

1 **Title:** Effects of plant evolution on nutrient cycling couple aboveground and belowground
2 processes

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9 ABSTRACT:

10 Plant strategies for nutrient acquisition and recycling are key components of ecosystem
11 functioning. How the evolution of such strategies modifies ecosystem functioning and
12 services is still not well understood. In the present work, we aim at understanding how the
13 evolution of different phenotypic traits link aboveground and belowground processes, thereby
14 affecting the functioning of the ecosystem at different scales and in different realms. Using a
15 simple model, we follow the dynamics of a limiting nutrient inside an ecosystem. Considering
16 trade-offs between aboveground and belowground functional traits, we study the effects of the
17 evolution of such strategies on ecosystem properties (amount of mineral nutrient, total plant
18 biomass, dead organic matter and primary productivity) and whether such properties are
19 maximized. Our results show that when evolution leads to a stable outcome, it minimizes the
20 quantity of nutrient available (following Tilman's R^* rule). We also show that considering the
21 evolution of aboveground and belowground functional traits simultaneously, total plant
22 biomass and primary productivity are not necessarily maximized through evolution. The
23 coupling of aboveground and belowground processes through evolution may largely diminish
24 predicted standing biomass and productivity (extinction may even occur), and impact the
25 evolutionary resilience (ie, the return time to previous phenotypic states) of the ecosystem in
26 face of external disturbances. We show that changes in plant biomass and their effects on
27 evolutionary change can be understood by accounting for the links between nutrient uptake
28 and mineralization, and for indirect effects of nutrient uptake on the amount of detritus in the
29 system.

30

31 **Key index words:** nutrient cycling, belowground-aboveground interactions, Tilman's R^*
32 rule, ecosystem functioning, plant evolution.

33

34 **Introduction**

35 Nutrient cycling is a key component of ecosystem functioning. It is strongly influential for
36 primary production and exerts a bottom-up control on the composition of food webs (i.e.,
37 primary producers, herbivores, predators) (Vitousek et al. 1997). Numerous plant traits (e.g.
38 nutrient uptake rate, biomass turnover, litter quality and influence on mineralization through
39 rhizosphere priming effect) influence the intensity of nutrient cycling rates (Chapin III et al.
40 2002). Such traits directly affect aboveground and belowground processes. For instance,
41 nutrient uptake rate and biomass turnover constrain aboveground biomass, while plant control
42 on mineralization can change belowground characteristics such as nitrogen or carbon
43 contents.

44 From a functional point of view (Chapin III et al. 2002) and, more recently from an
45 evolutionary point of view (Loeuille et al. 2002; Loeuille and Loreau 2004; Loeuille and
46 Leibold 2008; Boudsocq et al. 2011), the links between nutrient uptake rate and plant
47 individual biomass turnover have been largely investigated. For example, to take up more
48 mineral nutrient plants may produce more thin and short-lived roots or sustain a large
49 mycorrhizal network, providing organic matter in exchange for mineral nutrients. Such
50 strategies incur allocation costs, diverting energy from plant individual growth or
51 reproduction (e.g., Cheng & Gershenson 2007). Such allocation costs explicitly link
52 aboveground (plant individual growth) and belowground (mineralization activation)
53 processes. The novelty of the present work lies in the investigation of how such a link affects
54 the evolution of plant strategies and ecosystem functioning.

55 Considering such a coupling, evolution of plant traits simultaneously affects food webs that
56 are often separated, i.e. belowground and aboveground food webs. Reciprocal effects between
57 aboveground and belowground topic currently raises increasing interest (Zou et al. 2016) and
58 the plant compartment is central in understanding this interaction. Evolutionary dynamics

59 may lead to contrasted outcomes regarding the quantities of nutrient stocked aboveground
60 (proportional to total plant biomass) vs belowground (detritus) with important consequences
61 for the global dynamics of ecosystems. While total plant biomass determines the amount of
62 energy available for higher trophic levels aboveground, the amount of detritus influences the
63 total energy available to belowground detritivore food webs. In turn, available energy largely
64 impacts the length of food chains (Oksanen et al. 1981; Loeuille and Loreau 2005) and food
65 web stability (Rosenzweig 1971). Evolutionary dynamics associated with these traits thus
66 have far reaching implications.

67 Our goal is to go beyond the traditional focus of evolutionary functional models modelling
68 plant growth and mortality traits, by linking such traits to belowground processes such as
69 mineralization. We model the evolution of nutrient uptake rate, and its consequences for
70 nutrient turnover and mineralization due to allocation trade-offs. We then assess the
71 evolutionary consequences for ecosystem properties. The evolutionary outcome critically
72 depends on the shape of the trade-off functions, but we only find three qualitatively different
73 ecological outcomes: extinction of the plant population, continuous accumulation of nutrient
74 during evolution, or evolution toward stable ecosystem properties. While the ecological
75 model is based on a previous article (Boudsocq et al. 2011), our approach is novel in at least
76 two ways. First, it focuses on different traits, with an explicit focus on mineralization, thereby
77 linking evolution to nutrient acquisition and retention explicitly. This allows a coupling
78 between aboveground and belowground processes, providing a more integrative view of eco-
79 evolutionary dynamics of plant strategies. Second, by considering that evolution involves
80 existing links between four different traits (basic growth rate, competitive ability, nutrient
81 turnover and mineralization), while Boudsocq *et al.* (2011) (and most evolutionary models in
82 ecology) couple only two traits in trade-off functions. The multi-dimensionality of
83 evolutionary dynamics is a rising and important question in evolutionary ecology (Gilman et

84 al. 2012) and we hope that our work may help to understand its implications for the evolution
85 of plant strategies.

