How harmful are exotic plantations for soils and its microbiome? A case study in an arid island

Adolfo Perdomo-González [a,*], Raquel Pérez-Reverón [a], Marta Goberna [b], Milagros León-Barrios [c], Manuel Fernández-López [d], Pablo J. Villadas [d], J. Alfredo Reyes-Betancort [e], Francisco J. Díaz-Peña [a,*]

[a] *Departamento de Biología Animal, Edafología y Geología, Universidad de La Laguna, 38200 San Cristóbal de La Laguna, Spain*
[b] *Departamento de Medio Ambiente y Agronomía, Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA-CSIC), Madrid, Spain*
[c] *Departamento de Bioquímica, Microbiología, Biología Celular y Genética, Universidad de La Laguna, 38200 San Cristóbal de La Laguna, Spain*
[d] *Grupo de Microbiología de Ecosistemas Agroforestales, Departamento de Microbiología del Suelo y la Planta, Estación Experimental del Zaidín, CSIC, 18008 Granada, Spain*
[e] *Jardín de Aclimatación de La Orotava, Instituto Canario de Investigaciones Agrarias (ICIA), 38400 Puerto de la Cruz, Spain*

HIGHLIGHTS

- Plantations with exotic species led to similar soil microbial diversity compared to native vegetation.
- Soil microbial communities' composition differed between exotic plantations and preserved native vegetation.
- Microbial activities were higher under native species and denote a higher conservation status.

GRAPHICAL ABSTRACT
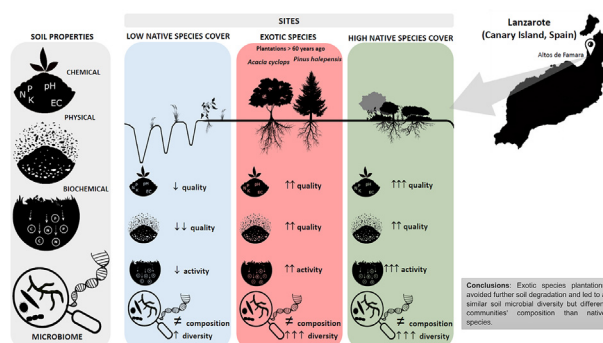
ABSTRACT

The plantation of exotic species has been a common practice in (semi-) arid areas worldwide aiming to restore highly degraded habitats. The effects of these plantations on plant cover or soil erosion have been widely studied, while little attention has been paid to the consequences on soil quality and belowground biological communities. This study evaluates the long-term (>60 years) effects of the exotic species *Acacia cyclops* and *Pinus halepensis* revegetation on soil properties, including microbiome, in an arid island. Soils under exotic plantation were compared to both degraded soils with a very low cover of native species and soils with well-preserved native plant communities. Seven scenarios were selected in a small area (~25 ha) with similar soil type but differing in the plant cover. Topsoils (0–15 cm) were analyzed for physical, chemical and biochemical properties, and amplicon sequencing of bacterial and fungal communities. Microbial diversity was similar among soils with exotic plants and native vegetation (Shannon's index = 5.26 and 5.34, respectively), while the most eroded soils exhibited significantly lower diversity levels (Shannon's index = 4.72). Bacterial and fungal communities' composition in degraded soils greatly differed from those in vegetated soils (Canberra index = 0.85 and 0.92, respectively) likely due to high soil sodicity, fine textures and compaction. Microbial communities' composition also differed in soils covered with exotic and native species, to a greater extent for fungi than for bacteria (Canberra index = 0.94 and 0.89, respectively), due to higher levels of nutrients, microbial biomass and activity in soils with native species. Results suggest that reforestation succeeded in avoiding further soil degradation but still leading to relevant changes in soil microbial community that may have negative effects on ecosystem stability. Information gained in this research could be useful for environmental agencies and decision makers about the controversial replacement of exotic plants in insular territories.

* Corresponding authors.
  E-mail addresses: apgonzalez@ull.edu.es (A. Perdomo-González), fjdiazpe@ull.edu.es (F.J. Díaz-Peña).

1. Introduction

Anthropogenic changes in vegetation cover are altering the dynamics and function, specifically the capacity to provide ecosystem services, of the world's natural ecosystems (IPBES, 2018; Gómez-Aparicio et al., 2022; Navarrete et al., 2023). Traditionally, restoration through the introduction of exotic species has been practiced as a strategy for the rapid structural recovery of degraded habitats, especially in areas where the original vegetation has been completely removed (Liu et al., 2014; Nkonya and Mirzabaev, 2016; Navarro-Cano et al., 2018). Globally, it is estimated that about 44 % of plantation forests, which are intensively managed for productive purposes, are composed mostly of introduced species (i.e., non-native or exotic species; FAO, 2020). The criteria for plant species selection, regardless of their origin, are mainly based on functional attributes of fast growth, high adaptability and reproductive capacity (Navarro-Cano et al., 2018), and often these plantations have been claimed to have positive effects for preventing soil erosion, mitigating global warming, and reducing biodiversity loss (Cifuentes-Croquevielle et al., 2020).

However, the invasion of habitats by exotic species typically represents a major threat to native species by reducing their genetic richness and diversity (Mologni et al., 2021; Stanek et al., 2020). Exotic plants may also trigger several potentially detrimental changes at the ecosystem level, such as modification in soil biological and physical-chemical properties, biogeochemical cycles, biotic homogenization processes and introduction of new pathogens (Cifuentes-Croquevielle et al., 2020; Mologni et al., 2021; Gómez-Aparicio et al., 2022). Those effects are especially pronounced on islands, where native species evolve with few competitors and strong predators due to geographical isolation (Kier et al., 2009; Mologni et al., 2021). This is the case of the Canary Islands Archipelago, a hotspot of biodiversity (Otto et al., 2012), where introduced plant species have been used for the revegetation of degraded arid and semiarid habitats (Kelt and Meserve, 2016). In particular, two tree species have served this purpose: *Acacia cyclops* A. Cunn. ex Don, a coastal shrub recognised for its highly invasive character and to endanger native species (Boudiaf et al., 2013; Cross et al., 2020), and *Pinus halepensis* Mill., a generalist conifer distributed in the north-western Mediterranean region, that has the ability to grow on different types of soil and actively colonize degraded areas, such as those affected by fires or human activities (Tatoni et al., 2005). The consequences of this introduction in the plant communities of the islands have been poorly studied (Arteaga et al., 2009; Bello-Rodríguez et al., 2020), and even to a lesser extent has the impact on soil properties and belowground diversity been assessed.

Among the ecological consequences of exotic plant plantation, the soil microbiome could be affected both directly, due to the new plant-microbe interactions, and indirectly through changes in the soil environment such as soil moisture, nutrient availability, and pH levels (Trentini et al., 2020). These variations can influence the biomass, activity and composition of soil microorganisms, which might in turn modify some soil properties such as aggregate stability, structure, nutrient availability and organic matter turnover rates (Hassani et al., 2018; Navarrete et al., 2023). It is well-known that plant species identity impacts soil microbial communities, which respond to variation in plant traits across species that change the quantity and quality of organic inputs into the soil, as well as the microclimatic conditions (e.g. water content and temperature) (Raposeiro et al., 2014; Fierer, 2017; Colin et al., 2019; Fernández-González et al., 2019). However, it is not clear how widely are the effects of exotics plants on soil properties and contradictory results have been reported depending on species composition and cover type, climate, soil environment, and interactions between native and exotic species (Zhou and Staver, 2019; McLeod et al., 2021; Xu et al., 2022). Additionally, the time elapsed after plantations can also play an important role (Li et al., 2015). Assessing these impacts provides essential information on soil processes (e.g., nutrient cycling, organic matter decomposition) that allows predicting the evolution of the dynamics and function of disturbed ecosystems (Vieira et al., 2022).

