



Anthropogenic vs. natural habitats: Higher microbial biodiversity pays the trade-off of lower connectivity

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ABSTRACT

Climate change and anthropogenic disturbances are known to influence soil biodiversity. The objectives of this study were to compare the community composition, species coexistence patterns, and ecological assembly processes of soil microbial communities in a paired setting featuring a natural and an anthropogenic ecosystem facing each other at identical climatic, pedological, and vegetational conditions. A transect gradient from forest to seashore allowed for sampling across different habitats within both sites. The field survey was carried out at two adjacent strips of land within the Po River delta lagoon system (Veneto, Italy) one of which is protected within a natural preserve and the other has been converted for decades into a tourist resort. The anthropogenic pressure interestingly led to an increase in the α -diversity of soil microbes but was accompanied by a reduction in β -diversity. The community assembly mechanisms of microbial communities differentiate in natural and anthropic ecosystems: for bacteria, in natural ecosystems deterministic variables and homogeneous selection play a main role (51.92%), while stochastic dispersal limitation (52.15%) is critical in anthropized ecosystems; for fungi, stochastic dispersal limitation increases from 38.1% to 66.09% passing from natural to anthropized ecosystems. We are on calcareous sandy soils and in more natural ecosystems a variation of topsoil pH favors the deterministic selection of bacterial communities, while a divergence of K availability favors stochastic selection. In more anthropized ecosystems, the deterministic variable selection is influenced by the values of SOC. Microbial networks in the natural system exhibited higher numbers of nodes and network edges, as well as higher averages of path length, weighted degree, clustering coefficient, and density than its equivalent sites in the more anthropically impacted environment. The latter on the other hand presented a stronger modularity. Although the influence of stochastic processes increases in anthropized habitats, niche-based selection also proves to impose constraints on communities. Overall, the functionality of the relationships between groups of microorganisms co-existing in communities appeared more relevant to the concept of functional biodiversity in comparison to the plain number of their different taxa. Fewer but functionally more organized lineages displayed traits underscoring a better use of the resources than higher absolute numbers of taxa when those are not equally interconnected in their habitat exploitation. However, considering that network complexity can have important implications for microbial stability and ecosystem multifunctionality, the extinction of complex ecological interactions in anthropogenic habitats may impair important ecosystem services that soils provide us.

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1. Introduction

The accelerating rate of habitat conversion is a prominent feature of the Anthropocene, which is significantly modifying the availability of terrestrial ecosystem resources and disrupting habitat connectivity (Ellis and Ramankutty, 2008; Birkhofer et al., 2017; Vega et al., 2020). These profound environmental changes cause biodiversity to be strongly affected (Geisen et al., 2019; Scholier et al., 2023). Indeed, not all species can tolerate or adapt to life in such a situation, with only 24% of species surviving in severely affected habitats (Dornelas et al., 2014; Newbold et al., 2015). As one of the largest pools of biodiversity on Earth, soil biodiversity is of significant importance in protecting and conserving the multiple ecosystem functions (Bardgett and Van Der Putten, 2014; Wagg et al., 2014; Delgado-Baquerizo et al., 2020). The soil biodiversity change driven by human activities could significantly diminish the benefits that people derive from ecosystem services (Cardinale et al., 2011; Isbell et al., 2017), which highlights the need for biodiversity surveys in understudied regions currently threatened by environmental change (i.e., to inform baseline conditions).

Soil microbes, as the critical and indispensable living beings in the soil environment, are extremely diverse and exhibit complex communities and interactions (Torsvik and Øvreås, 2002; Faust and Raes, 2012). The ability of soils to provide various ecological services, including nutrient cycling, decomposition, carbon storage, ruling plant productivity and diversity, and regulation of human immune responses, is highly dependent on soil microbial diversity and community composition (Boetius, 2019; Crowther et al., 2019; Jansson and Hofmockel, 2020; Guerra et al., 2021; Banerjee and van der Heijden, 2023; Sun et al., 2023). The microbial diversity and assemblages could have the potential to be efficient biological indicators for the environmental health of the terrestrial ecosystem (Astudillo-García et al., 2019). There is a strong need to investigate how soil microbial communities are influenced by anthropogenic pressure, to better help determining the consequence of multiple stress factors on ecosystem sustainability (Yang et al., 2022a).

Anthropogenic pressure is often hypothesized to alter community assembly processes that determine the presence and abundance of species. In order to investigate the underlying processes governing microbial community assembly, Stegen et al. (2012) developed 'null models' that couple phylogenetic community composition with randomization procedures, thereby characterizing how the relative influences of stochastic and deterministic processes. Indeed, studies have been conducted in a wide range of terrestrial habitats, including those of hypolithic communities (Stomeo et al., 2013), successional soils (Tripathi et al., 2018), a salt marsh (Dini-Andreote et al., 2015), incipient basaltic soil (Sengupta et al., 2019), subsurface sediment (Stegen et al., 2013), and a grassland (Li et al., 2015). The research suggested that microbial community assembly is simultaneously affected by deterministic processes, which involve selection due to environmental filtering and species interactions, and stochastic processes, which encompass unpredictable disturbances, probabilistic dispersal, and random birth-death events (Chase, 2010; Ofițeru et al., 2010; Vellend, 2010; Langenheder and Székely, 2011). Moreover, the relative importance of community assembly processes may depend on a variety of factors, such as initial conditions, soil chemical properties, disturbance, degree of change in environmental variables, etc. (Zhang et al., 2011; Ferrenberg et al., 2013; Zhang et al., 2016; Tripathi et al., 2018; Yang et al., 2022b). For example, soil pH mediates the balance between the stochastic and deterministic assembly of bacteria, and extreme soil pH will lead to the deterministic assembly of soil bacterial communities (Tripathi et al., 2018). At the regional scale, the variation in soil organic matter could regulate the dominance of deterministic or stochastic processes in shaping soil bacterial communities (Feng et al., 2018). However, our ability to predict changes in community diversity patterns following human activities is still extremely limited.

The limits between resistance to an endurable stress and failed

resilience vs. the opposite, when seen in evolutionary time scales is recognized as the result of fruitful interconnectivity among community members (Fierer et al., 2012; Messier et al., 2013; Yi and Jackson, 2021; Angeler et al., 2023). Assessing and detecting the potential patterns of soil microbial communities under habitat fragmentation and/or habitat conversion conditions requires the characterization of the differences between community composition and diversity in natural and anthropogenic habitats and a proper understanding of the mechanisms of microbial community assembly in both types. Hence, our research investigates the soil microbial across an environmental and landscape gradient, having individuated a suitable site between land and sea where two iso-pedological, iso-climatic adjacent coastal strips presented in one case an extended peninsula featuring a successional vegetation series, protected by the law within a restricted-access natural reserve, facing an originally identical island that had been instead turned into a recreational resort, paved with roads, covered with bungalows and heavily exploited by tourism for over fifty years. Compared to natural habitats, anthropogenic habitats are strongly affected by habitat fragmentation and/or habitat conversion, such as sealing, mixing, and incorporation of novel anthropogenic materials, and microbial community results significantly affected by human management (Mo et al., 2022). This perfect setting with a pristine control and an artificialized terrain allowed to test the outcomes of a measurable ecological disturbance by analyzing soil bacteria and fungi and asking whether and how new equilibria would be reached by reorganization upon impact and which alpha and beta diversities would be presented across and within these paired-sites communities, for which we had a uniquely arranged setting.

Specifically, we compared α and β -diversity and inferred assembly mechanisms within natural and anthropogenic landscapes within the Po River delta lagoon system, located in the southern part of Veneto, Italy. Due to different management practices, the two peninsular strips of land (i.e. Porto Caleri and the Island of Albrella) make excellent model sites, differing only by the anthropic pressure for assessing the effect of human activities and land use change on microbial diversity and assembly processes at local and regional scales. We postulated that physicochemical properties and ecosystem processes related to anthropogenic ecosystems would differ from those of natural ecosystems, likely resulting in distinct microbial assembly patterns. The specific research questions, expanding beyond extant knowledge (Farooq et al., 2023; He et al., 2023; Heděnc et al., 2023) were: 1) To what extent are soil environmental features and microbial community structures affected by anthropogenic management or disturbances? 2) Which specific mechanisms allow certain microbes to persist under anthropogenic pressures or environmental modifications while others decline or disappear? 3) Can communities of natural environments be less biodiverse and/or endowed by higher measurable phylogenetic signal, than those occurring in man-impacted ones?

The findings led to questioning and resizing the phylogenetic signal relevance but at the same time opened novel interesting evidence and perspectives to address how the soil microbial network in natural systems can provide a basis for understanding soil microbial communities in response to anthropogenic pressures and what specific management strategies can be implemented to promote sustainability by assessing species presence-absence and abundance, ecological assembly processes, and species coexistence patterns.

