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Community patterns of soil bacteria and nematodes in relation to geographic distance

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ABSTRACT

Ecosystems consist of aboveground and belowground subsystems and the structure of their communities is known to change with distance. However, most of this knowledge originates from visible, aboveground components, whereas relatively little is known about how soil community structure varies with distance and if this variability depends on the group of organisms considered. In the present study, we analyzed 30 grasslands from three neighboring chalk hill ridges in southern UK to determine the effect of geographic distance (1–198 km) on the similarity of bacterial communities and of nematode communities in the soil. We found that for both groups, community similarity decayed with distance and that this spatial pattern was not related to changes either in plant community composition or soil chemistry. Site history may have contributed to the observed pattern in the case of nematodes, since the distance effect depended on the presence of different nematode taxa at one of the hill ridges. On the other hand, site-related differences in bacterial community composition alone could not explain the spatial turnover, suggesting that other factors, such as biotic gradients and local dispersal processes that we did not include in our analysis, may be involved in the observed pattern. We conclude that, independently of the variety of causal factors that may be involved, the decay in similarity with geographic distance is a characteristic feature of both communities of soil bacteria and nematodes.

1. Introduction

The recognition of patterns in the spatial turnover of species is an important first step to understand the factors that determine their distribution and diversity. Distribution patterns will vary among groups of organisms because of large differences in traits such as body size, reproductive rates and dispersal abilities (Krebs, 2001). These differences are the basis for the expected divergence in biogeographical patterns between micro- and macroorganisms (Martiny et al., 2006). Dispersal abilities of microorganisms and small organisms in general (less than 1 mm in length), are often assumed to be much greater than those of macroorganisms, thereby preventing geographic differentiation in the composition of their communities (Fenchel et al., 1997; Fenchel and Finlay, 2004). However, the studies testing this hypothesis have led to conflicting results (Cermeño and Falkowski, 2009; Finlay et al., 2001; Hubert et al., 2009; Lawley et al., 2004; Telford et al., 2006), suggesting that biogeographic patterns of small organisms strongly depend on the group considered, the geographic scale and the type of environment.

In terrestrial ecosystems, microorganisms and small invertebrates account for the main part of the biodiversity in the soil (Lavelle and Spain, 2001). Life history strategies and distribution patterns of soil organisms are constrained by the characteristics of the soil environment, formed by a heterogeneous organic-mineral matrix that favors species with small body sizes and limits active dispersal. As a consequence, soil organisms often show patchy distribution patterns and opportunistic population growth caused by local fluctuations in resource availability (Lavelle and Spain, 2001). The soil matrix may also act as a physical barrier limiting

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passive dispersal of soil organisms, favoring isolation between populations and therefore local differentiation at local spatial scales (Vos and Velicer, 2008). These factors, together with the structural complexity of the soil matrix, are expected to have a significant effect on the patterns of diversity in soil organisms (Wardle, 2002). Currently, unraveling such patterns is of main interest as a critical step in further understanding the factors that contribute to soil biodiversity and the ecosystem services that may result from it (Fierer et al., 2009; Strickland et al., 2009; Wardle et al., 2004; Yergeau et al., 2010a).

If the soil environment limits dispersal processes of small organisms, these organisms should show significant decays in community similarity with geographic distance. To test this hypothesis, we assessed the spatial turnover of soil bacterial and nematode taxa between a series of chalk grasslands. Among the temperate biomes, grasslands show the highest amount of soil microbial and faunal biomass in relation to plant biomass (Fierer et al., 2009). Most of this microbial biomass is made up by bacteria (Bardgett et al., 1999; Fierer et al., 2009), which play a central role in decomposition and mineralization of organic matter in the rhizosphere and of global nitrogen and carbon cycles. Soil bacterial communities are extremely diverse (Curtis et al., 2002) and include not only organic matter decomposers, but also plant pathogens, plant mutualists and natural enemies of the root herbivores (Lavelle and Spain, 2001).

