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# 1 Evolution of nutrient acquisition: when space matters

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## 10 Summary

11 **1.** Evolution of nutrient acquisition by plants should depend on two forces: local competition is  
12 based on the capacity to exploit the local nutrient resource, and regional competition is based on  
13 the capacity to occupy the whole landscape through seed production and dispersal.

14 **2.** We build a spatially-explicit simulation model where a limiting nutrient is recycled in each  
15 local patch of a lattice by individual plants. The model includes both local and regional  
16 competition.

17 **3.** Heterogeneity in nutrient availability and dispersal limitation mitigate the effect of  
18 competition for the local nutrient resource and allow the evolution of lower rates of nutrient  
19 uptake. Our spatially explicit model suggests that evolution in richer ecosystems selects  
20 "expensive" strategies (high acquisition, low conservation of resources) compared to poor  
21 ecosystems.

22 4. Low rates of nutrient acquisition can be considered as a form of altruism because they leave  
23 more resource available for other individuals. Our model thus suggests that the influence of  
24 spatial processes on the evolution of altruism is pervasive and is linked to key aspects of  
25 ecosystem functioning.

26 5. Because our model both includes regional and local competition, evolution does not minimize  
27 the availability of mineral nutrient, though evolution or species replacement is often thought to  
28 minimize the availability of nutrient. Taken together, our work confirms that the interplay  
29 between local and regional competition is critical for the evolution of plant nutrient strategies  
30 and its effect on ecosystem properties.

31 **Key words:** nutrient acquisition, nutrient conservation, spatial model, local vs. regional  
32 competition, evolution of altruism, spatial heterogeneity, dispersal, plant traits, eco-evolutionary  
33 dynamics, nutrient enrichment.

## 34 Introduction

35 Spatial heterogeneity in the availability of mineral nutrients and the spatial structure of plant  
36 populations must be taken into account to predict the evolution of plant strategies to acquire  
37 mineral nutrients because: (1) Individual growth and reproduction depend on the local  
38 availability of the mineral resource. (2) A mutant can establish locally only competing with  
39 locally growing individuals and not with the whole resident population. (3) The ability of a  
40 mutant to establish locally depends on the modifications it may impose to the local nutrient  
41 availability even if its density is negligible at the population scale, i.e. the local success of a  
42 mutant depends on positive or negative feedbacks it builds with its local environment. These

43 points emphasize local processes, but these processes only take place because the mineral  
44 resource and plant individuals are spatialized.

45         Studies of adaptive plant strategies have already pointed out the importance of nutrient  
46 heterogeneity and the ecological and evolutionary influences of two scales of competition  
47 (Loreau 1998; Barot *et al.* 2014). (1) Within-cycle competition (local competition throughout  
48 this paper) arises between strategies/individuals that are locally competing for the same nutrient  
49 resource (thus sharing the same material cycle). (2) Between-cycle competition (regional  
50 competition throughout this paper) arises between strategies/individuals growing spatially-apart,  
51 therefore not directly competing for the same local resources (not sharing the same material  
52 cycle) but competing regionally for space and access to the regional pool of nutrient. While local  
53 competition is based on the capacity to exploit the local nutrient resource (which for example  
54 involves the investment into a dense root system), regional competition is based on density-  
55 dependence and the capacity to occupy the whole landscape (e.g. the whole surface of a plot, all  
56 local patches of a spatial model) through the production of seeds and their dispersal. Thus, these  
57 two scales of competition may lead to conflicting selection pressures because the strategy (i.e.  
58 the resource allocation) maximizing the exploitation of a local resource and its accumulation into  
59 the biomass is likely to be different from the strategy maximizing the number of individuals and  
60 their distribution over the whole landscape (Loreau 1998; Barot *et al.* 2014). This is likely to  
61 impede the minimization of nutrient availability predicted by the  $R^*$  theory (Tilman 1982). Most  
62 evolutionary models of nutrient cycling are mean-field models (Loeuille, Loreau & Ferrière  
63 2002; Menge, Levin & Hedin 2008; Boudsocq, Barot & Loeuille 2011) and only predict the  
64 evolutionary consequences of local competition. On the one hand, some models have addressed  
65 the evolution of nutrient cycling related traits in a spatial context (de Mazancourt, Loreau &

66 Dieckmann 2001; Loeuille & Leibold 2008). However, these studies do not directly aim at  
67 assessing the respective influence of local and regional competition. On the other hand, many  
68 models address the interplay between local and regional competition but without addressing  
69 explicitly evolutionary issues (e.g. Tilman 1994; Gravel *et al.* 2010) (see also a review  
70 Fagerström & Westoby 1997).

71 At least two types of process should influence the respective importance of local and  
72 regional competition on the evolution of nutrient acquisition by plants. First, the primary  
73 producer capacity to colonize new patches through dispersal influences the intensity of local  
74 competition between local mutants and the resident population through density-dependant  
75 effects. Second, lateral fluxes of nutrient between patches may decrease the heterogeneity in  
76 nutrient availability. Hence, both dispersal and nutrient fluxes between patches mitigate the  
77 effect of regional competition (Loeuille & Leibold 2008). Through these processes, the whole  
78 nutrient resource tends to be shared at the regional scale between all individuals and between the  
79 various nutrient strategies they may display. This should increase the strength of selective  
80 pressures for the uptake of local resources and should thus push towards the evolution of higher  
81 rates of nutrient acquisition. Taken together, a mean-field model should lead to the evolution of  
82 higher rates of mineral nutrient acquisition than a spatial model and, in a spatial model,  
83 increasing seed dispersal and homogenizing fluxes of mineral nutrients should lead to the  
84 evolution of higher rates of nutrient acquisition.

85 To assess the influence of local and regional competition and the impact of seed dispersal  
86 and homogenizing nutrient fluxes on the evolution of nutrient acquisition we developed a  
87 spatially-explicit model where primary producers compete locally for a heterogeneously  
88 distributed limiting nutrient and regionally through seed production and their dispersal. Our

89 model is based on two previously published models: (1) a mean-field analytical model  
90 (Boudsocq, Barot & Loeuille 2011) that predicts the evolution of nutrient acquisition, (2) a  
91 spatially-explicit and individual-based model (Barot *et al.* 2014) that predicts the evolution of  
92 plant capacity to control the mineralization of their litter. In the non-spatial model (Boudsocq,  
93 Barot & Loeuille 2011), the fitness of a mutant only depends on the immediate balance between  
94 acquisition and turnover of nutrient and this balance does not depend on inputs of nutrients to the  
95 ecosystem, nutrient losses from the ecosystem or mineralization. Thus the mutant fitness cannot  
96 depend on its capacity to modify its local environment. In contrast, in our spatial model, the  
97 fitness of a mutant depends, through the building of local feedback loops and through  
98 heterogeneity in nutrient availability, on complex interactions between all nutrient fluxes and the  
99 mutant strategy for nutrient acquisition.

100 Taken together, the characteristics of our model should allow the evolution of the  
101 diversity of plant strategies observed in different environments (Grime 2001; Craine 2009) and,  
102 in particular, to conservative (low rate of nutrient uptake and efficient conservation of the  
103 nutrient within the biomass) and acquisitive plants (high rate of nutrient uptake and poor  
104 conservation of the nutrient within the biomass). Using this model we test the following  
105 hypotheses: (1) The evolution of nutrient acquisition strategies depends on the relative strength  
106 of local versus regional competition and spatial processes that influence this strength: dispersal  
107 and lateral nutrient fluxes. More specifically, we expect increasing dispersal and lateral fluxes of  
108 nutrients to select for higher rates of nutrient uptake. (2) The evolution of nutrient acquisition  
109 depends on the nutrient richness of the ecosystem and all fluxes influencing this richness.  
110 Namely, a gradient of nutrient enrichment leads to the evolution of Stress-tolerators with low  
111 rates of nutrient uptake at the nutrient-poor end of the gradient and Competitors with high rates

112 of nutrient uptake at the other end of the gradient (Chapin III 1980; Grime 2001; Loeuille &  
113 Loreau 2004). (3) Ecosystem properties should be impacted by the evolution of nutrient  
114 acquisition. It has been proposed that local resource competition should allow the species that  
115 minimizes resource availability to exclude all other species and this should maximize the  
116 biomass of primary producer and primary production (Tilman 1982; Loreau 1998). On the  
117 contrary regional competition should impede this minimization of the availability of mineral  
118 nutrients (Loreau 1998).

## 119 **Description of the Model**

### 120 MODEL STRUCTURE

121 The model (see Fig. S1-A and Fig. S1-B and the list and description of parameters in Table 1) is  
122 a spatial and individual-based version of a mean-field model of recycling of a limiting mineral  
123 nutrient (Boudsocq, Barot & Loeuille 2011) between plants ( $P$ ), dead organic matter ( $D$ ) and  
124 mineral nutrient ( $N$ ). The limiting nutrient can virtually be any of the mineral nutrients that limit  
125 primary production (generally nitrogen or phosphorus). Note that this previous model was not  
126 individual-based. Here, the spatial features and the dynamics of individuals are modelled as in  
127 Barot et al.'s model (Barot *et al.* 2014). Sessile terrestrial plants interact locally with soil nutrient  
128 cycling and disperse through space by seed production. Our model thus couples a nutrient  
129 cycling model with a spatial demographic model.

130 Space is described as a lattice of contiguous patches, each containing two abiotic nutrient  
131 compartments ( $D$ ,  $N$ ) and one nutrient compartment for each locally growing plant individual ( $P_i$ ,  
132 Fig. S1-A). Nutrient cycling and individual plant growth is modelled through the integration of a  
133 system of differential equations in each patch. There is one equation for each plant individual so



134 that demographic events lead to the suppression (death) and addition (birth) of equations. We  
135 assume that one time step corresponds to one year so that demographic events occur at the end of  
136 each year whereas nutrient cycling is calculated on a sub-year basis through the integration of the  
137 differential equations.

138 The model takes into account three types of ecological processes that are detailed next  
139 section: (1) within-patch nutrient dynamics, (2) between-patch nutrient dynamics, corresponding  
140 to fluxes of mineral nutrient that tend to homogenize resource availability and (3) demography of  
141 plants. In order to assess the importance of space in the observed model dynamics, we compare  
142 simulations with a 400 patch lattice to others where the lattice has only one larger patch (non-  
143 spatial model). Individual plants growing in the same patch are competing for mineral nutrient  
144 within this patch, as implemented in many spatial and individual-based models of plant growth  
145 and competition (Czárán & Bartha 1992; Berger *et al.* 2008). There is a single source of  
146 heterogeneity: the interaction between nutrient cycling and plant demography, and the  
147 underlying stochasticity. More mineral nutrient is transiently available in local patches that  
148 contain fewer individual plants or a lower total biomass of plants.

149 The size of the patches has to be chosen appropriately, so that they only host a relatively  
150 low number of plant individuals that belong to the same competitive neighbourhood. More  
151 precisely, this number of individuals and patch size are determined by inputs of mineral nutrient  
152 and organic matter (see below). For example, patches of one square meter (as implemented in  
153 our simulation, see below) would be relevant to model small and short-lived herbaceous plants  
154 for which about 50 individuals may be thought as locally competing. If plants live longer,  
155 individuals may grow larger (e.g. perennial bunch grasses) and only a few individuals compete

156 for the same nutrient resource in each one-square-meter patch. The different parameters of the  
 157 model and their default values are given in Table 1.

## 158 ECOLOGICAL DYNAMICS

159 *Within-patch nutrient dynamics:* In each patch (subscript  $j$ ), the limiting nutrient is recycled  
 160 within the patch (through the absorption of mineral nutrient, the turnover of the biomass of the  
 161 primary producer, and the mineralization of the resulting dead organic matter) and each patch  
 162 receives inputs and loses nutrients. In contrast to the original non-spatial model, each patch of  
 163 the lattice can be occupied by several individuals (index  $i$ , nutrient content  $P_{j,i}$ ) that compete for  
 164 the local pool of mineral nutrient (thus the number of differential equations for each patch varies  
 165 with the number of individuals growing in the patch). We assume that plants are identical for all  
 166 parameters except their rate of nutrient uptake ( $u_{Nj,i}$ ) and their rate of nutrient turnover to the  
 167 ecosystem ( $d_{Pj,i}$ ). There is a rate of mineralization ( $m_D$ ) and a rate of nitrogen fixation ( $f_P$ , if the  
 168 limiting nutrient is nitrogen and if the plant is able to fix nitrogen). Nutrient inputs in its organic  
 169 matter form ( $R_D$ ) and in its mineral form ( $R_N$ ) are independent of the size of the nutrient pools.  
 170 Nutrients diffuse out of the ecosystem through fixed rates, respectively  $l_P$ ,  $l_D$ , and  $l_N$  for the P, D  
 171 and N compartments respectively.  $l_P$  denotes losses of nutrients through fires in terrestrial  
 172 ecosystems. Dead organic matter is lost through erosion and leaching ( $l_D$ ). Mineral nutrients are  
 173 lost through leaching and denitrification ( $l_N$ ). For each patch of the lattice, the equations thus  
 174 become:

$$175 \quad \frac{dP_{j,i}}{dt} = u_{Nj,i} N_j P_{j,i} - (d_{Pj,i} + l_P - f_P) P_{j,i} \quad (\text{for each individual } i \text{ of local patch } j),$$

$$176 \quad \frac{dD_j}{dt} = \sum_i d_{Pj,i} P_{j,i} + R_D - (m_D + l_D) D_j,$$

$$177 \quad \frac{dN_j}{dt} = m_D D_j + R_N - \left( \sum_i u_{N_j,i} P_{j,i} + l_N \right) N_j + H (\bar{N} - N_j). \text{ (Eq 1)}$$

178 *Between-patch nutrient dynamics.* These dynamics correspond to processes leading to an  
 179 homogenization of nutrient content between patches. To do so, the quantity  $H (\bar{N} - N_j)$  is  
 180 added to the derivative of the  $N_j$  value of each patch.  $H$  varies between 0 and  $+\infty$  and  $\bar{N}$  is the  
 181 mean nutrient availability calculated over all patches of the lattice. Nutrient availability tends to  
 182 homogenize at the regional scale when  $H$  increases (all local  $N_j$  values are equal to  $\bar{N}$ ), i.e.  
 183 higher  $H$  values correspond to a higher rate of nutrient mixing among patches. When  $H$  increases  
 184 the mineral resource is more and more shared between all individuals of the population and  
 185 competition for nutrient acquisition is no longer purely local, i.e. between individuals growing in  
 186 the same patch. Hence, studying the effect of  $H$  constitutes a theoretical experiment to determine  
 187 the influence of the way the mineral resource is shared at the population scale.

