Unraveling biogeographical patterns and environmental drivers of soil fungal diversity at the French national scale

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Abstract

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The fungal kingdom is among the most diversified kingdoms on earth with estimations up to 12 million species. Yet, it remains poorly understood with only 150,000 fungal species currently described. Given the major ecological role of fungi in ecosystem functioning, these numbers stress the importance of investigating fungal diversity description across different ecosystem types. Here, we explored the spatial distribution of the soil fungal diversity on a broad geographical scale, using the French Soil Quality Monitoring Network that covers the whole French territory (2,171 soils sampled along a systematic grid). Fungal alpha-diversity was assessed directly from soil DNA using a metabarcoding approach by targeting the 18S rDNA gene. The total accumulated fungal diversity across France included 136,219 OTUs, i.e., about 1% of worldwide soil fungal diversity (based on a maximum diversity estimate of 12 million) for a territory representing only 0.3% of terrestrial surface on Earth. Based on this dataset, the first extensive map of fungal alpha-diversity was drawn and evidenced a heterogeneous and spatially structured distribution in large biogeographical patterns of 231 km radius for richness (Hill diversity of order 0) and smaller patterns of 36 km radius for dominant fungi (Hill diversity of order 2). As related to other environmental parameters, the spatial distribution of fungal diversity (Hill numbers based on different orders of diversity) was mainly influenced by local filters such as soil characteristics and land management, but also by global filters such as climate conditions with various relative influences. Interestingly, cropped soils exhibited the highest pool of fungal diversity relatively to forest and vineyard soils. In complement, soil fungal OTUs network interactions were calculated under the different land uses across France. They varied hugely and showed a loss of 75% of the complexity in crop systems and grasslands compared to forests, and up to 83% in vineyard systems. Overall, our study revealed that a nation-wide survey with a high spatial resolution approach is relevant to deeply investigate the spatial distribution and determinism of soil fungal diversity. Our findings provide novel insights for a better understanding of soil fungal ecology across the 18S rDNA gene and upgrade biodiversity conservation policies by supplying representative repositories dedicated to soil fungi.

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a supprimé: As related to other environmental parameters, the spatial distribution of fungal diversity was mainly influenced by local filters such as soil characteristics and land management, but also by global filters such as climate conditions. The spatial distribution of abundant and rare fungi was determined by distinct or similar filters with various relative influences.

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1. Introduction

The fungal kingdom has been evolving continuously for more than 800 million years to adapt to and colonize a large number of habitats on Earth (Loron et al., 2019; Naranjo-Ortiz and Gabaldón, 2019; Li et al., 2021; Bonneville et al., 2020; Berbee et al., 2020). This heterotrophic kingdom represents about 2% of the global biomass on Earth (Bar-On et al., 2018) and is among the most diverse kingdom in the Eukaryota domain (Mora et al., 2011; Blackwell, 2011; Taylor et al., 2014; Hawksworth and Lücking, 2017). Recent extrapolations based on environmental DNA characterization using a metabarcoding approaches with mainly the internal transcribed spacer (ITS), evaluated that the total number of fungal taxa ranged from 6.28 million to 12 million (Baldrian et al., 2022; Wu et al., 2019; Phukhamsakda et al., 2022). To date, only 150,000 fungal species have been described by the scientific community to date (Species Fungorum 2022, http://www.speciesfungorum.org/Names/Names.asp), namely only 1.25-2.4% of the whole estimated fungal diversity.

The majority of fungi is found in terrestrial ecosystems, especially in soils; only 4,000 extant fungi from freshwater habitats are presently listed (Calabon et al., 2022). Fungi play crucial ecological roles in soils by contributing to their proper functioning due to a wide range of functional guilds (Bar-On et al., 2018; Frac et al., 2018). Fungi are keystones of the soil food web, both in biogeochemical cycles and in interactions with other macro- and microorganisms (de Vries et al., 2013; Treseder and Lennon, 2015; Hannula and Träger, 2020). The functions of fungal communities provide many ecosystem services that promote mineral nutrition of plants linked to soil organic matter turnover, phosphorus and nitrogen availability (Miyauchi et al., 2020; Ward et al., 2022). They are important decomposers (saprotrophs) of organic matter: they break down complex biopolymers and play a key role in organic matter recycling (Hage and Rosso, 2021). Regarding symbiotic interactions, there are no less than 50,000 mycorrhizal fungi interacting with 340,000 land plants representing 90% of beneficial symbiosis with a host plant association (Genre et al., 2020). Fungal pathogens and parasites can cause diseases and important crop losses and have a significant economic impact (Möller and Stukenbrock, 2017; Fausto et al., 2019). Some of them are also identified as biocontrol agents and are involved in plant protection through the regulation of pathogenic microorganisms and insect pests (Peng et al., 2021). Fungi are also known as ecosystem engineers contributing to soil aggregation and maintenance. Thus, the stability of the soil structure largely depends on mycelium density and the pool of fungal enzymatic activities (Lehmann et al., 2020).

The spatial distribution of fungal diversity has been more recently and less studied than the spatial distribution of bacterial diversity, in particular when it comes to identifying and

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ranking the local and global filters that influence species richness (Griffiths et al., 2011; Terrat et al., 2017; Fierer and Jackson, 2006; Delgado-Baquerizo et al., 2018; Ranjard et al., 2013; Tedersoo et al., 2021). In 2014, Tedersoo and collaborators generated the first global map of fungal richness by using the ITS marker and revealed that fungi are spatially structured and exhibit biogeographical patterns (Tedersoo et al., 2014). One major hotspot of fungal diversity was located in Latin America and a cold-spot in the Sahel region, whereas fungal diversity distribution was shown homogeneous across Europe. A second global map of fungal diversity was drawn from a meta-analysis of the *chao* index (Větrovský et al., 2019). Conversely to Tedersoo and collaborators (2014), they highlighted a lower fungal diversity in Latin America and a higher in North Africa (Větrovský et al., 2019). In parallel, Ma and collaborators (Ma et al., 2017) revealed a heterogeneous spatial distribution according to a gradient of forest soils at the continental scale in Eastern China. These differences and even discrepancies in the location of biogeographical patterns at global scale reflect the huge gap of knowledge in fungal diversity distribution and the need to complete these studies with high resolution approaches at a finer scale.

Soil fungal communities are constantly subjected to natural biotic and abiotic stresses, but also to human activities through global warming, deforestation, and land use intensification. These stresses altogether have a significant influence on fungal abundance, diversity and community assembly and lead to an overall impact on soil functions (Pärtel et al., 2017; Geisen et al., 2019; Thomson et al., 2015; Tsiafouli et al., 2015; Shi et al., 2019). Several large- and small-scale studies showed that fungal richness is driven by land uses, edaphic factors, climate conditions, and spatial descriptors (Ma et al., 2017; Větrovský et al., 2019; George et al., 2019a). Farming practices on cropped soils such as tillage, fertilization or crop rotation can have an influence on fungal diversity (Sommermann et al., 2018; Sadet-Bourgeteau et al., 2019; Stefan et al., 2021; Finn et al., 2021; Tedersoo et al., 2014) or not (Lentendu et al., 2014). Altogether, soil pH emerges as the strongest driver of fungal alpha-diversity, similar to bacteria at global or territorial scales (Delgado-Baquerizo et al., 2018; Terrat et al., 2017). Some studies indicate a positive effect of soil pH on fungal richness at the national (George et al., 2019b) and global (Bastida et al., 2021) scales, whereas others show a negative effect on a global scale (Tedersoo et al., 2014). In 2020, Tedersoo and collaborators also proposed a unimodal relationship between soil pH and fungal richness / Shannon diversity (Tedersoo et al., 2020). Fungal richness also appears higher in fine soil textures than in coarse soil textures (George et al., 2019b). In the same vein, plant cover – especially increased tree richness – shows a positive impact on fungal richness and Shannon diversity (Tedersoo et al., 2020). Soil carbon is also an

important driver of fungal diversity, with a positive (Maestre et al., 2015; Yang et al., 2019; Bastida et al., 2021) or a negative effect (George et al., 2019b), depending on the territory studied, the scale investigated and the molecular marker used. Other findings show that soil calcium and phosphorus, the C:N ratio, bulk density, some spatial descriptors (e.g., latitude, longitude, altitude), and climate conditions also have an influence on fungal alpha-diversity (Maestre et al., 2015; Bastida et al., 2021; Tedersoo et al., 2014).

