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# Arable plant communities as a surrogate of crop rhizosphere microbiota

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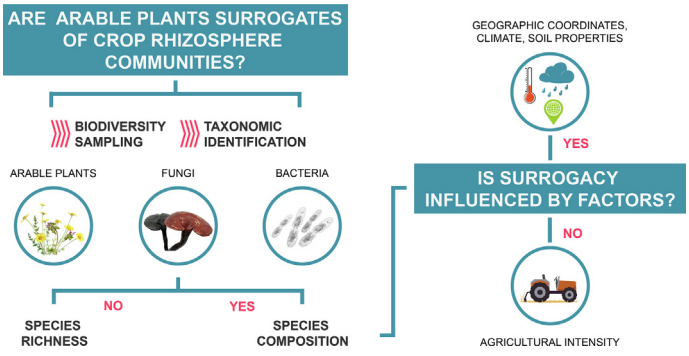
## HIGHLIGHTS

- Indicators for crop rhizosphere microbiota are needed.
- Arable plants were not surrogates of microbial species richness.
- Arable plants were surrogates of microbial species composition.
- Arable plants were predictive of fungal species composition.

## GRAPHICAL ABSTRACT

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## ABSTRACT

Soil microbiota is a crucial component of agroecosystem biodiversity, enhancing plant growth and providing important services in agriculture. However, its characterization is demanding and relatively expensive. In this study, we evaluated whether arable plant communities can be used as a surrogate of bacterial and fungal communities of the rhizosphere of Elephant Garlic (*Allium ampeloprasum* L.), a traditional crop plant of central Italy. We sampled plant, bacterial, and fungal communities, i.e., the groups of such organisms co-existing in space and time, in 24 plots located in eight fields and four farms. At the plot level, no correlations in species richness emerged, while the composition of plant communities was correlated with that of both bacterial and fungal communities. As regards plants and bacteria, such correlation was mainly driven by similar responses to geographic and environmental factors, while fungal communities seemed to be correlated in species composition with both plants and bacteria due to biotic interactions. All the correlations in species composition were unaffected by the number of fertilizer and herbicide applications, i.e., agricultural intensity. Besides correlations, we detected a predictive relationship of plant community composition towards fungal community composition. Our results highlight the potential of arable plant communities to be used as a surrogate of crop rhizosphere microbial communities in agroecosystems.

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## 1. Introduction

Biodiversity plays key roles in the maintenance of ecosystem functionality, providing irreplaceable services (Díaz et al., 2019). This is especially true in man-made ecosystems, such as agroecosystems (Altieri et al., 2017). In the latter, soil microbiota performs crucial functions from both an environmental and a production perspective (Rillig et al., 2018; Costantini and Mocali, 2022). Soil microorganisms such as bacteria and fungi play key roles in plant growth promotion processes, in the maintenance of nutrient cycling, and in the preservation of soil physical structure and water regime. In particular, rhizosphere microbiota can provide useful services to crop production, improving the growth and health of cultivated plants, controlling root pathogens, and improving soil fertility without the use of chemicals (Singh et al., 2011). This prompts for an appropriate knowledge of soil microbial communities in agroecosystems. However, assessing the taxonomic composition of soil microbiota is still challenging and relatively expensive (Singh et al., 2011; Francioli et al., 2021; Lansac-Tôha et al., 2022). In fact, although recent improvement of high-throughput DNA sequencing and "omics" technologies helped to get a better insight into soil biodiversity, with particular emphasis on microbial communities, such technologies are currently susceptible to limitations and biases that are common to all molecular techniques applied to soil (Nannipieri et al., 2014). Moreover, a large part of the existing soil microorganisms is still unknown (Larsen et al., 2017). Thus, reliable indicators for assessing soil biodiversity are urgently needed (Veerman et al., 2020). To overcome these issues, a useful and easier strategy is to find potential surrogate organisms that are indicators of the variation of soil microbial communities.

Over the last 20 years, there was growing interest in exploring cross-taxon congruence, i.e., using surrogate taxa or biodiversity correlates to optimize resources and sampling efforts under the assumption that these organisms are potential indicators of the total biodiversity or of specific taxonomic groups (Chiarucci et al., 2005; Rodrigues and Brooks, 2007; Brunbjerg et al., 2020). Investigating cross-taxon congruence allows understanding how communities of different organisms covary in space and/or time in response to changing conditions and detecting surrogate organisms that are indicators of such variations (Duan et al., 2016). The drivers of covariation between different taxonomic communities include a similar biogeographical history, comparable responses to certain environmental gradients, or interactions between organisms (Rooney and Azeria, 2015; Barbato et al., 2019; Bazzato et al., 2023). Though their surrogacy power varies across spatial scales and taxa and it is more effective within the same realm (terrestrial, marine, etc.), cross-taxon surrogates work better than other surrogates, e.g., environmental features (Rodrigues and Brooks, 2007; Heino, 2010; Qian and Kissling, 2010).