Nematodes are also very abundant in grasslands, and consist of species groups that vary widely in resource use (Yeates et al., 1993). Root-feeding nematodes are the main group of root herbivores in temperate grasslands and they can consume as much as a quarter of the plant biomass in these biomes (Stanton, 1988). Their feeding activities affect plant abundance, plant quality and plant community composition (De Deyn et al., 2003, 2004; Viketoft et al., 2009). Bacterivorous nematodes are the most important consumers of bacteria among soil invertebrates (Ekelund and Rønn, 1994) and they influence decomposition and nutrient mineralization processes in grassland soils (Stanton, 1988). Furthermore, grassland soils also contain fungal feeding, omnivorous and carnivorous nematodes (Hodda and Wanless, 1994). In spite of the potential role of bacteria and nematodes in processes related to vegetation dynamics and nutrient cycling, their spatial distribution patterns in the field are poorly known.

In the present study, we collected and analyzed soil samples from 30 chalk grasslands in southern UK to investigate how similarity patterns of soil bacteria and nematodes decay with distance at an intermediate geographic scale (1–198 km). We took a molecular approach to determine presence/absence of dominant bacterial taxa, while nematode taxa were identified using morphological traits. We tested the hypothesis that soil bacteria and nematodes show significant patterns of taxa turnover over distance. We also analyzed soil chemical characteristics and plant community composition in order to assess the influence of these environmental factors on the spatial variability of soil communities. We discuss the results in relation to the possible causes of the distance-related decay in community similarity of soil biota. We comment on the relevance of finding non-random patterns of taxa turnover for bacteria and nematodes, also considering the differences in their life histories, and in the identification methodology.

2. Materials and methods

2.1. Study area and sampling design

The study area was located in southern UK, between 50°44′–51°57′ N and 2°32′ W–0°14′ E. The sampling sites comprised 30 grasslands on ex-arable land separated from each other by distances ranging from 1 to 198 km (Fig. 1). The grasslands occurred on three different chalk hill ridges: the Chiltern Hills (CH), South Downs (SD) and South Wessex Downs (SW). On each chalk hill ridge soil samples were collected from 10 fields, leading to a total of 30 samples. During the past 8–19 years, some of the fields had been sown with a mix of grassland species while others were left to natural colonization. As a result, there was some variation in plant community composition among the fields, but this variation did not relate to distance. Further information about the time of abandonment and the restoration strategy of the fields can be found in Yergeau et al. (2010a). The fields varied in size between one and a few hectares. Within each field a representative sampling area of approximately 50 m × 100 m was selected. The sampling area was situated at a distance of at least 20 m away from the field boundary. Within the sampling area a structured 'W'-shaped walk was carried out, where soil and plant community samples were collected from five 2 m × 2 m plots. The soil samples were analyzed to determine soil chemical properties, bacterial and nematode community composition. In the field, we determined the percentage cover of each plant species present in each of the plots.

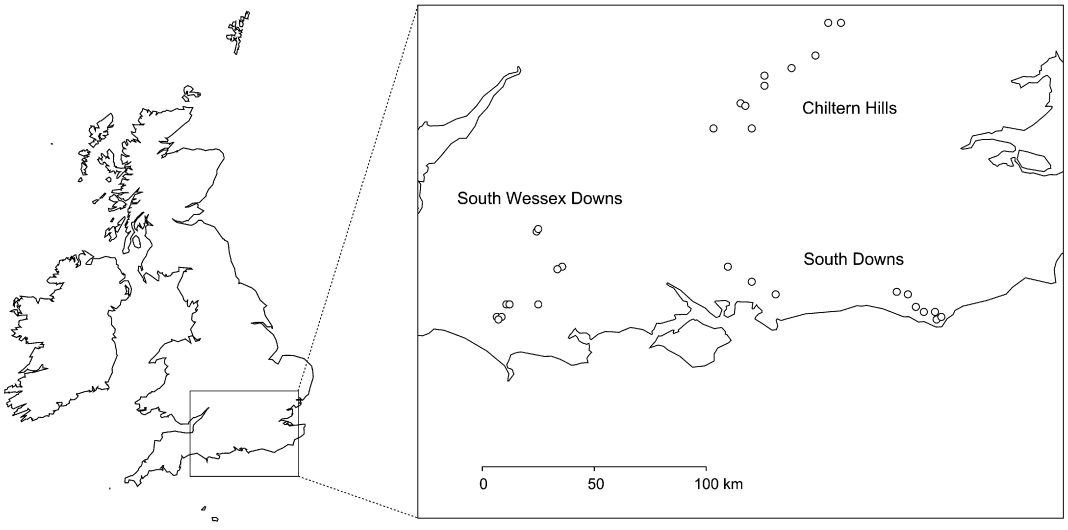

Fig. 1. Map of southern UK with the location of the 30 restoration grasslands used in this study and the names of the three different sampling regions.

