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Differences between soil ammonium and nitrate spatial pattern in six plant communities. Simulated effect on plant populations

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Abstract

Geostatistical descriptions of soil heterogeneity patterns for plant communities are abundant in literature, however no effort has been done to compare spatial structure of different nutrients, and to look for a common pattern in different plant communities. Furthermore, there is no information on the consequences of different soil spatial patterns on resource availability for plant populations. Conditional simulations on the spatial distribution of soil NH_4-N and NO_3-N were carried out in order to study the effect of contrasted patch sizes on N availability for individuals with increasing root system size. The semivariogram range (an indication of patch size) for soil NH_4-N and NO_3-N in six plant communities was found to be very variable, and was higher for soil NH_4-N than for soil NO_3-N in each community. A positive correlation was observed between organic matter and NH_4-N spatial ranges in the six plant communities, but not between NO_3-N and NH_4-N. Probabilities of finding a high soil N concentration within simulated plant populations depended on N patch size and root system size. Thus, a population taking up NH_4-N (higher spatial range values) would be more heterogeneous (i.e. individuals will have differing probabilities of finding a high soil N concentration) than the same population taking up NO_3-N. Likewise, a seedling population taking up NH_4-N or NO_3-N would be more heterogeneous than a large tree population in the same area, where individuals would have similar probability of finding a high soil N concentration. These results showed that the spatial patch size of limiting resources has important consequences at the population level, since it determines the probability of finding a favorable site, and therefore differing performances of individuals within a population.

Introduction

Spatial heterogeneity of physical factors or resources could allow the coexistence of species by favoring different species at different points in space (Tilman, 1982; Tilman and Pacala, 1993). Spatial heterogeneity of essential resources for plants at different spatial scales is a ubiquitous feature of natural ecosystems (Gallardo, 2003a; Guo et al., 2002; Jackson and Caldwell, 1993; Nicotra et al., 1999; Robertson et al., 1997; Schlesinger et al., 1996).

Geostatistical techniques have permitted the quantification of soil heterogeneity pattern and scale in a number of natural communities (Robertson, 1987; Robertson and Gross, 1994; Rossi et al., 1992). Spatial structure is frequently described using two semivariogram parameters: the range (a measure of the patch size) and the percentage of total variance explained by spatial dependence (a measure of uncertainty in spatial

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prediction). In addition to the above descriptive studies, there has been a simultaneous increasing interest on the effect of soil heterogeneity on plant performance (e.g. Caldwell et al., 1996; Hutchings et al., 2003; Reynolds et al., 1997; Ryel and Caldwell, 1998; Wijesinghe et al., 2001). Most of these studies examine the effect of fine-scale heterogeneity (within root systems of individual plants or where root systems overlap), and focus on the effect of spatial heterogeneity on individual performance or pairwise competition. However, less attention was paid to the effects at the population and community levels. Furthermore, information on the effect of heterogeneity on plant performance at scales larger than the rooting area of a plant is scarce, despite the fact that it is likely to affect relative plant performance and contribute to the maintenance of species diversity (Casper and Jackson, 1997; Reynolds et al., 1997; Tilman and Pacala, 1993).

Nitrogen is the element that more frequently limits the primary production in terrestrial ecosystems, therefore its transformations in soil have called the attention of numerous authors (Vitousek and Howarth, 1991). Ammonium derived from organic matter mineralization is being transformed into nitrate through the nitrification process. Both ions are presented in variable concentrations in different ecosystems, and frequently plants show preferences for one or another nitrogen form (Haynes and Goh, 1978). Their different origin and behavior in soils does probably determine different spatial distribution. Comparisons of the spatial distribution of nutrients has received little attention, despite the variability and size of nutrient patches may determine roots proliferation in soils.

The aim of this paper was (i) to study the differences on spatial pattern and scale between soil NH_4 and NO_3 in six natural plant communities, which are generated by independent (but

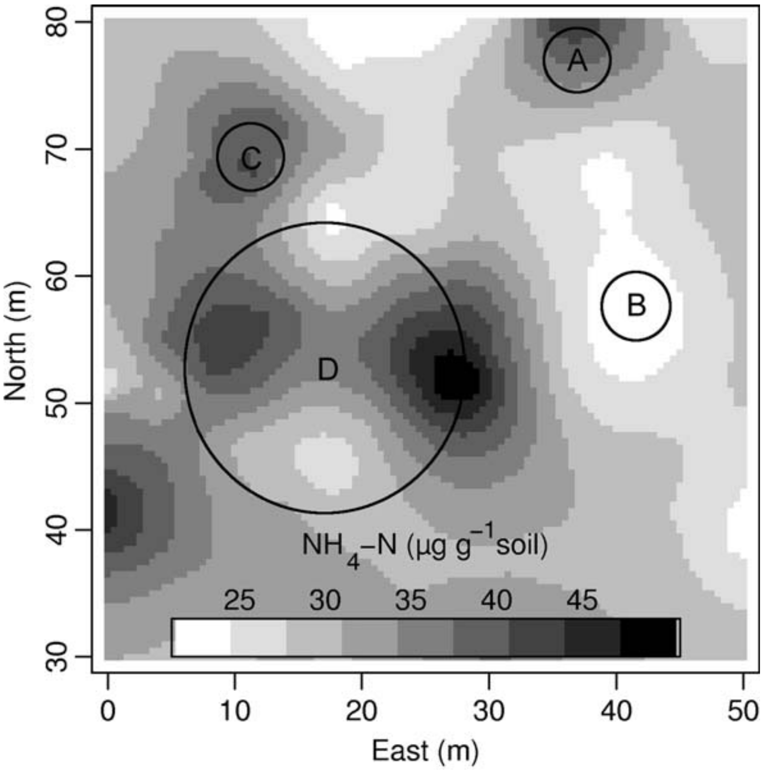

Figure 1. Map of soil NH_4-N concentration obtained by kriging interpolation methods in a section of the pine forest plot. The circles represent the area explored by hypothetical root systems growing on the plot. Small individuals (A, B and C) can be placed on areas with either a high, medium or low mean soil NH_4-N concentration. Large trees (such as D) would occupy a heterogeneous area covering most soil heterogeneity.

connected) microbial processes. Second, how these differences affect N-distribution between individuals of a simulated plant population. We used patches of either NH_4 or NO_3 concentration found in these plant communities to simulate the share of these resources among individuals within a population. Our starting hypothesis was that if nutrient patch size was smaller than the root system size, all individuals within the population would have similar availability of this resource. However, if nutrient patch size was larger than the root system size, individuals would be found in either a high, low or intermediate amount of available resource (Figure 1).

