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Evolution of nutrient acquisition: when space matters

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Summary

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

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

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

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

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

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

Introduction

Spatial heterogeneity in the availability of mineral nutrients and the spatial structure of plant populations must be taken into account to predict the evolution of plant strategies to acquire mineral nutrients because (i) individual growth and reproduction depend on the local availability of the mineral resource; (ii) a mutant can establish locally only competing with locally growing individuals and not with the whole resident population; and (iii) the ability of a mutant to establish locally depends on the modifications it may impose to the local nutrient availability even if its density is negligible at the population scale; that is, the local success of a mutant depends on positive or negative feedbacks it builds with its local environment. These points emphasize local processes, but these processes only take place because the mineral resource and plant individuals are spatialized.

Studies of adaptive plant strategies have already pointed out the importance of nutrient heterogeneity and the ecological and evolutionary influences of two scales of competition (Loreau 1998; Barot *et al.* 2014). (i) Within-cycle competition (local competition throughout this paper) arises between strategies/individuals that are locally competing for the same nutrient resource (thus sharing the same material cycle). (ii) Between-cycle competition (regional competition throughout this study) arises between strategies/individuals growing spatially apart, therefore not

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*Correspondence author. E-mail: sebastien.barot@ird.fr directly competing for the same local resources (not sharing the same material cycle) but competing regionally for space and access to the regional pool of nutrient. While local competition is based on the capacity to exploit the local nutrient resource (which, for example, involves the investment into a dense root system), regional competition is based on density dependence and the capacity to occupy the whole landscape (e.g. the whole surface of a plot, all local patches of a spatial model) through the production of seeds and their dispersal. Thus, these two scales of competition may lead to conflicting selection pressures because the strategy (i.e. the resource allocation) maximizing the exploitation of a local resource and its accumulation into the biomass is likely to be different from the strategy maximizing the number of individuals and their distribution over the whole landscape (Loreau 1998; Barot *et al.* 2014). This is likely to impede the minimization of nutrient availability predicted by the R* theory (Tilman 1982). Most evolutionary models of nutrient cycling are mean-field models (Loeuille, Loreau & Ferrière 2002; Menge, Levin & Hedin 2008; Boudsocq, Barot & Loeuille 2011) and only predict the evolutionary consequences of local competition. On the one hand, some models have addressed the evolution of nutrient cycling-related traits in a spatial context (de Mazancourt, Loreau & Dieckmann 2001; Loeuille & Leibold 2008). However, these studies do not directly aim at assessing the respective influence of local and regional competition. On the other hand, many models address the interplay between local and regional competition but without addressing explicitly evolutionary issues (e.g. Tilman 1994; Gravel *et al.* 2010) (see also a review Fagerström & Westoby 1997).

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

To assess the influence of local and regional competition and the impact of seed dispersal and homogenizing nutrient fluxes on the evolution of nutrient acquisition, we developed a spatially explicit model where primary producers compete locally for a heterogeneously distributed limiting nutrient and regionally through seed production and their dispersal. Our model is based on two previously published models: (i) a mean-field analytical model (Boudsocq, Barot & Loeuille 2011) that predicts the evolution of nutrient acquisition, (ii) a spatially explicit and individual-based model (Barot *et al.* 2014) that predicts the evolution of plant capacity to control the mineralization of their litter. In the non-spatial model (Boudsocq, Barot & Loeuille 2011), the fitness of a mutant only depends on the immediate balance between acquisition and turnover of nutrient and this balance does not depend on inputs of nutrients to the ecosystem, nutrient losses from the ecosystem or mineralization. Thus, the mutant fitness cannot depend on its capacity to modify its local environment. In contrast, in our spatial model, the fitness of a mutant depends, through the building of local feedback loops and through heterogeneity in nutrient availability, on complex interactions between all nutrient fluxes and the mutant strategy for nutrient acquisition.

Taken together, the characteristics of our model should allow the evolution of the diversity of plant strategies observed in different environments (Grime 2001; Craine 2009) and, in particular, to conservative (low rate of nutrient uptake and efficient conservation of the nutrient within the biomass) and acquisitive plants (high rate of nutrient uptake and poor conservation of the nutrient within the biomass). Using this model, we test the following hypotheses: (i) the evolution of nutrient acquisition strategies depends on the relative strength of local vs. regional competition and spatial processes that influence this strength: dispersal and lateral nutrient fluxes. More specifically, we expect increasing dispersal and lateral fluxes of nutrients to select for higher rates of nutrient uptake. (ii) The evolution of nutrient acquisition depends on the nutrient richness of the ecosystem and all fluxes influencing this richness. Namely, a gradient of nutrient enrichment leads to the evolution of stress tolerators with low rates of nutrient uptake at the nutrient-poor end of the gradient and competitors with high rates of nutrient uptake at the other end of the gradient (Chapin 1980; Grime 2001; Loeuille & Loreau 2004). (iii) Ecosystem properties should be impacted by the evolution of nutrient acquisition. It has been proposed that local resource competition should allow the species that minimizes resource availability to exclude all other species and this should maximize the biomass of primary producer and primary production (Tilman 1982; Loreau 1998). On the contrary, regional competition should impede this minimization of the availability of mineral nutrients (Loreau 1998).