In order to fill in the knowledge gap on the impact of planted exotic species on the soil microbiome of arid insular territories, this study evaluates the long-term (>60 years) effects of revegetating with *A. cyclops* and *P. halepensis* in comparison to both degraded soils (i.e., soils with very low native vegetation cover and under intense erosion processes) and preserved or recovered native communities (i.e., soils with high coverage of remnant native vegetation). We studied a small area (~25 ha) of high ecological value with uniform edaphoclimatic conditions, with the aim to: *i)* determine the extent to which exotic and native plants harbor different bacterial and fungal communities, and *ii)* identify the main soil abiotic predictors of bacterial and fungal community composition, and their impact on main soil functions related to organic matter decomposition (respiration rates) and nutrient cycling (enzymatic activities). Based on the poor observed effects of introduced *Pinus* and *Acacia* species on the soil conditions in long-term monospecific plantations in their natural distribution areas (e.g., Goberna et al., 2007; Derbel et al., 2009), we hypothesized that exotic plant species are not able to restore the soil conditions and microbial communities under more stressful environments such as that in the study area.

## 2. Material and methods

2.1. Study area

This study was carried out on Lanzarote, the northeastern most island of the Canary Island Archipelago (Spain), located in the Atlantic Ocean between 29° 14′ 41″ and 28° 50′ 28″ N and 13° 28′ 06″ and 13° 47′ 46″ W, and approximately 130 km of NW African coast (Fig. 1a). It is 862 km² in size and formed by basaltic volcanic rocks. Most parts of the island receive an average of 150 mm of rainfall per year with no parts receiving >250 mm. The rainfall is seasonal, from October to March, with high inter-annual variability. Mean monthly temperature ranges from 17.5 to 25.2 °C (AEMET 2022), with elevated solar radiation intensity (annual average of ~8 h sunshine per day) and an annual average wind speed of approximately 5–7 m s^{-1}. The combination of these climatic factors leads to high potential evapotranspiration rates (ET$_o$ ~ 1200–1400 mm year^{-1}) (Stevenson et al., 2021). There is also high relative humidity (above 80 %) and considerable day–night temperature fluctuations (Tejedor et al., 2004). The Aridity Index calculated as the ratio P/PET varies between 0.05 and 0.2 which allows classifying Lanzarote as arid land (Cherlet et al., 2018).

This territory is heavily affected and threatened by desertification and particularly by water erosion processes (Tejedor et al., 2003). Current distribution of the vegetation derives from extreme aridity and a history of extensive agriculture, grazing and timber harvesting, so that only 24 % of all the potential vegetation and just 9.3 % of the climatophilous vegetation remains (del Arco Aguilar et al., 2010).

The soil study was conducted on a landscape known as Altos de Famara, which is part of the Archipelago Chinijo Natural Park, and located in the northern coast of the Lanzarote island (Fig. 1a). This area is a cliff-top plain at approximately 580 m above sea level and it has a surface of about 25 ha (Supplemental Fig. S1). The soils can be classified as Paleargids and Calciargids (Aridisols; Soil Survey Staff, 2014). These soils are highly susceptible to water erosion processes, which limits its productive potential, mainly due to the high clay content that decreases infiltration and permeability to water, generating even in areas with low to moderate slopes (1–5 %) and without vegetation coverage numerous streams and gullies (*Badland*). As is typical for drylands, native vegetation forms scattered plant patches including ephemeral grasses, xerophytic shrubs and thermosclerophyllous scrubs (Stevenson et al., 2021).

2.2. Experimental design

Seven different sites were delimited in the study area according to the type of vegetation (Fig. 1b). Two degraded sites with very low native vegetation coverage: (1) *Badland*, highly eroded soils with a vegetation cover <2 % (mainly *Launaea arborescens, Frankenia ericifolia, Helianthemum canariense, Sonchus pinnatifidus* and *Aeonium lancerottense*); and (2) *Plain,*
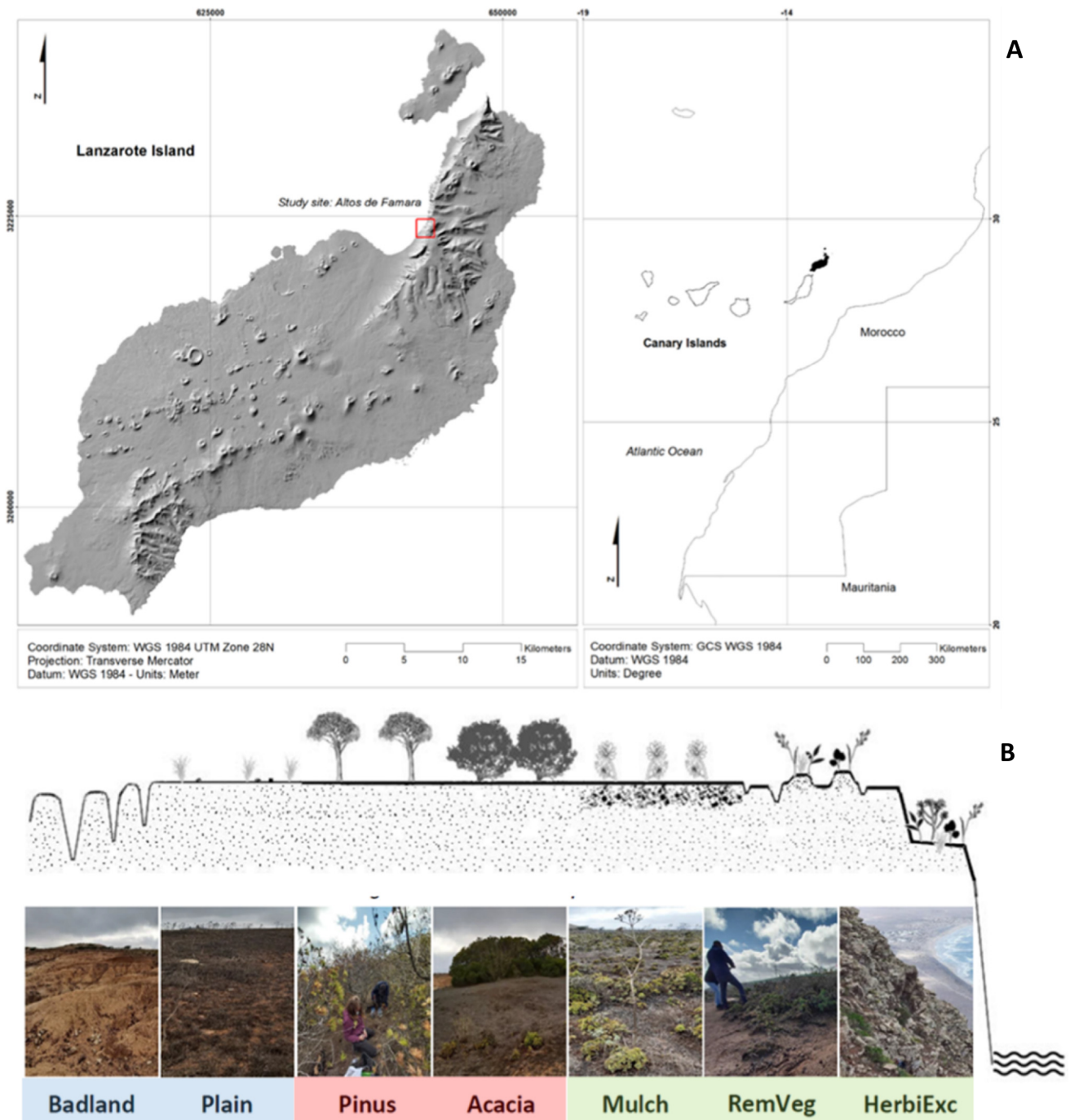
Fig. 1. (A) Location of the Canary Islands Archipelago, Lanzarote Island, and study area (Altos de Famara). Image obtained using ArcGIS Desktop software (ESTI's ArcGIS Desktop 10.8 software). (B) Experimental sites in the study area. Low native species cover: "*Badland*" badlands soils; "*Plain*" sheet erosion affected soil with seasonal vegetation (blue). Exotic species: "*Pinus*" *Pinus halepensis* reforested soils; "*Acacia*" *Acacia cyclops* reforested soils (red). High native species cover: "*Mulch*" lithic-mulch soil recolonised by native vegetation; "*RemVeg*" soils with remnant vegetation (native plants isolated cores); "*HerbiExc*" soils with herbivory exclusion supporting native vegetation (green).