Materials and methods

Study sites

All sites except the Mediterranean Dehesa are located in the SW of Galicia (NW Spain). These sites are grassland, scrubland, shrubland, pine forest and floodplain forest. The climate is warm-temperate with a slight Mediterranean influence, which produces scarce precipitation during the summer months. Mean annual precipitation is about 1800 mm, and mean annual temperature is about 15 °C. Soils of the shrubland, grassland and the pine forest communities were classified as Humic Cambisol. In the floodplain forest, soils ranged from Umbric Cambisols in the higher terraces to Histosols in the lower ones. Soils from all these five plant communities are slightly acidic (pH $\approx$4.5), and derived from the weathering of either coarse grain granitic or biotite gneiss bedrock.

The Mediterranean Dehesa (oak savanna) is located at the foothills of the Sierra Morena mountains (Northeast of Seville, SW Spain). The climate is subhumid Mediterranean with temperate winters. Mean annual precipitation is about 650 mm and mean annual temperature is about 17 °C. The soil, which is of an acidic brown type has been classified as Haplic Acrisol and overlies granitic bedrock. More details on climate and chemical characteristics of this soil can be found in Gallardo et al. (2000) and Gallardo (2003b). Vegetation was composed of a herbaceous stratum and a tree canopy stratum of *Quercus ilex* (holm oak).

Grassland, scrubland, shrubland and pine communities form the different successional stages in NW Spain. The pine forest was a 35-year-old maritime pine forest (*Pinus pinaster*). The stratum under the pine canopy was composed mainly of young (ca. 10- to15-year-old) pedunculate oak trees (*Quercus robur*). The shrubland was dominated by *Ulex gallii* and *Erica umbellata*, with the occasional presence of *Erica cinerea* and *Genista tridentata,* and represented a community that was developed under recurrent wildfires. The scrubland community was composed of *Rubus ulmifolius* and *Pteridium aquilinum* that invaded a recently burned area which had been formerly occupied by a maritime pine forest. The grassland was composed of perennial herbs and forbs under moderate-to-high levels of herbivory, with a few scattered invading shrublands. The floodplain forest was dominated by deciduous trees *Quercus robur*, *Salix atrocinerea* and *Alnus glutinosa*. More details on this site can be found in Gallardo (2003a). The vegetation in the Mediterranean Dehesa was composed of a herbaceous stratum and a tree canopy stratum of *Quercus ilex*. Details on this site can be seen in Gallardo (2003b).

Field sampling and laboratory analysis

A 20 m × 20 m grid was used on the grassland, shrubland and the Mediterranean Dehesa sites. Soil samples were taken at intervals of 2 m, inside the grid. Within this grid, sampling was carried out on a finer scale of 0.5 m within five nested 2 m × 2 m grids, totaling 220 samples for each site. In the case of the Ulex–Erica scrubland, samples were taken at intervals of 1 m in a 14 m × 10 m grid, with additional random samples totaling 179 soil cores. For the pine forest, an area of about 120 m × 120 m was selected from within the study site. An irregular plot was marked inside this area to leave out apparently disturbed surfaces. All young oak trees (totaling 125 trees) in the plot were tagged and mapped using the computer program INTERPNT, based on tree diameter and tree-to-tree distance measurements (Boose et al., 1998). Four soil samples were taken at 0.7 m from the center of each tree along the principal cardinal directions (N, S, E, W), These four points formed a 1 m × 1 m square around each tree. To study spatial dependence at a smaller spatial scale, additional samples separated by 0.25 cm were taken from within these squares, totaling 523 soil samples. In the floodplain forest, sampling design was based on Gross et al. (1995). In an area of 1 ha, ten parallel 40-m transects were randomly placed in the NE–SW direction. Base points were marked at 4 m intervals along the entire length of each parallel. A 2-m transect was drawn through each base point using different cardinal directions (N, E, SE, S, W, NW). This 2-m transect was marked at 0.5 m, 1 m, and at 2 m intervals. This gave a total of 400 sampling points. Four additional transects were placed to cover large non-sampled areas. A total of 541 soil samples were taken from the field. In all cases, a 10.5 cm diameter × 25 cm high metallic cylinder was used for sampling the top 10 cm of soil profile. This depth was chosen because in these soils most soil nutrients concentrate on the top 10–15 cm (Ah horizon, data not shown).

Each soil sample was sieved (< 2 mm) in field-moist condition, air-dried (30–50 °C) and then analyzed for organic matter, ammonium and nitrate. Organic matter was estimated in the samples by the loss-on-ignition method (Nelson and Sommers, 1996). In order to extract mineral N from soil, 10 g of the sample was shaken with 80 mL of a 1 M KCl solution for 1 h, and the suspension was filtered through a 0.45-μm Millipore filter. Aliquots of this solution were transferred in three batches on to microplates. Nitrate was reduced to ammonium by allowing the Devarda alloy to react with the extract overnight. Samples were then transferred to another microplate and its mineral N content was determined colorimetrically using a microplate reader (Sims et al., 1995).

