

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

Lingzi Mo, Augusto Zanella, Andrea Squartini, Giulia Ranzani, Cristian Bolzonella, Giuseppe Concheri, Massimo Pindo, Francesca Visentin, Guoliang Xu



PII: S0944-5013(24)00052-1

DOI: <https://doi.org/10.1016/j.micres.2024.127651>

Reference: MICRES127651

To appear in: *Microbiological Research*

Received date: 14 November 2023

Revised date: 23 January 2024

Accepted date: 16 February 2024

Please cite this article as: Lingzi Mo, Augusto Zanella, Andrea Squartini, Giulia Ranzani, Cristian Bolzonella, Giuseppe Concheri, Massimo Pindo, Francesca Visentin and Guoliang Xu, Anthropogenic vs. natural habitats: higher microbial biodiversity pays the trade-off of lower connectivity, *Microbiological Research*, (2024) doi:<https://doi.org/10.1016/j.micres.2024.127651>

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2024 Published by Elsevier.

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

Lingzi Mo^a, Augusto Zanella^{b*}, Andrea Squartini^c, Giulia Ranzani^b, Cristian Bolzonella^b, Giuseppe Concheri^c, Massimo Pindo^d, Francesca Visentin^e, Guoliang Xu^a

^a School of Geography and Remote Sensing, Guangzhou University, Guangzhou 510006, Guangdong, China (LM: lingzi.mo@gzhu.edu.cn ; GX: xugl@gzhu.edu.cn)

^b Department Land Environment Agriculture and Forestry, University of Padua, Viale dell'Università 16, 35020 Legnaro, Italy (AZ: augusto.zanella@unipd.it; GR: giulia.ranzani@studenti.unipd.it; CB: cristian.bolzonella@unipd.it)

^c Department Agronomy, Food, Natural Resources, Animals, Environment, University of Padua, Viale dell'Università 16, 35020 Legnaro, Italy (AS: squart@unipd.it; GC: giuseppe.concheri@unipd.it)

^d Fondazione Edmund Mach, 38098 San Michele all'Adige, Italy (MP: massimo.pindo@fmach.it)

^e Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, 43124 Parma, Italy (FV: francesca.visentin@unifi.it)

* Corresponding author. E-mail address: augusto.zanella@unipd.it .

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.

Keywords: Soil biodiversity; Soil microbial community; Co-occurrence pattern; Phylogenetic turnover; Anthropogenic habitat

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.*, 2022).

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 hypothec soils(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). 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; Polverigiani *et al.*, 2018; 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 physiochemical 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; Heděnec *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 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 50m 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, Arboreous 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* (1m)), 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 subsamples, 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.

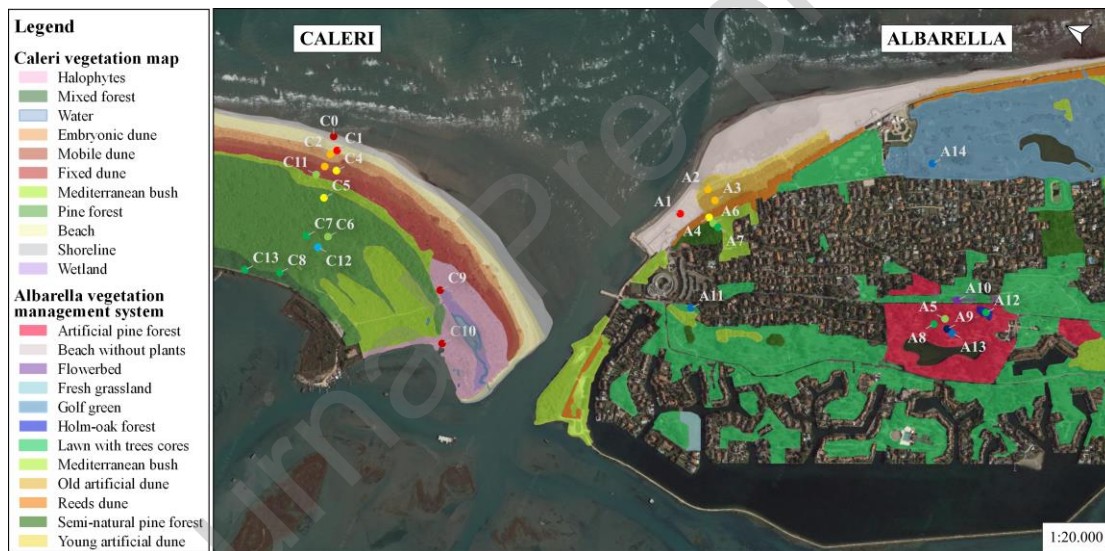


Fig. 1. Left Southern end of the Porto Caleri natural reserve; Right Northern end of the Island of Albarella. The sampling points of Caleri range from C0 to C13, while those of Albarella range from A1 to A14. The colors of the points correspond to those in the vegetation legend.

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 'permutetest' 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 $|RC_{Bray}| < 0.95$ indicates the influence of the "non-dominant" fraction. To assess the relative influence of assembly processes, we compared all possible pairwise comparisons of β NTI values with each major environmental variable

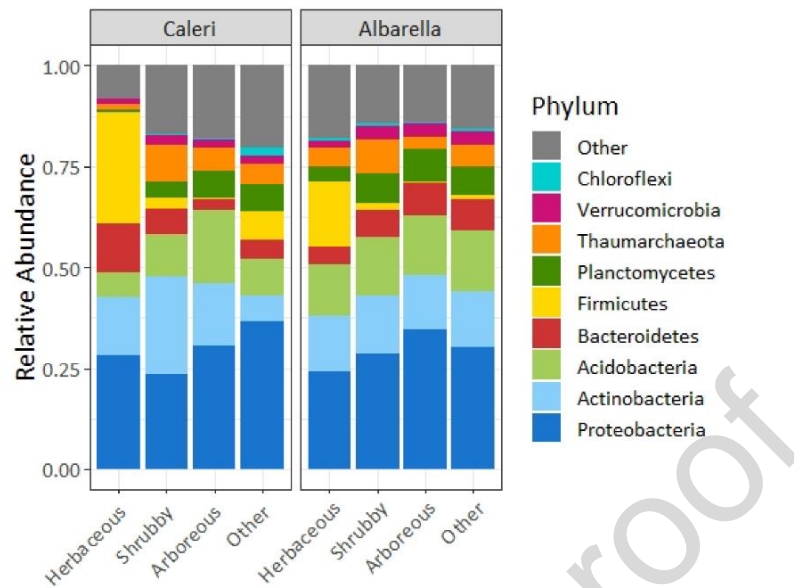
by using the 'mantel' function of the 'vegan' package in R(Ovaskainen *et al.*, 2017), and the statistical significance of these comparisons was determined with 999 permutations.

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).

A. Bacteria



B. Fungi

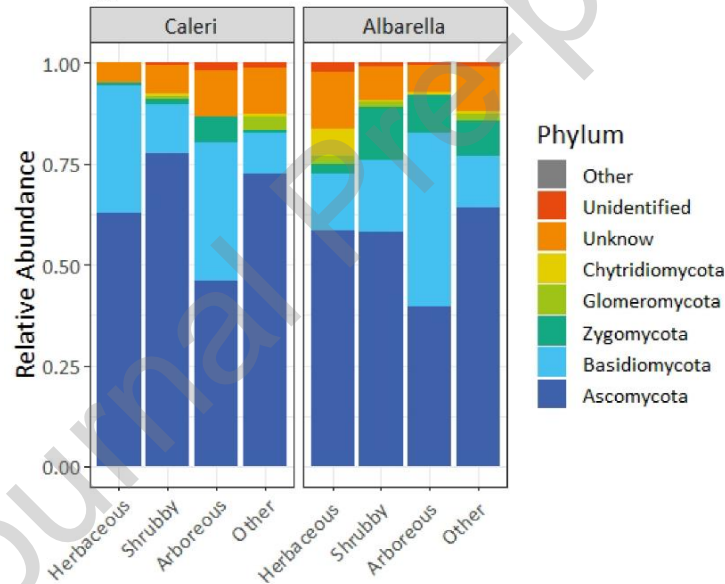


Fig. 2. Relative abundances of soil bacterial(A) and fungal(B) community in Caleri and Albarella