Compared to many other organisms, vascular plants are relatively easier to survey (Santi et al., 2010a), besides being good surrogates of other taxonomic groups and of the total biodiversity (Gioria et al., 2010; Westgate et al., 2017; Zara et al., 2021). Both bulk soil and rhizosphere microbial diversity are strictly related to above-ground plant diversity (Eisenhauer, 2016; Jambon et al., 2018), suggesting that vascular plant communities may be good surrogates of soil microbial communities. Arable plants are all those plants that can live in arable land, among crop species (Holzner, 1978). Arable plant communities evolved under millennia of adaptations to agricultural practices, and they are deeply connected to the communities of other organisms (Bretagnolle and Gaba, 2015). Usually undesired by farmers, their importance is so far widely acknowledged. Maintaining spontaneous plant diversity in arable fields benefits both biodiversity and crop production. For instance, the presence of species-rich arable plant communities mitigates crop yield loss, compared to the presence of species-poor communities with few dominant and harmful species (Adeux et al., 2019). Arable plants are by far the best studied organisms in agroecosystems, but their suitability as biodiversity surrogates is still largely unexplored. Some evidence about their congruence with insect communities is available (Corcos et al., 2021), but no study has investigated cross-taxon congruence between vascular plants and soil microbiota in arable land.

Detecting cross-taxon congruences between vascular plants and microbiota in arable land would imply a considerable reduction of the economic and time efforts required for biodiversity studies in agroecosystems. Given the functional importance of microbial communities in agriculture and the major challenges implied by their characterization, in this study we aimed at assessing the effectiveness of arable plants, a very well-known and easy to sample group of organisms, as surrogates of crop rhizosphere microbiota in annual crops, which would allow obtaining indications on the type of microbial communities that develop in the crop rhizosphere without using molecular techniques. We carried out a plot-based survey on vascular plant and crop rhizosphere fungal and bacterial communities in eight fields of a traditional Elephant Garlic crop of central Italy (*Allium ampeloprasum* L.), located in four farms. We aimed at: i) assessing the correlations in species richness and composition between the three communities and testing the predictive power of plant community composition towards bacterial and fungal community composition, using both presence-absence and abundance data to account for the influence of the type of predictor data on the results (Santi et al., 2016); ii) highlighting which drivers are responsible for the possible co-variation between the communities, such as biotic interactions or external factors, testing the role of geographic position, climate, soil properties, and agricultural practices, which are known to affect both arable plant and microbial diversity (Gleeson et al., 2016; Fanfarillo et al., 2020a; Fanfarillo et al., 2023).

## 2. Methods

### 2.1. Study area

We carried out our study in eight fields of a traditional Elephant garlic crop (*Allium ampeloprasum* L.) of Tuscany (central Italy), located in four farms. The specific ecotype is locally known as "Aglione della Valdichiana" ("Valdichiana Elephant Garlic"), historically cultivated in the Valdichiana area, a wide alluvial plain characterized by intensive cultivation of cereals, fruit, and horticultural crops. The fields are located between 250 and 500 m a.s.l., in different landscape contexts. The climate is Mediterranean or Temperate sub-Mediterranean, with mean annual precipitations between 730 and 800 mm and mean annual temperatures around 13–14 °C (Pesaresi et al., 2017).

### 2.2. Biodiversity sampling

In late May 2020 and 2021, we carried out a plot-based probabilistic sampling of arable plant communities in the eight fields described above. Three square plots of 4 $m^2$ size were randomly selected within each field. Thus, we sampled a total of 24 plots, 6 in May 2020 and 18 in May 2021. In each plot, we recorded all the occurring plant species and attributed to each of them a cover value according to the Braun-Blanquet seven-degree ordinal scale (Braun-Blanquet, 1964). Plant abundance values were then converted into percentage covers, using the central value of each Braun-Blanquet class. In the same period and in the same plots, we collected one Elephant garlic plant with the soil surrounding the root system from the center of the plot to obtain rhizospheric soil for the characterization of bacterial and fungal communities.

### 2.3. Taxonomic identification

Vascular plants were identified according to Pignatti et al. (2017–2019). Fungi and bacteria were identified according to Federhen (2012). Taxonomic nomenclature follows the Portal to the Flora of Italy v. 2021.2 (2020) for vascular plants, the NCBI taxonomy database (Federhen, 2012) for bacteria and fungi.