86 We focus on a restricted number of issues: How is the phenotypic composition of the plant
87 community modified through evolution? What are the ecosystem properties associated to
88 these evolutionary outcomes (amount of mineral nutrient, total plant biomass, dead organic
89 matter and primary productivity)? Are these properties maximized as a result of evolution?
90 We show that coupling aboveground and belowground processes strongly modifies predicted
91 dynamics, even in the case of the non-spatial model we employ here. The coupling can
92 enhance or reduce predicted standing biomass and productivity, affecting the evolutionary
93 resilience (i.e., the time it takes for evolutionary dynamics to go back to the selected strategy)
94 in the face of environmental perturbations (such as climate change, increase of fertilizers,
95 fires, erosion).

96

97

Methods

98 We model the dynamics of a limiting nutrient inside an ecosystem composed of three
99 compartments: inorganic nutrient (N), plants (P) and dead organic matter (D) (Figure 1). N , P
100 and D correspond to the quantity of limiting nutrient in each compartment (most usually,
101 nitrogen). While compartments are quantified in terms of limiting nutrient, we do not account
102 for plastic or evolutionary variations in stoichiometric ratios or in organism size, thus
103 implicitly assuming them constant, so we refer to P as plant biomass hereafter. Time variation
104 of nutrient stocks can be written:

$$\left\{ \begin{array}{l} \frac{dN}{dt} = I - l_N N - \frac{\beta N}{\delta + N} P + \alpha D \\ \frac{dP}{dt} = \frac{\beta N}{\delta + N} P - \gamma P \\ \frac{dD}{dt} = \gamma P - \alpha D - l_D D \end{array} \right. \quad (1)$$

105

106 Parameters β and δ define the plant growth rate using a classical Monod function. Primary
107 productivity ϕ is defined by the uptake term $\beta NP/(\delta+N)$. Parameter γ defines the turnover rate
108 of plant biomass. Through evolution and trade-offs (see below), traits β , γ and δ influence the
109 mineralization rate α . The model thus couples aboveground (eg, plant growth/production) and
110 belowground processes (nutrient uptake, mineralization) explicitly. Parameters describing
111 global inputs and outputs of nutrient are I and I_N, I_D respectively. The model is simple as it
112 focuses on one plant compartment with one limiting factor (a nutrient). Including other
113 density dependent effects (due to space or light competition) or community aspects (multiple
114 species) would of course make it more realistic. We do not account for such additional
115 components to keep the evolutionary dynamics tractable and focused on existing links
116 between aboveground and belowground processes. For more details on the parameters of the
117 model and parameter values, see Table S1.

118 *Relation between internal cycling rates – plant strategy trade-offs*

119 The model assumes that different aspects of plant life history–competitive ability, biomass
120 turnover, mineralization—are directly linked to intrinsic growth and reproduction due to
121 allocation constraints. Intrinsic growth and reproduction, being the rate of increase in plant
122 biomass when nutrient is not limiting, corresponds to β . Competitive ability, as measured by
123 the rate of growth when nutrient is rare, is directly (and negatively) linked to δ . Biomass
124 turnover is proportional to γ , and we consider this turnover to be either intrinsic (e.g., root or
125 leaf loss) or due to enemies (herbivores, pathogens, etc.). Mineralization is constrained by
126 parameter α . It embodies both intrinsic properties such as litter degradability and the
127 activation of decomposers (e.g., microbes) by the plant, through the release of activating
128 compounds.

129 To account for allocation costs, we propose to write parameters describing nutrient uptake and
130 recycling as: $(\alpha, \delta \text{ or } \gamma) = (k_1 * \beta + k_2)^g$ (see table 1 for the relationships and their biological

131 justifications). We use such functions because of their flexibility. They may be linear,
132 concave or convex depending on the value of exponent g . Such a flexibility is desirable,
133 because the shape of trade-off functions is usually not known empirically, but largely matters
134 for the outcome of evolutionary dynamics (de Mazancourt and Dieckmann 2004; Loeuille and
135 Loreau 2004).

136 Because of these trade-off functions, our model links aboveground and belowground
137 processes in a single evolutionary framework. Parameters β and δ for instance determines the
138 nutrient uptake (belowground), but also the increase in plant biomass (part aboveground, part
139 belowground). Parameter γ describes the loss of plant biomass (again, part aboveground, part
140 belowground) to the detritus compartment. Finally, α represents the belowground process of
141 mineralization.

142 *Adaptive dynamics of plant phenotypic traits*

143 We study the evolutionary dynamics of nutrient uptake β using the adaptive dynamics
144 methodology (Dieckmann and Law 1996; Geritz et al. 1998). The other traits are deduced
145 from the allocation trade-offs (Table 1). Because these functions are strictly monotonic,
146 choosing another trait as a basis instead of nutrient uptake β would produce similar results.
147 Adaptive dynamics model the evolution of phenotypic traits based on clonal reproduction,
148 leaving out the genetic basis, and assuming that evolutionary dynamics are sufficiently slower
149 than ecological dynamics. Although these hypotheses may seem restrictive, they allow a
150 thorough analytical study of selective regimes and of their consequences for ecological
151 systems. Evolution proceeds by the successive replacements of one phenotype by another, a
152 process shown to be similar to expected patterns of trait-based community assembly. While
153 the initial derivation of adaptive dynamics is strongly grounded in evolutionary perspectives,
154 results often extend to other types of adaptation (eg, changes in behaviour, plasticity: Abrams

155 2005). Evolution of nutrient uptake β is modeled using the canonical equation of adaptive
 156 dynamics:

$$157 \quad \frac{d\beta}{dt} = K\mu\sigma^2 P^0(\beta) \left(\frac{\partial W_{P_m}(\beta_m, \beta)}{\partial \beta_m} \right)_{\beta_m \rightarrow \beta} \quad (5)$$

158 where the fitness of the mutant β_m is deduced from its population dynamics:

$$159 \quad W_{P_m}(\beta_m, \beta) = \frac{1}{P_m} \frac{dP_m}{dt} \Big|_{P_m \rightarrow 0, P \rightarrow P^0} \quad (6)$$

160 and with K : scaling constant, μ : per unit biomass mutation rate, σ^2 : variance of the amplitude
 161 of mutations, P^0 : plant biomass at ecological equilibrium.