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

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

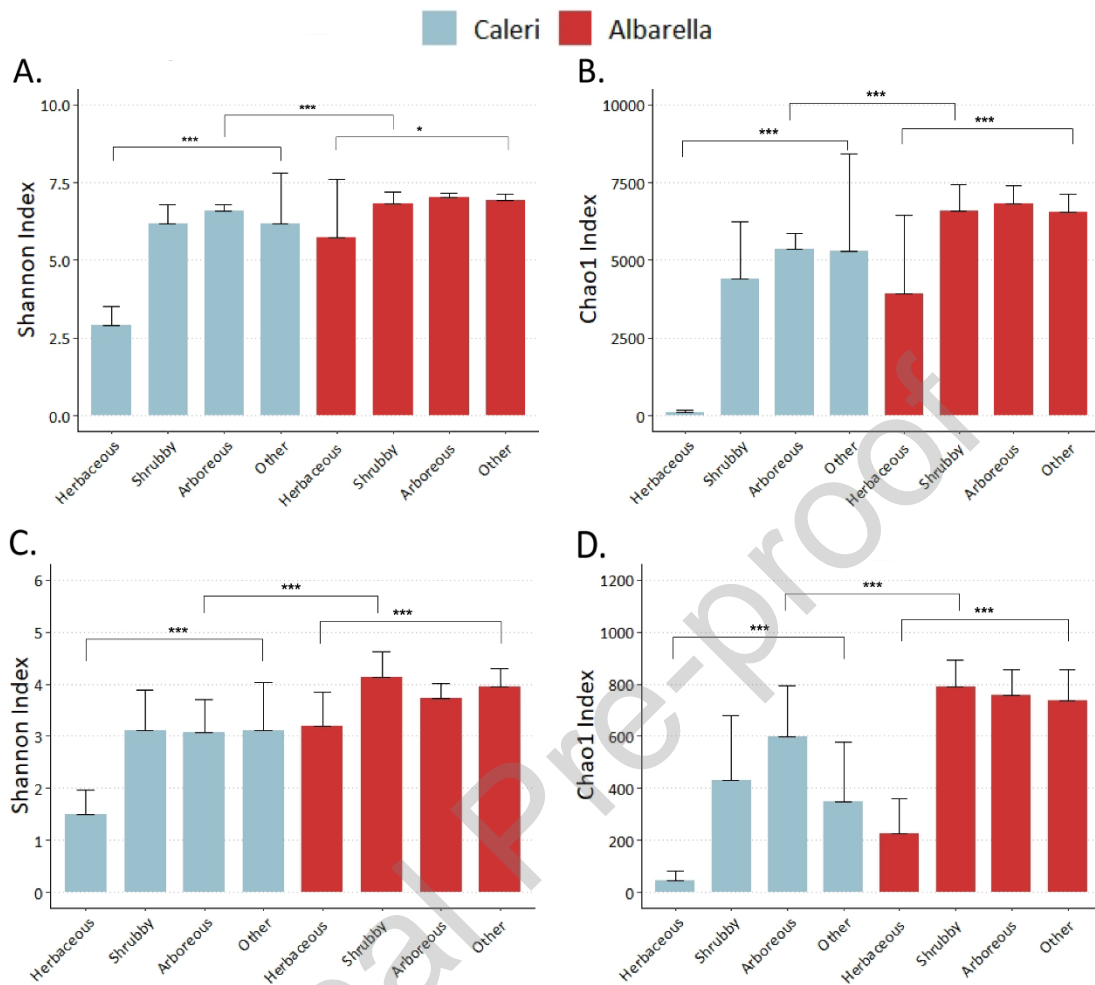


Fig. 3. Differences in soil bacterial (A, B) and fungal diversity (C, D) between Caleri and Albarella. All data are presented as the mean and standard error. Asterisks indicate that a horizon has significant influence (***) indicates $p < 0.001$; ** indicates $p < 0.01$; * indicates $p < 0.05$; ns indicates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

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, $p < .001$ 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).

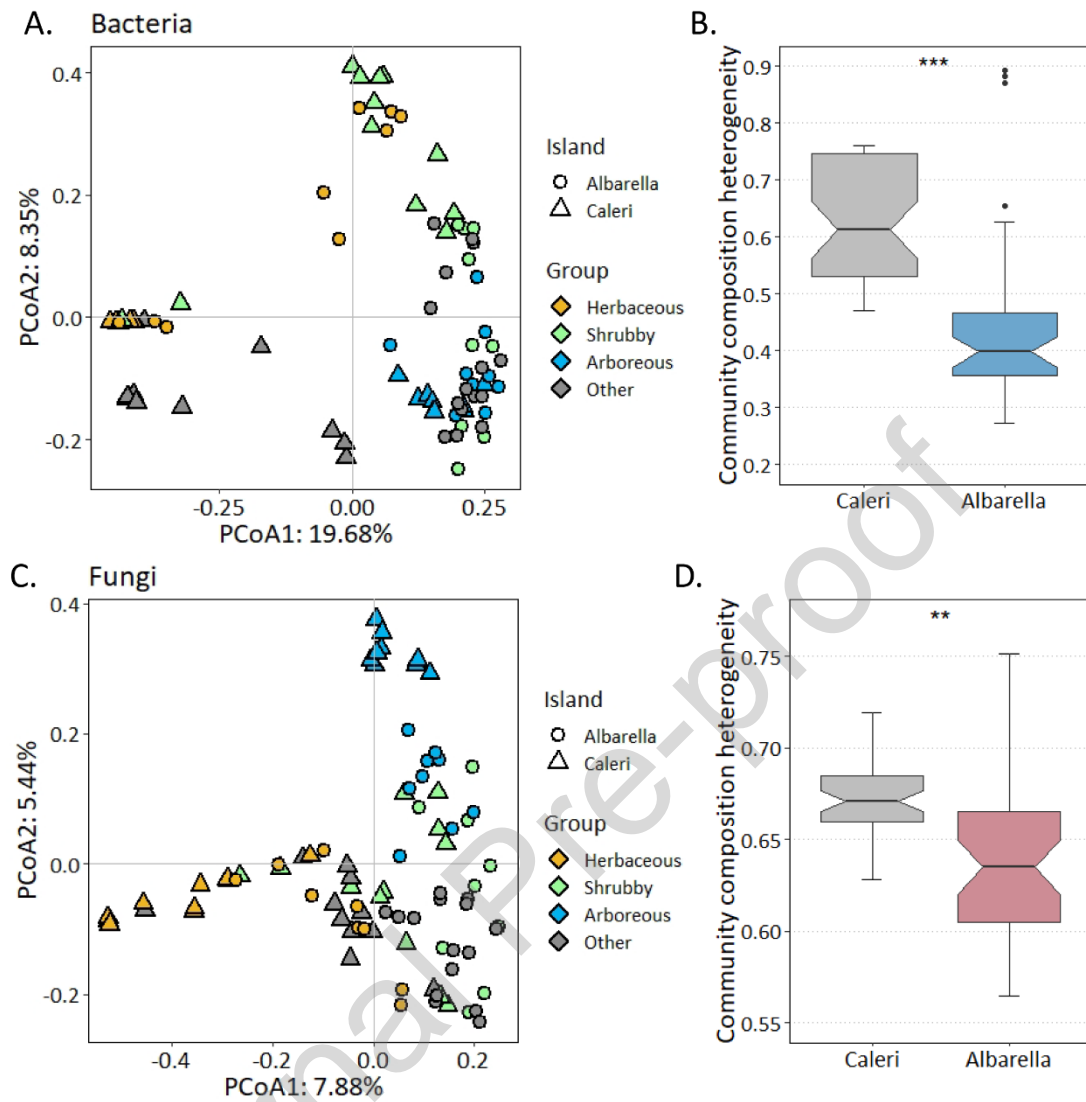


Fig. 4. PCoA of bacterial and fungal community composition across all soil samples in Caleri and Albarella (A and C). The soil community composition heterogeneity of the soil bacterial and fungal in Caleri and Albarella ecosystems (B and D). Asterisks indicate significant differences in compositional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

