Spatial soil ecology

Christien H. Ettema and David A. Wardle

Although spatial variability in distributions of soil organisms is generally regarded as random noise, this variability often has a predictable spatial structure. Recent studies have provided evidence that a spatially explicit approach to soil ecology can enable identification of factors that drive the spatial heterogeneity of populations and activities of soil organisms, at scales ranging from millimeters to hundreds of meters. Furthermore, there is increasing evidence that spatial soil ecology can yield new insights with regard to understanding the factors that maintain and regulate soil biodiversity, as well as to how the spatial distributions of soil organisms influence both plant growth and plant community structure.

There is increasing recognition of the fundamental role of space in population, community and ecosystem processes [1,2]. For example, it is well recognized that habitat spatial heterogeneity can be an important contributor to the coexistence of species in communities [3–5], and population persistence [6]. In spite of this, within spatial ecology, empirical and modeling studies have concentrated on aboveground biota, limiting belowground detail, if any, to abiotic properties, such as soil moisture and nutrients [7,8]. However, spatial patterns of soil biota, and the factors that determine them, will influence spatial patterns of decomposition, nutrient supply and root herbivory and, ultimately, the spatial structure of plant communities.

Except for a few early efforts [9,10], spatial patterns of soil biota have been explicitly studied only in the past decade, which partly explains the minimal contribution of soil biology to spatial ecology research. Although these studies indicate spatially predictable patterns at various scales, variability in soil organism densities is often still regarded as 'noise', hampering quantification of soil populations, the processes that they drive and the variables by which they are driven. As such, spatial variability is perceived as a problem for understanding how highly species-rich soil communities are maintained, and what their ecosystem functions are. However, taking lessons from spatial ecology, it is likely that spatial variability is the key, rather than the obstacle, to understanding the structure and function of soil biodiversity.

Here, we evaluate empirical evidence and theoretical arguments on the importance of a spatially explicit approach to the study of soil communities. Specifically, we address (1) What are the scales, patterns and causes of spatial variability in soil organism distributions? (2) What are the implications of spatial variability for the structure and function of soil communities? And (3) How do spatial properties of the soil biota influence plant communities?

Spatial distributions of soil organisms

Spatial patterning of soil biota can occur both vertically, through the soil profile, and horizontally.

Here, we focus on horizontal patterns, because these are less well documented than are vertical gradients, and most spatial studies report data integrated over soil cores. We derive most examples from spatially explicit studies that quantify spatial patterns using geostatistics, the most robust and commonly used method for analysing distributions of soil properties (Box 1). These studies show that soil organisms are usually not randomly distributed, but exhibit spatially predictable, aggregated patterns over scales ranging from hectares to square millimeters, with scale-dependent controls (Fig. 1, Table 1).

At the field scale, distributions of soil biota are often spatially structured over distances of tens to hundreds of meters, depending on the organism, the system studied and the minimum and maximum spacing of the samples (Table 1). These spatial patterns can often be related to large-scale landscape gradients. For example, Fromm *et al.* [11] found that, in an agroecosystem, soil microbial biomass and collembola were spatially dependent over ranges of >200 m, reflecting large-scale soil carbon gradients and cultivation practices. Similarly, Crist [12] found that, in a short-grass steppe, spatial patterning of termites over a range of 330 m was related to large-scale topography and vegetation patchiness. However, Ettema *et al.* [13] showed that, for a riparian wetland, heterogeneity in bacterivorous nematode species distributions, with patch sizes of up to 67 m, was related to soil resource gradients only for some genera, and that these correlations were inconsistent over time. Spatial patterns of soil biota at the field scale might exist both because of and in spite of human activity. For example, Robertson and Freckman [14] found strong aggregations of major feeding groups of nematodes in an agroecosystem, with patch sizes of 6–80 m, in spite of the homogenizing influence for many years of soil tillage and monoculture cropping. By contrast, Webster and Boag [15] suggested that spatial patterns of cyst nematodes *Globodera rostochiensis* and *Heterodera avenae* in an arable field could be explained by cultivation, spreading nematodes from small human-caused foci of contamination.