162 The selection gradient $\left(\frac{\partial W_{P_m}(\beta_m, \beta)}{\partial \beta_m} \right)_{\beta_m \rightarrow \beta}$ determines the direction of evolutionary

163 trajectories. Evolutionary singularities β^0 are obtained for $\left(\frac{\partial W_{P_m}(\beta_m, \beta)}{\partial \beta_m} \right)_{\beta_m \rightarrow \beta} = 0$.

164 The second derivatives of plant individual fitness with nutrient uptake β_m and β give the
 165 properties (invasibility and convergence) of evolutionary singularities (Geritz et al. 1998). A
 166 singularity is convergent provided:

$$167 \quad \left(\frac{\partial^2 W_{P_m}(\beta_m, \beta)}{\partial \beta_m^2} \right)_{\beta_m \rightarrow \beta \rightarrow \beta^0} + \left(\frac{\partial^2 W_{P_m}(\beta_m, \beta)}{\partial \beta \partial \beta_m} \right)_{\beta_m \rightarrow \beta \rightarrow \beta^0} < 0 \quad (7)$$

168 Convergence insures that selection will favor strategies closer to the singularity in its vicinity.

169 The strategy is non-invasible when:

$$170 \quad \left(\frac{\partial^2 W_{P_m}(\beta_m, \beta)}{\partial \beta_m^2} \right)_{\beta_m \rightarrow \beta^0} < 0 \quad (8)$$

171 Then, no mutant can invade at the evolutionary singularity. When both equations (7) and (8)
 172 are satisfied, β° is a continuously stable strategy CSS (Eshel 1983), noted β_{CSS} . Evolution
 173 stops once β_{CSS} is reached.

174 Because we have analytical expressions of the ecological equilibrium (N^0 , P^0 , D^0), it is
 175 possible to determine how evolution impacts ecosystem stocks and primary productivity. We
 176 compute their derivatives regarding nutrient uptake β and combine them with equation (5).

177 Let X° denotes one of these variables:

$$178 \quad \frac{dX^\circ}{dt} = \frac{\partial X^\circ}{\partial \beta} \frac{d\beta}{dt} \quad (9)$$

179 Results

180 *Impacts of evolution on system functioning*

181 We here summarize the main results. For detailed information, see appendix 2. Setting
 182 equations (1) to zero determines the position of the ecological equilibrium. A unique
 183 nontrivial equilibrium exists:

$$184 \quad \left(N^0 = \frac{\gamma \delta}{\beta - \gamma}, P^0 = \frac{\alpha + l_D}{\gamma} D^0, D^0 = \frac{I - l_N N^0}{l_D} \right) \quad (10)$$

185 While nutrient uptake β , biomass turnover γ and competitive ability δ influence all three
 186 compartments, mineralization α only influences P^0 .

187 Variables N , P and D being positive, it is necessary that:

$$188 \quad \beta > \gamma \left(1 + \frac{\delta l_N}{I} \right) \quad (11)$$

189 If this condition is satisfied, the equilibrium is also stable.

190 The fitness of a mutant is:

$$191 \quad W(\beta_m, \beta) = \frac{1}{P_m} \frac{dP_m}{dt} \Big|_{P_m \rightarrow 0} = \frac{\beta_m N^0(\beta)}{\delta(\beta_m) + N^0(\beta)} - \gamma(\beta_m) \quad (12)$$

192 Note that a direct implication of equation (12) is that the mutant can invade (ie, W is positive)

193 if and only if $N^0(\beta) > \frac{\gamma(\beta_m)\delta(\beta_m)}{\beta_m - \gamma(\beta_m)}$, which, given equation 10, can be rewritten

194 $N^0(\beta) > N^0(\beta_m)$. It follows that the mutant can invade only provided it leaves less nutrient at
195 equilibrium than the resident, following Tilman's R^* rule (Tilman 1982).

196 From (12), the selection gradient is:

197
$$\left(\frac{\partial W(\beta_m, \beta)}{\partial \beta}\right)_{\beta_m \rightarrow \beta} = \frac{N^0(\beta)(\delta(\beta) + N^0(\beta) - \beta\delta'(\beta))}{(\delta(\beta) + N^0(\beta))^2} - \gamma'(\beta) \quad (13)$$

198 Only two types of evolutionary dynamics can take place. (1) runaway evolution, nutrient
199 uptake β being always selected (figure 2a) or counterselected; (2) a β_{CSS} exists and evolution
200 eventually settles there, provided the CSS allows the existence of the system (ie, it satisfies
201 condition (11) and allows the positivity of equation (4a) (Table 1)). Following Boudsocq *et*
202 *al.* (2011), we propose to categorize these evolutionary outcomes depending on their
203 consequences for ecosystem functioning (for exact conditions, see appendix 3):

204 1) “Explosive R^* scenarios” (eg, figure 2A). In such scenarios, we have a continuous
205 evolution of traits that leads to ever-increasing plant biomass (hence "explosive"), while
206 mineral nutrient are minimized, in agreement with Tilman's R^* rule (hence " R^* "). Eventually,
207 crucial hypotheses of the ecological model will be violated, as another constraint (space, light,
208 water, alternative nutrient) will become limiting.

209 2) “Tragic R^* scenarios” (eg, figure 2B). In such scenarios, evolution selects for traits
210 that either continuously erode plant biomass and productivity, or lead the system out of the
211 range of existence (figure 2B), hence the "tragic". Inorganic nutrient is still minimized (hence
212 " R^* "). Note that such scenarios may happen either because runaway evolution continuously
213 erodes plant biomass, such that it may become vulnerable to demographic stochasticity, or
214 because β_{CSS} falls outside of the range of existence (equations 4a (Table 1) and 11).

215 3) “Realized R^* scenarios” (eg, figure 2c, 2d). In such instances, evolution leads to a
216 stable functional state in which plant biomass and productivity is positive (hence “realized”)
217 while inorganic nutrient is still minimized (hence “ R^* ”). Two situations are then possible:
218 either nutrient uptake β always increases through evolution, while nutrient stocks
219 asymptotically tend toward positive values or nutrient uptake β eventually settles at a CSS
220 value where ecosystem compartments have positive nutrient mass (figure 2c-d). In both cases,
221 the system reaches a stable and feasible functional state.

