Soil health is linked to primary productivity across Europe

Ferran Romero*[1], Maëva Labouyrie[1,2,3], Alberto Orgiazzi[3,4], Cristiano Ballabio[3], Panos Panagos[3], Arwyn Jones[3], Leho Tedersoo[5], Mohammad Bahram[6,7], Linnea C. Smith[8,9], Carlos A. Guerra[8,9], Emanuele Lugato[3], Nico Eisenhauer[8,10], Manuel Delgado-Baquerizo[11], Marcel G.A. van der Heijden*[1,2]

[1]Plant-Soil Interactions group, Agroscope, Reckenholzstrasse 191, 8046 Zurich, Switzerland

[2]Department of Plant and Microbial Biology, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland

[3]European Commission, Joint Research Centre Ispra (JRC Ispra), Via Enrico Fermi 2749, 21027 Ispra, Italy

[4]European Dynamics, Brussels, Belgium

[5]Mycology and Microbiology Center, University of Tartu, Liivi 2, 50409 Tartu, Estonia

[6]Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, Liivi 2, 50409 Tartu, Estonia

[7]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

[8]German Center for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[9]Institute of Biology, martin Luther University Halle Wittenberg, Halle (Saale), Germany

[10]Institute of Biology, Leipzig University, Leipzig, Germany

[11]Laboratorio de Biodiversidad y Funcionamiento Ecosistémico. Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, Av. Reina Mercedes 10, E-41012, Sevilla, Spain.

*Authors for correspondence: Ferran Romero (ferran.romeroblanch@agroscope.admin.ch) and Marcel van der Heijden (marcel.vanderheijden@agroscope.admin.ch)

Abstract

The role of soil biodiversity and soil health in regulating primary productivity across different land use types is still poorly understood, hindering our ability to predict the impact of soil degradation on essential ecosystem services such as food provision. To address this gap, we conducted a pan-European observational field study using data from 588 sites and 27 countries to investigate the linkages between soil microbial diversity, soil health, and primary productivity across three major land use types: woodlands, grasslands, and croplands. We demonstrate that a combination of climatic and edaphic factors, together with soil biodiversity parameters, explained between 20.76% and 31.20% of the variability in primary productivity across contrasting land use types. Our study further revealed a general positive effect of soil health (i.e., microbial biomass, soil nitrogen and carbon content, and microbial diversity) on primary productivity, particularly for croplands (R^2 = 0.16) and grasslands (R^2 = 0.18). The effects of soil microbial diversity depended on the microbial group and the land use type considered. In general, higher diversity of beneficial groups (e.g., Acidobacteria, Mortierellomycota) was linked to increased productivity, while the opposite was found for plant pathogens (particularly in croplands). Together, our results provide insights into the importance of soil biodiversity and soil health for maintaining essential ecosystem functions across contrasting land use types and highlight the need for land-use specific management strategies for preserving belowground diversity and primary productivity.

Introduction

Plant productivity is a crucial ecosystem process that supports essential services necessary for human welfare on Earth (Barrios, 2007). A range of studies have shown that plant diversity in ecosystems promotes plant productivity and yield (Dietrich et al., 2023; Fraser et al., 2015; Isbell et al., 2011; Le Provost et al., 2023; Tilman et al., 1997). On the contrary, it is still poorly understood whether the diversity of soil biota (i.e., belowground organisms) influences plant productivity. In addition to this, our understanding of how soil health relates to primary productivity at large scales remains poorly understood.

Soil health is a composite measure and refers to the capacity of soils to support plant productivity and other functions (Lehmann et al., 2020; Qiao et al., 2022). Soil health assessments have traditionally focused on soil properties including microbial biomass, available nutrients, and organic carbon (Bünemann et al., 2018). However, advanced molecular methods such as next-generation sequencing techniques offer the possibility to include a microbial component (e.g., soil biodiversity) into soil health indices, providing a more comprehensive view of the wide range of properties that characterize soils and influence ecosystem functioning. Although there is much interest globally on soil health, current scientific evidence that demonstrates the importance of soil health at large scale is missing (Lehmann et al., 2020; Rinot et al., 2019). Despite of this, a recent study assessing croplands in China demonstrated that soil health is positively linked to plant yield (Li et al., 2021). However, systematic comparisons of the relative importance that soil health has across contrasting ecosystems (i.e., woodlands, grasslands) have received less attention. Moreover, the studies performed so far have largely focused on chemical and physical properties, often ignoring biological measure (Van Bruggen & Semenov, 2000). The few studies including biological measures in soil quality have mostly focused on the activity of soil microorganisms (e.g., enzymatic activities), but biodiversity *per se* has received less attention (Alkorta et al., 2003).

Experiments performed in experimental microcosms where soil biodiversity can be manipulated (i.e., reduced) have demonstrated that a reduction of microbial diversity (e.g., number of bacterial and fungal taxa) leads to altered microbial mediated functions, less nutrient uptake by plants, and reduced productivity (Chen et al., 2020; Luo et al., 2023; Romero, Hilfiker, et al., 2023; van der Heijden et al., 1998; Wagg et al., 2019). However, only recently medium to large-scale monitoring studies have started to uncover the role that belowground diversity plays in ecosystem productivity (Anthony et al., 2022; Delgado-Baquerizo et al., 2016, 2020; Fan et al., 2021; Hu et al., 2021; Liu et al., 2022). Most of these studies have so far focused on natural or

semi-natural land use types (e.g., grasslands), or contained a limited number of study sites (Delgado-Baquerizo et al., 2020; Fan et al., 2023; Hu et al., 2021). Moreover, the specific drivers of plant productivity, especially in intensively managed ecosystems (i.e., croplands) are still poorly understood, and it is widely debated whether soil microbial diversity and microbiome complexity are important for plant productivity in these ecosystems (van der Heijden & Wagg, 2013; Xiong & Lu, 2022).