In the face of these discrepancies and given the essential role of fungi for ecosystem functioning and sustainability, it is essential to deeply characterize soil fungal diversity – in terms of alpha- and beta-diversity –, using the most recent molecular and high-throughput methods to better decipher the impacts of global and local filters (Chu et al., 2020; Hyde, 2022). In this context, we investigated the French Soil Quality Monitoring Network (RMQS) using a metabarcoding approach to determine the soil fungal diversity at a national scale. Based on a regular grid of 2,171 sites across France, this survey captured the various land uses, climates, geomorphology types, and soil characteristics. Located in Western Europe, France is the third largest European country and exhibits the third highest pedological diversity across the world according to the WRB classification (Minasny et al., 2010), and is also known to exhibit diversified land use and climate conditions (Ballabio et al., 2016; Karimi et al., 2020). Main land uses in France are dominated by croplands, grasslands, and forests. Climate conditions are also among the most diverse ones in Europe and organized in three major poles: oceanic, Mediterranean, and mountainous. All these facts lead us to conclude that France could be considered as an ideal national-scale observatory for monitoring the variations of biotic and abiotic components of soil ecosystems. The RMQS soil sampling strategy is probably one of the most intensive and extensive national soil sampling strategies in the world, and this systematic random sampling leads to good spatial coverage profitable both for mapping soil characteristics and unraveling environmental variation. Using this soil survey, a substantial body of scientific knowledge on soil bacterial biogeography has been produced by the use of molecular tools (Ranjard et al., 2013; Terrat et al., 2017; Karimi et al., 2018, 2020), associated with several technical developments to standardize metabarcoding, associated bioinformatics, and statistical analysis (Djemiel et al., 2020; Terrat et al., 2019, 2012).

Here, we explored the spatial distribution of the soil fungal communities on a broad geographical scale in order to better understand fungal diversity determinism according to environmental filters using high-throughput sequencing of the small 18S rDNA gene subunit directly amplified from soil DNA. In most studies, alpha-diversity is characterized by one index. However, in order to obtain a global overview of fungal diversity in a biogeographical

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context, it is important to explore deeper the distribution of rare and dominant taxa and ranking the influence of environmental filters in a deterministic process (Jousset et al., 2017; Rivett and Bell, 2018; Jiao and Lu, 2020). To reach this objective, we used Hill numbers to combine complementary diversity indexes such as richness, exponential Shannon diversity, and inverse Simpson. Methods based on spatial prediction (geostatistics) were applied to the data to map and explore the macro-ecological patterns of soil fungal diversity along the environmental gradients encountered in France. We used a set of environmental datasets – including soil physico-chemical characteristics, climate conditions, and land use – to explain variations in soil fungal diversity and rank the environmental filters structuring the spatial fungal distribution on a wide extent. Finally, we compared the variations of fungal diversity across different land uses plus climate types with the variations of the complexity of the fungal interaction networks by inferring co-occurrence networks at the operational taxonomic unit (OTU) level.

2. Methods

2.1. Soil sampling design

Soils were sampled from 2,171 locations across France between June 2000 and June 2009 as part of the RMQS set up to monitor the quality of French soils. As described previously (Ranjard et al., 2013), these sites included a wide range of land uses: forests (n=589), grasslands (n=537), crops (n=886), vineyards/orchards (n=65), and low anthropized environments (n=94), and eight climatic regions: type 1 (n=284), type 2 (n=270), type 3 (n=545), type 4 (n=418), type 5 (n=265), type 6 (n=86), type 7 (n=94), and type 8 (n=95). In France, low anthropized environments group wetlands, peatlands, sclerophyllous forests, natural grasslands, sparsely vegetated areas, and bare rocks (Karimi et al., 2020). Inside each of the 2,171 cells of a regular 16 km × 16 km grid throughout France, a smaller 20 m × 20 m grid was used for sampling where 25 core samples of topsoil (approximately 0-30 cm depth) were taken. The core samples were pooled and homogenized to obtain a composite sample. The sampling protocols applied on the RMQS are available through the RMQS2 manual (Jolivet et al., 2022). Each sample was air-dried following a standardized procedure at 35°C until the soil humidity was below 1%, then sieved to 2 mm and separated into two sub-samples. The first sub-sample was frozen at -40 ºC for molecular analyses, while the second sub-sample was used for physico-chemical analyses. A detailed description of the physico-chemical analyses performed in this study (soil pH, texture, organic carbon, nitrogen, and phosphorus) is accessible from (Jolivet et al., 2006). All the data are available in dataverse Gis Sol (https://doi.org/10.15454/QSXKGA).

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2.2. Molecular characterization of fungal communities

2.2.1. Soil DNA extraction

Soil DNA was extracted from 1g of soil using the GnS-GII standard procedure (Terrat et al., 2012, 2015). Briefly, the soil underwent two lysis steps, i.e., mechanical lysis and chemical lysis. In both cases, the soil was ground and homogenized for 90 s with 2 g of 0.1 mm diameter silica beads, 2.5 g of 1.4 mm diameter ceramic beads, and 4 glass beads of 4 mm diameter in 5 ml of a mix solution containing 100 mM Tris-HCl (pH 8), 100 mM EDTA (pH 8), 100 mM NaCl, 2% (wt/vol) sodium dodecyl sulfate, and up to 2.5 ml ultrapure water using a Fast-Prep-24 classic kit, and then incubated at 70 °C for 30 min. The mixture was centrifuged (7,000 g, 20 °C, 5 min) to retrieve the lysate. A deproteinization step was necessary using 1/10th of volume with 3 M potassium acetate (pH 5.5) followed by a centrifugation step (14,000 g, 4 °C, 5 min) to recover the supernatant containing the soil DNA. DNA was precipitated using isopropanol at -20 °C, and stored at -20 °C for 30 min. The last step consisted in washing the DNA pellet with ethanol and resuspending it in 200 µl of ultrapure water. Then, crude DNA were purified with NucleoSpin Soil kits following the manufacturer's instructions (NucleoSpin Soil, Macherey-Nagel). The purified DNA were quantified by fluorescence (QuantiFluor, Promega) using an Infinite® 200 PRO plate reader (Tecan) and then normalized to 1 ng/µl.

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2.2.2. Library preparation for sequencing

The V7-V8 regions of the fungal 18S rDNA gene were amplified from purified DNA using forward primer FR1 and reverse primer FF390 (Chemidlin Prévost-Bouré et al., 2011) with a two-step PCR. Both amplifications were carried out in a total volume of 25 µl using 1 to 5 ng of DNA, 4 µl of 5x HOT FIREPol® Blend Master Mix with 7.5 mM $MgCl_2$ (Solis Biodyne, Tartu, Estonia), and 1 µl (10 µM) of each primer (Eurogentec). The first step amplified the target region under the following conditions: initial denaturation at 94 °C for 3 min, followed by 35 cycles of 94 °C for 30 s; 52 °C for 1 m; 72 °C for 1 mn, and final extension at 72 °C for 5 min. The 18S PCR products were purified using an AMPure bead kit (Beckman) and quantified using a QuantiFluor staining kit (Promega, USA). The second amplification was performed to add barcodes for multiplexing samples. The conditions of the second PCR were similar, with a reduced number of cycles (seven) and a specific purification with a MinElute kit (Qiagen). Library preparation for the 2,171 samples was conducted at the GenoSol platform; Illumina HiSeq 2 × 250 bp paired-end sequencing was conducted by Genoscope (Evry, France).

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2.3. Bioinformatic analysis

We used BIOCOM-PIPE v.20 pipeline (https://forgemia.inra.fr/biocom/biocom-pipe) to process the 18S rRNA gene sequences (Djemiel et al., 2020). FASTQ paired-end raw reads were filtered with PRINSEQ to keep the good-quality sequences and then overlapped with FLASH to form contiguous reads. The libraries were demultiplexed and trimmed with zero difference between the barcode and primer sequences. The sequences were aligned with the Infernal tool based on RNA structures (Nawrocki and Eddy, 2013). Chimeras were removed by a "hunting-recovering" step specific to BIOCOM-PIPE (Djemiel et al., 2020). An additional step allowed us to check whether all our sequences were indeed affiliated to fungal sequences. Following this, a global clustering at 95% similarity was performed with the cleaned sequences, to cluster into Operational Taxonomic Units (or OTUs), followed by a post-clustering step with ReClustOR to improve the clustering (Terrat et al., 2019). All our diversity indices (geostatistical modeling, variance partitioning) and co-occurrence networks analyzes are performed on this OTU-based approaches with a post-clustering step for consistence with the evaluations of fungal diversity generally described in the literature (Terrat et al., 2015; Karimi et al., 2019).

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2.4. Statistical analysis

Hill numbers were calculated to estimate alpha-diversity and compare samples on a linear scale to provide a complete interpretation of alpha-diversity through different metrics. Hill numbers with q = 0 corresponded to the OTU richness observed in a sample (emphasizes rare fungal OTUs), q = 1 to the exponential of Shannon diversity (correspond to "typical" or "common" fungal OTUs), and q = 2 to inverse Simpson index (correspond to dominant fungal OTUs) (Alberdi and Gilbert, 2019). We tested if the variables were normally distributed or approximately so, using the *shapiro.test* function (R "stats" package). Depending on the result, we applied a boxcox transformation if the gaussian assumption was not satisfied. To compute the boxcox transformation from the "forecast" R package (Hyndman et al., 2020), we estimated the lambda value with the *BoxCox.lambda* function and applied the transformation with the *BoxCox* function. Outliers were tracked using the *grubbs.test* function in the "outliers" R package (Komsta and Komsta, 2011) for each Hill number dataset. Once the outliers were removed, to estimate the multiple comparisons across the modalities (land uses or climate types), analyses of variance (ANOVAs) were used, and we verified the normality assumption of residuals. If it was satisfied, we used a Least Significant Difference (LSD) test with adjusted p-value < 0.05; if it was not satisfied, we used a nonparametric test with *kruskal* function from "agricolae" package and a correction by the Bonferroni method for the multiple comparisons.