Nested within large-scale structures, soil organisms also exhibit patchy distributions at the scale of centimeters to meters, even where topography and soil texture are relatively uniform. Spatial patterns of soil biota at this scale are structured primarily by plant growth, and vary with plant size, growth form and spacing (Table 1). In forests, spatial distributions often reflect the zone of influence and positioning of single trees, such that patch sizes are one to several meters for soil microbes [16,17],

Christien H. Ettema
Subdept of Soil Quality, Dept of Environmental Sciences, Wageningen University, PO Box 8005, 6700 EC Wageningen, The Netherlands.

David A. Wardle*
Dept of Animal and Plant Sciences, University of Sheffield, Sheffield, UK S10 2TN.
*e-mail:
d.wardle@sheffield.ac.uk

Box 1. Definition and quantification of variability and heterogeneity

Variability and heterogeneity have many context-dependent meanings. Here, unless noted otherwise, the following definitions apply:

- Variability: a general term indicating changes, over space (or time), in the value of a given property. It can be quantified using standard parametric statistics, such as the coefficient of variation, and can be random or have a spatial structure. In the latter case, we use the term heterogeneity.
- Heterogeneity (patchiness): variability with a spatial structure, such that spatial distributions are not uniform or random, but aggregated (patchy, clumped). By quantifying its patterns and scales, the controls and consequences of heterogeneity can be assessed. For soil biotic and abiotic properties, heterogeneity is most often quantified using geostatistics, because of its robust characteristics and mapping possibilities [a]. At the heart of geostatistics is autocorrelation analysis.
- Autocorrelation (spatial dependence): the statistical term for heterogeneity in spatial data. It quantifies the resemblance between neighbors as a function of spatial separation distance. When near neighbors are more similar than are far neighbors (as is the case in aggregated distributions), data are autocorrelated, violating the assumption of data independence in standard parametric statistics [b]. Autocorrelation is calculated using the semivariance statistic $\gamma(h)$ for a range of distance intervals h (Eqn I):

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{n} [z(s_i) - z(s_i + h)]^2 \qquad [\text{I}]$$

where $N(h)$ is the number of observation pairs separated by distance h, $z(s_i)$ is the value of the variable of interest at location s_i, and $z(s_i+h)$ is its value at a location at distance h from s_i. When spatial dependence is present at the scale sampled, semivariance will be low at short distances, increase for intermediate distances, and typically reach an asymptote ('sill') when data separated by large distances become spatially independent, as shown by Fig. I. The model fitted to the semivariogram quantifies the scale of heterogeneity (patch size) and the spatially dependent predictability of the property. In addition, it allows for interpolation ('kriging'), which provides optimal, unbiased estimates of points not sampled, including estimation error. The resulting maps provide powerful visualizations of pattern (Fig. II).

- Spatial sampling: detection of spatial pattern is highly dependent on the organism studied, the characteristics of
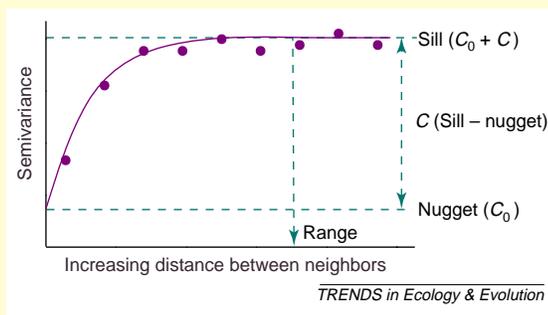