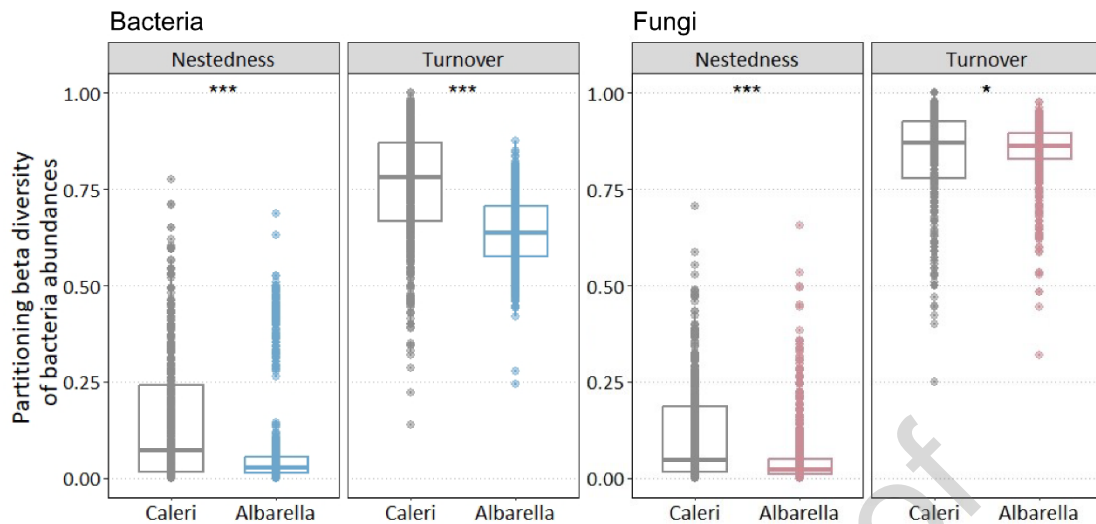


Fig. 5. Differences in bacterial and fungal communities' turnover component and nestedness-resultant fraction between Caleri and Albarella. Asterisks mean significant difference examined using the Wilcox test (***) indicates $p < 0.001$; ** indicates $p < 0.01$; * indicates $p < 0.05$).

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. Figure 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.

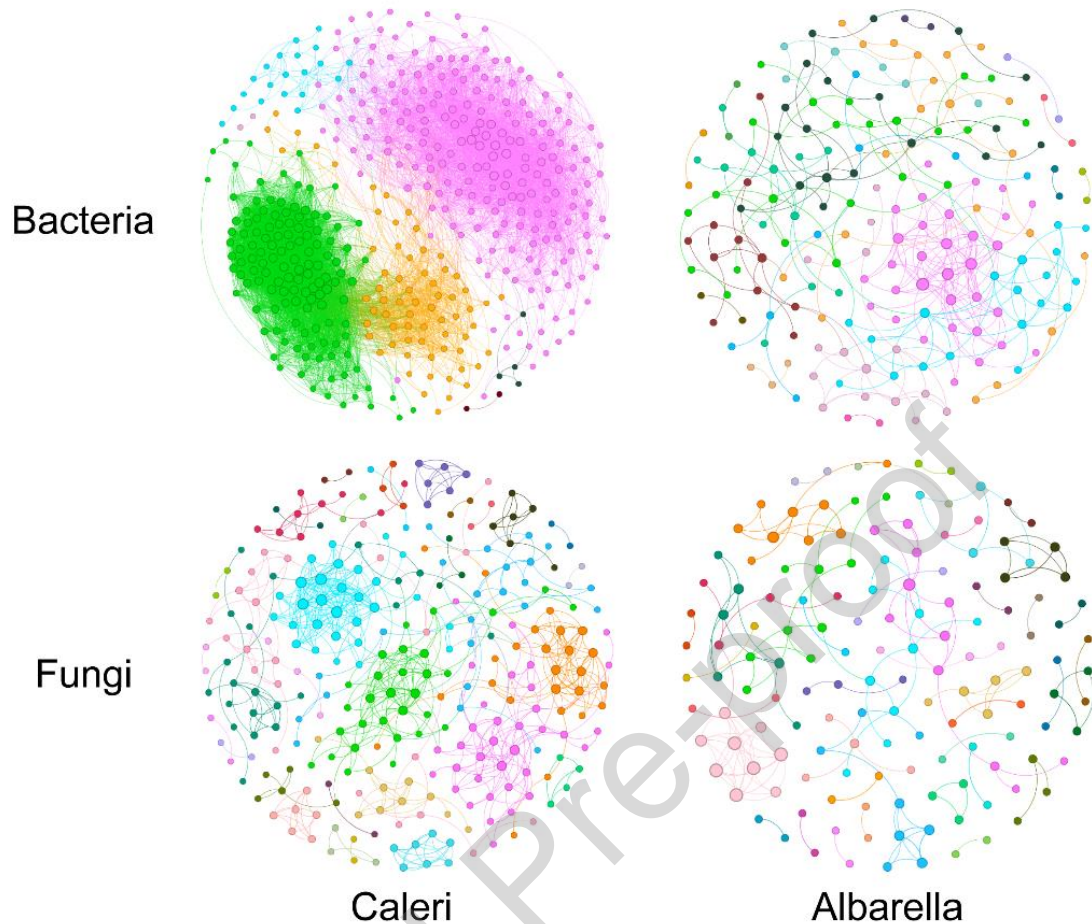


Fig. 6. Co-occurrence networks of soil microbial community in Caleri and Albarella.

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

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 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.

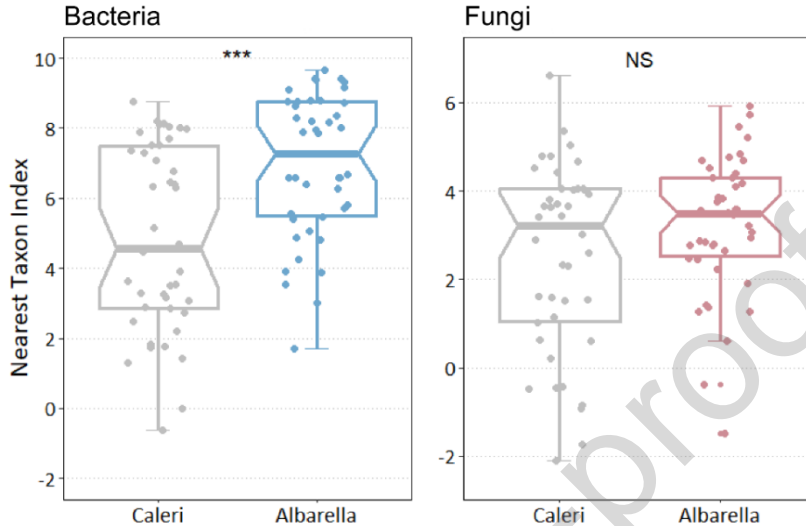


Fig. 7. Differences in soil bacterial and fungal nearest taxon index between Caleri and Albarella. Asterisks mean significant difference examined using the Wilcox test (***) indicates $p < 0.001$; NS indicates $p > 0.05$).

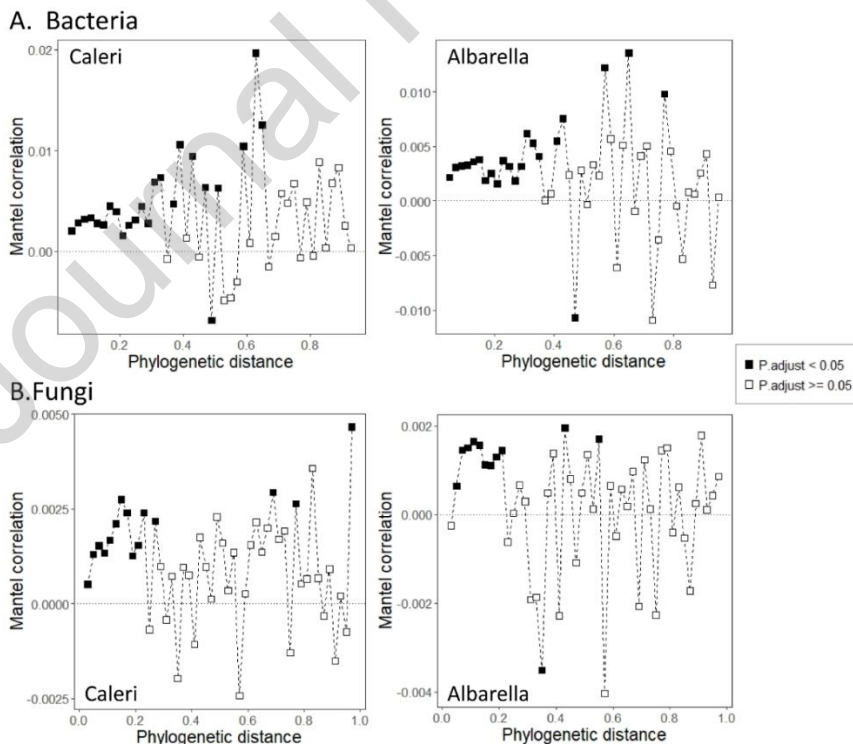


Fig. 8. Phylogenetic Mantel correlogram showing significant phylogenetic signal across phylogenetic distances. Solid and open symbols denote significant and nonsignificant correlations, respectively, relating between-OTU niche differences to between-OTU phylogenetic distances, across a given phylogenetic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

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 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.