2. Materials and methods

2.1. Study area description and sampling

The study was conducted at two peninsular strips of land within the Po River delta lagoon system, located in the southern part of Veneto, Italy (Fig. 1). A century ago these two territories were covered by the same vegetation. The Porto Caleri peninsula (45°05'53"N 12°19'27"E), also known as the 'Giardino Botanico Litoraneo del Veneto', is a nature



Fig. 1. Left Southern end of the Porto Caleri natural reserve; Right Northern end of the Island of Albarella. The sampling points of Caleri range from C0 to C13, while those of Albarella range from A1 to A14. The colors of the points correspond to those in the vegetation legend.

preserve and wild botanical garden, and represents such natural control ecosystem. It is still well preserved only in the first strips that today cover Caleri towards the sea. The composition of the Caleri forest has instead undergone silviculture and planting operations. The adjacent Island Albarella (45°04'32"N 12°20'38"E) with many lodging accommodations, leisure facilities, and economic activities, so the largest part of the area is occupied by houses, apart from the Mediterranean scrub area which is difficult to access, the rest has undergone important changes in structure and floristic composition. As anthropogenic ecosystems, it provides an attractive model to investigate the influence of human activities on soil biodiversity when compared to sites that feature isogenic soil, vegetation, and climate conditions but are spared from human settlement exploitation. We had previously studied⁴⁷ two series of 10 sample areas - one series in a rather natural environment, Porto Caleri, and one in the rather anthropized environment, Albarella - along a gradient that goes from the sea to the inland. For the phytosociological study and the survey of the distribution of the vegetation units, the information contained in specific works applied to the local flora was used, combining observation with Google Earth and classification of the species and units in the field in Albarella and Caleri (Piva and Scortegagna, 1993; Ballasso, 1998; Sanità, 1998; Buffa et al., 2007; Caniglia, 2007; Buffa et al., 2012).

After the first campaign, we refined the study of the vegetation, encountering environments that could complete the first series and which were included in the new sampling plan, in particular a holm-oak wood, a mixed forest, a new shrubland, a reeds dune, a lawn with trees cores, fresh grassland and a new wetland. Previously, the points had been marked in the different natural phytocoenoses; then we looked for the corresponding phytocoenoses (point by point) in equivalent anthropized environments, finding some still close in composition to the natural ones, while others were quite transformed into new phytocoenoses. In the present campaign, we took a series of sample plots lying in a line approximately from sea to inland following the natural vegetation succession in Porto Caleri, equidistantly at about 50 m every from each other. The vegetation series in Albarella was cut into pieces by roads and bungalows, and we made sample plots tailored as much as possible to correspond to the Porto Caleri habits in plant-covered areas. There are some particular vegetation types in both natural and anthropized environments, totally 14 sampling points in each site (Fig. 1). Sampling points in Porto Caleri: Herbaceous with *Ammophila arenaria* = C1, C2, and C3, Shrubby with *Juniperus communis*, *Phillyrea angustifolia*,

Hippophae rhamnoides and *Ligustrum vulgare* = C4, C6, and C11, Arborescous with *Pinus pinaster*, *Quercus ilex* and *Ulmus minor* = C7, C8, and C13. Other = C0 (beach without plant), C5 (low meadow with *Tortula ruralis* moss), C9 (moist lawn based on *Limonium narbonense*), C10 (wetland perennial *Juncus acutus*), and C12 (pine forest on the edge of a brackish pond), corresponding to vegetation particular to Porto Caleri only. Sampling points in Albarella: Herbaceous with *Ammophila arenaria*, *Ambrosia psilostachya* and *Asparagus acutifolius* = A1, A2, and A3, Shrubby with *Hippophae rhamnoides*, *Juniperus communis* and *Ligustrum vulgare* = A4, A5, and A6, Arboreous with *Pinus pinea* and *Quercus ilex* = A7, C8, and A12. Other = A9 (new plantation of small *Pinus pinea* and *Quercus ilex* and *Acer campestre*, *Populus alba* (1 m)), A10 (flowerbed with *Adonis* spp., *Bellis* spp., *Dianthus* spp.), A11 (*Populus x canescens* on lawn of *Arenaria serpyllifolia*, *Geranium molle*, etc.), A13 (managed lawn with *Dactylis glomerata*, *Avena fatua*, *Carex flacca*, *Holcus lanatus*, *Taraxacum officinalis*, etc.), and A14 (golf green with *Poa* spp., *Carex flacca*, *Plantago lanceolata*, *Geranium molle* etc.), corresponding to vegetation particular to Albarella only. Each sample was composed of three sub-samples, equidistantly every 5 m from each other. The litter layer was removed before sampling collection. The soils are all calcic Arenosol (WRB, 2022), while the humus systems varying from Aqueous (in the tidal zone) to Histic (inland with outcropping aquifer) to Terrestrial (dunes) (Zanella et al., 2022). In such humus systems, the most common humus forms are respectively Tidalic Redoxitidal in tidal zone, Saprianmoor in peat environment and Eumull, Hemimoder and Eumoder for terrestrials on the dune for herbaceous, shrubby and forest ecosystems. The organic carbon content in the first 30 cm of soil varies from the sea towards the innermost forest from 6 t/ha to more than 250 t/ha, also considering the litter when present. For the study of soil microorganisms, soil samples from the 0–10 cm profile were taken with a brass tube (1.3 cm diameter × 10 cm depth). A total of 84 soil samples were collected (14 sample points × 3 replicates per site × 2 ecosystems). For the study of soil properties, soil samples from the 0–10 cm profile were taken with tubes (10 cm diameter × 10 cm depth), which correspond to the plots investigated for microorganisms.

2.2. DNA extraction, sequencing, and bioinformatics

These have been carried out as previously described (Mo et al., 2022). The BioProject accession number for these SRA data is: PRJEB68196; <https://www.ncbi.nlm.nih.gov/sra/PRJEB68196>.

2.3. Soil properties analysis

Edaphic variables, including pH, total carbon (TC), total nitrogen (TN), total phosphorous (TP), total potassium (TK), soil organic carbon (SOC), available phosphorous (AP), and available potassium (AK), were measured using standard analytical methods. For a complete list of environmental parameters, see Table S1 in the supplemental material.

2.4. Statistical analysis

Taxonomic alpha diversity was calculated as estimated community diversity by the Shannon index and Chao 1 index. The diversity indices were analyzed by the Wilcoxon test or Kruskal-Wallis test to determine significant differences among the samples. Beta diversity was calculated using species occurrence data, which was then partitioned into turnover and nestedness components by applying the 'betapart' function within the R 'betapart' package (Baselga and Orme, 2012). The principal coordinates analysis (PCoA) was selected to illustrate the clustering of different samples, which was carried out using the 'pcoa' function in R package 'ape' (Paradis and Schliep, 2019). Subsequently, the permutational multivariate analysis of variance (PERMANOVA) was used to determine the distances of each sample to the group centroid in a PCoA and to provide a p-value for the significance of the grouping, which was implemented using the 'adonis' function in the R 'vegan' package (Ovaskainen et al., 2017). To test for a homogenization effect of natural and anthropic ecosystems on the soil microbial, we used the 'betadisper' function in the R 'vegan' package to calculate the dispersion within each group, and the 'permutest' function was used to compare dispersions between natural ecosystems (Ovaskainen et al., 2017).

Co-occurrence network analysis was conducted according to Spearman's correlations between OTUs computed by 'picante' package (Kembel et al., 2010), and the connections were considered statistically robust if the Spearman's correlation coefficients ($r \geq 0.7$ as well as p-values < 0.05) (Guseva et al., 2022). Moreover, network-level topological features were also calculated for each network including node numbers (Nodes), edge numbers (Edges), average weighted degree, average clustering coefficient, average path length, diameter, centralization of eigenvector centrality, and modularity. The network was visualized by using Gephi software (V0.9.2).