Data analysis

Spatial dependence of the samples was analyzed using geostatistical analyses (Isaaks and Srivastava, 1989). A semivariogram was calculated to show the average variance found in comparisons of samples taken at an increasing distance from one another – the lag interval. For randomly distributed data, there is little change in the semivariance encountered with increasing distance, and the variogram is essentially flat. For patterned data, the semivariogram first rises for comparisons of neighboring samples that are similar and autocorrelated, and then levels off at the sill (asymptote), indicating the distance (known as range) beyond which samples are independent. Variance that exists at a scale finer than our minimum lag intervals found at 0 lag distance is known as nugget variance (C_0). A high nugget variance indicates either that most variance occurs over short distances or that there is sampling and/or analytical error. The spatial variance (C) is the sill minus the nugget variance. A high ratio of spatial variance (C) to sill variance ($C_0 + C$) is an indication of a spatial pattern in the data. By common convention, data analysis is restricted to distances of half the smallest dimension of the study area. The model fitted to the semivariogram allows for interpolation ('kriging'), which provides optimal, unbiased estimates of non-sampled points.

The interpolation of points using semivariograms 'kriging' requires the stationarity assumption, that is, the mean and variance of the data are the same in the various parts of the area under study (Legendre and Fortin, 1989). A large spatial trend across the site in the data violates the stationarity assumption. Trend can be thought of as a pattern whose dimensions are larger than the sampling space. This large-scale trend, if reflected in the semivariogram, may mask small-scale structures in the data. Thus, the presence of a large-scale trend was removed by detrending when required. Detrending was accomplished by fitting a regression to the trend and using only the residuals for semivariance analysis.

Soil properties were log-transformed when the Shapiro–Wilk test indicated lack of normality. When this transformation failed, we used a Box–Cox transformation (Box and Cox, 1964). All the empirical semivariograms were fitted to a spherical model to facilitate comparisons. The spherical model, unlike other commonly used models, has a true range (i.e., a distance at which the variogram is constant. See equation in Table 2 and graphics in Figure 3).

Modeling

Interpolation by block kriging allowed us to estimate the mean and standard deviation of N concentration for any area (block) in the map of each plant community (the 'prior distribution'). However, there is no guarantee that the map obtained using kriging has the same variogram and variance as the original data (i.e. we were smoothing the map, and not retaining the dispersion characteristics of the original data). Simulation allowed us to come up with theoretically an infinite number of realizations of the map each of which has approximately the same variogram and variance of the original data (Chilès and Delfiner, 1999). We performed 1000 simulations on each block representing the area explored by roots. Each simulation assumes a range of values based on the 'prior distribution' at each block. The 1000 simulation gave us the 'posterior distribution' which allowed us to calculate the probability for each individual within the plant population to obtain an amount of NH_4-N or NO_3-N under their root explored area. We calculated the probability for each individual to reach a N value higher than the median value of the original data (hereafter 'probability to be located on a nutrient rich patch'). The use of another threshold value (as the mean) gave us similar results. We used circular blocks instead of the most commonly used square blocks to better simulate the shape of root systems, however the model is little sensitive to block shape. To avoid overlapping of root systems in the simulation, each plant population was composed of regularly spaced individuals separated by a distance longer than the maximum root size allowed for each plant community. These individuals were kept on the same place in each study area, and for each nutrient (NH_4 or NO_3), we repeated the simulations with different root system sizes (by increasing the block size) to estimate the mean concentration of either nutrient under the area explored by each individual. The diameters of the blocks (lateral root spreads) were arbitrarily chosen to simulate root systems from seedlings to adult trees or shrubs in each community. We were interested in simulating the effect of different root and nutrient patch sizes on N-availability prior to any phenotypic response and overlapping between roots (e.g. in seedlings stabilized on a empty (perturbed) site, a new restored plant community or a new tree plantation). Consequently, simulations assume roots from all individuals in each population to be circular and uniform in size. Thus, our intention was to test the effect of different patch size (NH_4 vs. NO_3) and different root system size on the soil N concentration in a plant population where all individuals have the same initial conditions.

Statistical and geostatistical analyses were performed with R 1.8 under a Linux platform (Ellner, 2001; R Development Core Team, 2004), using the geostatistical modules geoR (Ribeiro and Diggle, 2001) and gstat (Pebesma and Wesseling, 1998)

Results

Soil organic matter ranged from 5.2% of soil mass for the Mediterranean Dehesa to 31.7% for the grassland site (Table 1). Soil NH_4-N concentration varied from 22.2 mg kg^{-1} for the Rubus–Pteridium shrubland to 363 mg kg^{-1} for the floodplain forest soil. Soil NO_3-N concentration was lower for all plant communities, with values ranging between 6.5 and 173 mg kg^{-1} soil.

Table 1. Univariate statistics for soil organic matter, ammonium and nitrate in several terrestrial ecosystems in Spain

	Organic matter (%)		NH_4-N (mg kg^{-1})		NO_3-N (mg kg^{-1})	
	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
Floodplain forest	29.9	51.2	363.4	90.5	173.5	132.3
Mediterranean Dehesa	5.2	27.4	50.1	54.6	12.3	20.7
Pine forest	17.2	21.6	31.1	40.8	6.5	55.2
Rubus–Pteridium shrubland	16.6	21.9	22.2	48.7	9.9	71.9
Ulex–Erica scrubland	13.8	21.3	63.5	63.2	11.1	62.2
Grassland	31.7	22.2	169.2	47.9	36.9	63.3

Table 2. Parametres for the spherical variogram model of soil organic matter, ammonium and nitrate in several terrestrial ecosystems in Spain

	Organic matter (%)		NH_4-N (mg kg^{-1})		NO_3-N (mg kg^{-1})	
	Range (m)	$C/(C_0+C)$	Range (m)	$C/(C_0+C)$	Range (m)	$C/(C_0+C)$
Floodplain forest	10.31	0.56	13.7	0.35	5.46	0.38
Mediterranean Dehesa	9.69	0.92	9.28	0.75	5.35	0.74
Pine forest	16.46	0.39	14.14	0.37	3.03	0.69
Rubus–Pteridium shrubland	3.14	0.69	5.91	0.47	2.11	0.44
Ulex–Erica scrubland	4.23	0.34	6.58	0.27	0.97	0.47
Grassland	7.38	0.49	8.28	0.51	6.24	0.43

All spherical model fits were statistically significant ($P < 0.05$). In the spherical model, the semivariance $= C_0 + C[(3h/2a)-(h^3/2a^3)]$ if $h \leq a$, otherwise semivariance $= C_0 + C$; where a is the range, and h is the lag distance.