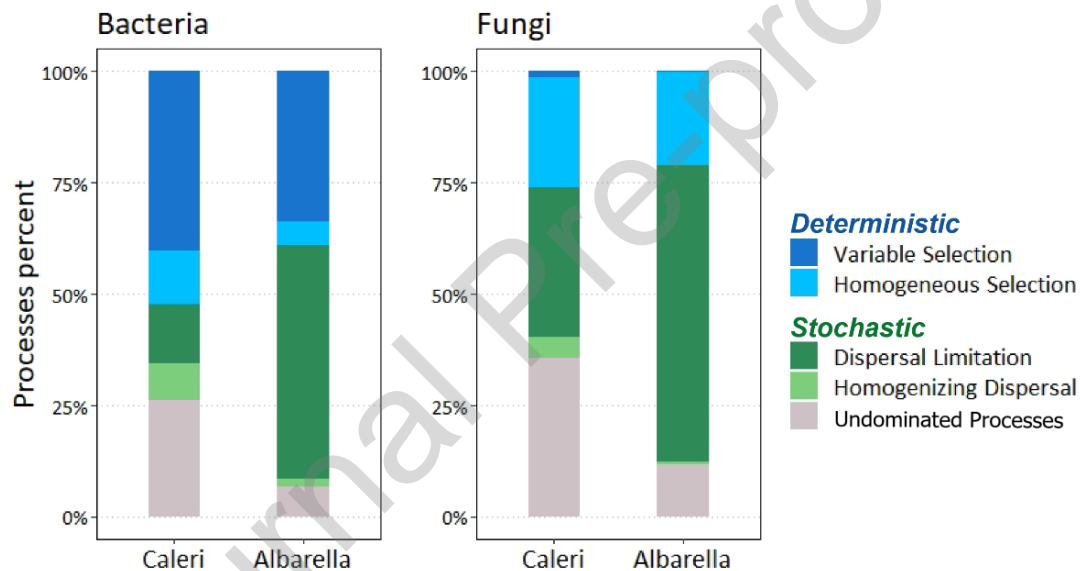


Fig. 9. The community assembly mechanisms of the bacterial and fungal communities

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.

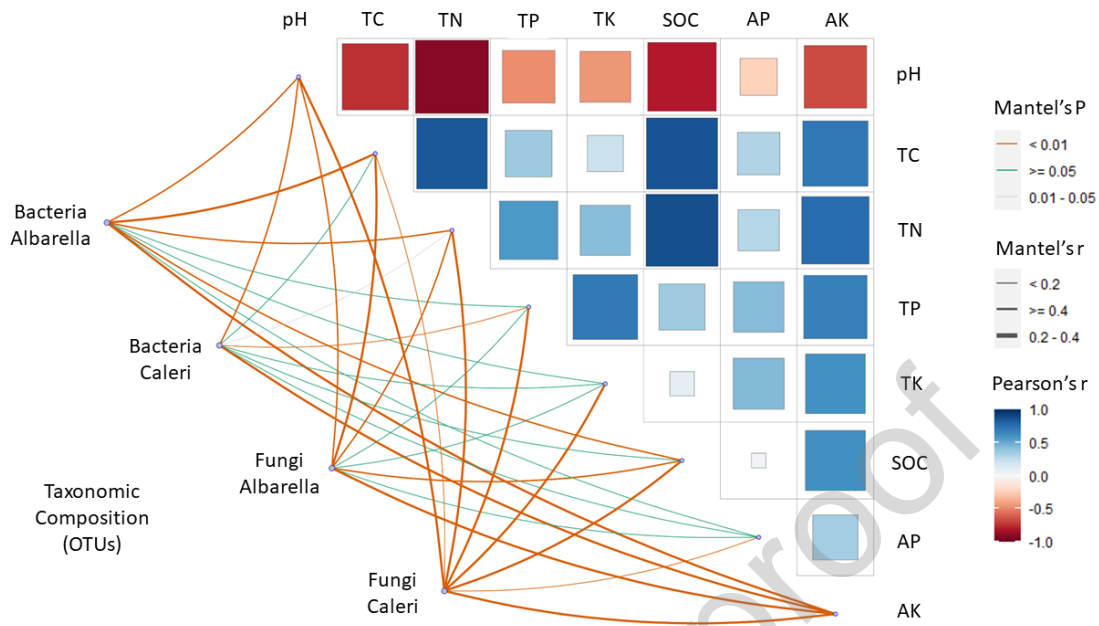


Fig. 10. Environmental factors influencing the taxonomic composition (OTUs level) of bacterial and fungal communities in Albarella and Caleri. Pairwise comparisons between environmental factors are shown in a color gradient. The composition of bacterial and fungal communities was related to each environmental 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.

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 $p < 0.05$).

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.

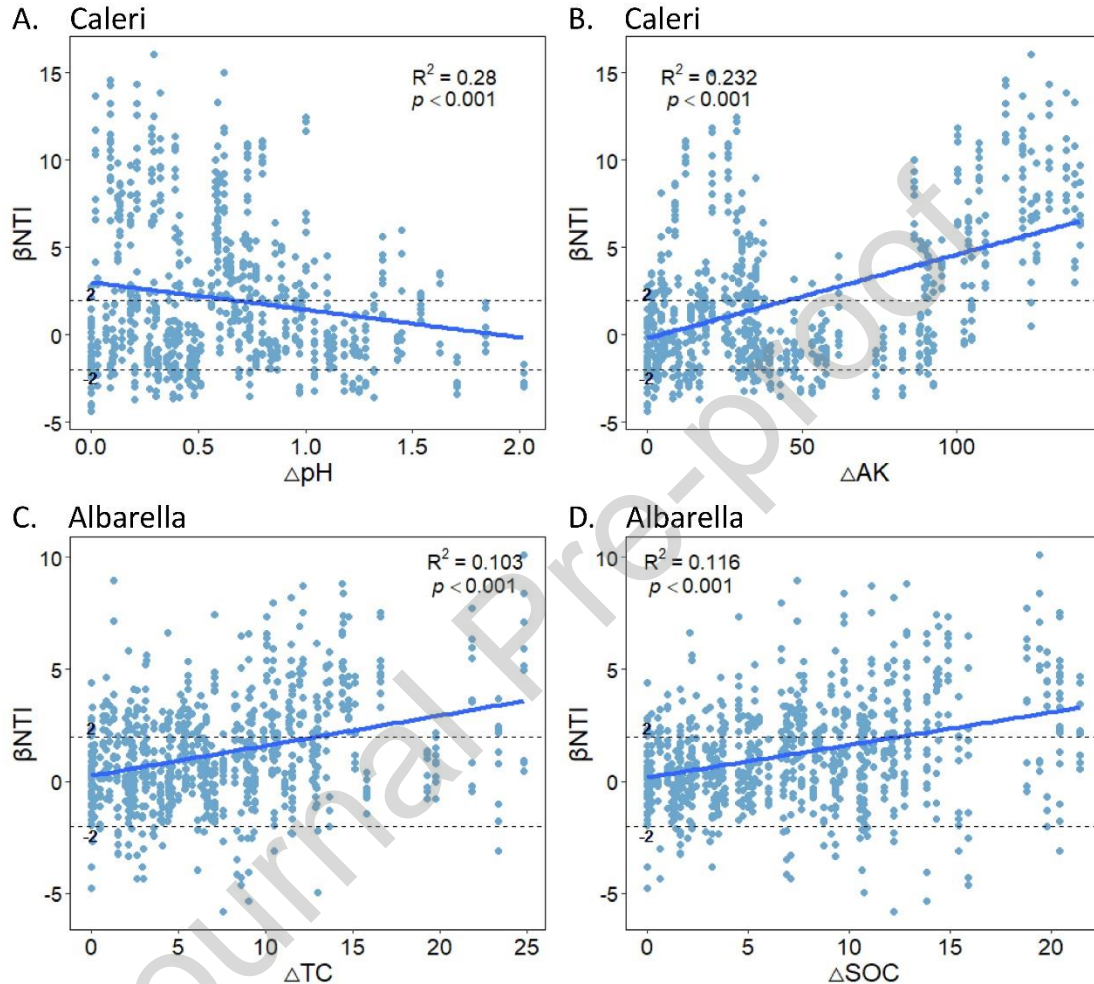


Fig. 11. The effect of environmental factors on bacterial deterministic and stochastic assembly processes in anthropogenic and natural ecosystems, respectively. The relationships between β NTI and differences in soil pH (A) and AK (B) were associated with the Caleri bacterial community while the differences 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.

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 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.

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 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 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.*, 2022). 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).