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The details of the removed samples (i.e., the samples considered to be outliers and the 'low anthropized environment' samples that we decided to exclude) in the different land uses are available in Supplementary Figure 1, as recommended by Dini-Andreote et al. (2021) (Dini-Andreote et al., 2021)), who developed a data management strategy with good practices for biogeographical studies.

The environmental data that did not follow a Gaussian distribution were log-transformed. Moreover, the soil pH covaries with land uses, with a majority of acidic soils in forests and a majority of neutral and basic soils in croplands and vineyards/orchards (Supplementary Figure 2). Therefore, we performed a polynomial transformation of degree 2 for the soil pH variable to improve the accuracy of fitting for the variance partitioning analysis.

Relationship between fungal alpha-diversity and environmental filters was assessed using variance partitioning. Briefly, the first step consisted in reducing the effect of model collinearity to obtain the most parsimonious models. We used the *vif* function (the variance inflation factors (VIF)) in the "usdm" R package (Naimi, 2015) and kept the explanatory variables with VIF $\leq$ 5. A second filtering step was performed to determine the best environmental variables using the *regsubset* function ("leaps" R package (Lumley and Lumley, 2013)) and based on the Bayesian information criterion (BIC) and adjusted R^2. Lastly, we conducted a redundancy analysis (Legendre, 2018) to model variation of the overall environmental filters using the *rda* and *ordiR2step* functions ("vegan" R package (Oksanen et al., 2013)). To select the best variables, we performed a forward multiple regression selection to build a model maximizing the adjusted R^2. We used the *ordiR2step* function with 10,000 permutations maximum and the *anova.cca* function ("vegan" R package) to evaluate the variance explained by the best explanatory environmental filtering variables.

Geostatistical modeling was used to assess the alpha-diversity spatial variations. We followed a standard approach as proposed in Granger and collaborators (2015). First, a variogram model was fitted to the experimental variogram computed using alpha-diversity observed at the sample sites. Then, we predicted the unsampled locations by a global kriging approach that used all the points in the dataset (global neighborhood). We implemented this approach with the "gstat" R package (Bivand et al., 2015). We tried to fit various authorized variogram models and kept the one that minimized the objective function. Then, we used the results of leave-one-out cross-validation (LOOCV) to evaluate the performance of the best fitted geostatistical model by computing the standardized squared prediction errors (Lark, 2002).

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To obtain the information of the putative OTU richness across France, we computed the rarefaction (interpolation) and prediction (extrapolation) curves for fungal richness (q=0) using the R package iNEXT (Hsieh et al., 2016).

2.5. Fungal co-occurrence networks

We used the methodological analysis previously described in Karimi and collaborators (2020, 2019) to compute the fungal co-occurrence networks between land uses and climate types. Briefly, two main steps were required: i) standardizing the number of soils (fixed at 60 samples for land uses and 83 for climate types) used to compute the networks per land use to avoid a sampling size effect, and ii) carrying out network repetitions (100 repetitions) to integrate the residual heterogeneity of the soils within each land use and climate type. Thus, the minimum number of combinations ensured that each network was computed from a unique combination of sites. Then, for each replicate, network computation was based on a contingency matrix of 136,219 fungal OTUs for the 60 or 83 randomly selected soil samples. The Spearman correlation coefficient for each pair of OTUs was used as a similarity index to estimate fungal OTU co-occurrence. A correlation was considered robust and non-random if the p-value was below 0.06 after correction using the false-discovery rate (FDR) method. To describe the topology of the networks, a set of metrics was calculated using "statnet" package (Handcock et al., 2019),), including the number of connected nodes, the proportion of connected nodes, the number of links, connectance, and the ratio between the positive and negative links. These metrics are defined in Karimi and collaborators (2017). We used a Kruskal-Wallis test with Bonferroni correction for the multiple comparisons of the fungal networks across land uses and climate types, using 100 repetitions. The median networks were mapped using Cytoscape software (v. 3.9.1) (Shannon et al., 2003).

3. Results

3.1. Evaluation and extrapolation of fungal alpha-diversity across France

Based on 18S rDNA amplicon sequencing to characterize the fungal diversity of the 2,171 sampled soils, we obtained a total of 180 million raw sequences. The use of bioinformatic filters (in BIOCOM-PIPE workflow) resulted in 2,060 samples with sufficient high-quality data for the assessment of fungal communities. Regarding the cumulated fungal diversity from the whole France, we identified 136,219 OTUs from the 2,060 samples. Thanks to our intensive soil sampling strategy combined with in-depth sequencing, we obtained an extrapolated total value of 186,794 fungal OTUs (Fig.1) at the national scale.

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a supprimé: Thanks to our intensive soil sampling strategy combined with in-depth sequencing, we extrapolated with iNEXT a total of 186,794 OTUs (Fig. 1) at the national scale.¶

3.2. Spatial distribution of fungal alpha-diversity across France

We generated three national maps showing the soil fungal alpha-diversity based on Hill numbers with orders of diversity of zero, one and two using a kriging interpolation approach (Fig. 2). The results of the LOOCV show very low R^2 values equal to 0.058, 0.057 and 0.038 for q=0, q=1 and q=2, respectively. However, the median and the mean of the SSPES are very close to the expected values (e.g., 0.45 and 1). The fitted variograms reveal different spatial structuring depending on the weighting of OTU relative abundances (Supplementary Table 1). Thus, the predicted map of fungal richness (Hill diversity of order 0) exhibited a heterogeneous and spatially structured distribution with a large autocorrelation distance of about 231-km radius (Fig. 2a, 2d). More or less wide regions with hot or cold spots of fungal diversity were observed. More specifically, soils from the north-west to the center of France support a high fungal richness whereas soils from the north-east, the south-east, and the southwest support a lower fungal richness.

The models fitted for q=1 (exp. Shannon diversity) and q=2 (inverse Simpson) exhibited the spottiest distribution with short autocorrelation distances (27-km radius and 36-km radius, respectively) (Fig. 2b, 2e and 2c, 2f). The hotspots observed for q=1 and q=2 were less diffuse and remained strongly present in the north-west to the center of France. This spotty distribution highlighted small hotspots of abundant fungal OTUs in certain geographical zones described as having low fungal diversity by q = 0, such as the south-east and the north-east of France.

3.3. Relationship between sets of environmental filters and fungal alpha-diversity

We used a variance partitioning approach to evaluate the relative share of fungal diversity explained variance by each set of environmental variables (soil characteristics, land use, climate conditions, and spatial descriptors) for the different Hill numbers in partial models using a redundancy analysis (RDA). Globally, environmental filters explained 20.1%, 15.52, % and 7.54% of the total variance of fungal richness for q=0, q=1 and q=2, respectively (Fig. 3a, 4a, 5a and Supplementary Table 2). For q=0, the main drivers of fungal richness variance were the soil characteristics (11.30%), and then to a lesser extent climate conditions (0.88%), land use (0.39%), and spatial descriptors (0.26%) (Fig. 3a). For q=1, the soil characteristics (9.30%) were the main drivers, and then to a lesser extent, spatial descriptors (0.90%), climate conditions (0.63%), and land use (0.44%) (Fig. 4a). For q=2, the soil parameters (4.25%) and land use (2.16%) were the main drivers, followed to a lesser extent by climate conditions (0.69%) and spatial descriptors (0.31%) (Fig. 5a). The percentage of interactions between the environmental

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filters decreased from 7.25% for q=0 to 4.25% for q=1, and neared zero for q=2 (0.12%). The main soil physical and chemical properties for each land use and climate condition are summarized in Supplementary Figures 3 and 4.

3.4. Influence of the soil characteristics on soil fungal alpha-diversity

The key determining soil parameter for fungal richness was pH (variation explained by 6.72%). A unimodal relationship was evidenced, with minimum fungal diversity in the most acidic and alkaline soils (Supplementary Figure 2). For q=0, a significant influence of the soil texture was also demonstrated, with a linear negative relationship observed with clay (2.38%) and silt (0.65%). Conversely, a positive relationship was observed with the total lead content (0.58%) and a negative relationship with the total nickel content (0.53%) and the total cadmium content (0.37%) (Fig. 3b).

For q=1, soil pH (6.30%) had a unimodal distribution and was also the strongest driver followed by the clay content (3%) with a negative linear correlation (Fig. 4b). For q=2, the soil pH remained the strongest driver with also a unimodal relationship, and organic carbon and the total iron content were also identified as secondary drivers, with a negative linear relationship (Fig. 5b). Moreover, a weak positive relationship was observed with silt (variation explained by 0.16% with a significance level of 0.1).

3.5. Influence of climate conditions on soil fungal alpha-diversity

The great diversity of climate conditions in France allowed us to compare fungal diversity across eight types of climates (Fig. 6a). Temperature, rainfall, and elevation are summarized in Supplementary Figure 4. Our analyses revealed that fungal diversity for q=0 and q=1 was highest under oceanic climate (type 5) and lowest under Mediterranean climate (types 6 and 8) and under the climate of the southwestern basin (type 7) (Fig. 6b and 6c). Moreover, we observed no significant difference from types 6, 7 and 8. Fungal diversities for q=0 and q=1 under mountain and continental climates had an intermediate value between oceanic and Mediterranean climates. Regarding the dominant OTUs (q=2), there was no significant difference in fungal diversity across the various climate types of France (Fig. 6d).