Description of the model

MODEL STRUCTURE

The model (see Fig. S1a,b, Supporting information, and the list and description of parameters in Table 1) is a

Table 1. Model parameters

Parameter type	Symbol	Default values	Definition
Nutrient recycling within a local patch	d_{P0}	0·275 year^{-1}	Initial rate of plant nutrient turnover through root and leaf turnover
	m_D	0·0766 year^{-1}	Mineralization of dead organic matter
	u_{N0}	1·43 dg^{-1} m^{2} year^{-1}	Initial uptake of mineral nutrient
Inputs of nutrient	R_D	2 dg m^{-2} year^{-1}	Mineral atmospheric deposition
	R_N	1·8 dg m^{-2} year^{-1}	Organic atmospheric deposition
	f_P	0 year^{-1}	Symbiotic nitrogen fixation
Losses of nutrient	l_P	l_P, 0 year^{-1}	Loss of nutrient from the ecosystem because of fires or human exportation of biomasses
	l_D	0·038 year^{-1}	Loss of dissolved organic matter or litter from the ecosystem
	l_N	0·05 year^{-1}	Nutrient leaching from soils, denitrification
Nutrient fluxes between patches	H	0 year^{-1}	Homogenizing lateral fluxes of nutrient
Demographic parameters	μ	0·5	Individual mortality
	γ	0·3 g	Nutrient content of a seed
	ρ	0·1	Percentage of the nutrient stock of plant individuals allocated to seed production
	σ	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

spatial and individual-based version of a mean-field model of recycling of a limiting mineral nutrient (Boudsocq, Barot & Loeuille 2011) between plants (*P*), dead organic matter (*D*) and mineral nutrient (*N*). The limiting nutrient can virtually be any of the mineral nutrients that limit primary production (generally nitrogen or phosphorus). Note that this previous model was not individual based. Here, the spatial features and the dynamics of individuals are modelled as in Barot *et al.*'s (2014) model. Sessile terrestrial plants interact locally with soil nutrient cycling and disperse through space by seed production. Our model thus couples a nutrient cycling model with a spatial demographic model.

Space is described as a lattice of contiguous patches, each containing two abiotic nutrient compartments (*D*, *N*) and one nutrient compartment for each locally growing plant individual (P_i, Fig. S1a). Nutrient cycling and individual plant growth are modelled through the integration of a system of differential equations in each patch. There is one equation for each plant individual so that demographic events lead to the suppression (death) and addition (birth) of equations. We assume that one time step corresponds to 1 year so that demographic events occur at the end of each year, whereas nutrient cycling is calculated on a subyear basis through the integration of the differential equations.

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

The size of the patches has to be chosen appropriately, so that they only host a relatively low number of plant individuals that belong to the same competitive neighbourhood. More precisely, this number of individuals and patch size are determined by inputs of mineral nutrient and organic matter (see below). For example, patches of one square metre (as implemented in our simulation, see below) would be relevant to model small and short-lived herbaceous plants for which about 50 individuals may be thought as locally competing. If plants live longer, individuals may grow larger (e.g. perennial bunch grasses) and only a few individuals compete for the same nutrient resource in each one-square-metre patch. The different parameters of the model and their default values are given in Table 1.

ECOLOGICAL DYNAMICS

Within-patch nutrient dynamics

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

$$\frac{\mathrm{d}P_{j,i}}{\mathrm{d}t} = u_{Nj,i}N_jP_{j,i} - (d_{Pj,i} + l_P - f_P)P_{j,i} (\text{for each individual } i \text{ of local patch } j), \quad \text{eqn 1}$$

$$\frac{\mathrm{d}D_j}{\mathrm{d}t} = \sum_i d_{Pj,i}P_{j,i} + R_D - (m_D + l_D)D_j, \quad \text{eqn 2}$$

$$\frac{\mathrm{d}N_j}{\mathrm{d}t} = m_DD_j + R_N - \left(\sum_i u_{Nj,i}P_{j,i} + l_N\right)N_j + H(\bar{N} - N_j). \quad \text{eqn 3}$$

Between-patch nutrient dynamics

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

Demography

Discrete demographic events, that is mortality and reproduction, occur at the end of every year (Fig. S1b). While $d_{Pj,i}$ denotes the rate of nutrient turnover of the primary producer because of the death of parts of the primary producer (death of roots and leaves, exudate production), μ denotes individual mortality (Table 1). The amount of nutrient contained in dead individuals is transferred to the local dead organic matter compartment (D_j).