The nearest-taxon index was used to estimate the mean phylogenetic relatedness between each OTU in a community and its nearest relative. The value of NTI is equivalent to -1 times the standardized effect size of MNTD (mean nearest-taxon distance) which was calculated by using the null model 'taxa.labels' (999 randomizations) in the 'ses.mntd' function in the "picante" R package (Kembel et al., 2010). To assess the process in the microbial community assemblies, the "mantel.correlog" function in the "vegan" package was used to test for significant phylogenetic signal (Ovaskainen et al., 2017). Then, the Raup-Crick index (RC_{Bray}) and β NTI were calculated using the scripts provided by Stegen et al. (2013) in R. $|\beta$ NTI > 2 indicates the dominance of deterministic processes with significantly less (homogeneous selection; β NTI < -2) or more (variable selection; β NTI > 2) phylogenetic turnover than expected. When $|\beta$ NTI < 2 , $RC_{Bray} < -0.95$ and $RC_{Bray} > 0.95$ represent the relative influences of homogeneous dispersal and dispersal limitation, respectively, and $|\beta$ NTI < 2 , $RC_{Bray} < -0.95$ and $RC_{Bray} > 0.95$ represent the relative influences of homogeneous dispersal and dispersal limitation, respectively, and $|\beta$ NTI < 2 , $RC_{Bray} < -0.95$ and $RC_{Bray} > 0.95$ represent the relative influences of homogeneous dispersal and dispersal limitation, respectively, and $|\beta$ NTI < 2 , $RC_{Bray} < -0.95$ and $RC_{Bray} > 0.95$ represent the relative influences of homogeneous dispersal and dispersal limitation, respectively.

3. Results

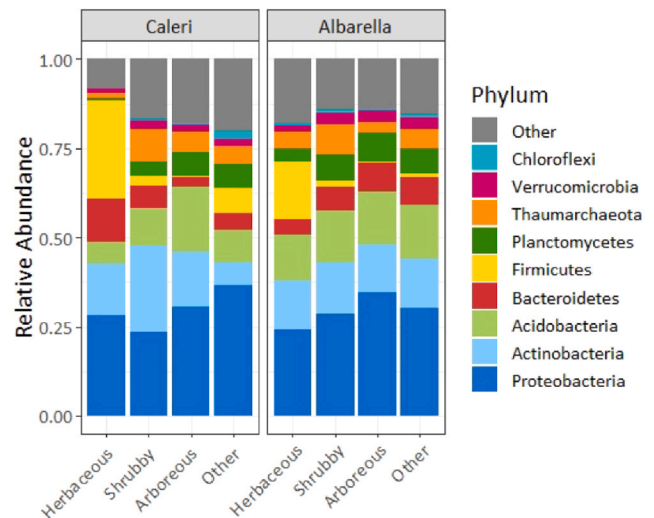
3.1. Composition and diversity of soil microbial community

Totally 52,756 of bacteria were identified after a sequence of

processing procedures. Overall, Proteobacteria, which occupied 23.48%–37.77% of the bacterial community, had the highest abundance, followed by Actinobacteria, Acidobacteria, Firmicutes (accounting for 6.23%–24.32%, 5.78%–18.28%, and 0.4%–27.32%, respectively. Fig. 2A.). Soil fungal sequences were identified into 11,676 OTUs. Ascomycota, Basidiomycota, and Zygomycota (accounting for 39.50% - 77.50%, 10.27% - 43.05%, and 0.53%–13.07% of the sequences, respectively) were the dominant phyla across all soil samples (Fig. 2B).

We compared the Shannon diversity index and Chao1 richness index for the Caleri and Albarella soil microbial to gain further insight into the relative diversities of the microbial communities. After checking the normality and homogeneity of all the diversity indices, the Wilcoxon test and the Kruskal-Wallis test were used to test differences between and within islands, respectively. There were large differences between Caleri and Albarella microbial diversity and richness indices ($p < 0.001$), and higher indices were found in Albarella (Fig. 3). In addition, both indices of soil microbial were significantly different between Caleri and Albarella. For bacterial communities, the Shannon-Wiener and Chao1 indices grew along the increasing complexity of vegetation, from herbaceous to shrubby and ending in arboreous (Fig. 3A, B). As for fungal communities, soils from the herbaceous had the lowest Shannon and Chao1

A. Bacteria



B. Fungi

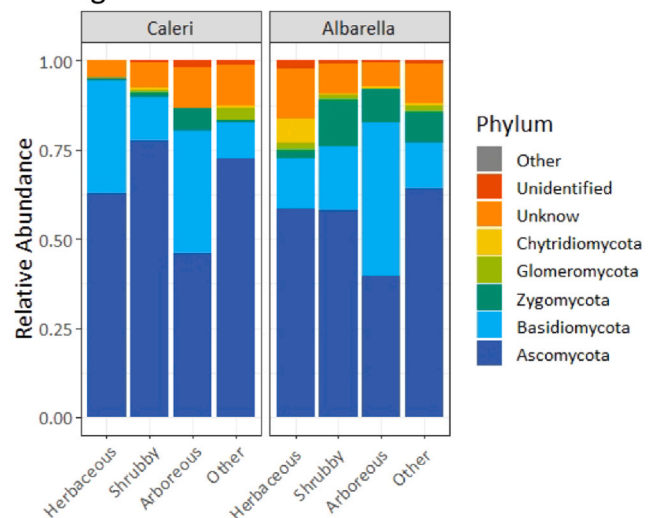


Fig. 2. Relative abundances of soil bacterial(A) and fungal(B) community in Caleri and Albarella.

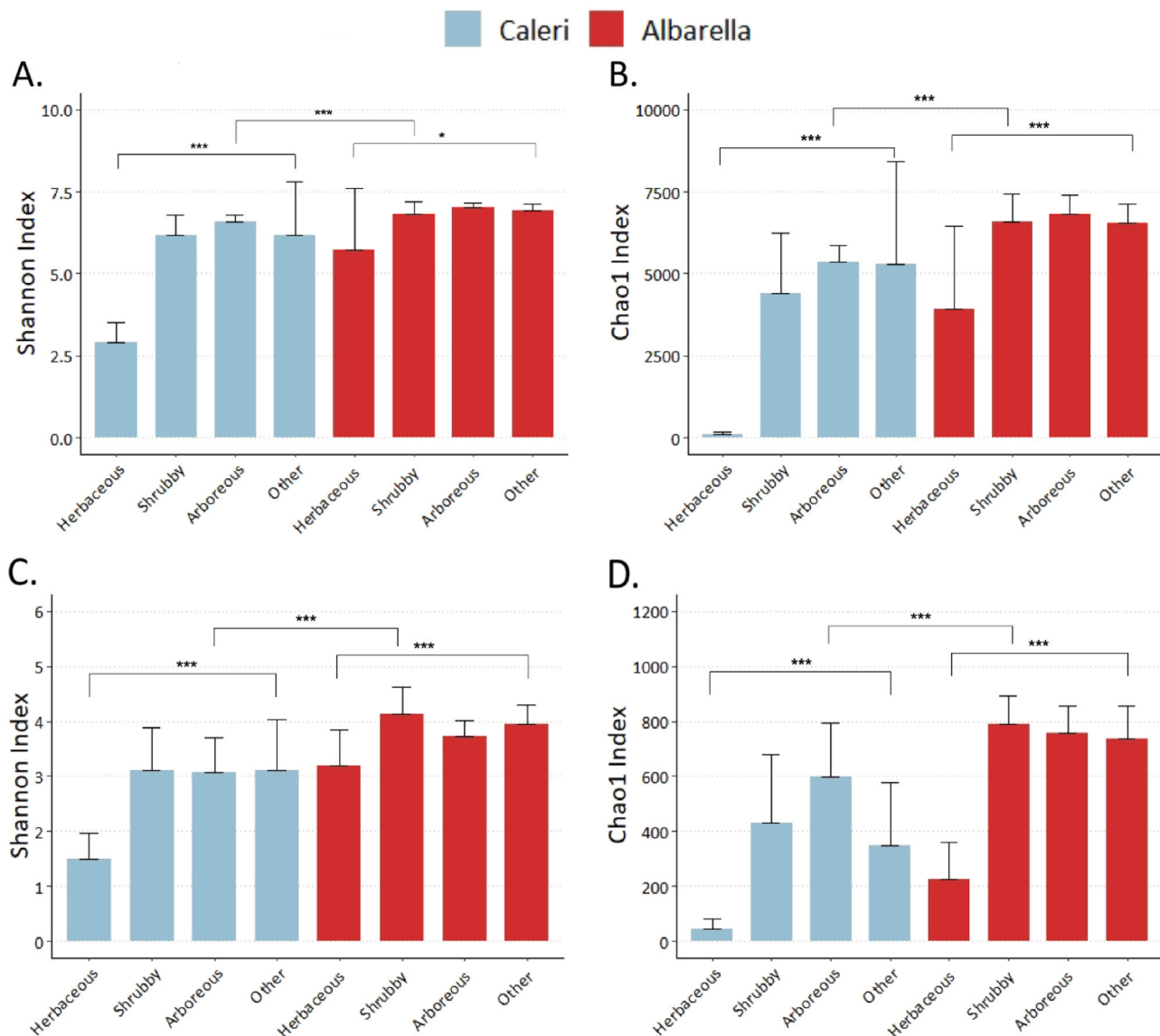


Fig. 3. Differences in soil bacterial (A, B) and fungal diversity (C, D) between Caleri and Albarella. All data are presented as the mean and standard error. Asterisks indicate that a horizon has significant influence (***) indicates $p < 0.001$; ** indicates $p < 0.01$; * indicates $p < 0.05$; ns indicates no significant difference).

indices, the highest value were found in the shrubby of Albarella (Fig. 3C, D).