Funding

This work was supported by the Uni-Impresa project 2020–2022 University of Padova, Italy; Associazione Comunione Isola di Albarella, Rovigo, Italy; The National Natural Science Foundation of China [grant number 42071061].

CRedit authorship contribution statement

Lingzi Mo: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing—Original draft preparation, Writing - review and editing. Augusto Zanella: Conceptualization, Data curation, Formal analysis, Funding Acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing—Original Draft Preparation, Writing - review and editing. Andrea Squartini: Conceptualization, Methodology, Supervision, Validation, Writing - review and editing. Giulia Ranzani: Data Curation, Investigation, Software, Visualization. Cristian Bolzonella: Data curation Investigation, Resources. Giuseppe Concheri: Investigation, Data Curation, Validation. Massimo Pindo: Investigation, Software, Data Curation, validation. Francesca Visentin: Investigation, Data Curation. Guoliang Xu: Writing - review and editing, Supervision, Funding Acquisition.

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 Statement

The sequences referred to in this work have been deposited in GenBank SRA archive under BioProject accession number PRJEB68196; <https://www.ncbi.nlm.nih.gov/sra/PRJEB68196>.

Acknowledgments

An affectionate thanks to Mauro Rosatti, Enrico Longo, and the inhabitants of the island of Albarella, for their collaboration with the university and the logistical support to the student teams.

References

Abrego, N. and I. Salcedo, 2013. Variety of woody debris as the factor influencing wood-inhabiting fungal richness and assemblages: Is it a question of quantity or quality? *Forest Ecology and Management*, 291: 377-385. DOI <https://doi.org/10.1016/j.foreco.2012.11.025>.

- Anderson, M.J., T.O. Crist, J.M. Chase, M. Vellend, B.D. Inouye, A.L. Freestone, N.J. Sanders, H.V. Cornell, L.S. Comita and K.F. Davies, 2011. Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecology letters*, 14(1): 19-28. DOI <https://doi.org/10.1111/j.1461-0248.2010.01552.x>.
- Angeler, D.G., J. Heino, J. Rubio-Ríos and J.J. Casas, 2023. Connecting distinct realms along multiple dimensions: A meta-ecosystem resilience perspective. *Science of The Total Environment*, 889: 164169-164169. Available from <https://linkinghub.elsevier.com/retrieve/pii/S0048969723027900>. DOI 10.1016/j.scitotenv.2023.164169.
- Astudillo-García, C., S.M. Hermans, B. Stevenson, H.L. Buckley and G. Lear, 2019. Microbial assemblages and bioindicators as proxies for ecosystem health status: Potential and limitations. *Applied microbiology and biotechnology*, 103: 6407-6421. DOI <https://doi.org/10.1007/s00253-019-09963-0>.
- Ballasso, A., 1998. Esperienze e nuove esigenze di tutela naturalistica: Flora e vegetazione del “giardino litoraneo” di porto caleri (rosolina mare – ro). Regione del Veneto, Assessorato agricoltura e foreste, Servizio forestale di Padova., Padova, Italy.
- Banerjee, S., M. Baah-Acheamfour, C.N. Carlyle, A. Bissett, A.E. Richardson, T. Siddique, E.W. Bork and S.X. Chang, 2016. Determinants of bacterial communities in Canadian agroforestry systems. *Environmental Microbiology*, 18(6): 1805-1816. DOI <https://doi.org/10.1111/1462-2920.12986>.
- Banerjee, S. and M.G. van der Heijden, 2023. Soil microbiomes and one health. *Nature Reviews Microbiology*, 21(1): 6-20. DOI <https://doi.org/10.1038/s41579-022-00779-w>.
- Bardgett, R.D. and W.H. Van Der Putten, 2014. Belowground biodiversity and ecosystem functioning. *Nature*, 515(7528): 505-511. DOI <https://doi.org/10.1038/nature13855>.
- Barnosky, A.D., N. Matzke, S. Tomiya, G.O. Wogan, B. Swartz, T.B. Quental, C. Marshall, J.L. McGuire, E.L. Lindsey and K.C. Maguire, 2011. Has the earth’s sixth mass extinction already arrived? *Nature*, 471(7336): 51-57. DOI <https://doi.org/10.1038/nature09678>.
- Baselga, A. and C.D.L. Orme, 2012. Betapart: An R package for the study of beta diversity. *Methods in ecology and evolution*, 3(5): 808-812. DOI <https://doi.org/10.1111/j.2041-210X.2012.00224.x>.
- Birkhofer, K., M.M. Gossner, T. Diekötter, C. Drees, O. Ferlian, M. Maraun, S. Scheu, W.W. Weisser, V. Wolters and S. Wurst, 2017. Land-use type and intensity differentially filter traits in above- and below-ground arthropod communities. *Journal of Animal Ecology*, 86(3): 511-520. DOI <https://doi.org/10.1111/1365-2656.12641>.
- Boetius, A., 2019. Global change microbiology—big questions about small life for our future. *Nature Reviews Microbiology*, 17(6): 331-332. DOI <https://doi.org/10.1038/s41579-019-0197-2>.
- Buffa, G., E. Fantinato and L. Pizzo, 2012. Effects of disturbance on sandy coastal ecosystems of n-adriatic coasts (italy). *Gbolagade Akeem Lameed*: pp: 339-372.
- Buffa, G., L. Filesi, U. Gamper and G. Sburlino, 2007. Qualità e grado di conservazione del paesaggio vegetale del litorale sabbioso del veneto (italia settentrionale). *Fitosociologia*, 44(1), 49-58. *Fitosociologia*, 44(1): 49-58.
- Caniglia, G., 2007. Stato attuale dei litorali del veneto. *Fitosociologia*, 44(1), 59-65. *Fitosociologia*, 44(1): 59-65.
- Cardinale, B.J., K.L. Matulich, D.U. Hooper, J.E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M.I. O'connor and A. Gonzalez, 2011. The functional role of producer diversity in ecosystems. *American*

- journal of botany, 98(3): 572-592. DOI <https://doi.org/10.3732/ajb.1000364>.
- Carmel, Y., Y.F. Suprunenko, W.E. Kunin, R. Kent, J. Belmaker, A. Bar-Massada and S.J. Cornell, 2017. Using exclusion rate to unify niche and neutral perspectives on coexistence. *Oikos*, 126(10): 1451-1458.
- Chase, J.M., 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science*, 328(5984): 1388-1391. DOI <https://doi.org/10.1126/science.1187820>.
- Chase, J.M., S.A. Blowes, T.M. Knight, K. Gerstner and F. May, 2020. Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature*, 584(7820): 238-243. DOI <https://doi.org/10.1038/s41586-020-2531-2>.
- Chau, J.F., A.C. Bagtzoglou and M.R. Willig, 2011. The effect of soil texture on richness and diversity of bacterial communities. *Environmental Forensics*, 12(4): 333-341. DOI <https://doi.org/10.1080/15275922.2011.622348>.
- Christel, A., S. Dequiedt, N. Chemidlin-Prevost-Bouré, F. Mercier, J. Tripied, G. Comment, C. Djemiel, L. Bargeot, E. Matagne and A. Fougeron, 2023. Urban land uses shape soil microbial abundance and diversity. *Science of The Total Environment*, 883: 163455. DOI <https://doi.org/10.1016/j.scitotenv.2023.163455>.
- Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecology letters*, 8(11): 1175-1182. DOI <https://doi.org/10.1111/j.1461-0248.2005.00820.x>.
- Crowther, T.W., J. Van den Hoogen, J. Wan, M.A. Mayes, A. Keiser, L. Mo, C. Averill and D.S. Maynard, 2019. The global soil community and its influence on biogeochemistry. *Science*, 365(6455): eaav0550. DOI <https://doi.org/10.1126/science.aav0550>.
- de Vries, F.T., R.I. Griffiths, M. Bailey, H. Craig, M. Girlanda, H.S. Gweon, S. Hallin, A. Kaisermann, A.M. Keith and M. Kretzschmar, 2018. Soil bacterial networks are less stable under drought than fungal networks. *Nature communications*, 9(1): 3033. DOI <https://doi.org/10.1038/s41467-018-05516-7>.
- Delgado-Baquerizo, M., D.J. Eldridge, Y.-R. Liu, B. Sokoya, J.-T. Wang, H.-W. Hu, J.-Z. He, F. Bastida, J.L. Moreno and A.R. Bamigboye, 2021. Global homogenization of the structure and function in the soil microbiome of urban greenspaces. *Science Advances*, 7(28): eabg5809. DOI <https://doi.org/10.1126/sciadv.abg5809>.
- Delgado-Baquerizo, M., F.T. Maestre, A. Gallardo, M.A. Bowker, M.D. Wallenstein, J.L. Quero, V. Ochoa, B. Gozalo, M. García-Gómez and S. Soliveres, 2013. Decoupling of soil nutrient cycles as a function of aridity in global drylands. *Nature*, 502(7473): 672-676. DOI <https://doi.org/10.1038/nature12670>.
- Delgado-Baquerizo, M., P.B. Reich, C. Trivedi, D.J. Eldridge, S. Abades, F.D. Alfaro, F. Bastida, A.A. Berhe, N.A. Cutler and A. Gallardo, 2020. Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nature Ecology & Evolution*, 4(2): 210-220. DOI <https://doi.org/10.1038/s41559-019-1084-y>.
- Dini-Andreote, F., M. de Cássia Pereira e Silva, X. Triado-Margarit, E.O. Casamayor, J.D. Van Elsas and J.F. Salles, 2014. Dynamics of bacterial community succession in a salt marsh chronosequence: Evidences for temporal niche partitioning. *The ISME Journal*, 8(10): 1989-2001.
- Dini-Andreote, F., J.C. Stegen, J.D. Van Elsas and J.F. Salles, 2015. Disentangling mechanisms that mediate the balance between stochastic and deterministic processes in microbial succession. *Proceedings of the National Academy of Sciences*, 112(11): E1326-E1332. DOI <https://doi.org/10.1073/pnas.1414261112>.