Studies to date have primarily focused on microbial-mediated functions such as carbon storage and nitrogen cycling, leaving a significant knowledge gap in understanding the broader effects of belowground diversity on other functions (i.e., plant productivity) across different ecosystems (Bissett et al., 2011; Huang et al., 2023; Wu et al., 2023). Malik and collaborators (2018) used 21 paired sites, comprising low- and high-intensity management practices (permanent grasslands *vs*. fertilized croplands), and observed higher carbon storage capacity attributed to enhanced microbial growth efficiency in undisturbed sites (grasslands) compared to heavily fertilized croplands. Similarly, Edlinger and collaborators (2023) observed lower soil aggregate stability and soil organic carbon content in croplands compared with neighboring grassland sites across a 3000 Km European gradient. Also recently, it was observed that soil microbial diversity at the European scale is highest in croplands compared to woodlands and grasslands (Karimi et al., 2019; Köninger et al., 2023; Labouyrie et al., 2023; Szoboszlay et al., 2017), but the question of whether productivity is similarly driven by belowground diversity across contrasting land use types (e.g., woodland and grasslands vs. cropland) remains unexplored, as a systematic large-scale comparison among different land uses is lacking and large scale soil monitoring efforts are scarce.

In this article, we tested the hypothesis of whether the relationship between soil health and primary productivity differs across contrasting land-use types. To that purpose, we used a pan-European observational field study to test the linkages between soil microbial diversity, soil properties, and primary productivity. We used fresh soil samples collected from 588 sites in 2018 and covering 27 countries and the three major land-use types in the European continent: woodlands (n = 185), grasslands (n = 126), and croplands (n = 277). Using next-generation sequencing methods targeting ribosomal marker genes, we obtained site-level information on the diversity of bacteria and fungi, as well as their major phyla, and functional groups (e.g., fungal pathogens, nitrogen-fixing bacteria). The analysis demonstrated that soil microbial diversity differed across land use types in Europe (Labouyrie et al., 2023). Here we used data from that earlier study and linked this with 11 variables representing information on climatic

109 and edaphic factor. Moreover, we used remote sensing to obtain primary productivity data
110 across the 588 sites. Subsequently we explored how soil health, soil microbial diversity and a
111 range of biotic and abiotic factors relate to primary productivity across contrasting land use
112 types.

113 Methods

114 *Field survey and soil sampling*

115 This study was carried out on the EU Statistical Office's Land Use and Coverage Area frame
116 Survey (LUCAS), the largest pan-European scheme for assessing soil characteristics in relation to
117 land cover and land use (Orgiazzi et al., 2018). As part of the 2018 LUCAS survey, 881 fresh soil
118 samples were collected across Europe and stored at -20°C before further processing (Orgiazzi et
119 al., 2022). The sampling followed a composite strategy: the final sample collected at each
120 location comprised five topsoil (0-20 cm) subsamples that are mixed to form a single composite
121 sample. The first subsample is taken at the precise GIS (geographical information system)
122 coordinates of the pre-established LUCAS point, and the remaining four subsamples are taken 2
123 m from the central one following the cardinal directions (North, East, South, and West). To avoid
124 seasonality and time effects, all samples were collected over the shortest possible timeframe
125 (spring 2018). For this study, we focused on 277 croplands, 126 grasslands, and 185 woodlands
126 from 881 LUCAS sites, across 27 countries (Figure 1). The selection was based on those samples
127 from which all variables (soil diversity, edaphic factors, and primary productivity) were available.
128 Sampling was based on a regular grid defined by the intersection points of a 2 km x 2 km grid
129 covering the European territory, and each sampling location was assigned to one of three land
130 use types (woodland, grassland, cropland) using orthophotos or satellite images (Orgiazzi et al.,
131 2018).

132 *Soil microbial diversity*

133 Soil DNA was extracted from each of the 588 composite soil samples using the Qiagen DNeasy
134 PowerSoil HTP 96 Kit Q12955-4. Three 0.2 g aliquots per sample were extracted and pooled
135 together. Negative and positive controls were included to determine the presence of any
136 external contamination. DNA extracts were quantified and checked for quality using a Qubit™
137 1X dsDNA HS Assay Kit and a Qubit™ 3 Fluorometer (Invitrogen). Primer sets for barcode
138 amplification were 515F (GTGYCAGCMGCCGCGGTAA) and 926R (GGCCGYCAATTYMTTTRAGTTT)
139 for the bacterial 16S region (Caporaso et al., 2011; Parada et al., 2016), and ITS9mun

(GTACACACCGCCCGTCG) and ITS4ngsUni (CGCCTSCSCTTANTDATATGC) for the fungal ITS region (Tedersoo & Anslan, 2019). Sequencing was performed by Illumina MiSeq platform with 2 x 300 paired-end mode for bacterial data and PacBio Sequel II platform for fungal data. Additional information including DNA amplification and library preparation is available in Labouyrie et al., 2023.