The soil samples used to characterize the microbial communities were maintained at 4 °C until the subsequent day when roots were well shaken to detach the not tightly adhering soil, then they were cut from bulbs and horizontally shaken for 30 min at 200 rpm in a Phosphate Saline Buffer

(pH = 7.4). Roots were removed and rhizospheric soil was collected by centrifugation and used for nucleic acid extractions using the commercial kit FastDNA™ SPIN Kit for Soil (MP Biomedicals, Santa Ana, California, USA). The DNA extract was eluted in sterile water and its integrity was verified by agarose gel electrophoresis (1 % *w/v*). The extracted DNA was preserved at −20 °C for further molecular analyses. The structure of the microbial communities was characterized by means of a high-throughput sequencing approach. For the bacterial communities, the V3-V4 region of the 16S DNA ribosomal gene was amplified with primers 341F (5′- CCTACGGGNBGCASCAG −3′) and 806R (5′- GACTACNVGGGTATCTAATCC -3′) (Takahashi et al., 2014). For the fungal communities, the ITS1 region was amplified with primers ITS1 forward (5'-TCCGTAGGTGAACCTGCGG −3′) and ITS4 reverse (5'-TCCTCCGCTTATTGATATGC -3′) (White et al., 1990). Libraries were sequenced on MiSeq instrument (Illumina, San Diego, CA) (Caporaso et al., 2012) using 300-bp paired-end mode (IGA Technology Services s.r.l., Italy). The Quantitative Insights Into Microbial Ecology (QIIME2) pipeline v2019.1.0 (https://qiime2.org/) method was used to process the obtained sequences (Bolyen et al., 2019). Paired-end sequences were denoised, dereplicated, and filtered for chimeras using the DADA2 plugin (Callahan et al., 2016), as implemented in QIIME 2. Sequences were trimmed in order to include only the bases with a median quality score higher than 30. Taxonomy was assigned to Amplicon Sequence Variants (ASVs) using the q2-feature-classifier at 97 % similarity (Bokulich et al., 2018). Representative sequences were classified against the SILVA database v138.1 for Bacterial 16S rRNA gene and against the UNITE database for Fungal ITS, using the function *assign Taxonomy* by applying a 99 % identity criterion to remove highly similar sequences. Plant, bacterial, and fungal community data are available in Tables S1, S2, and S3, respectively.

### 2.4. Geographic and environmental data

Since geographic location, climate, and soil properties are important determinants of both arable plant and microbial communities (Gleeson et al., 2016; Fanfarillo et al., 2023), we compiled a database containing such information for our sampling sites. Geographic coordinates (WGS 84) were recorded for each plot using a GPS device. For each field, we retrieved information about yearly positive temperature (expressed in yearly accumulated degree days - DD - above 0 °C as a proxy of the growth season) and year total precipitation from Pesaresi et al. (2017). Using the soil samples collected to characterize microbial communities, we carried out soil physical and chemical analyses. For the latter procedure, we pooled the three soil samples from each field and analysed the pooled sample, as this procedure allows reducing analytical efforts without affecting the results of organism-soil interaction analyses (Allen et al., 2021). We measured pH, Electric Conductivity (μS/cm at 20 °C), Organic C (cmol/Kg), Ca (mg/kg), Mg (mg/kg), Na (mg/kg), K (mg/kg), Al (mg/kg), CEC (cmol/kg), % sand, % silt, and % clay. The soil samples were dried at 40 °C using a ventilated oven. Then, the soils were sieved at 2 mm, homogenized by quartering and mechanically pulverized before the analysis. Soil pH and conductivity were measured in 1:2.5 (*w/v*) soil:water suspension by methods III.1 and IV.1 of Italian Legislative Decree 248/99. To determine the soil texture, expressed as the percent content of sandy, silty, and clayey granulometric fractions, we used the hydrometer method (Gee and Bauder, 1986). The procedure of Hendershot and Duquette (1986) was utilized to calculate the effective cation exchange capacity (CEC) by determining Ca, Mg, K, Na, and Al concentrations. Finally, according to the Walkley–Black procedure (1934) the organic carbon content was measured. Principal Component Analysis (PCA) was performed on geographic and environmental variables (geographic coordinates, soil variables, and climate data), using the function *rda* in the *vegan* package of R v. 4.3.0 (Oksanen et al., 2019; R Core Team, 2023). The scores of the samples along the first axis of the PCA (PC1) were used for further analyses as a measure of the main geographical-environmental gradient. Geographic coordinates and environmental variables are available in Table S4.