Fig. I. Generalized semivariogram, showing semivariance estimates for hypothetically observed distance classes (filled circles) and the fitted model (solid line). The sill ($C+C_0$) provides an estimate of total population variance. The intercept C_0 (nugget) represents the variance due to sampling error and/or spatial dependence at scales not explicitly sampled. The difference between the sill and the nugget, C, indicates the spatially dependent predictability of the property (spatially structured variance). A larger value of C relative to C_0 corresponds to a smaller degree of 'noise' (unpredictable error) in the data. The distance at which the asymptote is reached signifies the range (extent or patch size) of heterogeneity, beyond which data are stochastically independent.
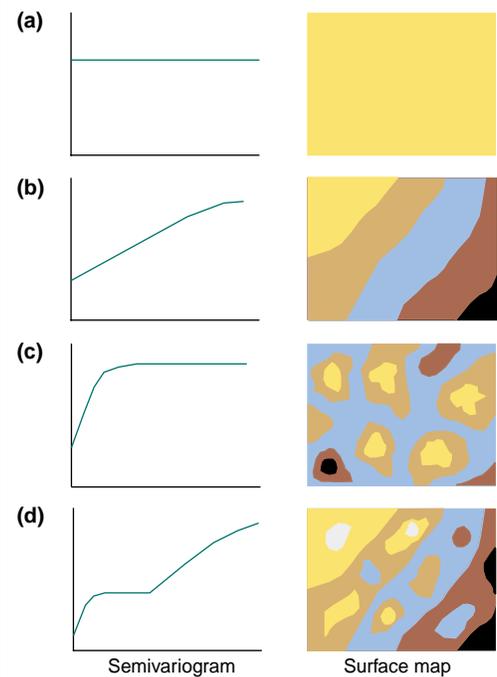
Fig. II. Hypothetical semivariograms with associated surface maps. (a) Pure nugget effect: at the scale sampled, the variance is not spatially structured. For interpolation, the population mean is the optimal estimate. (b) Large-scale heterogeneity: patches are few, large and smoothly continuous, reflecting gradients. (c) Small-scale heterogeneity: patches are many, small and more sharply discontinuous, reflecting hot and cold spots. (d) Nested heterogeneity: multiple scales of patchiness occur because factors influencing pattern operate at different scales. For a–d, patchiness at scales lower and higher than the scale sampled remains possible. The semivariogram is strongly influenced by the sampling design, specifically the minimum and maximum distance sampled.

the study area, and the spacing of the samples. Simple a priori sampling designs are not available, because spatial aggregations of soil biota are inherently cryptic. A nested spatial sampling design is useful to explore spatial aggregation among a range of scales [c]. For patch size estimation and mapping at a particular scale, the spatial sampling design can be optimized using simulation [d]. To increase statistical power in belowground field experiments and monitoring programs, exploratory spatial sampling and geostatistical analysis can be used to design a 'hotspot stratified sampling' scheme [e].

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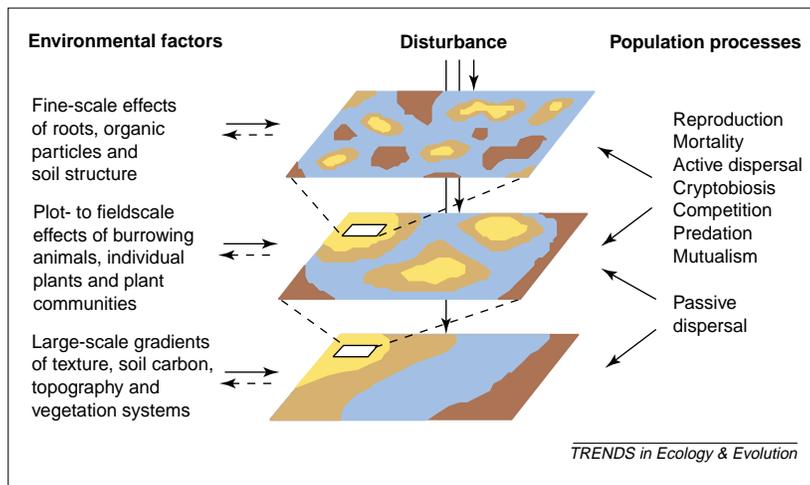
Fig. 1. Determinants of spatial heterogeneity of soil organisms. Spatial heterogeneity in soil organism distributions occurs on nested scales, and is shaped by a spatial hierarchy of environmental factors, intrinsic population processes and disturbance. Disturbance operates at all spatial scales and can be a key driver of spatial heterogeneity, for example through biomass reduction of dominant organisms or alteration of the physical structure of the soil substrate. Feedbacks between spatial patterns of soil biotic activity and heterogeneity of environmental factors add further complexity (dotted arrows). The scales at which population processes operate are dependent on soil organism body size, dispersal mechanisms and life-history characteristics.

