

Evolution of nutrient acquisition: when adaptation fills the gap between contrasting ecological theories

S. Boudsocq^{1,*}, S. Barot² and N. Loeuille^{3,4}

¹Laboratoire d'Ecologie, UMR 7618, Ecole Normale Supérieure, 46 Rue d'Ulm, 75230 Paris Cedex 05, France

²Laboratoire d'Ecologie, UMR 7618, IRD, 32 Avenue Henri Varagnat, 93143 Bondy Cedex, France

³Laboratoire d'Ecologie, UMR 7625, Université Pierre et Marie Curie, 4 Place Jussieu, 75005 Paris, France

⁴Ecologie des Populations et Communautés, USC 203, INRA, 75005 Paris, France

Although plant strategies for acquiring nutrients have been widely studied from a functional point of view, their evolution is still not well understood. In this study, we investigate the evolutionary dynamics of these strategies and determine how they influence ecosystem properties. To do so, we use a simple nutrient-limited ecosystem model in which plant ability to take up nutrients is subject to adaptive dynamics. We postulate the existence of a trade-off between this ability and mortality. We show that contrasting strategies are possible as evolutionary outcomes, depending on the shape of the trade-off and, when nitrogen is considered as the limiting nutrient, on the intensity of symbiotic fixation. Our model enables us to bridge these evolutionary outcomes to classical ecological theories such as Hardin's tragedy of the commons and Tilman's rule of R^* . Evolution does not systematically maximize plant biomass or primary productivity. On the other hand, each evolutionary outcome leads to a decrease in the availability of the limiting mineral nutrient, supporting the work of Tilman on competition between plants for a single resource. Our model shows that evolution can be used to link different classical ecological results and that adaptation may influence ecosystem properties in contrasted ways.

Keywords: adaptive dynamics; nutrient accumulation; nutrient recycling; nutrient uptake evolution; R^* ; tragedy of the commons

1. INTRODUCTION

The link between evolution and population/community dynamics has led to numerous models. Most of them focus on the evolution of predator–prey, host–parasite, mutualism and competitive interactions [1–3]. These models usually study the evolution of traits determining population dynamics but not ecosystem functioning. In most of these studies, the limiting resources for which organisms compete, for example prey, ‘disappear’ once consumed. Thus far, few studies have tackled the evolution of traits governing the use of a recycled resource [4–6], like traits allowing plants to influence nutrient cycling. Such traits are important because they are likely to determine key ecosystem properties [7–9]. We set out from the premise that evolution shapes ecosystems through the selection of biological traits that can have direct or indirect consequences on ecosystem properties, such as biomass, productivity, fertility or material and energy cycling [4,10–14]. The aim of this study is to examine the evolution of a trait influencing nutrient cycling—here the ability of plants to take up nutrients—and to determine the subsequent consequences for primary productivity and the distribution of nutrients among the different compartments of the ecosystem.

A number of theories have been proposed to predict general trends during the development and evolution of ecosystems [15,16]. Increase in living biomass or optimization of resources and energy use are among the normative predictions that have been made. Concerning primary productivity, the ability of plants to take up the limiting nutrient should be critical, and the evolution of this biological trait could lead to important environmental feedbacks, which could in turn have consequences on a plant's own fitness. Intuitively, the more resources a plant can absorb, the higher its biomass productivity, and the higher its fitness. We investigate this issue and test whether evolution of nutrient uptake capacity can improve or optimize primary productivity. Working on the evolution of such a biological trait implies determining its associated cost and benefit for the evolving organism. Conceivably, the more a plant invests its resources and energy into the root system as well as the uptake and assimilation of nutrients, the less resources and energy can be allocated to maintenance functions. Several studies show the existence of trade-offs between nutrient uptake ability and anti-herbivore defences at interspecific and intraspecific levels [17–20]. Other studies show that fast-growing plants tend to produce high amounts and quality of litter, whereas slow-growing plants tend to produce low amounts and quality of litter [21]. As a result, we chose to link the plant nutrient uptake capacity to its mortality rate: the more nutrients the plant absorbs, the higher its mortality rate. Including this trade-off enables us to study different plant strategies

* Author for correspondence (boudsocq@biologie.ens.fr).

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to acquire nutrients, and to find out under what conditions each strategy has a positive effect on the fitness of the plant. Are there situations where natural selection leads to an overconsumption of resources until they reach a too low level to enable plants survival (tragedy of the commons)? Does the R^* rule—according to which the plant with the lowest steady-state resource level is selected by evolution—always apply [22–24]? Can other strategies be selected?

To tackle these issues, we apply the adaptive dynamics framework [25–27] to a simple and general model of limiting nutrient cycling composed of three compartments and integrating the trade-off between nutrient uptake capacity and plant mortality. We focus on three questions: (i) given the trade-off we consider, what are the qualitative evolutionary outcomes, and how do they depend on the ecological scenario and trade-off shape? (ii) how do these outcomes relate to classical ecological theories? and (iii) what are their consequences in terms of ecosystem functioning?

2. THE ECOLOGICAL MODEL

(a) Model description

Our model describes the dynamics of the principal limiting nutrient of primary productivity in a simple three-compartment ecosystem: plants (P), dead organic matter (D) and inorganic nutrients (N) (figure 1). The model is described by the following set of differential equations:

$$\left. \begin{aligned} \frac{dP}{dt} &= u_N NP - (d_P + l_P - f_P)P, \\ \frac{dD}{dt} &= d_P P + R_D - (m_D + l_D)D \\ \text{and } \frac{dN}{dt} &= m_D D + R_N - (u_N P + l_N)N. \end{aligned} \right\} \quad (2.1)$$

The definitions of all parameters are in electronic supplementary material, appendix S1. Plants build up their biomass by absorbing nutrients from the N compartment, following a simple Lotka–Volterra function with the uptake rate u_N . In turn, plant biomass mortality leads to a flux of nutrients from the P compartment to the D compartment, following a mortality rate d_P . The D compartment includes all types of dead organic matter. This dead organic matter is mineralized, leading to a flux of nutrients to the N compartment with a rate m_D .

Each compartment is subject to losses. Fire, for example, can cause losses for plant and dead organic matter compartments, which leads to important fluxes in many ecosystems [28,29]. In agricultural ecosystems, harvest causes a net loss for the plant compartment. Erosion and leaching lead to losses of dead organic matter and the nutrients it contains. Inorganic nutrients can also be lost: for instance, mineral nitrogen is subject to volatilization, leaching and denitrification. These losses (nutrients going out of the ecosystem) are, respectively, modelled for the P , D and N compartments with the rates l_P , l_D and l_N .

There are different nutrient inputs to the ecosystem: atmospheric deposits of inorganic and organic nutrients brought by winds and rains (R_N and R_D , respectively).

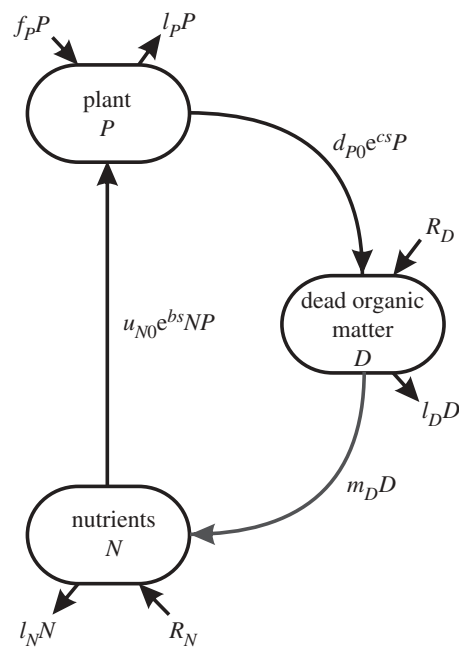


Figure 1. General model of nutrient cycling in an ecosystem. Arrow labels indicate the formula used for the corresponding flux. Definitions of parameters can be found in electronic supplementary material, appendix S1.

If the limiting nutrient is nitrogen, N_2 fixation by rhizospheric bacteria constitutes another input considered as proportional to the plant compartment size (with the rate f_P). It must be noted that f_P is null if the considered plant is non-leguminous or when plants are limited by other types of nutrients. Nitrogen fixation by free-living N -fixers constitutes another source of nutrients included in constant organic inputs (R_D).