### 2.5. Agricultural management data

The intensity of agricultural management has an essential role in determining the features of plant and microbial communities in arable land (Jangid et al., 2008; Fanfarillo et al., 2023). All the farmers compiled a diary annotating each single agricultural practice they carried out before and during crop growing, i.e., type of tillage, herbicide spraying, and fertilizing, including details on the used products and the day on which the operation was performed. Two of the studied farms are under conventional management and the other two are under organic management. However, past investigations revealed that this distinction is few informative of the effects of agriculture on biotic communities in our specific case, due to the high variability of farming practices in both conventional and organic farming (Fanfarillo et al., 2022). Thus, taking account of nitrogen input (number of fertilizations) and pesticide use (number of applications), we quantified the intensity of agricultural management by calculating an agricultural intensity index at the farm level (Herzog et al., 2006), modified according to the available information, i.e., we did not take account of livestock density and quantified nitrogen input through the number of fertilizations instead than in Kg/ha. Agricultural management variables are available in Table S4.

### 2.6. Statistical analyses

To assess the congruence in species richness between the plant, bacterial, and fungal communities, we calculated the Spearman correlation coefficient ($\rho$) using the *cor.test* function of the *stats* package (R Core Team, 2023). Partial correlations by the function *pcor.test* in the *ppcor* package were used to partial out the effect of geographic and environmental factors (PC1) and of the agricultural intensity index (Kim, 2015). Species richness was measured as the number of species per plot for plant communities and as the number of ASVs per plot for bacterial and fungal communities.

Congruence in community composition was evaluated using three independent tests: (i) Mantel test, (ii) Partial Mantel test, and (iii) Co-Correspondence analysis (hereafter Co-CA).

Mantel test was chosen to assess correlations in community composition since our data could be compared using distance matrices (Legendre and Fortin, 2010). The Mantel tests could indicate the presence of cross-taxon congruence in community composition without considering if relationships were direct or indirect, i.e., mediated by other factors (Rzanny and Voigt, 2012). Thus, we carried out a series of partial Mantel tests to determine the effect of environmental variables (PC1) and of the agricultural intensity index on the congruence in community composition. Mantel and partial Mantel tests were first performed using presence-absence data, for each pair of the investigated groups. Then, we carried out the same tests on abundance data with Hellinger transformation of species abundances (standardization and square root transformation), using Bray-Curtis dissimilarity, Pearson correlation, and 4999 permutations. We used the *mantel* and *mantel.partial* functions of the *vegan* package (Oksanen et al., 2019).

We applied an asymmetric, predictive form of the Co-CA, setting 4999 permutations in the *coca* function in the *cocorresp* package (Simpson, 2009) to directly correlate two different communities, identify common patterns between them and quantify the ability of each community in predicting the composition of the other communities. This method finds the weighted average species scores that maximize the weighted covariance between the site scores of the two communities of interest (ter Braak and Schaffers, 2004). We detected the minimum sufficient number of Co-CA axes to be used by means of the cross-validatory method, through the function *crossval* in *cocorresp*. We assessed the significance of Co-CA axes by means of permutation tests using the function *permutest.coca* in *cocorresp* (4999 permutations). Moreover, we fitted environmental variables (PC1) and the agricultural intensity index on the Co-CA ordination axes to highlight the underlying ecological gradients, assessing the significance of the correlation between the variables and community composition by means of the squared Pearson correlation coefficient ($r^2$) (function *envfit* in the package *vegan*). Despite the environmental variables being highly negatively correlated with the agricultural intensity index (Spearman's $\rho$ =

**Table 1**
Spearman correlations ($\rho$) and partial correlations between plant, bacteria, and fungi species richness. No comparison was statistically significant. PC1 = geographic coordinates, climate, and soil.

| | Simple correlation | | | Partial correlation (PC1) | | | Partial correlation (Agricultural intensity index) | |
|---|---|---|---|---|---|---|---|---|
| | Plants | Bacteria | | Plants | Bacteria | | Plants | Bacteria |
| Plants | – | 0.209 | Plants | – | 0.185 | Plants | – | 0.089 |
| Bacteria | 0.209 | – | Bacteria | 0.185 | – | Bacteria | 0.089 | – |
| Fungi | −0.095 | 0.174 | Fungi | −0.218 | 0.156 | Fungi | 0.014 | 0.218 |

$-0.96, p < 0.001$), we fitted both the variables in the Co-CA analyses since they have a different explanatory potential against community correlations.

We carried out an abundance-based indicator species analysis to detect the indicator species of plants, bacteria, and fungi of the four investigated farms. We used the function *multipatt* in the package *indicspecies*, which performs an improved version of indicator species analysis by considering all the possible combinations of groups of sites and then selecting the combination for which the species is the best indicator (De Cáceres and Legendre, 2009).