At the end of each year, individuals in the lattice may produce seeds that are dispersed on the lattice. Parameter ρ is the percentage of the stock of nutrient contained in each individual at the end of the year that is allocated to seed production. γ is the quantity of nutrient in a seed. The number of seeds produced by the individual i (in patch j) is thus the largest previous integer of $P_{j,i}\rho/\gamma$. Seed dispersal is modelled by moving each seed and creating a new individual with a nutrient content γ in another patch. We choose a random angle (between 0 and 360°) to determine the direction of dispersal and consider that the dispersal distance from the centre of the patch of the mother primary producer follows a centred normal distribution (mean = 0) with standard deviation σ (if the distance is negative, 180° is added to the original angle): when σ increases, dispersal distance tends to increase. There is no habitat choice. For simplification, production of seed starts at the age of 1 for individuals that are large enough at this age ($P_{j,i}\rho > \gamma$). Note that individuals falling under a threshold nutrient stock (i.e. the nutrient content of a seed) are also considered to die.

EVOLUTIONARY DYNAMICS

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

$$u_{Nj,i} = u_{N0}e^{bs_{j,i}}, \quad \text{eqn 4}$$

$$d_{Pj,i} = d_{P0}e^{cs_{j,i}}. \quad \text{eqn 5}$$

This trade-off is justified by several complementary mechanisms (see details in the Discussion). For example, the more a plant invests into the development of its root system, the uptake and assimilation of nutrients, the less resource is allocated to maintenance and defence functions. Indeed, the existence of trade-offs between nutrient uptake and anti-herbivore defences has been documented (Herms & Mattson 1992; Mauricio 1998). This mechanism should increase the turnover of the plant biomass and losses of mineral nutrients contained in this biomass.

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

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

IMPLEMENTATION

A simulation platform has been implemented in the Java programming language (1.5). The integration of the differential equations is based on the classical fourth-order Runge-Kutta method with an integration step $\Delta t = 0{\cdot}1$ year. In our simulations, H varies between 0 (no homogenization) and 10 (strong homogenization). Figure S6 shows that $H = 10$ leads to a null standard deviation of nutrient availability (perfect homogenization of the mineral nutrient availability).

Parameters chosen for nutrient cycling are adapted from Woodmansee, Vallis & Mott (1981) who describe nitrogen cycling in a temperate grassland (see Table 1). Unless stated in figure captions (main text and the supplementary material), we keep these parameter values. We consider one-square-metre-wide patches. Unless stated, the primary producer is considered to be a short-lived plant. For mutations, we always used $p_m = 10^{-4}$ and $m = 0{\cdot}05$. The grid size is always 20×20 patches except in one occasion (hereafter one-patch model) where only one patch is modelled but increasing accordingly input of mineral nutrients and organic matter (×400) to support the same total biomass as in the 20×20 patch model. This corresponds to a shift between 400 one-square-metre patches to one single 400-m^2 patch. The lattice is wrapped on a torus to handle seed dispersal. Variables following normal distribution (dispersal distance and mutation size) are simulated using the polar method (Marsaglia & Bray 1964).

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

Results (Figs 1 and 2) are presented using locally weighted polynomial regressions to compute trend lines. All figures were produced using R 2.10 (2010). In the main text, we focus on the evolutionary effects of inputs of mineral nutrient to the ecosystem. Figure S3 displays results concerning the effects of the rate of mineral nutrient losses from the ecosystem and the rate of dead organic matter mineralization that also influence the availability of mineral nutrient.

Results

EVOLUTIONARY DYNAMICS

The simulation model leads to the same types of evolutionary outcomes as the analytical model of Boudsocq, Barot and Loeuille (2011): (i) a stable evolutionary equilibrium (continuously stable strategy (CSS), Eshel 1983), (ii) a tragedy of the common scenario (Hardin 1968) where the primary producer compartment asymptotically decreases, while uptake and productivity increase, eventually leading to the primary producer extinction, and (iii) an accumulation of nutrient in all compartments due to an efficient recycling (inputs of nutrient are higher than outputs). In this last case, the model predicts the infinite accumulation of the limiting nutrient, which is not realistic but denotes cases where evolution drives the primary producer to switch to another limiting factor. Evolutionary branching does not occur.

