SPECIAL FEATURE

THE TREE OF LIFE IN ECOSYSTEMS

Nutrient enrichment and local competition influence the evolution of plant mineralization strategy: a modelling approach

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Summary

1. It is important to study how evolution impacts on plant functional traits and to determine how this subsequently determines ecosystem functioning. We tackle this general issue by studying the evolution of plant strategies that affect mineralization through the chemical quality of their own litter and their position on the leaf economic spectrum. This spectrum allows us to classify all plants on a single axis ranging from resource-acquisitive to resource-conservative strategies.

2. We build a spatially explicit and individual-based simulation model: individual plants grow in the cells of a lattice and the limiting nutrient is recycled locally in these cells. Individual plants may die and produce seeds that are dispersed. Mutants with different mineralization strategies appear stochastically. A trade-off is implemented between the rate of nutrient loss from plants and litter mineralization.

3. In the spatial-explicit model, plant capacity to increase mineralization evolves and reaches an evolutionary equilibrium in most cases. The evolved mineralization decreases with plant longevity, seed dispersal efficiency, spatial homogenization of mineral nutrient availability and inputs of mineral nutrient to the ecosystem.

4. The evolved mineralization strategies neither maximize plant biomass, nor minimize the availability of mineral nutrient or the stock of dead organic matter. The evolutionary and ecological impacts of nutrient enrichment on the stock of organic matter are different.

5. *Synthesis*. Our results suggest that plant mineralization strategy may evolve provided that the mineral resource is not fully shared by all individuals. Such an evolution modifies soil capacity to store organic carbon thereby being relevant in the context of the current climate change and global nutrient enrichment. Indeed, our model shows that evolutionary feedbacks of plants to nutrient enrichment are likely to differ from purely ecological feedbacks.

Key-words: adaptive dynamics, evolution of altruism, leaf economic spectrum, leaf traits, litter quality, nutrient cycling, plant–soil (below-ground) interactions, response and effect traits, spatial individual-based model

Introduction

It has been recognized for a long time that plants may partially control mineralization through the quality of their litter. Litters that have a high content in mineral nutrients tend to decompose faster (Melillo, Aber & Muratore 1982; Aerts 1997) and some plants accumulate metabolites such as tannins that slow down litter decomposition (Grime *et al.* 1996; Schimel, Cates & Ruess 1998). It has already been suggested that plant litter decomposability influences plant fitness (Wedin & Tilman 1990; Berendse 1994), and models have shown that this decomposability may determine the outcome of competition between

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plant strategies (Miki & Kondoh 2002; Clark *et al.* 2005). Data are now gathering to show that leaf traits linked to litter decomposition are submitted to evolutionary pressures (Donovan *et al.* 2011). However, functional ecology and soil ecology are less theory-oriented than other fields of ecology (Barot *et al.* 2007) and, as far as we know, no model has been built to predict the evolution of plant mineralization strategies and factors influencing this evolution.

The general idea that emerges from the literature is that higher mineralization rate increases primary production (Vitousek 1982). Accelerating nutrient recycling releases mineral nutrients that can be again taken up by plants. However, three arguments suggest that plant species should not evolve the maximum possible mineralization. (i) As all traits allowing organisms to modify their abiotic environment, a higher mineralization rate may benefit all neighbouring plants because released mineral nutrients are available to them all. If all individuals share the same mineral resource (as might be the case in aquatic systems), mutants increasing mineralization might not be favoured as there might not be any selection pressure on the mineralization strategy. In contrast, if the mineral resource is not fully shared among all primary producers (as for terrestrial plants), mutants increasing mineralization might benefit from the local increase in mineral nutrient availability and could be selected. (ii) Successful plants in nutrient competition are supposed to be the ones that reduce the availability of mineral nutrient to lower levels than their competitors (Tilman 1988) while mineralization increases nutrient availability. (iii) Controlling mineralization has also disadvantages and impacts other plant traits. Increasing litter mineralization through high nitrogen content, low nutrient resorption, reduction in defensive traits (e.g. low content in lignin or tannins) should lead to higher losses of mineral nutrients from plants (higher rates of herbivory, lower leaf life span) (Vitousek 1982; Grime *et al.* 1996; Aerts 1997; Cornelissen *et al.* 1999; Cornwell *et al.* 2008; Endara & Coley 2011). Conversely, plants that reduce their nutrient losses are likely to support lower rates of nutrient return due to the lower mineralization of their litter. Evolution is likely to have selected diverse strategies leading to wide-ranging mineralization strategies and corresponding to different positions on the leaf economic spectrum. This spectrum allows classifying all plants according to their leaf traits along a single axis of variation ranging from resource-acquisitive to resource-conservative strategies (Wright *et al.* 2004).

Inputs of mineral nutrient to ecosystems influence their fertility and should impact the evolved mineralization strategy. Studying this impact is relevant for two main reasons. First, plants from fertile and unfertile habitats have contrasting growth strategies. Plants from nutrient-poor habitats tend to have litters that decompose slowly due to high concentrations in secondary compounds (e.g. tannins) and low concentrations in mineral nutrients. The reverse should hold for plants of nutrient-rich habitats. While data give some support to these views (Grime 1977; Pastor, Aber & McClaugherty 1984; Aerts & Chapin 2000), the ultimate causes of this pattern are not clear but can be investigated with an evolutionary model. Secondly, global changes and increased human pressures on the functioning of the biosphere (Vitousek *et al.* 1997b) have increased mineral nutrient availability in many ecosystems, for example through the use of mineral fertilizers and fossil fuel combustion. This nutrient enrichment has many known consequences for ecosystem functioning (Vitousek *et al.* 1997a). It should also impact the evolution of plant strategies, for example their mineralization strategy. While evolutionary impacts of global changes have already been studied (Jump & Peñuelas 2005; Bradshaw & Holzapfel 2006), evolutionary responses of functional traits have been studied infrequently. Such evolutionary responses could be critical as they likely feedback on global change. For example, if the global nutrient enrichment drives plant evolution towards lower mineralization, this could allow ecosystems to store more dead organic matter and could partly compensate the climatic effect of the current increase in CO_2 atmospheric concentration.