Expressions for the ecological equilibrium (denoted by an over-bar) are found stating that derivatives (see equation (2.1)) are equal to 0:

$$\left. \begin{aligned} \bar{P} &= \frac{\alpha_P}{d_P} (\alpha_D R_D + R_N - l_N \bar{N}) \frac{1}{1 - \alpha_P \alpha_D}, \\ \bar{D} &= \frac{\alpha_D}{m_D} (R_D + \alpha_P R_N - l_N \alpha_P \bar{N}) \frac{1}{1 - \alpha_P \alpha_D} \\ \text{and } \bar{N} &= \frac{d_P}{\alpha_P u_N}, \end{aligned} \right\} \quad (2.2)$$

with

$$\left. \begin{aligned} \alpha_P &= \frac{d_P}{d_P + l_P - f_P} \\ \text{and } \alpha_D &= \frac{m_D}{m_D + l_D}. \end{aligned} \right\} \quad (2.3)$$

These two lumped parameters were chosen to make our results more concise and easier to understand. Equilibrium primary productivity (uptake and symbiotic fixation fluxes of nutrients to the P compartment) reads as follows:

$$\begin{aligned} \bar{\phi}_P &= u_N \bar{N} \bar{P} + f_P \bar{P} \\ &= \frac{d_P + l_P}{d_P + l_P - f_P} (\alpha_D R_D + R_N - l_N \bar{N}) \frac{1}{1 - \alpha_P \alpha_D}. \end{aligned} \quad (2.4)$$

(b) Equilibrium conditions

Independent conditions must be fulfilled to ensure that all model compartments can reach a positive equilibrium. As nutrient stocks are by definition positive, we disregard parameter sets that lead to negative equilibrium values of these stocks. Therefore, because of equation (2.2), only positive values of α_P are considered in the following analysis. Moreover, the term $1/(1 - \alpha_P\alpha_D)$ must also be positive to prevent an unrealistic nutrient accumulation [8,9], so that we only consider cases where

$$0 < \alpha_P < \frac{1}{\alpha_D}. \quad (2.5)$$

For the \bar{N} equilibrium stock to be positive, the following condition must be respected:

$$\bar{N} > 0 \Leftrightarrow \frac{d_P}{\alpha_P u_N} > 0 \Leftrightarrow \alpha_P > 0 \Leftrightarrow d_P > f_P - l_P. \quad (2.6)$$

If $l_P - f_P > 0$, then equation (2.6) is always met. On the contrary, if $l_P - f_P < 0$, there is a minimum plant mortality rate corresponding to the maximum α_P value allowed for the model to reach equilibrium.

The following condition must also be met:

$$\alpha_P < \frac{1}{\alpha_D} \Leftrightarrow d_P > \frac{f_P - l_P}{1 - \alpha_D}. \quad (2.7)$$

We always have $0 \leq 1 - \alpha_D \leq 1$, so that $(f_P - l_P)/(1 - \alpha_D) \geq f_P - l_P$ and equation (2.7) implies that equation (2.6) is met.

We must also have $\bar{P} > 0$ and $\bar{D} > 0$, so that

$$\bar{P} > 0 \Leftrightarrow \bar{N} < \frac{\alpha_D R_D + R_N}{l_N} \quad (2.8)$$

and

$$\bar{D} > 0 \Leftrightarrow \bar{N} < \frac{(1/\alpha_P)R_D + R_N}{l_N}. \quad (2.9)$$

Since $0 < \alpha_P < 1/\alpha_D$ for the model to reach equilibrium (see equation (2.5)), whenever equation (2.8) is true, so is equation (2.9). Thus, the necessary condition that must be fulfilled to have $\bar{P} > 0$ and $\bar{D} > 0$ is

$$\alpha_P > \frac{d_P}{u_N} \frac{l_N}{(\alpha_D R_D + R_N)}. \quad (2.10)$$

Finally, for an ecological equilibrium to exist, \bar{N} , \bar{P} and \bar{D} must be positive and the system must not accumulate nutrients infinitely. If $l_P - f_P < 0$, then equations (2.5) and (2.10) must be met. If $l_P - f_P > 0$, only equation (2.10) must be fulfilled. Using the Routh–Hurwitz criterion, it is possible to show that whenever an equilibrium is possible (positive stocks values), it is locally stable [30].

3. EVOLUTIONARY DYNAMICS

We assume that nutrient uptake and plant mortality rates are constrained by a trade-off, i.e. the higher the investment in nutrient uptake, the lower the investment in maintenance and defences, and hence the lower the survival rate. Mathematically, this trade-off is expressed using a common trait, s , which determines both the uptake rate

and the mortality rate through two exponential functions:

$$\left. \begin{aligned} u_N &= u_{N0} e^{bs} \\ \text{and } d_P &= d_{P0} e^{cs}. \end{aligned} \right\} \quad (3.1)$$

The relation between b and c (which can have any positive value) determines the strength of the trade-off: if $b < c$, as s increases, the relative increase in mortality is higher than the relative increase in nutrient uptake (and vice versa). The different types of curves that can be obtained following this trade-off are displayed in the electronic supplementary material, appendix S2.

Including equation (3.1) in equation (2.1) gives

$$\left. \begin{aligned} \frac{dP}{dt} &= (u_{N0} e^{bs} NP) - (d_{P0} e^{cs} + l_P - f_P)P, \\ \frac{dD}{dt} &= d_{P0} e^{cs} P + R_D - (m_D + l_D)D \\ \text{and } \frac{dN}{dt} &= m_D D + R_N - (u_{N0} e^{bs} P + l_N)N. \end{aligned} \right\} \quad (3.2)$$

We can express the constraints (equation 2.7) and (equation 2.10) in terms of the phenotypic trait s : when $l_P - f_P < 0$ (high rate of symbiotic fixation),

$$\alpha_P(s) < \frac{1}{\alpha_D} \Leftrightarrow s > \frac{1}{c} \ln \left(\frac{f_P - l_P}{d_{P0}(1 - \alpha_D)} \right), \quad (\text{see equation (2.7)})$$

whatever the sign of $l_P - f_P$,

$$\bar{P}, \bar{D} > 0 \Leftrightarrow \alpha_P(s) > \frac{d_{P0}}{u_{N0}} \frac{l_N}{(\alpha_D R_D + R_N)} e^{(c-b)s}. \quad (\text{see equation (2.10)})$$

Note that from equation (2.10) emerges a set of values of s (or α_P) enabling ecological equilibrium, which is bound by the solution(s) of

$$\alpha_P(s) = \frac{d_{P0}}{u_{N0}} \frac{l_N}{(\alpha_D R_D + R_N)} e^{(c-b)s}$$

(see the electronic supplementary material, appendix S3). These boundaries are called $\alpha_{P\text{lim}}$ (for cases with only one limit), $\alpha_{P\text{lim}1}$ and $\alpha_{P\text{lim}2}$ (for cases with two limits) and are reported in figure 2.

To study the joint evolution of the nutrient uptake rate and the primary producer mortality rate, we have studied the evolution of the trait s that links the uptake and mortality through a trade-off. During the evolution, the fitness of a mutant (denoted by subscript m) is defined by its *per capita* growth rate in the resident population at equilibrium [26,31]:

$$W_{P_m} = \frac{1}{P_m} \frac{dP_m}{dt},$$

and given equation (3.2),

$$W_{P_m}(s_m, s) = u_{N0} e^{bs_m} \frac{d_{P0} e^{cs}}{\alpha_P(s) u_{N0} e^{bs}} - (d_{P0} e^{cs_m} + l_P - f_P). \quad (3.3)$$

If this invasion fitness (equation 3.3) is positive, then the mutant can invade the resident population and s_m becomes the new resident trait for the plant population [31,32].