In particular, when the benefit of the investment in nutrient acquisition is low in comparison with its cost ($b < c$) and when inputs of nutrient to the primary producer compartment (nitrogen fixation) are equal or lower to its rate of mineral nutrient turnover ($f_P \le l_P$), simulations lead to a CSS we note s^*. Simulations with identical parameter values always lead qualitatively to the same results, but the inherent stochasticity of the model (mortality,

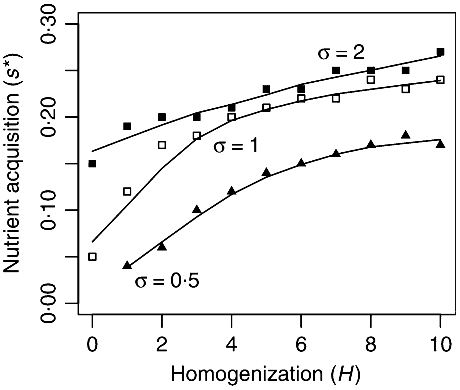

Fig. 1. Effect of the spatial homogenization of the mineral nutrient resource (H) on the evolved capacity for nutrient acquisition (s^*) for different dispersal capacities (σ). A point is missing for $\sigma = 0{\cdot}5$ and $R_N = 0$ because these parameters lead to a non-viable population. See Table 1 for parameter values.

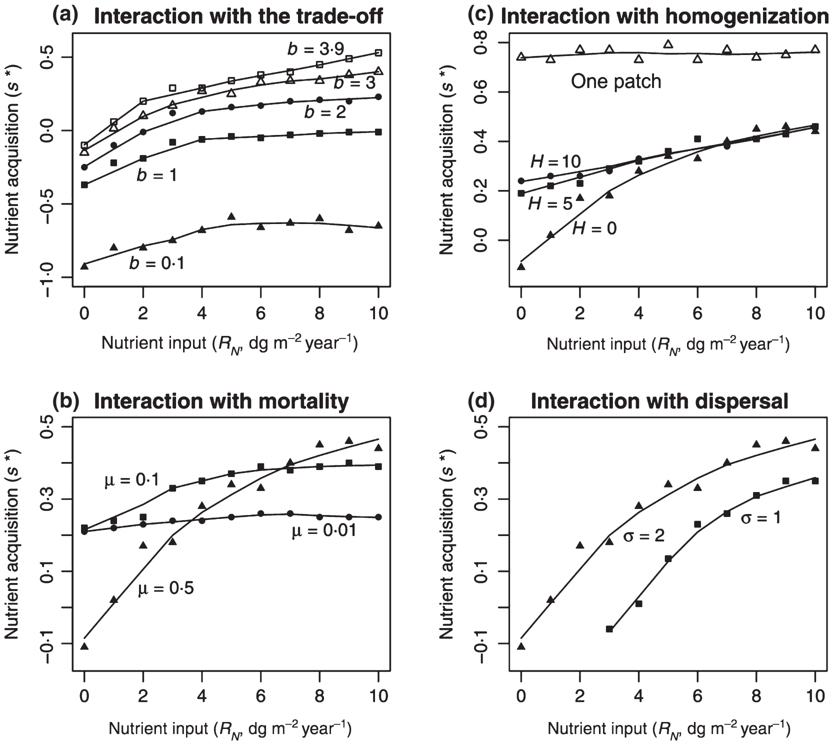

Fig. 2. Effect of the inputs of mineral nutrients (R_N) on the evolved capacity for nutrient acquisition (s^*), as a function of four cofactors: (a) the trade-off parameter b, (b) individual mortality μ, (c) homogenization of the availability of the mineral resource H (in this case '1 patch' denotes non-spatial simulations with only one patch) and (d) efficiency of dispersal (σ). See Table 1 for parameter values.

seed dispersal and mutations) may lead to small differences in the s^* observed at the end of a simulation. All the results displayed hereafter correspond to CSS cases because of the parameter values we choose ($f_P = l_P = 0$). To insure the meaningfulness of the results, we always run simulations long enough to reach the evolutionary equilibrium (400 000 time steps while 100 000 time steps are generally enough to reach the CSS). Figure S2 displays an example of evolutionary dynamics leading to an evolutionary equilibrium together with the corresponding pairwise-invisibility plot (Geritz *et al.* 1998) that proves that this is a case of CSS. Such dynamics have been simulated for each point of Figs 1 and 2.