We profiled the similarity of the soil bacterial and fungal community composition in Albarella and Caleri using Principal coordinates analysis (PCoA). The compositions of soil bacteria and fungi differed significantly across Albarella and Caleri (PERMANOVA: $R^2 = 0.07826$ and $F = 6.9617$ for bacteria, $R^2 = 0.04319$ and $F = 3.7013$ for fungi, $p < 0.001$ in both cases, Fig. 4A, C). In addition, our analyses also revealed that Albarella tended to host more homogeneous microbial communities than those found in Caleri (Betadisper: $p < 0.001$ for bacteria, and $p < 0.01$ for fungi; Fig. 4B, D). In other words, our analyses show a greater similarity in the community composition of bacteria and fungi across the anthropic ecosystem than across the corresponding natural ecosystems (Fig. 4).

3.2. Co-occurrence network of soil microbial community

The co-occurrence network of the soil microbial community in Caleri and Albarella was compared. After Modular analysis, closely linked species belonged to one module and were marked with the same color. Fig. 6 shows 7 and 20 modules in bacterial networks in Caleri and

Albarella, respectively. There are 32 and 41 modules in fungal networks in Caleri and Albarella, respectively. This indicated that the network structure of the soil microbial community had substantial differences in Caleri and Albarella. The microbial networks in the natural environment showed a more complex and relatively close relationship than that in the artificial environment.

Table 1 shows the microbial network topological features in Caleri and Albarella. Microbial networks in Caleri had a higher number of network nodes and edges than Albarella, as well as average path length, average weighted degree, average clustering coefficient, and density. However, the microbial network in Albarella presented relatively stronger modularity. These results indicated that the soil microbial network in Caleri was relatively larger and more complex.

3.3. Quantitative analysis of assembly processes in soil microbial

In order to measure the phylogenetic relatedness of microbial communities, we tested the level of phylogenetic clustering of soil microbial communities in both island ecosystems by using the nearest taxon index (Fig. 7) (Stomeo et al.). High or positive (low or negative) NTI values indicated that microbial communities had a tendency to be more

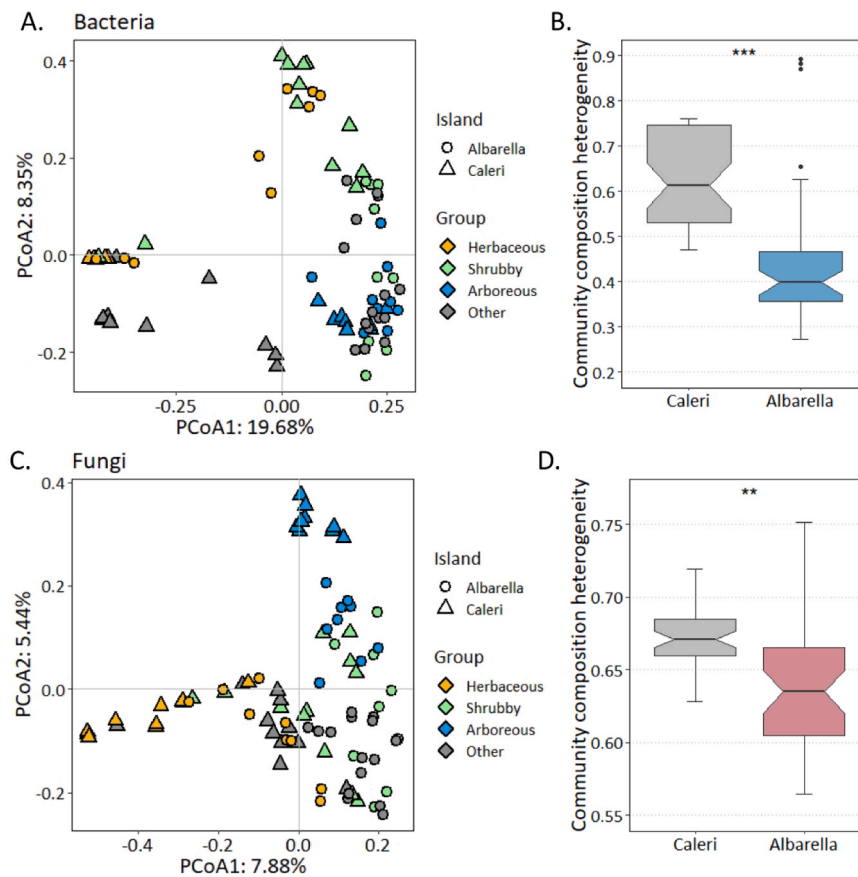


Fig. 4. PCoA of bacterial and fungal community composition across all soil samples in Caleri and Albarella (A and C). The soil community composition heterogeneity of the soil bacterial and fungal in Caleri and Albarella ecosystems (B and D). Asterisks indicate significant differences in compositional heterogeneity based on the permutation test for homogeneity of multivariate dispersions (***) indicates $p < 0.001$; ** indicates $p < 0.01$).

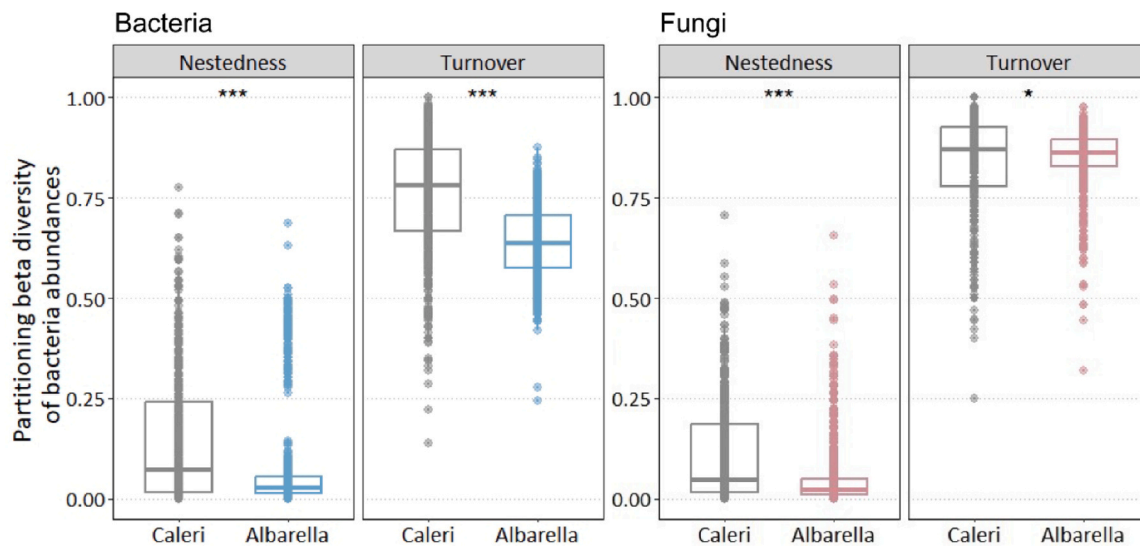


Fig. 5. Differences in bacterial and fungal communities' turnover component and nestedness-resultant fraction between Caleri and Albarella. Asterisks mean significant difference examined using the Wilcox test (***) indicates $p < 0.001$; ** indicates $p < 0.01$; * indicates $p < 0.05$).

phylogenetically clustered (overdispersion) than expected by chance (Webb, 2000; Horner-Devine and Bohannan, 2006). The bacteria NTI of Albarella was significantly higher than Caleri ($p < 0.001$) which suggested there were more phylogenetically clustered across the Albarella. The NTI of the fungi community was not significantly different between

the two ecosystems.