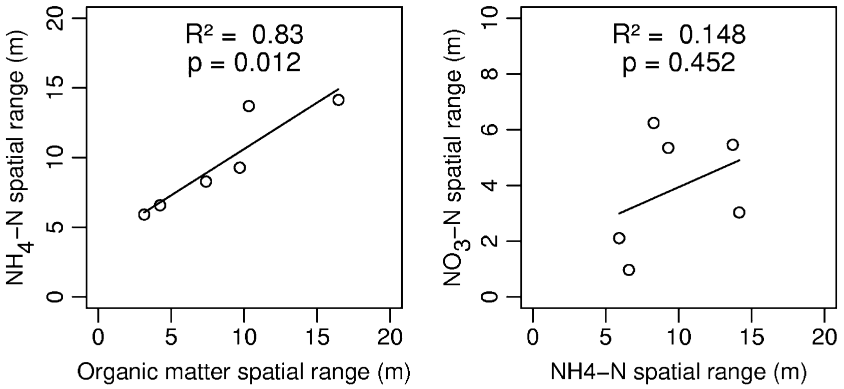

Figure 2. Relationship between soil NH_4-N and organic matter and between NO_3-N and NH_4-N semivariogram range values for the six studied plant communities.

Organic matter showed the lowest coefficient of variation, with the highest values corresponding to soil NO_3-N.

Fits of empirical variograms to the spherical model were all significant ($P < 0.05$). The fraction of total variance explained by spatial variance (C/C_0+C) ranged from 0.27 for soil NH_4-N concentration in the Ulex–Erica shrubland to 0.92 for the soil organic matter content in the Mediterranean Dehesa (Table 2). The model range (distance beyond which samples are spatially independent, and an indicator of the patch size) varied between a highest value of 16.5 m for NH_4-N in the pine forest, and a minimum value of 0.97 m for NO_3-N in the Ulex–Erica shrubland community. Range values of soil organic matter were of the same magnitude as NH_4-N for all plant communities, and they were positively correlated (Table 2, Figure 2). However, range values for NO_3-N were not correlated with NH_4-N, and they were consistently lower than those for organic matter and NH_4-N for all sites (Table 2, Figure 3). Consequently, while mapping of soil organic matter showed similar patch size and patch location than NH_4-N, mapping of soil NO_3-N showed different spatial properties than those showed by organic matter and NH_4-N (Figure 4).

The probabilities of locating individuals on a nutrient rich patch within the simulated populations were very variable for all plant communities, and depended on the form of nitrogen and root system size (Figures 5 and 6 show the two plant communities with the highest contrast between NH_4-N and NO_3-N range values, i.e., the Ulex–Erica and Pine forest sites). As can be seen in these figures, the distribution of probabilities among individuals narrowed as the soil area