All the statistical analyses were carried out in the R environment for statistical computing (R Core Team, 2023).

## 3. Results

### 3.1. General results

The γ-diversity consisted of 84 species of vascular plants, 1064 Amplicon Sequence Variants (ASVs) of bacteria, and 691 ASVs of fungi. The taxonomic richness per sampling unit was the highest in bacterial communities and the lowest in plant communities (Tables S4 and S5). The first axis of the PCA performed on geographic and environmental variables mainly showed a gradient of decreasing temperature and increasing soil Ca content (PC1 in Table S4).

### 3.2. Congruence in species richness

We did not find any statistically significant correlation in species richness between the three taxonomic communities, even after removing the effect of the geographic coordinates, of the environment, and of agricultural intensity (Table 1).

### 3.3. Congruence in community composition

The Mantel tests revealed correlations in composition between all the investigated communities (Table 2). However, partial Mantel tests highlighted that when the effect of the geographic position and environment was removed, the correlation between plant and bacterial communities disappeared and the others slightly decreased in magnitude. When the effect of agricultural intensity was removed, all the correlations remained significant, albeit with a little decrease in magnitude. The same results were obtained using presence-absence and abundance data.

For all the Co-CA analyses, we interpreted the first two axes. The results highlighted a significant predictive power of plant community composition *vs* fungal community composition both using presence-absence and abundance data. Conversely, the predictive value of plant community composition *vs* bacterial community composition was partially significant only using presence-absence data (Table 3, Fig. 1).

Both geographic-environmental variables (PC1) and the agricultural intensity index were always highly correlated with the composition of plant, bacterial, and fungal communities (Table 4).

### 3.4. Groups of indicator taxa

All the investigated farms had statistically significant associations with certain groups of taxa for all the three communities. The plant species with the highest indicator values in each farm (a, b, c, and d) were a) *Cota tinctoria, Sherardia arvensis,* and *Cirsium vulgare*; b) *Lamium purpureum, Rumex pulcher*, and *Stellaria media*; c) *Mercurialis annua* and *Datura stramonium*; d) *Sonchus asper* and *Erigeron sumatrensis* (Table S6). The bacterial ASVs with the highest indicator values were a) *Tabrizicola, Euzebyaceae,* and *Polyangia*; b) Defluviicoccales, Nitrosomonadaceae, and *Schlesneria*; c) *Novosphingobium* and *Neorhizobium*; d) AKYG1722, *Terribacillus*, and *Serratia* (Table S7). As for the fungal ASVs, those with the highest indicator values were a) Aspergillaceae, Thelephoraceae, and Agaricomycetes; b) *Septoriella,* Phaeosphaeriaceae, and *Bipolaris*; c) *Ganoderma, Scutellospora,* and *Ramicandelaber*; d) Microbotryomycetes, *Mortierella*, and Sordariomycetes (Table S8).

**Table 2**
Correlation in composition between the surveyed communities according to Mantel tests and to partial Mantel tests, using presence-absence and abundance data; PC1 = geographic coordinates, climate, and soil.

| Presence-absence | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Mantel test | | | Partial Mantel test (PC1) | | | Partial Mantel test (Agricultural intensity index) | |
| | Plants | Fungi | | Plants | Fungi | | Plants | Fungi |
| Plants | – | – | Plants | – | – | Plants | – | – |
| Fungi | 0.23** | – | Fungi | 0.16* | – | Fungi | 0.16** | – |
| Bacteria | 0.24** | 0.62*** | Bacteria | 0.08 | 0.58*** | Bacteria | 0.22*** | 0.61*** |
| **Abundance** | | | | | | | | |
| | Mantel test | | | Partial Mantel test (PC1) | | | Partial Mantel test (Agricultural intensity index) | |
| | Plants | Fungi | | Plants | Fungi | | Plants | Fungi |
| Plants | – | – | Plants | – | – | Plants | – | – |
| Fungi | 0.27*** | – | Fungi | 0.15* | – | Fungi | 0.17** | – |
| Bacteria | 0.21** | 0.69*** | Bacteria | 0.05 | 0.61*** | Bacteria | 0.13* | 0.68*** |

Significance codes: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$.

**Table 3**
Summary of the co-correspondence analyses; p/a = presence-absence data; ab = abundance data.

| | Inertia | Cross-validatory % fit |
|---|---|---|
| Vascular plants *vs* bacteria (p/a) | | |
| Axis 1 | 0.851 | 0.061 |
| Axis 2 | 0.789 | 0.055 |
| Vascular plants *vs* fungi (p/a) | | |
| Axis 1 | 2.608 | 0.153* |
| Axis 2 | 2.454 | 0.124 |
| Vascular plants *vs* bacteria (ab) | | |
| Axis 1 | 0.563 | 0.059 |
| Axis 2 | 0.504 | 0.072 |
| Vascular plants *vs* fungi (ab) | | |
| Axis 1 | 1.871 | 0.172** |
| Axis 2 | 1.699 | 0.140 |

Significance codes: ** = $p < 0.01$; * = $p < 0.05$.