3.6. Variation of soil fungal diversity as related to land uses

By comparing fungal richness (q=0) across the different land uses encountered in France (Fig. 7a), we observed several significant differences (Fig. 7b). Forest and vineyard/orchard soils

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harbored lower fungal richness than grassland and agricultural soils, and can be ranked as follows: vineyards/orchards ($\bar{x}$ = 1,384 OTUs) ≤ forests ($\bar{x}$ = 1,393 OTUs) < grasslands ($\bar{x}$ = 1,469 OTUs) ≤ crops ($\bar{x}$ = 1,498 OTUs) (Fig. 7b). The same trend was observed for q=1 (Fig. 7c) but was different for q=2 (Fig. 7d). For q=2, fungal diversity in grassland and vineyard soils appeared lowest compared to forest and crop soils.

Within the four major land uses of French soils, we identified and compared more precisely land managements (Fig. 8). For example, forests can be categorized into three groups – deciduous forests, coniferous forests, and mixed forests. Among forest managements, we observed significant differences between deciduous and mixed forests: the lowest richness was found in mixed forests (Fig. 8a). For q=1, fungal diversity in deciduous forests was significantly higher than in coniferous and mixed forests (Fig. 8b), while no difference was detected for q=2 (Fig. 8c). Significant differences were also recorded by comparing the different land managements of the crop systems: whatever the metrics, soil fungal diversity was higher under crops with a grassland rotation than under crops without a grassland rotation. No significant difference was recorded between vineyards and orchards or between the various grassland managements (Fig. 8).

3.7. Comparison of soil fungal co-occurrence networks between land uses and climate types

The networks were graphically composed of connections (links) between the nodes corresponding to the OTUs. The links represented the significant positive and negative correlations between the OTUs occurring in the soils under the respective land uses or climate types (Fig. 9). A visual analysis of the networks obtained for the different land uses revealed a significant shift in structure ranging from a highly connected, tightly closed structure in forests to a sparse, open structure in vineyards (Fig. 9a). In grassland and crop soils, the networks exhibited an intermediate structural complexity in terms of their numbers of links and connected OTUs (Fig. 10a). Statistical comparisons of the network metrics between land uses confirmed a highly significant decreasing gradient of network complexity, with a pattern: forest >> grassland ≥ crop system > vineyard & orchard soils (Supplementary table 3, Fig. 10a). The average number of links significantly decreased by 84% from forest to vineyard soils, and by 76% from forest to field crop and grassland soils. The average connectance also progressively decreased by 81% from forest to vineyard soils, and by 78% from forest to field crop and grassland soils. The ratio between the positive and negative links was lower in forest soil and higher in vineyard & orchard soil (Fig. 10a). The fungal networks across the eight climate types exhibited a progressive decrease in connectivity between climate types 1, 2, 3 and 4, then a very

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significant drop for types 5 and 7, and the greatest connectivity for types 6 and 8 (Figs. 9b and 10b, Supplementary table 4). Conversely, the highest ratio between the positive and negative links was observed in networks within types 5 and 7, and the lowest one for type 8.

4. Discussion

Two molecular markers are commonly used to explore fungal diversity thanks to metabarcoding approaches: the internal transcribed spacer (ITS) region, accepted as a universal barcode, and the 18S rRNA gene as an alternative, the two being considered today as complementary. Both have advantages and drawbacks, in particular to observe specific functional groups. For example, members of the class Glomeromycetes are better characterized using 18S rDNA than ITS, especially in the soil microbiota, and this could have a significant impact on fungal diversity metrics (George et al., 2019b). In addition, important reference sequences are only annotated at the phylum level in the international databases (Nilsson et al., 2012, 2016; Banos et al., 2018). Moreover, a recent study highlighted that national-scale fungal biogeography studies based on 18S rDNA were robust and sensitive to decipher the relationships between fungal diversity and environmental filters (George et al., 2019b). For all these reasons, the use of 18S rDNA gene to characterize fungal alpha-diversity in soil can be relevant. Once the molecular marker was chosen, the hypervariable region had to be selected for sequencing. Various criteria had to be taken into account such as amplicon length in relation to the sequencer, or the desired taxonomic and phylogenetic resolution. We sequenced the V7-V8 regions because they appeared to be the most promising regions for fungal diversity assessment (Banos et al., 2018). The last tricky step of a fungal diversity study is the bioinformatics analysis, which is dependent on the pipeline (Pauvert et al., 2019). Nevertheless, our previous studies on bacterial biogeography showed that our metabarcoding pipeline and associated tools were highly appropriate to analyze large microbial datasets (Djemiel et al., 2020; Terrat et al., 2019).

As for the alpha-diversity analysis, we chose to use the Hill numbers – which have several advantages (Roswell et al., 2021) – to provide an overview of fungal diversity for each site. This allowed us to observe all OTUs – "typical" OTUs and dominant ones –, based on their abundance frequencies (Chao et al., 2014), especially as fungal diversity can be represented by a few dominant species with a high relative abundance (Egidi et al., 2019a).

The first predictions of worldwide fungal diversity ranked from 2.2 to 3.8 million species (Hawksworth and Lücking, 2017), but recent molecular works updated estimations up

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to 6,28 to 12 million species predicted by computing several hundreds of international studies (Phukhamsakda et al., 2022; Wu et al., 2019; Baldrian et al., 2022). At the national scale, this question remains unexplored for soil ecosystems. In our study, we predict total fungal richness at a national scale for the first time by an extrapolation analysis from metabarcoding at the OTU levels. Compared to the estimated worldwide diversity, France exhibits a very high cumulated soil fungal richness (about 1% of the global soil fungal diversity based on a maximum diversity estimate of 12 million) relative to its small surface (0.3 % of terrestrial land). Independently to the molecular marker used, this suggests that global soil fungal richness is under-estimated worldwide partly due to the poor intensive sampling strategy that has only been extensive to date, with few sampling sites. Consequently, this strategy seems relatively inefficient to capture the local environmental heterogeneity that hosts and shapes fungal richness. Therefore, it is important to gather several deeply investigated national surveys to estimate global soil fungal diversity more robustly (Dini-Andreote et al., 2021). Another example of soil fungal diversity estimation at a national scale has been described in Wales, where 437 samples were collected in sites on a surface area of 20 x 10^3 km^2, leading to a total evaluation of 4,408 OTUs based on 18S rDNA characterization (George et al., 2019b).

Our first maps of the three Hill numbers were provided to describe the spatial distribution of soil fungal alpha-diversity across France, as previously done for molecular microbial biomass and bacterial richness (Dequiedt et al., 2011; Terrat et al., 2017). The heterogeneous spatial distribution of fungal diversity observed in France is not congruent with several studies using ITS marker (Větrovský et al., 2019; Tedersoo et al., 2014), which did not observe significant variations across Europe with a global soil mapping approach. The two studies computed 365 and 3,085 soil samples across the world, respectively, compared to 2,171 in the present study at the scale of France. In addition, these global sampling strategies were based on non-random designs that generally left aside difficult access (polar, arid, mountainous) regions, hence with possible biases on the environmental representativeness of soil fungal habitats. A recent study in northern Europe generated an extrapolated fungal richness map of Estonia using ITS marker that confirmed a heterogeneous geographic distribution with hot- and cold-spots at the national scale (Tedersoo et al., 2020). Altogether, these observations stress the need to assess more intensive samplings at different scales in order to describe robustly the global distribution of soil fungal diversity and its determinism (Dini-Andreote et al., 2021).

The soil fungal community is well known to be largely dominated by a few highly abundant taxa and to include a large number of rare taxa (Egidi et al., 2019). Few biogeography studies have focused on abundant and rare taxa through the different alpha-diversity metrics (e.g., Hill

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a supprimé: Compared to the estimated worldwide diversity, France exhibits a very high cumulated soil fungal richness (of about 1%) relative to its small surface (0.3 % of terrestrial land)

a supprimé: This suggests that global soil fungal diversity is strongly under-estimated worldwide mainly due to the poor intensive sampling strategy that has been to date only extensive with few sampling sites

a supprimé: For other soil organisms, total bacterial richness has been evaluated to reach a total of 188,030 OTUs across France (Terrat et al., 2019). Earthworm richness has been evaluated more globally by compiling 6,928 sites in 57 countries, leading to an estimated 1,376 cumulated species across the world (Phillips et al., 2019).

