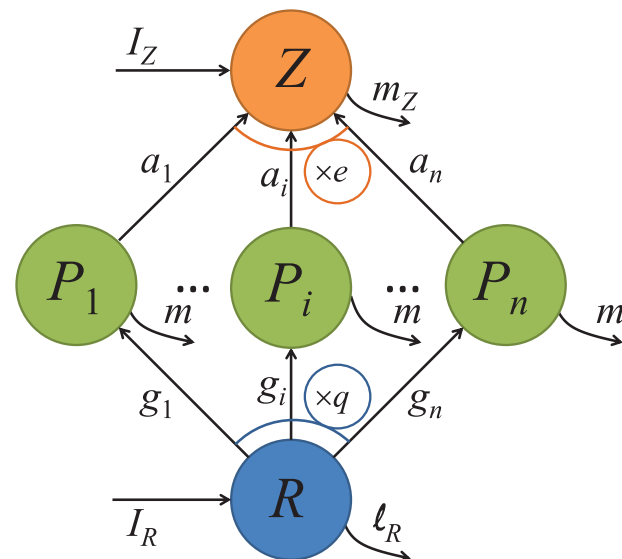
retical ecology (e.g., Holt et al. 1994; Leibold 1996; Grover and Holt 1998). It represents a community of  $n$  different plant species, whose population densities are denoted  $P_i$  ( $i = 1, \dots, n$ ), consuming a limiting resource with availability  $R$  and themselves being consumed by a single herbivore species with density  $Z$  (fig. 1). We model the dynamics of the food web module using the following ordinary differential equations:

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

$$\frac{dP_i}{dt} = [g_i(R) - a_i Z - m] P_i \quad i = 1, \dots, n, \quad (1b)$$

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

This model, directly applicable to phytoplankton communities, was parametrized on a nitrogen-phytoplankton-*Daphnia* system from a chemostat model (Grover 1995). All the state variables and parameters, as well as their numerical values and units, are summarized in table 1. The abiotic resource is supplied at input rate  $I_R$  and lost at first-order rate  $\ell_R$ . Herbivores can immigrate into the system at rate  $I_Z$  and die at per capita rate  $m_Z$ . Allowing for herbivore immigration is natural within this theoretical framework and makes it possible to independently vary the top-down and bottom-up controls on the plant, but most of our results will focus on the zero-immigration limit, as it is both more realistic for plankton communities and more directly com-



**Figure 1:** Schematic representation of the diamond-shaped food web module, where the shaded boxes represent the state variables of the system and the arrows represent the fluxes of matter.

Table 1: Model notation

Symbol	Meaning	Value used	Units
State variables:			
$R$	Resource availability	...	$\mu\text{mol L}^{-1}$
$P_i$	Plant species $i$ density	...	Plants $\text{L}^{-1}$
$Z$	Herbivore density	...	Animals $\text{L}^{-1}$
Ecological parameters:			
$g_i$	Plant $i$ growth rate	...	$\text{Day}^{-1}$
$m$	Plant basal death rate	.07	$\text{Day}^{-1}$
$a_0$	Herbivore basal attack rate on plant	.1	$\text{Day}^{-1} \text{ L animals}^{-1}$
$\alpha_i$	Plant $i$ resource affinity (0 to $\alpha_{\max}$ )	0–100	$\text{Day}^{-1} \text{ L } \mu\text{mol}^{-1}$
$\mu_i$	Plant $i$ maximal growth rate (0 to $\mu_{\max}$ )	0–2	$\text{Day}^{-1}$
$\rho_i$	Plant $i$ resistance (0 to $\rho_{\max}$ )	0–1	...
$a_i = a_0(1 - \rho_i)$	Herbivore attack rate on plant $i$	0–.1	$\text{Day}^{-1} \text{ L animals}^{-1}$
$e$	Plant-herbivore conversion efficiency	$5.7 \times 10^{-7}$	Animal plant $^{-1}$
$q$	Plant-resource conversion efficiency	$9.1 \times 10^{-9}$	$\mu\text{mol plant}^{-1}$
$m_Z$	Herbivore death rate	.215	$\text{Day}^{-1}$
$I_Z$	Herbivore immigration rate	Variable	Animals $\text{L}^{-1} \text{ day}^{-1}$
$I_R$	Resource supply rate	Variable	$\mu\text{mol L}^{-1} \text{ day}^{-1}$
$\ell_R$	Resource loss rate	.05	$\text{Day}^{-1}$
Allocation parameters			
$X_j$	Trait $j$ allocation	0–1	...
$X_{\rho, \max}$	Necessary $\rho$ allocation for complete resistance	.95	...
$f_j$	Trait $j$ return-on-allocation function	...	...
$\epsilon_j$	Trait $j$ allocation shape parameter	Variable	...

Note: Definitions, numerical values, and units of the state variables and parameters of the model. The model was parametrized using Grover's (1995) data on a nitrogen-phytoplankton-*Daphnia* food web module in a chemostat. "Plants" and "animals" both designate numbers of individuals.

parable to previous work (Oksanen et al. 1981; Mittelbach et al. 1988; Leibold 1996). Plants interact with their environment via two distinct trophic transfers. First, plants from species  $i$  grow at per capita growth rate  $g_i(R)$  by acquiring the resource  $R$ . Second, plants  $i$  are consumed by herbivores  $Z$  through a mass-action law with attack rate  $a_i$ . To facilitate the formulation of our evolutionary model later, we parameterize  $a_i$  in terms of resistance  $\rho_i$  as  $a_i = a_0(1 - \rho_i)$ , where  $a_0$  is the basal attack rate on a nonresistant plant. Both trophic transfers are characterized by constant conversion coefficients, respectively, the resource use efficiency of plants  $q$  and the efficiency of herbivore assimilation  $e$ . Finally, plants experience a basal, herbivore-independent per capita mortality rate  $m$ .

In contrast to previous models that used type I functional responses, our model requires a type II functional response of plants on the resource to distinguish between resource acquisition and tolerance:

$$g_i(R) = \frac{\mu_i \alpha_i R}{\mu_i + \alpha_i R}. \quad (2)$$

When the resource is scarce, growth is limited by resource acquisition and the growth rate of species  $i$  given by equation (2) is proportional to resource availability  $R$  through resource affinity  $\alpha_i$  (resource $^{-1}$  time $^{-1}$ ). Conversely, abun-

dant resources lead to saturation of the functional response toward maximal growth rate  $\mu_i$  (time $^{-1}$ ), a parameter directly related to plant tolerance to herbivory. Both  $\alpha_i$  and  $\mu_i$  contribute to growth, but their relative importance is driven by resource availability  $R$ . Note that we assumed for simplicity that parameters  $q$ ,  $e$ , and  $m$  do not differ between plant species  $i$  as we focus on their variation in affinity  $\alpha_i$ , maximal growth rate  $\mu_i$ , and resistance  $\rho_i$ .

Our analysis of this ecological model will focus on finding its stable equilibria to identify the conditions of a species' presence and the variation in resource level and herbivore density along the resource gradient. These results are critical to understanding how the selective pressure varies along such a gradient and eventually drives plant adaptation in "Eco-Evolutionary Results." The particular structure of equation (1), where the per capita growth rates of plant  $i$  depend only on two regulating factors, namely, the resource availability  $R$  and herbivore density  $Z$ , simplifies its analysis due to the competitive exclusion principle (CEP; Levin 1970; Meszéna et al. 2006). In our model, the CEP implies that at most two different plant species can stably coexist at equilibrium. Indeed, the presence of the herbivore allows for a second plant species to coexist despite competition for a single resource (Holt et al. 1994). This restricts the analysis to three different cases: absence of plants, one plant species only, or two coexisting plant species. The details

of the calculations can be found in appendix A (apps. A–G are available online).

