Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2011) **20**, 641–652

A Journal of Macroecology

Global Ecology and Biogeography

RESEARCH PAPER

Biogeographical patterns of soil molecular microbial biomass as influenced by soil characteristics and management

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ABSTRACT

Aim The spatial organization of soil microbial communities on large scales and the identification of environmental factors structuring their distribution have been little investigated. The overall objective of this study was to determine the spatial patterning of microbial biomass in soils over a wide extent and to rank the environmental filters most influencing this distribution.

Location French territory using the French Soil Quality Monitoring Network. This network covers the entire French territory and soils were sampled at 2150 sites along a systematic grid.

Methods The soil DNA extracted from all these soils was expressed in terms of soil molecular microbial biomass and related to other soil and land-use data over French territory.

Results This study provides the first extensive map of microbial biomass and reveals the heterogeneous and spatially structured distribution of this biomass on the scale of France. The main factors driving biomass distribution are the physico-chemical properties of the soil (texture, pH and total organic carbon) as well as land use. Soils from land used for intensive agriculture, especially monoculture and vineyards, exhibited the smallest biomass pools. Interestingly, factors known to influence the large-scale distribution of macroorganisms, such as climatic factors, were not identified as important drivers for microbial communities.

Main conclusions Microbial abundance is spatially structured and dependent on local filters such as soil characteristics and land use but is relatively independent of global filters such as climatic factors or the presence of natural barriers. Our study confirms that the biogeography of microorganisms differs fundamentally from the biogeography of 'macroorganisms' and that soil management can have significant large-scale effects.

Keywords
France, land use, microbial biomass, soil, soil properties, spatial distribution.

INTRODUCTION

Although microorganisms are the most diverse and abundant living organisms on earth, and despite their key role in a wide range of biogeochemical cycles, their distribution on small to large scales is poorly documented (Martiny *et al.*, 2006; Ranjard *et al.*, 2010). This knowledge gap might be partly explained by intrinsic characteristics such as (1) their minute size, resulting in poor accessibility in environmental matrices, (2) their high density (i.e. more than 1 billion per gram of soil) and (3) their huge diversity (from 1000 to 1,000,000 species per gram of soil), but also by the lack of robust techniques to characterize them (Torsvik & Øvreås, 2002).

Community assembly and abundance on small to very large spatial extents have been intensively investigated for macroorganisms, have been demonstrated to be strongly dependent on

DOI: 10.1111/j.1466-8238.2010.00628.x
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geographical location and have been related to site temperature, latitude and other climatic variables and/or to geographical isolation (MacArthur & Wilson, 2001; Martiny *et al.*, 2006). More precisely, precipitation gradients, water availability and evapotranspiration have been shown to be the most important factors influencing regional plant community distribution (Kreft & Jetz, 2007). However, the distribution of the abundance and diversity of microbial communities on small and large extents has been shown to be heterogeneous and spatially structured. Such variations in microbial diversity do not support the cosmopolitanism of microbes deduced from the old paradigm of Baas-Becking (1934) 'everything is everywhere' based on the works of Beijerinck (1913). On a microscale, the heterogeneous distribution of soil microbes is mainly determined by soil structure and porosity and by organic carbon content (governing trophic resources) (for a review see Ranjard & Richaume, 2001). On a field scale, the main factors structuring community abundance and assembly are the physicochemical characteristics of the soil, such as soil texture (Johnson *et al.*, 2003), soil pH (Bååth *et al.*, 1995) and soil organic status (Lejon *et al.*, 2007), but also soil management (Nicolardot *et al.*, 2007) and plant cover (Lejon *et al.*, 2005). Studies that aimed to investigate the spatial patterning of microorganisms on very wide extents (landscape, province, territory or continent) are, in comparison, very recent and few in number (Papke & Ward, 2004; Ranjard *et al.*, 2010). One of the main examples of a nationwide study of soil microorganisms is the Biological Indicator System for Soil Quality (BISQ) of the Dutch soil monitoring network (Rutgers *et al.*, 2009). Such investigations have demonstrated that the distribution of microorganisms is heterogeneous and structured by local environmental filters such as soil properties or land use (Green *et al.*, 2004; Horner-Devine *et al.*, 2004; Fierer & Jackson, 2006; Martiny *et al.*, 2006; Dequiedt *et al.*, 2009; Rutgers *et al.*, 2009) but also by more global parameters such as climatic factors (Drenovsky *et al.*, 2010). In addition, weak taxa–area relationships were observed for soil microorganisms suggesting that microbial biogeography is fundamentally different from the biogeography of macroorganisms (Green *et al.*, 2004; Horner-Devine *et al.*, 2004; Papke & Ward, 2004).

During the last two decades, novel molecular and robust methods have been developed that were well-suited to characterize soil microbial communities as they provided access to previously hidden genetic resources (for review see Torsvik & Øvreås, 2002). These methods were essentially based on soil DNA characterization and most efforts were devoted to optimizing the procedure of extracting soil DNA to obtain representative and suitable extracts for the characterization of microbial communities (Zhou *et al.*, 1996; Jackson *et al.*, 1997; Kuske *et al.*, 1998; Frostegård *et al.*, 1999; Ranjard *et al.*, 2003). At the same time, several studies demonstrated a highly positive relationship between the yield of DNA recovered and the measurement of carbon biomass in agricultural, grassland and forest soils, this latter being indicative of the size of microbial biomass (Marstorp *et al.*, 2000; Bundt *et al.*, 2001; Blagodatskaya *et al.*, 2003; Leckie *et al.*, 2004; Hartman *et al.*, 2006; Widmer *et al.*, 2006; Bouzaiane *et al.*, 2007). For example, Marstorp *et al.* (2000) and Widmer *et al.* (2006) demonstrated a high correlation ($r = 0.96$ and 0.75, respectively) between soil DNA content and microbial biomass estimated by chloroform fumigation, and they concluded that these two methods were equivalent to measuring soil microbial biomass.