soils affected by sheet and rill erosion and with intermittent seasonal vegetation which at the time of sampling covered ~5 % (mainly *Helianthemum canariense, Scorpiurus sulcatus, Dipcadi serotinum, Emex spinosa, Ferula lancerottensis* and *Erodium* sp.). Two plantation sites with exotic plants: (3) *Pinus*, soils planted 60 years ago with *Pinus halepensis* showing an average cover of 95 % (mainly *Ferula lancerottensis, Helianthemum canariense, Sonchus pinnatifidus, Allium canariense,* and *Asteriscus intermedius* as companion species); and (4) *Acacia*, soils planted about 60 years ago with *Acacia cyclops* presenting an average cover of 90 % (mainly *Ferula lancerottensis, Asteriscus intermedius, Asparagus horridus,* and *Euphorbia regis-jubae* as

companion species). And three sites with high native vegetation coverage: (5) *Mulch,* lithic-mulch soils from farmlands abandoned about 50 years ago and recolonised by native plants (55 % of vegetation coverage) such as *Aeonium lancerottense, Asteriscus intermedius, Sonchus pinnatifidus, Fagonia cretica, Helianthemum canariense, Euphorbia regis-jubae,* and *Ferula lancerottensis*; (6) RemVeg, isolated cores of soils with remnant native vegetation (90 % average coverage), that have been protected from water erosion due to the presence of nurse plant species not palatable to herbivores and with very deep root systems such as *Lycium intricatum* (mainly *Sonchus pinnatifidus, Aeonium lancerottense, Euphorbia regis-jubae, Asparagus horridus,*

Asteriscus intermedius, Bupleurum handiense and *Kleinia neriifolia* as companion species*;* and (7) *HerbiExc*, soils located on the cliff ledge, and thus naturally avoiding anthropogenic and herbivore disturbance, presenting a rich native flora (around 26 species; 75 % of vegetation cover) that in many cases have disappeared from other parts of the island (Fig. 1b). A full plant inventory is included in Table S1 of the Supplementary Material. All the vascular plant species in the different sites were listed and total vegetation cover (percentage) was visually quantified as described in Arévalo et al. (2016). The authority of plant species follows those of BIOTA (2022).

2.3. Soil sampling

Within each of the seven chosen sites, ten plots 2.5 × 2.5 m in size were established. The average distance between plots taking all sites was 322.3 ± 210.3 m, and the average distance between plots within each site was: *Badland*, 203.6 ± 121.5 m; *Plain*, 121.8 ± 75.7 m; *Pinus*, 15.3 ± 7.4 m; *Acacia*, 180.4 ± 145.6 m; *Mulch*, 40.9 ± 19.9 m; *RemVeg*, 181.9 ± 125.8 m; and *HerbiExc*, 446.1 ± 266.0 m. Soil samples were collected in December 2020 after the first rain event of the season in order to find an enhanced microbial activity. Each plot was divided into four quadrants and a topsoil sample (0–15 cm) was taken at the centre of each quadrant and combined to form a single composite sample per plot for subsequent analysis (N = 70). Samples were stored at 4 °C and transported to laboratory. Soil samples were homogenized, sieved (<2 mm) and divided into three subsamples: one was stored at room temperature for physical and chemical analysis, another one was stored at 4 °C for biochemical analysis, and the third subsample was stored at −20 °C for DNA extraction. Analysis was performed in the next four weeks following the sampling date. Additionally, one soil sample per plot was collected from the topsoil (5–10 cm depth) using stainless-steel core samplers (5 cm in diameter and 5 cm height) to determine bulk density.

2.4. Physical, chemical and biochemical soil characterization

Soil samples were air-dried and the following parameters were assessed: particle size (i.e., sand, silt and clay) using a hydrometer; pH and electrical conductivity (EC) in saturated paste extracts; soluble cations (Ca^{2+}, Mg^{2+}, Na^+, and K^+) in saturated paste extract by ion chromatography; sodium adsorption ratio (SAR) from Ca^{2+}, Mg^{2+} and Na^+ concentrations in the saturated paste extract; exchangeable sodium percentage (ESP_c) was indirectly calculated from SAR values (U.S. Salinity Laboratory Staff, 1969); calcium carbonate equivalent ($CaCO_3$) using gravimetric determination by reaction with hydrochloric acid; soil organic carbon (SOC) by chromic acid wet oxidation method; soil labile organic carbon (SLOC) by potassium permanganate oxidation (Weil et al., 2003); total nitrogen content (N) by dried combustion and measurement in the resulting gases with a thermoconductivity cell from LECO CN828 equipment; available phosphorus (P) by the Olsen method; and bulk density (BD) was determined from weighing soil cores after drying at 105 °C during 24 h. All physical and chemical analyses were performed following Standard Methods (Soil Survey Staff, 1996).

Regarding the biochemical parameters, microbial biomass carbon (MBC) was determined by the fumigation-extraction method from Vance et al. (1987); soil basal respiration (BR) was estimated based on the method of Öhlinger (1993) by direct measurement of CO_2 trapped in an alkali solution incubated at 28 °C for three days together with 50 g of sieved soil at 60 % humidity of its field capacity; β-glucosidase activity (bGlu) was obtained by the method of Strobl and Traunmüller (1993); Urease activity (Ure) was carried out as described by Kandeler and Gerber (1988); and alkaline phosphatase (Phosp) using the method proposed by Tabatabai and Bremner (1969).

2.5. DNA extraction and bacterial and fungal sequencing

Soil bacterial and fungal communities were analyzed using 16S rRNA and ITS2 region deep sequencing. DNA was extracted from each sample using the Power Soil DNA Isolation kit (MoBio, Laboratories Inc., CA) and stored at −80 °C until sequencing. Extracted DNA was checked, quantified, and sent for sequencing with the Illumina MiSeq platform. A prokaryotic library was constructed by amplifying the hyper-variable regions V3-V4 of the 16S rRNA gene, and another eukaryotic library was constructed by amplifying the ITS2 region. Raw sequences were processed following the workflow created by Wentzien (2021). Taxonomy was assigned with the Ribosomal Data Base Project (RDP-II). Sequences <0.005 % of total counts were removed. The prokaryotic dataset had 2,273,263 reads classified as Bacteria and clustered in 3480 ASVs, and the eukaryotic dataset had 4,679,804 reads classified as fungi and clustered in 1490 ASVs. All community ASV tables were rarefied to the minimum library size prior to analysis (10,309 for bacteria and 13,991 for fungi). For complete information on the extraction and sequencing of DNA and the processing of genetic data, see extension of the section in Supplementary Material.

2.6. Statistical analysis

Statistical methods were performed using R version 4.1.2 (R Core Team, n.d.). Significant differences in soil properties, biodiversity index (Shannon index) and phyla relative abundances between study sites were assessed by one-way ANOVA followed by the *post-hoc* Tukey HSD. The non-parametric Kruskal-Wallis test with Nemenyi *post-hoc* was applied when parameters did not conform to a normal distribution (Shapiro-Wilk normality test) and homogeneity of variance (Bartlett test). Differences between sites in the structure of microbial communities were determined by permutational multivariate analysis of variance (PERMANOVA). To assess compositional differences between communities Canberra dissimilarity index (values closer to 1.00 indicates greater dissimilarity; Legendre and Legendre, 2012) were calculated using the R vegan 2.5-7 package (Oksanen et al., 2020).