We found a significant phylogenetic signal for bacteria and fungi in Albarella and Caleri (Fig. 8). Collectively, the community assembly mechanisms of microbial communities with different ecosystems resulted differently (Fig. 9). The bacterial community assembly of Caleri

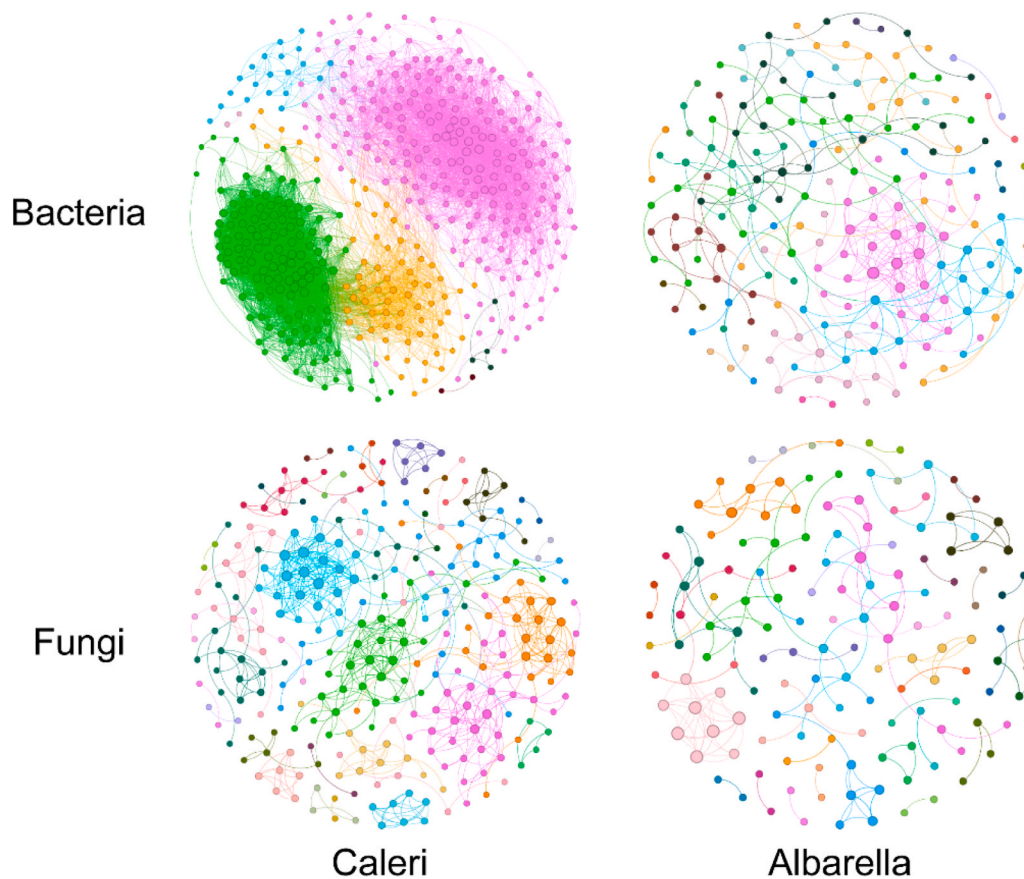


Fig. 6. Co-occurrence networks of soil microbial community in Caleri and Albarella.

Table 1
Network topological features of Caleri and Albarella.

Network Indexes	Bacteria		Fungi	
	Caleri	Albarella	Caleri	Albarella
Nodes	434	187	279	146
Edges	9133	300	655	164
Average weighted degree	33.385	2.397	3.781	1.803
Average clustering coefficient	0.650	0.365	0.614	0.637
Average path length	3.352	7.736	6.327	2.584
Diameter	11	22	17	9
Centralization of eigenvector centrality	0.068	0.013	0.339	0.015
Density	0.097	0.017	0.017	0.015
Modularity	0.526	0.781	0.856	0.909

appeared mainly driven by variable selection (40%) and homogeneous selection (11.92%), while undominated processes (26.03%) also seem to have played an important role. Dispersal limitation (52.15%) resulted to have played a main role in the assembly of the bacterial community of Albarella, and the contribution of selection (38.91%) to the assembly of all the sub-communities was pointed out to be also important by the analysis output. As for the fungal community, the community assembly of Caleri appeared driven by selection (25.9%), dispersal (38.1%), and undominated processes (35.19%) together. The assembly of the Albarella fungal community was indicated as mainly driven by dispersal, especially dispersal limitation (66.09%), while the contribution of heterogeneous selection and homogenizing dispersal to the assembly of the community was almost negligible.

3.4. The relative influence of environmental factors on microbial community composition and phylogenetic turnover

The intrinsic factors driving the community variation were explored. We performed Kruskal–Wallis and Wilcoxon tests to examine soil samples from herbaceous, shrubby, arboreous, and unique habitats (other) taken from Caleri and Albarella (Supplementary Table S1). When comparisons were performed between Caleri and Albarella, the pH was significantly lower in Albarella, while TC, TN, TK, SOC, AP, and AK were significantly higher. Then, we identified correlations between microbial taxonomic composition and environmental factors (Fig. 10). The bacterial composition of Albarella was significantly correlated with pH, TC, TN, SOC, and AK, while the Caleri bacterial composition was significantly correlated with pH, TN, TP, and AK. Moreover, the fungal composition of Albarella was significantly correlated with pH, TC, TN, SOC, and AK, and Caleri fungal composition was significantly correlated with all factors.

Mantel test results showed that soil AK, SOC, TC, and TN were important environmental variables in assembly processes in the bacterial communities in Caleri, while two more variables pH and AP (in order of decreasing significance: TN, SOC, TC, pH, AK, and AP) resulted the predominant variables that contribute to the bacterial communities in Albarella (Table 2). As for fungi, pairwise comparisons of β NTI values for the fungal communities in Caleri appeared significantly correlated with TK, AP, and SOC, but all measured environmental variables were not significantly correlated with fungal phylogenetic turnover in Albarella.

Linear models were used to further investigate the relationships between the β -nearest taxon index (β NTI) and major environmental variables used to infer changes in the relative influences of assembly processes. Pairwise comparisons of β NTI values for bacterial

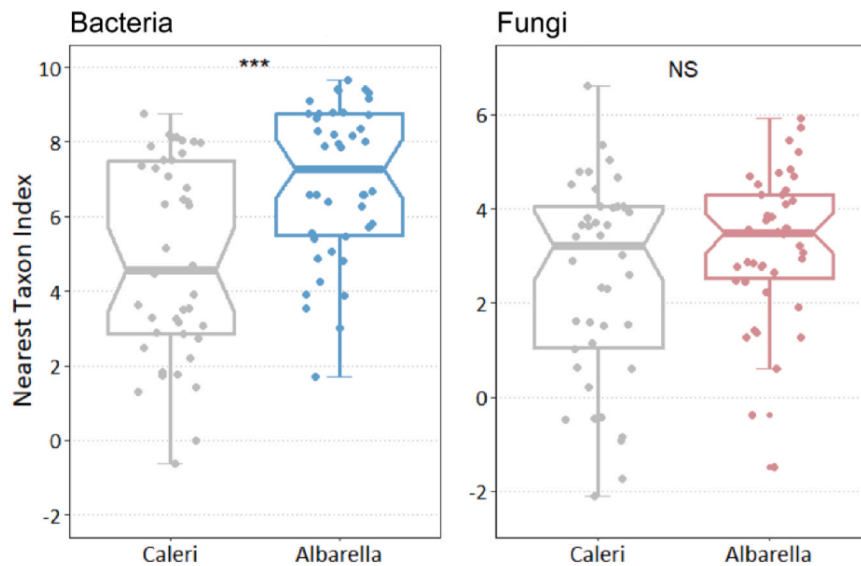


Fig. 7. Differences in soil bacterial and fungal nearest taxon index between Caleri and Albarella. Asterisks mean significant difference examined using the Wilcox test (***) indicates $p < 0.001$; NS indicates $p > 0.05$.