As the size of the soil microbial biomass is one of the key factors determining a soil's biological quality via its role in the regulation of the transformation and storage of nutrients (Horwath & Paul, 1994), the relevance of measuring the variations in DNA recovery between soils became apparent. In addition, microbial biomass has also been demonstrated as a sensitive and early indicator of changes in soil management (agricultural practices, soil contamination, etc.; Ranjard *et al.*, 2006). Compared with classical measurements of soil microbial biomass, the better practicality and efficiency of automated medium-throughput soil DNA extraction and quantification procedures justify interest in them as indicators of soil microbial abundance that are potentially applicable to large-scale soil sampling. However, few studies have evaluated soil DNA yield in relation to soil characteristics, climatic properties and land use (Feinstein *et al.*, 2009), and when this has been done, between-study comparisons and generalization of the observed results have been limited by the variety of procedures used (Feinstein *et al.*, 2009).

In this study, we extracted and quantified soil DNA from a large national soil survey network. DNA was extracted directly and quantified from 2150 soils sampled from the French Soil Quality Monitoring Network (the 'Réseau de Mesures de la Qualité des Sols', RMQS), which consists of a systematic sampling grid extending over the whole of France. The sampling strategy thus covered a huge diversity of physico-chemical soil characteristics, plant cover, land use and climatic conditions. A single soil DNA extraction procedure was used so that a universal set of DNA extracts from French soils could be compiled and interpreted in terms of molecular microbial biomass. As each soil was precisely geopositioned, the distribution of soil molecular microbial biomass was mapped on the scale of France. In order to analyse macroecological patterns, we computed the partition of the variations between the soil molecular microbial biomass among sets based on: soil physico-chemical characteristics, climatic conditions and land use. The objectives of the present study were: (1) to define the biogeographical patterns of soil molecular microbial biomass along environmental gradients encountered in French territory; and (2) to rank the most important environmental filters structuring the distribution of microbial biomass over a wide extent.

MATERIALS AND METHODS

Soil sampling strategy

Soils were sampled from the RMQS, a soil sampling network based on a 16 × 16 km systematic grid covering the whole of France (Arrouays *et al.*, 2002). The RMQS includes 2150 monitoring sites, each one located at the centre of a 16 × 16 km cell (Fig. 1). Each site has been geopositioned with a precision of

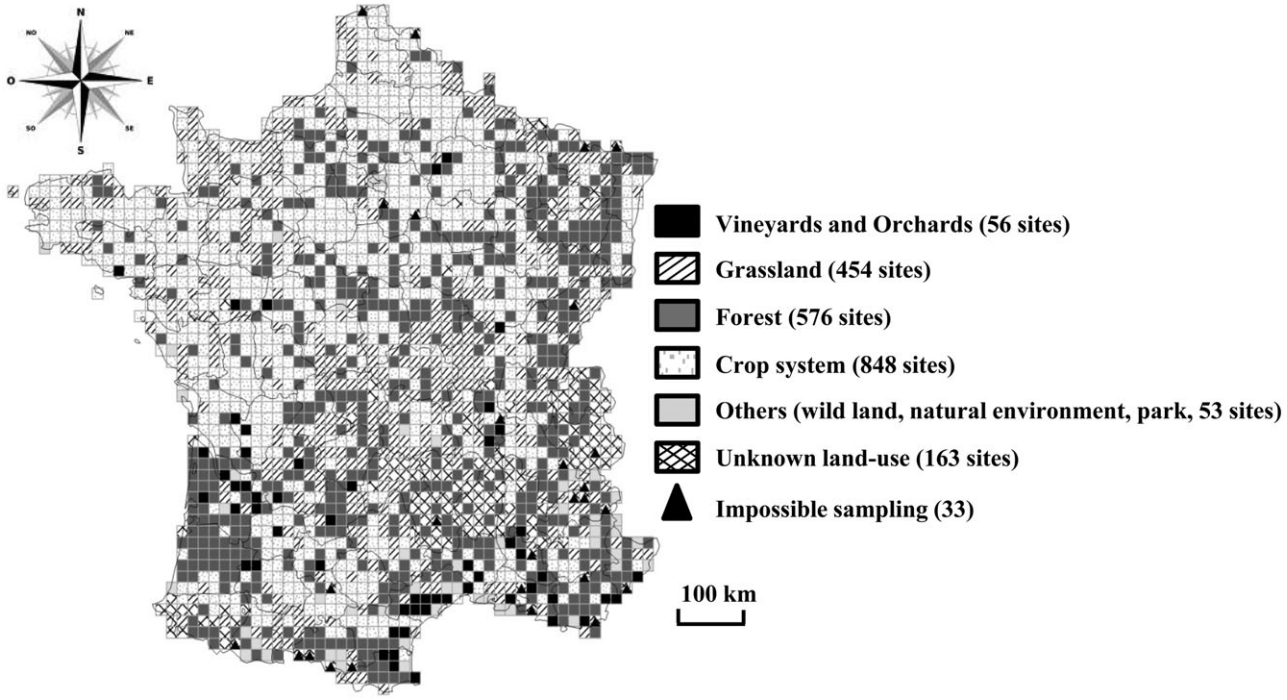

Figure 1 Location of sampling sites in the systematic sampling grid of the French Soil Quality Monitoring Network (RMQS) criss-crossing the whole French territory. Legends indicate the various types of land use encountered in France on this scale. Unknown land use corresponds to present missing data. Sites impossible to sample corresponded to inaccessible sites (mountain zone) or sites without natural soils (urban zone, rocky zone, etc.).