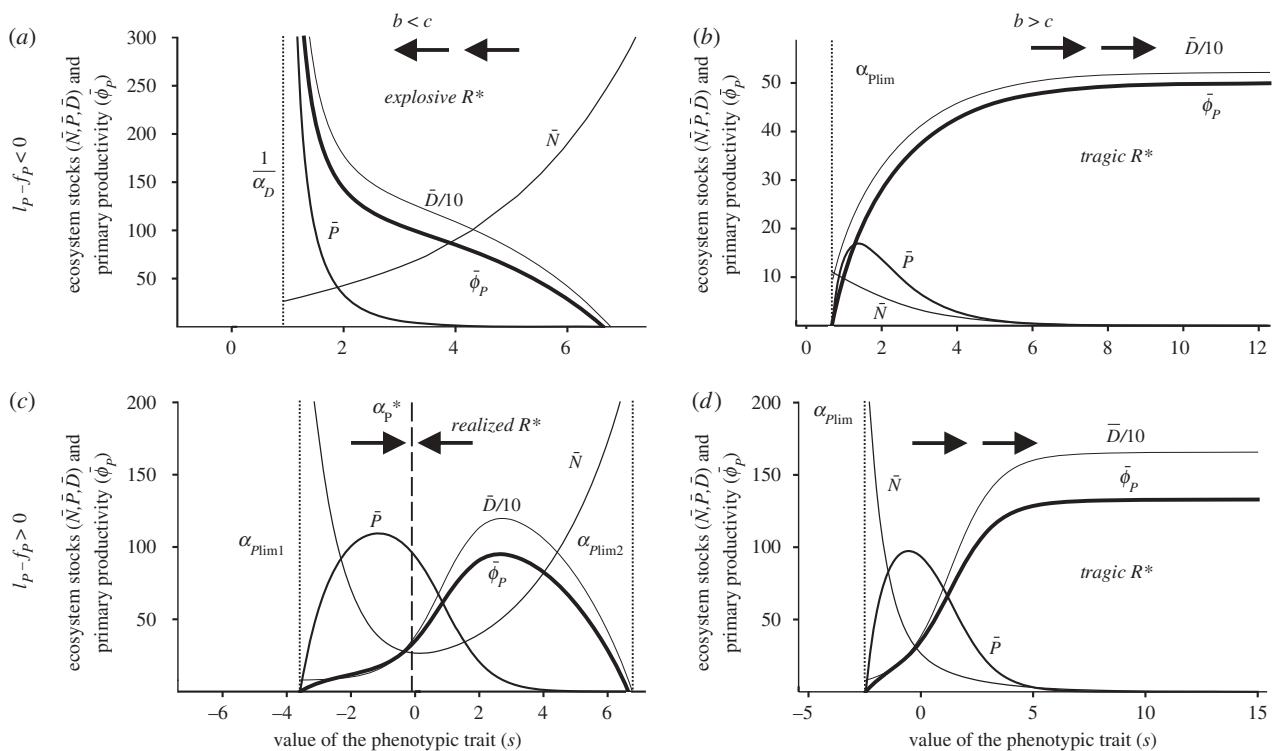


Figure 2. Variations in the size of ecosystem compartments (\bar{N} , \bar{P} and \bar{D} , in $\text{kg nutrient ha}^{-1}$) and primary productivity ($\bar{\phi}_P$, in $\text{kg nutrient ha}^{-1} \text{yr}^{-1}$) as functions of the trait (s). For the sake of readability, the tenth of the \bar{D} stock is displayed here. The arrows indicate the direction(s) of evolution. The dotted vertical lines illustrate the threshold beyond which the limiting nutrient accumulates indefinitely ($1/\alpha_D$), and beyond which the quantity of nutrients in the ecosystem is insufficient to allow plants to persist ($\alpha_{P\text{lim}}$). Parameters leading to these numerical simulations were chosen to obtain pedagogic representations of the different evolutionary cases. (a) Case 1.1, (b) case 1.3, (c) case 2.1 and (d) case 2.2. The values of the different parameters can be found in the electronic supplementary material, appendix S1.

Mutation after mutation, the value of s changes on the evolutionary time scale. This succession of discrete changes can be modelled using the canonical equation of adaptive dynamics [26,33]:

$$\frac{ds}{dt} = \frac{1}{2} K \mu \sigma^2 \bar{P} \left(\frac{\partial W_{P_m}}{\partial s_m} \right)_{s_m \rightarrow s}. \quad (3.4)$$

Here, K is a parameter scaling plant biomass to the evolving trait value, μ is the per-individual mutation rate and σ^2 is the variance of the amplitude of mutations. So, $\mu \sigma^2 \bar{P}$ corresponds to the phenotypic variability added by the mutation process. The fitness gradient $(\partial W_{P_m} / \partial s_m)_{s_m \rightarrow s}$ embodies the selection pressures acting on s . Using equations (3.2) and (3.4) provides the complete dynamics of the ecosystem, accounting simultaneously for variations on the ecological and evolutionary time scales. To reach an evolutionary equilibrium, the fitness gradient must be null:

$$\left(\frac{\partial W_{P_m}}{\partial s_m} \right)_{s_m \rightarrow s} = d_{P0} e^{cs} (b - c) + b(l_P - f_P) = 0. \quad (3.5)$$

Since α_P is a bijective function of s , so that to each value of α_P corresponds one value of s and reciprocally, studying variations of α_P or of s along the evolutionary trajectory is strictly equivalent. When the fitness gradient vanishes, the corresponding values of the phenotypic trait are known as 'evolutionary singular strategies':

(i) when $l_P - f_P > 0$ and $b - c > 0$, then $(\partial W_{P_m} / \partial s_m)_{s_m \rightarrow s} > 0$, so that there is no singular strategy and s increases along the evolutionary walk; (ii) on the contrary, when $l_P - f_P < 0$ and $b - c < 0$, then $(\partial W_{P_m} / \partial s_m)_{s_m \rightarrow s} < 0$; there is no singular strategy and s always decreases; and (iii) finally, when $l_P - f_P > 0$ and $b - c < 0$, or when $l_P - f_P < 0$ and $b - c > 0$, equation (3.5) has a solution and there is a singular strategy. We note ' s^* ' the trait value corresponding to this situation and ' α_{P^*} ' the corresponding α_P . Solving equation (3.5) leads to

$$s^* = \frac{1}{c} \ln \left(\frac{b(l_P - f_P)}{(c - b)d_{P0}} \right) \quad (3.6)$$

and $\alpha_{P^*} = \frac{b}{c}$.

To establish the properties of the singular strategy, we must determine the signs of the second-order derivatives of the fitness gradient at the evolutionary equilibrium:

$$\left. \begin{aligned} \left(\frac{\partial^2 W_{P_m}}{\partial s_m^2} \right)_{s_m \rightarrow s^*} &= bc(l_P - f_P) \\ \text{and } \left(\frac{\partial^2 W_{P_m}}{\partial s_m^2} \right)_{s_m \rightarrow s^*} &= -bc(l_P - f_P). \end{aligned} \right\} \quad (3.7)$$

The signs in these equations (3.7) characterize the conditions of invasibility and convergence of the singular

Table 1. Recapitulation of the model evolutionary outcomes, equilibrium formulae and their conditions.

symbiotic fixation	high: $l_P < f_P$			low, null or other limiting nutrient than nitrogen: $l_P > f_P$	
	case 1.1	case 1.2	case 1.3	case 2.1	case 2.2
cases	case 1.1	case 1.2	case 1.3	case 2.1	case 2.2
trade-off type	$0 < \frac{b}{c} \leq 1$	$1 < \frac{b}{c} < \frac{1}{\alpha_D}$	$\frac{1}{\alpha_D} < \frac{b}{c}$	$0 \leq \frac{b}{c} < 1$	$1 < \frac{b}{c}$
$\alpha_{P\text{initial}}$	$\alpha_{P\text{initial}} > \frac{b}{c}$	$\alpha_{P\text{initial}} < \frac{b}{c}$		$\alpha_{P\text{initial}} < \frac{b}{c}$ or $\alpha_{P\text{initial}} > \frac{b}{c}$	$\alpha_{P\text{initial}} < \frac{b}{c}$
outcome	explosive R^*	tragic R^*		realized R^*	tragic R^*
evolution of s	$s \rightarrow \frac{1}{c} \ln \left(\frac{(f_P - l_P)}{d_{P0}(1 - \alpha_D)} \right)$	$s \rightarrow +\infty$		$s \rightarrow s^*$	$s \rightarrow +\infty$
evolution of α_P	$\alpha_P \rightarrow \frac{1}{\alpha_D}$	$\alpha_P \rightarrow 1$		$\alpha_P \rightarrow \alpha_P^*$	$\alpha_P \rightarrow 1$
evolution of plant recycling rate	$d_P \rightarrow 0$	$d_P \rightarrow +\infty$		$d_P \rightarrow \frac{(l_P - f_P)\alpha_P^*}{(1 - \alpha_P^*)}$	$d_P \rightarrow +\infty$
evolution of plant uptake rate	$u_N \rightarrow 0$	$u_N \rightarrow +\infty$		$u_N \rightarrow u_{N0} \left(\frac{d_P}{d_{P0}} \right)^{\alpha_P^*}$	$u_N \rightarrow +\infty$
\bar{P} formula	$\bar{P} \rightarrow +\infty$	$\bar{P} \rightarrow 0$		$\bar{P} \rightarrow \frac{\alpha_D R_D + R_N - l_N \bar{N}}{\frac{1}{1 - \alpha_P^*} (l_P - f_P) (1 - \alpha_D \alpha_P^*)}$	$\bar{P} \rightarrow 0$
\bar{D} formula	$\bar{D} \rightarrow +\infty$	$\bar{D} \rightarrow \frac{R_D + R_N}{l_D}$		$\bar{D} \rightarrow \frac{R_D + R_N \alpha_P^* - l_N \bar{N} \alpha_P^*}{m_D (1 - \alpha_P^*) + l_D}$	$\bar{D} \rightarrow \frac{R_D + R_N}{l_D}$
\bar{N} formula	$\bar{N} \rightarrow \frac{d_P \alpha_D}{u_N}$	$\bar{N} \rightarrow 0$		$\bar{N} \rightarrow \frac{1}{u_N} \frac{1}{1 - \alpha_P^*} (l_P - f_P)$	$\bar{N} \rightarrow 0$
$\overline{\phi_P}$ formula	$\overline{\phi_P} \rightarrow +\infty$	$\overline{\phi_P} \rightarrow \frac{\alpha_D R_D + R_N}{1 - \alpha_D}$		$\overline{\phi_P} \rightarrow \frac{\alpha_D R_D + R_N - l_N \bar{N}}{1 - \alpha_D \alpha_P^*}$	$\overline{\phi_P} \rightarrow \frac{\alpha_D R_D + R_N}{1 - \alpha_D}$

strategy [34]. These signs depend here on the sign of $l_P - f_P$. We thus can distinguish two different cases.

- If $l_P - f_P > 0$ and $b - c < 0$, then the singular strategy is a continuous stable strategy (CSS): s evolves towards the evolutionary attractor s^* (convergence stable) and remains there once established (evolutionarily stable [35]).
- If $l_P - f_P < 0$ and $b - c > 0$, then the singular strategy is an evolutionary repeller and the trait s evolves away from s^* .

In §3a we study the evolutionary outcomes of the model. Figure 2 shows the ecological consequences of the different evolutionary scenarios.