- Dornelas, M., N.J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers and A.E. Magurran, 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science*, 344(6181): 296-299. DOI <https://doi.org/10.1126/science.1248484>.
- Ellis, E.C. and N. Ramankutty, 2008. Putting people in the map: Anthropogenic biomes of the world. *Frontiers in Ecology and the Environment*, 6(8): 439-447. Available from <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/070062>. DOI <https://doi.org/10.1890/070062>.
- Farooq, B., S. Anjum, M. Farooq, A. Nazir, M.U. Farooq, S. Yousuf, N. Shafi and J.A. Parray, 2023. Overview of soil microbe dynamics in different biosystems. pp: 33-49.
- Faust, K. and J. Raes, 2012. Microbial interactions: From networks to models. *Nature Reviews Microbiology*, 10(8): 538-550. DOI <https://doi.org/10.1038/nrmicro2832>.
- Feng, Y., R. Chen, J.C. Stegen, Z. Guo, J. Zhang, Z. Li and X. Lin, 2018. Two key features influencing community assembly processes at regional scale: Initial state and degree of change in environmental conditions. *Molecular ecology*, 27(24): 5238-5251. DOI <https://doi.org/10.1111/mec.14914>.
- Ferrenberg, S., S.P. O'Neill, J.E. Knelman, B. Todd, S. Duggan, D. Bradley, T. Robinson, S.K. Schmidt, A.R. Townsend and M.W. Williams, 2013. Changes in assembly processes in soil bacterial communities following a wildfire disturbance. *The ISME journal*, 7(6): 1102-1111. DOI <https://doi.org/10.1038/ismej.2013.11>.
- Fierer, N., C.L. Lauber, K.S. Ramirez, J. Zaneveld, M.A. Bradford and R. Knight, 2012. Comparative metagenomic, phylogenetic and physiological analyses of soil microbial communities across nitrogen gradients. *The ISME Journal*, 6(5): 1007-1017. Available from <http://www.nature.com/articles/ismej2011159>. DOI 10.1038/ismej.2011.159.
- Geisen, S., D.H. Wall and W.H. van der Putten, 2019. Challenges and opportunities for soil biodiversity in the anthropocene. *Current Biology*, 29(19): R1036-R1044. DOI <https://doi.org/10.1016/j.cub.2019.08.007>.
- Geng, M., W. Zhang, T. Hu, R. Wang, X. Cheng and J. Wang, 2022. Eutrophication causes microbial community homogenization via modulating generalist species. *Water research*, 210: 118003. DOI <https://doi.org/10.1016/j.watres.2021.118003>.
- Gossner, M.M., T.M. Lewinsohn, T. Kahl, F. Grassein, S. Boch, D. Prati, K. Birkhofer, S.C. Renner, J. Sikorski and T. Wubet, 2016. Land-use intensification causes multitrophic homogenization of grassland communities. *Nature*, 540(7632): 266-269. DOI <https://doi.org/10.1038/nature20575>.
- Guerra, C.A., R.D. Bardgett, L. Caon, T.W. Crowther, M. Delgado-Baquerizo, L. Montanarella, L.M. Navarro, A. Orgiazzi, B.K. Singh and L. Tedersoo, 2021. Tracking, targeting, and conserving soil biodiversity. *Science*, 371(6526): 239-241. DOI <https://doi.org/10.1126/science.abd7926>.
- Guseva, K., S. Darcy, E. Simon, L.V. Alteio, A. Montesinos-Navarro and C. Kaiser, 2022. From diversity to complexity: Microbial networks in soils. *Soil Biology and Biochemistry*, 169: 108604. DOI <https://doi.org/10.1016/j.soilbio.2022.108604>.
- He, P., N. Ling, X.-T. Lü, H.-Y. Zhang, C. Wang, R.-Z. Wang, C.-Z. Wei, J. Yao, X.-B. Wang, X.-G. Han and Z. Nan, 2023. Contributions of abundant and rare bacteria to soil multifunctionality depend on aridity and elevation. *Applied Soil Ecology*, 188: 104881-104881. Available from <https://linkinghub.elsevier.com/retrieve/pii/S0929139323000793>. DOI 10.1016/j.apsoil.2023.104881.
- He, Q., S. Wang, W. Hou, K. Feng, F. Li, W. Hai, Y. Zhang, Y. Sun and Y. Deng, 2021. Temperature and

- microbial interactions drive the deterministic assembly processes in sediments of hot springs. *Science of the Total Environment*, 772: 145465.
- Heděnc, P., H. Zheng, D. Pessanha Siqueira, Q. Lin, Y. Peng, I. Kappel Schmidt, T. Guldborg Frøslev, R. Kjøller, J. Rousk and L. Vesterdal, 2023. Tree species traits and mycorrhizal association shape soil microbial communities via litter quality and species mediated soil properties. *Forest Ecology and Management*, 527: 120608. Available from <https://www.sciencedirect.com/science/article/pii/S0378112722006028>. DOI <https://doi.org/10.1016/j.foreco.2022.120608>.
- Horner-Devine, M.C. and B.J. Bohannan, 2006. Phylogenetic clustering and overdispersion in bacterial communities. *Ecology*, 87(sp7): S100-S108. DOI [https://doi.org/10.1890/0012-9658\(2006\)87\[100:PCAOIB\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[100:PCAOIB]2.0.CO;2).
- Isbell, F., P. Balvanera, A.S. Mori, J.S. He, J.M. Bullock, G.R. Regmi, E.W. Seabloom, S. Ferrier, O.E. Sala and N.R. Guerrero-Ramírez, 2023. Expert perspectives on global biodiversity loss and its drivers and impacts on people. *Frontiers in Ecology and the Environment*, 21(2): 94-103. DOI <https://doi.org/10.1002/fee.2536>.
- Isbell, F., A. Gonzalez, M. Loreau, J. Cowles, S. Díaz, A. Hector, G.M. Mace, D.A. Wardle, M.I. O'Connor and J.E. Duffy, 2017. Linking the influence and dependence of people on biodiversity across scales. *Nature*, 546(7656): 65-72. DOI <https://doi.org/10.1038/nature22899>.
- Jansson, J.K. and K.S. Hofmockel, 2020. Soil microbiomes and climate change. *Nature Reviews Microbiology*, 18(1): 35-46. DOI <https://doi.org/10.1038/s41579-019-0265-7>.
- Jiao, S. and Y. Lu, 2020. Soil pH and temperature regulate assembly processes of abundant and rare bacterial communities in agricultural ecosystems. *Environmental Microbiology*, 22(3): 1052-1065. DOI <https://doi.org/10.1111/1462-2920.14815>.
- Jiao, S., Y. Yang, Y. Xu, J. Zhang and Y. Lu, 2020. Balance between community assembly processes mediates species coexistence in agricultural soil microbiomes across eastern china. *The ISME Journal*, 14(1): 202-216. DOI <https://doi.org/10.1038/s41396-019-0522-9>.
- Karimi, B., C. Meyer, D. Gilbert and N. Bernard, 2016. Air pollution below who levels decreases by 40% the links of terrestrial microbial networks. *Environmental Chemistry Letters*, 14: 467-475. DOI <https://doi.org/10.1007/s10311-016-0589-8>.
- Kembel, S.W., P.D. Cowan, M.R. Helmus, W.K. Cornwell, H. Morlon, D.D. Ackerly, S.P. Blomberg and C.O. Webb, 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26(11): 1463-1464. DOI <https://doi.org/10.1093/bioinformatics/btq166>.
- Labouyrie, M., C. Ballabio, F. Romero, P. Panagos, A. Jones, M.W. Schmid, V. Mikryukov, O. Dulya, L. Tedersoo and M. Bahram, 2023. Patterns in soil microbial diversity across europe. *Nature Communications*, 14(1): 3311. DOI <https://doi.org/10.1038/s41467-023-37937-4>.
- Langenheder, S. and E.S. Lindström, 2019. Factors influencing aquatic and terrestrial bacterial community assembly. *Environmental microbiology reports*, 11(3): 306-315. DOI <https://doi.org/10.1111/1758-2229.12731>.
- Langenheder, S. and A.J. Székely, 2011. Species sorting and neutral processes are both important during the initial assembly of bacterial communities. *The ISME journal*, 5(7): 1086-1094. DOI <https://doi.org/10.1038/ismej.2010.207>.
- Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, 23(11): 1324-1334. DOI <https://doi.org/10.1111/geb.12207>.
- Li, B., W. Tan, L. Wen, X. Zhao, B. Peng, J. Yang, C. Lu, Y. Wang and G. Lei, 2020. Anthropogenic habitat