< 0.5 m and the soil profile, site environment, climatic factors, vegetation and land use described. In the middle of each 16 × 16 km square, 25 individual core samples were taken from the topsoil (0–30 cm) using an unaligned sampling design within an area of 20 × 20 m. The core samples were bulked to obtain a composite sample for each site. The soil samples were gently air-dried, sieved to 2 mm and stored at −40°C before analysis.

Several physico-chemical parameters were measured for each soil, i.e. particle-size distribution, pH water, organic C, N, C/N ratio, soluble P contents, calcareous, cation exchange capacity (CEC) and exchangeable cations (Ca, Mg). Physical and chemical analyses are available for 2131 soils and were performed by the Soil Analysis Laboratory of INRA (Arras, France, http://www.lille.inra.fr/las). Available climatic data were monthly rain, evapotranspiration (ETP) and temperature at each node of a 12 × 12 km grid, averaged for the period 1992–2004. These climatic data were obtained by interpolating observational data using the SAFRAN model (Quintana-Seguí *et al.*, 2008). The RMQS site-specific data were linked to the climatic data by finding for each RMQS site the closest node within the 12 × 12 km climatic grid. Land cover was recorded according to the CORINE land-cover classification (IFEN, http://www.stats.environnement.developpement-durable.gouv.fr) (Fig. 1). Coarse and refined levels of land-cover classification were used (Fig. 1). The coarse level consisted of a rough descriptive classification into five classes: forest, crop systems, grassland, others and soils under vineyards or orchards. The refined level included more detailed land cover for forests, crop systems and grassland soils. All these data were available for 2004 soils in the DONESOL database (Jolivet *et al.*, 2006; http://www.gissol.fr/programme/rmqs/RMQS_manuel_31032006.pdf).

Soil DNA extraction

DNA was extracted from 2150 soils from the RMQS grid, using a single procedure optimized by Ranjard *et al.* (2003) and recently confirmed by the GenoSol platform (http://www.dijon.inra.fr/plateforme_genosol; Ranjard *et al.*, 2009) as being reliable and robust for the routine analysis of several hundreds of different soils. Briefly, 1.5 g (dry weight) of soil sample was mixed with 5 ml of a solution containing 100 mM TRIS (pH 8.0), 100 mM ethylenediaminetetraacetic acid (EDTA; pH 8.0), 100 mM NaCl and 2% (w/v) sodium dodecyl sulphate. Two grams and 0.4 g of 106 µm and 2-mm diameter glass beads, respectively, were added in a bead-beater tube and the samples were homogenized for 30 s at 1600 r.p.m. in a mini bead-beater cell disruptor (Mikro-dismembrator S.B. Braun Biotech International, Melsungen, Germany). The samples were then incubated for 30 min at 70 °C, and then centrifuged at 7000***g*** for 5 min at 15 °C. Supernatants were collected and incubated for 10 min on ice with 1/10 volume of 3 M potassium acetate (pH 5.5) and centrifuged at 14,000***g*** for 5 min. After precipitation with one volume of ice-cold isopropanol, the nucleic acids were washed with 70% ethanol and resuspended in 100 µl of sterile ultrapure water. This procedure is currently being standardized

at an international (ISO/DIS11036) level (F. Martin and A. Bispo, personal communication) as the reference procedure for DNA extraction from soils.

Quantification of DNA extracts

Crude DNA extracts were resolved by electrophoresis in a 0.8% agarose gel, stained with ethidium bromide and photographed (Infinitycapt, Vilber Lourmat, Marne la Vallée, France). Dilutions of calf thymus DNA (Bio-Rad, Hercules, CA, USA) were included in each gel and a standard curve of DNA concentration (500, 250, 125, 62.5 to 31.25 ng) was used to estimate the final DNA concentration in the crude extracts (Ranjard *et al.*, 2003). The ethidium bromide intensity was integrated with ImageQuaNT software (Molecular Dynamics, Evry, France). The reliability of this method in limiting bias due to soil impurities that can hamper DNA quantification has been confirmed (Ranjard *et al.*, 2003).

Mathematical analysis of metadata

Mapping of soil DNA recovery

A map of DNA recovery was produced by applying the method of geostatistical interpolation using the spatial analysis GeoR R package (Ribiero & Diggle, 2001). Full details for the geostatistical interpolation are given in Webster & Oliver (2007). We therefore present an outline of our methodology below.

As the data were highly skewed, a Box–Cox transform (Box & Cox, 1964) was applied to make them more closely conform to a Gaussian distribution. The maximum likelihood methodology has been used to fit the Box–Cox parameter. The spatial correlation structure of the transformed data was described by a Matérn function which was fitted by the method of moments using the iterative weighted least squares algorithm (Cressie, 1985). Indeed, the Matérn function has a smoothness parameter that gives this function flexibility for modelling the spatial covariance, particularly for small distances. Minasny & McBratney (2005) describe in greater detail the different forms that the Matérn function can take.

Recent studies have shown a high short-range variability in the spatial organization and spatial dependence of microorganisms (Grundmann & Debouzie, 2000; Philippot *et al.*, 2009). Thus, hot-spots of microorganisms are likely to occur at scales smaller than our sampling grid spacing. The existence of these spatial outliers justifies the use of robust geostatistics (Lark, 2000).

Therefore, a robust Dowd estimator (Dowd, 1984) was used instead of the classical Matheron estimator so that the model of the underlying variation was not overly influenced by these outliers. Finally, the map of DNA recovery was produced after backtransforming the predicted median by ordinary kriging.