Our objectives are to: (i) show that plant mineralization strategies may evolve, only if the mineral nutrient resource is not shared among all individuals, (ii) determine how the evolved plant mineralization strategies change along a fertility gradient, (iii) analyse the impacts of evolved mineralization strategy on ecosystem properties and on their capacity to stock dead organic matter. To reach these goals, we build two evolutionary models considering a trade-off between plant capacity to influence the mineralization of its litter and plant nutrient turnover. First, we use an analytical mean-field model of nutrient cycling (Boudsocq, Barot & Loeuille 2011). Using adaptive dynamics (Dieckmann & Law 1996; Geritz *et al.* 1998), we show that this model does not allow for the evolution of higher mineralization rates. Secondly, based on this first model, we built a spatially explicit individual-based model that simulates the recycling of a limiting nutrient in the cells of a lattice and competition between individuals that may have different mineralization strategies. Using this model, we compare non-spatial simulations (only one large cell) to spatial simulations (20 × 20 smaller cells) test whether only spatial simulations allow for a realistic evolution of litter mineralization.

Note that objective (ii) emphasizes that plant traits determining litter quality and subsequently its mineralization are response traits (i.e. traits that affect plant fitness), while objective (iii) emphasizes that the same traits modify ecosystem functioning, that is, they are also effect traits (Lavorel & Garnier 2002). We thus model here a case where effect and response traits are correlated. We do not tackle the evolution of effect traits influencing mineralization together with response traits, for example seed size, that are not directly linked to these effect traits.

Materials and methods

THE ANALYTICAL MEAN-FIELD MODEL

Our analytical model is derived from a simple non-spatial model of the recycling of a limiting nutrient between three compartments: plants (*P*), dead organic matter (*D*) and mineral nutrient (*N*) (Boudsocq, Barot & Loeuille 2011). This model is based on the stocks of

mineral nutrient that are expressed as a quantity of mineral nutrient by surface unit (decigram m^{-2}, hereafter dg m^{-2}). The nutrient is recycled via internal recycling rates: the rate of nutrient loss of plants (d_P), the mineralization rate of dead organic matter (m_D) and the uptake of the mineral nutrient by P (u_N). All corresponding fluxes are considered to be donor-controlled (e.g. the flux of mineralized nutrient is $m_D D$) except for nutrient uptake that is proportional to the product of plant and mineral nutrient compartments. The ecosystem is considered open. Nutrient inputs are fixed and independent of the size of the nutrient pools of the ecosystem: inputs of nutrient in its organic (R_D) and mineral (R_N) forms are considered. Nutrients diffuse out of the ecosystem through fixed rates, respectively 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 (dissolved organic matter) (l_D). Mineral nutrients are lost through leaching and denitrification (l_N). This leads to the following system of equations:

$$\frac{dP}{dt} = u_N NP - (d_P + l_P)P \qquad \text{eqn 1}$$

$$\frac{dD}{dt} = d_P P - (m_D + l_D)D + R_D \qquad \text{eqn 2}$$

$$\frac{dN}{dt} = m_D D - l_N N - u_N NP + R_N \qquad \text{eqn 3}$$

This non-spatial model was first used to study the evolution of the mineralization strategy using the analytical adaptive dynamics framework (Dieckmann & Law 1996; Geritz *et al.* 1998) as achieved before for the evolution of primary producer capacity to take up mineral nutrients (Boudsocq, Barot & Loeuille 2011). We consider that a trait s_m (the mineralization strategy) evolves and is linked to mineralization and the rate of nutrient loss from plants:

$$m_D = m_{D0} e^{b s_m} \qquad \text{eqn 4}$$

$$d_P = d_{P0} e^{c s_m} \qquad \text{eqn 5}$$

b and c are real-valued coefficients defining the trade-off between mineralization and nutrient losses from plants (see justification for this trade-off in introduction). The relation between b and c determines the shape of the trade-off if $b < c$ ($b > c$), the trade-off function is convex (concave); if $b = c$ the trade-off is linear. These two parameters describe quantitatively the trade-off introduced in the introduction between litter mineralization and nutrient losses from the plants due to litter production. They take into account two types of mechanism (Vitousek 1982; Grime *et al.* 1996; Aerts 1997; Cornelissen *et al.* 1999; Cornwell *et al.* 2008; Endara & Coley 2011): (i) Poorly defended leaves tend to decompose faster but are shorter-lived, which leads to high nutrient losses. (ii) Plants with leaves and roots with high nutrient contents and that are not efficient in nutrient resorption support high rates of nutrient losses.

THE SPATIALLY EXPLICIT SIMULATION MODEL

The spatially explicit and individual-based model describes the coupling between competition for a limiting mineral nutrient and the demography of a plant population (see parameters Table 1). It is derived from the mean-field analytical model with two differences: (i) The environment is composed of a lattice of cells. Each cell hosts a local nutrient cycling. (ii) In each cell, there is one nutrient compartment for dead organic matter, a compartment for the mineral nutrient under its mineral form (expressed in dg of mineral nutrient m^{-2}) and one nutrient compartment for each plant individual growing in this cell (expressed in dg of mineral nutrient by individual). Competition for

mineral nutrients is local between individuals growing in the same cell, but there is also competition at the plot scale through seed dispersal. At the end of each time step (i.e. at the end of a vegetation cycle), some individual plants stochastically die and some individuals reproduce (if they are large enough) and their seeds are dispersed. During each time step, growth of individuals occurs in interaction with nutrient cycling, following eqns 6–11 below. Beyond the initial heterogeneity in nutrient availability (availability of mineral nutrient is randomized at the start of each simulation), heterogeneity emerges from local nutrient cycling, plant demography and the underlying stochasticity. Taken together, the model both accounts for stocks and fluxes of the limiting nutrient and for densities and fluxes of individual plants (i.e. death and seed production). The detailed description of the model is given below.