188 *Demography.* Discrete demographic events, i.e. mortality and reproduction, occur at the  
 189 end of every year (Fig. S1-B). While  $d_{P_j,i}$  denotes the rate of nutrient turnover of the primary  
 190 producer because of the death of parts of the primary producer (death of roots and leaves,  
 191 exudate production),  $\mu$  denotes individual mortality (Table 1). The amount of nutrient contained  
 192 in dead individuals is transferred to the local dead organic matter compartment ( $D_j$ ).

193 At the end of each year, individuals in the lattice may produce seeds that are dispersed on  
 194 the lattice. Parameter  $\rho$  is the percentage of the stock of nutrient contained in each individual at  
 195 the end of the year that is allocated to seed production.  $\gamma$  is the quantity of nutrient in a seed. The  
 196 number of seeds produced by the individual  $i$  (in patch  $j$ ) is thus the largest previous integer of  
 197  $P_{j,i} \rho / \gamma$ . Seed dispersal is modelled by moving each seed and creating a new individual with a

198 nutrient content  $\gamma$  in another patch. We choose a random angle (between 0 and 360°) to  
 199 determine the direction of dispersal and consider that the dispersal distance from the centre of the  
 200 patch of the mother primary producer follows a centred normal distribution (mean=0) with  
 201 standard deviation  $\sigma$  (if the distance is negative 180° is added to the original angle): when  $\sigma$   
 202 increases dispersal distance tends to increase. There is no habitat choice. For simplification,  
 203 production of seed starts at age 1 year for individuals that are large enough at this age  
 204 ( $P_{j,i} \rho > \gamma$ ). Note that individuals falling under a threshold nutrient stock (i.e. the nutrient content  
 205 of a seed) are also considered to die.

## 206 EVOLUTIONARY DYNAMICS

207 As in the original non-spatial model (Boudsocq, Barot & Loeuille 2011), we study the evolution  
 208 of a trait  $s$  that can be considered as the investment of the primary producer into the acquisition  
 209 of mineral nutrient. The trait  $s$  can be either negative or positive. When  $s$  increases, both the  
 210 investment into nutrient acquisition and nutrient turnover increase. For any individual  $i$  of trait  
 211  $s_{j,i}$ , the nutrient uptake rate and the nutrient turnover of the primary producer are linked via the  
 212 following trade-off equations:

$$213 \quad u_{Nj,i} = u_{N0} e^{bs_{j,i}},$$

$$214 \quad d_{Pj,i} = d_{P0} e^{cs_{j,i}}.$$

215 This trade-off is justified by several complementary mechanisms (see details in the Discussion).  
 216 For example, the more a plant invests into the development of its root system, the uptake and  
 217 assimilation of nutrients, the less resource are allocated to maintenance and defence functions.  
 218 Indeed, the existence of trade-offs between nutrient uptake and anti-herbivore defences have

219 been documented (Herms & Mattson 1992; Mauricio 1998). This mechanism should increase the  
220 turnover of the plant biomass and losses of mineral nutrients contained in this biomass.

221 The relation between  $b$  and  $c$  (real-valued positive parameters) determines the strength of  
222 the trade-off: if  $b < c$ , the trade-off function displaying  $d_{Pj,i}$  as a function of  $u_{Nj,i}$  is convex  
223 (curving up); otherwise if  $b > c$  the trade-off function is concave (curving down); if  $b=c$  the  
224 nutrient turnover increases linearly with the uptake capacity. Taken together,  $b$  determines the  
225 benefit of the investment into nutrient uptake ( $s$ ), while  $c$  determines its cost. Because of this  
226 trade-off,  $s$  can be viewed either as a strategy of nutrient capture or a strategy of nutrient  
227 turnover. Since the model is not analytically tractable, numerical simulations have to be run.  
228 Each new seed has a probability  $p_m$  of being a mutant for  $s$ , in which case the size of the mutation  
229 is drawn from a centred normal distribution with a standard deviation  $m$ .

230 The capacity of a strategy to persist or to invade a resident strategy, and thus evolutionary  
231 dynamics, depend (1) on the effect of the investment into nutrient acquisition on individual  
232 growth in local patches, (2) the capacity to disperse from patch to patch through seed production.  
233 Thus selection occurs via the growth of individuals during each time step (the growth of each  
234 individual depends on its strategy for nutrient acquisition), and via demography at the end of  
235 each time step: the size of individuals having a non-optimal uptake strategy decreases and reach  
236 the threshold under which they die, i.e. the size of a seed (see above in the section about  
237 demography), and larger individuals produce more seeds.

## 238 IMPLEMENTATION

239 A simulation platform has been implemented in the Java programming language (1.5). The  
240 integration of the differential equations is based on the classical fourth-order Runge-Kutta

241 method with an integration step  $\Delta t = 0.1$  year. In our simulations  $H$  varies between 0 (no  
242 homogenization) and 10 (strong homogenization). Fig. S6 shows that  $H=10$  leads to a null  
243 standard deviation of nutrient availability (perfect homogenization of the mineral nutrient  
244 availability).

245 Parameters chosen for nutrient cycling are adapted from Woodmansee et al. (1981) who  
246 describe nitrogen cycling in a temperate grassland (see Table 1). Unless stated in figure captions  
247 (main text and the supplementary material) we keep these parameter values. We consider one  
248 square meter wide patches. Unless stated, the primary producer is considered to be a short-lived  
249 plant. For mutations we always used  $p_m = 10^{-4}$  and  $m = 0.05$ . The grid size is always 20 X 20  
250 patches except in one occasion (hereafter one-patch model) where only one patch is modelled but  
251 increasing accordingly input of mineral nutrients and organic matter (X400) to support the same  
252 total biomass as in the 20X20 patch model. This corresponds to a shift between 400 one square  
253 meter patches to one single 400 m<sup>2</sup> patch. The lattice is wrapped on a torus to handle seed  
254 dispersal. Variables following normal distribution (dispersal distance and mutation size) are  
255 simulated using the polar method (Marsaglia & Bray 1964).

256 Simulations are initialized with a single seed in each patch and a fixed amount of mineral  
257 nutrient (20 dg m<sup>-2</sup>). 0 is always chosen as a starting value for  $s$ . Preliminary analyses have  
258 shown that results are not sensitive to these initial conditions in terms of ecological ( $N^*$ ,  $D^*$ ,  $P^*$ )  
259 and evolutionary equilibriums ( $s^*$ ), provided that these conditions allow for the initial survival of  
260 the plant species.

261 Results (Fig. 1, 2) are presented using locally-weighted polynomial regressions to  
262 compute trend lines. All figures were produced using R 2.10 (2010). In the main text we focus on  
263 the evolutionary effects of inputs of mineral nutrient to the ecosystem. Fig. S3 displays results

264 concerning the effects of the rate of mineral nutrient losses from the ecosystem and the rate of  
265 dead organic matter mineralization that also influence the availability of mineral nutrient.

## 266 **Results**

### 267 EVOLUTIONARY DYNAMICS

268 The simulation model leads to the same types of evolutionary outcomes as the analytical model  
269 of Boudsocq et al. (2011): (i) a stable evolutionary equilibrium (Continuously Stable Strategy or  
270 CSS, Eshel 1983), (ii) a tragedy-of-the common scenario (Hardin 1968) where the primary  
271 producer compartment asymptotically decreases, while uptake and productivity increase,  
272 eventually leading to the primary producer extinction, and (iii) an accumulation of nutrient in all  
273 compartments due to an efficient recycling (inputs of nutrient are higher than outputs). In this  
274 last case, the model predicts the infinite accumulation of the limiting nutrient, which is not  
275 realistic but denotes cases where evolution drives the primary producer to switch to an other  
276 limiting factor. Evolutionary branching does not occur.

277 In particular, when the benefit of the investment in nutrient acquisition is low in  
278 comparison to its cost ( $b < c$ ) and when inputs of nutrient to the primary producer compartment  
279 (nitrogen fixation) are equal or lower to its rate of mineral nutrient turnover ( $f_p \leq l_p$ ),  
280 simulations lead to a CSS we note  $s^*$ . Simulations with identical parameter values always lead  
281 qualitatively to the same results, but the inherent stochasticity of the model (mortality, seed  
282 dispersal and mutations) may lead to small differences in the  $s^*$  observed at the end of a  
283 simulation. All the results displayed hereafter correspond to CSS cases because of the parameter  
284 values we choose ( $f_p = l_p = 0$ ). To insure the meaningfulness of the results we always run  
285 simulations long enough to reach the evolutionary equilibrium (400000 time steps while 100000

286 time steps are generally enough to reach the CSS). Fig. S2 displays an example of evolutionary  
287 dynamics leading to an evolutionary equilibrium together with the corresponding pairwise-  
288 invisibility plot (Geritz *et al.* 1998) that proves that this is a case of CSS. Such dynamics have  
289 been simulated for each point of Fig. 1 and 2.

290 Besides, for any set of ecological parameters leading to a CSS and for any  $s$  value, the  
291 ecological dynamics leads to equilibrium values for  $P$  (sum of  $P_i$  of all individuals in a local  
292 patch),  $N$  and  $D$  when their values are averaged over all patches of the model (see also Fig. S2).  
293 We use the same notation (\*) for these ecological equilibriums ( $P^*$ ,  $N^*$ ...) at the evolutionary  
294 equilibrium (CSS,  $s^*$ ).

#### 295 CAPACITY TO ACQUIRE NUTRIENTS AT THE EVOLUTIONARY EQUILIBRIUM

296 Consistent with our predictions, the homogenization of mineral nutrient and the dispersal  
297 capacity of the primary producer increase the evolved primary producer capacity for nutrient  
298 acquisition (Fig. 1).

299 The evolved capacity for nutrient acquisition ( $s^*$ ) increases with inputs of mineral  
300 nutrient to the ecosystem ( $R_N$ ) whatever the trade-off shape (Fig. 2 A), the individual mortality  
301 (Fig. 2 B), the intensity of mineral nutrient homogenization (Fig. 2 C), or the dispersal capacity  
302 (Fig. 2 D). The less restrictive the trade-off (increasing  $b$  values), the higher the evolved  $s^*$   
303 values. For increasing individual mortality rates the amplitude of the effect of nutrient inputs on  
304 the evolved nutrient acquisition becomes higher. As in Figure 1, homogenization of mineral  
305 nutrient and seed dispersal increases the evolved capacity for mineral nutrient acquisition. This  
306 effect of nutrient homogenization disappears for high inputs of mineral nutrients. In other words,  
307 the evolved capacity for nutrient acquisition always increases with nutrient inputs but this effect  
308 is weaker when nutrient homogenization increases. The non-spatial model (only one patch) leads



309 to a much higher value ( $s^*=0.77$ , Fig. 2 C) of the capacity for nutrient acquisition than the  
310 maximum rate of nutrient homogenization and a very efficient seed dispersal ( $s^*=0.27$ , Fig. 1).  
311 Perfect homogenization brought by the non-spatial model (one patch) leads to a higher evolved  
312 capacity for nutrient acquisition than the mere homogenization ( $H=10$ ) of mineral nutrient  
313 availability (Fig. 2 C). In the case of perfect homogenization, inputs of nutrient no longer impact  
314 the evolved capacity for nutrient acquisition.

315         Increasing the mineralization rate and decreasing the rate of mineral nutrient loss from  
316 the ecosystem have the same effect on the evolution of nutrient acquisition as increasing nutrient  
317 inputs (Fig. S3).

#### 318 ECOSYSTEM PROPERTIES AT THE EVOLUTIONARY EQUILIBRIUM

319         Figure 3 describes the ecological effect of the investment into nutrient acquisition ( $s$ ) and  
320 nutrient inputs ( $R_N$ ) on the average availability of mineral nutrient and the mean size of the  
321 primary producer compartment (for each combination of  $R_N$  and  $s$ , the model is run till an  
322 ecological equilibrium is reached but without allowing evolution). There is always a unique  $s$   
323 value that minimizes the mean  $N$ , or maximizes the mean  $P$ , for each  $R_N$  value. However, the  
324 values that minimize  $N$  and maximize  $P$  are always distinct. On the same figure is plotted the  
325 outcome of the evolution of  $s$  for each  $R_N$  value. Evolution neither minimizes  $N$  nor optimizes  $P$ .  
326 Similarly, evolution does not maximize primary production (results not shown). The difference  
327 between the evolved  $N^*$  value and the lowest possible  $N^*$  value increases with nutrient  
328 enrichment (Fig. 3, see also confirmation in Fig. S4).