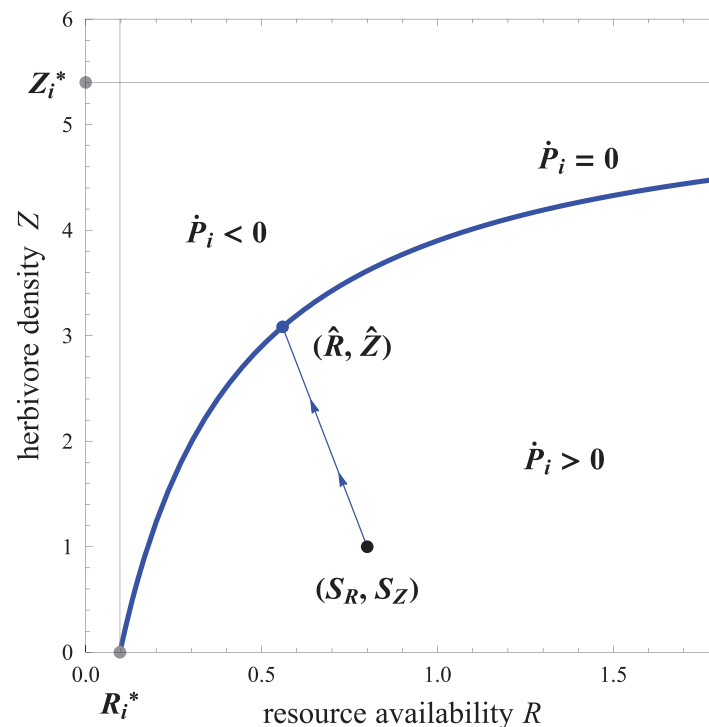
### One Species: The Graphical Ingredients

Following Leibold (1996), we graphically derive and represent the resulting equilibria of the ecological system along environmental gradients (Tilman 1980, 1982; Chase and Leibold 2003) made of varying resource supply and herbivore immigration. We use a graphical method that consists of two steps: (1) invasion analysis, which determines the equilibrium conditions under which a given species can grow and not be outcompeted by others, and (2) supply point map, which identifies the point along the environmental gradients for which these equilibrium conditions can be reached. These two steps rely on three ingredients—supply points, zero net growth isoclines (ZNGIs), and impact vectors—that are detailed below.

The supply point ( $S_R, S_Z$ ) is the resource and herbivore densities at equilibrium in the absence of plants, respectively given by  $S_R = I_R/\ell_R$  and  $S_Z = I_Z/m_Z$  (black dot in fig. 2). Note that  $S_Z = 0$  in the absence of herbivore immigration.

The ZNGI performs an invasion analysis by separating the environmental ( $R$ - $Z$ ) plane into regions where plant  $i$

can grow and regions where it cannot (fig. 2). It is obtained by setting net growth, the right-hand side of equation (1b), equal to 0, imposing a necessary link between  $R$  and  $Z$  when plant  $i$  persists at equilibrium. A typical ZNGI is represented in figure 2, with positive net growth under the ZNGI and negative net growth above it. Contrary to a type I functional response, a typical ZNGI in our model is not linear but concave (cf. Leibold 1996; Chase et al. 2000). The ZNGI crosses the  $R$ -axis at  $R_i^* = 1/\alpha_i \cdot \mu_i m_i / (\mu_i - m_i)$ , the minimal resource level to sustain species  $i$  in the absence of herbivores. According to Tilman's  $R^*$  theory, this measures this species' competitive ability at low resource levels (the smaller the better). Similarly, the ZNGI asymptotically saturates at  $Z_i^* = 1/a_0 \cdot (\mu_i - m_i) / (1 - \rho_i)$  for high  $R$  values, the maximal herbivore density a plant population can tolerate when resources are not limiting (fig. 2). This  $Z^*$  plays a symmetrical role relative to  $R^*$ , as emphasized in the apparent competition framework (Holt 1977; Holt et al. 1994): the most (apparent-) competitive species under high  $R$  values is the one with the largest  $Z^*$ . The analytical expression of  $Z_i^*$  shows that there are two ways to deal with herbivores: either with high  $\rho_i$  (resistant strategies) or with high  $\mu_i$  (tolerant strategies). Note that a completely resistant strategy with  $\rho_i = 1$  has an infinite  $Z_i^*$ , leading to a straight, vertical ZNGI.



**Figure 2:** Illustrative zero net growth isocline (ZNGI; thick blue line), impact vector (thin blue line), and supply point (black dot) for a plant species  $i$ . The ZNGI is similar in shape to the uptake function  $g_i(R)$  of equation (2), except that it starts on the  $X$ -axis at  $R_i^*$  and saturates at  $Z_i^*$  (gray lines and points). The impact vector maps this particular supply point to the corresponding equilibrium point  $(\hat{R}, \hat{Z})$  on the ZNGI (blue dot).

The impact vector of plant  $i$ , whose coordinates are given by the coefficients in front of the  $P_i$  terms in equation (1a) and (1c), represents how the biomass  $P_i$  affects both the resource level and the herbivore density in the system (Leibold 1996). The supply point map, which graphically solves for the equilibria of the system, is obtained by combining the impact vectors with the ZNGI and the supply points. How does the supply point map work in practice? For environmental conditions corresponding to a given supply point, the impact vectors map this supply point to the values of the corresponding resource availability and herbivore density at equilibrium ( $\hat{R}$ ,  $\hat{Z}$ ) on the ZNGI (fig. 2; eq. [A2] in app. A). Not surprisingly, the presence of a plant decreases resource levels by consuming it and increases herbivore abundance by feeding them. Another way to summarize these results consists of drawing the ZNGI and a family of impact vectors directly in the supply point two-dimensional parameter space or supply point plane. This leads to a bifurcation diagram, as the region spanned by the impact vectors corresponds to conditions leading to the plant's presence while the other region above the ZNGI corresponds to its absence, denoted region 0 (fig. 3A). Note that the slope of the impact vectors varies with resource level and herbivore density (see app. A).

It is also insightful to represent how equilibrium resource level and plant and herbivore densities vary along a gradient in resource supply in the absence of herbivore immigration (fig. 3B). A major difference with the classic food chain patterns (Oksanen et al. 1981; Mittelbach et al. 1988; Leibold 1996) can be identified: the combination of a saturating plant growth rate  $\mu$  and top-down control by the herbivores implies the saturation of herbivore density as the resource supply increases. As plant density is also kept in check by herbivory, only the resource pool is left to absorb this excess supply. In any case, it is important to note that increasing the resource supply indirectly benefits the herbivores through trophic transfers from the plant population. This leads the plant to switch abruptly from bottom-up to top-down control as resource availability increases, explaining why defense is so crucial for the plant at high resource levels and thus strongly influencing plant defense patterns, as we will see later in "Eco-Evolutionary Results."

### Two-Species Competition

The graphical approach previously described is especially useful when two or more different plant species are present along the resource gradient. A multispecies invasion analysis is performed by superimposing their corresponding ZNGIs: in the case of two plant species, the portion of a species  $i$ 's ZNGI that is located above the other species  $j$ 's ZNGI corresponds to uninvadable equilibria with species  $i$  present and species  $j$  absent, while the other portion is discarded as invadable by species  $j$  (fig. 3C). Coexistence occurs only at

points where the two ZNGIs intersect. This happens when there is a trade-off such that one species is more competitive in the absence of herbivores (i.e., has a smaller  $R_i^*$ ) and the other is more apparent-competitive when resources are nonlimiting (i.e., has a larger  $Z_i^*$ ). This trade-off between resource- and apparent-competitive abilities can emerge from an allocation model between plant traits, as will be seen in "Eco-Evolutionary Analysis." When the ZNGI portions corresponding to the different uninvadable single-species equilibria are coupled to their impact vectors, this leads to a multispecies bifurcation diagram. The regions spanned by the impact vectors of species 1 or 2 respectively correspond to species 1 or 2 only (blue and green in fig. 3C), while the cone originating from the ZNGI intersection and delimited by impact vectors 1 and 2 corresponds to the coexistence region 1&2 (gray in fig. 3C).

The equilibrium resource level, plant, and herbivore densities in the two-species case (fig. 3D) vary along the resource gradient in a way relatively similar to the single-species case (fig. 3B). The only difference with the latter comes from the presence of the coexistence region where  $\hat{R}$  and  $\hat{Z}$  variations are buffered, associated with a rapid increase in total plant density as species 1 replaces species 2.