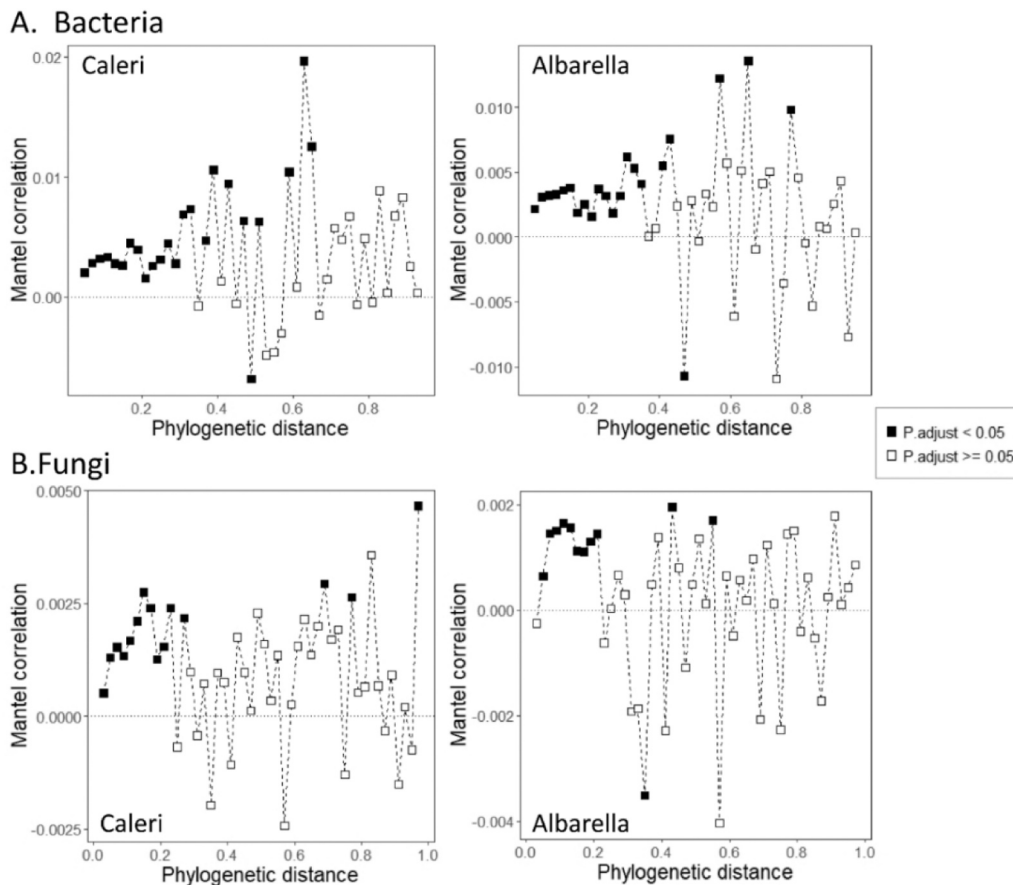


Fig. 8. Phylogenetic Mantel correlogram showing significant phylogenetic signal across phylogenetic distances. Solid and open symbols denote significant and non-significant correlations, respectively, relating between-OTU niche differences to between-OTU phylogenetic distances, across a given phylogenetic distance.

communities in Caleri were significantly and negatively correlated with differences in soil pH and positively correlated with differences in AK (Fig. 11A and B), indicating that in the natural ecosystem, an increasing divergence of pH led to a shift from variable selection to stochasticity while increasing divergence of AK led to a shift from stochasticity to variable selection. In Albarella, pairwise comparisons of bacterial β NTI

values were significantly and positively correlated with differences in soil TC and SOC (Fig. 11C and D), suggesting that the relative influence of variable selection increased with increasing differences in TC and SOC. However, no environmental variables significantly correlated with the β NTI of fungal communities in both ecosystems.

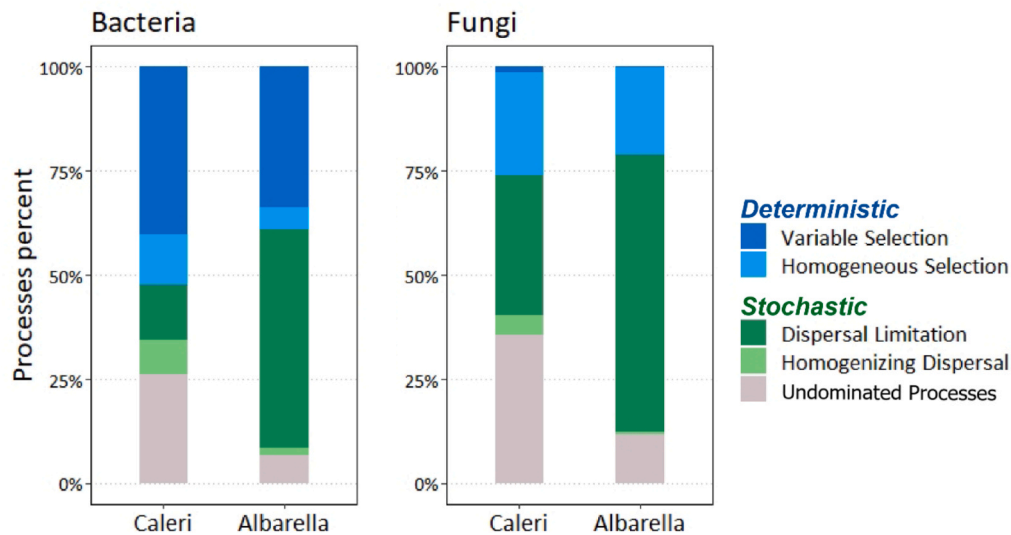


Fig. 9. The community assembly mechanisms of the bacterial and fungal communities.

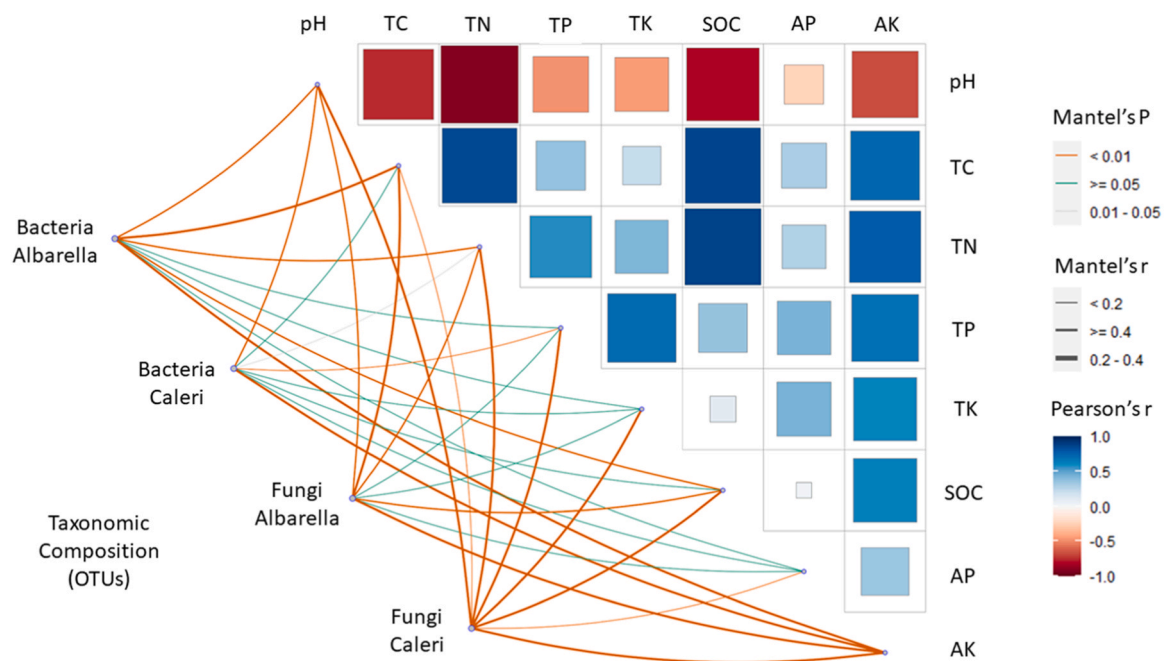


Fig. 10. Environmental factors influencing the taxonomic composition (OTUs level) of bacterial and fungal communities in Albarella and Caleri. Pairwise comparisons between environmental factors are shown in a color gradient. The composition of bacterial and fungal communities was related to each environmental factor by partial Mantel tests. Edge width corresponds to the Mantel's r statistic for the corresponding distance correlations, and edge color corresponds to Mantel's p denoting the statistical significance based on 999 permutations. TC, total carbon; TN, total nitrogen; TP, total phosphorous; TK, total potassium; SOC, soil organic carbon; AP, available phosphorous; AK, available potassium, the same below.

4. Discussion

4.1. Anthropogenic pressures promote soil microbial alpha diversity but cause the homogenization of microbial communities

The diversity of the soil microbial community is crucial for preserving the function of the soil ecosystem (Bardgett and Van Der Putten, 2014; Wagg et al., 2014; Delgado-Baquerizo et al., 2020). Understanding the ecological mechanisms that drive the responses of microbial communities to global environmental changes is a central aim of current microbial ecology (Nemergut et al., 2013). In line with this pursuit, our study findings demonstrate substantial alterations in soil bacterial and fungal diversity within anthropogenic ecosystems when compared to

neighboring natural ecosystems. Overall, the diversity and richness of soil microbial appears to increase in the anthropogenic ecosystems (Fig. 3). These results might seem positive and contrast with predictions of a decline in global terrestrial biodiversity (Barnosky et al., 2011; Chase et al., 2020; Lu et al., 2020; Isbell et al., 2023). Different types of organisms probably respond differently to global change (Gossner et al., 2016). Such relatively higher microbial diversity could be hypothesized to depend on the complexity of human activities and landscape fragmentation in anthropogenic systems. The intermediate disturbance hypothesis states that environmental heterogeneity can be increased by intermediate interferences, which create a more diversified microenvironment for species cohabitation or more independent ecological niches (Mayor et al., 2012), then increasing the possibility of multiple species

Table 2

Mantel tests of environmental variables against the phylogenetic turnover (β -nearest taxon index) of microbial communities in Caleri and Albarella.