329 **Discussion**330 SPATIALIZATION AND LOW HOMOGENIZING FLUXES ALLOW FOR THE  
331 EVOLUTION OF ALTRUIST NUTRIENT STRATEGIES

332 Increasing dispersal and lateral fluxes of nutrient simultaneously homogenizes the availability of  
333 the mineral resource and increases the evolved capacity for nutrient acquisition at the CSS ( $s^*$ ).  
334 This happens because these two processes mitigate the influence of regional competition and  
335 increase the evolutionary influence of local competition for a shared mineral resource, which  
336 tends to push towards less altruist strategies, i.e. towards the evolution of higher uptake rates of  
337 this resource. This interpretation is detailed below and is supported by three converging lines of  
338 researches: (1) models and experiments showing that heterogeneity in resource availability and  
339 spatial structuration of populations promote the evolution of altruism (Lion & van Baalen 2008;  
340 Bachmann *et al.* 2013), (2) the framework of the tragedy of the common that shows that  
341 competition for a common resource pushes towards the evolution of higher rates of consumption  
342 of this resource (Rankin, Bargum & Kokko 2007), (3) researches suggesting that a low rate of  
343 resource consumption can be considered as altruist (Pfeiffer, Schuster & Bonhoeffer 2001; Kreft  
344 2004; Burtsev & Turchin 2006).

345       It is logical that increasing dispersal and increasing resource homogeneity lead to  $s^*$   
346 values closer to the ones obtained for the non-spatial model (only one patch) where only local  
347 competition occurs. The non-spatial model, resource homogenization, and efficient dispersal lead  
348 to high  $s^*$  values because competition for a shared resource favours strategies that increase the  
349 acquisition of the resource (Rankin, Bargum & Kokko 2007). In the non-spatial model, the  
350 resource is fully shared by all individuals, while with homogenizing fluxes of nutrient the  
351 resource is only partially shared. In the same vein, when dispersal ability increases, plants with

352 alternative competing strategies are more likely to compete for the same local resource in the  
353 same patches. In the non-spatial model and in the fully-homogenized version of the model the  
354 mineral resource is fully-shared by all individuals, but the former case leads to much higher  $s^*$   
355 values. Indeed, in the non-spatial model, only local competition for the nutrient acts as a  
356 selective pressure unaltered by any spatial process while, in the homogenized models, mutants  
357 are locally selected by local competition but still have to invade the whole population, which  
358 requires producing seeds and dispersing them, thus involving regional competition.

359 Our evolutionary results reveal the essence of the tragedy of commons (Rankin, Bargum  
360 & Kokko 2007): competition for a shared nutrient resource drives the evolution towards higher  
361 rates of resource use thereby forbidding the maximization of collective properties (e.g.  
362 population biomass). Such a scenario has already been pointed out for roots and soil resources  
363 (Gersani *et al.* 2001; Craine 2006). A low rate of resource or social good acquisition is  
364 considered as a form of altruism since it leaves more resource available for other individuals  
365 (Burtsev & Turchin 2006; Rankin, Bargum & Kokko 2007). This follows classical definitions of  
366 altruism (Hamilton 1963; West, Griffin & Gardner 2007): having a low rate of nutrient uptake  
367 deprives a plant of an available resource, and can thus be considered as costly, while this benefits  
368 to other plants for which more resource is available. As in all cases of evolution of an altruist  
369 trait, the obvious cost of the altruist trait must be counterbalanced by indirect fitness benefits  
370 (West, Griffin & Gardner 2007). In our model, such indirect benefits emerge from the interaction  
371 between spatial variations in resource availability and dispersal processes. As such, our results  
372 are consistent with other observations of the emergence of altruism due to spatial structure (Kerr  
373 *et al.* 2006; Bachmann *et al.* 2013).

374 Our results can therefore be interpreted in terms of evolution of altruism and are  
375 consistent with the established finding that it is promoted by heterogeneity, low dispersal and  
376 spatial isolation of strategies (Lion & van Baalen 2008). This is also consistent with the fact that  
377 low dispersal increases the impact of kin selection and facilitates group selection (Lion & van  
378 Baalen 2008) that are also known to foster the evolution of altruism (Nowak 2006). Indeed, in  
379 our model, the mixture of regional and local competition allows for the apparition of selection at  
380 the scale of local patches. Evolution of altruism has often been studied from the point of view of  
381 social interactions (Ferrière & Michod 1995). Our results and others on the evolution of bacteria  
382 (Pfeiffer, Schuster & Bonhoeffer 2001), predators (Goodnight *et al.* 2008) and parasites  
383 (Haraguchi & Sasaki 2000) suggest that the influence of spatial processes on the evolution of  
384 altruism is pervasive and that many key aspects of ecosystem functioning should be analysed  
385 through this prism.

#### 386 NUTRIENT ENRICHMENT SELECTS FOR HIGHER RATES OF RESOURCE 387 ACQUISITION

388 In our spatial model, increasing nutrient inputs to the ecosystem (Fig. 2), increasing the  
389 mineralization rate and decreasing the rate of nutrient loss from the ecosystem (Fig. S3) lead to  
390 the evolution of higher rates of nutrient acquisition. These three parameters influence three  
391 features in interactions along the eco-evolutionary dynamics implemented in the model: the  
392 mean availability of mineral nutrient, the variability in this availability and the number of  
393 individual plants in each patch. Two arguments support the important role played by  
394 heterogeneity in nutrient availability and the number of individuals in a patch: First, in the mean-  
395 field analytical model (Boudsocq, Barot & Loeuille 2011) and in the non-spatial version of our  
396 simulation model (only one patch), the evolutionary effect of resource enrichment disappears. In

397 our spatial model, individuals with a higher rate of nutrient uptake benefit more from this  
398 strategy, on the average, if the heterogeneity in nutrient availability is low. Indeed, in a patch  
399 with a low nutrient availability a higher rate of nutrient uptake leads for an individual to a low  
400 increase in the nutrient acquired by this mutant that nevertheless pays a high cost for this  
401 increase in terms of nutrient turnover because of the trade-off. Second, we have shown that  
402 homogenizing fluxes affect the evolution of the investment into nutrient acquisition because they  
403 modulate the respective influence of local and regional competition, which is an other way to  
404 state that they modulate the number of individuals that are locally competing for the same  
405 resource. Thus, the evolved investment into nutrient acquisition should increase with the mean  
406 number of individuals in each patch, i.e. in each competitive neighbourhood, as with  
407 homogenizing fluxes.

408 This general rationale is supported by complementary results. An important difference  
409 between the spatial and non-spatial models is that spatial models allow for heterogeneity in  
410 nutrient availability. In our simulation model this heterogeneity is sustained by the stochasticity  
411 in plant demography. For example, if several individuals die at the same time in a patch, more  
412 mineral nutrient is likely to be locally available (more organic matter to be mineralized and less  
413 biomass to take up mineral nutrients). Thus, the local dynamics of nutrient pools are a permanent  
414 succession of transient dynamics (see Fig. S5). This allows an increase in nutrient inputs ( $R_N$ ), an  
415 increase in the mineralization rate ( $m_D$ ) and a decrease in the rate of nutrient loss from the  
416 ecosystem ( $l_N$ ) to modify the average mineral nutrient availability and the spatial and temporal  
417 variability in this availability (see Fig. S6 for nutrient inputs). On the contrary, in the analytical  
418 non-spatial model, nutrient availability is kept at an equilibrium that does not depend on nutrient  
419 inputs, mineralization or the rate of mineral nutrient loss from the ecosystem (see formula for the

420 ecological equilibrium, Boudsocq, Barot & Loeuille 2011). Fig. S6 shows that at the ecological  
421 scale (the acquisition of mineral nutrient is not allowed to evolve) the variability in the  
422 availability of mineral nutrient always decreases with inputs of mineral nutrient while the mean  
423 availability of mineral nutrient may increase or decrease with these inputs. Moreover, at the  
424 evolutionary equilibrium, the number of individuals by patch also always increases with nutrient  
425 inputs (see Fig. S7).

426 While it is beyond the objective of this article to fully disentangle the ecological and  
427 evolutionary feedbacks between local resource availability, its heterogeneity and the local  
428 density of plants, a way to study these feedbacks is to disrupt them. Fig. S8 shows that  
429 constraining the maximum number of individuals to one individual reverses the effect of nutrient  
430 inputs: increasing nutrient inputs decreases the evolved investment into nutrient acquisition. This  
431 suggests that: (1) When a maximum of one individual by patch is allowed, increasing nutrient  
432 inputs leads to the evolution of lower rates of nutrient uptake because more resource becomes  
433 available for a single individual and because lower rates of uptake allow absorbing large quantity  
434 of nutrient. (2) When the number of individuals by patch is allowed to increase due to an  
435 increase in nutrient inputs (see S6 and S7), higher uptake rates evolve precisely because the  
436 number of individuals sharing the local resource increases. These results, the comparison  
437 between the spatial and non-spatial models and the effects of homogenizing fluxes confirm that  
438 heterogeneity in nutrient availability and local density in competitors determine the evolutionary  
439 effects of nutrient enrichment. This general interpretation is parsimonious: the effects of nutrient  
440 enrichment, seed dispersal, and heterogeneity in nutrient availability would all be linked to the  
441 way these processes modulate the balance between local and regional competition and the  
442 number of individuals sharing the same local mineral resource. When nutrient inputs increase,

443 the number of locally competing individuals increases, which leads to a stronger evolutionary  
444 influence of local competition, and a stronger selection for nutrient acquisition, as when seed  
445 dispersal or homogenizing fluxes of nutrient increase. In both cases (homogenizing fluxes and  
446 nutrient enrichment), the local pools of mineral nutrient are more shared or shared among more  
447 individuals.

#### 448 EVOLUTION OF ACQUISITIVE AND CONSERVATIVE PLANTS

449 One of our main conclusions is that, whatever the underlying mechanisms, when nutrient  
450 resource is not fully shared by all competitors and is heterogeneously distributed, nutrient  
451 enrichment drives the evolution towards higher rates of nutrient acquisition. Because of the  
452 trade-off between nutrient acquisition and nutrient turnover in primary producers, this also  
453 means that strategies more conservative for nutrient evolve in nutrient poor ecosystems.  
454 Moreover, our rate of nutrient acquisition is analogous to a relative growth rate (rescaled by the  
455 availability of nutrient). Consequently, our results are consistent with Grime's theory about the  
456 evolution of terrestrial plants in nutrient-rich and nutrient-poor ecosystems: Competitors (i.e.  
457 acquisitive plants) have evolved high relative growth rates in nutrient-rich ecosystems, while  
458 Stress-tolerators (i.e. conservative plants) have evolved lower relative growth rates and lower  
459 nutrient turnovers in nutrient-poor ecosystems (Grime 1977; Grime 2001).

460 Our model is too simple to predict specific traits of low- and high- nutrient plants such as  
461 shoot root-ratio, root length or defences against herbivores. Similarly, it does not take into  
462 account the interactions between competition for light (i.e. carbon) and nutrient (see above).  
463 However, the generality of our model uncovers fundamental aspects of the evolutionary  
464 consequences of competition for a limiting but recycled resource: (1) The trade-off we  
465 implement is the most fundamental one concerning the management of a resource by an

466 organism. How efficiently does the organism capture the resource? How long is it able to  
467 conserve it? (2) The existence of this trade-off that constrains the evolution of acquisitive and  
468 conservative plants is supported by several documented mechanisms. First, the investment into  
469 nutrient acquisition may reduce the investment into defences against herbivores and protective  
470 structures (Herms & Mattson 1992). Note that this suggests that our results also give an  
471 evolutionary support for plants in nutrient-poor environments to be more defended against  
472 herbivores (Coley, Bryant & Chapin 1985). Second, plants that absorb large amounts of mineral  
473 nutrient tend to have higher nutrient concentrations in their biomass, which decreases the  
474 longevity of roots and leaves and leads to stronger herbivore attacks (Eissenstat *et al.* 2000; Silla  
475 & Escudero 2004; Endara & Coley 2011). Third, increasing the capacity to uptake mineral  
476 nutrients requires increasing the biomass of roots and especially of thin roots that have a short  
477 life-span. These three mechanisms should increase the turnover of plant biomass and the  
478 turnover of the nutrients contained in this biomass. Taken together, our results give some  
479 evolutionary support for the existence of a root economic spectrum (Reich & Cornelissen 2014)  
480 that parallels the leaf-economic spectrum (Wright *et al.* 2004).

481 We have shown that the evolution of nutrient acquisition depends on individual mortality:  
482 the evolutionary effect of nutrient enrichment depends on longevity, and the higher the longevity  
483 the less sensitive the evolved investment into nutrient acquisition to nutrient availability. The full  
484 interpretation of this result goes beyond the objectives of this article, but this confirms that  
485 nutrient acquisition strategies should interact with life-history traits (e.g. individual mortality,  
486 investment into reproduction, age at first reproduction, seed size, dispersal...). Together, they  
487 modulate the influence of local and regional competition and influence plant capacity to  
488 conserve mineral nutrients (e.g. long-lived plants conserve mineral nutrients longer than



489 annuals). Our framework could thus allow testing further the evolutionary background of plant  
490 functional classifications that also involve plant life-histories (Grime 2001; Craine 2009). This  
491 would require studying the joint evolution of functional and demographic traits and should lead  
492 to the evolution of ruderals –the third strategy of Grime's CSR theory– that have not appeared in  
493 our present model (see for example in Bornhofen, Barot & Lattaud 2011).