The limiting nutrient is recycled on a lattice of cells: in each cell (subscript j), nutrient cycling is simulated using a modified version of the original non-spatial equations. To simulate the evolution of plant mineralization strategy, the model incorporates competition among individuals (index i) growing in the same cell. These individuals potentially impose different mineralization rates ($m_{Dj,i}$) to the dead organic matter they have produced ($D_{j,i}$) through the quality of their litter (content in mineral nutrients, phenols, lignin, etc.). Mineralization is linked to nutrient losses from plants via the trade-off implemented in the non-spatial model (eqns 10 and 11), so that different individuals may have different nutrient turnover rates ($d_{Pj,i}$, all other parameters remaining equal between all individuals). For each cell j of the lattice the equations thus become:

$$\frac{dP_{j,i}}{dt} = u_N N_j P_{j,i} - (d_{Pj,i} + l_P)P_{j,i} \quad \text{(for each individual } i \text{ of cell } j) \qquad \text{eqn 6}$$

$$\frac{dD_{j,0}}{dt} = -(m_{D0} + l_D)D_{j,0} + R_D \qquad \text{eqn 7}$$

$$\frac{dD_{j,i}}{dt} = d_{Pj,i}P_{j,i} - (m_{Dj,i} + l_D)D_{j,i} \qquad \text{eqn 8}$$
(for each pool i of dead organic matter of cell j)

$$\frac{dN_j}{dt} = \sum m_{Dj,i}D_{j,i} - \left(u_N \sum_i P_{j,i} + l_N\right)N_j + H(\bar{N} - N_j) + R_N \qquad \text{eqn 9}$$

$$m_{Dj,i} = m_{D0} e^{b s_{m j,i}} \quad \text{(for each individual } i \text{ of cell } j) \qquad \text{eqn 10}$$

$$d_{Pj,i} = d_{P0} e^{c s_{m j,i}} \quad \text{(for each individual } i \text{ of cell } j) \qquad \text{eqn 11}$$

D_0 is the pool of organic matter resulting from inputs of organic matter entering into the ecosystem (wet and dry deposits). It has its own mineralization rate (m_{D0}).

We consider the possibility of a homogenization of mineral nutrient availability between cells by adding the quantity $H(\bar{N} - N_j)$ to the N_j value of each cell. H varies between 0 and $+\infty$ and $\bar{N}$ is the mean nutrient availability calculated over all cells of the lattice. This simulates the result of lateral fluxes of mineral nutrient: for $H = 0$, there are no lateral fluxes of mineral nutrient (all local values are kept unchanged). When H increases, lateral fluxes of nutrient increase and nutrient availability tends to homogenize at the plot scale (all local N_j values are equal to $\bar{N}$). When H increases, mineral nutrients produced locally by local plants are more and more shared by all plants of the population. Studying the impact of H constitutes a theoretical experiment to determine the influence of the way the mineral resource is shared at the population scale.

One time step corresponds to a vegetation cycle so that demography is modelled on a per-season basis. In addition to the continuous dynamics described so far, discrete demographic events, that is, mortality and reproduction, occur every time step. While $d_{Pj,i}$ denotes nutrient losses from individual plants due to the death of parts of plants (roots, leaves),

Table 1. List of parameters describing the different nutrient fluxes and the demography of the plants. Default values for the parameters are given

Parameter type	Symbol	Values	Definition
Nutrient recycling within a local cell	d_{P0}	0.275 year^{-1}	Initial rate of nutrient loss through the death of parts of plants (roots, leaves…)
	m_D	0.0766 year^{-1}	Mineralization of dead organic mater
	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
Losses of nutrient	l_P	l_P, 0 year^{-1}	Loss of nutrient due to fires, herbivores or human exportations (forestry, agriculture)
	l_D	0.038 year^{-1}	Loss of dissolved organic matter from soils or water bodies
	l_N	0.05 year^{-1}	Nutrient leaching from soils, denitrification, fluxes of water out
Nutrient fluxes between cells	H	0	Effect of lateral fluxes of nutrient on the heterogeneity in nutrient availability
Demographic parameters	μ	0.5	Individual mortality
	γ	0.3 g	Quantity of nutrient in a seed
	ρ	0.1	The percentage of the nutrient stock of a plant individual allocated to the production of seeds
	σ	1 m	Standard deviation of the cantered normal distribution that determines seed dispersal distances
Trade-off parameters	c	0.25	Costs of the investment in nutrient acquisition in terms of nutrient loss
	b	1	Benefits of the investment in nutrient acquisition

μ denotes individual mortality. The modelled ecosystem thus hosts a unique plant species that can be either long-lived (high μ) or short-lived (low μ). The amount of nutrient contained in dead individuals is transferred to the corresponding dead organic matter compartment ($D_{j,i}$). The parameter ρ defines the proportion of each plant nutrient that is allocated to seed production per season. γ denotes the quantity of nutrients in a seed. The number of produced seeds for individual i is thus int$\left(\frac{P_{j,i}\rho}{\gamma}\right)$, where int denotes the largest previous integer. Seed dispersal is modelled as follows: (i) We choose a random angle (between 0 and 360°) to determine the direction of dispersal. (ii) Dispersal distance follows a centred normal distribution (mean = 0) with standard deviation σ (if the distance is negative 180° is added to the original angle). (iii) Depending on the angle and the distance of dispersion the seed stays in the cell of the parent plant or is moved to another cell. Individuals falling under a threshold stock of mineral nutrient (i.e. the stock of mineral nutrient of a seed, γ) because they have many competitors and do not have a suitable nutrient strategy also die. When a new seed is dispersed or when an individual dies, the corresponding $P_{j,i}$ (eqn 6) differential equation is created or suppressed in the relevant cell.

As the model cannot be analysed analytically, we rely on numerical simulations. Each seed had a probability of mutation p_m and the size of the mutation was drawn randomly using a centred normal distribution with a standard deviation m. Mutants that have a favourable mineralization strategy (i.e. that allow them to grow through the uptake of mineral nutrient, survive and produce more or higher quality seeds) are able to invade the resident population. Note that the term 'mutants' can here be understood literally to refer to individuals of the modelled species that have a genotype and thus a mineralization strategy slightly different from the resident strategy. The term can also refer to seeds of other species that have been dispersed to the modelled plot and that differ from the resident species by their mineralization strategies. Our model thus predicts changes in the mineralization strategy that arise either through in situ evolutionary processes or through replacement by species representing different evolutionary lineages.