The Illumina and PacBio amplicon data (for bacteria and fungi, respectively) were demultiplexed using LotuS2 (Özkurt et al., 2022), and paired-end reads were assembled setting a minimum overlap of 10 bp using FLASH 1.2.10 (Magoč & Salzberg, 2011). Reads failing to merge were removed from the final dataset. For bacteria, operational taxonomic units (OTUs) were generated with the usearch option (version 10.0.024) available in UPARSE (Edgar, 2013). Merged reads were truncated up to the 16S primer sequences (i.e., 515F and 926R) and filtered for the presence of primer sequences (allowing a maximum of 2 mismatches). Merged reads were further quality-filtered with usearch by removing sequences with more than one expected error, and duplicated sequences were collapsed with fqtrim version 0.9.7 (Pertea, 2015). Obtained OTUs were annotated with the taxonomy data available from the Ribosomal Database Project (Cole et al., 2014). To avoid sequencing artifacts, only OTUs with at least 50 read counts and present in at least 10 samples were kept. For fungi, 98%-OTUs were obtained as described in Tedersoo et al., 2021. Fungal taxonomic annotation was performed using BLAST+ version 2.11.0 (Camacho et al., 2009) against the UNITE 9.1 database (Nilsson et al., 2019). Bacterial and fungal datasets were further normalized to comparable sequencing depths (bacteria: 40,109 reads; fungi: 502 reads) using the Scaling with Ranked Subsampling (SRS) method (Beule & Karlovsky, 2020). Normalized datasets were used to obtain values of total richness (i.e., OTU number), community composition (extracted values from the first dimension of NMDS), and the richness of major microbial groups (i.e., phyla). Normalized datasets were also used to obtain the richness of major functional groups as retrieved from the FAPROTAX (bacteria) and FungalTraits (fungi) databases (Louca et al., 2016; Põlme et al., 2020). Further details on bacterial/fungal sequence processing, filtering, and taxonomic/functional annotation are available in Labouyrie et al., 2023.

Edaphic and climatic factors

The following measurements were undertaken for each sampling site to ensure a comprehensive understanding of climatic and edaphic factors. Total nitrogen and phosphorus content were assessed to determine nitrogen and phosphorus availability in the soil. Soil organic carbon was quantified to estimate the amount of carbon stored in the soil organic matter. Soil

pH and microbial biomass were used as measures of acidity and activity of the living component of the soil, respectively. The bulk density was used as a surrogate of soil compactness. Soil texture was characterized by measuring silt, sand, and clay content. Additionally, to capture the broader climatic context of each site, mean annual precipitation and mean annual temperature were retrieved from the WorldClim database (www.worldclim.org) . These parameters collectively provided a detailed profile of the environmental and soil conditions at each sampling site. Specific details on the methods employed for these measurements are available in Labouyrie et al., 2023 and Smith et al., 2021.

Primary productivity

The normalized difference vegetation index (NDVI) was calculated from images taken with the NASA satellites Terra and Aqua using moderate resolution imaging spectroradiometer (MODIS) technology. The NVDI is a simple indicator for the health and abundance of vegetation in a particular area and is calculated using the difference between the amount of light reflected by vegetation in the near-infrared range and the amount of light reflected in the red range (Pettorelli et al., 2005). The NDVI is widely accepted as a proxy for plant biomass and photosynthetic efficiency (Camps-Valls et al., 2021; Jobbágy et al., 2002; Joiner et al., 2018; Paruelo et al., 1997) across different ecosystems, and has previously been used to investigate the relationship between soil biodiversity and plant productivity (Delgado-Baquerizo et al., 2016, 2020; Fan et al., 2023; Liu et al., 2022). Here, we used averaged NVDI values obtained for the months before, during, and after sampling at each location. This index was calculated in the same way for croplands, grasslands, and woodlands.

Statistics

Statistical analyses were performed using R software, version 4.2.1. Only soil samples for which all explanatory variables (i.e., soil biodiversity and climatic, edaphic, and spatial factors) were available were used for this study, so none of the values in any explanatory variables was inferred or calculated from the median value of the respective dataset. A total of 588 sites were used for this study, including 277 croplands, 126 grasslands, and 185 woodlands. To assess the most important drivers of primary productivity within the three land-use systems, we performed a three-step model-selection approach (Edlinger et al., 2022).

First, we selected a wide range of explanatory variables including biodiversity indicators (i.e., OTU richness, diversity, community composition), together with climatic and edaphic factors.

Total number of explanatory variables was 34 (Table S1). We then investigated the correlation among all variables to ensure there was no strong co-correlation among them, and reduced variables that were strongly correlated (i.e., Spearman rank correlation coefficient higher than +0.90, or lower than -0.90). Correlations were run using the corr function within the corrplot package (Wei & Simko, 2017). This approach reduced the 34 explanatory variables to 29 (Table S1). The five variables removed included Shannon's diversity index for bacteria and fungi (strong correlation with OTU richness), total nitrogen (strong correlation with soil organic carbon), richness of chemoheterotrophic bacteria (strong correlation with Actinobacteria and total bacteria), and Proteobacteria (strong correlation with total bacterial richness and Bacteroidetes). Some of the resulting variables (selection based on Lehmann et al., 2020, see Table S2) were used to build a soil health index: this was calculated using z-score transformation: each variable was standardized to have a mean of 0 and a standard deviation of 1. The soil health index for each site was then computed by summing its respective z-scores. This approach allowed us to integrate multiple soil health indicators into a single composite index, facilitating a comprehensive assessment.

The second step involved a multi-model inference approach using the R package glmulti (Calcagno & de Mazancourt, 2010). This package automates the process of exploring different combinations of explanatory variables and selects the most appropriate model to explain variability in each outcome (here, primary productivity). Multi-model inference approach resulted in a high number of possible linear models, ranked by Akaike information criterion (AIC). In the last step, the best models that fell within an AIC range of two were averaged to obtain a conservative estimate and relative importance of the most important predictors using the MuMin package (Barton, 2012). Briefly, this package combines the results of multiple models to get more robust and reliable estimates. We used ΔAIC values to compute the Akaike weight of each of the selected models and computed a weighted-average model. The relative importance of each explanatory variable was estimated by taking all the models into consideration as the sum of the weights/probabilities for the models in which the variable appears.