2.7. Data visualization

Non-metric multi-dimensional scaling (NMDS) analysis of bacterial and fungal community's composition among seven study sites and its correlation with soil parameters and microbial functions were performed based on Canberra distance using the metaMDS and "envfit" functions from the R *vegan 2.5-7* package (Oksanen et al., 2020). Hierarchically clustered heatmaps were developed based on the standard Euclidean distance with the Microbiome Analyst web server (Dhariwal et al., 2017; Chong et al., 2020) in order to display bacterial and fungal families that exhibited relevant changes in abundance among sites. Due to the large number of families of microorganisms detected in the studied soils (a total of 168 bacteria and 159 fungi), about fifty from each kingdom were selected to simplify the results. This selection was made according to their dominance which is determined by low count filtering (based on the prevalence of a number of reads in a percentage of the plots) and low variance filtering (using inter-quantile range -IQR- groups with lowest variance were excluded).

3. Results

3.1. Soil properties

The results for physical, chemical and biochemical properties of the top 15 cm depth layer in soils planted with exotic species and adjacent soils with low and high native vegetation coverage are shown in Table 1. All soils were rich in fine particles (clay to clay loam textures) with clay contents ranging from 33 % in *Mulch* to 62 % in *Badland*. BD average values were around 1.0–1.1 g cm⁻³ for most sites with the exception of *Badland* where it reached 1.7 g cm⁻³ in some samples and soils of *HerbiExc* where BD averaged 0.8 g cm⁻³. Soil reaction ranged from slightly to moderately alkaline (average pH 7.7–8.2), with soils of *Acacia* showing the lowest value. Calcium carbonate was present in all sites varying in content from 18.8 g kg⁻¹ in *Mulch* to 258 g kg⁻¹ in *Badland*. According to EC average values, *Plain* and *Mulch* soils can be considered non-saline (<2 dS m⁻¹),

Table 1

Soil physical, chemical and biochemical properties from the seven sites (n = 10). Data are mean ± standard deviation; different letters indicate significant differences among sites ($p < 0.05$).

Soil properties/sites	Low native species cover		Exotic species		High native species cover		
	Badland	*Plain*	*Pinus*	*Acacia*	*Mulch*	*RemVeg*	*HerbiExc*
Texture	Clay	Clay	Clay	Clay	Clay-loam	Clay	Clay-loam
Sand (g kg^{-1})	129.6 ± 22.6 a	122.1 ± 19.2 a	228.7 ± 32.4 b	172.9 ± 29.2 ab	398.2 ± 54.9 c	228.0 ± 31.6 b	401.1 ± 124.8 c
Silt (g kg^{-1})	256.0 ± 20.3 a	318.3 ± 18.0 b	256.8 ± 11.0 a	321.0 ± 23.5 b	268.8 ± 22.8 a	272.6 ± 30.0 a	248.6 ± 44.3 a
Clay (g kg^{-1})	614.4 ± 41.0 c	559.6 ± 21.4 bc	514.5 ± 30.8 b	506.1 ± 35.6 b	333.0 ± 38.5 a	499.4 ± 44.4 b	350.2 ± 93.1 a
BD (g cm^{-3})	1.4 ± 0.2 c	1.1 ± 0.1 b	1.0 ± 0.1 b	1.0 ± 0.1 ab	1.1 ± 0.1 b	1.0 ± 0.2 ab	0.8 ± 0.1 a
CaCO$_3$ (g kg^{-1})	257.8 ± 124.1 d	24.8 ± 19.1 ab	188.3 ± 39.6 cd	58.9 ± 60.9 ab	18.8 ± 7.7 a	179.9 ± 95.2 cd	117.9 ± 69.4 bc
pH	8.1 ± 0.3 cd	8.2 ± 0.3 d	7.9 ± 0.1 abc	7.7 ± 0.1 a	7.9 ± 0.1 ab	7.8 ± 0.1 a	8.1 ± 0.2 bd
EC (dS m^{-1})	5.9 ± 2.2 b	1.1 ± 0.2 a	2.2 ± 0.6 a	5.0 ± 1.3 b	1.7 ± 0.3 a	5.4 ± 1.5 b	4.7 ± 1.7 b
SOC (g kg^{-1})	3.2 ± 0.7 a	6.0 ± 2.4 ab	18.3 ± 2.8 bc	29.0 ± 8.3 cd	31.9 ± 10.6 d	38.2 ± 13.0 d	40.4 ± 16.4 d
SLOC (mg kg^{-1})	14.9 ± 26.3 a	151.2 ± 97.2 a	554.5 ± 100.6 b	638.0 ± 177.1 b	585.5 ± 69.0 b	786.5 ± 259.3 bc	1032.7 ± 452.6 c
ESP$_c$ (%)	23.6 ± 5.0	13.6 ± 2.0 a	12.3 ± 0.3 a	10.8 ± 0.6 a	12.1 ± 1.3 a	12.3 ± 1.3 a	13.0 ± 3.9 a
N (g kg^{-1})	0.4 ± 0.1 a	1.1 ± 0.1 a	1.1 ± 0.2 a	2.0 ± 0.4 b	2.5 ± 0.5 bc	2.7 ± 1.0 bc	3.3 ± 1.1 c
P (mg kg^{-1})	4.0 ± 0.9 a	2.9 ± 1.0 a	5.9 ± 0.9 ab	8.3 ± 2.8 ab	15.3 ± 4.6 b	12.6 ± 4.3 ab	30.5 ± 18.2 c
MBC (mg kg^{-1})	356.1 ± 103.4 a	679.8 ± 218.5 a	1425.9 ± 197.6 b	1374.8 ± 620.1 b	1561.1 ± 421.9 b	1609.8 ± 448.5 b	2408.5 ± 789.0 c
BR (mg$_{C-CO_2}$ kg^{-1} d^{-1})	16.6 ± 2.7 a	17.7 ± 2.1 a	25.5 ± 1.7 ab	25.8 ± 1.8 ab	31.0 ± 6.8 bc	37.6 ± 7.1 c	52.0 ± 18.4 d
bGlu (nmol$_{saligenin}$ g^{-1} h^{-1})	0.1 ± 0.0 a	0.1 ± 0.1 ab	0.3 ± 0.0 bc	0.3 ± 0.1 cd	0.4 ± 0.1 cd	0.5 ± 0.1 d	0.7 ± 0.3 e
Ure (nmol$_{ammonia}$ g^{-1} h^{-1})	0.1 ± 0.1 a	0.7 ± 0.4 ab	1.4 ± 0.2 bc	1.6 ± 0.4 cd	2.4 ± 0.5 e	2.2 ± 0.5 de	3.9 ± 1.2 f
Phosp (nmol$_{p\ nitrophenol}$ g^{-1} h^{-1})	0.3 ± 0.1 a	1.9 ± 1.0 ab	3.1 ± 0.6 bc	5.5 ± 1.5 de	4.2 ± 1.2 cd	7.1 ± 2.2 e	7.1 ± 1.3 e

"BD" bulk density; "CaCO$_3$" calcium carbonate equivalent; "EC" electrical conductivity; "SOC" soil organic carbon; "SLOC" soil labile organic carbon; "ESP$_c$" exchangeable sodium percentage; "N" total nitrogen content; "P" available phosphorus content; "MBC" microbial biomass carbon; "BR" basal respiration; "bGlu" beta-glucosidase activity; "Ure" urease activity; "Phosp" phospho-monoesterase (alkaline phosphatase) activity. Low native species cover: "*Badland*" badlands soils; "*Plain*" sheet erosion affected soil with seasonal vegetation. Exotic species: "*Pinus*" *Pinus halepensis* reforested soils; "*Acacia*" *Acacia cyclops* reforested soils. High native species cover: "*Mulch*" lithic-mulch soil recolonised by native vegetation; "*RemVeg*" soils with remnant vegetation (native plants isolated cores); "*HerbiExc*" soils with herbivory exclusion supporting native vegetation. F-values and significance levels are shown in Table S3.