## 4. Discussion

Our study is the first one to assess the effectiveness of arable plant communities as surrogates of crop rhizosphere microbiota. We showed that arable plant communities are good surrogates of crop rhizosphere bacterial and fungal communities in terms of composition, but not of species richness. Such results are relevant from the perspective of the conservation and improvement of biodiversity and its services in arable crops, especially considering the functional importance of crop rhizosphere microbiota in agriculture (Jambon et al., 2018). In fact, our evidence lays the bases for more detailed investigations to identify specific plant communities that are indicators of specific microbial communities on a broad scale, in the light of the high amount of available data about arable plants (Fanfarillo et al., 2020b; Küzmič et al., 2020). This would allow indicating the presence of certain microbial communities, and consequently of their conservation status, their functions, and their environmental and agronomic services, through the sole analysis of arable plant communities, with a considerable reduction in economic and time efforts in both agronomic and environmental practice. From this perspective, we underline the importance of assessing the several aspects of cross-taxon congruence, since the patterns of community co-variation may vary if either correlation, predictive power, or species co-occurrences are investigated and they can show contrasting trends in terms of species richness and species composition.

Our evidence that plant species richness is not a good surrogate of microbial taxonomic richness is consistent with findings from other types of ecosystems (Schuldt et al., 2015). In general, cross-taxon congruence in species richness is highly variable, and it is rarely observed compared to congruences in community composition (Bilton et al., 2006; Keith et al., 2012). Moreover, cross-taxon congruence in species richness varies according to the spatial scale of observation, and it could be better detectable at a regional scale than at a local scale (Heino, 2010; Qian and Kissling, 2010). Concerning agroecosystems, no previous studies assessed the congruence in species richness between arable vascular plants and crop rhizosphere microbial communities.

All the correlations in community composition were significant, despite their magnitude was not particularly high. We observed different patterns and drivers of congruence between the three communities. The correlation in composition between plants and bacteria was driven by similar responses to location and environmental factors, as commonly observed in a wide range of biotic communities (Axmacher et al., 2009; Duan et al., 2016; Barbato et al., 2019). Fungi showed persistent correlations with both plants and bacteria almost regardless of the environment and agricultural õintensity, suggesting the existence of biotic interactions driving such congruences in community composition. In fact, many types of interactions occurring between plants and fungi were described so far (Zeilinger et al., 2016; Bennett and Groten, 2022). Moreover, fungi and bacteria co-occur in many different microhabitats and are connected by a wide range of interactions, thus forming dynamic networks and co-evolving communities (Deveau et al., 2018). Regardless of the drivers of correlation, our results show that, in terms of taxonomic composition, arable plants were suitable indicators of both bacterial and fungal communities of the crop rhizosphere.

The predictive power of arable plants towards soil microbiota was never assessed so far. However, vascular plant communities are known to be predictive of other taxonomic groups such as amphibians, ants, carabids, lichens, and water beetles (Gioria et al., 2010; Santi et al., 2010b; Santi et al., 2016; Zara et al., 2021). Despite the correlations in composition between plant and crop rhizosphere microbial communities, we observed a significant predictive relationship only of plants towards fungi. Such predictive power was stronger using abundance data, suggesting that such relationship concerns not only the occurrence of taxa, but also their variation in abundance. This is consistent with previous evidence on the congruence between vascular plants and macrofungi in forests, which was higher when taking account of species abundance (Landi et al., 2015). Our results highlight that arable plant communities are better surrogates of the fungal than of the bacterial communities of Elephant Garlic rhizosphere. This may be due to the co-variation in composition between plants and bacteria being driven by geographic location and environmental factors, whereas plants and fungi had stronger relationships probably due to biotic interactions. Such finding is consistent with the global evidence that the composition of vascular plant communities is an important driver of fungal community composition (Tedersoo et al., 2014).