The validity of the fitted geostatistical models was assessed in terms of the standardized squared prediction errors using the results of a leave-one-out cross-validation. If the fitted model is a valid representation of the spatial variation of the soil property, then these errors have a χ^2 distribution which has a mean of 1 and median 0.455 (Lark, 2002). At some sites, the fitted spatial model might not approximate the behaviour of the property due to large and local outlier values of the DNA recovery. If an appropriate model is fitted by a robust variogram estimator, the mean will be then greater than 1.0 and the median will be close to 0.455 because the median is a more robust statistic. The mean and median values of θ were also calculated for 1000 simulations of the fitted model to determine the 90% confidence limits.

Statistical analysis

Physicochemical and climatic characteristics were available for 2131 of the 2150 soils studied. Pedo-climatic data were organized in a data matrix which was subjected to a principal components analysis (PCA) on a correlation matrix using ADE-4 software (Thioulouse *et al.*, 1997). This method provided an ordination of the soils in a factorial map based on the scores of the first two principal components. The corresponding correlation circle was drawn to highlight the relative contribution of each climatic and physico-chemical characteristic to the distinction of the soils. DNA yields were included as additive data to highlight the relationships between soil characteristics and DNA recovery.

Coarse level of land cover was available for 2004 RMQS soils. The effect on soil DNA yield was tested by a nonparametric Kruskal–Wallis test. Differences between means were tested by paired multiple comparison with Bonferroni correction. All the statistical analyses were performed in R packages.

RESULTS

Molecular microbial biomass in French soils

The amount of DNA recovered from the 2150 RMQs soils ranged from 0.1 μg DNA g^{-1} soil to 41.8 μg DNA g^{-1} soil (Fig. 2). The mean recovery was 9.9 ($\pm$ 5.7) μg DNA g^{-1} soil. The distribution of soil DNA recovery between French soils was neither normal nor lognormal but better fitted with the classical lognormal distribution of bacterial population size. Most of the soils (71.6%) yielded DNA concentrations between 5 and 15 μg DNA g^{-1} soil, 13.8% yielded more than 15 μg and 14.6% less than 5 μg DNA g^{-1} soil (Fig. 2).

Soil DNA recovery mapping

The robust Dowd variogram of the transformed DNA recovery is shown in Fig. 3 with the fitted Matérn model (nugget = 98.5, sill = 86.5, range = 62 km and ν = 0.35). The fitted Matérn parameters yielded good cross-validation results (median of θ = 0.473 which is within the 95% confidence interval of about 0.455). The nugget/(sill+nugget) ratio is substantial (0.53) and represents the variance that cannot be explained by the model. The value of this ratio shows that much of the nugget will be the result of spatial correlation over distances less than the 16 km grid size. The fitted model gave an effective range of 160 km

showing a large autocorrelation distance. However, the ν parameter which controls the smoothness of the spatial process was small, indicating a rough spatial process at small distance.

The map of DNA recovered revealed a heterogeneous distribution of microbial biomass which was, to a large extent, spatially structured in geographical patterns (Fig. 4). Three regions exhibited low DNA recovery: the Landes (L-zone 1), the eastern Mediterranean coast (L-zone 2) and the Paris Basin (L-zone 3). In contrast, four regions exhibited high DNA recovery: the north-east (H-zone 1), the east (H-zone 2), the south-west (H-zone 3) and the Massif Central (H-zone 4). The other regions of France exhibited a medium and rather homogeneous amount of soil DNA, although some outliers of high and low soil DNA recovery were also observed throughout the country (Fig. 4).

Relationships between DNA recovery and pedo-climatic characteristics

Relationships between DNA recovery, physico-chemical characteristics and climatic conditions were statistically related by a correlation circle corresponding to the PCA ordination of soils (Fig. 5). DNA recovery was positively correlated with CEC, clay

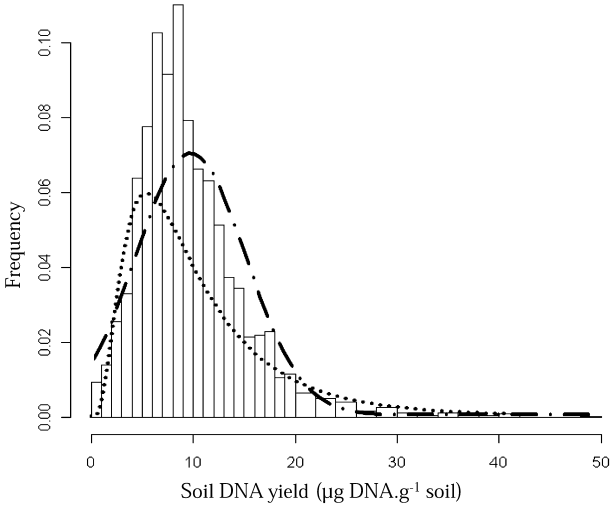

Figure 2 Distribution of DNA yields in French soils. The curves correspond to simulation of normal (dotted line) and lognormal (dashed and dotted line) distributions.

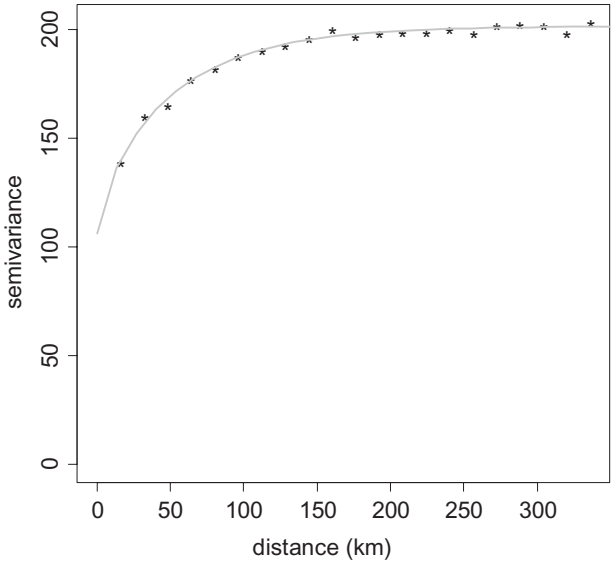

Figure 3 Robust variograms of soil molecular microbial biomass on the scale of French territory. The grey line shows the fitted Matérn function on the Dowd's variograms (*).