IMPLEMENTATION

A simulation platform, Evolutionary Nutrient Cycling Simulator, has been implemented in Java programming language. The resolution of the differential equations is based on the classical fourth-order Runge–Kutta method with an integration step of $\Delta t = 0.1$. Homogenizing fluxes of mineral nutrient are described by the parameter H that varies between 0 and $+\infty$. In our simulations, H ranged between 0 and 10 because preliminary simulations showed that $H = 10$ leads to a homogeneous mineral nutrient availability. The grid size was always composed of 20×20 one-square-metre wide cells except on one occasion (here after one-cell model) where only one cell was modelled but by increasing input of mineral nutrients and organic matter accordingly ($\times 400$) to support the same total biomass as in the 20×20 cells model. This corresponds to a shift from 400 one-square-metre cells to a single 400-m^2 cell. The boundaries of the lattice were wrapped around as a torus.

Parameters chosen for nutrient cycling were inspired from a temperate grassland (Woodmansee, Vallis & Mott 1981) considering one-square-metre wide cells and unless stated: d_{P0}, 0.275 year^{-1}; m_{D0}, 0.0766 year^{-1}; u_N, 1.43 dg^{-1} m^2 year^{-1}; R_D, 2 dg m^{-2} year^{-1}; R_N, 1.8 dg m^{-2} year^{-1}; l_P, 0 year^{-1}; l_D, 0.038 year^{-1}; l_N, 0.05 year^{-1}; b, 1; c, 0.25. Unless stated, we consider a short-lived plant with the following demographic parameters: μ, 0.5; ρ, 0.1; γ, 0.3 g; σ, 1 m. One was always chosen as a starting value for s_m in evolutionary simulations that lead to Figs 2 and 3. For mutations, we always used $p_m = 10^{-4}$ and $m = 0.05$. All simulations were run for 400 000 time steps.

Due to the time duration of simulations, only one replicate simulation was run for each parameter combination. Results (Figs 2 and 3) are smoothed using locally weighted polynomial regressions to better visualize trends.

Results

EVOLUTION OF MINERALIZATION STRATEGY IN THE ANALYTICAL MEAN-FIELD MODEL

During evolution, the fitness of a mutant ($W_{P'}$) with a mineralization strategy s'_m within a resident population with a mineralization strategy s_m is defined by the per capita growth rate of its biomass ($\overset{.}{P'}$) in the resident population at equilibrium

(Metz, Nisbet & Geritz 1992; Dieckmann & Law 1996):

$$W_{P'}\left(s'_m, s_m\right) = \frac{1}{P'}\frac{dP'}{dt} = u_N N^* - (d'_P + l_P)$$

where N^* is the mineral nutrient compartment at its ecological equilibrium imposed by the resident strategy (this assumes a separation between ecological and evolutionary time-scales). Using equation 1–3 to derive the equilibrium formula (see also Boudsocq, Barot & Loeuille (2011), eqn 2.2), this leads to:

$$W_{P'}\left(s'_m, s_m\right) = u_N \frac{d_{P0}e^{cs_m} + l_P}{u_N} - (d_{P0}e^{cs'_m} + l_P)$$
$$= d_{P0}\left(e^{cs_m} - e^{cs'_m}\right).$$

This invasion fitness is positive if and only if the mutant has a lower value for the evolving trait s_m. The precise expression of the invasion fitness indeed depends on the mathematical expressions we chose for nutrient fluxes. However, the general result arises from a general hypothesis of the adaptive dynamics framework. Mutants start from a very low biomass and cannot influence their environment (here the availability of mineral nutrient) at an early stage of their invasion (Metz, Nisbet & Geritz 1992). Consequently, in a non-spatial analytical model, evolutionary dynamics always pushes towards lower s_m values and thus to lower mineralization.

DIFFERENT TYPES OF EVOLUTIONARY DYNAMICS IN THE SIMULATION SPATIAL MODEL

Figure 1 displays the evolutionary dynamics we encountered with the simulation spatial model. Panels A, C, E and G display for four contrasted cases pairwise invasibility plots (PIP, Geritz *et al.* 1998) that describe the result of an invasion of a resident strategy (s_{m1}) by a mutant (s_{m2}) at low density. Panels B, D, F and H give examples of evolutionary dynamics in the same four cases and with different starting values for s_m. Black dots represent successful invasions (panels A, C, E, G). As opposed to the analytical mean-field model, the invasion of a resident strategy by another strategy becomes a stochastic process in the simulation model. This explains the fuzziness of the observed patterns.

When a single large cell was modelled, we never found any directional evolution (Fig. 1b). The PIP (Fig. 1a) shows that there were very few cases of invasion of the resident population (only a few black dots instead of a black area) and invasion was not more likely when the mutant had a higher or lower s_m value than the resident population (blacks dots are evenly distributed above and below the first diagonal).

With a lattice of 20 × 20 cells, two types of evolutionary dynamics were possible: evolution towards a continuously stable strategy or runaway evolution. In most cases, simulations led to an evolutionary equilibrium, s_m^*. The invasion of resident strategies below s_m^* is only possible for mutants with higher s_m values than the resident strategy (black area above the diagonal), while the reverse was true for resident strategies above s_m^* (Fig. 1c). Evolution through successive
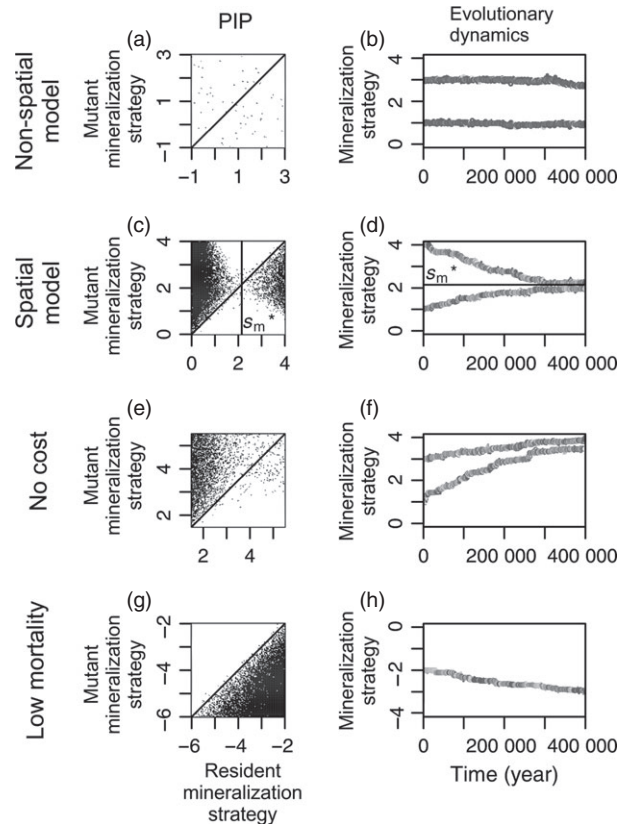