#### 494 IMPACT OF EVOLUTION ON MINERAL NUTRIENT AVAILABILITY

495 That evolution does not maximize the biomass of the primary producer is caused, as in  
496 the original mean field analytical model (Boudsocq, Barot & Loeuille 2011), by the basic  
497 functioning of selection: selection is based on the per capita growth rate of mutants and not on  
498 the ultimate biomass or primary productivity. The non-minimization of the evolved average  
499 nutrient availability ( $N^*$ ) contradicts both the non-spatial evolutionary model (Boudsocq, Barot  
500 & Loeuille 2011) and Tilman's  $R^*$  theory (Tilman 1982). This influential theory suggests that  
501 the ecological dynamics of species replacement due to competition for a limiting single resource  
502 should lead to the exclusion of all species but the one that reduces the most the mineral resource  
503 availability at equilibrium. Our new result must stem from the combination of local and regional  
504 competition and the impeding of the minimization of nutrient availability by regional  
505 competition (Loreau 1998). Indeed, local competition is only based on plant capacity to absorb  
506 mineral nutrient while regional competition requires plant individuals to be large enough and to  
507 be able to invest enough resource into seed production and seed dispersal. Local competition  
508 thus tends to select for high rates of nutrient uptake while regional competition tends to select, in  
509 a density-dependent way, for lower rates of nutrient uptake allowing plants to be larger and to  
510 invest more into seed production. Besides, homogenization of the availability of the mineral  
511 resource and an efficient dispersal increase the influence of competition for the mineral resource

512 because these processes drive this resource to be more evenly distributed among individual  
513 plants and the strategies they represent. Therefore, homogenization of the resource and seed  
514 dispersal decrease the difference between the evolved availability of mineral nutrient and the  
515 lowest possible availability of mineral nutrient (Fig. S4), this difference being caused by regional  
516 competition. As aquatic systems are supposedly more homogeneous than terrestrial systems, our  
517 results might explain why most conclusive positive tests of the  $R^*$  theory have been achieved in  
518 aquatic systems (Miller *et al.* 2005) and very few, apart from Tilman's initial papers (Tilman &  
519 Wedin 1991; Wedin & Tilman 1993), in terrestrial systems.

## 520 CONCLUSION

521 Our results about the evolution of nutrient acquisition in a spatial context and former results  
522 about the evolution of plant capacity to control mineralization (Barot *et al.* 2014) support each  
523 other and are complementary. Since mineralization does not impact individual fitness directly,  
524 but only through a modification of the availability of the mineral resource, higher mineralization  
525 cannot evolve at all in a non-spatial model. On the contrary, nutrient acquisition directly impacts  
526 individual fitness so that spatial processes only modify the evolution of nutrient acquisition  
527 predicted by the non-spatial model (Boudsocq, Barot & Loeuille 2011). However, in both cases  
528 the relative influence of local and regional competition determines the evolutionary dynamics  
529 and leads to comparable results: (1) In Barot *et al.* (2014) homogenization (through seed  
530 dispersal or homogenizing fluxes of nutrient) leads to the evolution of lower mineralization rate  
531 while in the present work homogenization leads to the evolution of higher rates of nutrient  
532 uptake. (2) In Barot *et al.* (2014) nutrient enrichment leads to lower mineralization rates while in  
533 the present work it leads to higher rates of nutrient uptake. (3) Both in Barot *et al.* (2014) and the  
534 present work, the mixture of local and regional competition does not lead through evolution to

535 the maximization of the plant biomass or the minimization of the availability of the mineral  
536 nutrient. We contend here that a low rate of nutrient uptake can be considered as an altruist  
537 strategy because it leaves more mineral nutrient available to other plants (see above and a  
538 classical definition, Hamilton 1963). Considering a high rate of mineralization as an altruist  
539 strategy is probably even more obvious because it directly increases the availability of the  
540 mineral resource for all plants of the local patch, while the plant that increases mineralization is  
541 the only one to bear the cost of this increase in mineralization (the plant losses more nutrient).  
542 With this joint interpretation of low rates of nutrient uptake and high rates of mineralization as  
543 altruist strategies the results of the present work and the model by Barot et al. (2014) are fully  
544 consistent. The higher the influence of local competition the less altruist the evolved strategy: the  
545 evolved rate of mineral nutrient acquisition becomes higher and the evolved decomposition rate  
546 lower. Similarly, an increase in nutrient inputs pushes plants towards less altruist strategies  
547 probably because an increase in nutrient inputs tends to increase the local densities in  
548 competitors (see above).

549 Starting from a very simple and general analytical model based on plant biomass we have  
550 added some realistic features of plant competition: interaction between local and regional  
551 competition and some simple features of plant demography. The resulting model remains general  
552 and theoretical. Some features of the model may appear as unrealistic, but our work has paved  
553 the way to the implementation of many other influential mechanisms to test the robustness of our  
554 results: (1) plasticity in the investment into nutrient acquisition depending on nutrient availability  
555 and local density of competitors (Cahill *et al.* 2010), (2) more refine functions for nutrient uptake  
556 and local competition (see for example results in Raynaud & Leadley 2004), (3) implementation  
557 of more realistic lateral nutrient fluxes corresponding to particular mechanisms (e.g. impact of

558 herbivores) and interactions between lateral fluxes of mineral nutrient and dead organic matter  
559 (Gravel *et al.* 2010), (4) more realistic life-cycles to represent particular plant types (e.g. size  
560 dependent survival, age at first reproduction, different seed sizes), (5) coevolution between  
561 nutrient acquisition and life-history traits such as the investment into seed production or dispersal  
562 (Craine 2009; Suzuki & Kimura 2011), (6) different shapes of trade-off (de Mazancourt &  
563 Dieckmann 2004) between nutrient acquisition and nutrient turnover. In particular, while our  
564 model always leads to the selection of a single nutrient uptake strategy, point (2) and the use of  
565 an uptake function increasing with biomass with a downward curvature (Rastetter & Ågren  
566 2002) should allow the coexistence of various strategies and may thus lead to the diversification  
567 of the strategy of nutrient acquisition through evolutionary branching (Geritz *et al.* 1998).

568 In conclusion, the merit of our study is to link demographic processes, functional  
569 processes, evolution and ecosystem properties, which still constitutes a very open research  
570 avenue (Fussmann, Loreau & Abrams 2007). This allows us to link theories that are usually  
571 developed independently, e.g. theories about the evolution of altruism and evolutionary impact  
572 of spatial processes (Lion & van Baalen 2008) vs. the existence of distinct plant strategies  
573 depending on resource availability (Grime 2001). In particular, while ecosystem ecology is not  
574 prone to evolutionary interpretations, we suggest that many aspects of ecosystem functioning are  
575 linked to the evolution of altruism.

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707 **Supporting information**708 **Figure S1.** General graphical description of the spatial model709 **Figure S2.** Example of evolutionary dynamics710 **Figure S3.** Effect of the mineralization rate ( $m_D$ ) and the rate of mineral nutrient loss from the  
711 ecosystem ( $l_N$ ) on the evolution of nutrient acquisition ( $s^*$ )712 **Figure S4.** Joint effect of the capacity for nutrient acquisition ( $s$ ) and the inputs of mineral  
713 nutrient ( $R_N$ ) on the availability of mineral nutrient at the ecological equilibrium ( $N^*$ ) for four  
714 combinations of dispersal and lateral nutrient fluxes715 **Figure S5.** Examples of ecological dynamics in one patch showing temporal variations in the  
716 availability of mineral nutrient and the number of plant individuals717 **Figure S6.** Ecological effects of nutrient inputs on the mean and standard deviation of the  
718 equilibrium nutrient availability and the number of plant individuals in each patch719 **Figure S7.** Evolutionary effect of inputs of mineral nutrient ( $R_N$ ) on the local density of plants720 **Figure S8.** Effect of the inputs of mineral nutrient ( $R_N$ ) on the evolution of nutrient acquisition  
721 ( $s^*$ ) when only one individual is allowed to survive in each patch

722 Table 1: Model parameters.

Parameter type	Symbol	Default values	Definition
Nutrient recycling within a local patch	$d_{P0}$	0.275 yr <sup>-1</sup>	Initial rate of plant nutrient turnover through root and leaf turnover
	$m_D$	0.0766 yr <sup>-1</sup>	Mineralization of dead organic mater
	$u_{N0}$	1.43 dg <sup>-1</sup> m <sup>2</sup> yr <sup>-1</sup>	Initial uptake of mineral nutrient
Inputs of nutrient	$R_D$	2 dg m <sup>-2</sup> yr <sup>-1</sup>	Mineral atmospheric deposition
	$R_N$	1.8 dg m <sup>-2</sup> yr <sup>-1</sup>	Organic atmospheric deposition
	$f_P$	0 yr <sup>-1</sup>	Symbiotic nitrogen fixation
Losses of nutrient	$l_P$	$l_P, 0$ yr <sup>-1</sup>	Loss of nutrient from the ecosystem because of fires or human exportation of biomasses
	$l_D$	0.038 yr <sup>-1</sup>	Loss of dissolved organic matter or litter from the ecosystem
	$l_N$	0.05 yr <sup>-1</sup>	Nutrient leaching from soils, denitrification
Nutrient fluxes between patches	$H$	0 yr <sup>-1</sup>	Homogenizing lateral fluxes of nutrient
Demographic parameters	$\mu$	0.5	Individual mortality
	$\gamma$	0.3 g	Nutrient content of a seed
	$\rho$	0.1	Percentage of the nutrient stock of plant individuals allocated to seed production
	$\sigma$	2 m	Standard deviation of the centred normal distribution that determines seed dispersal distances
Trade-off parameters	$c$	4	Costs of the investment into nutrient acquisition
	$b$	3.5	Benefits of the investment into nutrient acquisition

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725 Figure 1. Effect of the spatial homogenization of the mineral nutrient resource ( $H$ ) on the  
726 evolved capacity for nutrient acquisition ( $s^*$ ) for different dispersal capacities ( $\sigma$ ). A point is  
727 missing for  $\sigma=0.5$  and  $R_N=0$  because these parameters lead to a non-viable population. See Table  
728 1 for parameter values.

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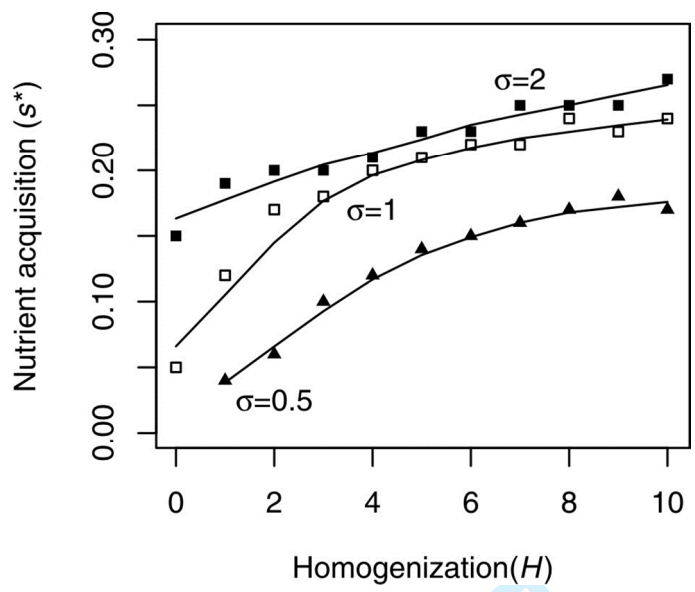
730 Figure 2. Effect of the inputs of mineral nutrients ( $R_N$ ) on the evolved capacity for nutrient  
731 acquisition ( $s^*$ ), as a function of four cofactors: (A) the trade-off parameter  $b$ . (B) individual  
732 mortality  $\mu$ , (C) homogenization of the availability of the mineral resource  $H$  (in this case “1  
733 patch” denotes non-spatial simulations with only one patch), (D) efficiency of dispersal ( $\sigma$ ). See  
734 Table 1 for parameter values.

735

736 Figure 3. Contour plots of the joint effect of the capacity for nutrient acquisition ( $s$ ) and the  
737 inputs of mineral nutrients into the ecosystem ( $R_N$ ) on (A) the mean availability of mineral  
738 nutrient ( $N$ ) and (B) the mean size of the primary producer compartment ( $P$ ). The thick solid  
739 lines denote the position of (A) the minimum  $N$  value, (B) the maximum  $P$  value for each  $R_N$   
740 value. The dots and the dashed lines denote the evolved capacity for nutrient acquisition ( $s^*$ ) for  
741 each  $R_N$  value. See Table 1 for parameter values.