Consistently with the detected relationships in community composition, each of the four investigated farms had distinct sets of indicator taxa of plants, bacteria, and fungi. This indirectly confirms that the presence of a certain arable plant species can be associated to specific microbic taxa in the crop rhizosphere. For instance, the plant *Cota tinctoria*, the bacterium *Tabrizicola* sp., and a fungus species from the family Aspergillaceae were the best indicators of farm "a", meaning that the presence of the plant can suggest the presence of the bacterium and of the fungus in the rhizosphere of Elephant Garlic in the light of the detected congruences in community composition. The same evidence emerged for the other farms, e.g., *Lamium purpureum* co-occurred with a bacterium of *Defluviicoccales* and *Septoriella* sp. in farm "b", *Mercurialis annua* with *Novosphingobium* sp. and *Ganoderma* sp. in farm "c", and *Sonchus asper* with the bacterium AKYG1722 and a fungus of *Microbotryomycetes* in farm "d". Such results are especially relevant in the light that, within the microbiota, we found plant growth promoting fungi (*Mortiriella*), ectomycorrhizal fungi (*Pisolithus*, *Rhizopogon*, *Tomentella*), bacteria involved in the removal of pollutants (Intrasporangiaceae), and bacteria involved in the control of the nitrogen cycle (Nitrosomonadaceae) (Parladé et al., 2004; Peralta et al., 2013; Stackebrandt et al., 2014; Ozimek and Hanaka, 2021; Põlme et al., 2021), whose presence could be indicated by arable vascular plants. Especially as regards fungi, some co-occurrences due to interactions could also be detected. For instance, the fungi *Septoriella, Bipolaris*, *Periconia, Pseudorobillarda* and *Arthrinium* are saprophytes or pathogens of Poaceae plant species and co-occurred with *Hordeum murinum* and *Poa annua* (Marin-Felix et al., 2019). Arable plant communities also included some useful species themselves, in terms of pathogen control (*Capsella bursa-pastoris, Chenopodium album*), improvement of soil fertility (*Cirsium arvense, Solanum nigrum*), and support to animals (*Cota tinctoria, Polygonum aviculare*) (Holland et al., 2006; Blaix et al., 2018).

This study revealed that arable plants are promising indicators of the composition of crop rhizosphere microbiota, and that they could thus be used as surrogates of certain microbial communities having specific values in terms of biodiversity, ecological functions, and ecosystem services. Such findings are important in the light of improving biodiversity knowledge in agroecosystems while optimizing the use of resources and efforts for sampling activities by focusing them on surrogate organisms, as well as for the development of new reliable indicators for assessing soil biodiversity. From this perspective, the restrained magnitude of the detected cross-taxon congruences suggests the need for further studies of this kind. This would allow highlighting if arable plant communities are better surrogates