(a) Evolutionary outcomes of the adaptive model

Although the trait subject to evolution is s , we chose to express our results as ecological limits and evolutionary equilibriums using α_P because this makes them easier to express and understand. For each case described below, evolution starts at the value of the initial α_P ($\alpha_{P\text{initial}}$), allowing for an ecological equilibrium (equations (2.5) and (2.10) met). Mathematical analyses of the model shows that evolution always drives \bar{N} towards smaller compartment sizes so that starting from a viable population at equilibrium, equation (2.8) and thus, equation (2.10) are always met (electronic supplementary material, appendix S4). The ecological equilibria, evolutionary outcomes and the conditions leading to them are summarized in table 1. According to their ecological meaning, we propose three categories of singularities: ‘explosive R^* ’, ‘tragic R^* ’

and ‘realized R^* ’. Each outcome is in accord with Tilman’s R^* theory [23]: evolution systematically pushes towards a decrease in the limiting nutrient stock. The ‘explosive’ case corresponds to a net accumulation of nutrients in the whole system, while the ‘tragic’ situation to an ever decreasing plant population. The ‘realized’ case is a CSS that has no other particularity than the reduction of the mineral nutrient pool to its lowest size. ‘Tragic’ and ‘explosive’ singularities eventually lead to cases for which some crucial hypotheses of the model would be violated. Accumulation of the limiting nutrient in plant biomass and dead organic matter stock should eventually lead to a limitation of the system by another nutrient or constraint, while a decrease in the plant population eventually leads to the incorporation of other processes (e.g. demographic stochasticity) that are not readily present in the model. We emphasize these cases because the transient evolutionary dynamics associated with them are informative, leading to more nutrients in the first case, and to an increasingly vulnerable plant population in the second.

When $l_P - f_P > 0$, α_P is an increasing function of s , and vice versa, and when $l_P - f_P < 0$, α_P is a decreasing function of s , we can thus distinguish two cases.

(i) Case 1. $l_P - f_P < 0$

This situation makes sense only when the model focuses on nitrogen cycling, with plants being able to fix atmospheric nitrogen ($f_P > 0$). When $l_P - f_P < 0$, we always have $\alpha_P > 1$, so that starting from an initial plant population at equilibrium, we necessarily have $\alpha_{P\text{initial}}$ in the interval $[1, 1/\alpha_D]$.

Case 1.1. Explosive R^* $0 < b/c \leq 1$

Here, $l_P - f_P < 0$ and the trade-off has a high cost: the mortality rate increases more with s than the uptake rate ($b \leq c$, electronic supplementary material, appendix S2), so that the fitness gradient is always negative ($(\partial W_{P_m}/\partial s_m)_{s_m \rightarrow s} < 0$). There is no singular strategy and s always decreases with evolution, so that uptake and plant mortality rates decrease while α_P increases. In this case, evolution drives α_P to a value higher than $1/\alpha_D$ and the system evolves towards an infinite accumulation of nutrients in plant biomass and dead organic matter compartments. Along the evolutionary trajectory, primary productivity (electronic supplementary material, appendix S5), plant biomass and dead organic matter stocks all increase, and soil nutrient content decreases (electronic supplementary material, appendix S4). These results are reported in figure 2.

Case 1.2. Explosive or tragic R^* $1 < b/c < 1/\alpha_D$

This situation corresponds to a 'low-cost' trade-off, where the mortality rate increases less with s than the uptake rate ($b > c$, electronic supplementary material, appendix S2). Two different cases arise here. The $\alpha_{P_{\text{initial}}}$ of the plant population can be higher or lower than the singular strategy (b/c). In the first situation, α_P^* being a repeller, evolution pushes α_P towards larger values, hence leading to nutrient accumulation as in case 1.1. In the other situation, $\alpha_{P_{\text{initial}}}$ is below b/c and α_P is repelled towards lower values, evolution then the driving plant strategy towards higher uptake and plant mortality rates. Primary productivity increases and can reach a plateau that corresponds to a minimal, intermediate or maximal flux, depending on the model parameters (electronic supplementary material, appendix S5). Moreover, the dead organic matter compartment increases towards its maximal size, whereas plant biomass and soil nutrient content (electronic supplementary material, appendix S4) decrease. As it represents an intermediate situation between the current and following cases, we have not displayed this scenario in figure 2.

Case 1.3. Tragic R^* $1/\alpha_D < b/c$

If the repelling singular strategy is higher than $1/\alpha_D$, the $\alpha_{P_{\text{initial}}}$ is always below α_P^* , so that α_P always decreases. This leads to an indeterminate level of primary productivity (electronic supplementary material, appendix S5), a maximal dead organic matter stock size and a total reduction of plant biomass and soil nutrient content (electronic supplementary material, appendix S4), as in case 1.2 when $\alpha_{P_{\text{initial}}}$ is below b/c (figure 2).

(ii) Case 2. $l_P - f_P > 0$

Since $l_P - f_P > 0$, $\alpha_{P_{\text{initial}}}$ necessarily lies below $\alpha_P = 1$. The limiting nutrient is not necessarily nitrogen and if it is, there is no or few symbiotic fixation. This case can be divided into two situations.

Case 2.1. Realized R^* $0 < b/c \leq 1$

This situation corresponds to an 'intermediate' trade-off strength, where $b \leq c$ (see the electronic supplementary material, appendix S2). In this case, mortality increases more with s than the uptake rate. Here, α_P evolves towards and reaches the evolutionary attractor α_P^* . It is a CSS, and the uptake and plant mortality rates reach intermediate

values. At the CSS, \bar{N} stock is at its minimum size (electronic supplementary material, appendix S4). Our results show that primary productivity (electronic supplementary material, appendix S5), \bar{P} and \bar{D} stocks are not maximized under this scenario (figure 2).

Case 2.2. Tragic R^* $1 < b/c$

This situation corresponds to a low-cost trade-off where $b > c$, i.e. mortality increases less with s than does nutrient uptake (electronic supplementary material, appendix S2). There is no singular strategy and the fitness gradient is always positive so that s and α_P always increase ($(\partial W_{P_m}/\partial s_m)_{s_m \rightarrow s} > 0$). In this case, the uptake and plant mortality rates always increase and evolution pushes primary productivity towards its maximum value if the condition $\alpha_D > f_P/l_P$ is met (see the electronic supplementary material, appendix S5). As in case 1.3 (and sometimes case 1.2), the dead organic matter compartment increases towards its maximal size while the plant and mineral nutrient (electronic supplementary material, appendix S4) compartments decrease (figure 2).

4. DISCUSSION

Our results show different possible evolutionary scenarios. We identified cases that have already been predicted and/or observed in the relevant literature, such as the R^* rule and the tragedy of the commons. We found that switches from one scenario to another depend on: (i) the strength of the cited trade-off (electronic supplementary material, appendix S2), and (ii) the relation between inputs and outputs of the limiting nutrient in the plant compartment—i.e. symbiotic fixation (when nitrogen is considered as the principal limiting nutrient) and losses of nutrients from the plant compartment. Taken together, our results show that the evolutionary dynamics of nutrient acquisition by plants bridges distinct ecological theories usually presented separately.

(a) Different evolutionary outcomes and consequences for the ecosystem

Whatever the evolutionary outcome, evolution leads to a minimization of soil mineral nutrient content (electronic supplementary material, appendix S4). This is the only feature that all outcomes have in common. Consequently, in our model, evolution always leads to the protection of the mineral nutrient stock from intense losses and increases the conservation of the limiting nutrient inside the ecosystem. From an evolutionary rationale, this confirms Tilman's R^* theory, which was originally based on an ecological argument [23]. The most obvious case is the R^* CSS, which we call the *realized R^** (case 2.1). This scenario is obtained with a high-cost trade-off (electronic supplementary material, appendix S2) and a net loss of nutrients for the plant compartment. On the one hand, the benefit of an increase in nutrient uptake is constrained by a greater cost: the higher s , the higher the death rate compared with the nutrient uptake rate. On the other hand, since plants draw nutrients from root uptake and not from symbiotic fixation, the nutrient uptake rate has to be sufficiently high to enable plants to grow and maintain themselves. In this scenario, s reaches and stays at the singular strategy (s^*) that allows the best use of mineral nutrients by plants, in the sense

that this strategy reduces \bar{N} to its lowest possible size. Plants that are not able to survive on such low quantities of resources are outcompeted by the resident.

These properties are in accordance with Tilman's R^* rule [23]. However, primary productivity is not maximized, as sometimes predicted in the literature [16]. This is owing to linking plant mortality to plant nutrient uptake ability through a trade-off. To our knowledge, such a trade-off has never been taken into account in studies focusing on the R^* rule [16,23]. We show at the evolutionary scale that the maximal depletion of nutrients by plants does not lead necessarily to the maximization of their biomass or primary productivity. Because selection is based on the *per capita* growth rate of mutants as a proxy for individual fitness and not on biomass or primary productivity, there is in fact no reason why maximal biomass or productivity should be obtained through evolution. For this reason, there can be some values of s maximizing plant biomass and/or productivity that are not selected by evolution (cases 1.1, 2.1 and 2.2). Finally, depending on the values of the trade-off parameters, different values of α_P can be selected at the CSS. The more constraining the trade-off, the lower α_P^* , and the lower the mineral nutrient pool and the higher the plant biomass (numerical simulations not shown).