nematodes [18,19] and microarthropods [19]. In mixed forests, litter quality differences among tree species can lead to further structuring [17,20], and differences among plant species might be key drivers of the spatial patterning of soil organisms and processes (Box 2). With decreasing zones of plant influence, patch sizes of soil organisms decline correspondingly. For example, whereas Saetre and Bååth [17] found ranges of 1–3 m for microbial lipid profiles in a spruce *Picea abies*–birch *Betula pubescens* forest, Cavigelli *et al.* [21] found ranges as

small as 5 cm in an arable field, possibly reflecting the different scale of influence of individual arable plants versus trees. In row crops, spatial ranges of soil respiration [22] and plant-parasitic nematodes [23] reflect inter-row distance. An important issue to consider is the plant legacy effect, where past vegetation remains influential through long-lasting effects on patterns of soil organic matter [24]. Finally, mound-building animals, such as gophers and ants, create patchiness that might interact with plants to affect the spatial patterns of soil biota [25,26].

Embedded in the heterogeneity present at the scale of centimeters to meters, fine-scale spatial structures occur when macroscopically uniform conditions are not perceived as such by microscopic soil organisms. For example, Mitchell *et al.* [27] found that, for a *Sphagnum* moss-covered surface (40×60 cm), testate amoebae were aggregated in patches of 1–10 cm, which partly reflected microtopographical differences of only a few millimeters. Often, fine-scale heterogeneity in soil populations is correlated to substrate hotspots. For example, using computer-assisted tomography of soil cores, Wachinger *et al.* [28] correlated high spatial heterogeneity in methanogenic Archaea and methane production to fine-scale distributions of fresh plant litter (and in one case, a decomposing earthworm). Similarly, Rønn *et al.* [29] found that population hotspots of microbes, protozoa and nematodes developed in buried root litter, and that this substrate effect was so local that no population increases were measured in bulk soil >1.8 mm from the litter patch. Clearly, there are methodological challenges to sampling and measuring soil microbiota at even smaller scales. Using a 1-mm-diameter needle as a soil corer, Grundmann and Debouzie [30] showed that *Nitrobacter* bacteria were spatially aggregated over ranges of just 2–4 mm, and the authors speculated that soil aggregates and fine roots contributed to this pattern.

The above examples indicate the importance of environmental controls on soil biota spatial patterns at various scales. However, spatial aggregation is also influenced by intrinsic population processes, such as dispersal, reproduction and competition (Fig. 1). Although these processes occur principally on small scales for soil microbiota, the more mobile macrofauna, such as earthworms, might be spatially structured at plot and field scales primarily as a result of population processes. For example, Rossi *et al.* [31] found that earthworms in a pasture were patchily distributed over ranges of 10–30 m, with smaller patch sizes for juveniles compared with adults, reflecting the clumped distribution of eggs and the dispersal behavior of adults. Furthermore, spatial patterns of soil biota are dynamic rather than static over time, and often show greater fluctuations than do underlying patterns of abiotic resources [18,22,32]. This provides indirect evidence for the contribution of intrinsic population processes and disturbance to spatial pattern formation.

Table 1. Influence of sampling scale, taxonomic resolution and ecosystem on the spatial heterogeneity in soil microbial properties

Property	Patch size (m)[a]	Distance sampled (m) Min.	Max.	Spatial structure[b]	Ecosystem studied	Main factors influencing microbial spatial pattern	Refs
Microbial biomass	250	50	1500	0.80	Arable and pasture	Land use and soil carbon	[11]
	21	5	1200	0.54	Arable	Topography, soil carbon and moisture	[59]
	7	2	20	0.50	Spruce–Birch	Tree species patch size	[20]
	1.00	0.10	18	0.70	Spruce	Tree size and spacing	[16]
	0.39	0.10	10	0.88	Chaparral	Bush size and spacing	[19]
FAME profiles[c]	0.05–0.97	0.02	80	0.25–1.00	Arable	Corn rhizosphere and plant spacing	[21]
NH$_4^+$-oxidizers	0.004	0.001	0.09	Not reported	Arable	Soil pores, aggregates and fine roots	[30]

[a]Estimated by the range parameter of the semivariogram model (Fig. I in Box 1).
[b]Spatially dependent predictability of the property, calculated as (C/C+C_0) (Fig. I in Box 1).
[c]FAME, fatty acid methyl ester (profiles characterizing biomass of specific microbial isolates).