222 The examples shown on figure 2 can give some insights regarding the mechanisms at
223 hand for falling in one or another category (see also supplementary information for more
224 general results). The shape of trade-off functions is particularly critical in this regard.
225 Consider fitness gradient (13). It clearly underlies the crucial role of variations in biomass
226 turnover γ and competitive ability δ with nutrient uptake β as constraints for the direction of
227 evolution. If the costs in terms of competitive ability (increasing δ) or in terms of biomass
228 turnover (increasing γ) are not strong (constant or concave functions, figure 2a, see also
229 supplementary information), evolution of ever-increasing nutrient consumption β is predicted.
230 Such an increase in nutrient uptake β can either lead to explosive R^* (on the condition that P^0
231 continuously increases when nutrient uptake β increases, ie, mineralization α increases faster
232 than biomass turnover γ with nutrient uptake β), or to a tragic R^* (when, conversely, P^0 is
233 negatively affected by increases in nutrient uptake β). On the contrary, when evolution of β is
234 quite costly (ie, competitive ability δ or biomass turnover γ varies in a linear or convex
235 fashion with β), then a selected strategy (CSS) exists (figure 2b-d). The position of such a
236 selected strategy may be outside the range of existence of the system, a “tragic R^* ” scenario
237 (figure 2b). However, increasing basic mineralization (figure 2b vs 2c,d) enlarge the range of
238 existence and allows a realized R^* scenario (figure 2c,d).

239 *Are the functional properties (nutrient stocks and primary productivity) maximized through*
240 *evolution?*

241 Because evolution is based on individual fitness (equation 12), links with emergent ecosystem
242 properties can only be indirect. *A priori*, there is no reason to expect that evolution optimizes
243 the system in any way. Evolution however leads to systematic variations in the compartments
244 and fluxes within the ecosystem, depending on the evolutionary scenario.

245 For “Explosive R* strategies” (Figure 2a), standing plant biomass increases by definition
246 through evolution. Primary productivity also increases. The quantity of inorganic nutrient is
247 minimized while the dead organic matter compartment is maximized. Higher nutrient input (I)
248 or lower detritus outputs (I_D), increase the detritus compartment, plant biomass and
249 productivity. This global redistribution of nutrient, from the inorganic compartment to the
250 other compartments can be explained again from trade-off shapes. Because loss terms are
251 bounded (γ is of concave shape), and because mineralization α increases with the evolution of
252 higher nutrient uptake β , plants acquire increasing amounts of nutrient. In the case of
253 “Realized R* strategies” contrasted outcomes are possible. In runaway evolution instances,
254 inorganic nutrient is minimized, plant biomass, primary productivity and dead organic matter
255 are all maximized (Table S5). If a CSS is reached (Figures 2c & 2d), inorganic nutrient is
256 minimized through evolution but plant biomass and primary productivity are not
257 systematically maximized nor minimized. Compare figure 2c and 2d. Evolution optimizes
258 productivity when it comes at no costs in mineralization α (figure 2d), but such an
259 optimization is not observed when such costs exist (figure 2c). When α is independent from β
260 (figure 2d), the impact of evolution involves less dimensions (ie, impacts less compartments
261 directly), so that this result confirms that evolution is more likely to be optimizing when the
262 number of dimensions is reduced (Metz et al. 2008).

263 We stress that in CSS instances, final biomass and primary productivity always depends on
264 basal biomass turnover γ_0 . (Table S4). In terms of management, it suggests that external
265 disturbances (fire, pollution) not only directly impact ecosystem processes due to extra-
266 mortality, but also further deteriorate their functional state by affecting evolutionary
267 dynamics.

268 *Functional consequences of coupling aboveground and belowground traits*

269 First, note that fitness (equation 12) is independent of belowground mineralization trait α .
270 This happens because the nutrient consumption part of fitness only depends on the total
271 amount of inorganic nutrient, as fixed by the resident population. Our model makes mean-
272 field hypotheses, all mineral nutrient being equally accessible to all plant individuals.
273 Differences in mineralization then add to the nutrient pool, at the advantage of any individual
274 of the population, regardless of its phenotype. Changes in mineralization do not create any
275 relative fitness difference. Consequently, existing links between β and α do not affect the
276 selection of traits in our model. In spite of this conservative approach of mineralization
277 effects, the coupling of aboveground and belowground processes still impacts the ecological
278 consequences of evolution.

279 From an ecological point of view, the link between β and α modifies the plant biomass and
280 productivity obtained through the evolutionary dynamics. Consider a model that would ignore
281 the links between nutrient uptake β and mineralization α . From equation (10), it is easy to
282 show that equilibrium plant biomass is then always increasing with β , as D^0 increases with β .
283 Linking β and α makes the variations more complex. If the relationship between β and α is
284 positive, D^0 and α are both positively impacted by increases in β so that such evolutionary
285 dynamics strongly increase expected plant biomass. Similarly, for situations in which the
286 system settles at a given β_{CSS} , if the relationship between uptake and mineralization is positive
287 ($r > 0$), then increasing this effect parameter r will in turn increase mineralization α , thereby

288 increasing plant biomass and productivity (figure 3A). On the contrary, if the relationship is
289 negative, the coupling between aboveground and belowground processes moderates the
290 impacts of evolution on plant biomass and productivity or even reverses them (figure 4).
291 Although the exact magnitude of change depends on parameter values, these results suggest
292 that predictions that ignore links between growth rate and mineralization rate can be vastly
293 misleading. Consequences may be far reaching: standing biomass and primary productivity
294 largely affect ecosystem services and set the energetic basis and nutrient constraints for
295 related food webs.