Fig. 1. Pairwise-invasibility plots (PIP, a, c, e, g) together with examples of corresponding evolutionary dynamics (b, d, f, h) of the mineralization strategy (s_m). These results were obtained with the simulation spatially explicit model. A, B, non-spatial model (only one cell); c, d, spatial model (20 × 20 cells); E, F, spatial model (20 × 20 cells) with no cost of the control of litter quality ($c = 0$); g, h, spatial model with lower mortality, $\mu = 0.1$. For PIPs, each black dot corresponds to a simulation that leads to the successful invasion of a resident population at its ecological equilibrium (value on the x axis) by a mutant (value on the y axis) starting at a very low density. In these simulations, s_m values are not allowed to evolve. s_m values for the resident populations and mutants were explored systematically with a step of 0.025 so that each PIP is based on 161 × 161 invasion simulations. Examples of evolutionary dynamics starting from different mineralization strategies are displayed in each case. A-B corresponds to an evolutionary drift (no directional selection), c–d to a CSS, E-F to a runaway evolution towards higher mineralization, G-H to a runaway evolution towards lower mineralization.

replacement by new mutants drove the mineralization strategy towards s_m^* (Fig. 1d). Because no strategy could invade a resident strategy at s_m^* (white areas above and below the diagonal at s_m^*), evolution stopped at s_m^*. This strategy is named continuously stable strategy (CSS, Geritz *et al.* 1998), because it can be reached through natural selection and cannot be invaded by any other strategy.

When there was no cost to an increased mineralization ($c = 0$), invasion by mutants was mostly possible when they had a higher s_m value than the resident population (black dots above the first diagonal, Fig. 1e). This led to a runaway evolution towards higher s_m, that is, plants kept evolving higher mineralization. However, the rate of evolution decreased for high s_m values (Fig. 1f). Relative fitness advantages became

progressively smaller when s_m increased. As the fitness landscape flattens, variations in trait became slow and s_m reached a pseudoequilibrium.

When mortality was low ($\mu = 0.1$) runaway evolution led to ever decreasing s_m values (Fig. 1g–h). In the PIP, this is shown by the black dots under the first diagonal. This type of evolutionary dynamics was also found (see Fig. 2) for $\mu = 0.01$ and for high dispersal capacities ($\sigma = 5$). In these cases, s_m did not reach an equilibrium but had lower values than the equilibrium values reached for higher mortality and lower dispersal.

IMPACT OF NUTRIENT ENRICHMENT ON THE EVOLVED MINERALIZATION STRATEGY

In most cases, regardless of the trade-off, mortality, homogenizing fluxes of nutrient and dispersal, the evolved s_m value decreased with nutrient inputs to the ecosystem, R_n (Fig. 2). The only exception was for the non-spatial, that is, only one cell, simulation model (Fig. 2c) that did not lead to any directional evolution (Fig. 1). Thus, in this case, the evolved s_m values did not change with nutrient inputs and only depended on the initial values chosen for s_m. In all cases leading to a CSS, s_m^* decreased with R_n. Even in cases of runaway evolution towards lower values (low mortality $\mu = 0.01$ or

$\mu = 0.1$; high dispersal, $\sigma = 5$), s_m values found at the end of the simulations followed the same rule.

As expected, the higher the cost of increasing mineralization (c), the lower the evolved mineralization (the lower s_m^*, Fig. 2a). The evolved mineralization increased with individual mortality (i.e. decreases with plant longevity, Fig. 2b). The evolved mineralization decreased with the intensity of lateral fluxes of nutrients (H, Fig. 2c) and with fluxes of seeds (dispersal, σ).

IMPACT OF THE EVOLUTION OF THE MINERALIZATION STRATEGY ON ECOSYSTEM PROPERTIES

Figure 3 (a,b) shows (in the case of a 20×20 lattice of cells) how evolution of the mineralization strategy impacted upon abiotic properties of the ecosystem such as the mean N and D stocks, once the mineralization strategy had reached its evolutionary equilibrium (s_m^*). These ecological properties at the evolutionary equilibrium are noted N^* and D^*. Values are displayed as a function of nutrient inputs and the trade-off shape (parameter c). Counter-intuitively, when nutrient inputs increased, N^* decreased or increased depending on the trade-off (Fig. 3a). Stocks of dead organic matter at the evolutionary equilibrium increased with nutrient inputs (Fig. 3b). This is due to the fact that increasing inputs of nutrient decreased
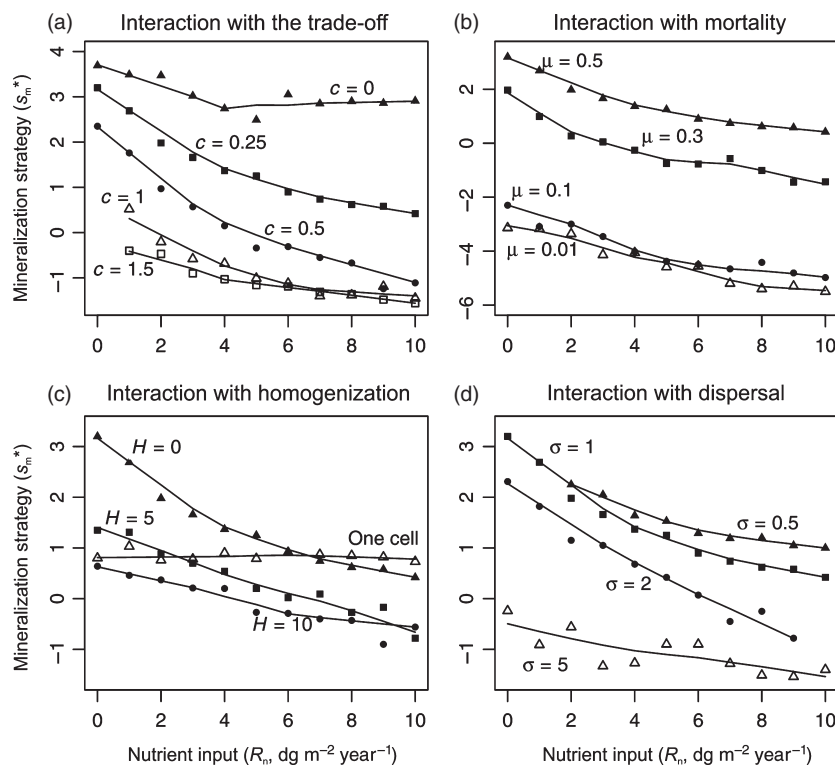