To further clarify the relative contribution of environmental factors and soil biodiversity to explain patterns in primary productivity, we conducted a classification Random Forest (RF) analysis. The RF analyses were performed independently for soil biodiversity, environmental parameters, and both combined. The RF were also performed for each land use type independently (croplands, grasslands, and woodlands). Therefore, a total of nine RF analyses were performed using the rfPermute package (Archer, 2016). For each RF, we obtained the

variation (as %) explained by the different predictors (soil biodiversity, environmental parameters, or both combined).

Results and discussion

This study represents the first continental-scale comparison of patterns on soil biodiversity-primary productivity across contrasting land uses. We surveyed 588 sites across the European continent including 277 croplands, 126 grasslands, and 185 woodlands (Figure 1). For each site, we gathered information on environmental parameters (i.e., climatic, and edaphic factors), together with information on soil microbial (i.e., bacterial, and fungal) diversity, and primary productivity (Table 1). Primary productivity was significantly lower in croplands, compared to grasslands and woodlands, in line with previous research (Krause et al., 2022) (Figure S1). Overall, our results demonstrate that a combination of climatic and edaphic factors, together with soil biodiversity, explain patterns in primary productivity across contrasting land use types at the European scale: our predictors explained 20.76% of the variability in primary productivity in grasslands, 23.80% in woodlands, and 31.20% in croplands (Figure 2). Moreover, we show that a soil health index built from soil chemical properties but also biodiversity (Table S2) positively correlates to primary productivity, especially in croplands (R^2 = 0.16) and grasslands (R^2 = 0.18).

We show that soil biodiversity accounts for a unique proportion of the variation in primary productivity, especially in grasslands. Among soil biodiversity components, bacterial richness (particularly the richness of Acidobacteria and Firmicutes) was positively associated to primary productivity in croplands and grasslands, while woodlands relied more on fungi (saprotrophic fungi and the phylum Mortierellomycota). Bacterial diversity (i.e., OTU number, Shannon's diversity index) was higher in croplands, followed by grasslands, and woodlands (Table 1, Figure S2). Fungal richness was highest in grasslands and lowest in woodlands. Fungal diversity (Shannon's index) was not significantly different between grasslands and croplands (Table 1, Figure S3). Regarding community composition, both bacterial and fungal communities markedly differed across land use types (Table 1, Figure S2, Figure S3). By-phylum richness analysis revealed that Acidobacteria, Basidiomycota, and Leotiomycetes (Ascomycota) were more numerous in woodlands, whereas Verrucomicrobia were more numerous in grasslands. Croplands showed the highest richness of Sordariomycetes (Ascomycota), Actinobacteria, Proteobacteria, Nitrospirae, Bacteroidetes, and Firmicutes (Table 1, Figure S4, Figure S5). At the functional level, nitrogen-fixing bacteria where more abundant in woodlands and grasslands

269 than in croplands. Croplands, however, displayed the highest abundance of bacterial
270 chemoheterotrophs and fungal plant pathogens (Table 1, Figure S6).

271 We used a multi-model inference approach followed by random forest regression to evaluate
272 the performance of predictor combinations in explaining patterns in primary productivity across
273 land use types. Moreover, we used 8 variables known to be often associated to soil health to
274 build a soil health index and observed positive correlations between this index and primary
275 productivity, especially in grasslands (R^2 = 0.18), and croplands (R^2 = 0.16) (Figure 3). Among the
276 different variables included in the index (see Table S2), the strongest correlations with primary
277 productivity were found for total nitrogen content, soil organic content, and microbial biomass
278 (Figure S7) Multi-model inference resulted in a high number of possible linear models, ranked
279 by their Akaike Information Criterion (AIC). We weighted the best models into an average model
280 (Table 2) and obtained a conservative estimate and relative importance of the most important
281 predictors (Figure 4) (Cade, 2015; Edlinger et al., 2022). In croplands, the model best explaining
282 patterns in primary productivity (AIC = 4780.66, p-value < 0.001) included the richness (OTU
283 number) of several microbial groups (i.e., Acidobacteria, Actinobacteria, Firmicutes,
284 Chytridiomycota) as well as three edaphic properties (sand content, pH, and microbial biomass).
285 Our results confirm previous evidence on the role of pH in driving crop productivity; accordingly,
286 we observed a clear decrease in cropland productivity in highly alkaline (pH > 8) soils (Figure S7)
287 (Couto, 2018).

288 Soil microbial biomass was also selected as an important variable explaining plant productivity.
289 Interestingly, a recent study indicated that high microbial biomass in croplands enhances
290 nutrient use efficiency and nutrient cycling of plants, so we argue that further work is necessary
291 to assess the importance of microbial biomass for agroecosystem performance (Toda et al.,
292 2023). Predictor ranking based on relative importance following multi-model averaging
293 indicated that the best predictor of primary productivity in croplands was the richness of
294 Acidobacteria (Figure 4). Acidobacteria are abundant soil-borne microorganisms known to be
295 involved in nutrient mineralization and organic matter degradation (Banerjee et al., 2016; Kielak
296 et al., 2016; Sikorski et al., 2022). Here we demonstrate for the first time that the positive effect
297 of Acidobacteria on primary productivity is comparatively higher in croplands than in woodlands
298 or grasslands (Figure S8). Our results align with a recent study where Acidobacteria positively
299 correlated with cropland productivity in a 4-decade fertilization experiment (Fan et al., 2021).
300 Finally, the richness of Chytridiomycota negatively correlated to productivity in croplands
301 (Figure S9). While this fungal group is best known for parasitizing vertebrates, some species are

responsible for plant disease in Europe (van de Vossenberg et al., 2022). In line with this, we observed a negative correlation between fungal plant pathogens and cropland productivity (Figure S10).