	Bacteria		Fungi	
	Caleri	Albarella	Caleri	Albarella
pH	-0.075	0.266 *	-0.01	-0.014
TC	0.249 **	0.302 **	0.085	-0.0205
TN	0.165 *	0.332 **	-0.117	-0.0671
TP	-0.066	-0.094	-0.117	0.095
TK	-0.037	0.069	0.147 **	0.023
SOC	0.266 **	0.328 **	0.124 *	-0.053
AP	0.007	0.17*	0.127 *	0.073
AK	0.358 **	0.212 **	0.022	-0.029

Note: the bold values represent significant variables (** indicates $p < 0.01$; * indicates $p < 0.05$).

coexisting in adjacent habitats without resource competition (Chau et al., 2011). Gossner et al. (2016) reported that high land-use intensity had neutral or positive effects on below-ground organisms. Higher soil bacterial and fungal diversity in highly disturbed environments than that in less-disturbed environments also has been observed previously (Delgado-Baquerizo et al., 2021; Xiong et al., 2021; Christel et al., 2023; Labouyrie et al., 2023). However, such results did not necessarily provide a more optimistic outlook for the future of the planet.

Our analyses show the homogenization effect for the soil microbial under anthropogenic pressures which means a decrease in the dissimilarity of soil microbial communities across locations, with communities

becoming more similar to each other. This was supported by a more concentrated cluster in Albarella than in Caleri in ordination plots (Fig. 4A and C), which is the predominant approach to quantify biotic homogenization with the dispersion metric calculated by the distance to group centroid in PERMDISP analysis (Fig. 4B and D). In a community, species presence-absence and abundance can be interpreted by species replacement and abundance difference (Legendre, 2014). We analyzed the nestedness and turnover of the paired Caleri and Albarella samples, the results showed that both ecosystems were dominated by turnover. That is, rather than the change in species richness, the difference in species composition among quadrats was mainly a result of species replacement.

4.2. Soil microbial networks become less connected under anthropogenic pressures

It is proposed that environmental filtering may be a strong mechanism for microorganisms' homogenization in assemblages (Zhang et al., 2019; Geng et al., 2022), and has been shown to cause phylogenetic clustering (Horner-Devine and Bohannan, 2006), because it tends to exclude intolerant species and harbor more adapted species, ultimately leading to regional soil microbial communities to become more similar through the range expansion of tolerant species or the decline of intolerant species. But the observed patterns of β -diversity alone cannot be used to unambiguously discern the relative importance of community assembly mechanisms. As noted by prior reports (Anderson et al., 2011), extreme caution should be taken in interpreting these relationships. In

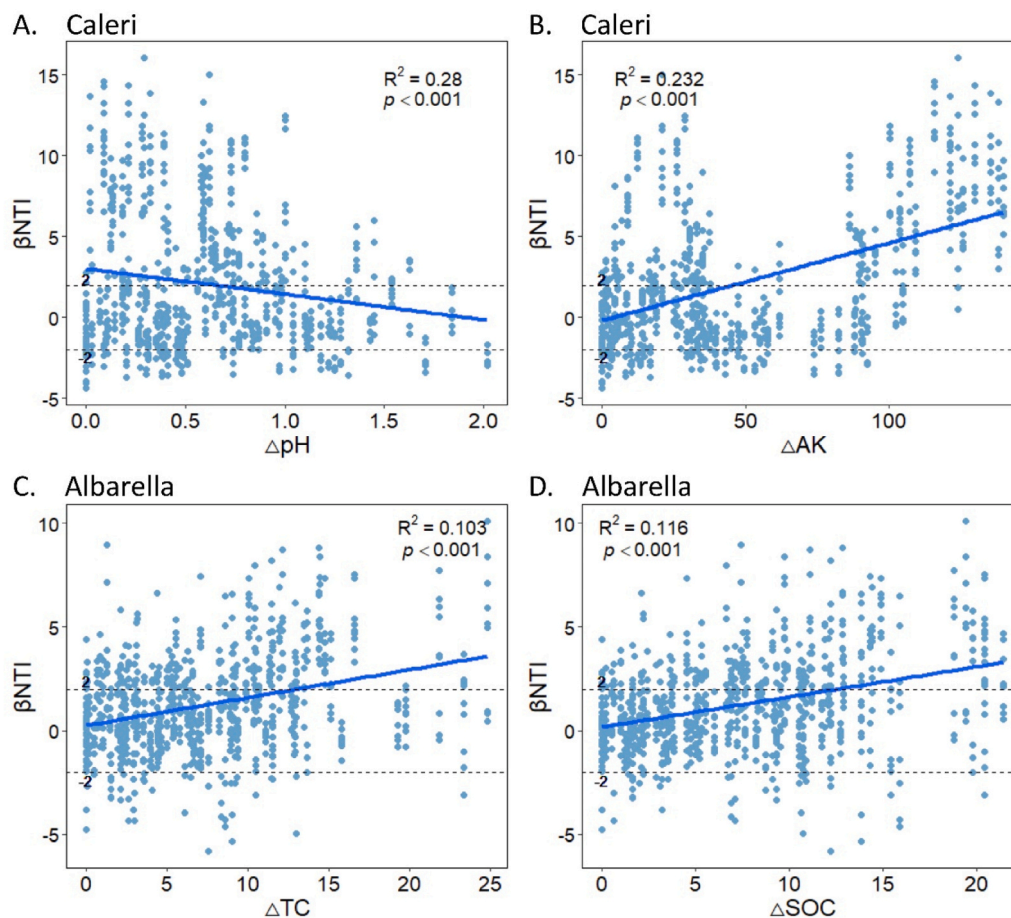


Fig. 11. The effect of environmental factors on bacterial deterministic and stochastic assembly processes in anthropogenic and natural ecosystems, respectively. The relationships between β NTI and differences in soil pH (A) and AK (B) were associated with the Caleri bacterial community while the differences in soil TC (C) and SOC (D) were observed for the Alberlla bacterial community. Linear regression models (shown as blue lines) and associated correlation coefficients are provided on each panel. Horizontal dashed lines indicate the β NTI thresholds of +2 and -2.

the present study, the positive NTI observed in both natural and anthropogenic systems indicates that species were more clustered in their distributions than expected by chance (Fig. 5). Moreover, the significantly lower mean NTI values obtained for natural ecosystems (Fig. 7) indicate that the bacteria in the natural environment are more distantly related than in the anthropogenic environment. In a mirror way, the bacterial communities of a more anthropized environment (es. Albarella) tend to be more grouped phylogenetically than if they were by chance, compared to those of a more natural environment (Caleri). At the level of organisms, Molleman et al. (2023) suggest that soil fauna profits from the resource concentration in local plant communities that are uniform in both functional traits and phylogenetic lineages (high phylogenetic signal). Soil fauna would hence benefit from co-occurrence of closely related plants that have conserved the same trait values, rather than of distantly related plants that have converged in traits. This might result in faster decomposition and positive feedback between trait conservatism and ecosystem functioning.

Is it therefore possible to distinguish man-made environments from natural ones, bringing to light differences in the functionality of the food web? Biotic interactions between soil microbial taxa should not be overlooked when analyzing community assembly. The anthropogenic pressures may lower the stabilizing properties in the bacterial and fungal interactive network, then finally disturb the soil microbial co-occurrence interactions, which indeed appears supported by a less complicated and weaker connectivity of bacterial and fungal nodes in Albarella (Fig. 6, Table 1). Simultaneously, the lower average degree values of bacterial and fungal networks in the Albarella ecosystem suggested that the interactions within microbial members were less intense (Table 1). It is generally accepted that network complexity and connectivity are usually positively correlated with the stability of the community and ecosystem multifunctionality (Mougi and Kondoh, 2012; Schmidt et al., 2017; Wagg et al., 2019; Qiu et al., 2021). A more clustered network structure and stronger connections between species could enhance the efficiency of resource and information transfer, which contribute to the high stability of community function (He et al., 2021). Previous studies showed that connectivity, the density of the links, and transitivity decrease in disturbed environments (Karimi et al., 2016; de Vries et al., 2018). Zhang et al. (2020) provided evidence that impervious surfaces coupled with human population density could affect microbial connectivity indirectly by changing soil physicochemical characteristics. A relatively higher soil bacterial diversity and an unstable community status were also found in the city of Chicago, and the main reason might be traced to the excessive anthropogenic interference (Wang et al., 2018). A higher modularity in the bacterial and fungal networks was observed in Albarella. The more the modules, the more niches overlap with each other, and a higher overlap of niches produces a neutral process (Banerjee et al., 2016; Carmel et al., 2017). Consequently, 1) networks of more stochastically assembled communities (in Albarella and anthropogenic systems in general) feature a greater number of modules than those mainly shaped by deterministic selection; 2) microbial networks of more deterministically assembled communities (as in Porto Caleri, representative of natural systems) show a higher number of network nodes and edges than those shaped by stochastic assembly mechanisms, as well as average path length, average weighted degree, average clustering coefficient, and density (Fig. 6). The soil microbial network in natural systems results relatively larger and more complex than in anthropogenic systems, albeit less biodiverse. This is particularly important, considering that network complexity can have important implications for microbial stability and ecosystem multifunctionality; our results suggest that anthropogenic disturbance generally decreases the complexity and stability of species interactions, possibly as a trade-off for biodiversity loss to support ecosystem function when faced with frequent disturbance.