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

CAPACITY TO ACQUIRE NUTRIENTS AT THE EVOLUTIONARY EQUILIBRIUM

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

The evolved capacity for nutrient acquisition (s^*) increases with inputs of mineral nutrient to the ecosystem (R_N) whatever the trade-off shape (Fig. 2a), the individual mortality (Fig. 2b), the intensity of mineral nutrient homogenization (Fig. 2c) or the dispersal capacity (Fig. 2d). The less restrictive the trade-off (increasing b values), the higher the evolved s^* values. For increasing individual mortality rates, the amplitude of the effect of nutrient inputs on the evolved nutrient acquisition becomes higher. As in Fig. 1, homogenization of mineral nutrient and seed dispersal increases the evolved capacity for mineral nutrient acquisition. This effect of nutrient homogenization disappears for high inputs of mineral nutrients. In other words, the evolved capacity for nutrient acquisition always increases with nutrient inputs but this effect is weaker when nutrient homogenization increases. The non-spatial model (only one patch) leads to a much higher value ($s^* = 0{\cdot}77$, Fig. 2c) of the capacity for nutrient acquisition than the maximum rate of nutrient homogenization and a very efficient seed dispersal ($s^* = 0{\cdot}27$, Fig. 1). Perfect homogenization brought by the non-spatial model (one patch) leads to a higher evolved capacity for nutrient acquisition than the mere homogenization ($H = 10$) of mineral nutrient availability (Fig. 2c). In the case of perfect homogenization, inputs of nutrient no longer impact the evolved capacity for nutrient acquisition.

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

ECOSYSTEM PROPERTIES AT THE EVOLUTIONARY EQUILIBRIUM

Figure 3 describes the ecological effect of the investment into nutrient acquisition (s) and nutrient inputs (R_N) on

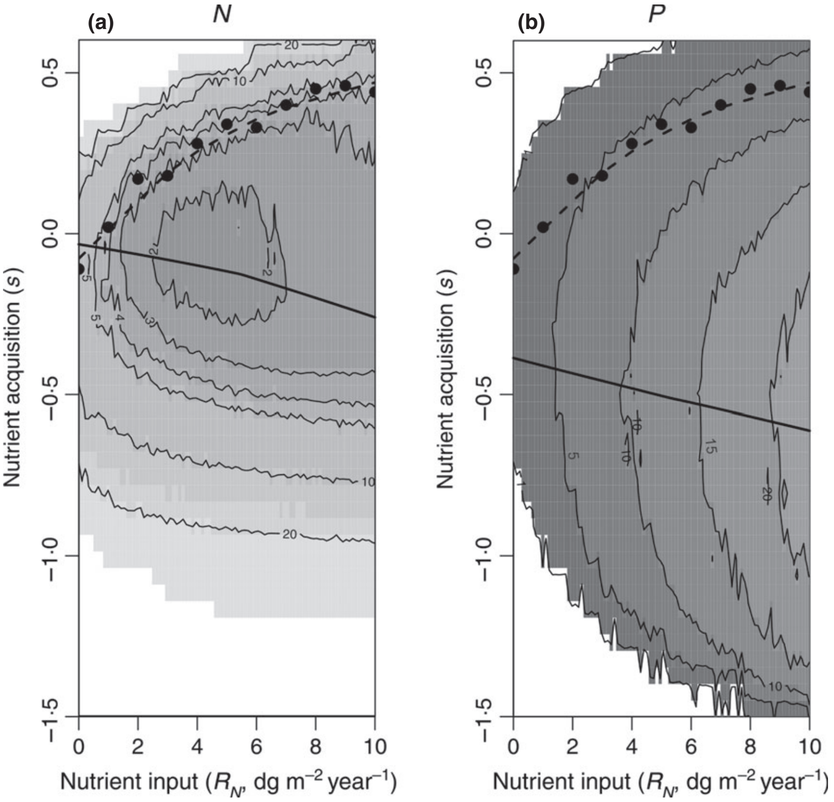

Fig. 3. Contour plots of the joint effect of the capacity for nutrient acquisition (s) and the inputs of mineral nutrients into the ecosystem (R_N) on (a) the mean availability of mineral nutrient (N) and (b) the mean size of the primary producer compartment (P). The thick solid lines denote the position of (a) the minimum N value, (b) the maximum P 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. See Table 1 for parameter values.