Our multi-model inference approach points towards soil organic carbon as a major predictor of grassland productivity (Figure 4). Grasslands store one third of the terrestrial carbon stock, and most of it is stored belowground as soil organic carbon (Conant, 2012). Recent studies show that plant diversity increases soil organic carbon storage in grasslands by elevating carbon inputs to belowground biomass and promoting microbial necromass contribution to soil organic carbon storage (Lange et al., 2015). Our results show that not only plant diversity is interlinked with soil organic carbon, but also plant productivity at the continental scale. We did not differentiate between necromass and living biomass in our study, but we also found positive correlations between bacterial richness/ microbial biomass and grassland productivity. As for croplands, pH and grassland productivity described a hump-shaped response, with productivity peaking at pH ≈ 6.

Soil organic carbon was also retained as an important predictor of primary productivity in woodlands (Figure 4). Other relevant environmental factors in woodland productivity were temperature, phosphorus, and clay content. However, the main predictors of primary productivity in woodlands according to our multi-model inference approach were bacterial and fungal community composition (NMDS1). Our results align with a recent study suggesting that fungal community composition outcompetes richness (number of fungal OTUs) as a driver of soil functioning in woodlands (Anthony et al., 2022; Osburn et al., 2023). We argue, however, that future studies at a large scale should include the bacterial compartment in their analyses, as both previous research and the findings of this study show that the distribution of bacterial groups plays a role in woodland productivity.

Previous studies have suggested that functional groups (e.g., mycorrhizal fungi, nitrogen-fixing bacteria, plant pathogens) might be better predictors of ecosystem functioning than the richness or diversity of taxonomy-based microbial groups (i.e., OTUs) (Delgado-Baquerizo et al., 2020; Liu et al., 2022). For example, Delgado-Baquerizo and collaborators (2020) observed positive relationships between the richness of mycorrhizal fungi and soil functions such as phosphorus mineralization and soil respiration. The same study observed no relationship between mycorrhizal or saprophytic fungi and primary productivity. Another large-scale study observed a positive relationship between saprophytic fungi and the stability of primary productivity, and no relationship between productivity and mycorrhizal fungi (Liu et al., 2022).

Our findings indicate a positive trend of increased productivity associated with higher mycorrhizal richness, especially within grassland ecosystems (Figure S11). We argue that the variability in outcomes across various large-scale studies underscores the urgency for additional research conducted under controlled conditions, aiming to elucidate the precise mechanisms through which mycorrhizal diversity fosters plant productivity (Romero et al., 2023) . Finally, our study aligns with previous research showing a decrease in cropland productivity with increasing pathogen richness (Liu et al., 2022).

In summary, our results provide compelling evidence that a combination of environmental factors and soil biodiversity relate to primary productivity at the continental scale. This study shows that between 20.76% and 31.2% of the variability in primary productivity can be explained from information on microbial (fungal and bacterial) community composition, and edaphic/ climatic parameters. We further demonstrate that bacterial community composition exerts a significant influence on primary productivity across diverse land use types, whereas in woodlands, fungal community composition also governs primary productivity. Overall, our study emphasizes the importance of addressing relationships between soil biodiversity and primary productivity across contrasting land use types, and further highlights the need to include microorganisms in soil monitoring schemes to gain a comprehensive understanding of ecosystem functioning in terrestrial ecosystems.