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743 Fig 1



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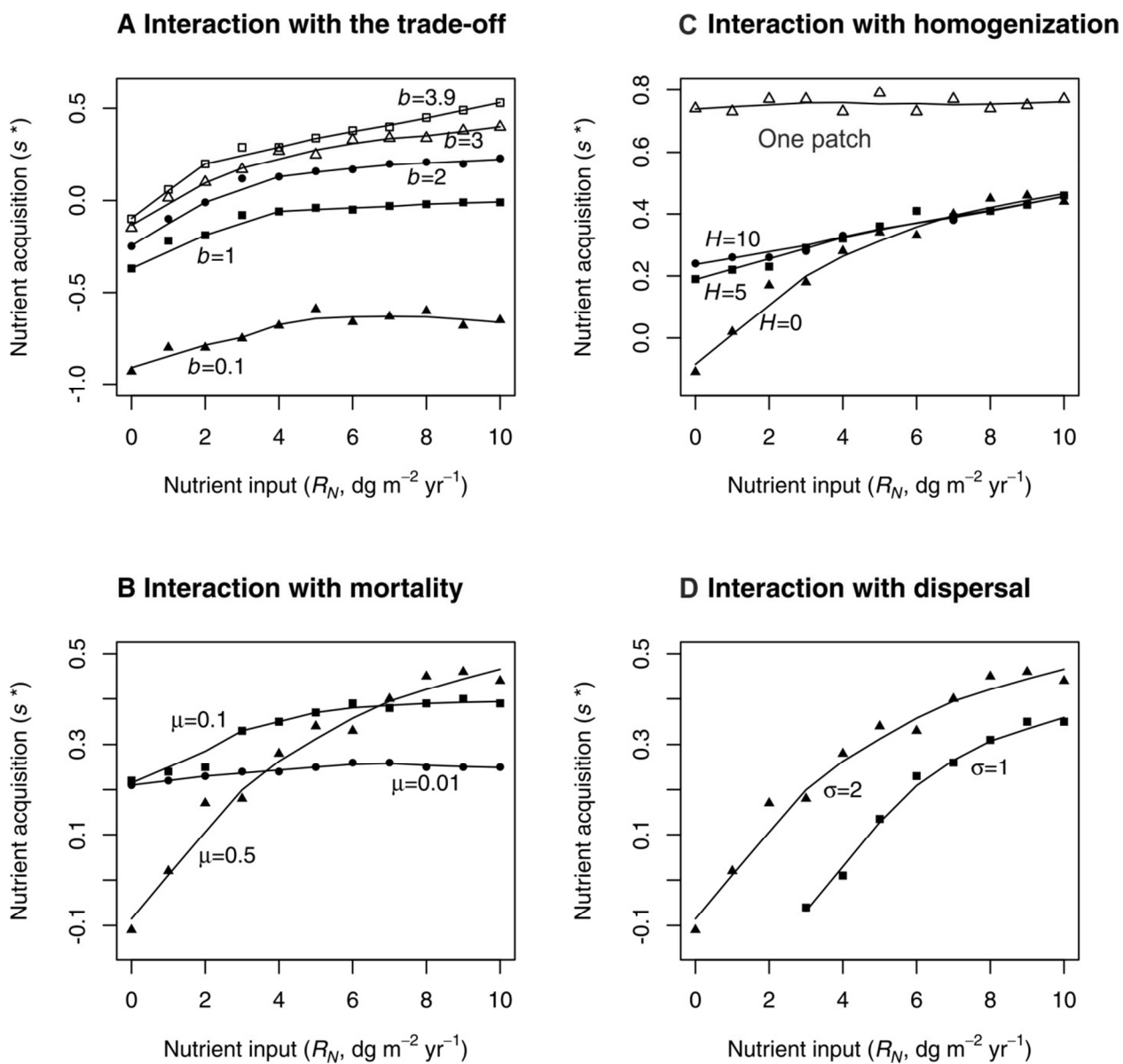
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747 Fig 2



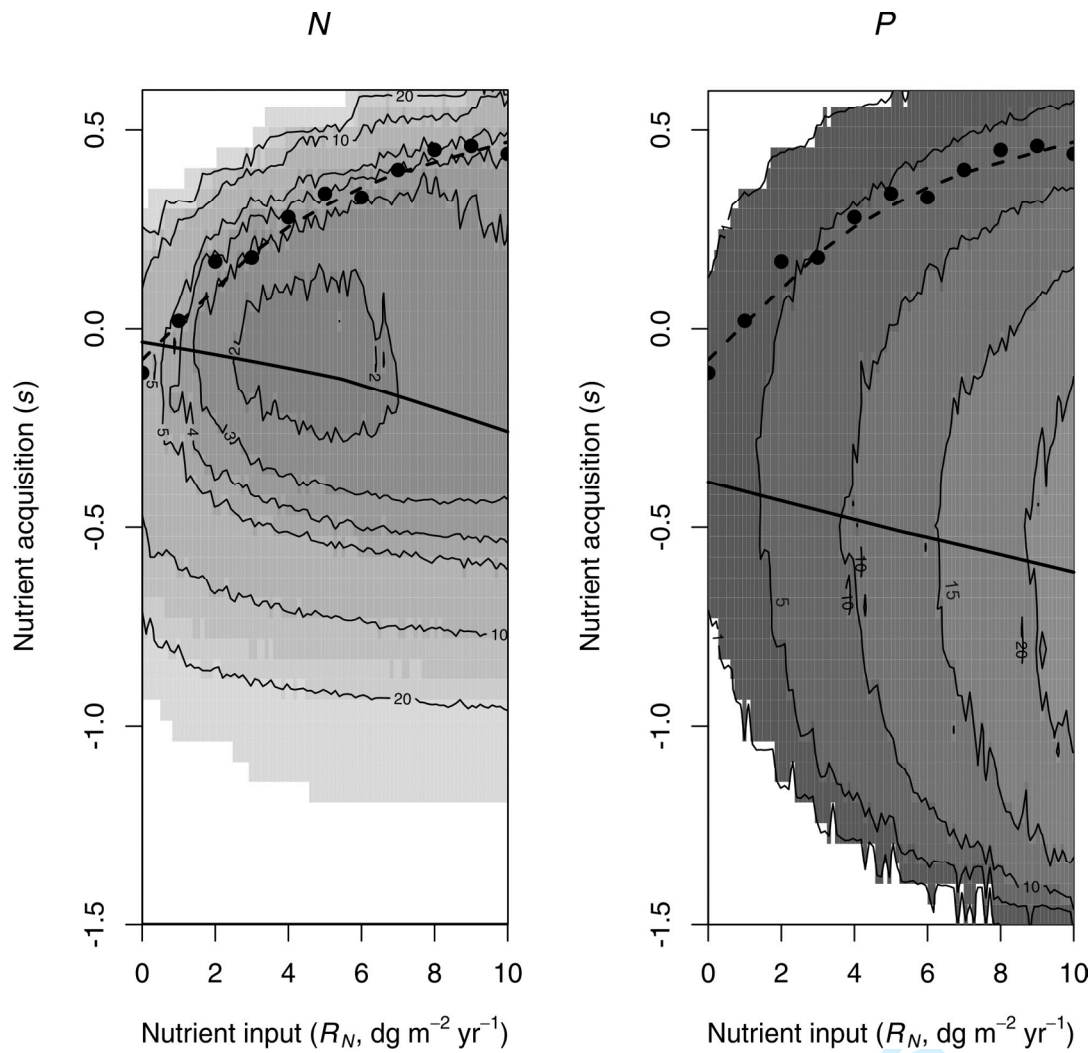
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750 Fig 3

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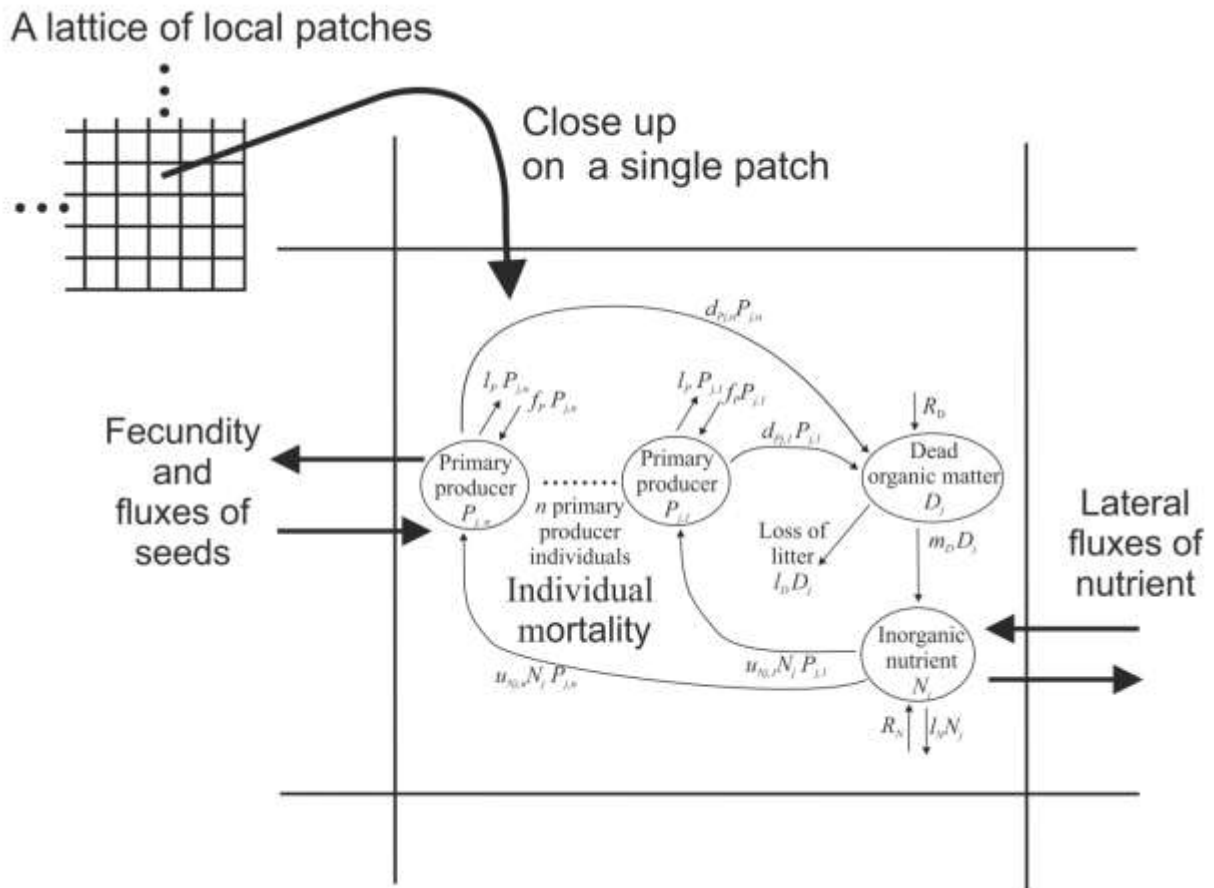
## Fig. S1. General description of the spatial model

Figure S1-A describes the spatial setting of the model and nutrient cycling while Figure S1-B describes the scheduling and implementation of the model.

Fig. S1-A first describes (central patch of the model) the nutrient cycling model (see Table 1 and text for detailed explanations) that allows the local competition between plant individuals ( $P_{j,1}, \dots, P_{j,n}$ ) sharing the same material cycle in a local patch (subscript  $j$ ) of the ecosystem, i.e. a local patch of the model. Second, Fig. S1-A shows that the model also allows for regional competition between individuals growing in different patches, thus not sharing the same local mineral resource: individuals die, reproduce and disperse seeds between local patches. Finally, the model also mimics lateral fluxes of mineral nutrient which allows modulating the heterogeneity in nutrient availability and the way nutrients are shared between the individuals of the population.

Fig. S1-B shows that during each year the system of differential equations is integrated in each cell to simulate the growth of each plant individual in interaction with local mineral resources. Discrete demographic events happen at the end of each year and are implemented through the suppression and addition of differential equations.