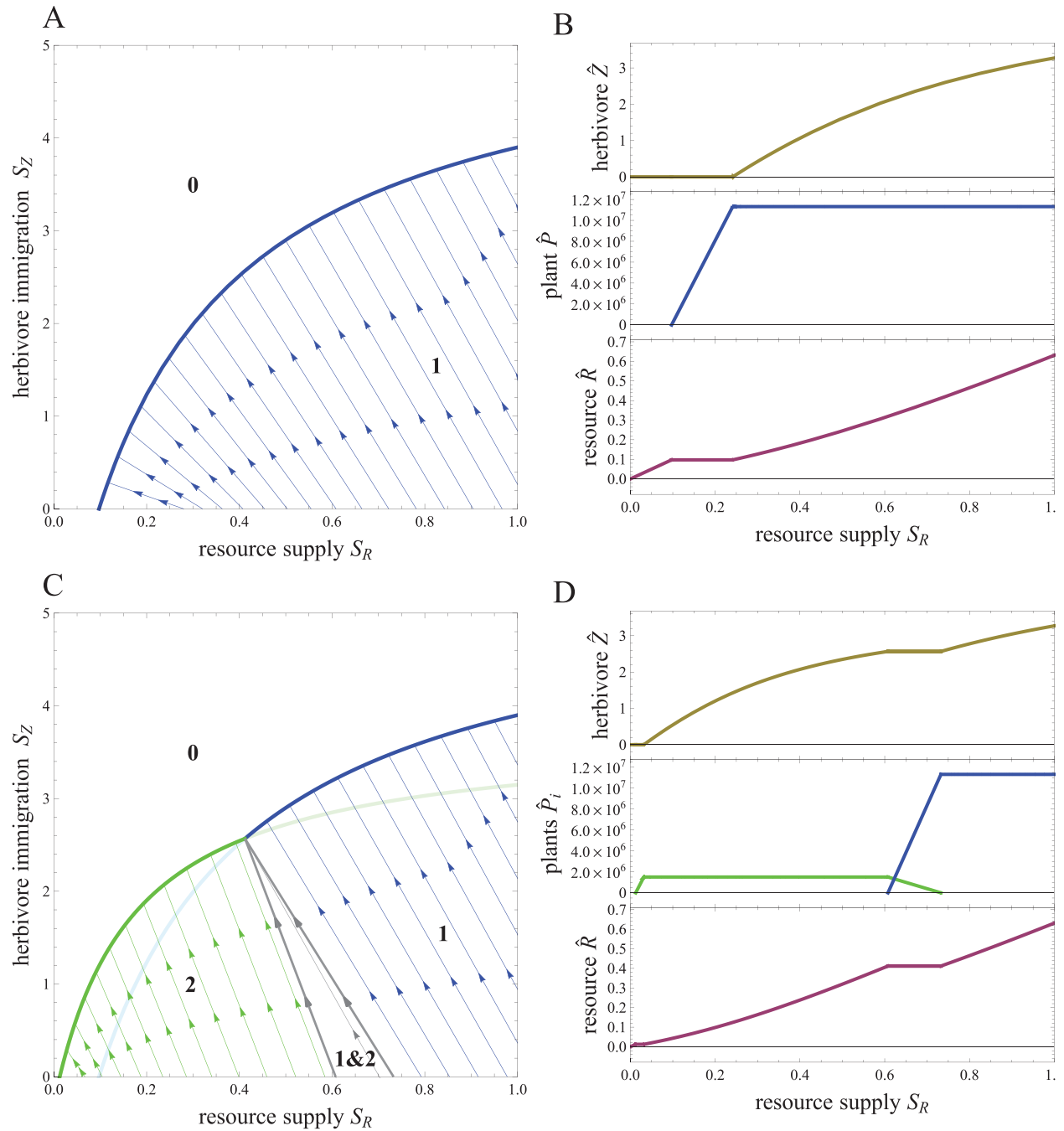
### Eco-Evolutionary Analysis

Building on the ecological system of the previous section, we now take a trait-based perspective where we consider competition between an arbitrary number of strategies defined by their allocation to resource acquisition, tolerance, and resistance. We focus on finding single strategies or pairs of strategies that render the community uninvadable when they are at their ecological equilibrium, called global evolutionarily stable strategies (ESSs) and communities (ESCs), respectively. There are at least three scenarios that can lead to global ESSs or ESCs (Abrams 2001; Bonachela et al. 2016): (1) asexual evolution by mutations of arbitrary size (adaptive dynamics but without the assumption of small mutations), (2) coevolution of a number of species that follow quantitative genetics, and (3) community assembly from a large range of extant species in the metacommunity.

### Linking Allocations and Traits

In this article, we focus our attention on the three traits associated with the fundamental ways that the plant interacts with its environment, that is, acquisition of the resource when scarce ( $\alpha$ ), fast growth when the resource is nonlimiting ( $\mu$ ), and resistance to herbivory ( $\rho$ ). A combination of these three traits defines a plant strategy, and the set of all these possible combinations defines the trait or strategy space. Due to its three-dimensional nature, this strategy space and the constraints that shape it are complex to describe. One way





**Figure 3:** A, C, Ecological bifurcation diagrams for the one-species (A) and two-species (C) cases, where species 1 (blue;  $\alpha_1 = 1$ ,  $\mu_1 = 0.25$ ,  $a_1 = 0.033$ ) and species 2 (green;  $\alpha_2 = 6$ ,  $u_2 = 1$ ,  $a_2 = 0.25$ ) both consume resource  $R$  and are consumed by herbivore  $Z$  along resource  $S_R$  and herbivore  $S_Z$  supply gradients. Species 1 and 2 differ in their relative competitive ability for  $R$  and defense against  $Z$ . Other parameters are from table 1. Region 1, located below species 1 zero net growth isocline (thick blue line) and spanned by species 1 impact vectors (thin blue lines) corresponds to species 1 only, while region 2 corresponds to species 2 only (green). In region 1 and 2 (gray), the two plant species coexist. In region 0, neither of the two species can persist. B, D, Equilibrium resource ( $R$ ), plant ( $P_i$ ), and herbivore ( $Z$ ) densities along the zero herbivore immigration ( $S_Z = 0$ ) cross section of the bifurcation diagrams for both the one-species (B) and two-species (D) cases.

to get around this problem consists of introducing a common currency, corresponding to the energy or material available to each organism, that is allocated between the three traits. We denote  $X_j$  such allocation to a trait  $j = \{\alpha, \mu, \rho\}$ . As each organism has only a limited amount—chosen to be equal to 1 in the appropriate units—of this currency to allocate, the sum of the three allocations has to satisfy the following constraint or trade-off:

$$X_\rho + X_\alpha + X_\mu \leq 1. \quad (3)$$

In practice, we take this constraint to be equal to 1, as there is no advantage to an underallocated strategy. As a result, the effective allocation space is two-dimensional, which facilitates its visualization (fig. 4A).

How are the traits linked to their allocations? First, we assume without any loss of generality that the trait value  $j = 0$  is obtained when  $X_j = 0$  and that an increase in allocation  $X_j$  always leads to an increase in trait  $j$  (i.e.,  $dj/dX_j > 0$ ). The maximal possible trait value  $j_{\max}$  is obtained when the maximal allocation to that trait  $X_{j,\max}$  is reached. Contrary to allocation to  $\alpha$  and  $\mu$ , for which we allow full allocation (i.e.,  $X_{\alpha,\max} = 1$  and  $X_{\mu,\max} = 1$ ), we cap the maximal allocation to  $\rho$  at a value  $X_{\rho,\max} < 1$  sufficient to reach perfect resistance ( $\rho_{\max} = 1$ ). This ensures

that a completely resistant strategy has some energy or material left to allocate to resource uptake and growth.

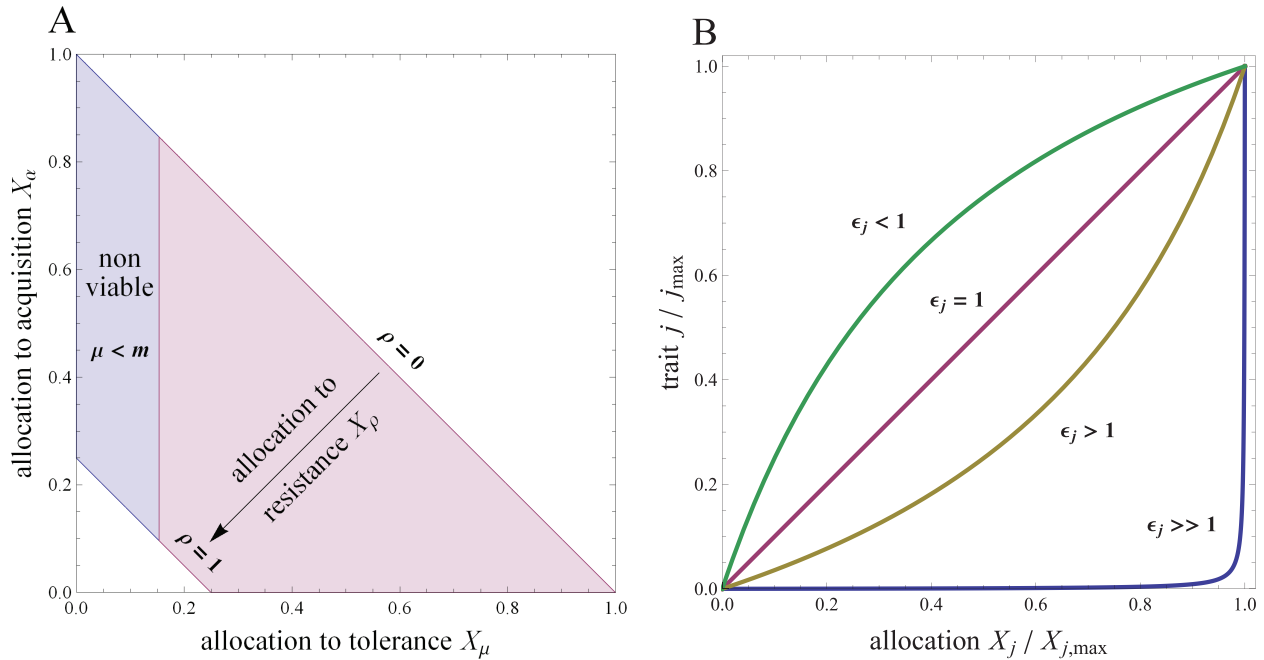
Second, we specify the shape of the return-on-allocation function  $f_j$  that links the allocation  $X_j$  to the obtained trait value  $j$ . Mathematically,