Box 2. Plant species effects on soil organisms

Over the past decade, there has been increasing interest in understanding how plant species differ in their effects on community and ecosystem properties. In ecosystems in which individuals of coexisting plant species influence the soil in the patch that they occupy, the spatial patterning of plant species should therefore directly influence the spatial patterning of soil organisms and the processes that they govern. Spatial analysis provides us with the tools for answering such questions. An example of such an application is presented by Saetre and Bååth [a] who used geostatistical approaches to study the spatial patterning of the soil microbial community associated with a mixed Norway spruce *Picea abies*–birch *Betula pubescens* stand in central Sweden. They sampled soil from a grid of 96 points, spaced 2 m apart in a 14 m × 22 m rectangle, and assessed microbial community composition in each sample. The main principal component summarizing microbial community structure was spatially dependent over a range of 4.6 m; this patterning was influenced by the positioning of individuals of the two tree species. Their results suggested that the tree species differed in their effects on the microbial community, and that there was a distinct subset of the microbial community that aggregated in small patches away from birch trees. It is not possible from such a study in isolation to determine whether tree species effects were responsible for spatial patterning of the soil microbial community, or whether the trees and microbes were both driven by the spatial patterning of a third, unmeasured variable. However, the trends identified by Saetre and Bååth were consistent with the results of a microcosm study in which microbial communities were measured in mixtures of humus from these two tree species [b]. This provides support that spatial patterning of microbial communities in these forests was driven to a large extent by differences in organic matter quality associated with the two species. Spatial analysis provides a useful tool for generating hypotheses about how plant species effect the belowground subsystem, and form the bases upon which mechanisms can be investigated through experimentation.

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Implications of spatial heterogeneity for soil biodiversity

Our understanding of the maintenance and function of soil biodiversity is hampered by the apparent contradiction of exceptionally high species richness of soil communities and low degrees of resource specialization of constituent species [33,34]. One key to the analysis of this problem involves consideration of the spatial patterning of environmental factors and soil populations, which profoundly influences the nature of species interactions and coexistence in several ways [3].

Most simply, spatial heterogeneity in soil resources results in microhabitat diversity, which can promote species coexistence through greater resource partitioning [33,35]. For example, in small soil and litter cores, the species richness of microarthropods increases with microhabitat diversity [36,37]. However, as a consequence of limited mobility of soil organisms and the complexity of the soil matrix, the importance of competition as a major structuring force is likely to be restricted to the small scales where potential competitors are using the same space. In a soil microcosm study, Sulkava and Huhta [38] found that soil microarthropod diversity was lower in systems where four resources were mixed together than in those where the same four resources were presented in patches, indicating that spatial separation decreased competitive pressure. Thus, spatial heterogeneity of soil resources not only promotes microhabitat diversity, but also enables spatial separation of potentially competing soil organisms.

Even when resources are homogeneous, interspecific spatial separation and the coupled reduction of competitive interactions might still occur, because intrinsic population processes, such as reproduction and limited dispersal, lead to intraspecific aggregation [39]. For example, the centimeter-scale spatial patterns of 13 testate amoebae species assessed by Mitchell *et al.* [27] show limited spatial overlap between species, and are likely to be caused, in part, by such intrinsic population processes. Furthermore, spatial models suggest that many species can coexist on a single resource when their mobility is low relative to the scale of resource patchiness [2]. With the exception of macrofauna, the active dispersal of soil organisms through the soil matrix is generally very limited (depending on the taxon, in the order of few millimeters to centimeters per day), although passive dispersal over larger distances is possible through accidental or specialized (soil) animal vectors, water and wind [40,41]. Because of the difficulty of measuring dispersal of soil organisms and the cryptic nature of soil resource patchiness, experimental testing of the effects of resource patch size and dispersal on spatial population dynamics has, to date, been limited to transient soil fauna, such as beetles [42].