Fig. 2. Effect of inputs of mineral nutrients to the ecosystem (R_n) on the mineralization strategy (s_m^*) that evolves in the simulation spatially explicit model. The impact of different cofactors is also displayed: (a) the trade-off parameter c. (b) individual mortality μ, (c) the intensity of homogenization H (in this case '1 cell' denotes non-spatial simulations with only one cell), (d) the efficiency of dispersal σ. Nearly, all points correspond to evolutionary equilibriums (CSS, see text for details), but long-lived plants ($\mu = 0.01$ or $\mu = 0.1$) or efficient dispersal ($\sigma = 5$) leads to run away evolution towards lower mineralization and the absence of a cost to increase mineralization ($c = 0$) leads to runaway evolution towards higher mineralization (see Fig. 1). In these cases, s_m values displayed are values obtained at the end of simulations and depend on initial s_m values. See Table 1 for parameter values.
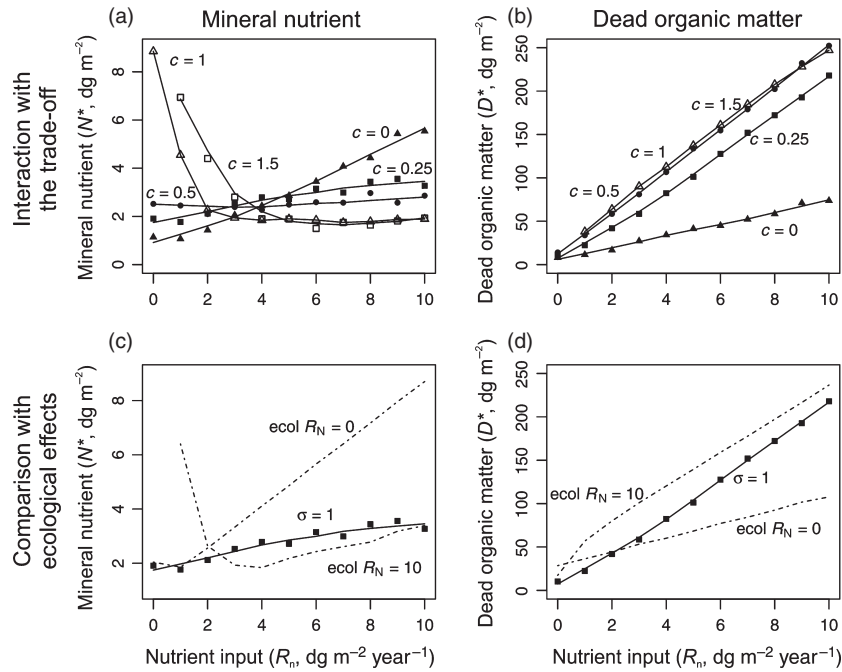
Fig. 3. Effect of inputs of mineral nutrients to the ecosystem (R_n) on the ecosystem characteristics (N^*, panels a, c; D^*, panels b, d) resulting from the evolution of the mineralization strategy (s_m). These results were obtained with the simulation spatially explicit model (20×20 cells) and as a function of the trade-off parameter c. Panels C and D compare the evolutionary effect of nutrient inputs with their ecological effects: the dashed lines are produced without allowing s_m to evolve either using for this trait the evolutionary equilibrium value obtained with low nutrient inputs (ecol $R_N = 0$) or high nutrient inputs (ecol $R_N = 10$). See Table 1 for parameter values.

mineralization at the evolutionary scale (Fig. 2). The evolutionary and ecological impacts of nutrient enrichment differed (Fig. 3c,d). Evolution decreased the response of the mineral nutrient pool (N^*) to nutrient enrichment (Fig. 3c). When s_m was fixed to its evolutionary equilibrium for low nutrient inputs, D^* increased with nutrient enrichment (Fig. 3d). When s_m was allowed to evolve, D^* increased in a much steeper way. When s_m was fixed to its evolutionary equilibrium for high nutrient inputs, D^* increased with nutrient enrichment slightly quicker than when s_m was allowed to evolve.

Figure 4 displays (in the case of a 20×20 lattice of cells) contour plots for N, P and D at their ecological equilibrium as a function of the mineralization strategy and nutrient inputs. To these contour plots, for each value of nutrient inputs, the evolved s_m^* equilibrium value is superposed as well as the s_m value that minimized N (Fig. 4a) and the value that maximized P (Fig. 4b). This shows that the evolved mineralization strategy neither minimized N nor maximized P. Similarly, the evolved mineralization strategy led to intermediate D values: lower/higher D values could be reached with higher/lower s_m values.