Evolution may also drive the plant population to values so low that it becomes vulnerable to demographic stochasticity and hence prone to extinction (*tragic R**). This scenario may be found under two very different sets of conditions (figure 2) and requires that the trade-off has a low cost (electronic supplementary material, appendix S2), so that the benefit of an increase in the mineral nutrient uptake capacity is higher than its cost. Again, \bar{N} decreases along the evolutionary time scale, leading to a minimization of soil mineral nutrient losses. But here, the plant compartment decreases in a parallel way. This can be explained by the fact that plant mortality rate increases quicker than plant capacity to take up nutrients. However, since the plant uptake rate also increases, plant productivity, which is the quantity of nutrients entering the plant compartment in a step of time, increases and can sometimes be maximized (electronic supplementary material, appendix S5). More nutrients thus enter into the plant compartment, but their residence time becomes shorter as the rate of nutrient uptake increases. Such cases constitute an evolutionary tragedy of the commons [22,24]. As plants exploit evermore intensively the limiting nutrients, they lead, in the long term to a critical reduction of the mineral nutrient pool and to the extinction of the population. In the past 15 years, the idea that evolution can lead a population to extinction has received important attention and has become known as evolutionary suicide [36–38]. We can consider that the tragedy of the commons is a case of evolutionary suicide where the limiting resource is depleted until no population can maintain itself.

The last evolutionary outcome is the accumulation of the limiting nutrient in plant biomass and dead organic matter compartments (see case 1.1, *explosive R**). This situation is obtained with a high-cost trade-off (electronic supplementary material, appendix S2), and for plants that are able to fix nitrogen symbiotically. s always decreases, leading to lower nutrient uptake and plant mortality rates. In this case, plants have a strategy that exploits

their ability to fix nitrogen. Indeed, the less they take up nutrients, the lower the mortality of their biomass and the nutrients it contains, and the higher the proportion of their nutrients coming from symbiotic fixation. This leads to an increase in α_P . The outcome of this scenario is an increase in plant biomass, dead organic matter stock and primary productivity, whereas the soil mineral nutrient pool tends to be reduced.

(b) Empirical implications

Though the model has been thought through for terrestrial plants, there is no reason why it could not work for aquatic ecosystems. We chose to build it in a simple way, so as to keep it easy to understand and analytically tractable. Many mechanisms have not been considered and we used simple mathematical expressions. It is thus difficult to discuss the relative probability of the eco-evolutionary scenarios when they differ only by the trade-off strength (1.1 versus 1.2 versus 1.3, and 2.1 versus 2.2) because of the lack of empirical knowledge on the cost and benefit associated to nutrient uptake investment. However, we can assume that cases 2.1 and 2.2 are more likely to occur than cases 1.1, 1.2 and 1.3, since these latter only concern leguminous plants limited by nitrogen availability. Cases 2.1 and 2.2 are more general and applicable to every limiting nutrient.

In the *explosive R** scenario, the final outcome (system explosion) seems impossible. However, if we assume—once a significant quantity of limiting nutrients has been reached in the modelled ecosystem—that the considered nutrient is no longer limiting, then we can expect that such a scenario is realistic until another factor becomes limiting. Actually, the conditions needed to meet this situation in our model correspond to a nitrogen-fixing plant that bears a high cost in investing its resources into mineral nitrogen absorption.

Concerning the two *tragic R** scenarios (see cases 1.3 and 2.2), the fact that nutrient uptake and mortality rates always increase is not realistic. Indeed, it can be supposed that these two traits are physiologically constrained by other factors that would prevent such increases. But it does not preclude the fact that directional selection may initially favour such strategies, thereby contributing to an increased vulnerability of the plant population. There is evidence that natural selection (at the individual scale) could lead to population rarefaction in nature, and then to extinction owing to demographic stochasticity [38]. Though such evidence is not common, this is at least partially owing to the fact that it is difficult to identify the causes of extinction of plants that are no longer present, and even more to quantify the role of evolution relative to other factors. In case 1.3 (*tragic R**), plants are able to fix nitrogen but benefit from increasing their uptake capacity and mortality. Conceivably, the benefit in fixing nitrogen symbiotically or not should depend on the availability of nitrogen in the exploited soil. Different studies support the idea that the cost of nitrogen fixation relative to the cost of nitrogen absorption is negatively correlated to the soil mineral nitrogen content [39–41]. Since biological nitrogen fixation is not subject to evolution in our study, we have not been able to pinpoint such scenarios where nitrogen absorption and fixation coevolve. Nevertheless, this case can be considered as a

leguminous species in an environment where fixation is more costly than nitrogen uptake (N-rich environment), so that evolution drives the plant to a strategy increasingly based on nitrogen absorption through its roots. Oppositely, case 1.1 (*explosive R**) can be considered as a leguminous species in an environment where nitrogen uptake is more costly than fixation, so that the plants invest more and more in fixation, but not in nitrogen uptake. Note that the two trade-off parameters, b and c , depend on the physiology and the allocation of resources and energy of the studied organism, but also on environmental factors such as climate, herbivory, light or fire, etc.

Case 1.2 is an intermediate situation that would occur if the costs of nitrogen uptake and fixation were assumed to be relatively similar, so that the evolutionary outcome would depend on the position of the singular strategy with regard to $\alpha_{P_{\text{initial}}}$. If $\alpha_{P_{\text{initial}}}$ is sufficiently high—i.e. the fixation rate is high enough in comparison to the net loss rate of plant nutrients—then the outcome of this scenario is the same as in case 1.1. If $\alpha_{P_{\text{initial}}}$ is not sufficiently high—i.e. the fixation rate is not high enough in comparison to the net loss rate of plant nutrients—then the outcome of this scenario is the same as in case 1.3.

(c) *Perspectives*

A shortcoming of our model is that nitrogen fixation is not allowed to evolve or to change in a plastic way, while it is well known that the intensity of nitrogen fixation and the distribution of legume species depend on nitrogen availability [5,39–41]. The way we chose to model the capacity of plants to take up nutrients, as well as to describe plant mortality, may seem overly simplistic. On the one hand, using exponential functions allow us to attribute any real number to s , so that we do not have mathematical limitations in the variation of the evolving traits. On the other hand, this formalism remains simple enough to keep the model analytically tractable. Implementing a type II or type III functional response for limiting nutrient uptake would certainly be more realistic.

We also chose to build a three-compartment model to keep it as simple and general as possible. It would surely be more realistic to represent other compartments such as microbial biomass or to distinguish litter from more complex soil organic matter. But this would not necessarily affect the evolutionary outcomes, as far as investment to mineral nutrient absorption is concerned. It would however help answer other questions: how has evolution shaped the properties of the microbial loop and competition between plant and micro-organisms for mineral nutrients [42]? Are there conditions for which evolution has selected plant strategies that enhance mineralization through the stimulation of micro-organisms and root exudates [43,44]?

5. CONCLUSIONS

Our model leads to contrasting evolutionary outcomes of the same ecological situation—i.e. competition for a limiting nutrient—and unites distinct theories concerning the exploitation of a limiting resource. To our knowledge, such a bridge between the R^* rule, the tragedy of the commons and nutrient accumulation has never been built. These theories are originally based on ecological arguments, and the conditions we have found for the different evolutionary outcomes are not obviously *a*

priori. Thanks to its simplicity, our model is one of the few models tackling the issue of the consequences of the evolution of biological traits on ecosystem functioning. Furthermore, it helps understanding of how ecosystems are shaped through the evolution of traits implicated in nutrient recycling. Since the evolutionary outcomes predicted by our model depend on the shape of the trade-off between biomass mortality and investment into nutrient uptake, it would be relevant to experimentally determine this shape for different plant species and environmental settings.

Nutrient loss rates and nutrient inputs have no influence on the model evolutionary outcomes. The same type of result was found by Menge *et al.* [5] for the evolution of symbiotic nitrogen fixation. This is probably owing to the use of a donor–recipient function for nutrient absorption. Another formalism, such as the one employed in Kylafis & Loreau's model [4], would have probably led to different results in which environmental factors influence plants' evolutionary dynamics. However, the shape of the trade-off depends on physiological constraints evolved by plant lineages, but is also likely to depend on environmental characteristics such as soil properties, nutrient availability or light availability. In this sense, the evolutionary outcomes of our model implicitly depend on environmental properties. Taking explicitly into account the influence of environmental properties on the trade-off could help link the different evolutionary scenarios to plant functional groups and environmental conditions.