The intrinsic heterogeneity in distributions of soil organisms interacts with soil resource heterogeneity to form the complex spatial patterns observed in soil communities, and these are, in turn, further altered by localized stochastic disturbances. For example, using geostatistical analysis on space–time species data, Ettema *et al.* [32] described how limited dispersal, soil resource patchiness and local disturbance led to complex spatiotemporal patterns of bacterivorous nematode species, and suggested that stochastic patch dynamics contributed to the maintenance of nematode diversity at the landscape scale. In patch dynamic models of coexistence, stochastic disturbances upset local competitive dynamics, creating 'empty' patches that can be exploited by different species depending on their relative competitive and dispersal abilities, and the tradeoffs between these traits [2,3]. In addition to competitive and dispersal strategies, the strategy of cryptobiosis (dormancy) might also be important in determining the abilities of soil organisms to survive and exploit local disturbances, analogous to soil seed banks in aboveground models. For example, Felske and Akkermans [43] showed that, for coexisting bacterial species in a grassland, a large fraction of the community was in a resting stage, and the spatial variability of metabolic activity of particular bacterial species (as measured by 16S rRNA fractions) was higher than the spatial variability of the abundance of these species (16S rDNA fractions). To assess further the importance of patch dynamics for soil communities, more spatiotemporal studies at the species-level of resolution are needed, as well as information on competitive, dispersal and dormancy strategies at a finer level of taxonomic resolution than is currently available.
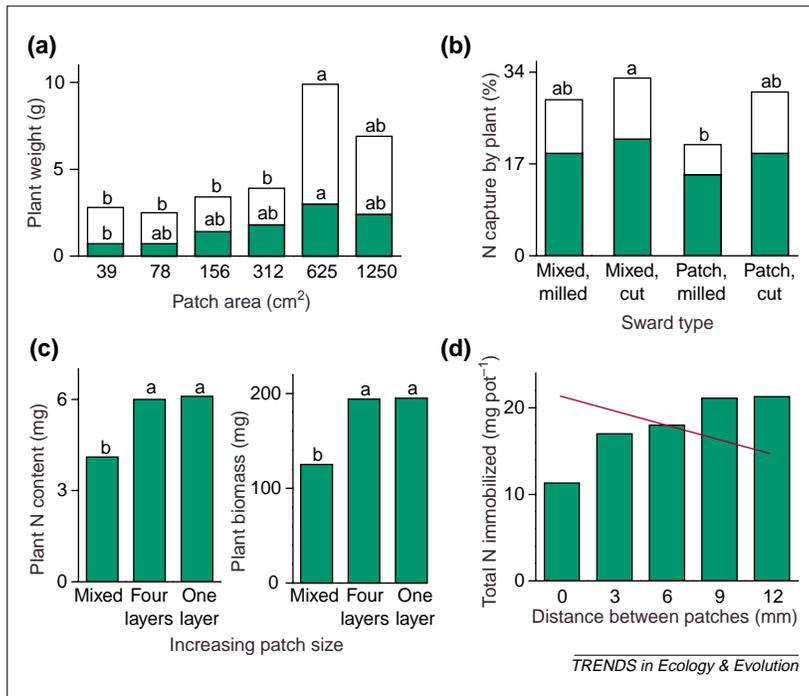
(a)

(b)

(c)

(d)