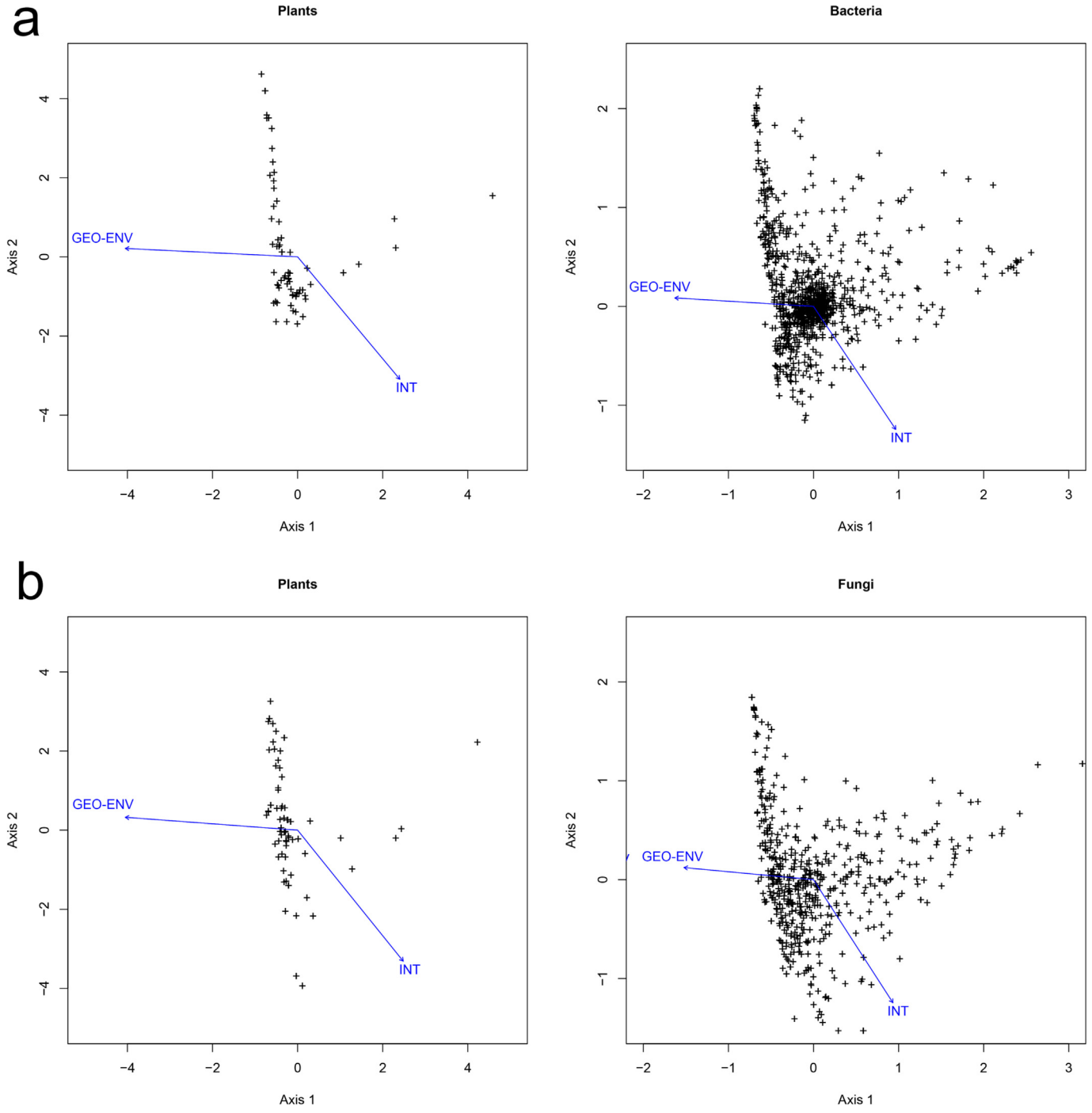


**Fig. 1.** Predictive Co-CA biplots of plant community composition *vs* (a) fungal and (b) bacterial community composition, based on abundance data. Black crosses = plant species, bacterial ASVs, and fungal ASVs. GEO-ENV = PC1 (geographic coordinates, climatic, and soil variables); INT = Agricultural intensity index.

of crop rhizosphere microbiota in other crop types or geographic and environmental contexts. The detected high variability of the studied communities within fields of the same crop underlines the importance of studying biodiversity for a better understanding of agroecosystems, and shows that the crop type itself is not a good indicator of its rhizosphere microbial communities. We provided the basis for further investigations in different crop types and agroecosystems, to better understand the nature of cross-taxon relationships between arable plants and crop rhizosphere microbial communities and their usefulness for the conservation and management of biodiversity and ecosystem services in agriculture. Besides, our findings are important to sensibilize both stakeholders and environmental scientists on the importance of arable plants in agroecosystems, to go beyond their common perception as weeds.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.165141.

## CRediT authorship contribution statement

**Emanuele Fanfarillo:** Conceptualization, Methodology, Investigation, Writing – original draft. **Claudia Angiolini:** Writing – review & editing. **Enrico Tordoni:** Methodology, Writing – original draft, Writing – review & editing. **Giovanni Bacaro:** Methodology, Writing – review & editing.

**Table 4**
Correlation between PC1 (geographic coordinates, climate, and soil), the agricultural intensity index, and composition of plant, bacterial, and fungal communities in the Co—Ca analyses. $r^2$ = squared Pearson correlation. p/a = presence-absence data; ab = abundance data.

| Vascular plants *vs* bacteria (p/a) | $r^2$ |
|---|---|
| PC1 | 0.687** |
| Agricultural intensity index | 0.553*** |
| Vascular plants *vs* fungi (p/a) | |
| PC1 | 0.692** |
| Agricultural intensity index | 0.266* |
| Vascular plants *vs* bacteria (ab) | |
| PC1 | 0.744*** |
| Agricultural intensity index | 0.695*** |
| Vascular plants *vs* fungi (ab) | |
| PC1 | 0.792*** |
| Agricultural intensity index | 0.823*** |

Significance codes: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$.

**Erika Bazzato:** Methodology, Writing – original draft, Writing – review & editing. **Maurizio Castaldini:** Investigation, Writing – original draft, Writing – review & editing. **Maria A. Cucu:** Investigation, Writing – review & editing. **Martina Grattacaso:** Writing – original draft, Writing – review & editing. **Stefano Loppi:** Writing – review & editing, Funding acquisition. **Michela Marignani:** Writing – review & editing. **Stefano Mocali:** Writing – review & editing. **Lucia Muggia:** Writing – original draft. **Elena Salerni:** Writing – original draft, Writing – review & editing. **Simona Maccherini:** Conceptualization, Methodology, Investigation, Supervision, Writing – review & editing, Funding acquisition.

## Data availability

All relevant data supporting the key findings of this study are available within the article and its Supplementary Information files.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Emanuele Fanfarillo reports financial support was provided by National Biodiversity Future Center.

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