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

Discussion

SPATIALIZATION AND LOW HOMOGENIZING FLUXES ALLOW FOR THE EVOLUTION OF ALTRUIST NUTRIENT STRATEGIES

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

It is logical that increasing dispersal and increasing resource homogeneity lead to s* values closer to the ones obtained for the non-spatial model (only one patch) where only local competition occurs. The non-spatial model, resource homogenization and efficient dispersal lead to high s* values because competition for a shared resource favours strategies that increase the acquisition of the resource (Rankin, Bargum & Kokko 2007). In the non-spatial model, the resource is fully shared by all individuals, while with homogenizing fluxes of nutrient, the resource is only partially shared. In the same vein, when dispersal ability increases, plants with alternative competing strategies are more likely to compete for the same local resource in the same patches. In the non-spatial model and in the fully homogenized version of the model, the mineral resource is fully shared by all individuals, but the former case leads to much higher s* values. Indeed, in the non-spatial model, only local competition for the nutrient acts as a selective pressure unaltered by any spatial process while, in the homogenized models, mutants are locally selected by local competition but still have to invade the whole population, which requires producing seeds and dispersing them, thus involving regional competition.

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

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

NUTRIENT ENRICHMENT SELECTS FOR HIGHER RATES OF RESOURCE ACQUISITION

In our spatial model, increasing nutrient inputs to the ecosystem (Fig. 2), increasing the mineralization rate and decreasing the rate of nutrient loss from the ecosystem (Fig. S3) lead to the evolution of higher rates of nutrient acquisition. These three parameters influence three features in interactions along the eco-evolutionary dynamics implemented in the model: the mean availability of mineral nutrient, the variability in this availability and the number of individual plants in each patch. Two arguments support the important role played by heterogeneity in nutrient availability and the number of individuals in a patch: first, in the mean-field analytical model (Boudsocq, Barot & Loeuille 2011) and in the non-spatial version of our simulation model (only one patch), the evolutionary effect of resource enrichment disappears. In our spatial model, individuals with a higher rate of nutrient uptake benefit more from this strategy, on average, if the heterogeneity in nutrient availability is low. Indeed, in a patch with a low nutrient availability, a higher rate of nutrient uptake leads for an individual to a low increase in the nutrient acquired by this mutant that nevertheless pays a high cost for this increase in terms of nutrient turnover because of the trade-off. Secondly, we have shown that homogenizing fluxes affect the evolution of the investment into nutrient acquisition because they modulate the respective influence of local and regional competition, which is another way to state that they modulate the number of individuals that are locally competing for the same resource. Thus, the evolved investment into nutrient acquisition should increase with the mean number of individuals in each patch, that is in each competitive neighbourhood, as with homogenizing fluxes.

This general rationale is supported by complementary results. An important difference between the spatial and non-spatial models is that spatial models allow for heterogeneity in nutrient availability. In our simulation model, this heterogeneity is sustained by the stochasticity in plant demography. For example, if several individuals die at the same time in a patch, more mineral nutrient is likely to be locally available (more organic matter to be mineralized and less biomass to take up mineral nutrients). Thus, the local dynamics of nutrient pools are a permanent succession of transient dynamics (see Fig. S5). This allows an increase in nutrient inputs (R_N), an increase in the mineralization rate (m_D) and a decrease in the rate of nutrient loss from the ecosystem (l_N) to modify the average mineral nutrient availability and the spatial and temporal variability in this availability (see Fig. S6 for nutrient inputs). On the contrary, in the analytical non-spatial model, nutrient availability is kept at an equilibrium that does not depend on nutrient inputs, mineralization or the rate of mineral nutrient loss from the ecosystem (see formula for the ecological equilibrium, Boudsocq, Barot & Loeuille 2011). Figure S6 shows that at the ecological scale (the acquisition of mineral nutrient is not allowed to evolve), the variability in the availability of mineral nutrient always decreases with inputs of mineral nutrient, while the mean availability of mineral nutrient may increase or decrease with these inputs. Moreover, at the evolutionary equilibrium, the number of individuals by patch also always increases with nutrient inputs (see Fig. S7).