Pinus soils were slightly saline (2–4 dS m^{-1}) and *Acacia*, *RemVeg*, *HerbiExc* and *Badland* were saline soils (4–8 dS m^{-1}). Highest salinity level was found in *Badland* site reaching maximum values of 9.3 dS m^{-1} in some samples. Soil solution was dominated by Na$^+$ and Cl$^-$ (data not shown) suggesting that the origin of the salts is the incidence of marine spray. Exchangeable sodium percentage was significantly higher in most degraded soils (*Badland*) and decreased by a factor of 2 in the rest of sites (23 vs.12 %). As expected, due to limited carbon sources, SOC and SLOC content were very low in soils devoid of permanent vegetation (i.e., *Badland* and *Plain*). Higher carbon contents were found in the rest of sites showing a gradual increase in the average values from exotic vegetation to native vegetation (e.g., average of 23.6 g kg^{-1} SOC in exotic vegetation cover vs. 36.9 g kg^{-1} in high native vegetation cover). Lowest concentration of nutrients N and P were found in *Badland*, *Plain* and *Pinus* (averages ranging from 0.4 to 1.1 g N kg^{-1}, and 4.0 to 5.9 mg P kg^{-1}). For the rest of sites, the mean levels of N and P increased reaching the highest values in *HerbiExc* (~3.3 g N kg^{-1} and 30 mg P kg^{-1}) which were significantly different from *Badland*, *Plain*, *Pinus* and *Acacia*. Soil MBC and BR rates increased from low native species cover followed by exotic species and high native species cover. Specifically, the MBC increased by a factor of 2.7 and 3.6 in exotic vegetation cover and dense native vegetation cover respectively, with regard to low native vegetation cover. In the case of BR, the increase factors were 1.5 and 2.3. Enzymes activities exhibited the same trend as MBC and BR (Table 1).

3.2. Microbial diversity and community structure

Bacterial Shannon index differed significantly across sites (Kruskal-Wallis chi-squared = 38.245, df = 6, p = 1.006e-06), although just *Badland* soils, with the lowest bacterial diversity (Shannon index = 5.5 ± 0.4), was significantly different from the rest of sites (Fig. 2a). No significant differences ($p > 0.05$) were detected in bacterial α-diversity between soils with exotic species (*Pinus* and *Acacia*) and high native species cover (*Mulch*, *RemVeg* and *HerbiExc*). A similar trend was observed for fungal α-diversity (Kruskal-Wallis chi-squared = 28.91, df = 6, p = 6.327e-05; Fig. 2b).

Soil microbial communities' structure varied significantly across sites for both bacteria (PERMANOVA; R^2 = 0.543; $p < 0.001$) and fungi

(R^2 = 0.45; $p < 0.001$). Clustering of samples based on the type of plant cover can be visualized through NMDS analyses (Fig. 3). Both for bacteria and fungi, *Badland* and *Plain* soil communities were clearly discriminated from the rest. This was mainly explained by their high contents in exchangeable sodium and clay, as well as their high bulk density. Soils covered with exotics (i.e., *Pinus* and *Acacia*) tended to cluster together and separate from those covered with native species, although this trend was clearer for fungi than for bacteria. This separation responded to the higher levels of salts (EC), nutrients (P), microbial biomass (MBC) and activity (BR, Phosp) in soils covered with native vegetation.

The Canberra dissimilarity index also revealed differences in microbial communities among site types. For bacteria, mean dissimilarity values were 0.88 (Low native cover vs. Exotic plantations), 0.83 (Low native cover vs. High native cover), and 0.89 (Exotic plantations vs. High native cover). For fungi, the mean values were 0.93, 0.91, and 0.94, respectively. A comparison to check the effects of the bareness in soil (Low native cover vs. the combined Exotic plantations and High native cover sites) was 0.85 for bacteria and 0.92 for fungi.

3.3. Microbial community composition

3.3.1. Bacteria

The taxonomic profile at the phylum level varied between soils with different vegetation cover and density (Fig. 4 and Table S2). The predominant bacteria phyla (up to 90 % of the total abundance) were *Actinobacteria*, *Proteobacteria*, *Acidobacteria*, *Bacteroidetes*, *Gemmatimonadetes*, candidate_division_WPS-1, *Chloroflexi* and *Verrucomicrobia* in all sites (Fig. 4). *Cyanobacteria* were included in "others" but reached >1 % only in *Badland* and *Plain* soils (23 % and 14 %, respectively). The relative abundances and differences for these and other phyla are reported in Table S2 in the *Supplementary Material*, where also the dominant groups are further explored in Figs. S2 and S3.

Some main bacteria phyla from soils with low native species cover showed significant differences compared to exotic species and high native species cover (Table S2). For example, *Gemmatimonadetes* and *Chloroflexi* were detected to be significantly more abundant in *Badland* (11 % and 6 %, respectively). In contrast, *Acidobacteria* decreased by up to a factor of 2.8 and 2.0 in *Badland* compared to exotic species and high native species
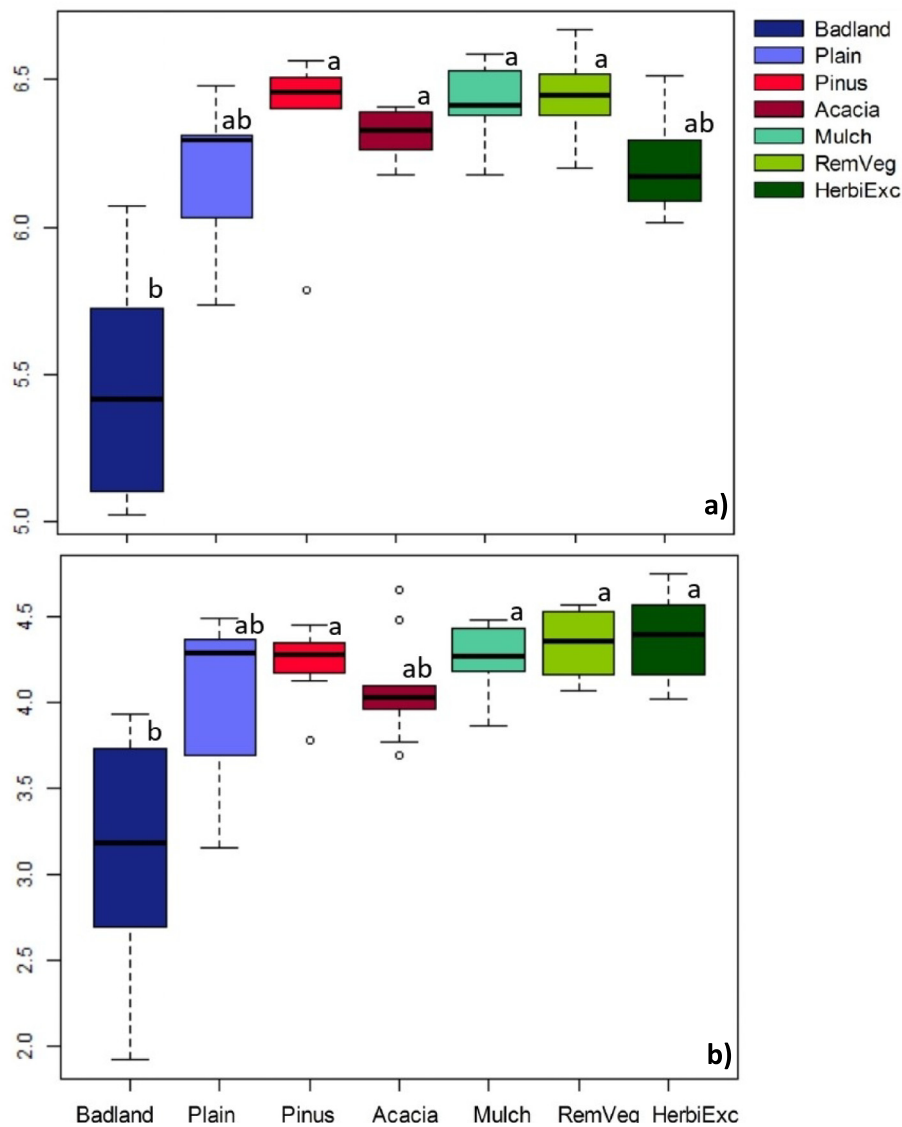
Fig. 2. Shannon index for α-diversity of the soil bacterial (a) and fungal (b) community from the seven study sites; n = 10 for each boxplot; boxes represent the middle 50 % of the data (interquartile range), with the line inside the box representing the median; the whiskers show the range of the data excluding outliers represented as isolated circles; different letters indicate significant differences among study sites ($p < 0.05$).