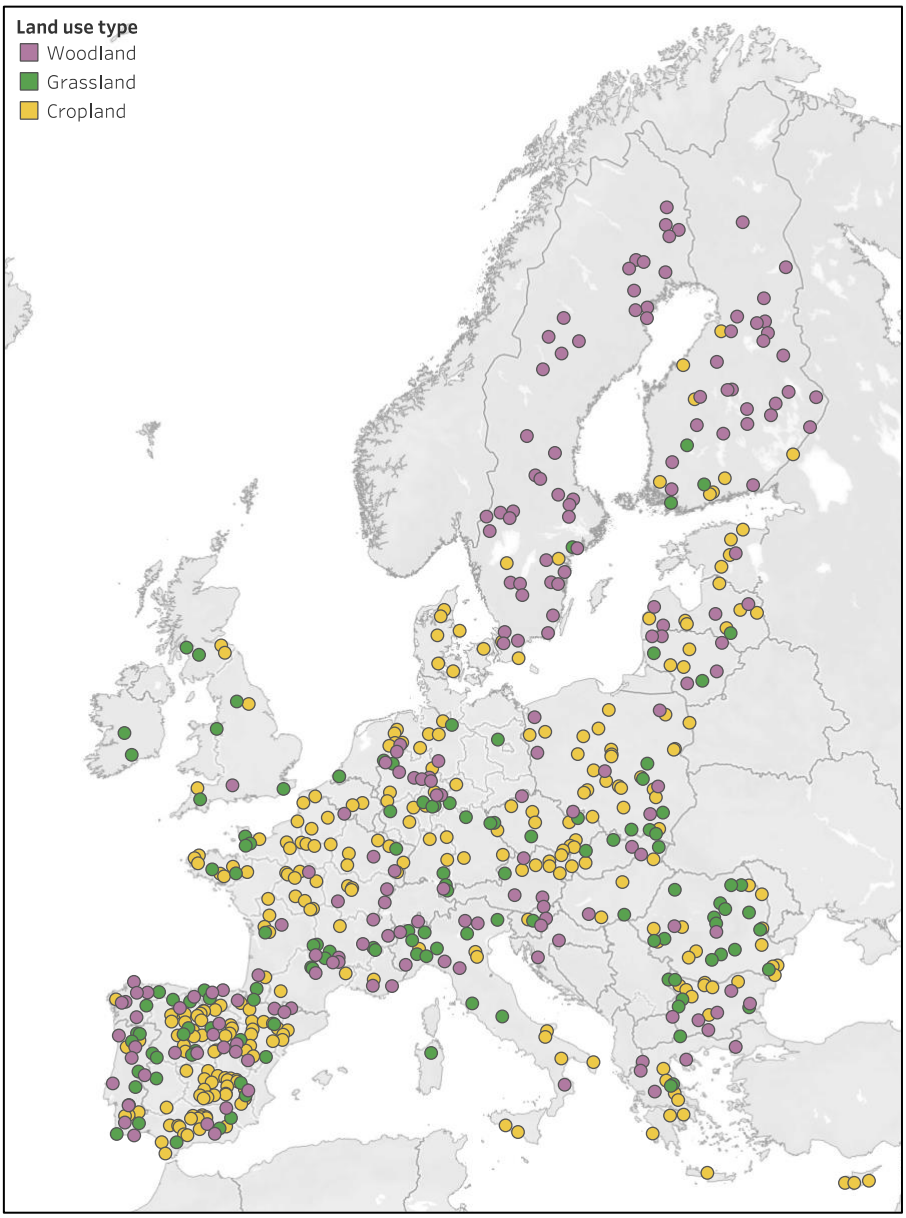
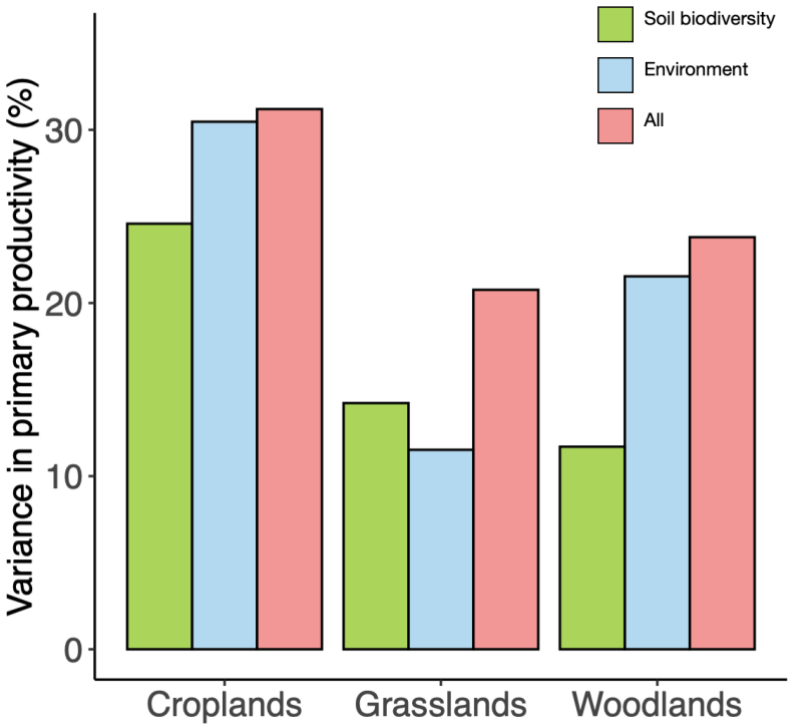


Figure 1. Study site locations. Geographic distribution across the European continent of the 589 locations used in this study. Three major land use types were covered in the survey: cropland (n = 277, yellow), grassland (n = 126, green), and woodland (n = 185, purple).



357

358 **Figure 2. Importance of soil biodiversity and environmental parameters in explaining**
359 **patterns in primary productivity**. Variance in primary productivity (%) as obtained from
360 random forest regression explained by soil biodiversity (bacteria and fungi), environmental
361 parameters (climate and edaphic factors), or the combination of both, across land use types
362 (croplands, grasslands, and woodlands).