- alternation significantly decreases α - and β -diversity of benthopelagic metacommunity in a large floodplain lake. *Hydrobiologia*, 847: 293-307. DOI <https://doi.org/10.1007/s10750-019-04091-2>.
- Li, X., J. Zhang, J. Gai, X. Cai, P. Christie and X. Li, 2015. Contribution of arbuscular mycorrhizal fungi of sedges to soil aggregation along an altitudinal alpine grassland gradient on the Tibetan plateau. *Environmental Microbiology*, 17(8): 2841-2857. DOI <https://doi.org/10.1111/1462-2920.12792>.
- Lu, Y., Y. Yang, B. Sun, J. Yuan, M. Yu, N.C. Stenseth, J.M. Bullock and M. Obersteiner, 2020. Spatial variation in biodiversity loss across China under multiple environmental stressors. *Science Advances*, 6(47): eabd0952.
- Luo, R., Y. Kuzyakov, B. Zhu, W. Qiang, Y. Zhang and X. Pang, 2022. Phosphorus addition decreases plant lignin but increases microbial necromass contribution to soil organic carbon in a subalpine forest. *Global Change Biology*, 28(13): 4194-4210. DOI <https://doi.org/10.1111/gcb.16205>.
- Mayor, S., J. Cahill Jr, F. He, P. Solyomos and S. Boutin, 2012. Regional boreal biodiversity peaks at intermediate human disturbance. *Nature Communications*, 3(1): 1142. DOI <https://doi.org/10.1038/ncomms2145>.
- Messier, C., K.J. Puettmann and K.D. Coates, 2013. Managing forests as complex adaptive systems. Building resilience to the challenge of global change. New York: Routledge.
- Mo, L., A. Zanella, C. Bolzonella, A. Squartini, G.-L. Xu, D. Banas, M. Rosatti, E. Longo, M. Pindo, G. Concheri, I. Fritz, G. Ranzani, M. Bellonzi, M. Campagnolo, D. Casarotto, M. Longo, V. Linnyk, L. Ihlein and A.J. Yeomans, 2022. Land use, microorganisms, and soil organic carbon: Putting the pieces together. *Diversity*, 14(8): 638-638. Available from <https://www.mdpi.com/1424-2818/14/8/638>. DOI 10.3390/d14080638.
- Molleman, F., N. Rossignol, J.F. Ponge, G. Peres, D. Cluzeau, N. Ruiz-Camacho, J. Cortet, C. Pernin, C. Villenave and A. Prinzing, 2023. Why phylogenetic signal of traits is important in ecosystems: Uniformity of a plant trait increases soil fauna, but only in a phylogenetically uniform vegetation. *Oecologia*, 202(1): 175-191. Available from <https://link.springer.com/10.1007/s00442-023-05384-z>. DOI 10.1007/s00442-023-05384-z.
- Mougi, A. and M. Kondoh, 2012. Diversity of interaction types and ecological community stability. *Science*, 337(6092): 349-351. DOI <https://doi.org/10.1126/science.12205>.
- Nemergut, D.R., S.K. Schmidt, T. Fukami, S.P. O'Neill, T.M. Bilinski, L.F. Stanish, J.E. Knelman, J.L. Darcy, R.C. Lynch and P. Wickey, 2013. Patterns and processes of microbial community assembly. *Microbiology and Molecular Biology Reviews*, 77(3): 342-356. DOI <https://doi.org/10.1128/mmb.00051-12>.
- Newbold, T., L.N. Hudson, S.L. Hill, S. Contu, I. Lysenko, R.A. Senior, L. Börger, D.J. Bennett, A. Choimes and B. Collen, 2015. Global effects of land use on local terrestrial biodiversity. *Nature*, 520(7545): 45-50. DOI <https://doi.org/10.1038/nature14324>.
- Ofiteru, I.D., M. Lunn, T.P. Curtis, G.F. Wells, C.S. Criddle, C.A. Francis and W.T. Sloan, 2010. Combined niche and neutral effects in a microbial wastewater treatment community. *Proceedings of the National Academy of Sciences*, 107(35): 15345-15350. DOI <https://doi.org/10.1073/pnas.1000604107>.
- Ovaskainen, O., G. Tikhonov, A. Norberg, F. Guillaume Blanchet, L. Duan, D. Dunson, T. Roslin and N. Abrego, 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, 20(5): 561-576. DOI

- <https://doi.org/10.1111/ele.12757>.
- Paradis, E. and K. Schliep, 2019. Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35(3): 526-528. DOI <https://doi.org/10.1093/bioinformatics/bty633>.
- Piva, E. and S. Scortegagna, 1993. Flora e vegetazione del delta del po: Le zone litoranee. Regione Veneto, Segreteria per le attività produttive ed economiche del settore primario.
- Polverigiani, S., M. Franzina and D. Neri, 2018. Effect of soil condition on apple root development and plant resilience in intensive orchards. *Applied Soil Ecology*, 123(in Press): 787-792. Available from <https://doi.org/10.1016/j.apsoil.2017.04.009>
<http://www.sciencedirect.com/science/article/pii/S0929139316306564>. DOI <https://doi.org/10.1016/j.apsoil.2017.04.009>.
- Qiu, L., Q. Zhang, H. Zhu, P.B. Reich, S. Banerjee, M.G.A. van der Heijden, M.J. Sadowsky, S. Ishii, X. Jia, M. Shao, B. Liu, H. Jiao, H. Li and X. Wei, 2021. Erosion reduces soil microbial diversity, network complexity and multifunctionality. *The ISME Journal*, 15(8): 2474-2489. Available from <https://doi.org/10.1038/s41396-021-00913-1>. DOI 10.1038/s41396-021-00913-1.
- Reese, A.T., A. Savage, E. Youngsteadt, K.L. McGuire, A. Kolling, O. Watkins, S.D. Frank and R.R. Dunn, 2016. Urban stress is associated with variation in microbial species composition—but not richness—in manhattan. *The ISME journal*, 10(3): 751-760. DOI <https://doi.org/10.1038/ismej.2015.152>.
- Sanità, N., 1998. Esperienze e nuove esigenze di tutela naturalistica: La vegetazione alofila del “giardino botanico litoraneo” di porto caleri, area di tutela dell’istituendo parco interregionale del delta del po. Regione del Veneto, Assessorato agricoltura e foreste, Servizio forestale di Padova., Padova, Italy.
- Schmidt, T.S.B., J.F. Matias Rodrigues and C. Von Mering, 2017. A family of interaction-adjusted indices of community similarity. *The ISME journal*, 11(3): 791-807. DOI <https://doi.org/10.1038/ismej.2016.139>.
- Scholier, T., A. Lavrinienko, I. Brila, E. Tukalenko, R. Hindström, A. Vasylenko, C. Cayol, F. Ecke, N.J. Singh and J.T. Forsman, 2023. Urban forest soils harbour distinct and more diverse communities of bacteria and fungi compared to less disturbed forest soils. *Molecular Ecology*, 32(2): 504-517. DOI <https://doi.org/10.1111/mec.16754>.
- Sengupta, A., J.C. Stegen, A.A. Meira Neto, Y. Wang, J.W. Neilson, T. Tatarin, E. Hunt, K. Dontsova, J. Chorover and P.A. Troch, 2019. Assessing microbial community patterns during incipient soil formation from basalt. *Journal of Geophysical Research: Biogeosciences*, 124(4): 941-958. DOI <https://doi.org/10.1111/mec.16754>.
- Stegen, J.C., X. Lin, J.K. Fredrickson, X. Chen, D.W. Kennedy, C.J. Murray, M.L. Rockhold and A. Konopka, 2013. Quantifying community assembly processes and identifying features that impose them. *The ISME journal*, 7(11): 2069-2079. DOI <https://doi.org/10.1038/ismej.2013.93>.
- Stegen, J.C., X. Lin, A.E. Konopka and J.K. Fredrickson, 2012. Stochastic and deterministic assembly processes in subsurface microbial communities. *The ISME journal*, 6(9): 1653-1664. DOI <https://doi.org/10.1038/ismej.2012.22>.
- Stomeo, F., A. Valverde, S.B. Pointing, C.P. McKay, K.A. Warren-Rhodes, M.I. Tuffin, M. Seely and D.A. Cowan, 2013. Hypolithic and soil microbial community assembly along an aridity gradient in the namib desert. *Extremophiles*, 17: 329-337. DOI <https://doi.org/10.1007/s00792-013-0519-7>.