cover, respectively (Fig. 4). Significant differences in phyla between exotic species and high native species cover were less frequent. Particularly, *Bacteroidetes* were more abundant in high native vegetated soils, with significantly higher values in *RemVeg* and *HerbiExc* soils (9 % in both cases). The opposite behavior was observed for Verrucomicrobia, which presented the lowest values in exotic vegetated soils (~1 % in *Pinus* and *Acacia*). Within soils with low native species cover, *Actinobacteria* were richest in the orders *Acidimicrobiales*, *Rubrobacterales* and *Egibacterales*. In soils with exotic species, *Gaiellales* and *Jiangellales* were especially abundant. While it was observed that *Mycobacteriales* and *Geodermatophilales* dominated in soils with higher native species diversity (Fig. S2).

In the bacterial heatmap (Fig. 5), seven clusters were identified according to the behavior of their family abundances. Families included in clusters 1 (e.g., *Blastocatellaceae* and *Rubrobacteraceae*) dominated in soils with low and high native vegetation cover, especially in *Badland* and *HerbiExc* soils. Families from cluster 4 (e.g., *Reyranellaceae* and *Bradyrhizobiaceae*) were abundant in exotic species, especially in *Acacia* samples. High native species cover was rich in families such as *Rhizobiaceae* and *Sphaerobacteraceae* from cluster 7.

3.3.2. Fungi

Predominant fungal phyla were *Ascomycota, Basidiomycota, Mortierellomycota* and *Chytridiomycota*. Except in *Badland*, in all sites almost 85 % of the fungi belonged to the phylum *Ascomycota* (Fig. 6 and Table S2). In *Badland* soil, *Ascomycota, Basidiomycota* and *Mortierellomycota* presented the lowest relative abundances (0.68, 0.04, and 0.01 %, respectively) with respect to soils with higher plant cover (Fig. 6 and Table S2). Soils with exotic plantations differed from the rest in two specific phyla, *Basidiomycota*, that accounted for up to 30 % of the fungi in some *Pinus* soil samples (Fig. 6), and *Mortierellomycota* that reached an average of 10 % of the total fungi in *Acacia* soils (Table S2). *Wallemiomycetes* and *Ustilaginomycetes* were particularly abundant in soils with low native species cover. *Pezizomycetes* showed a preference for soils with higher plant cover, especially in those with exotic species, while *Lecanoromycetes* were striking at both extremes of conservation (i.e., *Badland* and *HerbiExc*) (Fig. S3).

Fungal heatmap highlighted seven family clusters (Fig. 7). Cluster 1 and 5 dominated in high native species cover (e.g., *Rhizophlyctidaceae*). Cluster 7 (e.g., *Walleamiaceae*) was associated with low native plant cover. Cluster
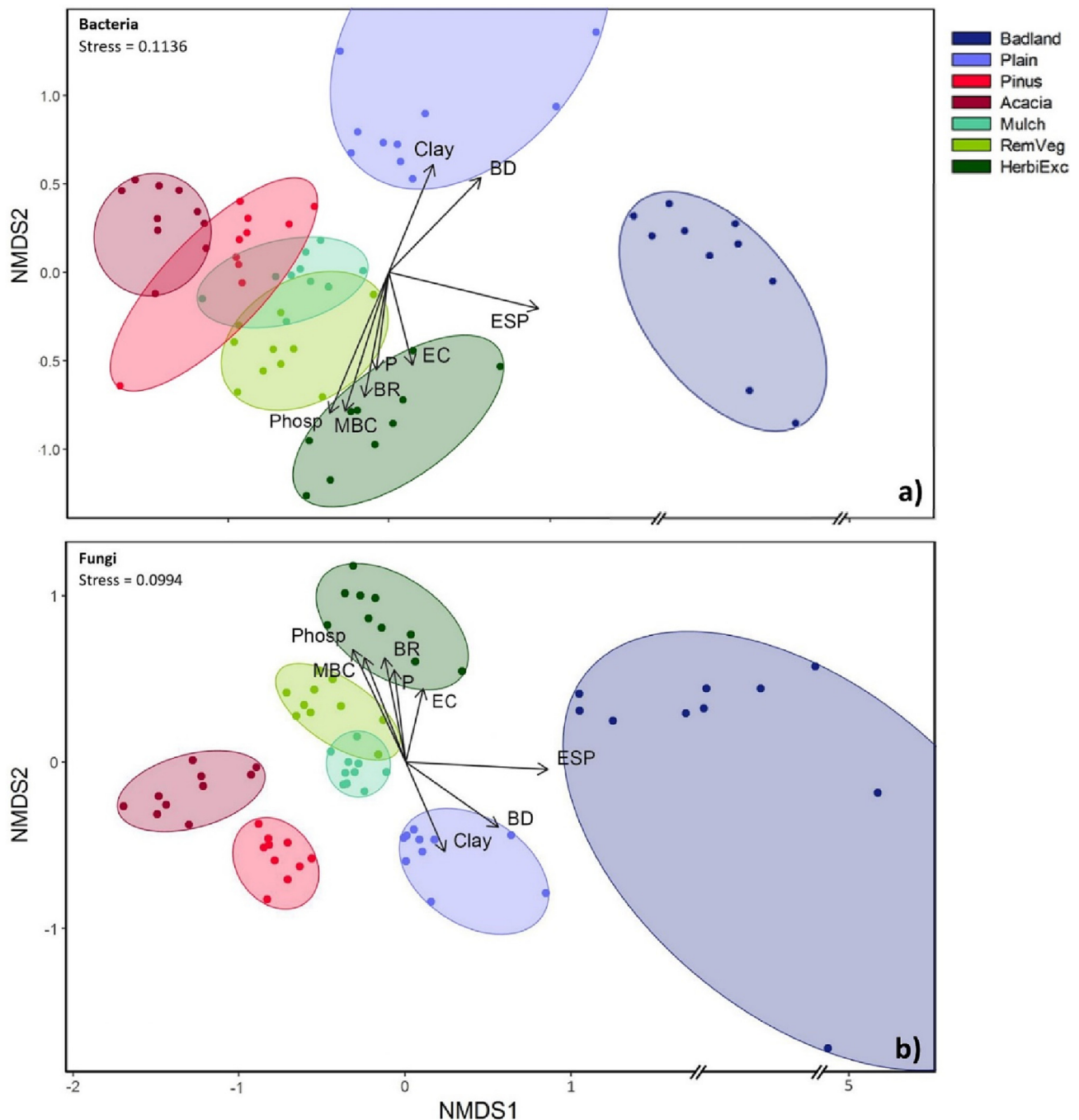
Fig. 3. Non-metric multidimensional scaling (NMDS) analysis based on Canberra distance of bacterial (a) and fungal (b) community from the seven sites. Soil variables were fit to the two-dimensional representation of the microbial communities; soil physical, chemical and biochemical properties are represented by arrows. "BD" bulk density; "EC" electrical conductivity; "P" available phosphorus content; "ESP$_c$" exchangeable sodium percentage; "MBC" microbial biomass carbon; "Phosp" phospho-monoesterase (alkaline phosphatase) activity. The NMDS1 axis was shortened for better visualization.