Fig. 2. Varied effects of patchiness of soil organic matter hotspots on plant growth and nitrogen (N) acquisition in four representative studies. In each case, the total amount of each type of material included in the experimental substrate remains constant but its spatial pattern is varied. (a) Effect of increasing the patch size of a constant amount of compost added to sand on the growth of the clonal herb *Glechoma hederacea*. Open and closed portions of each bar represent shoot and root mass, respectively. Data from [8]. (b) Effect of the nature of addition of a set amount of organic matter (N-rich *Lolium perenne* shoots) to a sand–soil growth medium on total uptake of N by a mixed sward of *Poa annua* (closed portions of bars) and *L. perenne* (open portions of bars). Data from [57]. (c) Effect of increasing patch size of a fixed amount of chopped *L. perenne* tissue added to soil on net N uptake and mass production of *L. perenne* seedlings. Treatments involve *L. perenne* tissue mixed with the soil, or arranged in one or four discrete layers. Data from [56]. (d). Effect of increasing distance between patches of a N-rich substrate (clover leaves) and a N-poor substrate (straw) added to soil on measured uptake of N by *Hordeum vulgare* plants (histogram bars) and N uptake by the soil microflora as estimated using a simulation model (line). Data from [58]. For (a–c), histogram bars topped by the same letter do not differ significantly at $P = 0.05$.

Aboveground consequences of belowground spatial patterning

There is an increasing awareness that the feedbacks among aboveground and belowground biota are major ecological drivers in terrestrial ecosystems [44]. Spatial patterning of soil biota and biotic activity can have important aboveground consequences, and this is apparent with regard to both plant community structure and the growth of individual plants [45].

Many soil macrofauna species create physical structures that contain different physical and chemical properties to those of the surrounding soil, and the spatial distribution of these structures is therefore a powerful determinant of plant community structure. Termite mounds in eastern Australia [46], ant mounds in The Netherlands [26] and gopher mounds in Californian grasslands [47] have all been shown to support vegetation types that are very different from those in the surrounding landscape, and these structures are important in determining both the dynamics and spatial patterning of plant communities.

Spatial distributions of soil organisms that form associations with plant roots can also influence spatial patterning of different plant species in a community,

and this is regulated by plant–soil feedbacks. For example, plant species can promote pathogenic fungi that contribute to their local decline. In a deciduous forest in Indiana, USA, Packer and Clay [48] demonstrated that seedlings of black cherry *Prunus serotina* showed very high mortality when planted in soil collected from under black cherry trees, but not in soil collected 25–30 m away from the trees. This was apparently a result of a build-up of pathogenic fungi *Pythium* spp. under the trees, and suggests that plant–soil feedback could influence tree spacing and distribution patterns. Root herbivores, such as nematodes [49] and insects [50], influence plant community structure through exhibiting differential feeding patterns on different plant species. Olff *et al.* [49] suggested that soil disturbances in grasslands by ants and rabbits in The Netherlands influenced the spatial distributions of plant-pathogenic soil nematodes, and that this, in turn, favored the grass *Festuca rubra* over the sedge *Carex arenaria* in the disturbed patches. Furthermore, plant–mycorrhizal associations can also influence spatial patterning of plant communities, either by promoting greater coexistence of plant species (apparently as a result of reduced competition intensity) [51], or by reducing coexistence by competitively excluding plant species not linked to the same hyphal network [52].

The spatial patterning of plants is likely to be influenced further by the spatial distributions of soil organisms active in decomposition and nutrient cycling. Plants of different species that are spatially separated might exert differential effects on the patterns of nutrient supply from the soil, which, in turn, can result in maintenance of each plant species on the patch that it occupies, promoting maintenance of a diverse plant community [7]. Such a mechanism is likely to involve different plant species selecting for different decomposer communities and activities, with subsequent feedbacks [44].

At smaller spatial scales, spatial patterning of the decomposers in the soil matrix can also influence the growth of individual plants, and this is determined ultimately by the spatial distribution and decomposition of organic matter hotspots. Sulkava and Huhta [38] provided evidence that a set quantity of litter arranged in patches was mineralized more rapidly than when mixed through the soil in the absence (but not in the presence) of soil fauna. Such hotspots can serve as localized ephemeral microsites of enriched mineral nutrient supply, and the ability of plants to utilize these microsites depends on the capacity of their roots to rapidly locate these patches and proliferate in them. Different plant species differ in their precision of foraging for patchily distributed nutrients [53,54]. Recent experiments that have aimed to determine how increasing resource patch size influences plant growth have found patterns that range from neutral [55] to positive [8,56] to negative [57] depending on the plant species used and the experimental conditions (Fig. 2). Competition