Figure S1-A

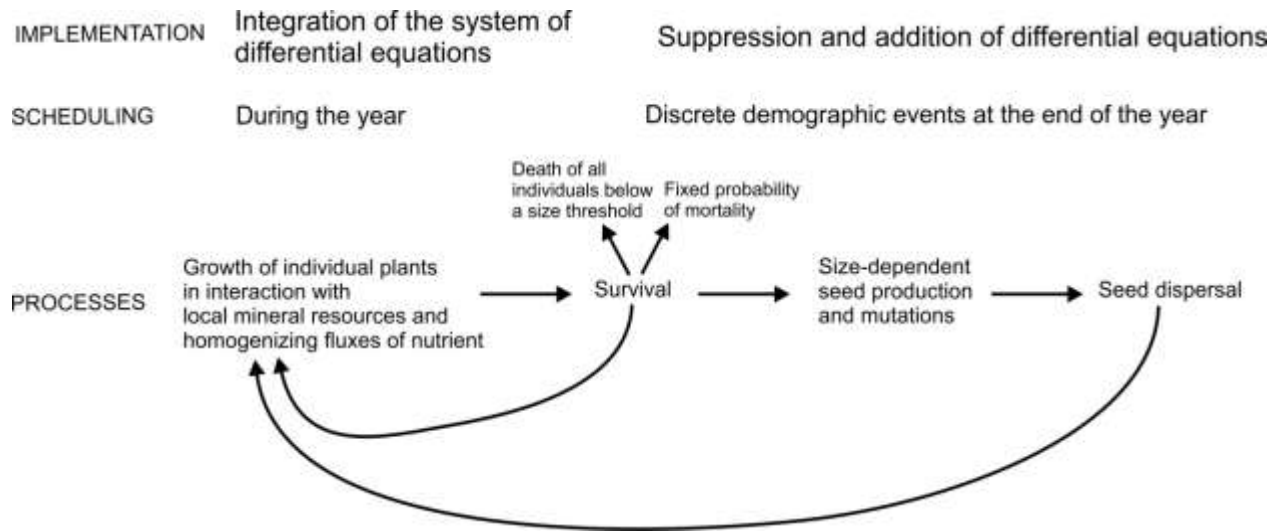


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Figure S1-B



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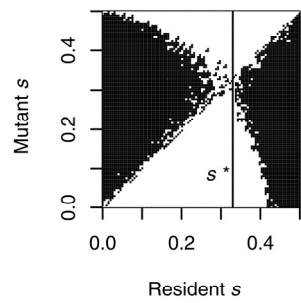
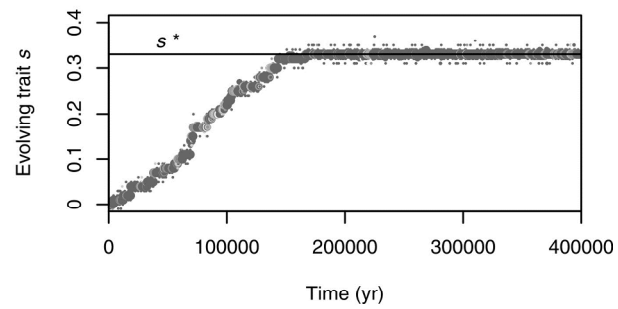
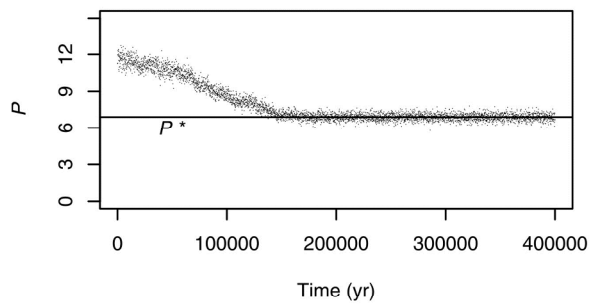
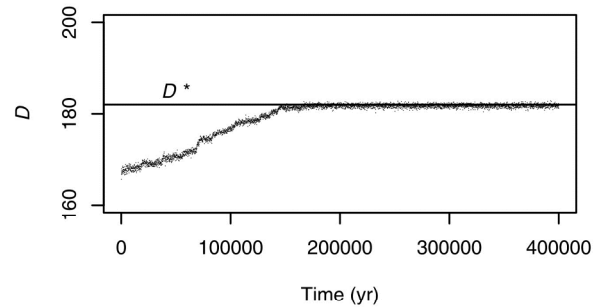
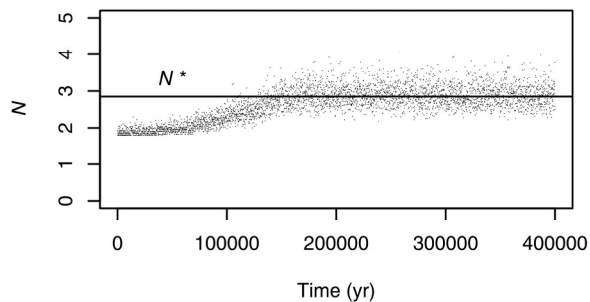
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## Fig. S2. Example of evolutionary dynamics

A: Pairwise-invasibility plot (PIP). Each black dot corresponds to a simulation that led to the successful invasion of a resident population at its ecological equilibrium ( $s$  value on the x axis) by a mutant ( $s$  value on the y axis) starting at a very low density. In these invasion simulations,  $s$  values are not allowed to evolve.  $S$  values for the resident populations and mutants are explored systematically with a step of 0.025 so that each PIP is based on 161X161 invasion simulations. For resident strategy of nutrient uptake below  $s^*$  invasion can only be successful for mutants with higher  $s$  values than the resident  $s$  (black area above the diagonal), while the reverse is true for resident strategies above  $s^*$ . Evolution through successive replacement by new mutants therefore pushes the strategy for nutrient uptake towards  $s^*$ . Since, no strategy can invade a resident strategy at  $s^*$  (white areas above and below the diagonal at  $s^*$ ) evolution stops at  $s^*$  an evolutionary type of singularity called Continuously Stable Strategy (Geritz et al. 1998).

B: Evolutionary dynamics. An example of evolutionary dynamics is displayed. It confirms the result suggested by the pairwise-invasibility plot: evolution drives the strategy for nutrient uptake towards the CSS  $s^*$ . Each dot corresponds to a different mutant. The larger and the darker a dot, the higher the biomass of the corresponding mutant.

C, B, D: changes in the size of the three ecological compartments through evolution.  $d_{p0}$ , 0.275  $\text{yr}^{-1}$ ;  $m_D$ , 0.0766  $\text{yr}^{-1}$ ;  $u_{NO}$ , 1.43  $\text{dg}^{-1} \text{m}^2 \text{yr}^{-1}$ ;  $R_D$ , 2  $\text{dg m}^{-2} \text{yr}^{-1}$ ;  $R_N$ , 6  $\text{dg m}^{-2} \text{yr}^{-1}$ ;  $l_P$ , 0  $\text{yr}^{-1}$ ;  $l_D$ , 0.038  $\text{yr}^{-1}$ ;  $l_N$ , 0.05  $\text{yr}^{-1}$ ;  $f_P$ , 0  $\text{yr}^{-1}$ ;  $b$ , 4;  $c$ , 3.

**A Pairwise-invasibility plot****B Evolutionary dynamics****C Primary producer****D Dead organic matter****E Mineral nutrient**

Geritz, S. A. H., E. Kisdi, G. Meszéna, and J. A. J. Metz. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* 12:35-57.

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**Fig. S3. Effect of the mineralization rate ( $m_D$ ) and the rate of mineral nutrient loss ( $I_N$ ) on the evolution of nutrient acquisition ( $s^*$ ).**

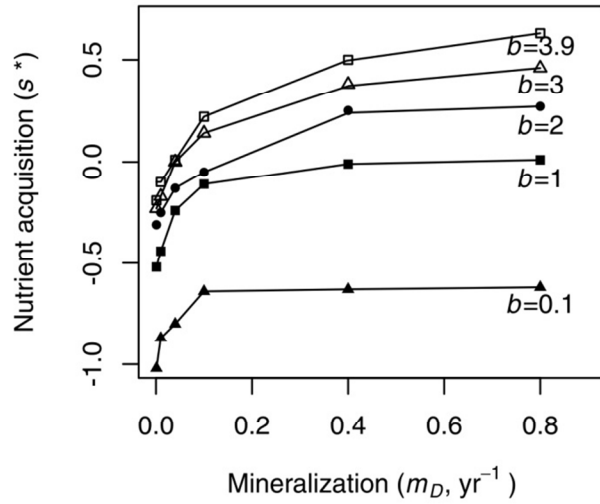
Effect of the mineralization rate ( $m_D$ ) on the evolution of nutrient acquisition ( $s^*$ ) with different cofactors: (A) the trade-off parameter  $b$ . (B) individual mortality  $\mu$ , (C) the intensity of homogenisation  $H$  (in this case “1 patch” denotes non-spatial simulations with only one patch), (D) the efficiency of dispersal  $\sigma$ .

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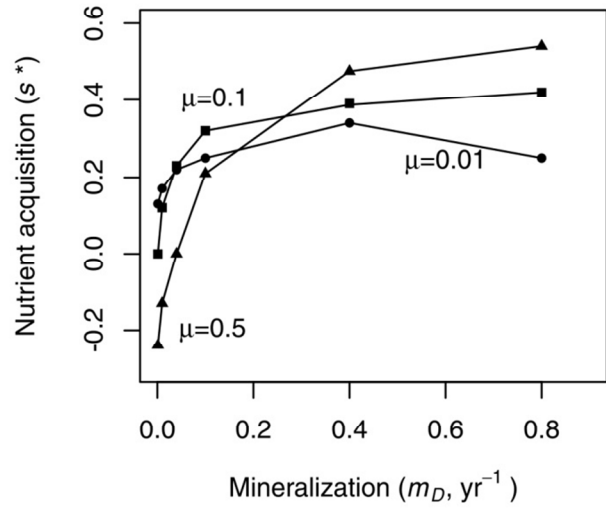
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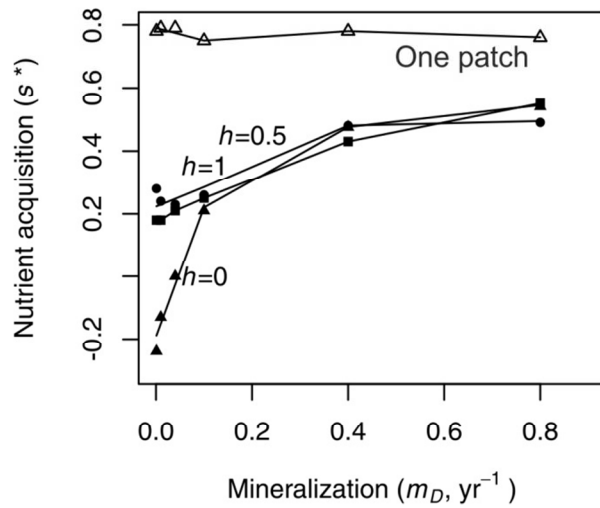
**A Interaction with the trade-off**



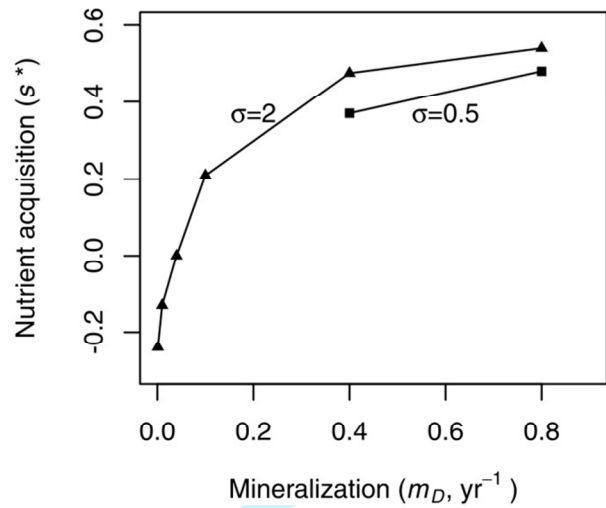
**B Interaction with mortality**



**C Interaction with homogenization**



**D Interaction with dispersal**

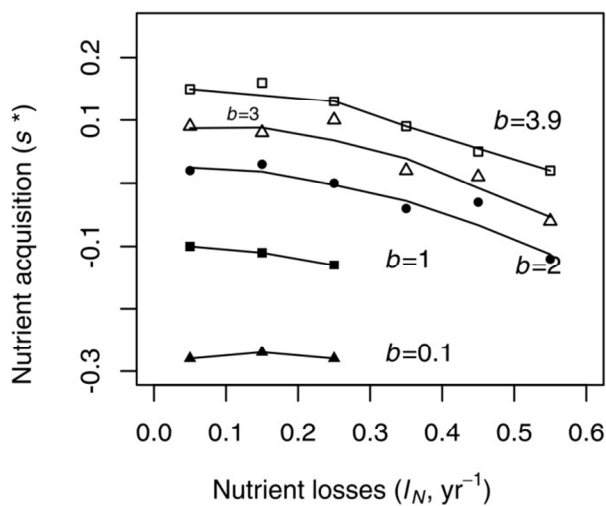


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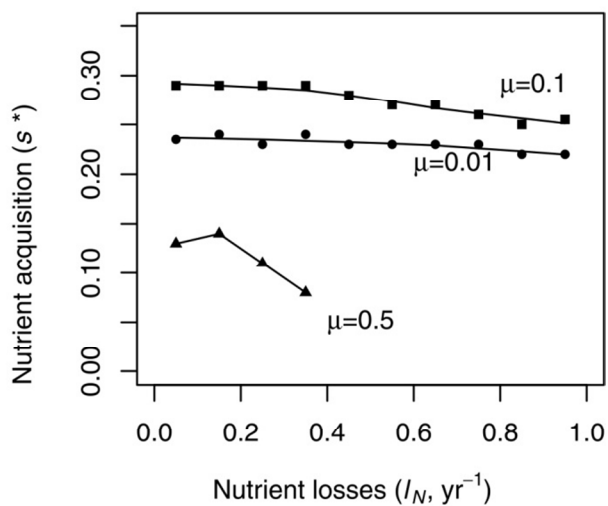


Effect of the rate of mineral nutrient loss ( $l_N$ ) on the evolution of nutrient acquisition ( $s^*$ ) with different cofactors: (A) the trade-off parameter  $b$ , (B) individual mortality  $\mu$ , (C) the intensity of homogenisation  $H$  (in this case 1 patch denotes non-spatial simulations with only one patch), (D) the efficiency of dispersal  $\sigma$ .