Discussion

EVOLUTION OF THE MINERALIZATION STRATEGY REQUIRES A SPATIALLY STRUCTURED RESOURCE

Our model suggests that spatial structuring in which local partitioning of nutrient pools exists allows the evolution of

stronger controls of mineralization by plants. Modelling the evolution of the mineralization strategy requires a spatially explicit model. The mean-field analytical approximation only leads to runaway evolution towards ever lower mineralization, because, within the adaptive dynamics framework (Metz, Nisbet & Geritz 1992), mutants start with a low biomass and cannot impact on their environment significantly. The one-cell version of the individual-based model does not allow for any directional evolution towards intermediate mineralization strategies. In such well-mixed conditions, the fitness of mutants only depends on the cost they pay for their mineralization strategy. Benefits in terms of mineral nutrient availability disappear as they are equally shared by all individuals regardless of their traits. Consider two scenarios, (i) when cells are small (one square metre), there is a low number of individuals (fewer than 50) competing for the local nutrient resource, (ii) when there is only one large cell ($400 \, \text{m}^2$), this cell contains a large number of individuals (several thousands). In the latter case, mutants triggering a higher mineralization rate have no chance to impact significantly the availability of mineral nutrients and cannot be favoured by evolution. On the contrary, in the former case, when only a few individuals compete for the local mineral resource, mutants with a higher mineralization rate have a chance to grow and reproduce in the local cell because they have a chance to increase significantly the availability of mineral resource and to benefit from this increase. Importantly, while the quantitative results we obtained with the mean-field analytical model and the spatial simulation model
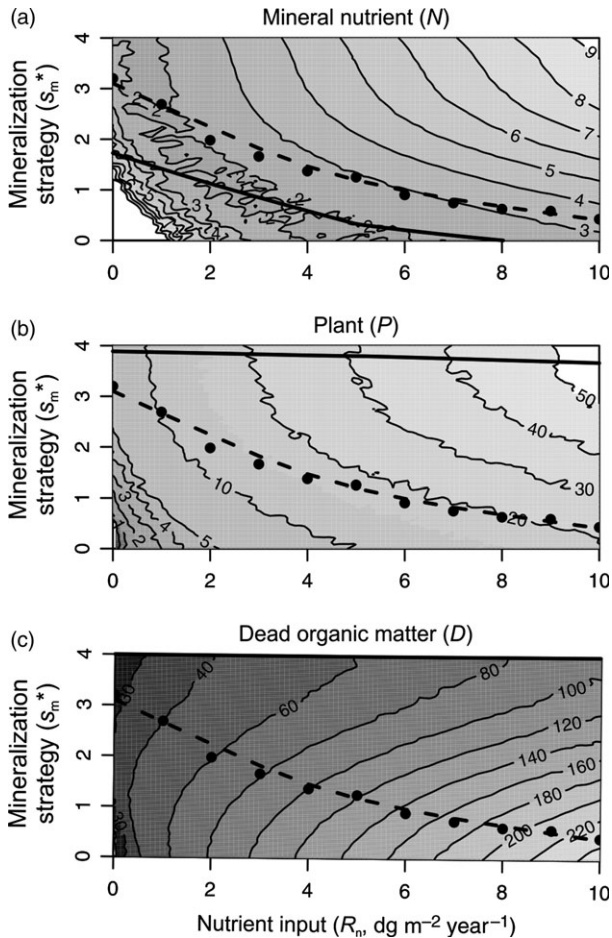
Fig. 4. Simulation spatially explicit model. Contour plot of the effect of the mineralization strategy (s_m) (20×20 cells) and the inputs of mineral nutrients into the ecosystem (R_N) on (i) the mean stock of mineral nutrient (N), (ii) the mean stock of mineral nutrient contained in the plant compartment, summing up the nutrient content of all individuals in each cell (P) and (iii) the mean stock of mineral nutrient contained in dead organic matter (D). For each R_N value, 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_m^*). See Table 1 for parameter values.

depend on the equations chosen for nutrient fluxes (e.g. nutrient uptake is proportional to the product of plant and mineral nutrient compartments), the rationale we develop here to explain why a spatial model is required to model the evolution of the mineralization strategy is general and does not depend on the precise formalism we have used.

We ran complementary simulations showing that evolution is possible as soon as the single 400-m² cell is replaced by 4 100-m² cells (decreasing the input of mineral nutrients to each cell accordingly), but in this case, there is runaway evolution towards ever decreasing mineralization. This result is consistent with our hypothesis that competition between many individuals for the same pool of mineral resource pushes towards the evolution of low mineralization. Indeed, 100-m² cells host about 100 times more individuals as 1-m² cells.

INCREASING MINERALIZATION AS AN ALTRUISTIC TRAIT

Large effects of lateral fluxes of mineral nutrients clearly hint at how important these spatial aspects are for the system's ecological and evolutionary dynamics. Lateral fluxes of nutrient somehow force individuals from different local cells to share their mineral resource. It increases the size of the local competitive neighbourhood. In the same way, if seed dispersal is efficient, mutants with different mineralization strategies are more likely to share their local mineral resource with individuals of the resident strategy. These mutants hardly modify the local availability in mineral nutrient and hardly benefit from such changes. Hence, both dispersal and homogenizing fluxes of nutrient mitigate the impact of spatialization. These processes lead to the evolution of lower mineralization. Based on these resource sharing arguments, increasing mineralization can be viewed as an altruistic trait. Increasing mineralization increases nutrient availability for all individuals sharing the local neighbourhood, even if these individuals do not share the same mineralization strategy and do not bear the cost of this strategy. Congruent with other studies (Pfeiffer, Schuster & Bonhoeffer 2001; Le Gaillard, Ferrière & Dieckmann 2003; Lion & van Baalen 2008), we suggest that evolution of altruistic traits may emerge from spatial heterogeneity and limited dispersal and that the evolution of such traits may be a determinant for many ecosystem properties.