While it is beyond the objective of this article to fully disentangle the ecological and evolutionary feedbacks between local resource availability, its heterogeneity and the local density of plants, a way to study these feedbacks is to disrupt them. Figure S8 shows that constraining the maximum number of individuals to one individual reverses the effect of nutrient inputs: increasing nutrient inputs decreases the evolved investment into nutrient acquisition. This suggests that (i) when a maximum of one individual by patch is allowed, increasing nutrient inputs leads to the evolution of lower rates of nutrient uptake because more resource becomes available for a single individual and because lower rates of uptake allow absorbing large quantity of nutrient; (ii) when the number of individuals by patch is allowed to increase due to an increase in nutrient inputs (see Figs S6 and S7), higher uptake rates evolve precisely because the number of individuals sharing the local resource increases. These results, the comparison between the spatial and non-spatial models and the effects of homogenizing fluxes confirm that heterogeneity in nutrient availability and local density in competitors determine the evolutionary effects of nutrient enrichment. This general interpretation is parsimonious: the effects of nutrient enrichment, seed dispersal and heterogeneity in nutrient availability would all be linked to the way these processes modulate the balance between local and regional competition and the number of individuals sharing the same local mineral resource. When nutrient inputs increase, the number of locally competing individuals increases, which leads to a stronger evolutionary influence of local competition, and a stronger selection for nutrient acquisition, as when seed dispersal or homogenizing fluxes of nutrient increase. In both cases (homogenizing fluxes and nutrient enrichment), the local pools of mineral nutrient are more shared or shared among more individuals.

EVOLUTION OF ACQUISITIVE AND CONSERVATIVE PLANTS

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

Our model is too simple to predict specific traits of low- and high-nutrient plants such as shoot–root ratio, root length or defences against herbivores. Similarly, it does not take into account the interactions between competition for light (i.e. carbon) and nutrient (see above). However, the generality of our model uncovers fundamental aspects of the evolutionary consequences of competition for a limiting but recycled resource: (i) the trade-off we implement is the most fundamental one concerning the management of a resource by an organism. How efficiently does the organism capture the resource? How long is it able to conserve it? (ii) The existence of this trade-off that constrains the evolution of acquisitive and conservative plants is supported by several documented mechanisms. First, the investment into nutrient acquisition may reduce the investment into defences against herbivores and protective structures (Herms & Mattson 1992). Note that this suggests that our results also give an evolutionary support for plants in nutrient-poor environments to be more defended against herbivores (Coley, Bryant & Chapin 1985). Secondly, plants that absorb large amounts of mineral nutrient tend to have higher nutrient concentrations in their biomass, which decreases the longevity of roots and leaves and leads to stronger herbivore attacks (Eissenstat *et al.* 2000; Silla & Escudero 2004; Endara & Coley 2011). Thirdly, increasing the capacity to uptake mineral nutrients requires increasing the biomass of roots and especially of thin roots that have a short lifespan. These three mechanisms should increase the turnover of plant biomass and the turnover of the nutrients contained in this biomass. Taken together, our results give some evolutionary support for the existence of a root economic spectrum (Reich & Cornelissen 2014) that parallels the leaf economic spectrum (Wright *et al.* 2004).

We have shown that the evolution of nutrient acquisition depends on individual mortality: the evolutionary effect of nutrient enrichment depends on longevity, and the higher the longevity, the less sensitive the evolved investment into nutrient acquisition to nutrient availability. The full interpretation of this result goes beyond the objectives of this article, but this confirms that nutrient acquisition strategies should interact with life history traits (e.g. individual mortality, investment into reproduction, age at first reproduction, seed size, dispersal). Together, they modulate the influence of local and regional competition and influence plant capacity to conserve mineral nutrients (e.g. long-lived plants conserve mineral nutrients longer than annuals). Our framework could thus allow testing further the evolutionary background of plant functional classifications that also involve plant life histories (Grime 2001; Craine 2009). This would require studying the joint evolution of functional and demographic traits and should lead to the evolution of ruderals – the third strategy of Grime's CSR theory – that have not appeared in our present model (see, e.g. Bornhofen, Barot & Lattaud 2011).

IMPACT OF EVOLUTION ON MINERAL NUTRIENT AVAILABILITY

That evolution does not maximize the biomass of the primary producer is caused, as in the original mean-field analytical model (Boudsocq, Barot & Loeuille 2011), by the basic functioning of selection: selection is based on the per capita growth rate of mutants and not on the ultimate biomass or primary productivity. The non-minimization of the evolved average nutrient availability (N^*) contradicts both the non-spatial evolutionary model (Boudsocq, Barot & Loeuille 2011) and Tilman's R* theory (Tilman 1982). This influential theory suggests that the ecological dynamics of species replacement due to competition for a limiting single resource should lead to the exclusion of all species but the one that reduces the most the mineral resource availability at equilibrium. Our new result must stem from the combination of local and regional competition and the impeding of the minimization of nutrient availability by regional competition (Loreau 1998). Indeed, local competition is only based on plant capacity to absorb mineral nutrient, while regional competition requires plant individuals to be large enough and to be able to invest enough resource into seed production and seed dispersal. Local competition thus tends to select for high rates of nutrient uptake, while regional competition tends to select, in a density-dependent way, for lower rates of nutrient uptake allowing plants to be larger and to invest more into seed production. Besides, homogenization of the availability of the mineral resource and an efficient dispersal increase the influence of competition for the mineral resource because these processes drive this resource to be more evenly distributed among individual plants and the strategies they represent. Therefore, homogenization of the resource and seed dispersal decrease the difference between the evolved availability of mineral nutrient and the lowest possible availability of mineral nutrient (Fig. S4), this difference being caused by regional competition. As aquatic systems are supposedly more homogeneous than terrestrial systems, our results might explain why most conclusive positive tests of the R* theory have been achieved in aquatic systems (Miller *et al.* 2005) and very few, apart from Tilman's initial studies (Tilman & Wedin 1991; Wedin & Tilman 1993), in terrestrial systems.