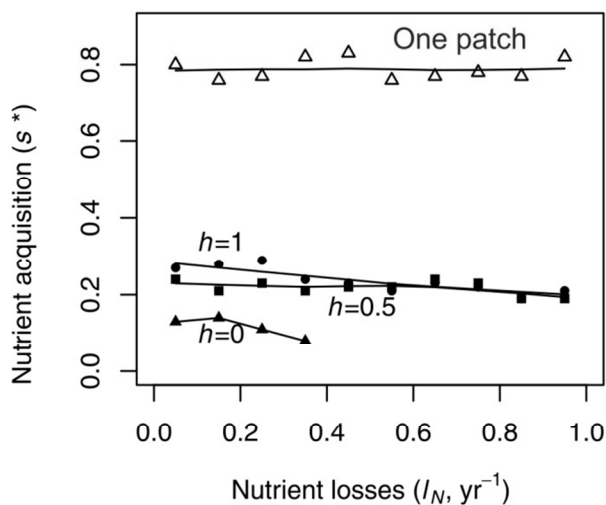
**A Interaction with the trade-off**



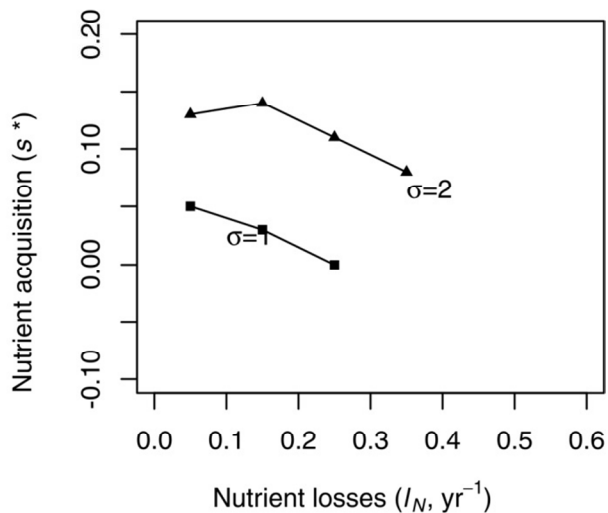
**B Interaction with mortality**



**C Interaction with homogenization**



**D Interaction with dispersal**



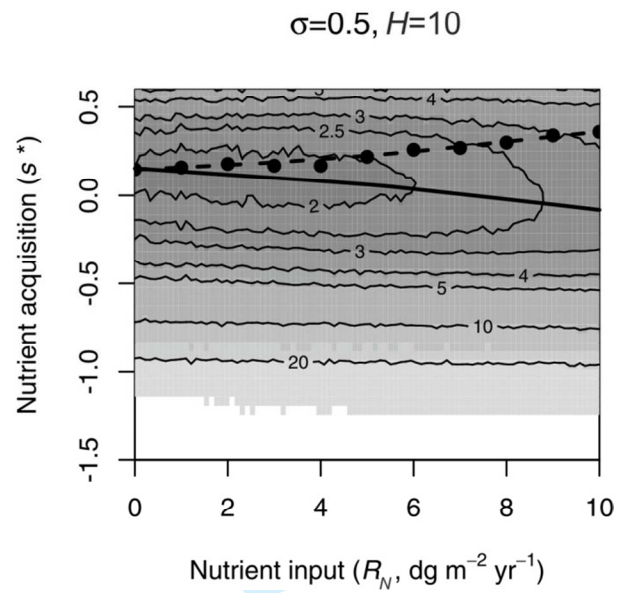
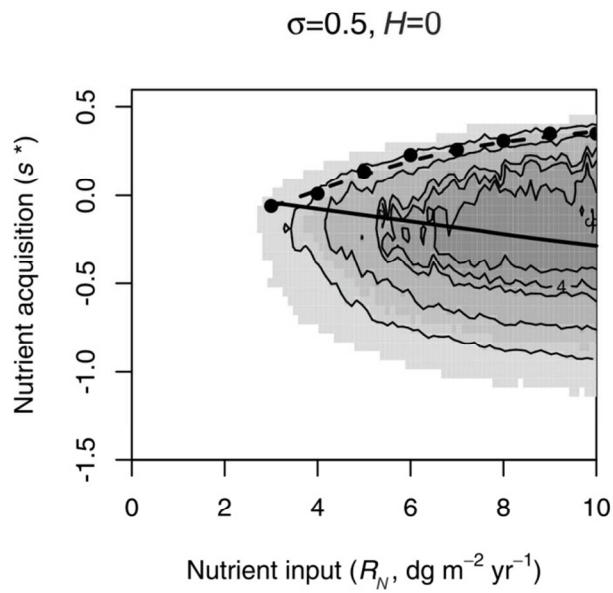
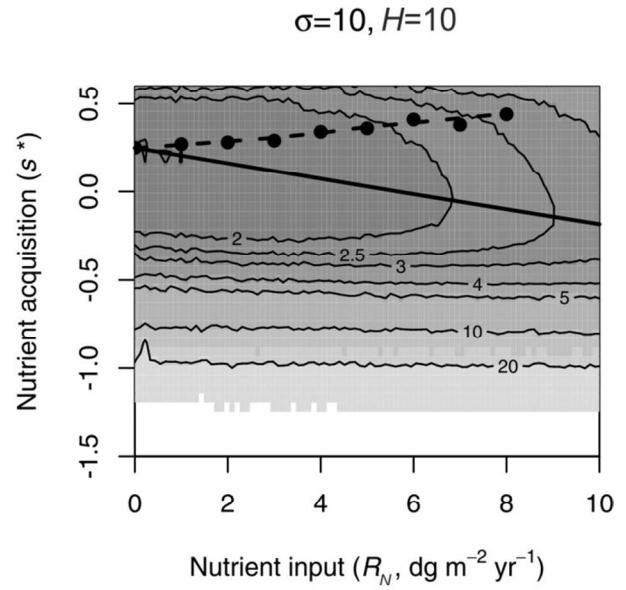
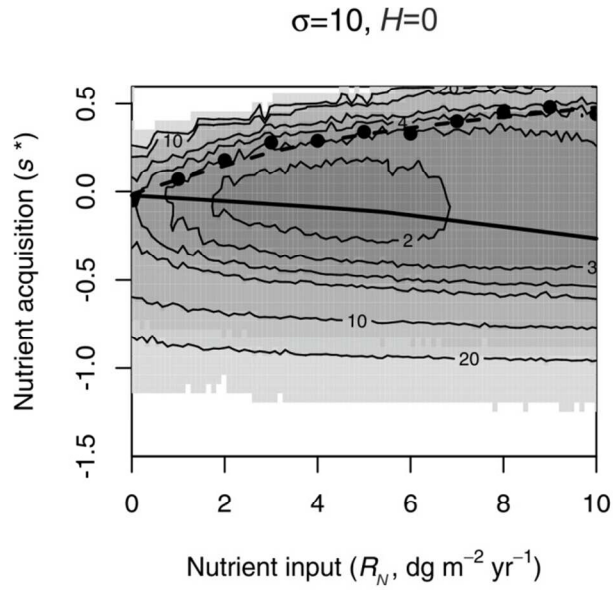
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**Fig. S4. Joint effect of the capacity for nutrient acquisition ( $s$ ) and the inputs of mineral nutrient ( $R_N$ ) on the availability of mineral nutrient at the ecological equilibrium ( $N$ ) for four combinations of dispersal and lateral nutrient fluxes.**

Contour plot of the joint effect of the capacity for nutrient acquisition ( $s$ ) and the inputs of mineral nutrients into the ecosystem ( $R_N$ ) on the availability of mineral nutrient ( $N$ ) in four cases: dispersal is either low ( $\sigma=0.5$ ) or high ( $\sigma=10$ ), and homogenization is either low ( $H=0$ ) or high ( $H=10$ ). The thick solid lines denote the position of the minimum  $N$  value for each  $R_N$  value. The dots and the dashed lines denote the evolved capacity for nutrient acquisition ( $s^*$ ) for each  $R_N$  value.

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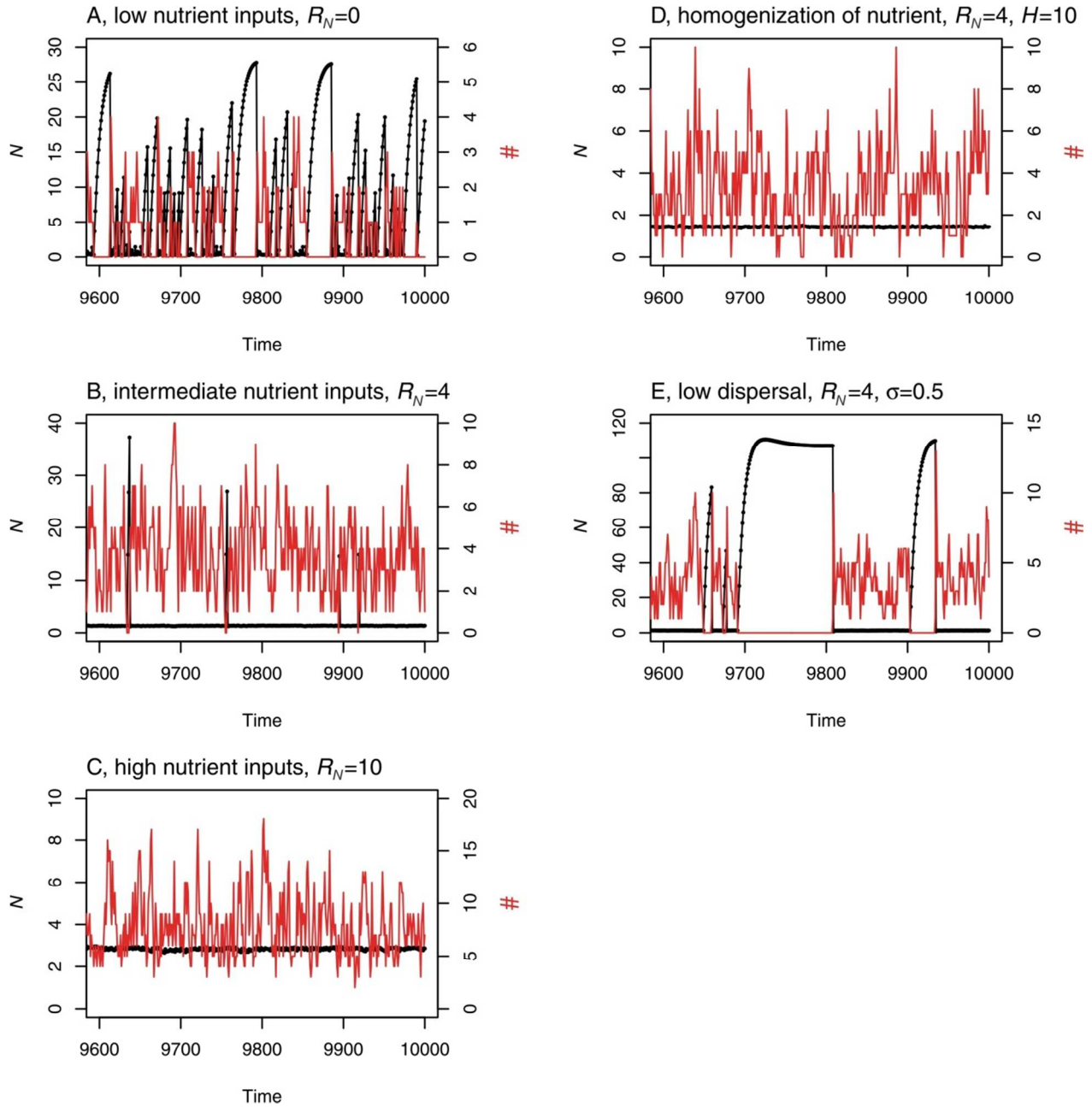
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### **Fig. S5. Examples of ecological dynamics in one local patch showing temporal variations in the availability of mineral nutrient**

The ecological dynamics in one patch of the 400-patch lattice is displayed: the availability of mineral nutrient (in black,  $N$ ) and the number of individuals (in red,  $\#$ ). The investment into the acquisition of mineral nutrient is not allowed to evolve ( $s=0$ ). Results are displayed for the period 9600-9800 years after the start of the simulation so that it can be considered that a steady-state has been reached. Each panel corresponds to different conditions: A-B-C corresponds to an increase in inputs of mineral nutrients; D and E correspond to an intermediate value of nutrient inputs. For D nutrient availability is homogenized ( $H=10$ ), while for E the capacity of seed dispersal is very low ( $\sigma=0.5$ ).