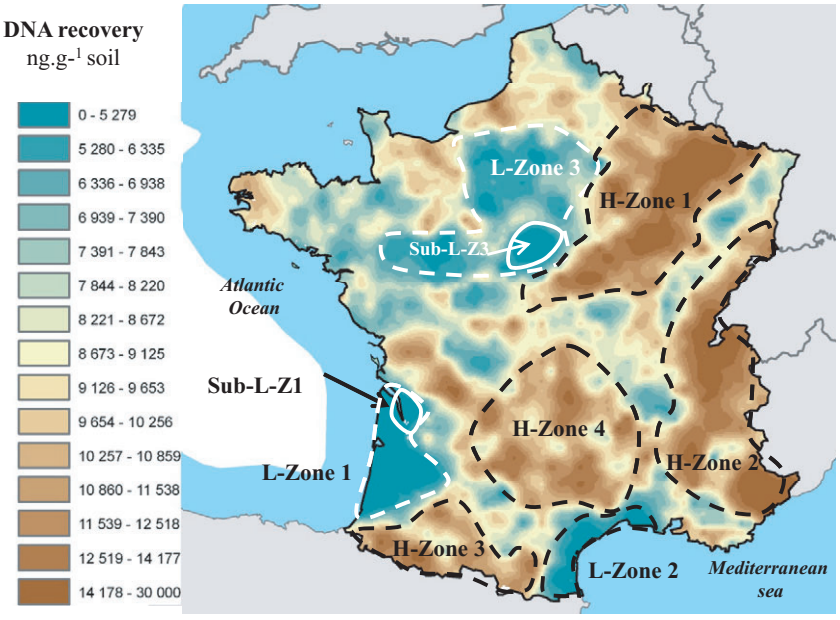

Figure 4 Mapping of soil molecular microbial biomass on the scale of the French territory. The L and H zones correspond to cold and hot spots of microbial biomass on a regional scale, respectively. Arrows indicate subzones with local cold and hot spots of microbial biomass.

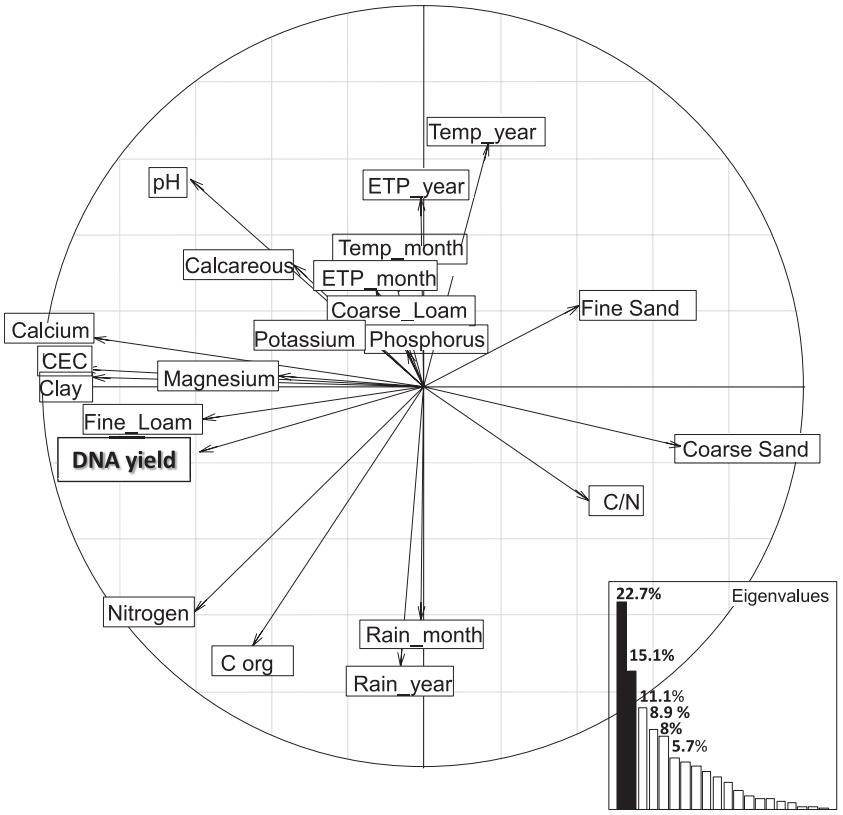

Figure 5 Correlation circle of the principal components analysis (PCA) on the correlation matrix of soil physicochemical characteristics, climatic conditions and DNA recovery data, showing factors contributing to distinction between the soil samples. C/N, carbon to nitrogen ratio; ETP, evapotranspiration; Temp, atmospheric temperature; CEC, cation exchange capacity.

and fine silt contents and, to a lesser extent, with pH, organic C and N contents. Inversely, DNA yields were negatively correlated with sand and coarse silt contents as well as with the C/N ratio. Climatic data, analysed in terms of mean value of temperature (°C), rainfall and ETP, were not correlated with DNA recovery.

Relationship between DNA recovery and land cover

The influence of soil management on the distribution of DNA yield was assessed according to coarse and fine levels of land-cover classification (Fig. 6a, b). Distribution of DNA yield showed significant differences between land-use categories based on the coarse level of classification (Fig. 6a, Table S1 in Supporting Information). The highest mean value was observed for grassland soils with 11.6 ± 5.8 µg DNA g^{-1} soil, and the lowest for vineyards and orchard soils with 5.7 ± 3.3 µg DNA g^{-1} soil. Other land-cover types, such as crop system and forests, exhibited significantly lower amounts than grassland, with 8.7 ± 3.9 µg DNA g^{-1} soil and 10.4 ± 7 µg DNA g^{-1} soil, respectively. The 'others' soil category, which included wild land, natural environments and urban parkland, exhibited intermediate values. Although the standard deviation of the calculated mean in each situation was large, the statistical tests significantly discriminated between DNA recoveries from forest, crop system and grassland, and from vineyards and orchards soils ($P < 0.001$, d.f. 4) (Fig. 6a, Table S1).