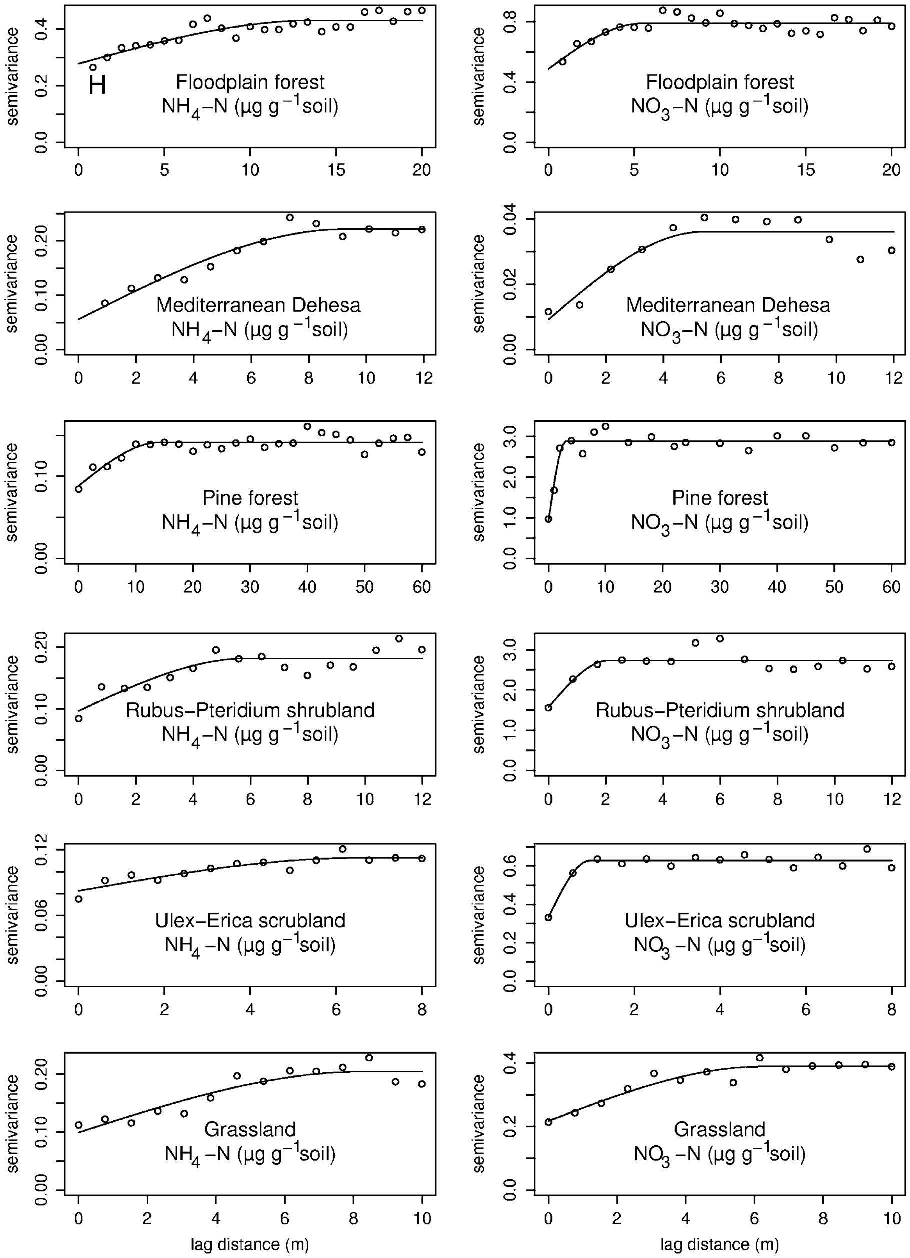

Figure 3. Semivariograms for soil NH_4-N and NO_3-N in six plant communities. The line represents the fitted spherical model. Semivariograms for the floodplain forest and the Mediterranean Dehesa were redrawn from Gallardo (2003a) and Gallardo et al. (2000), respectively.

explored by roots increased. For example, for small plants (root explored area < 0.79 m^2), the probabilities of location on an area with high NH_4-N concentration were evenly distributed between 0 and 1 among the population individuals in the Ulex–Erica site (Figure 5). Comparatively, large individuals (root explored area of 28.3 m^2) placed on the same locations would concentrate on central probability values. Same result was observed for a simulated population taking up NO_3-N in the Ulex–Erica site and for both forms of mineral N on the pine site (Figure 6). Furthermore, differences were also observed in the distribution of probabilities between populations

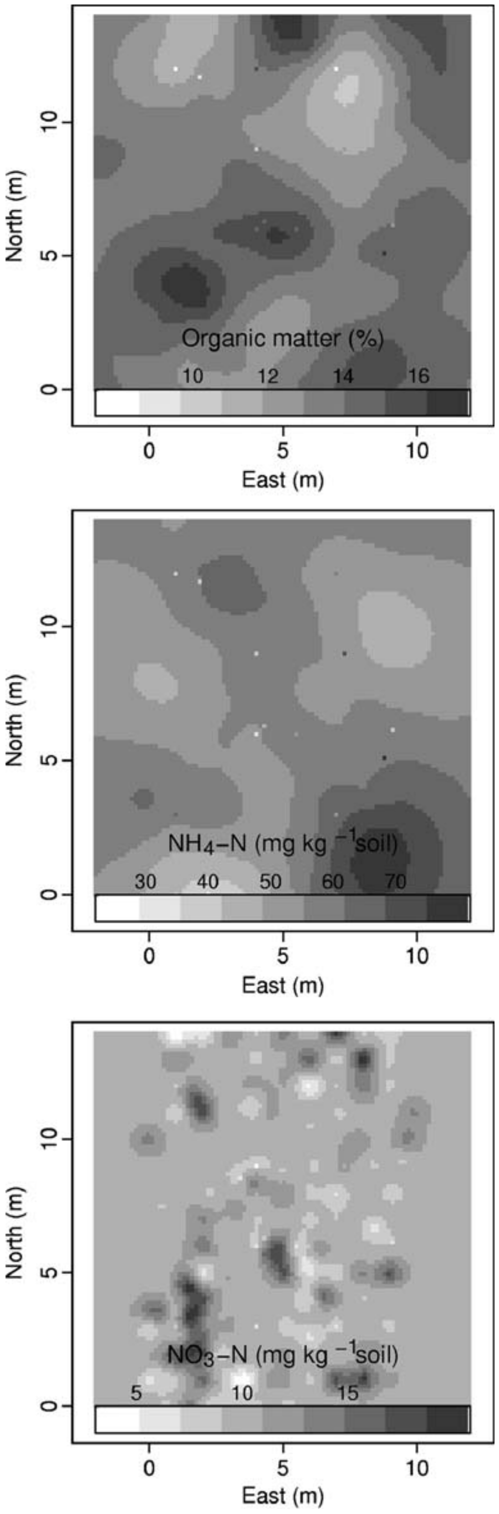

Figure 4. Maps of organic matter, NH_4-N and NO_3-N obtained by kriging interpolation techniques in the Ulex–Erica scrubland.

taking up NH_4-N or NO_3-N. The probability of locating individuals on an area with high N concentration was less variable for NO_3-N than for NH_4-N for any simulated plant root size (Figures 5 and 6). Similar results were observed for simulations on the grassland, shrubland and floodplain forest soils, but data were not shown for simplicity. The choice of a different threshold to define a high nutrient concentration in the root explored area would change the probability distributions in each case, but not the pattern of change between plants of different sizes, or nutrients with different spatial patch size (data not shown).

Discussion

Our analyses were based on the observed spatial structures of soil N concentrations. This approach only represents N availability for plants on a very short-term basis (hours to few days). However, other approaches to soil nitrogen availability (such as mineralization rates or ion exchange membranes) also showed spatial dependency in natural ecosystems (Cain et al., 1999; Robertson et al., 1997). Thus, as far as long-term patterns of N availability were correlated with spatial short-term patterns, our major conclusions might be extrapolated to these other measurements.