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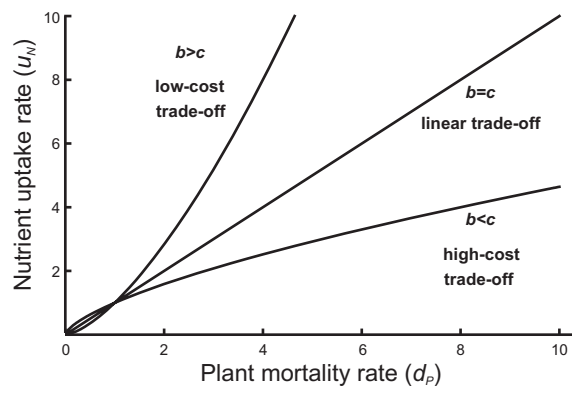
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APPENDIX 1

Parameter	Case 1.1	Case 1.3	Case 2.1	Case 2.3	Dimension	Definition
f_P	0.1	0.1	0.01	0.01	yr^{-1}	Annual symbiotic nitrogen fixation rate
d_{P0}	0.275	0.275	0.275	0.275	yr^{-1}	Annual plant mortality rate
l_P	0.01	0.01	0.1	0.1	yr^{-1}	Annual plant loss rate
R_D	6.7	10	6.7	6.7	$\text{kg nutrient ha}^{-1} \text{yr}^{-1}$	Annual organic nutrient input
m_D	0.0766	0.0766	0.0766	0.0766	yr^{-1}	Annual dead organic matter recycling rate
l_D	0.0077	0.0383	0.0077	0.0077	yr^{-1}	Annual dead organic matter loss rate
u_{NO}	0.0137	0.0137	0.0137	0.0137	$\text{ha kg nutrient}^{-1} \text{yr}^{-1}$	Annual inorganic nutrient uptake rate
l_N	0.05	1.5	0.05	0.05	yr^{-1}	Annual inorganic nutrient loss rate
R_N	6	10	6	6	$\text{kg nutrient ha}^{-1} \text{yr}^{-1}$	Annual inorganic nutrient input
b	1	1.6	1	1.375	dimensionless	Benefit of the nutrient uptake capacity
c	1.375	1	1.375	1	dimensionless	Cost of the nutrient uptake capacity

APPENDIX 2



APPENDIX 3

In this appendix, we study the condition allowing $\bar{P} > 0$ and $\bar{D} > 0$. The following inequality must be verified:

$$\alpha_p(s) > \frac{d_{p0}e^{cs}}{u_{N0}e^{bs}} \frac{l_N}{\alpha_D R_D + R_N} \quad (10)$$

We thus have to determine the set of s values (and hence α_p) that verify condition (10).

Given $\alpha_{p_{critical}}(s) = \frac{d_{p0}e^{cs}}{u_{N0}e^{bs}} \frac{l_N}{\alpha_D R_D + R_N}$, the solution(s) of the equality $\alpha_p(s) = \alpha_{p_{critical}}(s)$ are

the boundaries of the set of s values that verify condition (10). Since $\alpha_p(s)$ is a bijective

function of s , limit values of α_p can also be determined. We show that depending on the

evolutionary outcome, $\alpha_p(s) = \alpha_{p_{critical}}(s)$ can have no, one, or two solutions that are called

$\alpha_{p_{lim}}$, $\alpha_{p_{lim1}}$ and $\alpha_{p_{lim2}}$, depending on the evolutionary outcome. To determine the number of

solutions of this equality, we study here the number of intersections between the curves

$\alpha_p(s)$ and $\alpha_{p_{critical}}(s)$ geometrically. It must be noted that evolution starts from a viable

population that must meet condition (10).

Study of $\alpha_p(s)$:

Given $\alpha_p(s) = \frac{d_{p0}e^{cs}}{d_{p0}e^{cs} + l_p - f_p}$, when $l_p - f_p > 0$, then $0 < \alpha_p(s) < 1$. When $l_p - f_p < 0$,

then $1 < \alpha_p(s)$.

The derivative of α_p relative to s reads as follow:

$$\alpha_p'(s) = c\alpha_p(s)(1 - \alpha_p(s))$$

It is then possible to determine the sign of this derivative.

If $l_p - f_p > 0$, then $0 < \alpha_p(s) < 1$ and $\alpha_p'(s) > 0$, so that $\alpha_p(s)$ increases.

If $l_p - f_p < 0$, then $1 < \alpha_p(s)$ and $\alpha_p'(s) < 0$, so that $\alpha_p(s)$ decreases.

Note that when $l_p < f_p$, there is a vertical asymptote for $s = (1/c)\ln((f_p - l_p)/d_{p0})$. On the left side of this asymptote, $\alpha_p(s)$ become negative, and equilibrium conditions are no longer respected.

In cases 1.1 and sometimes 1.2, the fitness gradient is negative so that s always decreases toward the asymptote. Since condition 7 is more constraining than condition 6, in these cases, we consider that the decrease of s stops before hitting the asymptote, because α_p increases exponentially and once a certain value of α_p is reached, nutrient accumulates and the model is no longer an approximation.

The second-order derivative enables us to determine the shape of $\alpha_p(s)$:

$$\alpha_p''(s) = c^2 \alpha_p(s) \left(2(\alpha_p(s))^2 - 3\alpha_p(s) + 1 \right)$$

$$\alpha_p''(s) \text{ becomes null when } \alpha_p = 0, \alpha_p = \frac{1}{2} \text{ and } \alpha_p = 1$$

When $0 < \alpha_p < \frac{1}{2}$, then $\alpha_p''(s) > 0$.

When $\frac{1}{2} < \alpha_p < 1$, then $\alpha_p''(s) < 0$.

So, when $0 < \alpha_p < 1$, the variation of $\alpha_p(s)$ is characteristic of a sigmoid shape.

When $1 < \alpha_p$, then $\alpha_p''(s) > 0$, so that the variation of $\alpha_p(s)$ is characteristic of an exponential shape.

In sum, when $l_p - f_p > 0$, then $0 < \alpha_p(s) < 1$ and $\alpha_p(s)$ is an increasing sigmoid function of s . When $l_p - f_p < 0$, then $1 < \alpha_p(s)$ and $\alpha_p(s)$ is a decreasing exponential function of s .

Study of $\alpha_{Pcritical}(s)$:

Given $\alpha_{Pcritical}(s) = \frac{d_{p0} e^{cs}}{u_{N0} e^{bs}} \frac{l_N}{\alpha_D R_D + R_N}$, the derivative of $\alpha_{Pcritical}$ relative to s reads as

follows:

$$\alpha_{Pcritical}'(s) = (c - b)\alpha_{Pcritical}(s).$$

So that when $b > c$, $\alpha_{Pcritical}'(s) < 0$ and $\alpha_{Pcritical}$ is a decreasing function of s .

When $b < c$, $\alpha_{Pcritical}'(s) > 0$ and $\alpha_{Pcritical}$ is an increasing function of s .

The second-order derivative enables us to determine the shape of $\alpha_{Pcritical}$.

$$\alpha_{Pcritical}''(s) = (c - b)^2 \alpha_{Pcritical}(s)$$

We thus always have $\alpha_{Pcritical}''(s) > 0$, so that $\alpha_{Pcritical}(s)$ always has an increasing slope, and the expression of $\alpha_{Pcritical}(s)$ proves that it is a decreasing or increasing exponential function.

To sum up, when $b > c$, $\alpha_{Pcritical}(s)$ is a decreasing exponential function of s that goes to 0 when s evolves toward $+\infty$ and goes to $+\infty$ when s evolves toward $-\infty$.

When $b < c$, $\alpha_{Pcritical}(s)$ is an increasing exponential function of s that goes to $+\infty$ when s evolves toward $+\infty$ and goes to 0 when s evolves toward $-\infty$.

We can now study the number of intersections between the curves $\alpha_p(s)$ and $\alpha_{Pcritical}(s)$.

Case 1.1) Explosive R*:

$$b \leq c \text{ and } l_p < f_p.$$

In this case $\alpha_p(s)$ is a decreasing exponential function of s and $\alpha_{Pcritical}(s)$ is an increasing exponential function of s . The curves thus always have one intersection so that there is always a unique solution of the equality $\alpha_p(s) = \alpha_{Pcritical}(s)$, which is called α_{Plim} . $\alpha_p(s)$ must hence be higher than α_{Plim} to enable $\bar{P} > 0$ and $\bar{D} > 0$.

Cases 1.2 & 1.3) Explosive or Tragic R*:

$$b > c \text{ and } l_p < f_p.$$

In these cases, $\alpha_p(s)$ and $\alpha_{Pcritical}(s)$ are decreasing exponential functions of s . When s evolves toward $-\infty$, as well as when s evolves toward $+\infty$ we always have:

$\alpha_p(s) > \alpha_{Pcritical}(s)$, so that $\bar{P} > 0$ and $\bar{D} > 0$ for these two extreme limits.

Three situations can occur:

- Either $\alpha_p(s)$ is always higher than $\alpha_{Pcritical}(s)$, so that there is no solution to the equality

$\alpha_p(s) = \alpha_{Pcritical}(s)$, and we always have $\bar{P} > 0$ and $\bar{D} > 0$.

- Either $\alpha_p(s)$ and $\alpha_{Pcritical}(s)$ are tangential, so that there always exists a unique solution to

the equality $\alpha_p(s) = \alpha_{Pcritical}(s)$, which is called α_{plim} , and which does not enable $\bar{P} > 0$ and

$\bar{D} > 0$.