4.3. Anthropogenically-induced SOC and soil pH change regulates the assembly processes of bacterial communities in anthropogenic ecosystems

The contemporary coexistence theory suggests that species pool, environmental filtering, dispersal assembly processes, ecological drift, and biotic interactions collectively determine the composition patterns of communities (Vellend, 2010; Stegen et al., 2012). Uncovering the balance between community assembly processes under different habitats could provide us with a better understanding of the maintenance of species diversity (Stegen et al., 2012; Nemergut et al., 2013; Langenheder and Lindström, 2019). Hence, we further examined the community assembly processes driving the respective relationships. In the present study, the deterministic assembly processes were dominant in the natural bacterial communities, while the dispersal limitation was found to be more important than selection in anthropogenic ecosystems (Fig. 9). As for fungi, the deterministic, stochastic, and undominated processes combined resulted to drive community assemblage in natural ecosystems, and anthropogenic ecosystems had relatively high dispersal limitations. To some extent, our results were supported by some previous observations reporting that anthropogenic pressure affects the assembly of soil microbial communities primarily by mediating stochastic processes (e.g., dispersal limitation) (Ferrenberg et al., 2013; Zhang et al., 2016), and stochastic assembly processes were dominant in high α -diversity communities (Xun et al., 2019). The environmental conditions within the natural ecosystem progressively exhibit spatial heterogeneity from seaside to inland, thereby exerting influence on the composition and distribution of species within the community (e.g., habitat specialization and strategy differentiation) (Dini-Andreote et al., 2014). Consequently, environmental constraints and selection assume a more pronounced role in natural systems, instead of stochastic processes. Soil microbes in the relatively natural environment may be less limited by dispersal than those in anthropogenic environments, and thus can sufficiently be delivered to suitable habitats with suitable environmental conditions (Cottenie, 2005). On the contrary, fragmentation of anthropogenic habitats not only causes loss of the area of natural habitat but also changes the properties of the habitat by creating small and isolated patches, that prevent microorganisms from dispersing into new habitats, thereby adversely affecting the ability of species to disperse among suitable habitat remnants (Li et al., 2020). Hence, it could be suggested that dispersal limitation emphasizes the retention of location-specific taxa. Jiao et al. (2020) suggested that in low environmental stress ecosystems which experience lower environmental heterogeneity, or in scenarios where competitive interaction among environmental generalists is diminished, stochastic assembly mechanisms have the potential to overrule deterministic processes.

It is essential to individuate the factors regulating the relative influences of stochastic and deterministic assembly processes of microbial communities, in order to advance mechanistic understanding of community assembly processes (Feng et al., 2018). Here, based on the mantel test and linear model, we found β NTI of bacterial communities in the natural system to be associated with differences in soil pH and AK, while the β NTI in the anthropogenic system was mostly affected by soil differences in TC and SOC (Table 2 and Fig. 11). We are on calcareous sandy substrate and in the natural ecosystems a variation of pH values favors the deterministic selection of bacterial communities, while a divergence of K availability favors stochastic selection. In more anthropized ecosystems, the deterministic variable selection is influenced by the values of SOC. It is not surprising that soil pH and carbon influence the assembly of bacterial communities, the major significance of these factors in soil microbial composition and diversity is well-known and supported by many previous studies (Feng et al., 2018; Tripathi et al., 2018; Zhang et al., 2019; Jiao and Lu, 2020). In this study, the differences in major factors that influenced soil bacterial assemblage might be ascribed to the divergences between human-managed and natural ecosystems. Long-term accumulation of soil carbon under natural vegetation is lower in comparison to

anthropogenic in this survey. However, land use change and related management practices (i.e. cropping, fertilization, and irrigation) are usually driving the dynamics of soil carbon stock in anthropogenic ecosystems. Soil bacterial communities respond quickly to changes in soil carbon changes because they are often C-limited (Delgado-Baquerizo et al., 2013; Luo et al., 2022; Yang et al., 2022a). In this case, we speculated that soil carbon might influence the bacterial community assembly via two mechanisms: (i) soil bacteria are directly involved in carbon cycling, and soil carbon indirectly interacts with plants to shape the bacterial community assembly. The fact that relationships between fungi and environmental factors were not observed may be due to the fungal compositional shifts being influenced to a larger extent by spatial restrictions (Abrego and Salcedo, 2013; Reese et al., 2016). Overall, the governing ecological processes exhibited the impacts of similarities of environmental conditions, as well as the potential impacts of anthropogenic disturbances, natural environmental selections, and stochastic interspecies interactions.

These results help to explain the forces responsible for the generation and maintenance of microbial diversity, and these factors should be considered when determining ecosystem management practices. However, our study was limited to two simple ecosystems, and a broader examination of more complex areas is warranted. Furthermore, a thorough vision of these phenomena still requires a better description and consideration of the context-dependency of the soil microbial processes with respect to biotic and abiotic environmental conditions.

5. Conclusions

The soil bacterial and fungal communities in natural and anthropogenic ecosystems were comparatively screened by amplicon sequencing and multiple statistical analyses. When the data were viewed at a local scale, anthropogenic pressure showed the potential to lead to an increase in species diversity of soil microbes within the different sample communities (i.e., α -diversity), but accompanied by a reduction in the variation in species composition among communities (i.e., β -diversity). This could be arguably due to the fact that although the influence of stochastic processes increases, niche-based selection also imposes some constraints on communities, following availability of SOC and consequent mineral nutrients, mediated by soil pH. Deterministic and stochastic processes can both be critical for bacterial and fungal communities. This suggests comprehensively considering multiple aspects of microbial communities when evaluating their assembly processes, which would improve our understanding of the assembly of soil microbial communities in a changing environment. Microbial networks in natural systems exhibit higher numbers of nodes and network edges, as well as averages of path length, weighted degree, clustering coefficient, and density than equivalent systems in more anthropized environments, the latter on the other hand presents a stronger modularity.

The microorganisms that coexist in communities of natural environments do not show a higher phylogenetic signal than those of communities of anthropized environments, or at least not in Caleri and Albarella, as cautiously suggested in a previous article (Mo et al., 2022). The explanation can be linked to the fact that horizontal gene transfer and illegitimate recombination events could have allowed the microorganisms that reproduce in a more natural environment to respond in a collaborative way to the selection imposed by the environment and consequently express a significant phylogeny, not stand up to the verification that we made in the present work (Fig. 8). The guess of our previous article has been confirmed by this widened analysis: the functionality of the relationships between groups of microorganisms co-existing in communities is more relevant to the concept of functional biodiversity than the plain number of their different taxa; fewer but well-organized lineages could make better use of the resources than many ones when those are not equally interconnected in their habitat exploitation (scientific and philosophical foundations with figure in Supplementary Materials. “Global impact: Do you like cycling?” And

Fig. S1).

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CRediT authorship contribution statement

Cristian Bolzonella: Data curation, Investigation, Resources. **Giulia Ranzani:** Data curation, Investigation, Software, Visualization. **Massimo Pindo:** Data curation, Software, Supervision. **Giuseppe Concheri:** Data curation, Investigation, Validation. **Guoliang Xu:** Funding acquisition, Supervision, Writing – review & editing. **Francesca Visentin:** Data curation, Investigation. **Lingzi Mo:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Andrea Squartini:** Conceptualization, Methodology, Supervision, Validation, Writing – review & editing. **Augusto Zanella:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Our data are deposited to a public database; a link to them is set in the article

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.micres.2024.127651](https://doi.org/10.1016/j.micres.2024.127651).

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