Conclusion

Our results about the evolution of nutrient acquisition in a spatial context and former results about the evolution of plant capacity to control mineralization (Barot *et al.* 2014) support each other and are complementary. Since mineralization does not impact individual fitness directly, but only through a modification of the availability of the mineral resource, higher mineralization cannot evolve at all in a non-spatial model. On the contrary, nutrient acquisition directly impacts individual fitness so that spatial processes only modify the evolution of nutrient acquisition predicted by the non-spatial model (Boudsocq, Barot & Loeuille 2011). However, in both cases, the relative influence of local and regional competition determines the evolutionary dynamics and leads to comparable results: (i) in Barot *et al.* (2014), homogenization (through seed dispersal or homogenizing fluxes of nutrient) leads to the evolution of lower mineralization rate, while in the present work, homogenization leads to the evolution of higher rates of nutrient uptake. (ii) In Barot *et al.* (2014), nutrient enrichment leads to lower mineralization rates, while in the present work, it leads to higher rates of nutrient uptake. (iii) Both in Barot *et al.* (2014) and in the present work, the mixture of local and regional competition does not lead through evolution to the maximization of the plant biomass or the minimization of the availability of the mineral nutrient. We contend here that a low rate of nutrient uptake can be considered as an altruist strategy because it leaves more mineral nutrient available to other plants (see above and a classical definition, Hamilton 1963). Considering a high rate of mineralization as an altruist strategy is probably even more obvious because it directly increases the availability of the mineral resource for all plants of the local patch, while the plant that increases mineralization is the only one to bear the cost of this increase in mineralization (the plant losses more nutrient). With this joint interpretation of low rates of nutrient uptake and high rates of mineralization as altruist strategies, the results of the present work and the model by Barot *et al.* (2014) are fully consistent. The higher the influence of local competition, the less altruist the evolved strategy: the evolved rate of mineral nutrient acquisition becomes higher and the evolved decomposition rate lower. Similarly, an increase in nutrient inputs pushes plants towards less altruist strategies probably because an increase in nutrient inputs tends to increase the local densities in competitors (see above).

Starting from a very simple and general analytical model based on plant biomass, we have added some realistic features of plant competition: interaction between local and regional competition and some simple features of plant demography. The resulting model remains general and theoretical. Some features of the model may appear as unrealistic, but our work has paved the way to the implementation of many other influential mechanisms to test the robustness of our results: (i) plasticity in the investment into nutrient acquisition depending on nutrient availability and local density of competitors (Cahill *et al.* 2010), (ii) more refine functions for nutrient uptake and local competition (see, e.g. results in Raynaud & Leadley 2004), (iii) implementation of more realistic lateral nutrient fluxes corresponding to particular mechanisms (e.g. impact of herbivores) and interactions between lateral fluxes of mineral nutrient and dead organic matter (Gravel *et al.* 2010), (iv) more realistic life cycles to represent particular plant types (e.g. size-dependent survival, age at first reproduction, different seed sizes), (v) co-evolution between nutrient acquisition and life history traits such as the investment into seed production or dispersal (Craine 2009; Suzuki &

Kimura 2011), (vi) different shapes of trade-off (de Mazancourt & Dieckmann 2004) between nutrient acquisition and nutrient turnover. In particular, while our model always leads to the selection of a single nutrient uptake strategy, point (ii) and the use of an uptake function increasing with biomass with a downward curvature (Rastetter & Ågren 2002) should allow the coexistence of various strategies and may thus lead to the diversification of the strategy of nutrient acquisition through evolutionary branching (Geritz *et al.* 1998).

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

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Data accessibility

This is a modelling paper. All information regarding the models is in the paper and supporting information.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

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

Fig. S2. Example of evolutionary dynamics.

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

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.

Fig. S5. Examples of ecological dynamics in one patch showing temporal variations in the availability of mineral nutrient and the number of plant individuals.

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.

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

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 patch.