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a supprimé: The community of soil microorganisms – especially fungi – is well known to be largely dominated by a few highly abundant taxa and to include a large number of rare taxa

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numbers) (Bent and Forney, 2008). Yet, comparing the spatial distribution of dominant and rare biosphere fungi is important to better grasp the environmental determinism that shapes soil fungal diversity (Mo et al., 2018). Mapping of richness (q=0, including all OTUs), and "typical" (q=1, including common fungal OTUs abundances) and dominant (q=2, including OTUs with high relative abundance) fungal OTUs revealed different spatial patterns, "patchier" (i.e., spatially more diffuse) for q=0 with 231 km radius, and "spottier" (i.e. spatially more restricted) for q=1 (27 km) and q=2 (36 km). These results altogether suggest a 'patchier' pattern, generally considered less stochastic than a 'spottier' distribution (Dequiedt et al., 2011; Terrat al., 2015). A similar observation was made in eastern China, with different spatial distributions of rare and dominant soil fungal OTUs based on ITS marker (the authors did not use Hill numbers but relative abundance and a threshold to group rare and dominant OTUs), suggesting differential sensitivity to various environmental filters leading to increase the endemicity of particular dominant taxa (Jiao and Lu, 2020).

The decrease of the explained variance between the q=0, q=1 and q=2 Hill numbers indicates that environmental and spatial characteristics had a low influence on the national distribution of dominant OTUs. These are generally considered as generalist and more driven by stochastic processes, whereas rare taxa are more driven by deterministic processes (Zhao et al., 2022; Jia et al., 2018; Xu et al., 2022b, a). The spottier distribution observed for q=2 could support this hypothesis of a more random distribution across France, less influenced by environmental filters. Whatever the Hill numbers, the main filters explaining the variance of fungal diversity were the soil characteristics: soil pH was the main driver, followed by clay content for q=0 and q=1, and the trophic conditions for q=2 (organic C and total Fe contents). Such an influence of soil trophic resources on dominant fungal OTU diversity seems in accordance with their generalist and copiotrophic strategy (Wang et al., 2021). Numerous studies have reported the importance of soil pH in the distribution of fungal richness across different scales (Rousk et al., 2010; Glassman et al., 2017; Tedersoo et al., 2014, 2020; George et al., 2019b). Interestingly, we revealed a unimodal relationship of soil pH with fungal diversity, whereas most studies found either a positive or a negative linear relationship (Tedersoo et al., 2014; Maestre et al., 2015; Bastida et al., 2021; Yang et al., 2019). Such a discrepancy could be partly explained by the large pH range recorded in France – 3.7 to 9 –, *versus* 3.6 to 5.2 in Wales (George et al., 2019b) or more surprisingly 3.34 to 10.43 at the European scale (Fernandez-Ugalde et al., 2022). Emphasizing our hypothesis, other studies report the same unimodal relationship for fungi by using ITS marker and even for bacteria (Bickel et al., 2019; Tedersoo et al., 2020). As for bacterial richness across France, fungal richness was lower in fine-textured soil, which is

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not congruent with the results obtained in Wales based on the 18S rDNA marker (George et al., 2019b). In France, we may think that fine-textured soils offer less diverse habitats for fungi, as previously reported (Witzgall et al., 2021; Tecon and Or, 2017). This might be partly explained by the decrease in microscale heterogeneity with increasing clay content, leading to a lower diversity of microbial habitats and a smaller hosting capacity for various indigenous microbial species (Tecon and Or, 2017). Finally, some soil heavy metals were minor but represented significant drivers of fungal richness. A positive relationship was observed with total lead, but a negative one with cadmium and nickel. These metallic elements occur naturally but also result from human activities and are known to be toxic for soil fungi when accumulated in the environment (Sun et al., 2022; Ding et al., 2022). In crop soils, significant Cd accumulation through the input of phosphate fertilizers extracted from contaminated limestone rocks has been observed (Khan et al., 2017) and our results could reflect the significant impact of this contamination on soil fungi at a broad scale.

Conversely to bacterial biogeography at the scale of France, climate conditions have been identified as important global filters of the distribution of fungal diversity across France for all Hill numbers based on three different orders of diversity (Terrat et al., 2017). The highest fungal richness and highest typical OTU diversity found under oceanic climate may be partly explained by particular conditions such as buffered mean temperature and humidity inducing soil homeothermy and stability of water availability favorable to fungal development (Canini et al., 2019; Jiao et al., 2021). On the contrary, the high variability of these conditions between seasons could explain the decline observed under Mediterranean climate. The poor influence of climate on the diversity of abundant fungal OTUs across France could reflect their generalist strategy better adapted to a high magnitude of environmental fluctuations over time, as previously observed in eastern China (Jiao and Lu, 2020). Moreover, our results indicate that rare fungi were more present in geographical regions with abundant annual rainfall and mild mean temperature, in line with the observation of increasing fungal richness with frequent rainfall (Tedersoo et al., 2014; Wang et al., 2018; Bahram et al., 2018).

In France, each land use corresponds to a particular intensity of soil disturbance resulting from the intensification of agricultural practices. We can rank the different land uses according to the intensity level of their soil disturbance as follows: forests < grasslands < crops < vineyards/orchards. The crop systems – vineyards in particular – use pesticides and soil tillage that have deleterious effects on fungal diversity (Karimi et al., 2021; Christel et al., 2021). We observed the highest richness (q=0) and typical (q=1) OTU diversity in grasslands and crops corresponding to the intermediate levels of disturbance. Similar observations have been

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reported about nematodes (Vazquez et al., 2019), bacteria (Delgado-Baquerizo et al., 2018; Terrat et al., 2017), and fungi by using 18S rDNA marker (George et al., 2019b) at different scales. Conversely, no difference has been reported between forest, grassland, and crop soils in Estonia (Tedersoo et al., 2020), and decreased fungal richness has been reported between temperate-forest and crop soils at a global scale (Bastida et al., 2021). Our observations support the intermediate disturbance hypothesis (IDH) stating that the species richness of an ecosystem is maximized when it is submitted to an intermediate disturbance, and minimized when it is submitted to either a low disturbance by a competitive exclusion process or to a high disturbance by a selection process (Connell, 1978; Wilkinson, 1999; Giller et al., 1998). More precisely, agricultural practices such as tillage can stimulate microbial richness in crop systems (Szoboszlay et al., 2017; Lienhard et al., 2013), and the highest level of richness is generally explained by the coexistence of microorganisms with different ecological strategies that promote ecosystem stability (Griffiths and Philippot, 2013). Interestingly, we also observed the highest diversity of dominant fungal OTUs (inverse Simpson, Hill q=2) in crop systems, *versus* lowest diversity in grasslands, in line with previous studies reporting a similar trend in grassland and crop soils (Xu et al., 2017; Zhang et al., 2022). This observation suggests that increased fungal diversity in intensive soil management crop systems is concurrent with decreased fungal evenness.

Analyzing fungal diversity according to the different land managements within each land use highlighted the highest fungal diversity in the agricultural systems when crop rotation included grasslands. Inserting temporary grasslands in the rotations is well known to improve soil quality in terms of nutrient provision and recycling, soil structure, and biological regulation (Martin et al., 2020) and could favor the development of soil fungi, as previously described at the landscape scale in Brittany by using 18S rDNA marker (Western France, Le Guillou et al., 2019). More fundamentally, this statement also raises the question of the influence of aboveground (plant) diversity on the abundance and diversity of belowground (micro-) organisms due to the maintenance of diverse habitats in soils and to changes in nutrient cycling poorly investigated in crop systems to date (Wardle et al., 2004). Among forest ecosystems, deciduous forests seem to provide the most favorable conditions for fungal diversity. Across France, deciduous forests present the highest tree family richness compared to mixed and coniferous forests (data not showed). Therefore, our results are in line with studies showing that plant species richness positively affects the soil fungal diversity (Tedersoo et al., 2016; Hiiesalu et al., 2017). The lowest fungal diversity observed in coniferous forest soil also confirmed the strong influence of the lower availability and/or degradability of organic substrates provided by

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this litter for microorganisms (Leckie et al., 2004; De Boer et al., 2005). However, other parameters such as plant genotype, forest stand age or tree density, not taken into account in the present study, could also affect fungal diversity (Tedersoo et al., 2016; Hazard and Johnson, 2018; Spake et al., 2015). In contrast, no difference related to the different types of grassland or to the distinction between vineyards and orchards was recorded.