- Either the curves $\alpha_p(s)$ and $\alpha_{Pcritical}(s)$ intersect together, so that there are always two

solutions to the equality $\alpha_p(s) = \alpha_{Pcritical}(s)$, which are called α_{plim1} and α_{plim2} . In this

situation, there is no equilibrium when $\alpha_{plim1} < \alpha_p < \alpha_{plim2}$. On the contrary, when

$\alpha_p < \alpha_{plim1}$ and $\alpha_p > \alpha_{plim2}$, $\bar{P} > 0$ and $\bar{D} > 0$.

Case 2.1) Realized R*:

$b \leq c$ and $l_p > f_p$.

In this case, $\alpha_p(s)$ is an increasing sigmoid function of s and $\alpha_{Pcritical}(s)$ is an increasing

exponential function of s . When s evolves toward $-\infty$, as when s evolves toward $+\infty$ we

always have: $\alpha_p < \alpha_{Pcritical}$, so that $\bar{P} < 0$ and $\bar{D} < 0$ for these two extreme limits.

Three situations can occur here:

- Either $\alpha_p(s)$ is always lower than $\alpha_{Pcritical}(s)$, so that there is no solution to the equality

$\alpha_p(s) = \alpha_{Pcritical}(s)$, and we always have $\bar{P} < 0$ and $\bar{D} < 0$. It must be noted that this situation

is impossible since evolution must start from a viable population that meets condition (10).

- Either $\alpha_p(s)$ and $\alpha_{Pcritical}(s)$ are tangential, so that there always exists a unique solution to the equality $\alpha_p(s) = \alpha_{Pcritical}(s)$, which is called α_{Plim} , and which enables $\bar{P} > 0$ and $\bar{D} > 0$.
- Either the curves $\alpha_p(s)$ and $\alpha_{Pcritical}(s)$ intersect together, so that there are always two solutions to the equality $\alpha_p(s) = \alpha_{Pcritical}(s)$, which are called α_{Plim1} and α_{Plim2} . In this situation, equilibrium lies only between these two solutions ($\alpha_{Plim1} < \alpha_p < \alpha_{Plim2}$).

Case 2.2) Tragic R*:

$$b > c \text{ and } l_p > f_p.$$

In this case, $\alpha_p(s)$ is an increasing sigmoid function of s and $\alpha_{Pcritical}(s)$ is a decreasing exponential function of s . The curves thus always have one intersection so that there is always a unique solution to the equality $\alpha_p(s) = \alpha_{Pcritical}(s)$, which is called α_{Plim} . $\alpha_p(s)$ must hence be higher than α_{Plim} to enable $\bar{P} > 0$ and $\bar{D} > 0$.

APPENDIX 4

In this appendix, we show that in all possible evolutionary scenarios, the size of the equilibrium mineral nutrient stock always decreases along the evolutionary walk ($\frac{d\bar{N}}{dt} < 0$), and that starting from a viable population, selection never drives this population toward a situation where the quantity of nutrients that are recycled inside the ecosystem is lower than the critical amount necessary for plants to survive.

Given that $\frac{ds}{dt}$ (the variation of s as a function of time, on an evolutionary timescale) is

proportional to the fitness gradient $\left(\frac{\partial W_{Pm}}{\partial s_m}\right)_{s_m \rightarrow s}$ (see equation 14), and since the sign of

$\frac{d\bar{N}}{ds} = c \frac{d_{P0} e^{cs}}{u_{N0} e^{bs}} - b \frac{d_{P0} e^{cs} + l_P - f_P}{u_{N0} e^{bs}}$ can easily be determined, we can thus know the sign of

$$\frac{d\bar{N}}{dt} = \frac{d\bar{N}}{ds} \frac{ds}{dt}.$$

Case 1.1) Explosive R*:

In this case, $\left(\frac{\partial W_{Pm}}{\partial s_m}\right)_{s_m \rightarrow s} < 0$, so that $\frac{ds}{dt} < 0$

Since $l_P < f_P$ and $b \leq c$, we find: $\frac{d\bar{N}}{ds} > 0$

So that $\frac{d\bar{N}}{ds} \frac{ds}{dt} < 0$, and thus $\frac{d\bar{N}}{dt} < 0$.

We can conclude here that \bar{N} decreases along the evolutionary walk.

Cases 1.2 & 1.3) Explosive or Tragic R*:

In these cases, $\left(\frac{\partial W_{Pm}}{\partial s_m}\right)_{s_m \rightarrow s} = 0$ has one solution, $s = s^* = \frac{1}{c} \ln \left(\frac{b(l_p - f_p)}{(c-b)d_{p0}} \right)$.

When $s < s^*$, then $\frac{ds}{dt} < 0$. Since $l_p < f_p$ and $b > c$, we find: $\frac{d\bar{N}}{ds} > 0$ for this interval. When

$s > s^*$, then $\frac{ds}{dt} > 0$. Since $l_p < f_p$ and $b > c$, we find: $\frac{d\bar{N}}{ds} < 0$ for this interval.

So, whatever the value of s , we always have $\frac{d\bar{N}}{ds} \frac{ds}{dt} < 0$, and thus $\frac{d\bar{N}}{dt} < 0$.

We can conclude here that \bar{N} decreases along the evolutionary walk.

Case 2.1) Realized R*:

In this case, $\left(\frac{\partial W_{Pm}}{\partial s_m}\right)_{s_m \rightarrow s} = 0$ has one solution, that is $s = s^* = \frac{1}{c} \ln \left(\frac{b(l_p - f_p)}{(c-b)d_{p0}} \right)$.

When $s < s^*$, then $\frac{ds}{dt} > 0$. Since $l_p > f_p$ and $b \leq c$, we find: $\frac{d\bar{N}}{ds} < 0$ for this interval.

When $s > s^*$, then $\frac{ds}{dt} < 0$. Since $l_p > f_p$ and $b \leq c$, we find: $\frac{d\bar{N}}{ds} > 0$ for this interval.

So, whatever the value of s , we always have $\frac{d\bar{N}}{ds} \frac{ds}{dt} < 0$, and thus $\frac{d\bar{N}}{dt} < 0$.

We can conclude here that \bar{N} decreases along the evolutionary walk until it reaches its

minimum value: $\bar{N} = \frac{1}{u_N} \frac{1}{1 - \alpha_p^*} (l_p - f_p)$

Case 2.2) Tragic R*:

In this case, $\left(\frac{\partial W_{Pm}}{\partial s_m}\right)_{s_m \rightarrow s} > 0$, so that $\frac{ds}{dt} > 0$.

Since $l_p > f_p$ and $b > c$, we find: $\frac{d\bar{N}}{ds} < 0$.

So that $\frac{d\bar{N}}{ds} \frac{ds}{dt} < 0$, and thus $\frac{d\bar{N}}{dt} < 0$.

We can conclude here that \bar{N} decreases along the evolutionary walk.

Finally, whatever the evolutionary scenario, \bar{N} always decreases along the evolutionary walk. This property leads to another important property: since \bar{N} decreases, and since evolution always starts from a viable population that meets the following condition for which

all compartments are positive: $\bar{P} > 0 \Leftrightarrow \bar{N} < \frac{\alpha_D R_D + R_N}{l_N}$ (6), then conditions (8) and (10)

are always met along the evolutionary walk and the sizes of the different compartments always remain positive.

APPENDIX 5

In this appendix, we show analytically for each evolutionary outcome how primary productivity varies along the evolutionary walk.

The most simplified expression that we found for the variation of primary productivity in function of s reads as follows:

$$\frac{\partial \bar{\phi}_P}{\partial s} = \frac{c\alpha_P(l_P\alpha_D - f_P)(\alpha_D R_D + R_N - l_N \bar{N}) + (d_{P0}e^{cs} + l_P)(b - c\alpha_P)(1 - \alpha_D\alpha_P)l_N \bar{N}}{(d_{P0}e^{cs} + l_P - f_P)(1 - \alpha_P\alpha_D)^2}$$

Starting from this derivative, we can determine its sign for each evolutionary outcome of the model.

Case 1.1) Explosive R*:

Here, the parameters satisfy these conditions: $l_P - f_P < 0$ and $0 < \frac{b}{c} \leq 1$. As seen in the results section, the model predicts these trends: $s \rightarrow -\infty$ and $\alpha_P \rightarrow +\infty$.

The system explodes when α_P reaches the ecological limit $\alpha_P = \frac{1}{\alpha_D}$

($s = s_0 = \frac{1}{c} \ln \left(\frac{(f_P - l_P)}{d_{P0}(1 - \alpha_D)} \right)$). Moreover, since condition (10) is always verified along the

evolutionary walk, we always have: $\alpha_D R_D + R_N - l_N (N)_{s=s_0} > 0$.