296 Many current works link the functioning of plant communities to their phenotypic
297 states (Lavorel and Garnier 2002; Wright et al. 2004; Shipley et al. 2006). To understand the
298 future functioning of ecosystems under disturbances, it may therefore be interesting to
299 understand their stability in terms of phenotypic composition. To study this question, we
300 analyze the "evolutionary resilience" of our system as measured by the return time to the
301 initial phenotypic state following a disturbance. This measure of resilience is quite different
302 from (but complementary to) the one classically used in ecology, as it is based on an analysis
303 of evolutionary dynamics (trait variation) rather than on an analysis of the ecological
304 equilibrium. On figure 3B, we show that this evolutionary resilience depends on the coupling
305 between nutrient uptake and mineralization. This may be understood by accounting for
306 changes in plant biomass observed in figure 3A.

307 Changes in plant biomass have important consequences for the pace of evolutionary
308 dynamics, as larger plant populations lead to higher genetic variabilities. This is visible in
309 equation (5), where the rate of change of the trait is linked to plant compartment size through
310 the mutation process. Again, this has important, applied consequences. Consider a change in
311 the phenotypic composition of plants. The return time to the evolutionary equilibrium (ie,
312 evolutionary resilience) depends on the coupling between aboveground and belowground

313 processes (Figure 3B). Consider an external disturbance that creates additional mortality, e.g.,
314 changing basal biomass turnover γ_0 therefore modifying β_{CSS} . Depending on the strength of
315 the link between aboveground and belowground processes, evolution toward the new
316 evolutionary equilibrium may be fast or slow, hence affecting the robustness of ecosystem
317 functioning. Here, the return time is much longer, as plant biomass is strongly reduced by a
318 negative β - α relationship. We stress that the exact time associated with such evolutionary
319 dynamics is generally unknown (it depends on the selective pressures, trade-off shape, genetic
320 variability, generation time, etc), but the change in evolutionary resilience incurred by
321 coupling aboveground and belowground processes is qualitatively robust.

322 In order to broaden the results illustrated by figure 3, we investigate how r , the
323 impact of nutrient uptake β on mineralization α , affects plant biomass and evolutionary
324 resilience (figure 4), compared to a reference scenario for which no impact exists ($r=0$). The
325 left column assumes a negative impact (panels A & C), while the right column assumes a
326 positive impact (panels B & D). As intuitively expected, when nutrient acquisition β and
327 mineralization α are negatively correlated, plant biomass is decreased compared to the
328 reference scenario (panel A). This is simply because evolutionary gain on one side (say,
329 increase in nutrient uptake), is traded-off against nutrient availability on the other side
330 (mineralization). Conversely, when the two traits are positively correlated, plant biomass is
331 positively affected (panel B). We also show how such effects depend on two parameters of
332 well-known functional importance: nutrient input (e.g., eutrophication), and basic turnover
333 rate (e.g., fire, herbivory). Results show that the effects on plant biomass are exacerbated
334 when nutrient input increases, or when basic turnover decreases. When the impact on
335 mineralization allows for higher plant biomass (panel B & D), evolution is accelerated and the
336 system more resilient (negative values on panel D: return time is reduced). Results illustrated
337 by figure 4 clearly stress that to predict the effects of evolutionary dynamics on the

338 functioning and resilience of the system one needs to know how aboveground and
339 belowground processes are coupled. Such a link arguably depends on the species and
340 ecosystem considered (table 1).

341

342 **Discussion**

343 Consider a landscape made of multiple separated ecosystems, where local environmental
344 conditions may involve changes in the trade-off shapes (Schluter 1995). Our results suggest
345 that such variations in trade-off and variations in the coupling of belowground and
346 aboveground processes strongly affect the functioning of the system. Ultimately, associated
347 evolutionary dynamics can produce a range of behaviors, ranging from extinction to the
348 maintenance of a stable ecosystem, or even the unstable accumulation of plant biomass.

349 Regardless of the scenario, N^o is minimized through evolution. This is in agreement
350 with the R^* rule proposed by Tilman (1982). However, depending on the strength and the
351 existence of trade-off constraints, three qualitatively different evolutionary outcomes have
352 been identified: explosive R^* , tragic R^* and realized R^* strategies. This last outcome
353 corresponds to an evolutionary stable and convergent equilibrium where ecosystem
354 functioning critically depends on the coupling between aboveground and belowground
355 processes. Also, we have proved that except for explosive R^* strategies, plant biomass,
356 primary productivity and dead organic matter are not necessarily maximized. In explosive R^*
357 strategies, the model cannot predict the future state of the system as another constraint will
358 eventually come into play (instead of the considered limiting nutrient). Such scenarios are
359 nevertheless interesting, as they pinpoint cases in which evolution by itself may allow the
360 system to escape from one constraint to another, with important implications for predictions
361 and management.

362 Even if the belowground trait α determining mineralization does not directly influence
363 selected traits, it affects final biomass, productivity and evolutionary speed. When there is a
364 strong link between aboveground and belowground processes, all aboveground phenotypic
365 modifications cascade to constrain the energy allocated to belowground traits. Our results
366 suggest that this can have important impacts on associated ecosystem services such as soil
367 fertility or primary productivity. Several empirical works have suggested couplings between
368 aboveground and belowground processes. For instance, evolution of plant defenses slows
369 recycling processes (Grime et al. 1996; Whitham et al. 2003). Because the production of such
370 defenses often incurs a cost in terms of growth (Herms and Mattson 1992), variations of
371 defenses and their impacts on recycling relate well to the hypotheses of our model. A
372 continental-scale study incorporating 13 vastly different ecosystems in North-America shows
373 that investment in aboveground growth and biomass is linked to belowground processes such
374 as the composition and mineralization activities of soil microbes (Zak et al. 1994). In spite of
375 this increasing recognition that selections on aboveground and belowground traits are largely
376 related, few evolutionary models incorporate this link explicitly (though see Reynolds and
377 Pacala (1993); Gersani et al. (2001) for models of root competition and shoot/root ratios).