The finer analysis of soils under crop systems did not reveal significant differences in DNA recovery between fallow and large-scale farming with rotation (alternated or not with temporary grassland), whereas soils under monocultures gave the lowest DNA recovery (Fig. 6b). No differences were recorded according to the level of intensification of grassland (ranging from seeded and fertilized to natural grassland), whereas for forest soils, significant differences were recorded between deciduous, coniferous and mixed forests, with the highest level of DNA detected in deciduous and the lowest in coniferous forests (Fig. 6b). Altogether, the lowest (and highly significant) DNA recovery in all the land-use categories studied at this level was obtained from vineyard soils.

Relationship between land cover and soil properties

A PCA correlation matrix of physico-chemical soil characteristics and climatic characteristics was used to compile a factorial map for each type of coarse level of land cover (Fig. S1a–d). For crop systems, forest and grassland the soils were uniformly distributed along axis 1 and also axis 2 (especially for forest and grassland soils), which suggested a weakly significant relationship between land cover and soil properties. In contrast, vineyard and orchard soils did not exhibit a uniform distribution along the two axes (Fig. S1d) and were preferentially associated with sandy soils with low organic C content and a high C/N ratio (as indicated by correlation circle of soil characteristics, Fig. S1e).

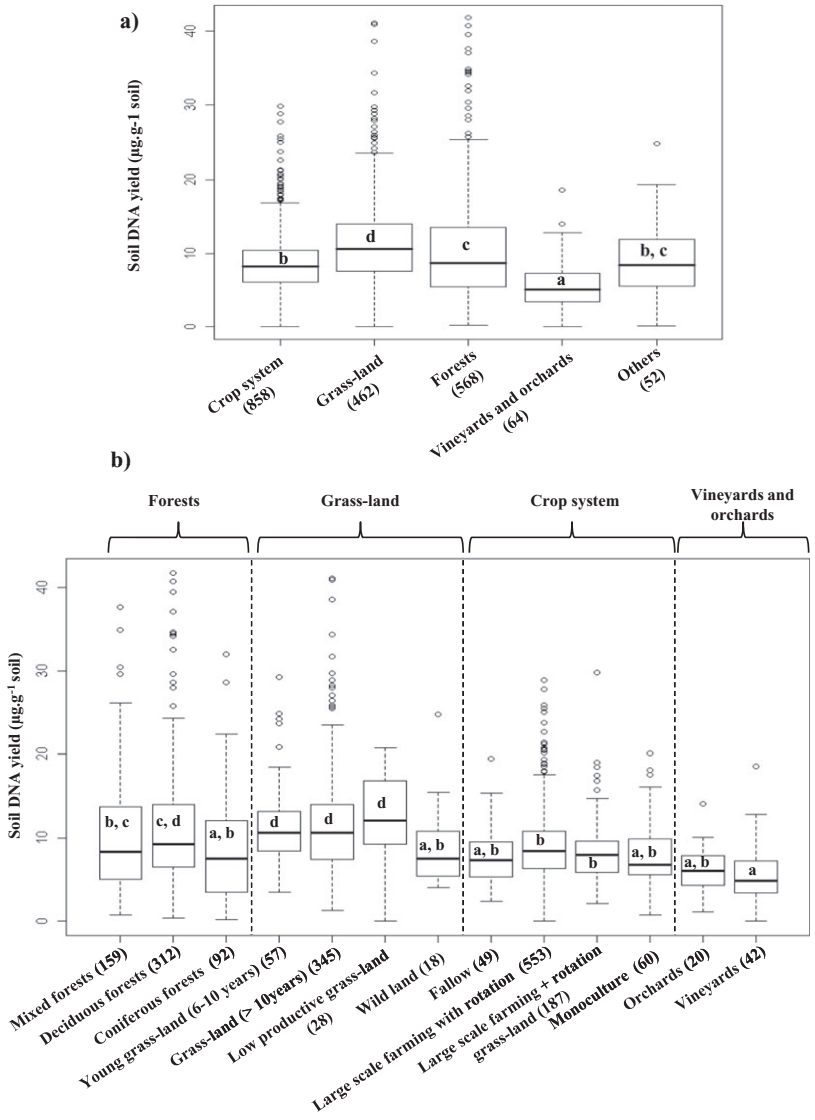

Figure 6 Distribution of the mean value of soil molecular microbial biomass according to the coarse (a) and fine level (b) of French Soil Quality Monitoring Network (RMQS) land cover. Numbers in parentheses indicate the number of corresponding soil samples. Superscript letters indicate significant differences between types of land cover ($P < 0.05$).

DISCUSSION

To date, most studies of soil microbial ecology on a field scale have focused on cataloguing microbial abundance and diversity in particular sites and describing how communities have been affected by local perturbations. As a result, microbial ecology studies suffer from a lack of systematic baseline information implying their poor capacity to predict microbial community abundance and assembly in soils subject to various perturbations. In this study, the French soil survey was used to characterize soil microbial biomass on a wide extent along environmental gradients of pedo-climatic and land-use conditions. A single procedure was used to extract the DNA, and therefore to quantify the molecular microbial biomass of all the RMQS soils as previously demonstrated (Marstorp *et al.*, 2000; Hartman *et al.*, 2006; Widmer *et al.*, 2006; Bouzaiane *et al.*, 2007). The efficiency of this procedure has already been demonstrated on different soil types, such as acidic forest soils (Lejon *et al.*, 2005), agricultural soils (Baudoin *et al.*, 2009), vineyard soils (Lejon *et al.*, 2007), clayey tropical soils (Jouquet *et al.*, 2005), soils contaminated with metals (Ranjard *et al.*, 2006), rhizosphere and detritusphere soils (Mougel *et al.*, 2006; Nicolardot *et al.*, 2007) and a large set of various soils on a regional scale (Dequiedt *et al.*, 2009).