The lower NO_3-N than soil NH_4-N concentration found in all communities did not necessarily mean less NO_3-N availability for plants due to the higher mobility and lower microbial competition for NO_3-N found in several ecosystems (e.g. Lin and Stewart, 1998; Nadelhoffer et al., 1985; Schimel et al., 1989). NH_4-N vs. NO_3-N nutrition has called the attention of numerous authors (Gutschick, 1981; Haynes and Goh, 1978). Species from habitats where NH_4-N is the dominant form of available N preferentially absorb NH_4-N relative to NO_3-N and vice-versa (Aerts and Chapin, 2000). Thus, relative soil concentrations of these ions are relevant to plants. We find that different spatial structures of NH_4-N and NO_3-N may be also relevant to plants. Thus, the semivariogram range – a measure of the patch size, was higher for NH_4-N than for NO_3-N for all plant communities. Furthermore, among the six plant communities, the

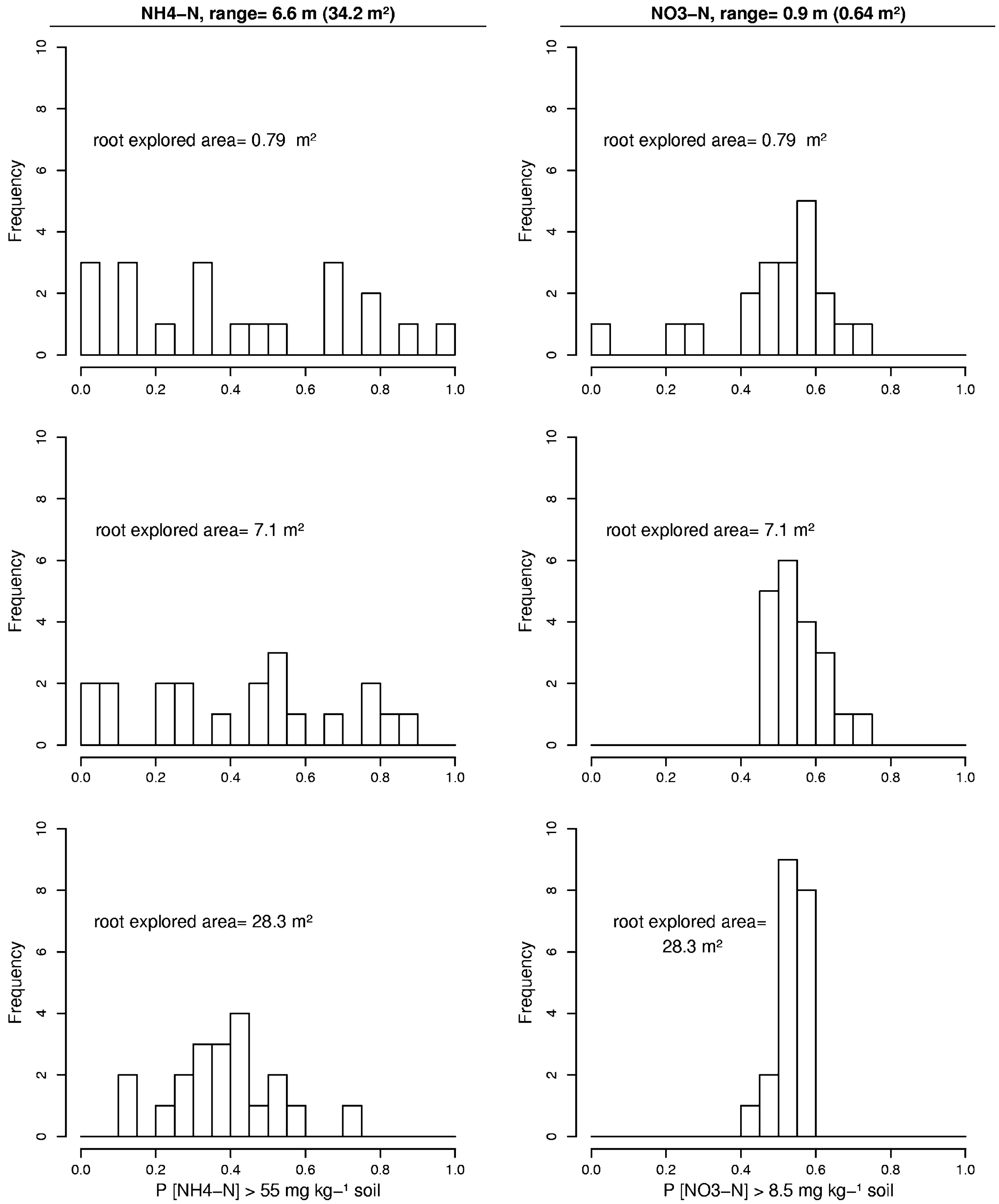

Figure 5. Histograms for the probability of locating plants on a NH_4-N or NO_3-N rich patch for different root system sizes in simulated populations standing on the Ulex–Erica scrubland plot.