2.2. Soil analysis

From each individual 2 m × 2 m quadrat, one soil core of 10 cm deep and 2.5 cm diameter was collected and a 10 g subsample was stored at −80 °C for molecular analysis. Afterward, the five samples from each field were pooled, gently sieved through a 2 mm mesh and homogenized. Part of this composite sample was air-dried at room temperature prior to the chemical analysis. Dry samples were used to determine pH and content of organic matter, C, N, P and K, following standard methods (Tan, 2005). The remaining fresh soil was used for nematode community analysis.

2.3. Nematode counts and identification

Nematodes were extracted from 100 g fresh soil samples (see above) using a modified Oostenbrink elutriator (Oostenbrink, 1960). The nematodes were heat killed and fixed in 4% formaldehyde. They were counted using a microscope at 100–400× magnification and identified to the family or genus level according to Bongers (1988). This was the highest achievable taxonomic resolution and is typically the finest resolution used in studies that report composition of soil nematode communities.

2.4. PCR-DGGE

Bacterial communities of the soil samples were analyzed by 16S rDNA-directed PCR-denaturing gradient gel electrophoresis (PCR-DGGE) profiling (Muyzer and Smalla, 1998). To maximize the number of bacterial species detected, three of the five available samples per field were selected to perform the analysis. The samples were kept separate and each sample was thoroughly homogenized before collecting a 0.25 g subsample for DNA extraction using the MOBIO soil DNA extraction kit according to the manufacturer's specifications. DNA was eluted in 50 µl 10 mM Tris, pH 8.0. The primers, thermocycling regimes and electrophoresis conditions used to analyze the bacterial community were those described by Yergeau et al. (2010a). The banding patterns of PCR-DGGE gels were analyzed using the Image Master 1D program (Amersham Biosciences, Roosendaal, The Netherlands). The resulting binary matrices were exported and used in statistical analyses as 'species' presence/absence matrices. The bacterial community at each grassland field was represented as the total number of bands of the three samples. The bands were considered to represent taxonomical units close to the species level because each of them constitutes a unique DNA-sequence type, which in turn corresponds to a discrete bacterial population (Fromin et al., 2002).

2.5. Data analysis

Data were analyzed using the R environment (R Development Core Team, 2011). Similarity in bacterial and nematode communities between field sites was assessed by means of Jaccard and Bray–Curtis indexes, respectively. Normalized Mantel tests (based on 10^4 permutations) were performed to test the correlation between those indexes and geographic distance, using the statistical package *vegan* (Oksanen et al., 2011). Since a previous study showed that the composition of bacterial and nematode communities depended on soil chemical characteristics and plant community composition (Yergeau et al., 2010a), Mantel tests were also calculated to verify that none of these variables were correlated with geographic distance. In order to substantiate the results of the Mantel tests, partial Mantel tests (Legendre and Legendre, 1998) were used to estimate the correlation between bacterial/nematode community similarity and geographic distance while controlling for the effect of soil chemistry and plant community composition.

We performed Principal Component Analysis (PCA) to check for possible differences in soil chemical characteristics and plant community composition between the three hill ridges. According to Yergeau et al. (2010a), the composition of the bacterial community differed between the Chiltern Hills and the other two regions of the study area. To check if these differences influenced the observed patterns of bacterial community similarity with distance, the Mantel test was recalculated after excluding bacterial communities from the Chiltern Hills. In the same way, we performed a PCA to check for differences in nematode community composition between the sampling regions. The Mantel tests for nematode data were recalculated according to the results of the PCA.

Sample-based rarefaction curves (Gotelli and Colwell, 2001) were used to evaluate the degree of patchiness in taxon abundance of bacteria and nematodes that resulted from the effect of geographic distance on taxa distribution. This was done by comparing the randomized taxa accumulation curves with the distance-based accumulation ones. Rarefaction curves were constructed by using the function betadiver( ) of the *vegan* package. Differences between curves were estimated using a permutation test (Edgington, 1980) based on 10^4 permutations, with the function compareGrowthCurves( ) of the package *statmod* (Smyth, 2011).