$$\frac{j}{j_{\max}} = f_j\left(\frac{X_j}{X_{j,\max}}\right), \quad (4)$$

where we choose to use the particular one-parameter function  $f_j$ :

$$f_j(x_j) = \frac{x_j}{\epsilon_j - (\epsilon_j - 1)x_j}, \quad (5)$$

where  $x_j = X_j/X_{j,\max}$ , and with the parameter  $\epsilon_j$  controlling the shape of the return on allocation from linear ( $\epsilon_j = 1$ ) to diminishing or concave ( $\epsilon_j < 1$ ) and accelerating or convex ( $\epsilon_j > 1$ ; fig. 4B). Such allocation and trade-off shapes are known to strongly affect the outcome of adaptation: accelerating returns tend to favor all-or-nothing allocation (i.e., specialists), while diminishing returns tend to favor intermediate allocation and thus generalists (Levins 1962; de Mazancourt and Dieckmann 2004; Kisdi 2015). Following the example of diffusion limitation's effect on resource acquisition (Pasciak and Gavis 1974; Armstrong 2008; Bona-



**Figure 4:** A, Visualization of the possible allocation strategies in the  $(X_\mu, X_\alpha)$  space. Allocation to resistance is given by  $X_\rho = 1 - X_\mu - X_\alpha$ . The truncated lower left corner expresses the fact that complete resistance is achieved with the allocation  $X_{\rho,\max} < 1$ , making further allocation to  $X_\rho$  meaningless. The strategies in the blue region are discarded as nonviable, because their maximal growth rate  $\mu$  does not exceed their mortality rate  $m$ . B, Visualization of the return-on-allocation function  $f_j$  linking the allocation  $X_j$  to the obtained trait value  $j$ , for various shape parameters  $\epsilon_j$ . This relationship is linear when  $\epsilon_j = 1$  (purple), concave when  $\epsilon_j < 1$  (green), and convex when  $\epsilon_j > 1$  (yellow). When  $\epsilon_j$  is close to 0 or  $\infty$ ,  $f$  tends toward a step function with an abrupt corner (blue).

chela et al. 2011), we here further assume that allocations to affinity and maximal growth rate satisfy linear or diminishing returns ( $\varepsilon_\alpha \leq 1$ ,  $\varepsilon_\mu \leq 1$ ). Depending on the details of the plant-herbivore interaction, returns on allocation to resistance could, however, be either diminishing or accelerating, as supported by empirical studies (Wetzel et al. 2016), so we consider both  $\varepsilon_\rho < 1$  and  $\varepsilon_\rho > 1$ .

### Adaptive Dynamics Techniques

Having defined the space of possible plant strategies, we can now couple it with the ecological model defined by equation (1) to investigate how competition leads to the eco-evolutionary response of plant communities along resource gradients. Following the adaptive dynamics framework (Hofbauer and Sigmund 1990; Dieckmann and Law 1996; Geritz et al. 1997, 1998; Champagnat et al. 2006), the invasion fitness  $w$  of an invading strategy with traits  $\mathbf{x}' = (\alpha', \mu', \rho')$  in a resident environment  $\hat{E} = (\hat{R}, \hat{Z})$  is given by

$$w(\mathbf{x}', \hat{E}) = \frac{1}{P} \frac{dP}{dt} = \frac{\mu' \alpha' \hat{R}}{\mu' + \alpha' \hat{R}} - a_0(1 - \rho') \hat{Z} - m, \quad (6)$$

where the environment  $\hat{E}$  is implicitly determined by the ecological equilibrium of the resident strategy  $\mathbf{x}$ . This feedback loop between the evolving population and its environment leads to density- and frequency-dependent selection, characteristic of game-theoretic approaches. **Introducing the fitness gradient**

$$s(\mathbf{x}) = \left. \frac{\partial w}{\partial \mathbf{x}'} [\mathbf{x}', \hat{E}(\mathbf{x})] \right|_{\mathbf{x}' = \mathbf{x}}, \quad (7)$$

**the evolutionary equilibria, or evolutionarily singular strategies,  $\hat{\mathbf{x}} = (\hat{\alpha}, \hat{\mu}, \hat{\rho})$ , are obtained by solving  $s(\hat{\mathbf{x}}) = \mathbf{0}$ . Their stability is assessed locally by second-order derivatives of the invasion fitness  $w$  and globally by evaluation of  $w$  across the trait space (Geritz et al. 1998).** Among these evolutionary equilibria, ESSs are of particular interest as they correspond to strategies that cannot be invaded by any other one. When an ESS is such that the eco-evolutionary dynamics converges toward it, it corresponds to a stable eco-evolutionary equilibrium of the system and is called a convergence stable strategy (CSS). Note that two coexisting strategies can together be an ESS, which we will refer to as an ESC.

In contrast with the standard approaches to adaptive dynamics, **we will focus on the global evolutionary stability of these equilibria.** Doing so implicitly assumes that all the strategies from the trait space are potential invaders, following an “everything is everywhere” (Baas Becking 1934; De Wit and Bouvier 2006) picture instead of a small mutations framework. This differs from the usual adaptive dynamics approach

because **we ignore branching point and local but not global ESS and ESC, as these kinds of singular points are invisable by some strategy from the trait space.** Our approach also implicitly assumes that mutation or immigration of plant strategies is frequent enough that all strategies are accounted for but not so frequent to have an effect on the population dynamics of plants through mass effects.

### Envelope-Based Approach

The strategy space of the three-way allocation problem is two-dimensional, **so pairwise invasibility plots, the standard graphical approach to find and characterize evolutionary equilibria, cannot be used.** To overcome this limitation, we used a recently developed extension to eco-evolutionary situations of the graphical approach to contemporary niche theory presented in “Ecological Analysis” (Koffel et al. 2016).

This envelope-based approach mimics the two steps of the graphical approach presented in “Ecological Analysis” (fig. 3A, 3C). First, a combination of local and global analysis selects from the whole strategy space the subset of strategies that are ESS and associates them with the corresponding equilibrium resource level and herbivore density. Graphically, this is equivalent to drawing all the possible ZNGIs from the plant strategy space and extracting their geometrical envelope. This is what we did in the ecological case when we drew the two ZNGIs and kept only the portions that were uninvadable (fig. 3C), except now it is with a whole continuum of ZNGIs instead of two. In this evolutionary context, an ESC made of two coexisting species appears at “kinks” in the envelope (Koffel 2016). Second, the supply point map combines the ZNGI envelope with the impact vectors to associate to each ESS their corresponding supply points. When represented in the supply point plane, this gives an eco-evolutionary bifurcation diagram that summarizes the outcome of plant adaptation along both resource and herbivore immigration gradients. From there, we can obtain and represent how plant adaptive traits (acquisition, tolerance, and resistance) and ecosystem properties (resource level, plant and herbivore densities) vary along the resource gradient.

### Eco-Evolutionary Results

#### Analytical Results for the Two-Way Allocation Problems

We now investigate how plant adaptive strategies and ecosystem equilibrium densities vary along the resource gradient. Before directly addressing the three-way allocation problem presented in “Linking Allocations and Traits,” we can obtain general analytical results by restricting the analysis to the three partial allocation problems obtained when only two traits can vary, holding the last trait fixed.