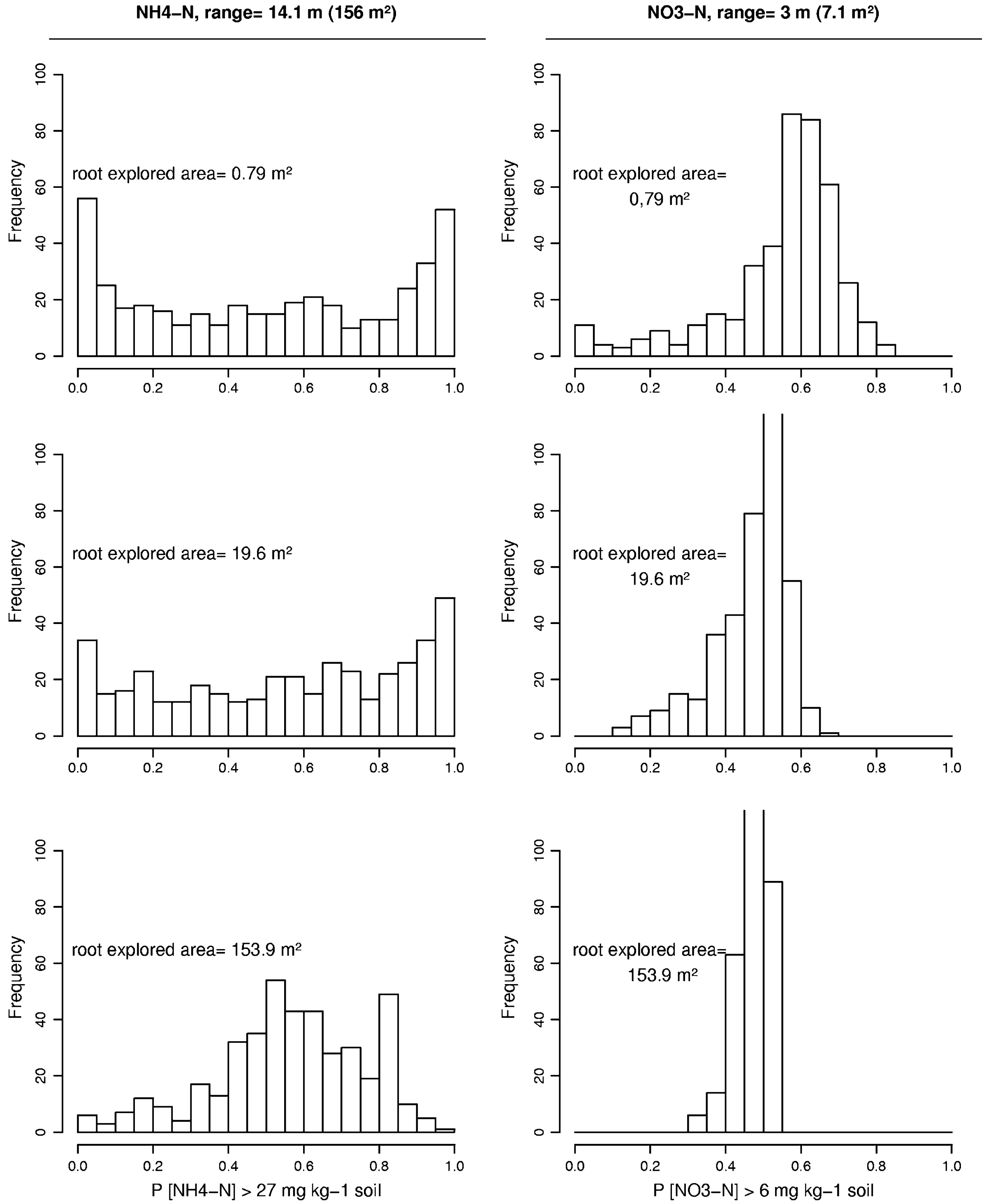

Figure 6. Histograms for the probability of locating plants on a NH_4-N or NO_3-N rich patch for different root system sizes in simulated populations standing on the Pine forest plot.

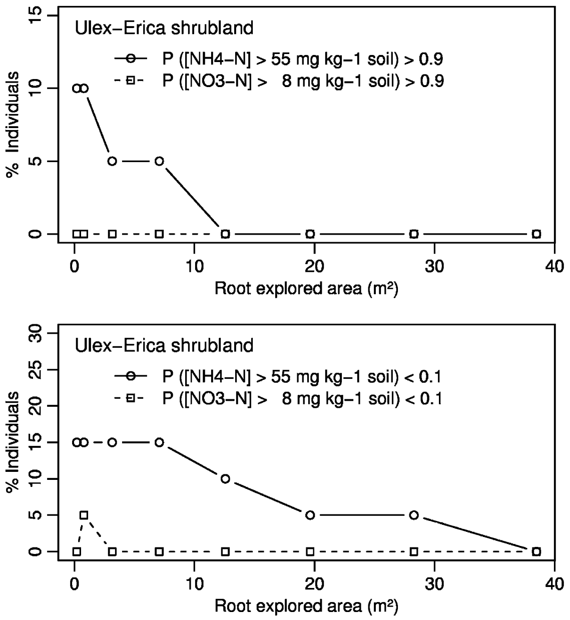

Figure 7. Percent of individuals within simulated plant populations of different root sizes that would have a high probability (successful individuals) or a low probability (unsuccessful individuals) of being located on a NH_4-N or NO_3-N rich patch in the Ulex–Erica scrub soil.

semivariogram range for organic matter was found to correlate with NH_4-N, but not with NO_3-N, suggesting that independent processes were responsible of their spatial structure. Heterotrophic microorganisms are responsible for the release of NH_4 from soil organic matter. The low NH_4 diffusion rate in temperate soils could result in high NH_4 concentration being associated with high organic matter content. This mechanism may explain the spatial coincidence between NH_4 and soil organic matter content, and the positive correlation between sizes of the spatial range of organic matter and NH_4 across the different ecosystems studied. On the contrary, nitrification rate is not directly related to ammonification rate, because nitrifiers, plants and other microorganisms compete for soil NH_4, and nitrification is frequently inhibited in low pH soils (Schlesinger, 1997). In these soils, nitrification may be restricted to favorable microhabitats, where competition for NH_4 is low and/or pH is high, showing an insignificant relationship with the spatial distribution of organic matter, and a lower spatial scale as seen in our study. Higher NH_4-N than NO_3-N semivariogram range (8.2 vs. 2.5 m) was also found by Gross et al. (1995) in a late successional forest in Michigan. However, differences in patch size between NH_4-N and NO_3-N were not found in agricultural soils and in arid or semiarid ecosystems (Gross et al., 1995; Hirobe et al., 2003; Jackson and Caldwell, 1993). Other authors found spatial structure for NO_3-N but not for NH_4-N (Cain et al., 1999; Lister et al., 2000). Thus, consistent differences between NH_4-N and NO_3-N spatial structure are far from universal, and they may be only apparent in acid soils and late-successional forests of mesic habitats with low nitrification rates. Nevertheless, spatial structure comparisons of NH_4-N and NO_3-N from literature were not straightforward because authors frequently did not use the same semivariogram model for the two ions, and most of them did not use detrended data. This last step may be critical because the existence of a large spatial trend in the data (as caused by slope or any other environmental gradient) has an immediate effect of elongating the autocorrelation distance (the semivariogram range).