EFFECT OF PLANT LIFE HISTORY

We suggest that long-lived plants should evolve much lower mineralization than short-lived plants. The interpretation would be that short-lived plants strongly depend on the immediate availability of mineral resource to growth and reproduce so that mining the local nutrient resource through mineralization would be very beneficial. On the contrary, long-lived plants may evolve lower mineralization, which leads to larger local stocks of dead organic matter, they can benefit from in the long term. This result is consistent with theories viewing short-/long-lived plants, respectively, as *r* vs. *K* selected organisms or 'Competitors' vs. 'Stress tolerators' that have, respectively, evolved strategies emphasizing the acquisition or the conservation of resources (Grime 2001). Indeed litter decomposition significantly differs between plant functional types, and long-lived, often ligneous, species tend to produce more recalcitrant litters that decompose slower (Cornelissen *et al.* 1999; Cornwell *et al.* 2008). However, the impact of longevity *per se* has not been tested. Surprisingly, litter of graminoids tends to decompose, on average, as slowly as the litter of woody species (Cornwell *et al.* 2008). According to our predictions, this may be due to the fact that many graminoids are long-lived.

Taken together, our results suggest that the evolution of the mineralization strategy likely depends on life-history traits (longevity and seed dispersal). Data confirm that leaf traits and demographic traits such as seed size are correlated (Cornelissen 1999; Westoby & Wright 2003; Wright *et al.* 2010). This means that whilst here we have modelled the

joint evolution of effect and response traits that are tightly linked because they depend on leaf traits, future work should model the joint evolution of the mineralization strategy and independent response traits such as seed size or seed dispersal (Diaz *et al.* 2013). Theoretical results already point to the importance of such joint evolutionary dynamics (Ravigne, Dieckmann & Olivieri 2009; Suzuki & Kimura 2011) that must likely be taken into account to fully understand the evolution of plant strategies (Grime 2001; Craine 2009).

EVOLUTIONARY IMPACT OF NUTRIENT ENRICHMENT

In nutrient-poor ecosystems, plant litter tends to decompose slowly because of its low nutrient content and defensive characteristics (high contents in lignin, tannins, low-specific leaf area). This could increase nutrient limitation (Vitousek 1982) through a positive feedback. The likely evolutionary mechanism causing this feedback is that plants in nutrient-poor environments should conserve mineral nutrient as much as possible. They should thus have long-lived highly defended nitrogen-poor leaves that decompose slowly. On the contrary, plants in nutrient-rich environments could afford leaves with opposite characteristics (Hobbie 1992; Cornelissen *et al.* 1999; Grime 2001). This has been verified in a global meta-analysis (Ordoñez *et al.* 2009).

The general understanding presented in the previous paragraph contradicts the results of our model that suggests that the evolved mineralization decreases with nutrient inputs. These results can be interpreted in two complementary ways. First, when more mineral nutrient is provided, plants depend less on mineral nutrients stored in dead organic matter. Hence, the cost of a higher mineralization likely outweighs potential benefits. Secondly, when nutrient inputs increase more individuals are allowed to survive locally (see Appendix S1) and share the local resource. This should lead to the evolution of lower mineralization (see the first two sections of the Discussion). It is difficult at this time to solve this contradiction but note that: (i) In this understanding the direction of causality is not clear: Is the evolution of plants leading to low nutrient availability or the reverse? (ii) Our model predicts that increasing nutrient inputs may either decrease or increase nutrient availability depending on the cost paid for mineralization. Hence, the link between overall fertility and nutrient availability is not straightforward. (iii) Our model makes the first general predictions on the evolution of plant mineralization strategy. It can thus be viewed as a null model to further disentangle the complex eco-evolutionary dynamics between ecosystem properties and traits that control nutrient cycling.

THE EVOLUTION OF THE MINERALIZATION STRATEGY IMPACTS ECOSYSTEM PROPERTIES

That evolution does not maximize plant biomass, contrary to earlier theories (Odum 1969), is due to the fact that evolutionary dynamics is based on the individual fitness of mutants and not on any collective properties at the ecological equilibrium (e.g. total biomass or primary production). That

evolution does not minimize the availability of mineral nutrient contradicts models predicting the exclusion of all species but the one that is able to minimize mineral nutrient availability (Tilman 1982). An evolutionary model also predicted the same pattern (Boudsocq, Barot & Loeuille 2011). In our spatial model, the optimization of the exploitation of the local resource is not the only evolutionary strength. Selected strategies must also disperse enough seeds to be competitive at the plot scale. This combination of local and regional competition leads to contradictory evolutionary forces and impedes the minimization of mineral nutrient availability (Loreau 1998).

We suggest that ecosystem responses to nutrient enrichment depend on plant evolution. This adds to ecological mechanisms through which nutrient enrichment enhances nutrient stocks. All else being equal and assuming a constant carbon-to-mineral nutrient ratio, we suggest that evolution could lead to a twofold increase in the stock of soil carbon. Hence, global nutrient enrichment of terrestrial ecosystems (Vitousek *et al.* 1997b; Galloway & Cowling 2002) could mitigate via the evolution of plant strategy the current elevation in atmospheric CO_2 and the subsequent global warming.

Conclusion

Beyond their functional and ecosystem significance, we confirm that traits determining plant position on the leaf economic spectrum and subsequently controlling litter mineralization may play an important role in plant demography and competition (Berendse 1994; Clark *et al.* 2005). In a world under global changes that exert strong selective pressures on ecosystems, understanding the coupling between evolutionary, demographic and functional aspects could be critical (Fussmann, Loreau & Abrams 2007; Matthews *et al.* 2011). Because our model applies virtually to any terrestrial ecosystem, testing our predictions with empirical data could be critical. The model applies both to true evolutionary dynamics and to changes in the mineralization strategy arising from the dynamics of species replacement. Such dynamics, in response to warming, have already been shown to decrease litter mineralization (Cornelissen *et al.* 2007). Species replacement likely leads to quicker changes in ecosystem functioning than evolution. However, world-wide nutrient enrichment is a long-term phenomenon and evolutionary processes are faster than originally assessed (Hairston *et al.* 2005) and may lead to significant evolution over a few generations. More data should be gathered to assess the relative impact of nutrient enrichment on (i) the effect trait composition of plant communities and (ii) the evolution of traits influencing mineralization. Furthermore, our model could be modified to predict the impact of the increase in atmospheric CO_2 and global warming on mineralization strategies and nutrient cycling rates.

Acknowledgments

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Supporting Information

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

Appendix S1. Effect of inputs of mineral nutrients and the mineralization strategy on the density of individuals.