We analyzed these three situations for completely general allocation functions ( $f_j$ ), that is, by assuming only that the traits  $j = \{\alpha, \mu, \rho\}$  are increasing functions of their allocations  $X_j$ . The  $\alpha$  versus  $\rho$  scenario ( $\mu$  fixed) can be seen as a generalization of Loeuille and Loreau's (2004) type I functional response results to the type II case (i.e., finite  $\mu$ ). **In each case, we analytically tracked plant adaptive traits  $\hat{\alpha}$ ,  $\hat{\mu}$ , and  $\hat{\rho}$  and consequent equilibrium densities  $\hat{R}$ ,  $\hat{P}$ , and  $\hat{Z}$  along a resource gradient in a food chain** (i.e., with a single CSS present; for the details of the calculations, see app. B). We did not investigate in this section the conditions under which evolutionarily stable coexistence in a diamond-shaped module is possible. Still, we know that when there is a two-species ESC, their traits,  $\hat{R}$  and  $\hat{Z}$ , remain constant along the resource gradient, as is expected for two evolving populations interacting with two regulating factors (Kisdi and Geritz 2016; Koffel et al. 2016). The population densities  $\hat{P}$ , of the two coexisting strategies of the ESC then vary along the resource gradient similarly to the ecological case (i.e., linearly, with one density usually going down and the other going up).

The results for a CSS involving a single strategy are summarized in table 2. Several general conclusions can be drawn from these results. First, concerning densities, both the resource ( $\hat{R}$ ) and the herbivore ( $\hat{Z}$ ) always increase with the increasing resource supply, thus not differing qualitatively from the purely ecological case. This is a direct consequence of the ecological structure of the food chain, that is, trophic transfers along the food chain coupled with top-down and bottom-up controls of the plant population. This means that the selective pressure coming from herbivore consumption systematically increases along the resource gradient, in stark contrast with nontrophic approaches where herbivore densities are assumed to stay fixed (Coley et al. 1985). Second, concerning traits, resource acquisition ( $\hat{\alpha}$ ) always decreases with resource supply when it is not fixed, confirming that the contribution of this trait to fitness automatically decreases as resource availability increases. Conversely, increased allocation to both tolerance ( $\mu$ ) and resistance ( $\rho$ ) can help the plant cope with increasing herbivore pressure, as shown in "Ecological Analysis." For this

reason, tolerance ( $\hat{\mu}$ ) increases along the gradient when resistance ( $\rho$ ) is fixed and resistance ( $\hat{\rho}$ ) increases along the gradient when tolerance ( $\mu$ ) is fixed, coinciding with increasing plant biomass  $\hat{P}$  in both cases. Finally, when resource acquisition ( $\alpha$ ) is fixed, these two defense options trade off, their variations thus being mutually exclusive. Increasing resistance ( $\hat{\rho}$ ) is then always the first adaptive response of the plant for low but increasing resource availability. This trend is then either sustained along the gradient or reversed toward increasing tolerance ( $\hat{\mu}$ ) when tolerance costs are small enough. Interestingly, the latter situation can lead to decreasing plant biomass  $\hat{P}$ , an intuitive population-level side effect of the evolution of tolerance.

### Three-Way Allocation Problem

With the results of the previous section in mind, we can now investigate how plant adaptive traits and consequent equilibrium densities vary along the resource gradient in the case of the full three-way allocation problem. As we already emphasized in "Linking Allocations and Traits," both accelerating and diminishing returns on allocation to resistance can be encountered in natural systems. As we will see, these allocation shapes deeply affect the eco-evolutionary outcome of the system along the resource supply gradient, such as the possibility of evolutionarily stable coexistence, the presence of a completely resistant strategy, and the evolution of tolerance or resistance under high resource supply. Examples from closely related models can be found in the literature (Abrams 2003; Jones and Ellner 2004; Zu et al. 2015). Here we focus our attention on two particular cases that have been selected for their ecological relevance as well as their representativeness of the model outcomes. Scenarios 1 and 2 investigate the effects of accelerating and diminishing returns on allocation to resistance, respectively, coupled with linear returns on the two other traits. In appendix D, a third scenario shows how a combination of accelerating and diminishing returns can lead to a hump-shaped allocation pattern in resistance along the resource supply gradient. Three other possible scenarios where complete resistance is not possi-

**Table 2:** Adaptive dynamics results for the two-way allocation problems

Case	$\hat{\alpha}$	$\hat{\mu}$	$\hat{\rho}$	$\hat{R}$	$\hat{P}$	$\hat{Z}$	Condition
$\mu$ vs. $\rho$	0	—	+	+	+	+	When $S_R$ is small but potentially not when $S_R$ is large <sup>a</sup>
$\mu$ vs. $\rho$	0	+	—	+	—, +	+	Potentially when $S_R$ is large <sup>a</sup>
$\alpha$ vs. $\rho$	—	0	+	+	+	+	...
$\alpha$ vs. $\mu$	—	+	0	+	+	+	...

Note: Effect of an increase in resource supply  $S_R$  on plant convergence stable strategy traits ( $\hat{\alpha}$ ,  $\hat{\mu}$ , and  $\hat{\rho}$ ) and equilibrium ecosystem densities ( $\hat{R}$ ,  $\hat{P}$ , and  $\hat{Z}$ ) for the three cases where one trait is kept fixed.

<sup>a</sup> See "Case  $\mu$  versus  $\rho$ " in app. B, available online, for the exact criterion and its derivation.

ble are described in appendix E, and a thorough exploration of all the possible scenarios along the three allocation shape parameters can be found in appendix F.

#### *Scenario 1: Accelerating Returns on Resistance Allocation*

For this first scenario, we assume accelerating returns on resistance allocation ( $\varepsilon_p > 1$ ). For simplicity, we also assume linear returns on the two other allocations ( $\varepsilon_\alpha = 1$  and  $\varepsilon_\mu = 1$ ). The adaptive strategy turnover along the resource gradient is displayed in figure 5A–5C. At very low resource levels, a completely nonresistant strategy ( $\hat{\rho} = 0$ ) with high allocation to affinity ( $\alpha$ ), so that its  $R^*$  is minimal, dominates as long as the herbivore is absent (green top left corner in fig. 5A, 5B). Then, increasing the resource supply allows the herbivore to invade, in turn leading to reallocation from acquisition to tolerance and thus faster growth, though still nonresistant (green line along the triangle edge in fig. 5A, 5B). As a consequence, herbivore abundance increases, releasing the top-down control of the resource by the plant and thus allowing the resource levels to increase as well (fig. 5D). At one point, the resource level in the system is high enough for a completely resistant strategy ( $\hat{\rho} = 1$ ) to invade (red dot and lines in fig. 5A–5C) and coexist with the fast grower it just invaded. This particular completely resistant strategy is the one with the lowest  $R^*$  among all completely resistant strategies. As resource supply increases further, the traits of these two strategies remain fixed as they continue to coexist, maintaining resource levels and herbivore abundances at a constant level (the kink in fig. 5C). The population size of the fast-growing species also stays constant, whereas the completely resistant population continues to increase as it absorbs all the exceeding resource supply. No partially resistant strategy appears in this case, being less competitive than the completely resistant and nonresistant ones: accelerating returns in resistance favors plant strategic specialization, which in turn favors coexistence.

#### *Scenario 2: Diminishing Returns on Resistance Allocation*

For this second scenario, we assume diminishing returns on resistance allocation ( $\varepsilon_p < 1$ ) and linear returns on the two other allocations ( $\varepsilon_\alpha = 1$  and  $\varepsilon_\mu = 1$ ). The absence of accelerating returns favors generalist plant strategies, and thus evolutionarily stable coexistence never occurs along the resource supply gradient. We again track the adaptive strategy turnover along the resource gradient ( $S_R$ ). Starting with an acquisition specialist, increasing resource supply again leads to reallocation to maximal growth rate while staying nonresistant (green line along the triangle edge in fig. 6A). This happens up to a point where allocation to resistance becomes adaptive. This correlates with a decrease in

growth allocation, which leads to a hump-shaped maximal growth rate allocation for intermediary supply (fig. 6B). Finally, allocation to resistance keeps increasing while never reaching complete resistance, even under very high resource supply. This happens because a completely resistant plant would drive herbivores extinct, undermining the competitive advantage brought by resistance. From an ecosystem perspective, evolution toward resistance allows the plant to escape top-down control by the herbivore with increasing plant biomass along the gradient, while both resource level and herbivore density reach saturation. As a whole, this situation largely echoes the previous one, the main difference being that coexistence between two specialist strategies is replaced by dominance by single generalists.