between plants and microorganisms for nutrients is an important determinant of plant nutrient acquisition, and its outcome could be influenced by the spatial separation of organic matter patches. For example, Korsaeth *et al.* [58] found that the competitive balance between plants and microbes for nitrogen switched from favoring microbes to favoring plants, as the distance between N-mineralizing hotspots (clover *Trifolium* sp. particles) and N-immobilizing hotspots (straw particles) increased.

Underlying themes

Although spatial variability in soil organism distributions is often regarded as random noise, understanding the drivers of this variability could help to develop insights as to the factors that regulate the soil biota, and their functional roles. Spatial hierarchies of environmental factors, intrinsic population processes and disturbance regimes operate to influence the patchiness of populations of soil organisms and the ecosystem processes that they carry out at scales ranging from millimeters to hundreds of meters. Characterization of these patterns is pivotal to improving quantification and our understanding of factors that drive soil organisms across spatial and temporal scales.

Spatially explicit approaches might help us to better understand factors responsible for the extremely high diversity of organisms that live in soils. Limited dispersability of much of the soil biota, soil resource heterogeneity and local disturbance regimes lead to stochastic patch dynamics, and this could have an important role in maintaining the magnitude and function of soil biodiversity. Furthermore, because of the role of spatial patchiness of the soil biota in regulating spatial distributions of plant nutrient supply, soil-borne mutualists and antagonists of plant roots, the spatial distribution of soil organisms is likely to operate as a driver of spatial patchiness of species within plant communities and, ultimately, plant community diversity. Finally, although there are challenges in working with soil biota because of taxonomic complexities and the opaque nature of the soil matrix, soil communities offer great potential for advancing our understanding of factors that spatially structure communities, species coexistence mechanisms and, ultimately, the functioning of ecological communities both aboveground and belowground.

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Gene flow and the limits to natural selection

Thomas Lenormand

In general, individuals who survive to reproduce have genotypes that work relatively well under local conditions. Migrating or dispersing offspring elsewhere is likely to decrease an individual's or its offspring's fitness, not to mention the intrinsic costs and risks of dispersal. Gene flow into a population can counteract gene frequency changes because of selection, imposing a limit on local adaptation. In addition, the migrant flow tends to be higher from densely populated to sparsely populated areas. Thus, although the potential for adaptation might be greatest in poor and sparsely populated environments, gene flow will counteract selection more strongly in such populations. Recent papers, both theoretical and empirical, have clarified the important role of migration in evolution, affecting spatial patterns, species ranges and adaptation to the environment; in particular, by emphasizing the crucial interaction between evolutionary and demographic processes.

Thomas Lenormand
CEFE – CNRS, 1919 route de Mende, 34293 Montpellier cedex 05, France.
e-mail: thomas.lenormand@cefe.cnrs-mop.fr

Under natural selection, individuals tend to adapt to their local environmental conditions, resulting in a pattern of LOCAL ADAPTATION (see Glossary). Local adaptation can occur if the direction of selection changes for an allele among habitats (antagonistic environmental effect), but it might also occur if the intensity of selection at several loci that are maintained as polymorphic by recurrent mutations covaries negatively among habitats. These two possibilities have been clearly identified in the related context of the evolution of senescence but have not have been fully appreciated in empirical and theoretical studies of local adaptation [1,2].

The interaction between directional selection and gene flow

When an allele with antagonistic environmental effects is maintained at a MIGRATION–SELECTION EQUILIBRIUM, gene flow changes allele frequencies in a direction opposite to natural selection, and each population is suboptimally adapted: that is, there is a MIGRATION LOAD. For small amounts of migration, this load per locus approximately equals the migration rate. If the migration rate is large compared with selection, the polymorphism is lost. When such GENE SWAMPING occurs, the alleles with the best average reproductive success across all populations tend to become fixed; therefore there is no local adaptation