3 and 6 (e.g., *Chaetomiaceae* and *Clavicipitaceae*) were especially abundant in exotic species (Fig. 7).

4. Discussion

The main goal of this research was to determine if restoration practices with exotic species have influenced soil microbial communities in comparison to reference degraded soils and target ecosystems with remnant native vegetation. We hypothesized that exotic plantations would not be able to successfully restore the physical, chemical, and biological quality of the soil in extreme environments, but the results do not fully support this initial

hypothesis. Results globally show that exotic plantations have led soil microbial communities to an intermediate conservation status between those two reference situations. This suggests that reforestation succeeded in avoiding further degradation of soils but still leading to relevant changes in soil microbial community composition with regard to native soils that may have negative effects on ecosystem stability.

4.1. Influence in soil properties

Several studies have shown that changes in vegetation alter soil properties, but there is strong controversy over the long-term role of exotic plants
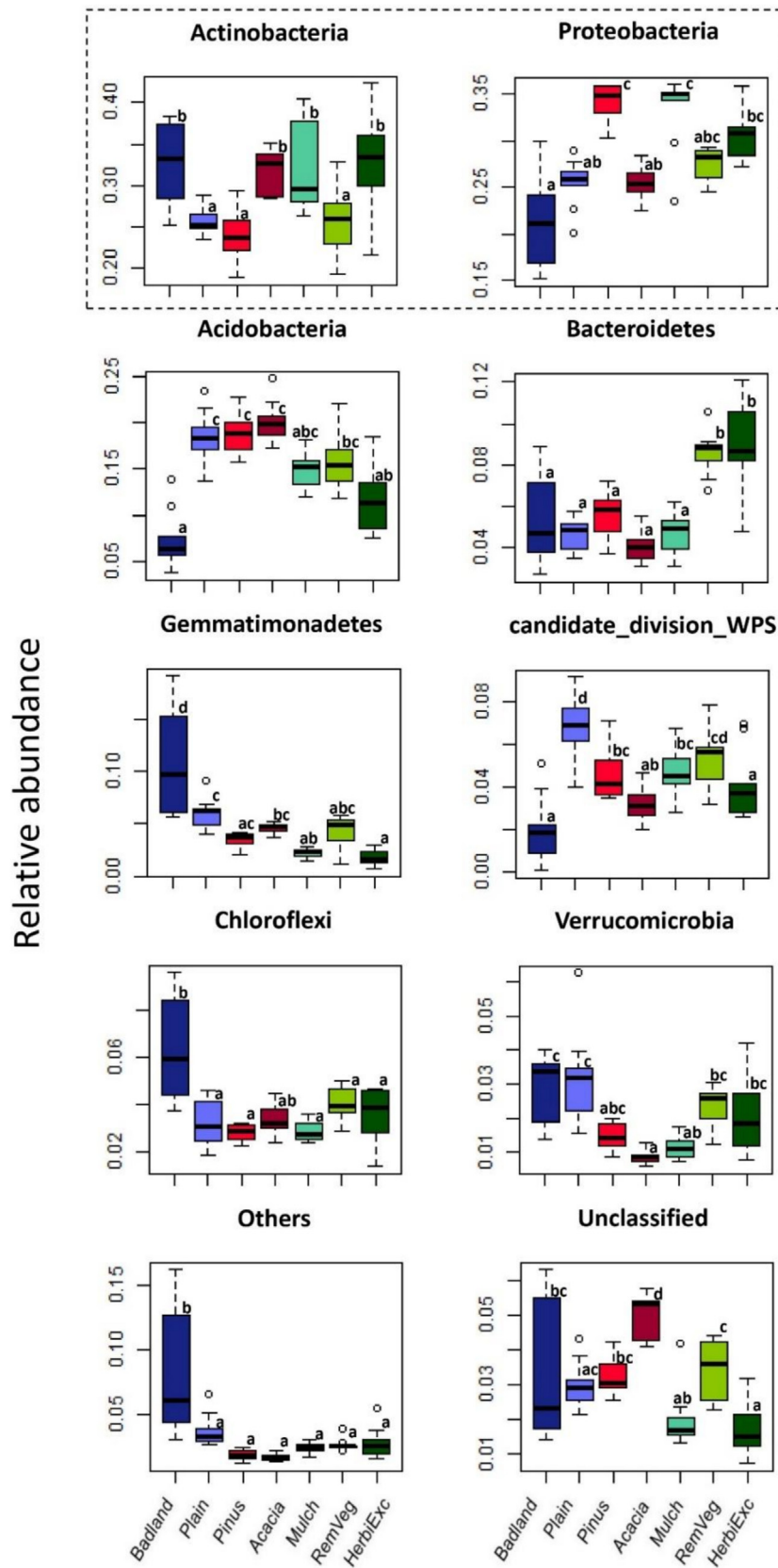
Fig. 4. Quantitative contribution of the sequences affiliated with different soil bacterial phyla to the total number of sequences in the seven sites; n = 10 for each boxplot; boxes represent the middle 50 % of the data (interquartile range), with the line inside the box representing the median; the whiskers show the range of the data excluding outliers represented as isolated circles; different letters indicate significant differences among study sites ($p < 0.05$). Sequences not classified to any known phylum are included as "unclassified". Phyla with relative frequency of <1 % are included as "others". Largest phyla in grey dashed boxes are further detailed in Fig. S2.
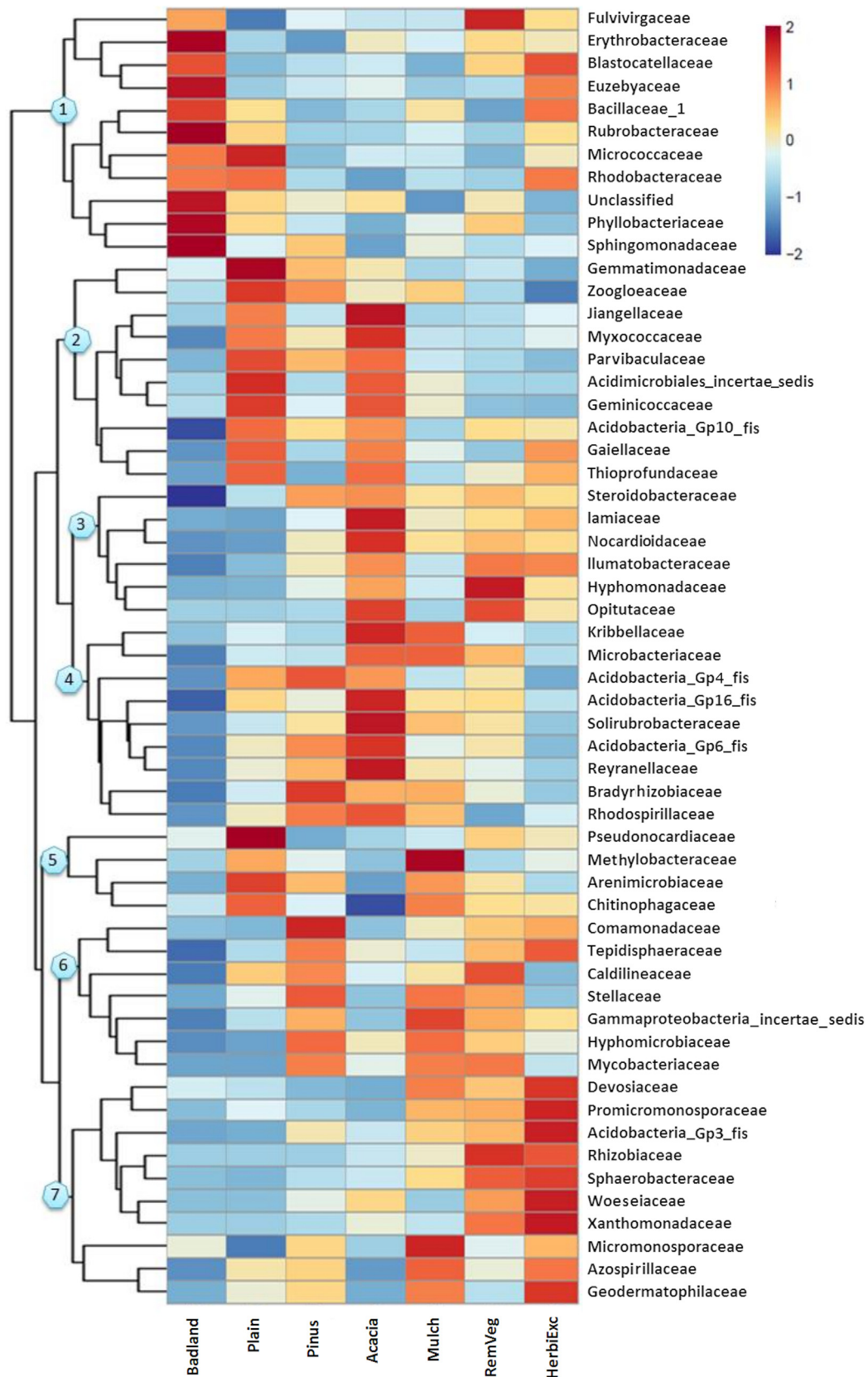
Fig. 5. Hierarchically clustered (using the standard Euclidean distance) heatmap displaying bacterial families that exhibited biologically relevant changes in abundance, determined by low count filter (based on the prevalence of at least 50 counts on the 30 % of the plots) and low variance filter (using inter-quantile range: 50 % of the groups with lowest variance are excluded). The scale represents the positive or negative increase of the standard deviation with respect to the mean of the relative abundances of a given taxon.
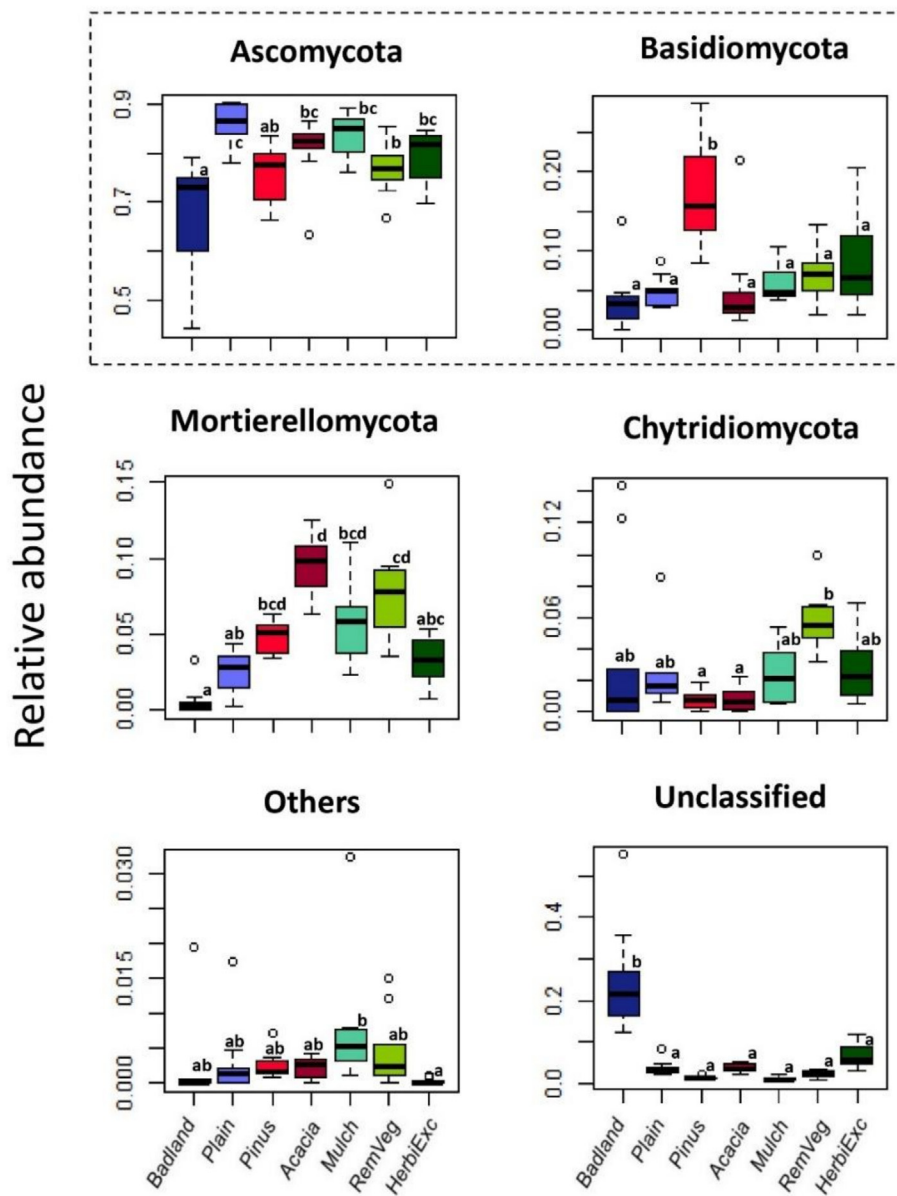
Fig. 6. Comparison of the quantitative contribution of the sequences affiliated with different soil fungal phyla to the total number of sequences among seven sites; n = 10 for each boxplot; boxes represent the middle 50 % of the data (interquartile range), with the line inside the box representing the median; the whiskers show the range of the data excluding outliers represented as isolated circles; different letters indicate significant differences among study sites ($p < 0.05$). Sequences not classified to any known phylum are included as "unclassified". Phyla with relative frequency of <1 % are included as "others". Largest phylum in grey dashed boxes is further detailed in Fig. S3.