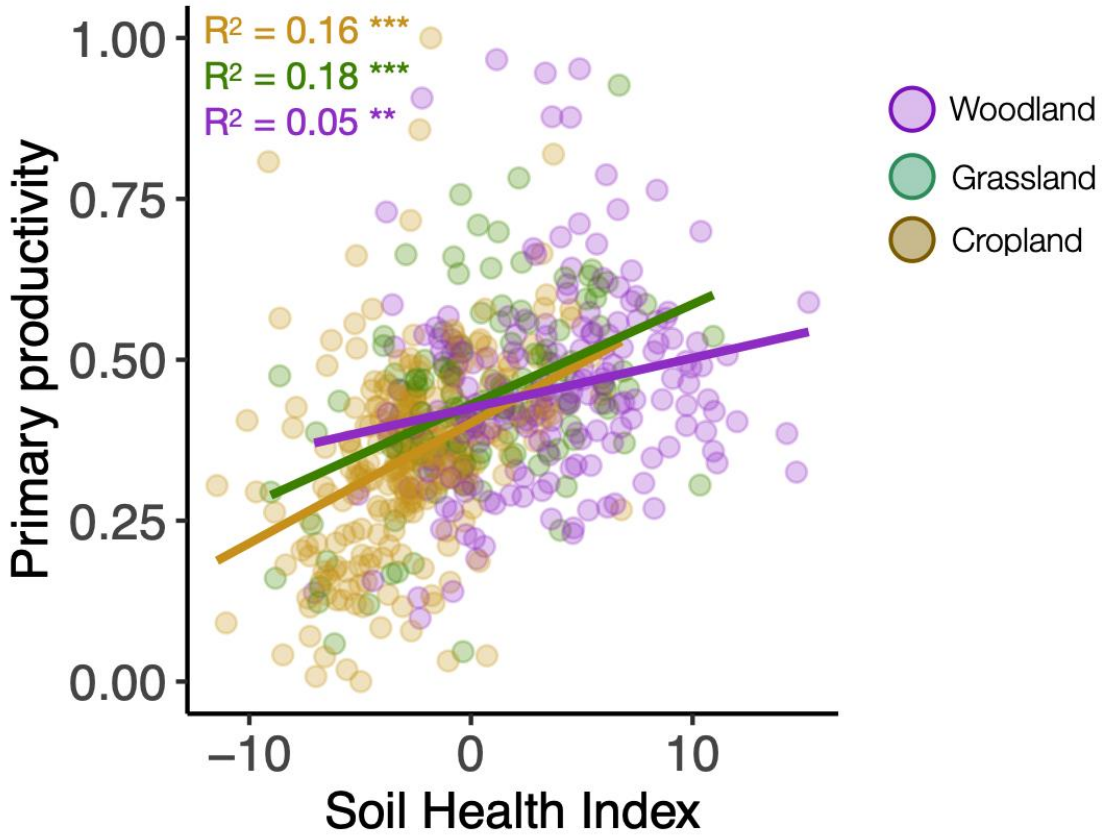


Figure 3. Relationship between soil health and primary productivity. Linear regressions were fitted to explore the relationship between the soil health index and primary productivity across land use types (woodlands, grasslands, and croplands). Explained variation is expressed as R^2, and significance is indicated by asterisks (***; p-value < 0.001, **; p-value < 0.010, *; p-value < 0.050). Non-significant (p-value > 0.05) regressions are denoted with "n.s.".

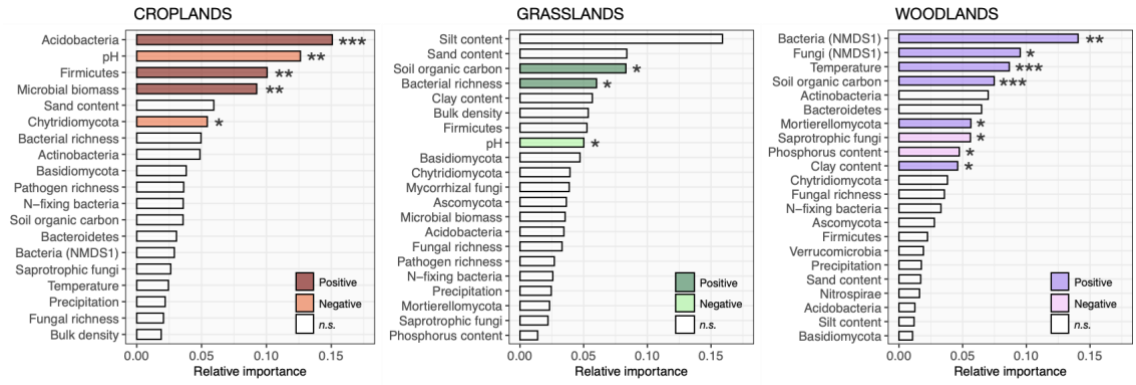


Figure 4. Relative importance of the main predictors on primary productivity. Relative importance of main predictors for primary productivity based on multi-model inference analysis in woodlands (n = 185), grasslands (n = 126), and croplands (n = 277). Dark colors indicate positive predictor effects on primary productivity, and light colors indicate negative effects. Asterisks indicate a significant effect based on the averaged model coefficients (***; p-value < 0.001, **; p-value < 0.010, *; p-value < 0.050).