Beyond fungal alpha-diversity, the analysis of co-occurrence networks is a relevant way of providing a more comprehensive view of fungal diversity and its interactions according to environmental variations on a broad scale (Karimi et al., 2017). As previously observed for bacterial co-occurrence networks across France, land use intensity affects the complexity of fungal networks (Karimi et al., 2019). Although forest ecosystems exhibited the lowest fungal richness, they harbored the highest complexity of fungal co-occurence networks. Strong losses of about 83% of the links between forests and vineyards and about 75% between 'forests' on the one hand and 'grasslands and crop systems' on the other hand were observed across France. A similar trend has been observed for bacterial networks across France (Karimi et al., 2019) and also for fungi along a transect from forest to vineyards in Australia (Xue et al., 2022). However, soil fungal interaction networks remain poorly described by comparing land uses on a broad scale. The lowest fungal diversity and lowest complexity of interaction networks observed in vineyard and orchard soils could be related to the intensification of agricultural practices in these systems (Karimi et al., 2019). Vineyard soils are indeed known to be strongly disturbed by intensive tillage, a restricted plant cover and large pesticide inputs (Quiquerez et al., 2022). This intensification of agricultural practices can lead to the isolation of fungal taxa and the loss of links between taxa in these soils by i) reducing microbial biomass, hence a lower probability of each cell encountering another and interacting with it (Dequiedt et al., 2011), ii) stimulating self-sufficient opportunistic microorganisms that do not interact with others (Lienhard et al., 2013), and iii) reducing spatial connectivity between soil ecological niches due to soil tillage and compaction, hence physical isolation of fungal taxa (Cordero and Datta, 2016). Altogether, our results confirm that forest soils remain a favorable habitat for soil fungi by representing a mosaic of connected ecological niches that are fully complete and shared by non-opportunistic taxa (Karimi et al., 2019). Interestingly, the highest fungal diversity and lowest complexity of interaction networks were observed in oceanic climate soils. The lowest fungal diversity and a very low complexity of interaction networks were also observed under the climate of the south-western basin. Finally, the lowest fungal diversity and lowest complexity of interaction networks were observed under Mediterranean climate (region types 6 and 8). The soils under Mediterranean climate presented the greatest level of stress, with the

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highest annual temperatures and the lowest annual precipitation, and did not provide favorable ecological niches for fungal diversity.

5. Conclusions

At the scale of France, by using 18S rDNA gene, the soil fungal diversity is driven by soil characteristics, land management and climatic conditions. Soil pH was the most important soil property explaining rare and abundant fungal diversity. The lowest fungal richness was found in less disturbed environments (forests) and highly disturbed environments (vineyards & orchards) compared to grasslands and croplands. Highly disturbed environments (crops, vineyards & orchards) harbored the lowest fungal network complexity compared to forest soils, which harbored the most connected networks. Our study confirms that a nation-wide survey is relevant to deeply investigate the spatial distribution and determinism of soil fungal diversity. In addition, compiling data obtained from different molecular markers (ITS and 18S rDNA) could also significantly improve the description and comprehensiveness of the soil fungal diversity. The multiplication and the sum of such studies conducted across the world could highly upgrade biodiversity conservation policies and provide representative repositories dedicated to soil microorganisms in a context of global change. To go further, it will be important to explore fungal beta-diversity and fungal taxonomy at the scale of France in order to reach a more comprehensive understanding of spatial distribution, ecological processes, and environmental filters. Finally, it will also be important to investigate the ecological and functional traits assignment of soil fungal communities, using recent tools and databases developed to better predict the shift in soil functioning according to land management intensity (Djemiel et al., 2022).

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Code and data availability

The fungal DNA sequencing datasets supporting the results presented in this article are available at the EBI ENA under accession number PRJEB57875. The code that supports the findings of this study are available from the first author upon request.

Authors' contributions

All authors conceptualized the research project. Claudy Jolivet coordinated the RMQS program and the soil sampling at the territory scale. Lionel Ranjard is the scientific coordinator of the different projects dealing with the characterization of the soil microbial communities at the

scale of France. Charles Guilland, Solène Perrin, Gwendoline Comment, Julie Tripied and Mélanie Lelièvre performed the molecular analyses. Patrick Wincker and Corinne Cruaud contributed to DNA sequencing. Christophe Djemiel and Sébastien Terrat performed the bioinformatic analyses. Claudy Jolivet, Nicolas P.A. Saby, Line Boulonne provided the environmental dataset. Christophe Djemiel, Samuel Dequiedt, Walid Horrigue, Arthur Bailly, and Nicolas P.A. Saby contributed to the statistical and geostatistics analyses. Christophe Djemiel and Lionel Ranjard wrote the original draft. Christophe Djemiel, Sébastien Terrat, Nicolas P.A. Saby, Claudy Jolivet, Line Boulonne, Antoine Pierart, Pierre-Alain Maron, and Lionel Ranjard reviewed and edited the final manuscript.

Competing interests

One author is member of the editorial board of SOIL journal. The peer-review process was guided by an independent editor, and the authors have also no other competing interests to declare.

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chemical analyses were supported by a French Scientific Group of Interest on soils: the "GIS Sol", involving the French Ministry for an Ecological Transition and Territorial Cohesion (MCT), the French Ministry of Agriculture and Food (MASA), the French Agency for Ecological Transition (ADEME), the French Biodiversity Agency (OFB), the National Institute of Geographic and Forest Information (IGN), the French Institute for Research and Development (IRD), the French Geological Survey (BRGM) and the National Research Institute for Agriculture, Food and Environment (INRAE). We thank all the soil surveyors and technical assistants involved in sampling the sites and the staff of the European Soil Samples Conservatory (INRAE Orléans) for preparing the soil samples. Calculations were performed using HPC resources from DNUM CCUB (Centre de Calcul de l'Université de Bourgogne). Thanks, are also extended to Frédérick Gavory for submitting dataset to EBI ENA, and Annie Buchwalter for correcting and improving English language in the manuscript.

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Figures

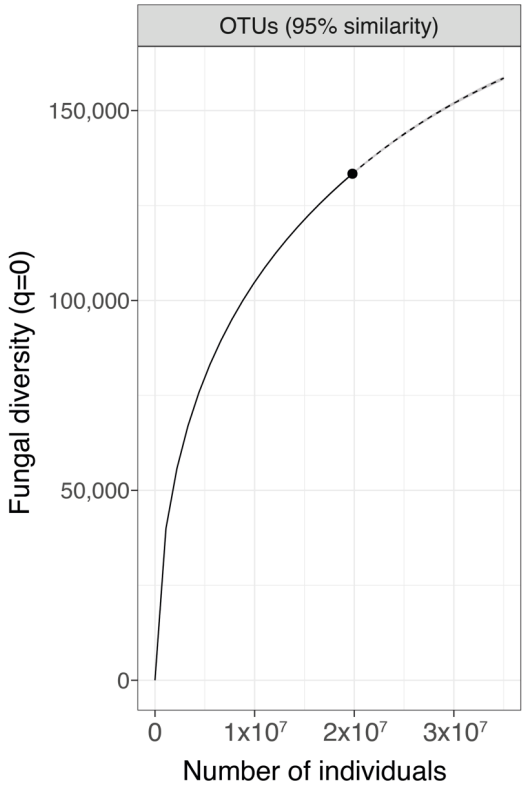


Figure 1

Fig. 1: Maximum number of fungal species expected across France based on OTUs. The analyses of fungal richness rarefaction (solid line segment) and extrapolation (dotted line segment) was performed with iNEXT.

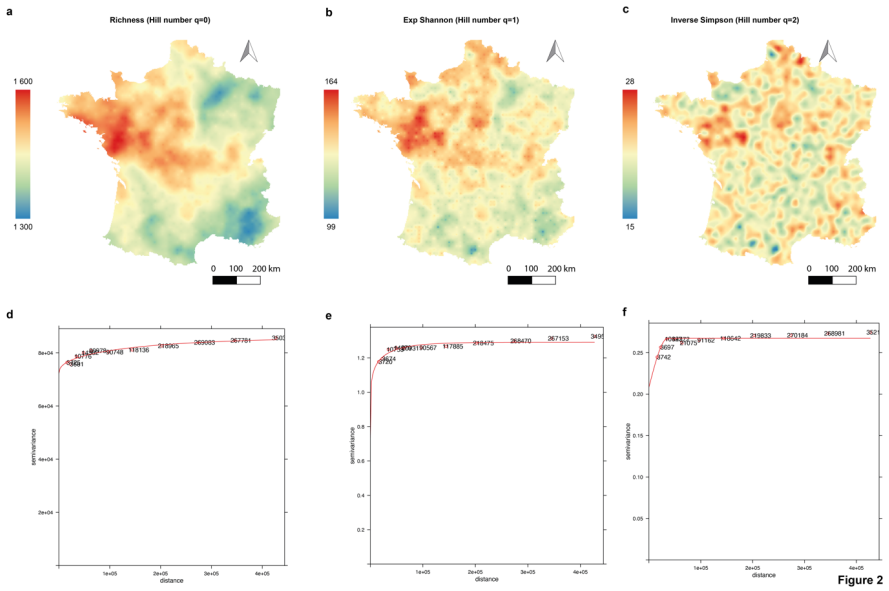


Figure 2

Fig. 2: National soil fungal alpha-diversity maps and robust variograms in France. Map of fungal richness (a). Map of fungal exponential of Shannon diversity (b). Map of fungal inverse Simpson (c). The variogram of fungal richness and the exponential of Shannon diversity are based on Matern model with M. Stein's parameterization (d and e). The variogram of fungal inverse Simpson is based on a spherical model. Colors correspond to the extrapolated values expressed as OTUs *per* soil sample (f).