- Sun, X., C. Liddicoat, A. Tiunov, B. Wang, Y. Zhang, C. Lu, Z. Li, S. Scheu, M.F. Breed and S. Geisen, 2023. Harnessing soil biodiversity to promote human health in cities. *npj Urban sustainability*, 3(1): 5. DOI <https://doi.org/10.1038/s42949-023-00086-0>.
- Torsvik, V. and L. Øvreås, 2002. Microbial diversity and function in soil: From genes to ecosystems. *Current Opinion in Microbiology*, 5(3): 240-245. Available from <http://www.sciencedirect.com/science/article/pii/S1369527402003247>. DOI [http://dx.doi.org/10.1016/S1369-5274\(02\)00324-7](http://dx.doi.org/10.1016/S1369-5274(02)00324-7).
- Tripathi, B.M., J.C. Stegen, M. Kim, K. Dong, J.M. Adams and Y.K. Lee, 2018. Soil ph mediates the balance between stochastic and deterministic assembly of bacteria. *The ISME journal*, 12(4): 1072-1083. DOI <https://doi.org/10.1038/s41396-018-0082-4>.
- Vega, G.C., P. Convey, K.A. Hughes and M.Á. Olalla-Tárraga, 2020. Humans and wind, shaping antarctic soil arthropod biodiversity. *Insect conservation and diversity*, 13(1): 63-76. DOI <https://doi.org/10.1111/icad.12375>.
- Vellend, M., 2010. Conceptual synthesis in community ecology. *The Quarterly review of biology*, 85(2): 183-206. DOI <https://doi.org/10.1086/652373>.
- Wagg, C., S.F. Bender, F. Widmer and M.G. Van Der Heijden, 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proceedings of the National Academy of Sciences*, 111(14): 5266-5270. DOI <https://doi.org/10.1073/pnas.132005411>.
- Wagg, C., K. Schlaeppi, S. Banerjee, E.E. Kuramae and M.G.A. van der Heijden, 2019. Fungal-bacterial diversity and microbiome complexity predict ecosystem functioning. *Nature Communications*, 10(1): 4841. Available from <https://doi.org/10.1038/s41467-019-12798-y>. DOI [10.1038/s41467-019-12798-y](https://doi.org/10.1038/s41467-019-12798-y).
- Wang, H., M. Cheng, M. Dsouza, P. Weisenhorn, T. Zheng and J.A. Gilbert, 2018. Soil bacterial diversity is associated with human population density in urban greenspaces. *Environmental science & technology*, 52(9): 5115-5124. DOI <https://doi.org/10.1021/acs.est.7b06417>.
- Webb, C.O., 2000. Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *The American Naturalist*, 156(2): 145-155. DOI <https://doi.org/10.1086/303378>.
- WRB, I.W.G., 2022. World reference base for soil resources. International soil classification system for naming soils and creating legends for soil maps 4th edition. 2022. 4th Edn., Vienna, Austria: IUSS - International Union of Soil Sciences.
- Xiong, Y., L. Ruan, Z. Li, S. Dai, Y. Pan, Y. Qiao, Y. Qi and L. Hu, 2021. Changes in metabolic functions of the soil microbial community in eucalyptus plantations along an urban-rural gradient. *Eurasian Soil Science*, 54: 1912-1920. DOI <https://doi.org/10.1021/acs.est.7b06417>.
- Xun, W., W. Li, W. Xiong, Y. Ren, Y. Liu, Y. Miao, Z. Xu, N. Zhang, Q. Shen and R. Zhang, 2019. Diversity-triggered deterministic bacterial assembly constrains community functions. *Nature Communications*, 10(1): 3833. DOI <https://doi.org/10.1038/s41467-019-11787-5>.
- Yang, G., M. Ryo, J. Roy, D.R. Lammel, M.-B. Ballhausen, X. Jing, X. Zhu and M.C. Rillig, 2022. Multiple anthropogenic pressures eliminate the effects of soil microbial diversity on ecosystem functions in experimental microcosms. *Nature Communications*, 13(1): 4260. DOI <https://doi.org/10.1038/s41467-022-31936-7>.
- Yang, Y., X. Chen, L. Liu, T. Li, Y. Dou, J. Qiao, Y. Wang, S. An and S.X. Chang, 2022. Nitrogen fertilization weakens the linkage between soil carbon and microbial diversity: A global meta-analysis. *Global Change Biology*, 28(21): 6446-6461. DOI <https://doi.org/10.1111/gcb.16361>.
- Yi, C. and N. Jackson, 2021. A review of measuring ecosystem resilience to disturbance. *Environmental*

Research Letters, 16(5): 053008-053008. Available from
<https://iopscience.iop.org/article/10.1088/1748-9326/abdf09>. DOI 10.1088/1748-9326/abdf09.

- Zanella, A., J.-F. Ponge, B. Jabiol, B. Van Delft, R. De Waal, K. Katzensteiner, E. Kolb, N. Bernier, G. Mei, M. Blouin, J. Juilleret, N. Pousse, S. Stanchi, F. Cesario, R.-C. Le Bayon, D. Tatti, S. Chersich, L. Carollo, M. Englisch, A. Schrötter, J. Schaufler, E. Bonifacio, I. Fritz, A. Sofo, S. Bazot, J.-C. Lata, J.-F. Iffly, C.E. Wetzel, C. Hissler, G. Fabiani, M. Aubert, A. Vacca, G. Serra, C. Menta, F. Visentin, N. Cools, C. Bolzonella, L. Frizzera, R. Zampedri, M. Tomasi, P. Galvan, P. Charzynski, E. Zakharchenko, S.M. Waez-Mousavi, J.-J. Brun, R. Menardi, F. Fontanella, N. Zaminato, S. Carollo, A. Brandolese, M. Bertelle, G. Zanella, T. Bronner, U. Graefe and H. Hager, 2022. A standardized morpho-functional classification of the planet's humipedons. *Soil Systems*, 6(3): 59. Available from <https://www.mdpi.com/2571-8789/6/3/59>. DOI 10.3390/soilsystems6030059.
- Zhang, X., E.R. Johnston, W. Liu, L. Li and X. Han, 2016. Environmental changes affect the assembly of soil bacterial community primarily by mediating stochastic processes. *Global Change Biology*, 22(1): 198-207. DOI <https://doi.org/10.1111/gcb.13080>.
- Zhang, X., W. Liu, Y. Bai, G. Zhang and X. Han, 2011. Nitrogen deposition mediates the effects and importance of chance in changing biodiversity. *Molecular Ecology*, 20(2): 429-438. DOI <https://doi.org/10.1111/j.1365-294X.2010.04933.x>.
- Zhang, Y., L. Cheng, K. Li, L. Zhang, Y. Cai, X. Wang and J. Heino, 2019. Nutrient enrichment homogenizes taxonomic and functional diversity of benthic macroinvertebrate assemblages in shallow lakes. *Limnology and Oceanography*, 64(3): 1047-1058. DOI <https://doi.org/10.1002/lno.11096>.
- Zhang, Y., G. Ji, T. Wu and J. Qiu, 2020. Urbanization significantly impacts the connectivity of soil microbes involved in nitrogen dynamics at a watershed scale. *Environmental Pollution*, 258: 113708. DOI <https://doi.org/10.1016/j.envpol.2019.113708>.

Declarations of interest:

none