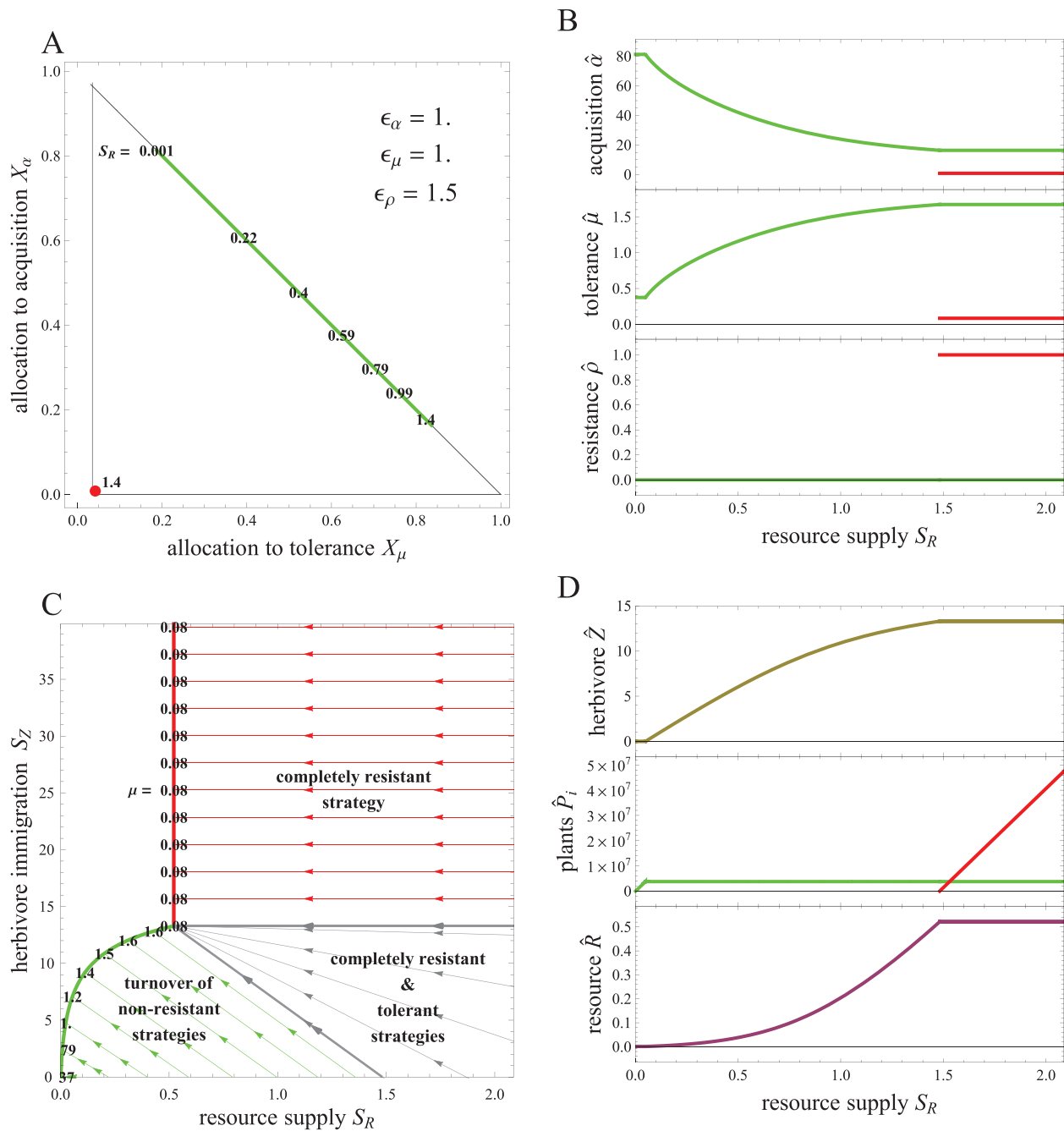
#### **Comparison to the Fitness Optimization Approach**

To compare our results with previous models of plant adaptation to herbivory (e.g., Coley et al. 1985), it is instructive to compare the plant adaptive strategies along the resource gradient obtained with our adaptive dynamics approach to the ones that would be given by a fitness optimization procedure without accounting for plants' feedback on resource and herbivore densities. This can be done by isolating plant equation (1b) from model (1) and considering  $R$  and  $Z$  as external parameters, replacing them directly by their supplies  $S_R$  and  $S_Z$ . Doing so, we neglect the feedback of the evolving population on its environment. The optimal strategy for a given supply is then the strategy with the highest per capita growth rate  $dP/(Pdt)$ .

#### *Analytical Results for the Two-Way Allocation Problems*

As in “Eco-Evolutionary Results,” it is insightful to first study the three partial allocation problems with one of the traits held constant. Again, these results were obtained for completely general allocation functions ( $f_i$ ). See appendix C for the details of the calculations. The results are synthesized in table 3. Note that coexistence cannot occur in the optimization approach, as having two strategies with the exact same growth rate is infinitely unlikely in the absence of the environmental feedback loop.

It is striking to see the difference with the adaptive dynamics approach (table 2). In the optimization approach, tolerance ( $\hat{\mu}$ ) appears to be systematically favored with increasing resource supply, against both resource acquisition ( $\hat{\alpha}$ ) and resistance ( $\hat{\rho}$ ). Indeed, in the absence of the environmental feedback loop, herbivore pressure does not increase along the resource gradient and resource availability is not made scarcer by consumption, so that the relative importance of herbivory compared to growth potential sharply decreases with increasing resource availability. When tolerance ( $\hat{\mu}$ ) is fixed, allocation to resource acquisition ( $\hat{\alpha}$ ) is favored



**Figure 5:** Scenario 1: eco-evolutionary results under accelerating returns on allocation to resistance ( $\epsilon_\rho > 1$ ) and linear returns on allocation to affinity and maximal growth rate ( $\epsilon_\alpha = \epsilon_\mu = 1$ ). A, Adaptive strategy turnover between nonresistant (green) and completely resistant (red) strategies in the allocation space ( $X_\mu$ ,  $X_\alpha$ ) 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. A nonresistant strategy coexists with a completely resistant one under high supplies ( $S_R > 1.4$ ). Parameters are from table 1.



**Table 3:** Optimization results for the two-way allocation problems

Case	$\hat{\alpha}$	$\hat{\mu}$	$\hat{\rho}$	Condition
$\mu$ vs. $\rho$	0	+	—	...
$\alpha$ vs. $\rho$	+	0	—	If $\hat{\alpha} < \frac{\hat{\mu}}{S_R}$
$\alpha$ vs. $\rho$	—	0	+	If $\hat{\alpha} > \frac{\hat{\mu}}{S_R}$
$\alpha$ vs. $\mu$	—	+	0	...

Note: Effect of an increase in resource supply  $S_R$  on plant optimal traits ( $\hat{\alpha}$ ,  $\hat{\mu}$ , and  $\hat{\rho}$ ), with each of the three traits kept fixed. Compare with table 2.

only when the resource is limiting and thus shifts to resistance ( $\hat{\rho}$ ) under high resource supplies.

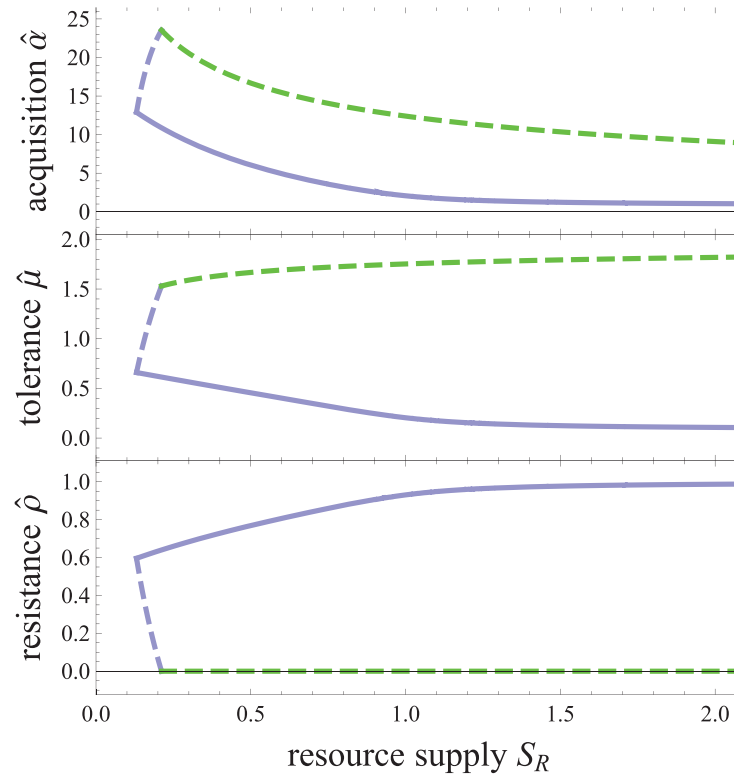
#### Optimization Approach under Scenario 2: Diminishing Returns on Resistance

The contrasting outcomes of the optimization approach can be further studied using the full three-way allocation problem. We focus here on scenario 2 because it illustrates the most striking differences between the adaptive dynamics

and optimization approaches, but similar results hold for scenario 1. Using the same parameters as in scenario 2, with the supplies  $S_R$  and  $S_Z$  directly playing the roles of  $R$  and  $Z$  in equation (1b), we determined the strategies maximizing plant growth rate for each supply point along the resource gradient. Note that in absence of trophic transfers, herbivore immigration ( $S_Z \neq 0$ ) is necessary for the herbivore population to be nonzero. The resulting optimal strategy against increasing resource supply  $S_R$  under high and constant herbivore immigration is shown in figure 7. The main difference along the increasing resource supply when compared to the adaptive dynamics results of figure 6 is that the optimal strategy sharply decreases its allocation to resistance until it hits 0 and then progressively reallocates from acquisition to tolerance.