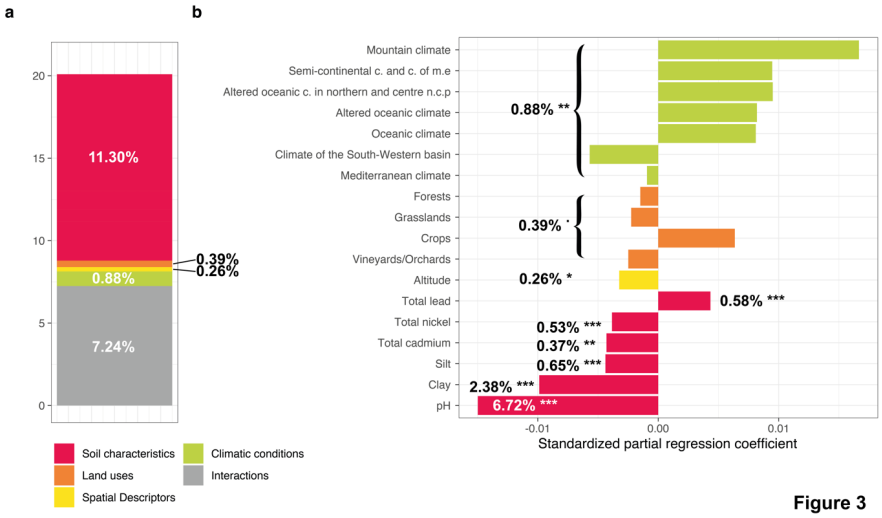


Figure 3

Fig. 3: Variance partitioning analysis to determine how local factors and factors related to global environmental filters explained variance in fungal richness (a). The amount of explained variance corresponds to the adjusted R^2 values of the contextual groups using partial redundancy analysis. (b) Model parameters for the distribution of fungal richness. Each parameter is presented with its estimated model coefficients and its marginal effect assessed by a permutation test. *P<0.1; **P<0.01; ***P<0.001. Missing values indicate that the variable was not retained in the model. Sand was removed prior to model evaluation since it was represented by the opposite of the sum of the silt and clay contents.

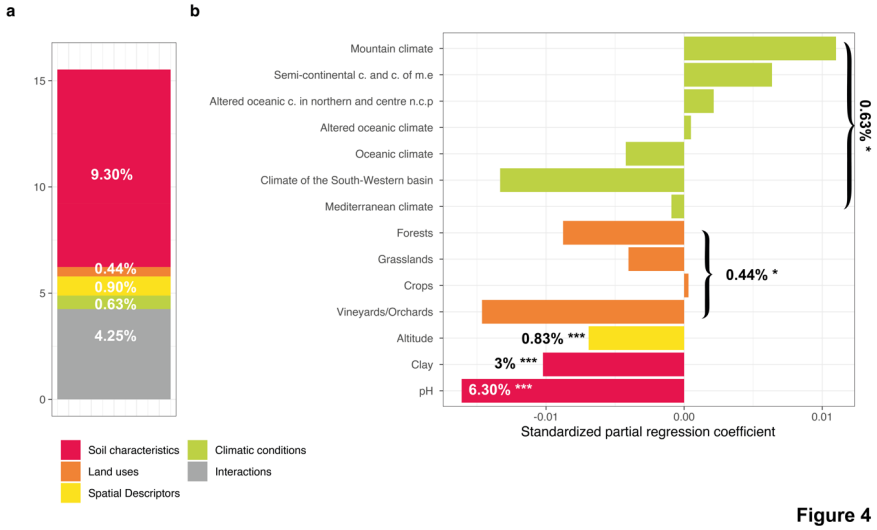


Figure 4

Fig. 4: Variance partitioning analysis to determine how local factors and factors related to global environmental filters explained variance in the exponential of fungal Shannon diversity (a). The amount of explained variance corresponds to the adjusted R^2 values of the contextual groups using partial redundancy analysis. Model parameters for the distribution of the exponential of fungal Shannon diversity (b). Each parameter is presented with its estimated model coefficients and its marginal effect assessed by a permutation test. *P<0.1; **P<0.01; ***P<0.001. Missing values indicate that the variable was not retained in the model. Sand was removed prior to model evaluation since it was represented by the opposite of the sum of the silt and clay contents.

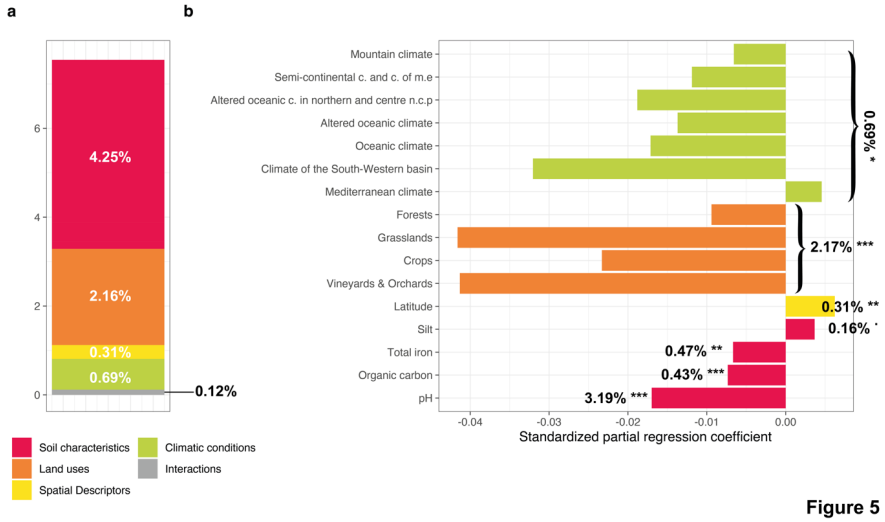


Figure 5

Fig. 5: Variance partitioning analysis to determine how local factors and factors related to global environmental filters explained variance in fungal inverse Simpson (a). The amount of explained variance corresponds to the adjusted R^2 values of the contextual groups using partial redundancy analysis. Model parameters for the distribution of fungal inverse Simpson (b). Each parameter is presented with its estimated model coefficients and its marginal effect assessed by a permutation test. *P<0.1; **P<0.01; ***P<0.001. Missing values indicate that the variable was not retained in the model. Sand was removed prior to model evaluation since it was represented by the opposite of the sum of the silt and clay contents.

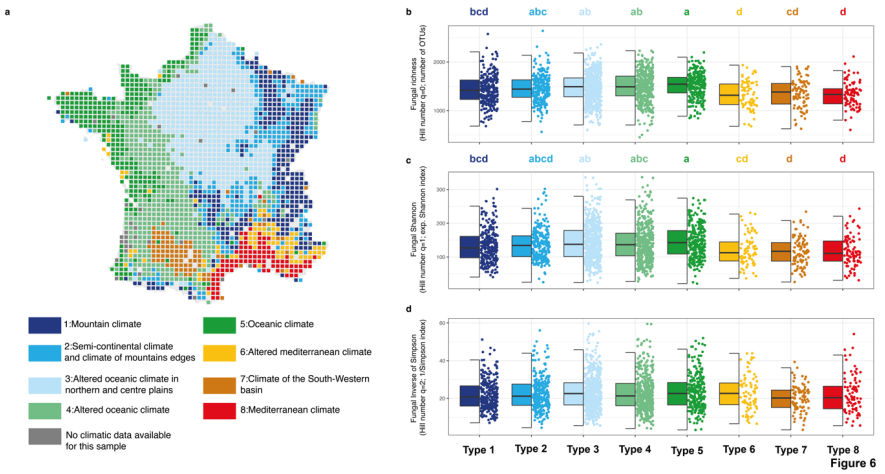


Figure 6

Fig. 6: Map of the RMQS sampling sites and classification of the eight climate types (a). Soil fungal alpha-diversity distribution across climate types for fungal richness (b), the exponential of fungal Shannon diversity (c), and fungal inverse Simpson (d). Different letters designate significantly different values following multiple comparisons.

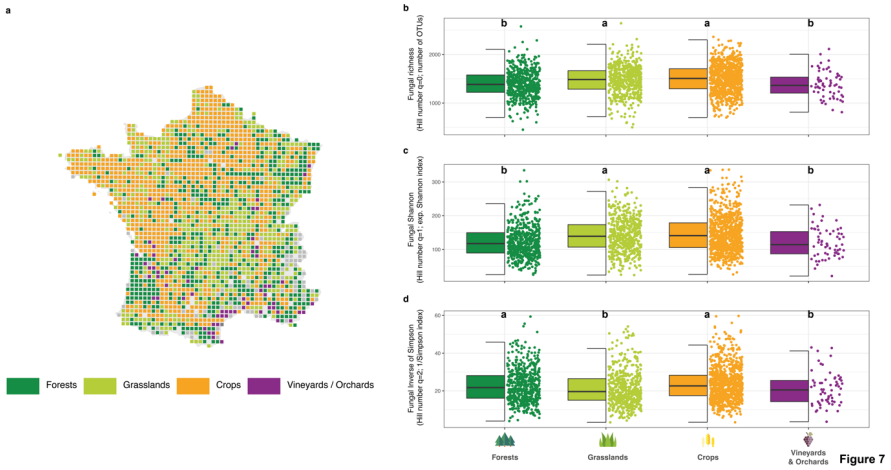


Figure 7

Fig. 7: Map of the RMQS sampling sites and classification for the four land uses (a). Fungal richness distribution across land uses (b). Distribution of the exponential of fungal Shannon diversity across land uses (c). Fungal inverse Simpson distribution across land uses (d). Different letters designate significantly different values following multiple comparisons.