378 Our results have several important consequences in terms of conservation. First, local
379 selection can decrease plant populations and negatively affect its role in the overall ecosystem
380 functioning (in the case of tragic R^* outcomes). Such outcomes occur when the benefit of an
381 increase in nutrient uptake is constrained by a stronger cost in competition ability or survival.
382 Such results are similar to those of other evolutionary models (Parvinen 2005; Boudsocq et al.
383 2011). Our study also gives new perspectives on existing links between plant evolution and
384 ecosystem functioning. Runaway evolution occurs for concave trade-offs and population
385 decreases (tragic scenarios) with convex trade-offs when inputs of nutrient are high and
386 outputs are low. Evolutionary equilibrium is reached for convex trade-offs when inputs of

387 nutrient are low and outputs are high. Even though an explicit test of these patterns is hardly
388 possible because trade-off shapes are usually unknown, such dynamics correspond to
389 contrasted situations that happen in nature and are usually considered separately (see also
390 Boudsocq *et al.* (2011)).

391 It has often been postulated that evolution should maximize nutrient fluxes and
392 increase primary productivity (e.g., Lotka 1922; Odum & Pinkerton 1955; Roff 1992).
393 However, as shown by our study, taking into account unavoidable trade-offs and measuring
394 fitness at the individual level, there is no reason to expect such effects. Some empirical
395 studies that considered plant individual competition for resources have shown that primary
396 productivity is not always maximized (e.g., Rankin, Bargum & Kokko 2007), in agreement
397 with our results. Such negative relationships between community performance and individual
398 competitiveness also have important implications for the improvement of crop yield potential
399 in agricultural ecosystems (Denison 2012; Loeuille *et al.* 2013). Similarly, and contrary to
400 predictions by Lotka (1922), aboveground and belowground selected strategies do not
401 necessarily lead to tighter nutrient cycling.

402 Most works in plant community focus on either one trait or two traits linked by one
403 trade-off function. An early example corresponds to the classical r/K theory, which organizes
404 plant species along the growth/competitiveness trade-off (Pianka 1970). Other examples include
405 colonization/competition (Tilman 1994) or growth/defense trade-offs (Herms and Mattson
406 1992). Such a focus on one or two traits allows a degree of simplicity and a mechanistic
407 understanding of eco-evolutionary dynamics (Boudsocq *et al.* 2011). A danger, however, is
408 that it also tends to yield an adaptationist view of evolution that disregards the fact that
409 individuals have many more traits, linked by multi-dimensional constraints (Gould and
410 Lewontin 1979). Accounting for this complexity is a major challenge for evolutionary and
411 community ecology. Here, we link four traits through allocation trade-offs. In spite of this

412 added complexity and of the large number of trade-offs we tested, we have found some
413 robustness in our results as only three qualitative functional outcomes have been identified.
414 The multi-dimensional trade-off approach allows links with other multi-dimensional
415 evolutionary theories of plant strategies (Grime 1977; Southwood 1988). For instance, some
416 outcomes of our models (predicting a decrease in trait β), produce a syndrome of slow-
417 growing conservative strategy very similar to stress-tolerant strategies introduced by Grime
418 (1977).

419 In a context where databases of plant traits are systematically studied to predict the
420 effects of global changes and the variations in ecosystem services (Lavorel and Garnier 2002),
421 an important issue remains open. Plant species can be classified along a trade-off between
422 acquisition and conservation of the resource (Díaz et al. 2004). Though this is clear for
423 aboveground traits that define the leaf economic spectrum (Wright et al. 2004), such a
424 spectrum for root traits is not fully clear. Mechanistic models could in the future help to
425 predict (1) whether, (2) when evolution should lead to positive or negative correlations
426 between aboveground and belowground traits and (3) the consequences for ecosystem
427 functioning. Our result particularly suggests that resilience in trait composition strongly
428 depends on how mineralization is linked to other traits such as nutrient uptake or turnover.

429 Because we focus on this issue of evolutionary multidimensionality, the ecological
430 structure of our model is kept simple. Two extensions of this work would be particularly
431 valuable. The first is related to the spatial context. In our model, the mean field hypothesis
432 explains why mineralization is not present in the fitness definition we get from the present
433 model. Accounting for spatial structures allows for a benefit of higher mineralization through
434 local recycling (Barot et al. 2014) and nutrient compartment are then no longer minimized
435 through evolution (Barot et al. 2015). Another extension is to account for other functional
436 groups, as they crucially modify nutrient cycles. Herbivores affect nutrient spatial dynamics

437 through dispersal at meta-ecosystem scale (McNaughton 1979). Gravel et al. (2010) have
438 shown that spatial flows of material due to the nutrient diffusion or to plant or herbivore
439 dispersal heavily impact the functioning of ecosystems. In fact, most instances of spatial
440 flows of material involve higher trophic levels (e.g., McNaughton 1979; Helfield & Naiman
441 2001). In addition to changing nutrient constraints, incorporating higher trophic levels may
442 constrain coexistence among plant phenotypes through apparent competition (P^* rule, Holt et
443 al. 1994).

444 Here we have shown how trade-offs between belowground (mineralization) and
445 aboveground processes can determine ecosystem functioning in general, and more
446 particularly plant productivity and ecosystem resilience. It would be relevant to test
447 empirically the eco-evolutionary consequences of other trade-offs between belowground and
448 aboveground functions. For example, by assessing the allocation of carbon and mineral
449 resources to root exudates, roots, mycorrhizae and the aboveground system, or the allocation
450 of belowground and aboveground defences against herbivores. Beyond the acknowledgment
451 of various trade-offs, understanding such evolutionary dynamics, involving the coevolution of
452 aboveground and belowground systems can profoundly change our view on the management
453 of ecosystems.

454

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559 Table 1: Biological justification of trade-off functions used in the present work.