#### Discussion

We studied the adaptive response of plants facing selective pressures from both resource competition and herbivory along a resource gradient. We showed that undefended,



**Figure 7:** Comparison of the adaptive strategy turnovers involving nonresistant (green) and partially resistant (blue) strategies along the resource gradient between the adaptive dynamics (solid lines) and fitness optimization (dashed lines) approaches for scenario 2 under high herbivore immigration  $S_Z = 10$ . Other parameters are similar to figure 6. In contrast with the results of the adaptive dynamics approach, plant allocation to resistance quickly drops to 0 at the low end of the gradient. The plant then remains nonresistant along the rest of the gradient while reallocating from acquisition to tolerance. Note that the strategy turnover starts at  $S_R = 0.13$  because no strategy can subsist under lower resource supplies.



competition-specialist strategies are expected to dominate under low resource supplies. Conversely, high resource supplies, which lead to high herbivore abundance because of trophic transfers, result in the dominance of either a very resistant strategy or evolutionarily stable coexistence between a completely resistant strategy and a fast-growing, tolerant one. Diminishing returns on allocations favors the first scenario, with an intermediate strategy, while accelerating returns favors the second one, with coexistence of two extreme strategies. Finally, we compared this density-dependent approach based on the environmental feedback loop to a more traditional, density-independent optimization approach. We showed that density dependence originating from trophic transfers was the cause of this increase in resistance along the resource gradient, as the frequency-independent model instead favored tolerant, fast-growing strategies over resistant ones.

#### *Variation in Plant Defense along the Resource Gradient*

By including three possible strategic archetypes—competitors that specialize in acquisition of scarce resources, fast-growing tolerant species, and herbivore-resistant strategies—our model enabled a nuanced exploration of possible plant adaptation to the joint selective pressure of resource acquisition and herbivory. We studied adaptive strategy turnovers along the resource gradient for various allocation shape parameters. At low resource levels, the best-adapted strategies are always good competitors specialized in resource acquisition, called “gleaners” by Grover (1997), as they are the only strategies that can survive in those very resource-limited conditions due to their low  $R^*$  and despite their sensitivity to herbivory. As these competitor strategies typically subsist at very low densities, this ensures that herbivore populations and thus their damages are low in the absence of herbivore immigration: the plants are essentially bottom-up controlled. On the contrary, both tolerance, through maximal growth rate, and resistance are adaptive under high resource supply because high resource supply leads to significant herbivore densities, meaning that plants are this time mostly top-down controlled (Armstrong 1979; Leibold 1996; Grover and Holt 1998). However, very resistant strategies, when viable, need to either coexist with a tolerant species or not be completely resistant so that herbivores remain present to maintain their selective advantage (Tiffin 2000). This explains why the completely resistant strategy is never present alone (unless there is significant herbivore immigration, as can be seen in the upper regions of the panels in figs. 5C, 6C).

Another interesting consequence of working with three traits is that tolerance ( $\mu$ ) and resistance ( $\rho$ ) need not be automatically anticorrelated, allowing mixed adapted strategies that are both tolerant and resistant, with their relative weights strongly depending on both the allocation parameters and

the resource supply. The existence of these mixed defense strategies has been observed empirically (Mauricio et al. 1997; Carmona and Fornoni 2013; Turley et al. 2013).

Strikingly, our results contrast with Coley’s resource gradient hypothesis, which used a density-independent optimization approach to predict that allocation to plant resistance should be favored under low resource availability (Coley et al. 1985). We suspect that the feedback loop between the plant population and its environment plays a central role in this discrepancy (McNickle and Dybzinski 2013), as underlined by our comparison between the adaptive dynamics and the optimization approaches. Indeed, the results from our optimization approach without the environmental feedback loop are consistent with these early optimization models, as they show that resistant strategies dominate only at the low end of the gradient (Coley et al. 1985). This is a consequence of a rapid decrease in the relative impact of herbivory on plant fitness along the resource gradient in the absence of the feedback loop. As pointed out by Loreau and de Mazancourt (1999), taking into account the effect of plant growth on the resource availability within a dynamical plant-resource model affected Coley et al.’s (1985) evolutionary predictions and led Loreau and de Mazancourt (1999) to conclude in their fixed herbivore density case that increasing resource supply does not influence plant strategies. Our approach follows this logic one step further by also including a dynamical herbivore population. In fact, our predictions—selection of defended strategies under high-resource environments—are consistent with previous ecological (Leibold 1996; Chase et al. 2000) and eco-evolutionary (Loeuille and Loreau 2004; Zu et al. 2015) approaches, as well as a recent review on intra-specific variation in plant defense (Hahn and Maron 2016). Our study gives a quantitative demonstration of Hahn and Maron’s (2016) intuition that the emergence of more defended strategies with increasing resource availability stems from increased herbivore pressure associated with these environments.

Nonetheless, not every plant population so directly controls the population growth of the herbivores that feed on it. We expect the strength of this environmental feedback loop to depend on both plant and herbivore relevant spatial and temporal scales. Among others, plant growth rate, spatial structure, and population size, as well as herbivore body size, generation time, dispersal, and mobility, affect the coupling between plant and herbivore population dynamics and thus the evolution of plant defense (Duffy and Hay 1994; Augner 1995; Underwood 1999; Tiffin et al. 2006). Within our model, this decoupling between plant and herbivore dynamics can be simulated by changing the balance between herbivore immigration and intrinsic growth through decreased transfer efficiency ( $e$ ). Interestingly, this leads to a decrease in defense allocation for a given resource supply but does not alter the qualitative allocation patterns along the gradient.

### *Diversification and Coexistence*

Our model makes clear the conditions under which diversification of the plant strategies dealing with both resource and herbivore selective pressure is possible. First, the shape of the allocation functions plays a crucial role. Accelerating returns on at least one trait appears to be necessary for evolutionarily stable coexistence to occur, consistent with classical results (Levins 1968). This also supports recent studies on diversification of an intermediate trophic level (Abrams 2003; Jones and Ellner 2004; Zu et al. 2015), after noting that accelerating returns on resistance ( $\rho$ ) is equivalent to diminishing returns on susceptibility ( $1 - \rho$ ) in their models. The cases of evolutionarily stable coexistence obtained here also suggest that when coexistence happens, one of the two coexisting strategies is always completely resistant, while the other one is more tolerant. Finally, coexistence happens only under high resource supply, which ensures that both resource availability and herbivore pressure are high enough for both strategies to be advantaged. All in all, our study shines a light on the conditions for initial diversification of nutrient-phytoplankton-zooplankton models (Armstrong 1994; Sauterey et al. 2015) and food web emergence.

Note that contrary to previous models (Chase et al. 2000), priority effects (i.e., dependency of the equilibrium strategy on the timing of arrival) between the tolerant and resistant strategies do not occur here. The reason is that the completely resistant strategy is regulated only by resource availability and has no impact on the herbivores. This prevents the situation where each strategy inhibits the other one more than it inhibits itself to happen, a necessary condition to switch from coexistence to priority effects (Tilman 1982; Leibold 1996; Chase and Leibold 2003). However, evolutionary priority effects are still possible between two mixed, partially resistant strategies along the decreasing branch of the hump-shaped allocation to resistance of scenario 3 (not shown here).

### *Effect of Plant Adaptation on Trophic Cascade*

Accounting for the evolution of plant tolerance along the resource gradient allowed for some generalizations and refinements compared to previous models (Oksanen et al. 1981; Leibold 1996; Loeuille and Loreau 2004). First, we showed in the three two-way allocation problems that equilibrium resource levels and herbivore densities could only positively (or neutrally) respond along the gradient when plant adaptation is accounted for. Based on our numerical explorations, this seems to hold true in the full three-way allocation problem, thus generalizing the previous results. Furthermore, plant biomass ( $\hat{P}$ ) also seems to generally increase along the resource gradient when resistance ( $\rho$ ) is fixed or increasing. However, we found some situations under both the two- and the three-way allocation problems where plant biomass could, at least

under intermediate resource supplies, respond negatively to enrichment (see table 2; app. D). This contrasts with previous studies (Leibold 1996; Loeuille and Loreau 2004) and corresponds to a situation in which it is more adaptive for the plant to decrease allocation to resistance and reallocate to maximal growth rate. These shifts from resistance to tolerance, by incurring a sudden increase of attack rate by the herbivore, can negate the positive effect of resource increase and thus lead to an overall decrease in plant density along increasing supply.