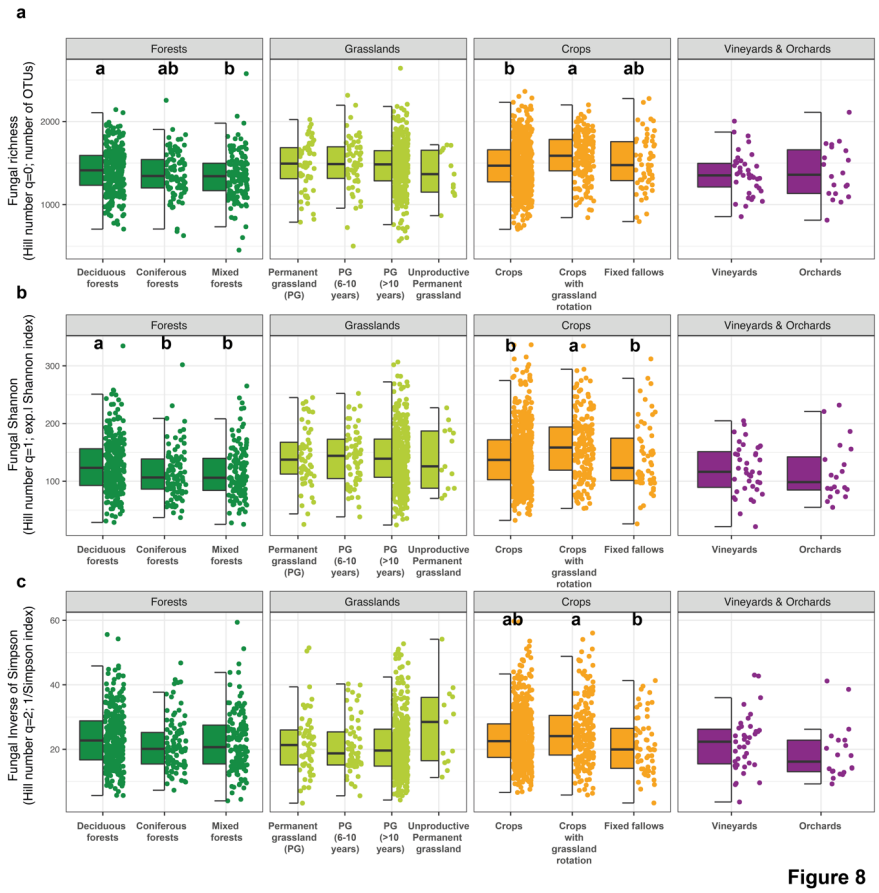


Figure 8

Fig. 8: Distribution of soil fungal alpha-diversity within the four major land uses of French soils according to a more precise land management characterization for fungal richness (a), the exponential of fungal Shannon diversity (b), and fungal inverse Simpson (c). Different letters designate significantly different values following multiple comparisons.

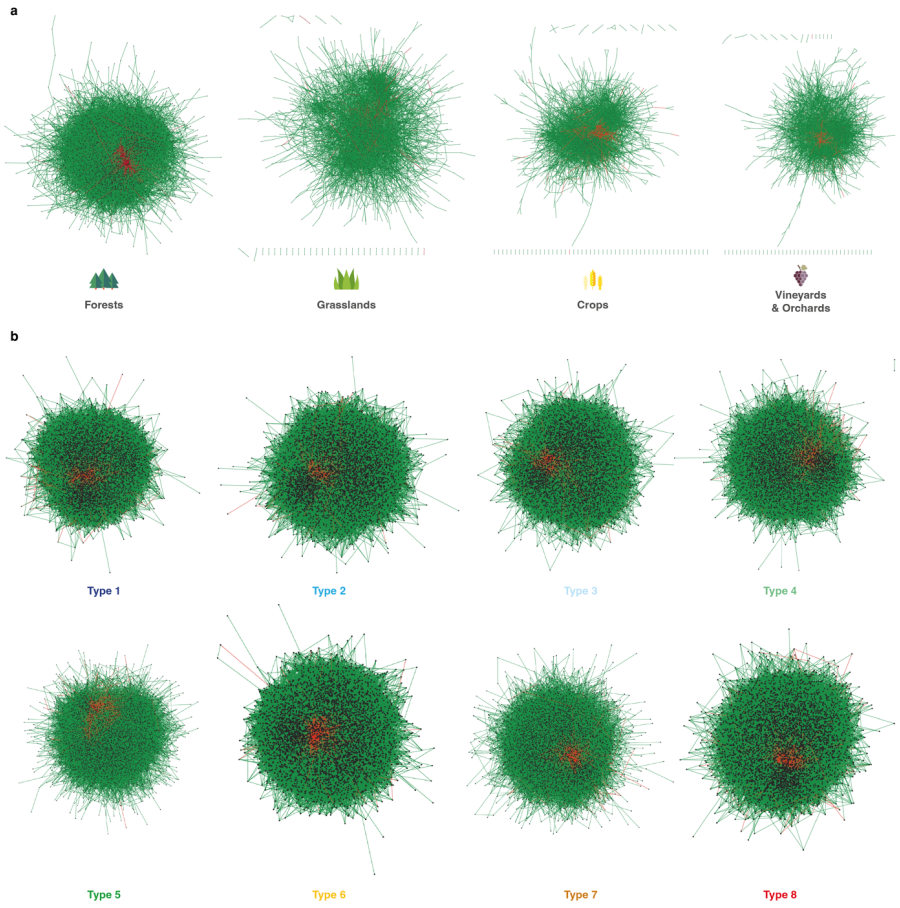
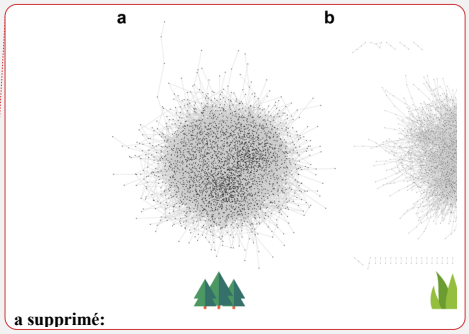


Figure 9

Fig 9. Co-occurrence networks of fungal OTUs across land uses (a) and climate types (b) in France. Among the 100 replicates of the 4 types of land cover or 8 climate types, we visualized the network closest to the median network based on the number of links and connectance. The red edges represent the negative links, and the green edges represent the positive links. Nodes,

a supprimé:



OTUs; edges, links between the nodes.

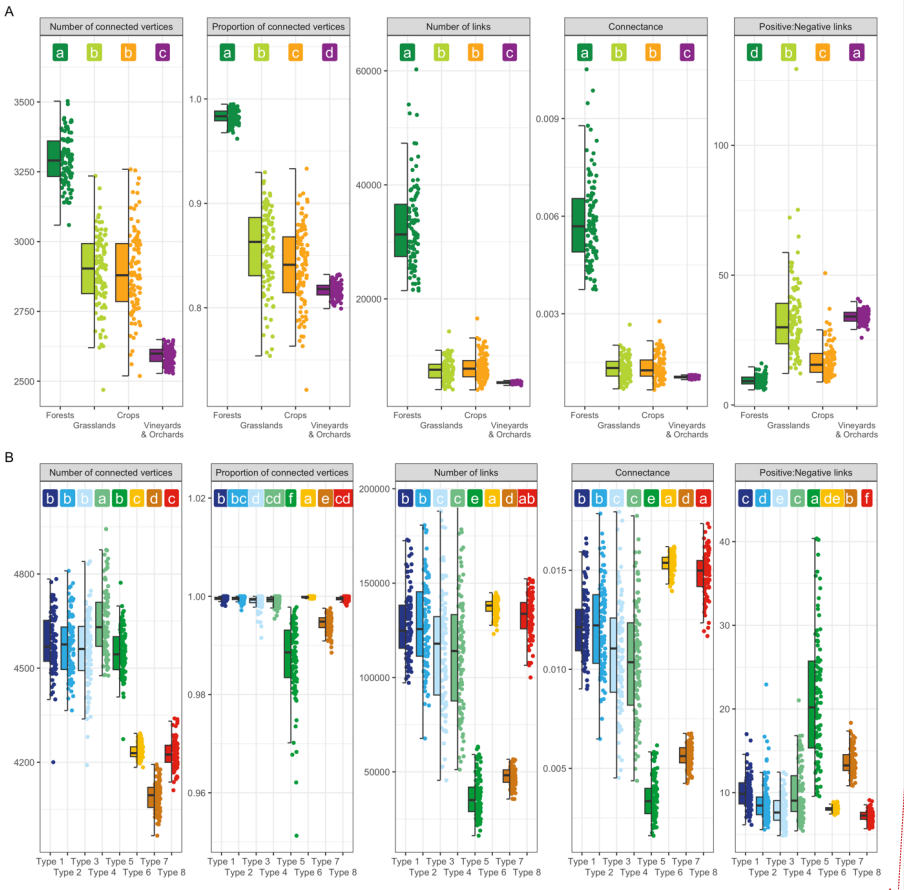


Fig 10. Fungal co-occurrence network metrics for the four land uses (a) and eight climate types (b) based on five indices. Different letters designate significantly different values following multiple comparisons.

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