3. Results

3.1. Bacterial communities

Similarity in the bacterial community composition of the fields was negatively correlated with geographic distance (Fig. 2a). In spite of the variation observed, this pattern of distance-decay in similarity was significant, as indicated by the Mantel test ($r = 0.27$, $P < 0.001$). The pattern remained significant ($r = 0.26$, $P < 0.001$) after removing the bacterial communities from the Chiltern Hills, which indicated that the distance-decay in community similarity was not primarily due to differences in bacterial community composition between the three sampling regions. There was no significant relationship between community similarity and geographic distance at the within-region scale (40–90 km wide; data not shown).

In order to check if this pattern of similarity decay of bacterial communities with distance may be due to environmental factors that may change with distance, we performed additional analysis. The analysis of the correlations between geographical distances, soil chemical characteristics and plant community composition did not reveal a significant relationship between distance and these environmental factors ($r = -0.07$, $P = 0.86$ for soil chemical composition; $r = 0.02$, $P = 0.38$ for plant communities). The results of the PCAs showed no differences either in the overall soil chemical characteristics or in plant community composition between chalk hill ridges (see Fig. S1). The use of partial Mantel tests supported the results of the Mantel tests and discarded any influence of these environmental factors on the similarity decay of the bacterial communities with distance ($r = 0.3278$, $P < 0.001$, while controlling for soil chemical composition; $r = 0.3292$, $P < 0.001$, while controlling for plant community composition).

The taxon accumulation curves showed a negative effect of proximity on the number of bacterial taxa. The richness of bacterial taxa in the distance-based accumulation curve was consistently lower than the expected values provided by the rarefaction one ($t = -7.42$, $P < 0.001$, Fig. 3a), indicating some degree of spatial aggregation of bacterial taxa collected by PCR-DGGE.

3.2. Nematode communities

As for bacteria, the similarity of the nematode communities was negatively correlated with geographic distance ($r = 0.40$, $P < 0.001$, Fig. 2b). This correlation was supported by the results of the partial Mantel tests, controlling for the influence of soil chemistry and plant community composition ($r = 0.3768$, $P < 0.001$, while controlling for soil chemical composition; $r = 0.3966$, $P < 0.001$, while controlling for plant community composition). However, the effect of distance depended on differences in nematode communities among the three sampling regions. The results of the PCA showed that especially South Wessex Downs harbored different nematode taxa than the other two chalk hill ridges (Fig. 4). After excluding the South Wessex Downs, the Mantel test indicated that the relationship between community similarity and geographic distance had lost its significance ($r = 0.10$, $P = 0.08$), even though the samples fell into the same range of distances (1 − almost 200 km). The other two possible region combinations, SW–CH and SW–SD, resulted in significant decays in nematode community similarity with distance ($r = 0.70$, $P < 0.001$ and $r = 0.60$, $P < 0.001$, respectively), indicating that at our level of taxonomic resolution, the observed distance effect was caused by the different nematode community composition of the South Wessex Downs region. Community similarity did not decrease with distance at the within-region scale (data not shown).

The nematode taxon accumulation curves showed a negative effect of geographical vicinity on the richness of the nematode community. The increase in the number of nematode taxa with distance was lower than predicted by random sampling ($t = -1.98$, $P < 0.001$, Fig. 3b), indicating spatial aggregation of the nematode taxa as identified at the genus or family level.

4. Discussion

Community similarity of soil bacteria and nematodes decayed significantly with geographic distance, indicating that distribution patterns for these organisms at a regional scale level were non-random. Remarkably, the distance-decay patterns occurred in both groups studied, in spite of their different functional characteristics, dispersal capacities, and the different types and levels of taxon identification that we applied. Therefore, our results suggest that the factors leading to geographic differentiation of soil communities may operate at similar scales for bacteria and