Our study represents the most extensive compilation of DNA yields from soil environments and highlights the great variation between soils (Fig. 2). In most French soils (about 72%) the DNA recovery ranged from 5 to 15 µg DNA g^{-1} soil (Fig. 2), which is of the same order of magnitude as that classically obtained in different soil environments with various protocols (Zhou *et al.*, 1996; Kuske *et al.*, 1998; Frostegård *et al.*, 1999; Ranjard *et al.*, 2003). The demonstration that soil DNA recovery did not follow a normal or lognormal distribution suggested that its distribution between French soils was non-stochastic,

and consequently that DNA recovery could be under the dependence of environmental parameters. Moreover, the great range of variations (from 0.1 to more than 40) recorded for molecular microbial biomass had not been previously observed with the classical fumigation/extraction procedure (Horwath & Paul, 1994). This discrepancy might be attributable either to our large sampling strategy, which allowed the comparison of various soil types and managements, or to the greater sensitivity of the molecular approach to detect differences in microbial abundance.

Soil DNA recovery was thus geostatistically interpolated to provide the first map on a large scale. As indicated by the parameters of the Matérn function of the variogram, the nugget/(sill+nugget) ratio observed was high (0.53), suggesting that a large proportion of the variance was unexplained. This might be due to technical variation in the soil DNA extraction procedure for a given soil as well as to the large scale of the sampling scheme. Indeed, our sampling scheme is not suitable for detecting local variations, as previously observed (Saby *et al.*, 2009). In addition, the autocorrelation distance of about 160 km (Fig. 3) suggests that soil DNA content is spatially organized in bio geographical patches of several hundreds of kilometres. This scale of spatial variation did not correspond to French climatic variations (http://eusoils.jrc.ec.europa.eu/projects/soil_atlas, climate p. 122) but could be matched with large pedological patterns (King *et al.*, 1995) and/or the coarse level of land-cover distribution described for France (Fig. 1; http://image2000.jrc.it/; http://eusoils.jrc.ec.europa.eu/projects/soil_atlas, land cover p. 123). This suggests that soil properties such as texture, which is strongly influenced by the parental material, and also land cover and management strongly influence the spatial distribution of soil DNA. In addition, the ν parameter of the fitted variogram, which controls the smoothness of the spatial process, is small, and indicates a rough spatial process over small distances. This observation supports the hypothesis that variations in soil DNA recovery are also structured over small distances and thus dependent on variations in local environmental filters.

The French atlas of soil DNA revealed a heterogeneous distribution with spatial patterning consisting of hot and cold spots on both large and small scales (Fig. 4). Consequently, the null hypothesis of microbial biogeography, implying a random distribution of microorganisms over space, could be rejected (Martiny *et al.*, 2006). However, the geographical location of these spots cannot be explained by a geographical isolation, due to the presence of natural barriers (mountain, sea, desert, etc.; http://eusoils.jrc.ec.europa.eu/projects/soil_atlas, elevation p. 121), or by particular climatic conditions (http://eusoils.jrc.ec.europa.eu/projects/soil_atlas, climate p 122). Consequently, these global factors, which are known to significantly affect the distribution of macroorganisms (MacArthur & Wilson, 2001; Martiny *et al.*, 2006), do not structure microbial biomass to a large extent.

On the other hand, the map of French soil types based on their physico-chemical characteristics (http://gissol.orleans.inra.fr/programme/bdgsf/carte.php) matched with certain hot or cold spots for biomass, thus supporting the hypothesis that the physico-chemical characteristics of soil have a strong influence. For example, in the Landes region (L-zone 1, Fig. 4) all soils were of sandy acidic type (podzol; IUSS Working Group WRB Report 2006) which would partly explain the small pool of molecular microbial biomass. Similar observations were made for a subzone in L-zone 3 (Fig. 4) characterized by acid sandy soils developed on detrital material (the Sologne region). Previous studies indicated a lower microbial biomass in acidic and coarse-textured soils, due to a poor carrying capacity for microbes combined with the stressing effect of a low pH leading to a reduce primary productivity (Johnson *et al.*, 2003; Lejon *et al.*, 2005; Mulder *et al.*, 2005). The correlation circle of the PCA correlation matrix, which included DNA recovery, physico-chemical soil characteristics and the climatic conditions of each studied site, confirmed the strong relationships between molecular microbial biomass and soil characteristics (Fig. 5). The main factors with a positive effect on soil DNA recovery could be ranked as follows: fine texture, CEC > organic C and N contents > soil pH >>> climatic conditions (rainfall, atmospheric temperature and evapotranspiration). In contrast, soil DNA was significantly negatively correlated with coarse textured soils and C/N ratio. Previous wide-extent studies have already revealed that soil texture, organic C content and especially pH are the main factors driving the numerical abundance of below-ground organisms (Bååth & Anderson, 2003; Johnson *et al.*, 2003; Mulder *et al.*, 2005) as well as their diversity (Fierer & Jackson, 2006).