For high resource supplies, both scenarios described in the main text lead to trophic dead ends, that is, reduced trophic transfers from resistant plants to herbivores that result in biomass accumulation at the intermediate trophic level. This can be related to cyanobacteria blooms, as some species are believed to be completely inedible by zooplankton, with significant environmental consequences (Lampert 1987; Wilson et al. 2006; but see Perga et al. 2013). However, when complete resistance is out of reach, the asymptotic strategies are either completely nonresistant or only partially resistant (see scenarios 1', 2', and 3' in app. F). In these cases, trophic transfers from plants to herbivores never stop, leading to linear increase in resource availability ( $\hat{R}$ ) and saturating plant ( $\hat{P}$ ) and herbivore ( $\hat{Z}$ ) biomasses, similarly to the purely ecological case. To conclude, our model predicts that plant adaptation toward either tolerance or resistance can strongly alter the standard patterns of trophic cascade along a resource gradient.

### *Generality of the Approach and Extensions*

Even though our model necessarily omits many of the details of plant interactions with herbivores, it provides the first theoretical study that considers the joint evolution of plant resistance and tolerance within a simple food web module using an allocation trade-off between three quantitative traits, paving the way toward the study of the evolution of plant defense in more complex ecological situations.

Our model probably overestimates the importance of allocation to resistance by ignoring seasonality, an important driver of plant and herbivore growth in both terrestrial and aquatic ecosystems (Klausmeier and Litchman 2012). During early growth following the start of a favorable season, the solutions from the density-independent optimization approach (i.e., fast-growing tolerant strategies) are selected. Including seasonality could thus reconcile the resource gradient hypothesis with our adaptive dynamics approach by creating a balance between early season and late season selective forces. This could select for strategies with intermediate characteristics or lead to diversification of seasonal specialists (Kremer and Klausmeier 2013; Miller et al. 2016). Seasonality could also delay herbivore growth and lead to

the succession of more resistant species over the course of a season (Klausmeier and Litchman 2012).

Taking into account elemental costs of resistance, generally carbon or nitrogen based (Bryant et al. 1983), and tolerance, demanding in phosphorus-rich ribosomal RNA (Elser 2006), could lead to a more mechanistic implementation of the trade-off linking plant traits (Branco et al. 2010). In turn, such a stoichiometrically explicit approach (Meunier et al. 2017) can help address large-scale biogeochemical patterns such as the constraints on the ratios of carbon, nitrogen, and phosphorus in plant biomass, known as Redfield ratios in the marine literature (Redfield 1958; Klausmeier et al. 2004; McGroddy et al. 2004).

While we used the generic term “plant” throughout this article, our model is best suited to phytoplankton communities for which individual growth and population growth coincide. Yet, there has been a tradition of applying such resource-based models to terrestrial plants (Tilman 1982; de Mazancourt et al. 1998; Menge et al. 2008; Loreau 2010), which suggests that our approach and some of our conclusion could apply more broadly to other plant-herbivore systems. There are, however, some acknowledged shortcomings (Peet 1989). Terrestrial plants present more complex ontogenies than their aquatic counterparts, leading to more complex patterns of tolerance and resistance in the course of their developmental trajectories or between individual growth and fecundity (Boege et al. 2011). Terrestrial plants also present differentiated organs—roots, stems, and leaves—that can be selectively targeted by herbivores (Rasmann and Agrawal 2008), and the combination of size and spatial structure leads to more complex mechanisms of competition, especially for light (Weiner 1990; Dybzinski et al. 2011). Accounting for such extra complexity in the model would inevitably increase the dimensionality of both the environment and the trait space, providing new directions for future work. Although overly simplistic from this perspective, the three-way trade-off in our model provides a first glimpse of possible allocation patterns in higher-dimensional strategy space, such as correlated allocations in plant traits.

Our results depend on having an herbivore on top of the food chain, inducing a top-down control on the plant population. The addition of a carnivore feeding on the herbivore would drastically change our predictions. Because of top-down control by the carnivore, herbivore density would not increase with increasing resource supply. This means that the best-adapted plant strategy would be the one with the smallest  $R^*$ , where mortality includes losses by this constant herbivore pressure, thus not depending on resource supply at all, similarly to Loreau and de Mazancourt's (1999) results. This reasoning could be extended to more complex food webs where the responses of the different compartments along a resource gradient have been identified (Wollrab et al. 2012). Another limitation of our approach is that only plants evolve.

A variety of different scenarios are possible when accounting for herbivore evolution, as was shown, for example, by Loeuille and Loreau (2004).

In our model, we have restricted plant resistance to the direct effect on the herbivore attack rate, for example, through deterring effects or gut passage survival. However, resistance could also affect other herbivore parameters (Grover 1995), such as decreasing conversion efficiency ( $e$ ) and increasing herbivore mortality ( $m_z$ ). Our model ignores these effects, but it is easy to see that they would affect only the plant impact vectors and thus the supply point map. The invasion analysis being completely independent of  $e$  and  $m_z$ , the singular points and their ESS properties would stay the same, leaving the general bifurcation diagrams and the trait responses to increased supply unchanged. Similarly, we suspect that taking into account herbivore handling time ( $h$ ) through a type II functional response instead of a type I would not qualitatively alter our results as long as the handling time is not too large. Indeed, the previous reasoning with  $e$  and  $m_z$  would still hold, as the fitness of a mutant would not depend on its own handling time ( $h$ ). Although the inclusion of a handling time could potentially destabilize the ecological dynamics (Hastings and Powell 1991; Abrams and Roth 1994), we predict that the main effect at equilibrium would be an increase in plant density and a decrease in both herbivore pressure and resource availability leading to a stronger bottom-up control of the plant by the resource, as a direct consequence of decreased herbivore efficiency (see app. G). This favors acquisition over tolerance and resistance for a given resource supply but leaves the global adaptive strategy turnover along the gradient qualitatively unchanged.

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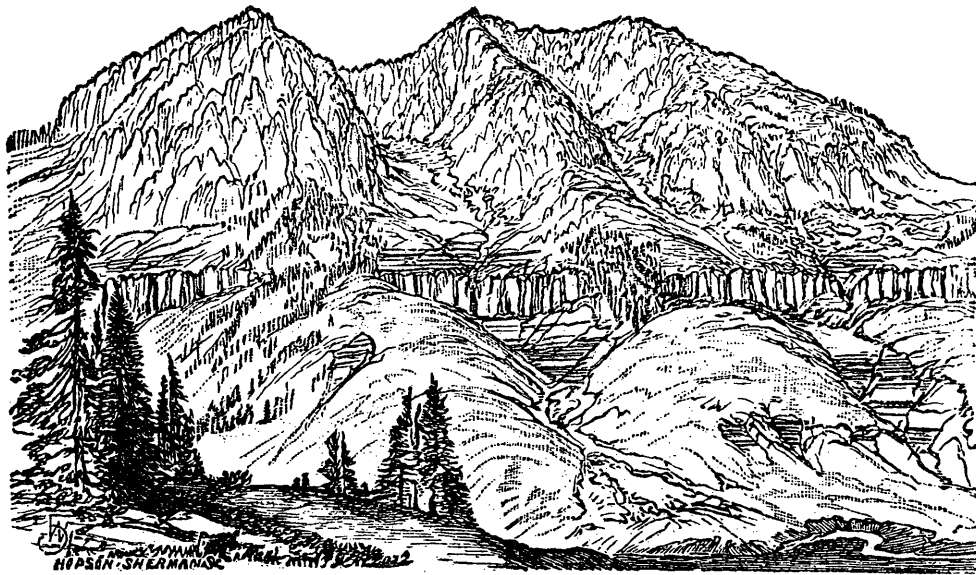


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“The elevated plateau and mountains of Colorado have a unique interest to the naturalist. Most interesting questions in the distribution of life, both horizontal and vertical; the relation of the physical aspects of Colorado as compared with the plateaux of Asia and the mountains arising from them, will find a partial solution in the data given in this report.” Figured: Gothic Mountain, Elk Range, Colorado. From the review of Hayden’s *Geology of Colorado* (*The American Naturalist*, 1875, 9:173–178).