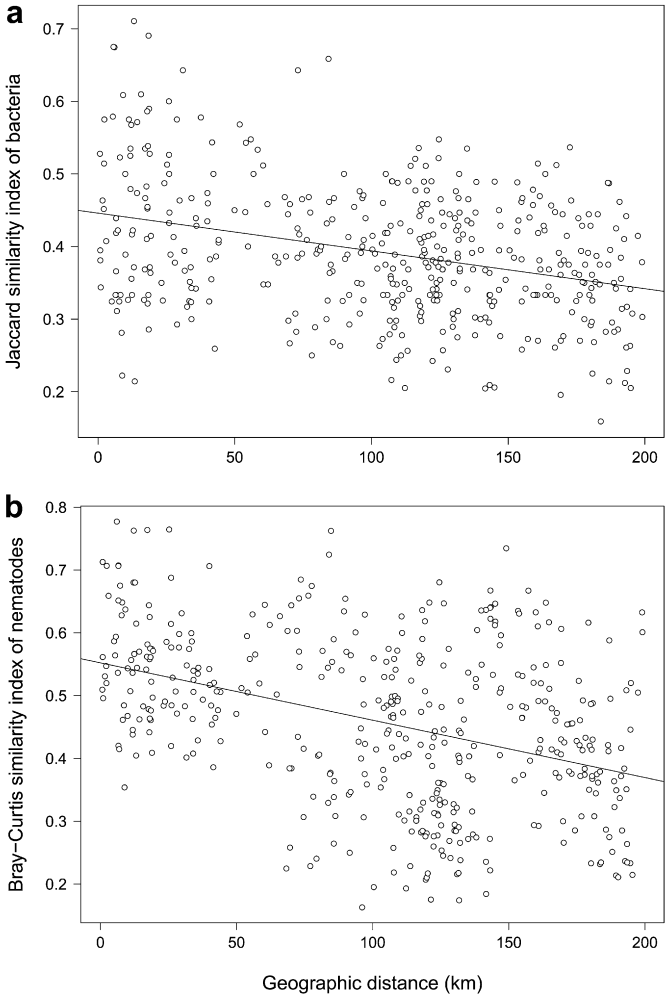

Fig. 2. Relationship between geographic distance and community similarity of soil bacteria (a) and soil nematodes (b). Points represent pair-wise distances (similarities) among all pairs of sampled sites ($N = 30$), resulting in $N(N-1)/2 = 435$ comparisons. The straight lines represent the linear relationships between the distance matrices.

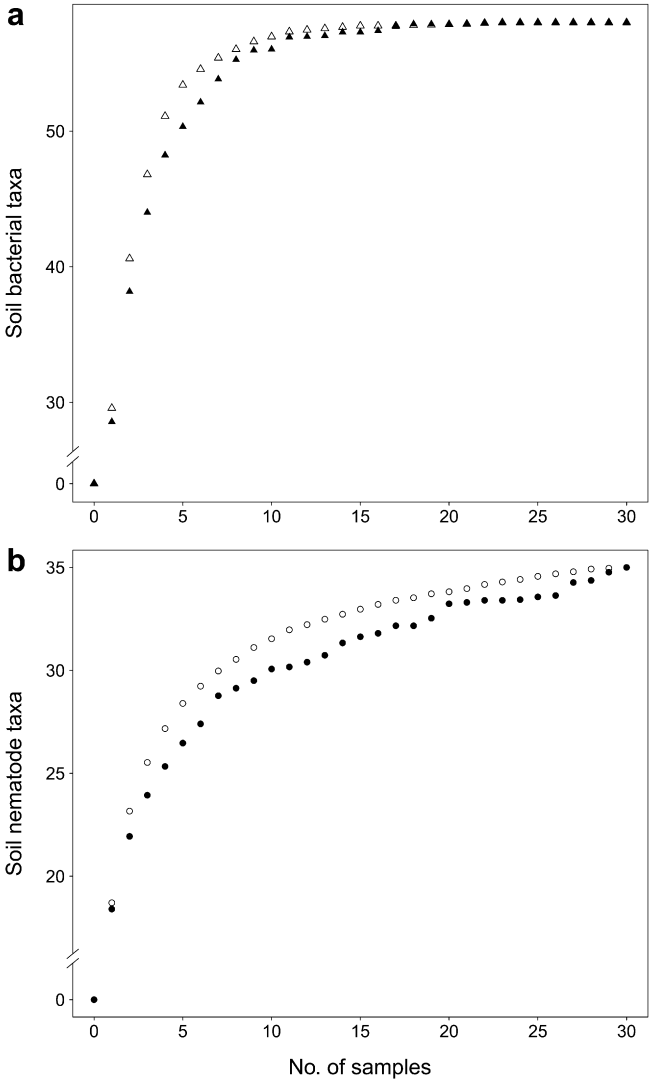

Fig. 3. Sample-based rarefaction (open symbols) and taxa accumulation by distance (solid symbols) curves for soil bacteria (a) and soil nematodes (b). For the rarefaction curves, the x axis indicates the number of random samples; for the distance-based curves, the number of most nearby samples. The rarefaction curves are based on 100 permutations.