		Units	Croplands (n = 277)		Grasslands (n = 126)		Woodlands (n = 185)		Kruskal-Wallis test (Chi-squared)	Kruskal-Wallis test (p-value)
Climatic factors	Precipitation	mm	48,54 ± 23,64	a	68,89 ± 28,57	b	64,07 ± 27,97	b	56,82	< 0,001
	Temperature	°C	17,3 ± 4,91	a	15,13 ± 3,5	b	14,44 ± 4,85	b	44,61	< 0,001
Edaphic factors	Clay content	(%)	23,31 ± 13,31	a	22,23 ± 11,35	a	14,73 ± 12,33	b	64,64	< 0,001
	Sand content	(%)	35,41 ± 26	a	36,61 ± 20,97	a	47,72 ± 24,54	b	30,57	< 0,001
	Silt content	(%)	41,13 ± 19,43	a	40,86 ± 16,76	a	37,53 ± 17,27	a	3,97	> 0,05
	pH	unitless	7,07 ± 1,02	a	6,29 ± 1,02	b	5,16 ± 1,12	c	222,42	< 0,001
	Microbial biomass	µg C/g soil	278,05 ± 156,11	a	455,45 ± 272,69	b	394,4 ± 335,85	c	44,53	< 0,001
	Organic carbon	g/Kg	18,61 ± 14,93	a	36,5 ± 33,8	b	59,23 ± 64,51	c	170,23	< 0,001
	Phosphorus content	mg/Kg	36,65 ± 30,45	a	22,81 ± 23,82	b	19,59 ± 21,41	b	60,48	< 0,001
	Nitrogen content	mg/Kg	1,82 ± 1,15	a	3,36 ± 2,54	b	3,25 ± 2,71	b	81,00	< 0,001
	Bulk density	g/cm3	1,23 ± 0,2	a	1,06 ± 0,23	b	0,77 ± 0,36	c	202,79	< 0,001
Biodiversity (fungi)	Total richness	OTU number	120,46 ± 26,67	a	129,48 ± 32,4	b	104,69 ± 30,2	c	57,91	< 0,001
	Shannon's index	unitless	3,86 ± 0,53	a	3,93 ± 0,64	a	3,48 ± 0,66	b	55,91	< 0,001
	Community composition (NMDS1)	unitless	0,10 ± 0,07	a	0,03 ± 0,09	b	-0,16 ± 0,16	c	277,43	< 0,001
	Basidiomycota	OTU number	17,34 ± 7,33	a	23,17 ± 10,94	b	33,23 ± 11,8	c	210,27	< 0,001
	Chytridiomycota	OTU number	8,61 ± 4,61	a	7,8 ± 4,87	a	2,39 ± 3,27	b	222,66	< 0,001
	Mucoromycota	OTU number	2,08 ± 1,97	a	3,72 ± 3,55	b	3,22 ± 3,06	b	30,47	< 0,001
	Ascomycota	OTU number	71,69 ± 17,66	a	68,52 ± 23,64	a	51,94 ± 20,51	b	100,01	< 0,001
	Mortierellomycota	OTU number	9,19 ± 4,02	a	9,4 ± 4,59	a	6,54 ± 4,84	b	58,42	< 0,001
Biodiversity (bacteria)	Total richness	OTU number	7417,12 ± 1122,83	a	6959,97 ± 1079,26	b	5797,98 ± 1648,39	c	111,54	< 0,001
	Shannon's index	unitless	7,92 ± 0,3	a	7,75 ± 0,32	b	7,34 ± 0,52	c	164,98	< 0,001
	Community composition (NMDS1)	unitless	-0,13 ± 0,14	a	-0,02 ± 0,15	b	0,21 ± 0,21	c	232,37	< 0,001
	Acidobacteria	OTU number	965,81 ± 251,36	a	1035,03 ± 230,47	b	1089,4 ± 210,19	c	30,44	< 0,001
	Actinobacteria	OTU number	1694,05 ± 328,01	a	1522,75 ± 428,15	b	1012,31 ± 561,86	c	154,85	< 0,001
	Proteobacteria	OTU number	2385,02 ± 426,75	a	2149,83 ± 402,81	b	1862,84 ± 587,83	c	102,79	< 0,001
	Bacteroidetes	OTU number	643,71 ± 214,04	a	529,41 ± 182,11	b	369,04 ± 228,53	c	138,8	< 0,001
	Nitrospirae	OTU number	19,6 ± 9,33	a	14,44 ± 9,73	b	6,27 ± 8,35	c	197,23	< 0,001
	Verrucomicrobia	OTU number	403,29 ± 134,63	a	441,89 ± 144,25	b	388,28 ± 126,25	a	11,95	< 0,001
	Firmicutes	OTU number	152,34 ± 81,8	a	118,16 ± 54,12	b	55,24 ± 47,4	c	228,84	< 0,001
Biodiversity (functional groups)	Bacterial chemoheterotrophs	OTU number	1676,78 ± 288,57	a	1339,74 ± 335,02	b	929,82 ± 472,29	c	246,99	< 0,001
	Nitrogen-fixing bacteria	OTU number	9,04 ± 4,68	a	9,87 ± 5,23	ab	9,94 ± 3,7	b	10,28	< 0,001
	Fungal saprotrophs	OTU number	71,44 ± 15,75	a	67,11 ± 19,95	a	50,41 ± 19,02	b	129,11	< 0,001
	Fungal plant pathogens	OTU number	11,01 ± 4,98	a	7,12 ± 4,81	b	1,55 ± 2,28	c	324,32	< 0,001
	Mycorrhizal fungi	OTU number	3,26 ± 4,52	a	6,61 ± 6,03	b	20,63 ± 12,05	c	286,89	< 0,001

Table 1. Mean values of spatial, climatic, and edaphic factors (± standard deviation) in soils from cropland (n = 277), grassland (n = 126), and woodland (n = 185) sites used in this study. Mean values of biodiversity measures are also shown for bacteria, fungi, and predicted functional groups. Kruskal-Wallis test was used to assess the overall effect of land use type on explanatory variables (chi-squared and p-value are indicated for each test). Grouping information following pairwise Wilcoxon test is indicated above each boxplot, different letters indicate significant differences ($p < 0.05$).

Land Use	Sites	Best model	AIC	p-value
Croplands	277	NPP ~ 1 + Acidobacteria + Actinobacteria + Firmicutes + Sand content + pH + Microbial biomass + Chytridiomycota	4780.66	< 0.001
Grasslands	126	NPP ~ 1 + Firmicutes + Bacterial richness + Clay content + Sand content + pH + Soil organic C + Phosphorus content + Soil density + Basidiomycota + Chytridiomycota + Mycorrhizal richness	2168.70	< 0.001
Woodlands	185	NPP ~ 1 + Bacteroidetes + Bacteria (NMDS1) + Clay content + Soil organic C + Phosphorus content + Temperature + Fungi (NMDS1) + Chytridiomycota + Mortierellomycota + Saprotrophic fungi	3208.55	< 0.001

Table 2. Output of model selection. Best models explaining variation in primary productivity across land use types following multi-model averaging inference.

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