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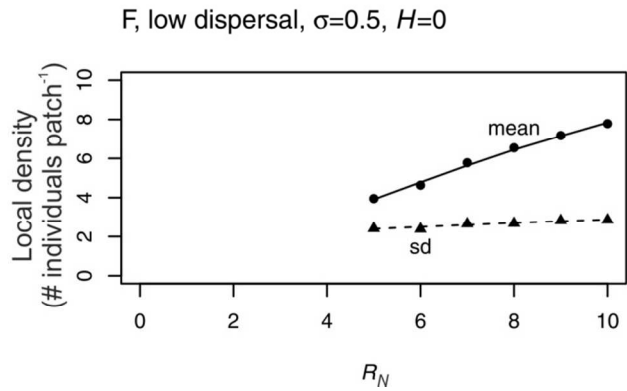
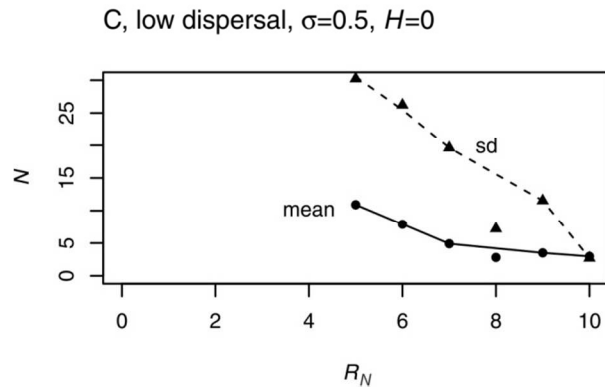
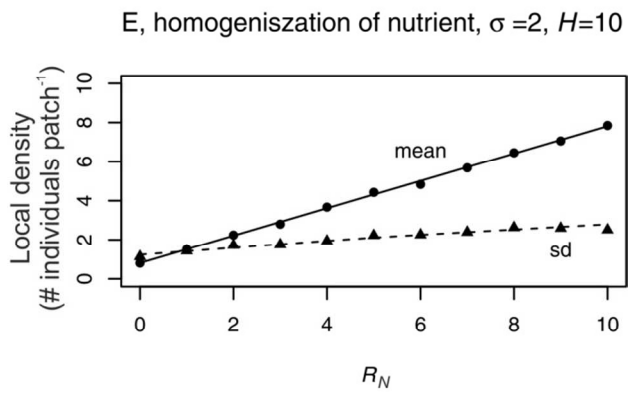
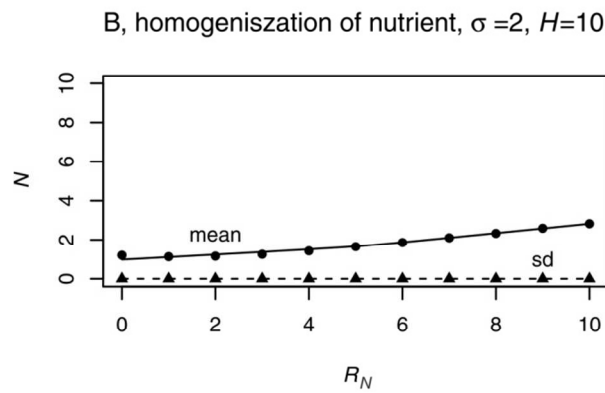
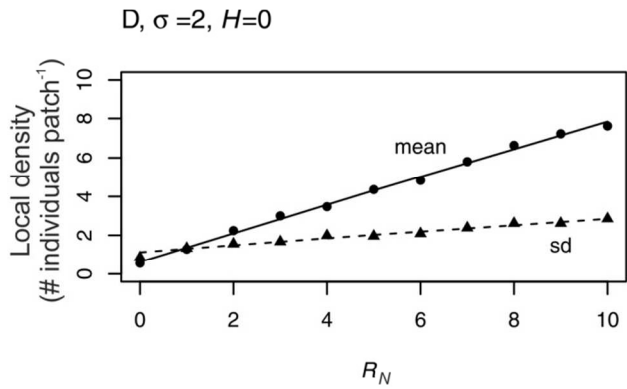
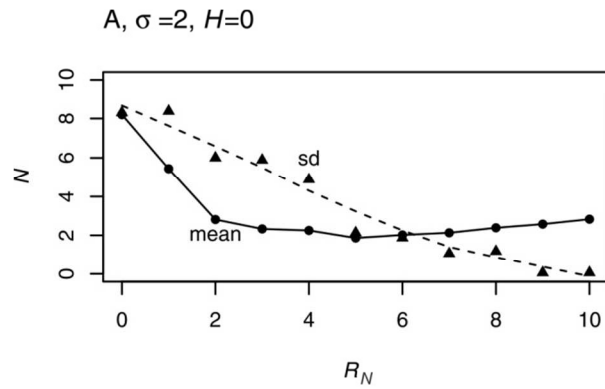
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**Fig. S6. Ecological effects of nutrient inputs on the mean and standard deviation of the equilibrium nutrient availability and the number of plant individuals in each patch**

Ecological effect of nutrient enrichment (increase in inputs of mineral nutrients) (1) on the mean and standard deviation (sd) of the availability of mineral nutrient (panels A, B, C), (2) on the mean and standard deviation of the number of individuals by patch (#, panels D, E, F). Means and standard deviations are computed over all the patches of the simulated lattice (20X 20 patches) at the end of 10000 years of ecological simulation. The investment into mineral nutrient acquisition is not allowed to evolve ( $s=0$ ) and it can be considered that an ecological steady state has been reached. Different situations are modeled: (A and D) no homogenization of mineral nutrient and high seed dispersal ability; (B and E) homogenization of mineral nutrient; (C and F) low seed dispersal. Missing points for low dispersal are due to the fact that, in this case, for low nutrient inputs populations of primary producers get extinct.

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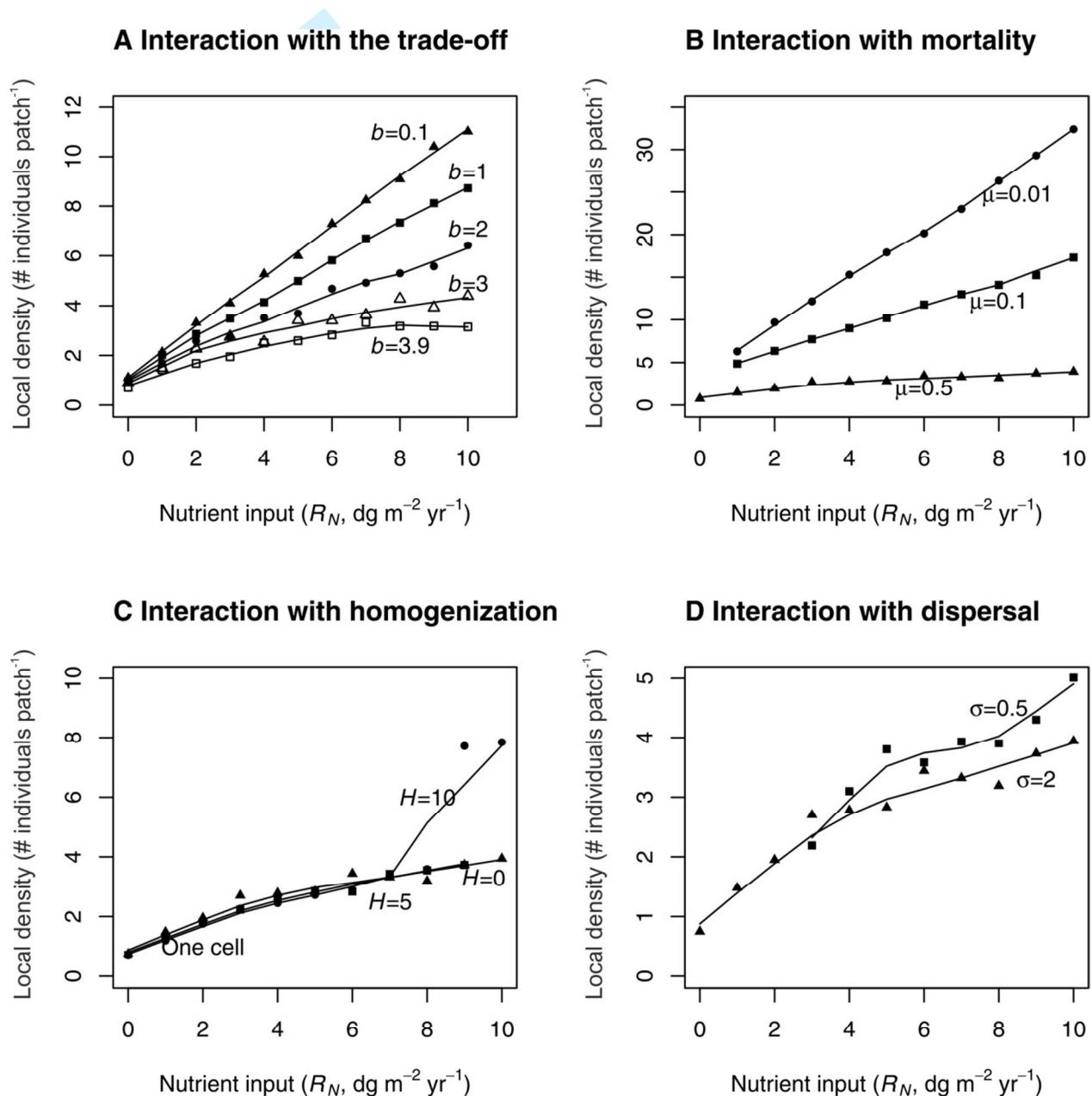


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## Fig. S7. Evolutionary effect of inputs of mineral nutrient ( $R_N$ ) on the local density of plants

Effect of inputs of mineral nutrient ( $R_N$ ) on the local crowding (mean number of individuals by local patch) with different covariables: (A) the trade-off parameter  $b$ . (B) individual mortality  $\mu$ , (C) the intensity of homogenisation  $H$ , (D) the efficiency of dispersal  $\sigma$ . The investment into nutrient acquisition ( $s$ ) is allowed to evolve and has reached an equilibrium.



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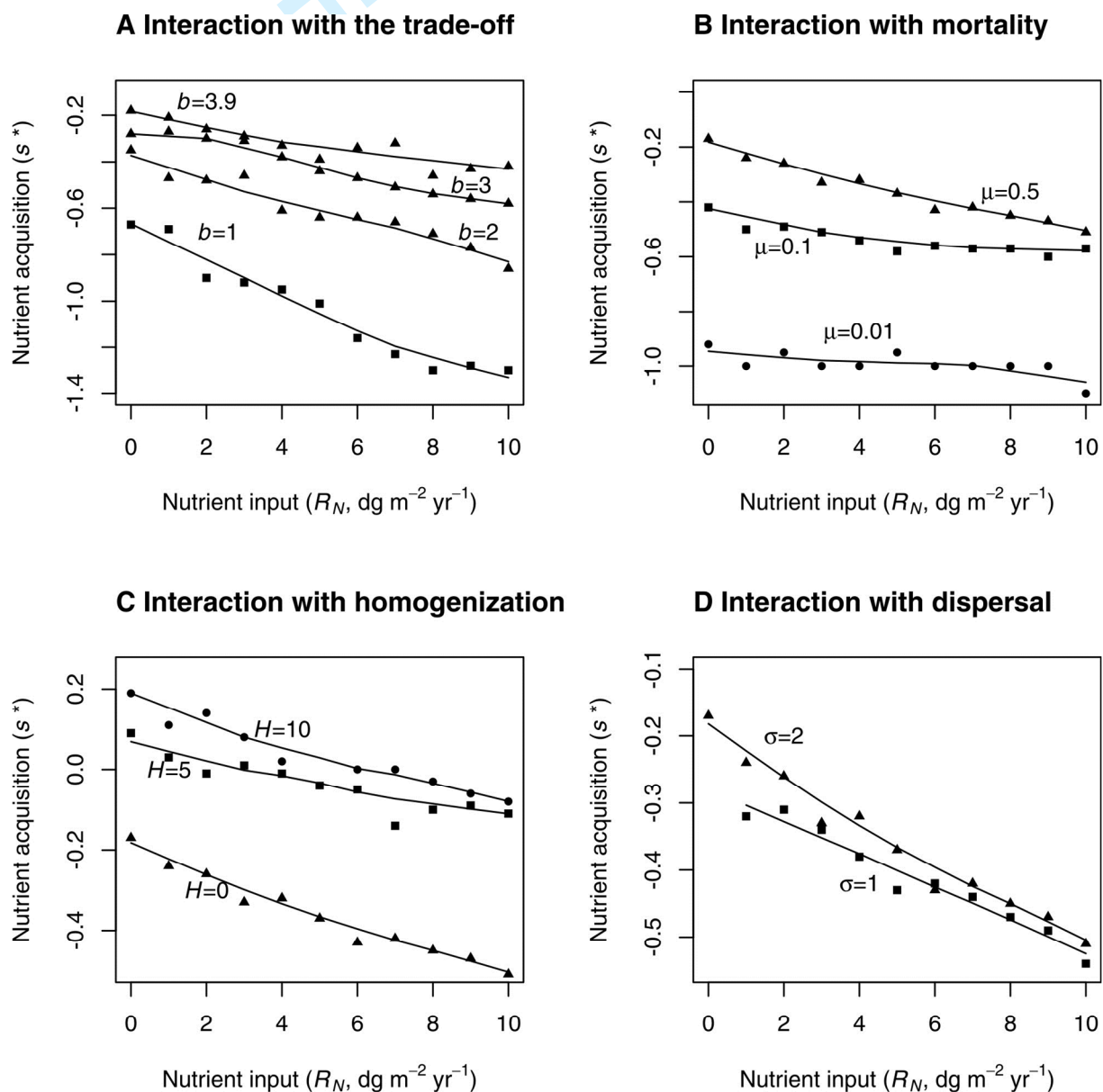
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### Fig. S8. Effect of the inputs of mineral nutrient ( $R_N$ ) on the evolution of nutrient acquisition ( $s^*$ ) when only one individual is allowed to survive in each local patch

Effect of the inputs of mineral nutrient to the ecosystem ( $R_N$ ) on the evolution of nutrient acquisition ( $s^*$ ) in the case where only one individual is allowed to survive in each local patch and with different cofactors: (A) the trade-off parameter  $b$ , (B) individual mortality  $\mu$ , (C) the intensity of homogenisation  $H$ , (D) the efficiency of dispersal  $\sigma$ .



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