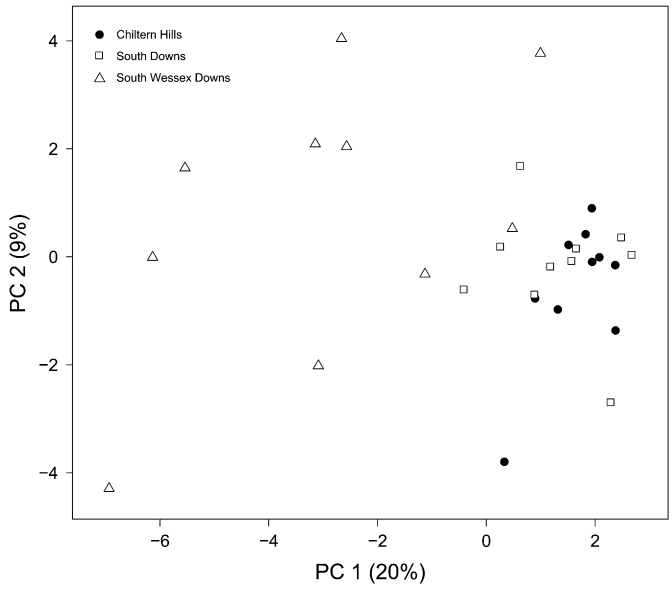

Fig. 4. Principal component analysis of the nematode communities of 30 semi-natural grassland fields in the Chiltern Hills, South Downs and South Wessex Downs in southern UK.

nematodes. Recent studies (Horner-Devine et al., 2007; Martiny et al., 2006) focusing on the biogeographic patterns of micro- and macroorganisms have provided insight into the possible factors driving the spatial structure of their communities. According to these studies, spatial patterns of distribution such as the ones we found are driven by processes such as competition, habitat configuration and historical effects. Dispersal limitation can also create correlation between nearby sites leading to the observed patterns of taxa turnover (Bell, 2001). These processes are not mutually exclusive and may operate together, resulting in a combination of spatial constraints whose relative importance probably depends on the geographic scale considered (Martiny et al., 2011).

The decay of community similarity with distance might be caused by an increased dissimilarity in environmental features (Nekola and White, 1999). In our grasslands, a previous study (Yergeau et al., 2010a) showed that the composition of the bacterial communities may be explained by both the plant community composition and the soil characteristics of the sampling sites. However, these environmental features only explained 9% of the observed variation, indicating that additional factors were shaping bacterial distribution. We found that the distance between locations is an additional explanatory factor for the observed variation in the composition of soil bacterial communities. Although distance-related changes in the community composition of sediment and soil bacteria have been previously reported at scales of 200–600 m (Horner-Devine et al., 2004; King et al., 2010), in those studies it was not possible to separate the effect of distance from the occurrence of gradients in plant community composition and soil chemistry. In our study, we were able to isolate the effect of geographic distance from those gradients by selecting fields with the same type of vegetation among different sampling regions. We cannot exclude that environmental gradients leading to soil community dissimilarity may act at scales that are not detected by conventional soil and plant sampling techniques (Yergeau et al., 2010b). For instance, gradients associated to unmeasured soil biotic factors, such as the presence of viruses, fungi, Protozoa and microarthropods could be responsible for the variation in bacterial and nematode communities.

The use of two different identification techniques may have influenced our estimate of the distance-decay in community similarity. In the case of bacteria, the use of PCR-DGGE enables the detection of taxa representing ~99% of the total community (Muyzer et al., 1993; Muyzer and Smalla, 1998). Although other bacterial taxa may occur at densities that are below the detection limit of this technique, the observed variation between bacterial communities indicates differences in their structure, i.e., in the identity of the main species present at each site (Fromin et al., 2002). Similar PCR-based approaches have been used to assess bacterial community composition and richness over different spatial scales (Bell et al., 2005; Fierer and Jackson, 2006; Van der Gucht et al., 2007). Since the main part of the bacterial community is screened with this technique, the detection of additional bacterial taxa is likely to result in proportional changes in all samples (Bell et al., 2005). These changes are not expected to alter our estimates of spatial turnover. In the case of nematodes, we used a morphological analysis with a taxonomic resolution at the family/genus level. However, the lack of information about species presence/absence is expected to underestimate the differences in community composition between samples. Therefore, the significant distance-decay we observed in nematode community similarity can be considered as a reliable measure.