Traits considered	Relationship	Biological justification	References	Function used
δ vs β	positive	High growth rate when rare incurs a cost in terms of competitive ability	r-K Theory (McArthur and Wilson 1967; Pianka 1970)	$\delta = (a\beta + \delta_0)^{g_1}$ (2)
γ vs β	positive	-Fast growing species have high nutrient uptake and large turnover rate -Investment in defenses reduce turnover, but incurs costs in growth or reproduction	Eissenstat <i>et al.</i> (2000) Herms & Mattson (1992)	$\gamma = (m\beta + \gamma_0)^{g_2}$ (3)
α vs β	negative	-Activation of decomposers (eg, microbes) increases mineralization α but is costly in terms of growth and reproduction -production of tough tissues reduces mineralization	Cheng & Gershenson (2007) Whitham <i>et al.</i> (2003) Grime <i>et al.</i> (1996)	$\alpha = (-r\beta + \alpha_0)^{g_3}$ (4a)
	positive	-For fast growing plant species, increased nutrient content in tissue makes litter more easy to mineralize -Increased carbon input in soil may accelerate litter decomposition (priming effect)	Chapin (1980) Berendse (1994) Fontaine, Mariotti & Abbadie (2003)	$\alpha = (r\beta + \alpha_0)^{g_3}$ (4b)

560

561 **Figures caption**

562 Figure 1:

563 Modeled nutrient compartments and fluxes. Circles represent ecosystem nutrient
564 compartments: inorganic nutrient (N), plants (P) and dead organic matter (D). Arrows and
565 correspond to nutrient fluxes.

566

567 Figure 2:

568 Variation in the size of ecosystem compartments ($N^\circ, P^\circ, D^\circ$) and primary productivity (ϕ°)
569 depending on trait β . N° : solid line, D° : dashed line, P° : Long-dashed line, ϕ° : dotted line.

570 Arrows indicate the direction of evolution. Vertical solid grey lines show the boundary of
571 existence for the model. Grey dashed vertical lines indicate the value of the selected strategy.

572 Insets indicate variations of α, β, γ with β (trade-off functions, see table 1). a: “Explosive R*
573 strategy”, while increasing β is selected, plant biomass and primary productivity increase
574 continuously. Compartments and productivity are rescaled: N° ($\times 1000$), D° ($\times 50$), ϕ° ($\times 0.5$). b:

575 “Tragic R* strategy”, β converges to α_0/r , at which point rate mineralization is null.

576 Compartments and productivity are rescaled: N° ($\times 10$), D° ($\times 25$), ϕ° ($\times 2$). c-d: “Realized R*
577 strategy” β converges to the selected strategy. Compartments and productivity are rescaled:

578 N° ($\times 10$), D° ($\times 10$). c: no maximization of the primary productivity. d: maximization of the
579 primary productivity.

580 Figure 3:

581 (a) Variation of the plant biomass P° (solid line) and the primary productivity ϕ° (dashed line)
582 at the CSS depending on the strength of the impact of the evolution of β on belowground
583 processes, r . β is fixed at the CSS value. A positive α - β relationship is assumed (eq 4b (Table

584 1)) (b) Variation of the evolutionary speed of β depending on whether coupling (dashed lines)

585 exists or not (solid lines) between aboveground and belowground processes. β_{CSS} is equal to

586 14.426. A negative α - β relationship is assumed (eq 4a (Table 1)). Parameters values: $K=1$;
587 $\mu=0.0001$; $\sigma=0.0001$.

588

589 Figure 4:

590 Variations in plant standing biomass (A, B) and resilience of the eco-evolutionary equilibrium
591 (C,D) when nutrient input I and basic turnover rates γ_0 vary, depending on the impact of
592 nutrient acquisition on mineralization rates (negative (see eq 4a (Table 1)): A & C; positive
593 (see eq 4b (Table 1)): B & D). In each panel, variations are represented as differences with a
594 reference no-coupling scenario where $r=0$ (ie, effect on plant biomass $\Delta P=(P_r)-(P_{r=0})$; effect
595 on return time $\Delta\tau=(\tau_r)-(\tau_{r=0})$), P standing for the plant biomass at the evolutionary
596 equilibrium, and τ for the return time to the evolutionary equilibrium following a disturbance
597 of 5%. Lighter shades correspond to higher values. Numbers on contours in panels are
598 expressed in thousand on panel A & C, and in million on panel B & D. Parameters values:
599 $K=1$; $\mu=0.0001$; $\sigma=0.0001$.

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604 **Figure 1**

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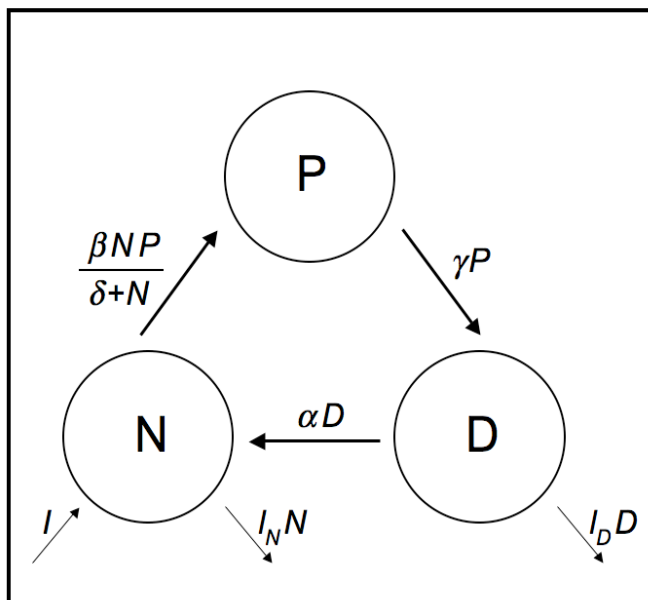


Figure 2:

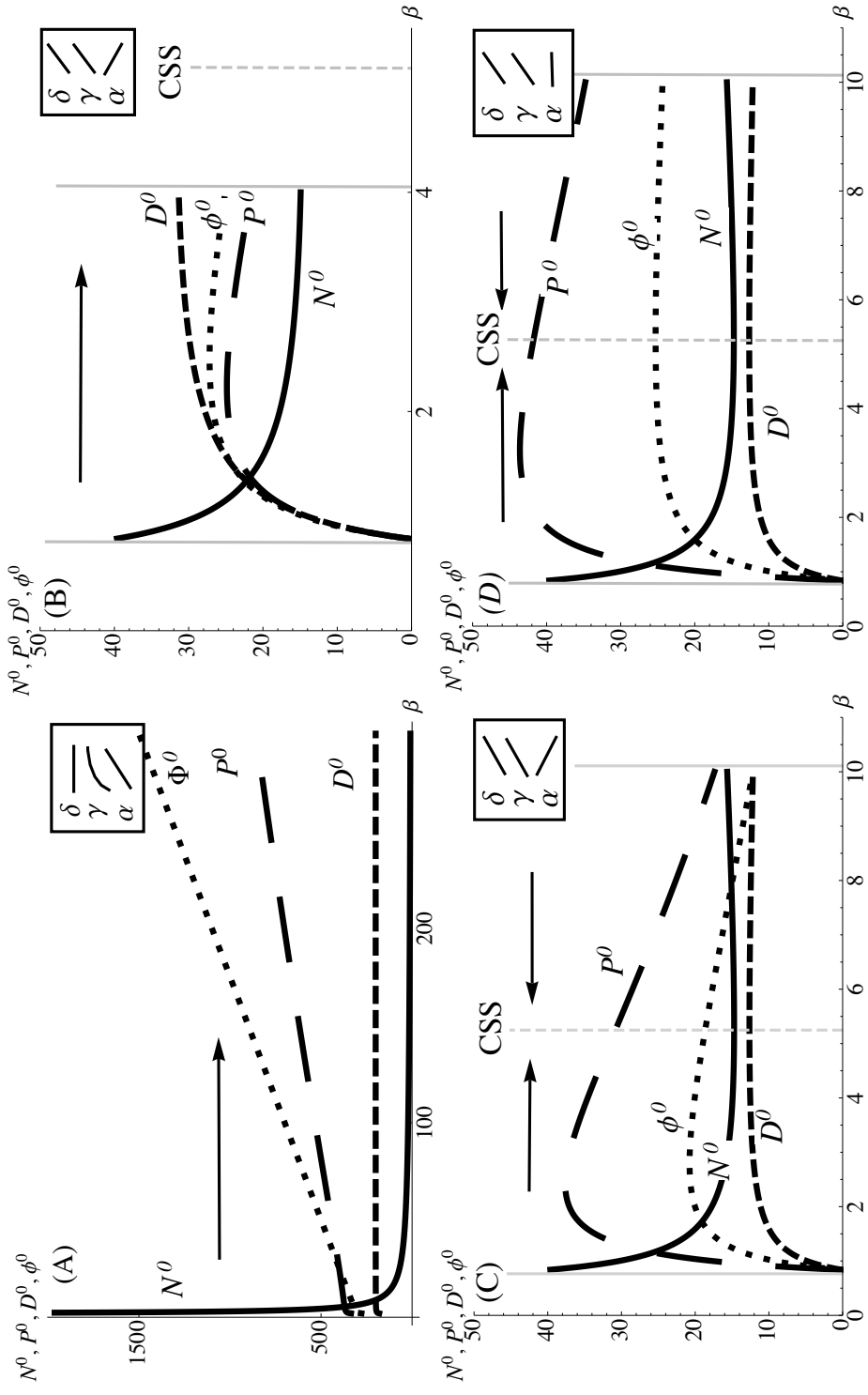
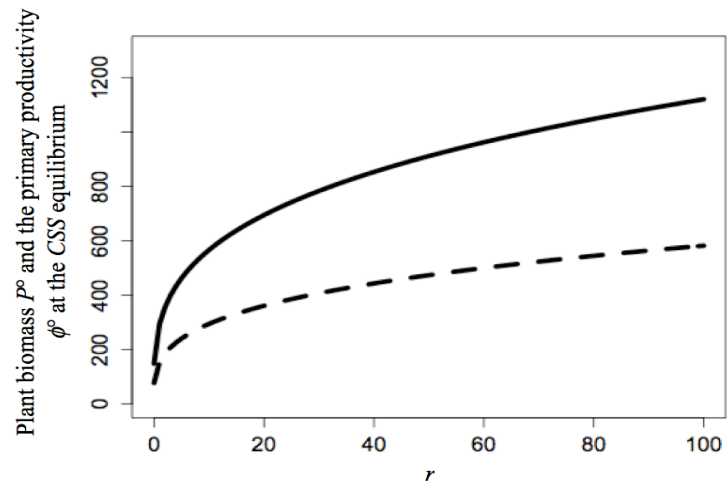


Figure 3:

(a)



(b)

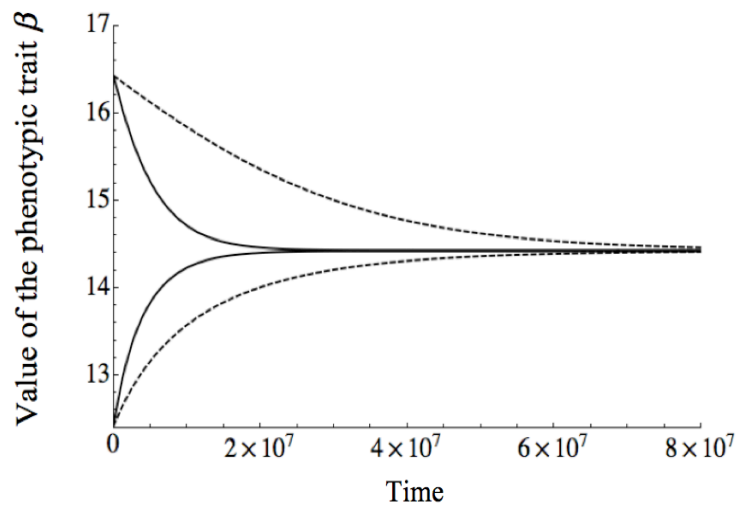


Figure 4