We can find the sign of the derivative of the primary productivity when $\alpha_P = \frac{1}{\alpha_D}$:

$$\lim_{s \rightarrow s_0} \left(\frac{\partial \bar{\phi}_P}{\partial s} \right) = \frac{c\alpha_P(l_P\alpha_D - f_P)(\alpha_D R_D + R_N - l_N \bar{N}) + (d_{P0}e^{cs} + l_P)(b - c\alpha_P)(1 - \alpha_D\alpha_P)l_N \bar{N}}{(d_{P0}e^{cs} + l_P - f_P)(1 - \alpha_P\alpha_D)^2}$$

$$\lim_{s \rightarrow s_0} \left(\frac{\partial \bar{\phi}_P}{\partial s} \right) = \frac{c \frac{1}{\alpha_D} (l_P\alpha_D - f_P)(\alpha_D R_D + R_N - l_N \bar{N}) + (0^-)}{0^+}$$

$$\lim_{s \rightarrow s_0} \left(\frac{\partial \bar{\phi}_P}{\partial s} \right) = \frac{-cte + 0^-}{0^+}$$

$$\lim_{s \rightarrow s_0} \left(\frac{\partial \bar{\phi}_P}{\partial s} \right) = -\infty$$

The primary productivity thus increases when s decreases, until α_P reaches the limit

$$\alpha_P = \frac{1}{\alpha_D}.$$

Case 1.3) Tragic R*:

Here, the parameters satisfy these conditions: $l_P - f_P < 0$ and $\frac{1}{\alpha_D} < \frac{b}{c}$. The model predicts

these trends $s \rightarrow +\infty$ and $\alpha_P \rightarrow 1$. We can find the sign of the derivative of the primary

productivity when $s \rightarrow +\infty$:

$$\lim_{s \rightarrow +\infty} \left(\frac{\partial \bar{\phi}_P}{\partial s} \right) = \frac{c\alpha_P (l_P \alpha_D - f_P) (\alpha_D R_D + R_N - l_N N^*) + (d_{P0} e^{cs} + l_P) (b - c\alpha_P) (1 - \alpha_D \alpha_P) l_N N^*}{(d_{P0} e^{cs} + l_P - f_P) (1 - \alpha_P \alpha_D)^2}$$

$$\lim_{s \rightarrow +\infty} \left(\frac{\partial \bar{\phi}_P}{\partial s} \right) = \frac{c\alpha_P (l_P \alpha_D - f_P) (\alpha_D R_D + R_N - l_N N^*)}{(d_{P0} e^{cs} + l_P - f_P) (1 - \alpha_P \alpha_D)^2} + \frac{\left(\frac{(1 - \alpha_D) d_{P0}^2 e^{2cs} + l_P - f_P}{u_{N0} e^{bs}} + l_P \frac{(1 - \alpha_D) d_{P0} e^{cs} + l_P - f_P}{u_{N0} e^{bs}} \right) (b - c\alpha_P) l_N}{(d_{P0} e^{cs} + l_P - f_P) (1 - \alpha_P \alpha_D)^2}$$

$$\lim_{s \rightarrow +\infty} \left(\frac{\partial \bar{\phi}_P}{\partial s} \right) = \frac{c\alpha_P (l_P \alpha_D - f_P) (\alpha_D R_D + R_N - l_N N^*)}{(d_{P0} e^{cs} + l_P - f_P) (1 - \alpha_P \alpha_D)^2} + (0^+ + 0^+) (b - c\alpha_P) l_N$$

$$\lim_{s \rightarrow +\infty} \left(\frac{\partial \bar{\phi}_P}{\partial s} \right) = \frac{c\alpha_P (l_P \alpha_D - f_P) (\alpha_D R_D + R_N - l_N N^*)}{(d_{P0} e^{cs} + l_P - f_P) (1 - \alpha_P \alpha_D)^2} + 0^+$$

To satisfy the model equilibrium conditions, we must have $\alpha_D R_D + R_N - l_N N^* > 0$.

Thus, $c\alpha_p(l_p\alpha_D - f_p)(\alpha_D R_D + R_N - l_N N^*) < 0$,

and then $\frac{c\alpha_p(l_p\alpha_D - f_p)(\alpha_D R_D + R_N - l_N N^*)}{(d_{p0}e^{cs} + l_p - f_p)(1 - \alpha_p\alpha_D)^2} = 0^-$,

so that

$$\lim_{s \rightarrow +\infty} \left(\frac{\partial \bar{\phi}_p}{\partial s} \right) = 0^- + 0^+$$

$$\lim_{s \rightarrow +\infty} \left(\frac{\partial \bar{\phi}_p}{\partial s} \right) = 0^\pm$$

The derivative is thus always null but we cannot determine whether primary productivity is increasing or decreasing before it reaches its plateau. So, we do not know whether the plateau corresponds to a maximal, minimal or intermediate flux of primary productivity.

Case 2.1) Realized R^* :

Here, the parameters satisfy these conditions: $l_p - f_p > 0$ and $0 < \frac{b}{c} \leq 1$. The model predicts

these trends: $s \rightarrow s^* = \frac{1}{c} \ln \left(\frac{b(l_p - f_p)}{(c-b)d_{p0}} \right)$ and $\alpha_p \rightarrow \frac{b}{c}$. We can find the sign of the derivative

of the primary productivity when $s \rightarrow \frac{1}{c} \ln \left(\frac{b(l_p - f_p)}{(c-b)d_{p0}} \right)$:

$$\left(\frac{\partial \bar{\phi}_p}{\partial s} \right)_{s=s^*} = \frac{c\alpha_p(l_p\alpha_D - f_p)(\alpha_D R_D + R_N - l_N N^*) + (d_{p0}e^{cs} + l_p)(b - c\alpha_p)(1 - \alpha_D\alpha_p)l_N N^*}{(d_{p0}e^{cs} + l_p - f_p)(1 - \alpha_p\alpha_D)^2}$$

$$\left(\frac{\partial \bar{\phi}_p}{\partial s} \right)_{s=s^*} = \frac{b(l_p\alpha_D - f_p)(\alpha_D R_D + R_N - l_N N^*)}{\left(\frac{c}{c-b} \right) (l_p - f_p) \left(1 - \frac{b}{c} \alpha_D \right)^2}$$

$$\left(\frac{\partial \bar{\phi}_p}{\partial s} \right)_{s=s^*} > 0 \Leftrightarrow \frac{b(l_p\alpha_D - f_p)(\alpha_D R_D + R_N - l_N N^*)}{\left(\frac{c}{c-b} \right) (l_p - f_p) \left(1 - \frac{b}{c} \alpha_D \right)^2} > 0$$

$$\left(\frac{\partial \bar{\phi}_P}{\partial s}\right)_{s=s^*} > 0 \Leftrightarrow l_P \alpha_D - f_P > 0$$

$$\left(\frac{\partial \bar{\phi}_P}{\partial s}\right)_{s=s^*} > 0 \Leftrightarrow \alpha_D > \frac{f_P}{l_P}$$

If $\alpha_D = \frac{f_P}{l_P}$, then $\left(\frac{\partial \bar{\phi}_P}{\partial s}\right)_{s=s^*}$ becomes null and the primary productivity reaches its maximal

flux:

$$\phi_P^* = \frac{1}{1 - \alpha_D} (\alpha_D R_D + R_N - l_N N^*).$$

If $\alpha_D \neq \frac{f_P}{l_P}$, the primary productivity is lower than its maximal value.

Case 2.2) Tragic R*:

Here, the parameters satisfy these conditions: $l_P - f_P > 0$ and $1 < \frac{b}{c}$. The model predicts these

trends: $s \rightarrow +\infty$ and $\alpha_P \rightarrow 1$. We can find the sign of the derivative of the primary

productivity when $s \rightarrow +\infty$:

$$\lim_{s \rightarrow +\infty} \left(\frac{\partial \bar{\phi}_P}{\partial s}\right) = \frac{c \alpha_P (l_P \alpha_D - f_P) (\alpha_D R_D + R_N - l_N N^*) + (d_{P0} e^{cs} + l_P) (b - c \alpha_P) (1 - \alpha_D \alpha_P) l_N N^*}{(d_{P0} e^{cs} + l_P - f_P) (1 - \alpha_P \alpha_D)^2}$$

$$\lim_{s \rightarrow +\infty} \left(\frac{\partial \bar{\phi}_P}{\partial s}\right) = \frac{c (l_P \alpha_D - f_P) (\alpha_D R_D + R_N - l_N N^*) + (d_{P0} e^{cs} + l_P) (b - c) (1 - \alpha_D) l_N N^*}{(d_{P0} e^{cs} + l_P - f_P) (1 - \alpha_D)^2}$$

$$\lim_{s \rightarrow +\infty} \left(\frac{\partial \bar{\phi}_P}{\partial s}\right) = 0$$

$$l_P \alpha_D - f_P > 0 \Leftrightarrow \lim_{s \rightarrow +\infty} \left(\frac{\partial \bar{\phi}_P}{\partial s}\right) = 0^+$$

$$l_p \alpha_D - f_p < 0 \Leftrightarrow \lim_{s \rightarrow +\infty} \left(\frac{\partial \bar{\phi}_p}{\partial s} \right) = 0^\pm$$

Thus, when $l_p \alpha_D - f_p > 0$, the derivative is always positive and tends toward 0 when $s \rightarrow +\infty$. Thus, primary productivity reaches a plateau that corresponds to its maximal value.

But if $l_p \alpha_D - f_p < 0$, we cannot determinate if the plateau corresponds to the maximal, minimal or to an intermediate value of primary productivity.