Spatial turnover of bacterial taxa may be favored by local differentiation processes (at scales between cm and m) in response to site-specific biotic or abiotic factors (Cho and Tiedje, 2000; Vos and Velicer, 2008). These processes occur in many microbial taxa and lead to geographic structuration and diversification of their populations (Whitaker, 2009), which in turn is expected to affect the composition of the microbial community. Nematode communities can also differ at distances less than 1 m (Ettema and Yeates, 2003), indicating a great potential for spatial patterning at larger scales. This variability may be driven by heterogeneity in the soil structure, but also by the patchy distribution showed by some of their natural enemies (Dabiré et al., 2005). Dispersal limitation is expected to maintain and even to enlarge these differences in community composition. Local dispersal leads to the spatial aggregation of individuals from the same species, increasing community similarity between nearby sites. Clumping affects niche-based processes such as intra- and interspecific competition, likely reinforcing this similarity pattern. The resulting patchiness would also allow ecological drift to increase differentiation between communities with geographic distance (Bell, 2001).

Another possible cause for the observed geographic pattern in bacterial and nematode communities is the persistence of temporal constraints, i.e., the influence of historical events such as past environmental conditions that led to local differentiation of soil organism communities (Martiny et al., 2006). Yergeau et al. (2010a) found a significant divergence between the bacterial community composition of the Chiltern Hills and the other two areas, and for nematodes we found that South Wessex Downs supported a different community composition than the Chiltern Hills and South Downs. These divergences were poorly explained by differences in plant composition and soil chemistry, suggesting that current bacterial and nematode communities may represent, at least to some extent, the biotic composition of their regions before the cessation of cultivation (Kardol et al., 2005; Kielak et al., 2008).

Since increasing distances in our pair-wise comparisons of community composition entailed comparison between fields from different regions, the distance-decay in community similarity could have been due to the observed differences in community composition between regions. Interestingly, this explanation appeared to apply to the nematode communities, at our level of identification,

but not to the bacteria, because the distance-decay in bacterial similarity was observed even when the outlying chalk hill ridge was omitted from the analysis. Therefore, the persistent pattern of distance-decay in the similarity of bacterial communities suggests that factors other than soil chemistry, plant community composition and site history may play an important role in structuring communities of soil bacteria.

The comparison between the rarefaction and the taxon accumulation curves confirmed the occurrence of non-random spatial patterns in the community composition of both bacteria and nematodes. For both groups, the sample-based rarefaction curves overestimated the number of taxa obtained by sampling neighboring areas, suggesting spatial segregation among taxa (Collins and Simberloff, 2009). Segregation patterns are characteristic of communities structured by competition processes (Gotelli, 2000), but other factors, such as dispersal limitation, habitat configuration and historical effects, could also explain why segregation among taxa is a common feature of microbial communities (Horner-Devine et al., 2007). In our study, the taxon accumulation curves were probably influenced by the differences in bacteria and nematode community composition between regions. Continuous sampling over distance would result in lower taxon accumulation due to the probability that the neighbor sampling point belongs to the same sampling region, provided there was some distance between regions.

5. Conclusions

We found a significant pattern of spatial turnover in soil bacteria and nematode communities in restored conservation grasslands on ex-arable land at three chalk hill ridges in southern UK. There were no spatial gradients either in plant composition or soil chemistry accounting for the effect of distance on the community composition of bacteria and nematodes. In the case of nematodes, the similarity decay with distance may be explained by differences in the community composition of these organisms between sampling regions. On the other hand, the observed pattern of dissimilarity in bacterial communities was independent of differences between regions, indicating that the spatial patterns of soil bacteria and nematodes may be shaped by different processes. The occurrence of biotic or abiotic gradients not included in our analysis and the possible role of dispersal limitation cannot be excluded as alternative explanatory factors. We conclude that the observed pattern of similarity decay with distance is a feature of both soil bacteria and nematode communities, and that it can be found at similar spatial scales, varying from 1 to almost 200 km, in spite of their different life histories and the identification methodology employed.

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Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.soilbio.2011.10.006.

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