Differences in patch size may have important consequences for individual performance (Antonovics et al., 1987; Miller et al., 1995; Wijesinghe and Hutchings, 1999). Campbell et al. (1991)

suggested that small-scale heterogeneity might be even more important than average soil nutrient levels in determining competitive outcome. Thus, the differences found in the NH_4-N vs. NO_3-N patch size may have important consequences for plant populations that prefer different forms of nitrogen.

Several recent papers have highlighted the importance of soil heterogeneity for plant populations (Hutchings et al., 2003 and references therein). Heterogeneity determined competitive interactions between plants, where a greater intensity of competition is found within nutrient-rich patches. However, mortality has been found to be higher under homogeneous conditions than under heterogeneous conditions (Casper and Cahill, 1996; Day et al., 2003a). Total yield and size hierarchy was either not affected by soil heterogeneity (Casper and Cahill, 1996, 1998) or was higher under heterogeneous conditions (Day et al., 2003b; Facelli and Facelli, 2002).

Most of these papers focused on the morphological responses of plants when patches of different quality are smaller than, or of a similar size to, the root systems of individual plants. Their experiments were done in controlled conditions in which the same total quantity of resources was provided in homogeneous and heterogeneous patterns. We developed a new and different approach, in which patches of soil N concentration found in several natural plant communities were used to simulate the nitrogen availability for a plant population with varying root size. Thus, we study the interaction between root size and patch size on the distribution of nitrogen availability inside a simulated population. Unlike the above-cited authors, we did not try to model individual responses to resource heterogeneity or the consequences for populations of these responses. We tried to find out how much N was available to each individual within a population for differing roots and nutrient patch sizes. Our results simulate the initial conditions for a population. For example, a new pine plantation, shrubs on a new restored area or seedlings emerging in a disturbed area. However, we sampled intact plant communities, and the spatial pattern observed might differ substantially from those observed following site restoration or disturbance. Some authors found that spatial pattern of soil N was quite stable after disturbance (Robertson et al., 1993), while others observed rapid temporal changes (Cain et al., 1999). Our results may be applied to plants if (1) the spatial structure stays after disturbance; and (2) this spatial structure is stable during all or part of the growing season. Beyond the initial conditions, and depending on the degree of resource heterogeneity, individuals will compete for nutrient rich patches, and their root systems will overlap with important consequences for plants described by other authors but not included in our model. Our results showed that individuals from a population that depend on a source of nitrogen with patches smaller than the root system size would all have a similar amount of available N. In this scenario each plant will perceive its soil environment as heterogeneous with important implications for population parameters (Hutchings et al., 2003), but our results emphasize that all individuals in the area will have similar probability to reach a nutrient rich patch. Alternatively, when a resource patch size is bigger than the root system size, the individuals of a population that take up this resource will find a wide range of favorable to unfavorable habitats. If patches were internally homogeneous, each plant would perceive the environment as uniformly good or bad as pointed out by Hutchings et al. (2003). However, patches in natural soils are not always internally homogeneous but frequently composed of concentric isolines (e.g. Figures 1 and 4), and therefore each plant perceives a soil gradient and some degree of heterogeneity. Based on our simulations, we found that populations depending on a limited resource with larger patch size (NH_4-N in our study) are more heterogeneous (i.e. the population is composed of individuals differing in the mean soil N concentration under their area of influence) than the same population when depending upon a limited resource with a smaller patch size (NO_3-N). Thus as far as plant growth is limited by N availability, individuals from the population taken up NH_4 will likely show a high variability in sizes and root-to-shoot ratios as compared with individuals from the same population taken up NO_3. The degree of heterogeneity in resource availability within a population will also depend on the ratio between root system size and patch size. If success for an individual (in terms of growth rate or survivorship) depends on the amount of limited resource available to it, in a seedling population we will find seedlings with high and low probability of success within the population. But with larger individuals, the probability of success will tend to be equal. For example, we can arbitrarily define a successful or an unsuccessful individual as one with a higher or lower probability ($P > 0.9$ or $P < 0.1$, respectively) of being located on a rich nutrient patch in the Ulex–Erica scrubland (Figure 7). A significant percent of the smaller individuals taking up NH_4-N will meet the successful or unsuccessful requirements. However, for small plants taking up just NO_3-N, only a few individuals within the simulated population will meet the successful or unsuccessful requirements. These results may have important consequences for plant populations. For example, given a known patch size of the limiting resource, the choice of planting seedlings or adult plants in ecosystem restoration may determine how many plants will survive and how many will grow on either a rich or poor nutrient patch during initial stages.

Our results represent a step beyond the interpretations of merely spatial descriptions of soil heterogeneity by geostatistical analysis. Our model shows that patch size of a limiting resource may determine the variability in terms of resource acquisition among individuals within a population. However, our model has important limitations. First, the patch size can be transient or can be modified by plant activity. Second, roots overlap, compete and show phenotypic plasticity. None of these characteristics are included in our model. Nevertheless, our approach suggested that patch size matters for populations as far as resource patches stay stable, and it may be expanded to other plant resources such as water or light availability, which has been found to be spatially structured in natural ecosystems (Guo et al., 2002; Nicotra et al., 1999).

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