Altogether, our data highlighted that fine-textured soils exhibited a high molecular microbial biomass, which is in agreement with the large number of bacterial and fungal organisms as well as the greater size of the microbial biomass generally observed in such types of soil (Chaussod *et al.*, 1988; Ranjard *et al.*, 2006; Lejon *et al.*, 2007; Rutgers *et al.*, 2009). Indeed, H-Zone 1 of eastern France is dominated by clayey and/or calcareous soils. Fine-textured soils represent a more favourable habitat for microbial growth than coarse ones, offering better protection from desiccation, gas diffusion, toxic exogenous compounds and predation by protozoa (Ranjard & Richaume, 2001). Furthermore, the availability of C and N nutrient resources for indigenous microbes is generally higher in fine-textured soils due to important primary productivity and better stabilization of the organic matter (Wang *et al.*, 2003). The fact that molecular microbial biomass was inversely correlated with C/N ratio confirmed the major contribution not only of the amount of organic matter but also of its biochemical quality in terms of availability and resistance to degradation by microbes (Houot & Chaussod, 1995; de Boer *et al.*, 2005; Lejon *et al.*, 2007). This result also demonstrated that sampling was realized in the absence of a recent influence of plant exudates (the rhizosphere generally exhibits a high C/N ratio) which is positively correlated with microbial biomass.

The low soil DNA recovery observed in Sub-L-Z1 and L-Zone 2 (Fig. 4) could be related to the distribution of particular land covers (Fig. 1), notably vineyards, in these regions. In contrast, hotspots of soil DNA (H-Zones 1, 2, 4 and the south of H-Zone 3, Fig. 4) seemed mainly to correspond to regions under forests and grassland. These observations support the hypothesis that

the autocorrelation distance might be partly driven by the influence of large patterns of land-cover distribution on microbial biomass. Conversely, part of the high nugget effect might be related to local variations in land cover or land-use practices. Similarly, Rutgers *et al.* (2009) demonstrated, by estimating bacterial biomass on the Dutch soil monitoring network, that soil microbial abundance could be significantly influenced by land use. To confirm these statements, soil DNA was related to the land-use data. Regarding the coarse level of land-cover classification, the highest DNA recovery occurred in grassland and forest soils and the lowest in vineyard and orchard soils (Fig. 6a). Although the high DNA yield under forest and grassland soils could not only be explained by the associated soil properties (Fig. S1), these soils are known to have a high organic matter content due to their management and land cover, whereas the stock of organic C in soils under crops is generally reduced (Fig. 6a; Arrouays *et al.*, 2001; Leckie *et al.*, 2004; Nicolardot *et al.*, 2007). Vineyard and orchard soils exhibited the lowest DNA recovery of all the different land covers present in France. Most vineyard soils exhibited particular soil properties such as a sandy texture, a high C/N ratio and low organic C content (Fig. S1), all these parameters being unfavourable for microbial growth. In addition, the low microbial biomass could also be explained by specific viticulture practices which are known to be deleterious to soil-living organisms. Indeed, the large inputs of metallic and organic pesticides, combined with mechanical and/or chemical removal of grass over a very long period, can have adverse effects on soil microbial life (Ranjard *et al.*, 2006; Komarek *et al.*, 2010).

Significant differences were also observed among crop systems and forest soils (Fig. 6b). In contrast, no differences related to the level of intensification of grassland (ranging from seeded and fertilized to natural grassland) were recorded. In forest soils, significant differences were observed between deciduous and coniferous forest soils that could partly be explained by differences in litter quality (Lejon *et al.*, 2005). The lower microbial biomass observed under coniferous forest confirmed the strong influence of the lower availability and/or degradability of organic substrates provided by this litter for microorganisms (Leckie *et al.*, 2004; de Boer *et al.*, 2005). Regarding crop systems, no significant differences were observed between large-scale farming with rotation and fallow, but a significantly lower biomass was observed under monoculture. Fundamentally, this statement raises the question of the influence of the above-ground (plant) diversity on the abundance and diversity of below-ground (micro-) organisms due to the maintenance of particular and diverse habitats in soils and to changes in nutrient cycling (Wardle *et al.*, 2004). To date, the ecological relationship between below- and above-ground organisms has been insufficiently investigated in crop soils (contrary to forest and grassland) and requires further specific experimental demonstration.

CONCLUSION

Altogether, our results indicate that microbial biomass can exhibit spatial variation on a wide extent organized in biogeographic patterns. Large pedological and land-cover patterns seem to be the environmental filters with the greater influence on this distribution in French territory. When considering this set of DNA recovery data as a reference system for biomass variation along environmental and anthropogenic gradients, we can evaluate the impacts of particular land management on soil microbial life with potentially strong repercussions for soil biological functioning and therefore for the sustainability of that land use. In this study, we observed entire French geographical regions that harbour a low level of microbial biomass and could therefore be unable to support certain land management systems deleterious for soil microorganisms. As a consequence, one of the outputs of our study will aim at defining a 'normal operating range' of soil biology according to biotic and abiotic parameters which may be useful for the definition of a more accurate strategy for land management and its spatial organization.

ACKNOWLEDGEMENTS

This study was supported by grants from ADEME (French Environment and Energy Management Agency) and by the French National Research Agency (program ANR-06-BDIV-011). RMQS soil sampling and physico-chemical analyses were supported by a French Scientific Group of Interest on soils: the 'GIS Sol', involving the French Ministry for Ecology and Sustainable Development (MEDAD), the French Ministry of Agriculture (MAP), the French Institute for Environment (IFEN), the Environment and Energy Management Agency (ADEME), the French Institute for Research and Development (IRD) and the National Institute for Agronomic Research (INRA). We thank all the soil surveyors and technical assistants involved in sampling the sites.

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SUPPORTING INFORMATION

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

Table S1 Paired multiple comparison with Bonferroni correction of soil DNA yield between coarse levels of land cover.
Figure S1 Factorial map of principal components analysis (PCA) correlation matrix of physico-chemical and climatic characteristics of soils under particular land-cover types.

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BIOSKETCHES

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Editor: Martin Sykes