(Custer and van Diepen, 2020; Parhizkar et al., 2021; Li et al., 2022). In this sense, some authors report that exotic species have a negative (Chen et al., 2013), neutral (Stefanowicz et al., 2016, 2019), or positive effect (Xu et al., 2022) on the soil physical-chemical and biochemical properties with regards to soils with native vegetation. Some key factors for these differences could be environmental conditions, type of plant species and soils, and the overall soil quality state at the beginning of the restoration (Stefanowicz et al., 2016; Parhizkar et al., 2021; Xu et al., 2022).

In our case, exotic vegetation has considerably improved the soil C pool (including labile and microbial biomass C) and microbiological activity with regard to non-restored soils, but still has not reached the levels of soils with native vegetation, particularly those not affected by herbivores (*HerbiExc*). These results suggest that exotic plants have slowed down or controlled soil degradation processes, such as surface sealing that strongly reduces water infiltration and dramatically diminishes water storage, as well as sheet, rill or gully erosion that usually remove the fertile topsoil layer (Gatiboni, 2018). Even in *Plain* soils vegetation communities flourish

after rain but ground cover is typically sparse before and during rainstorms leaving the soil surface exposed to raindrop impact, soil surface sealing, and overland flow (McCool and Williams, 2008). Eroded soils have higher bulk density and are poorer in nutrients making plant establishment difficult, leading to low organic matter input and biological activity (Olson et al., 2016). In turn, the lack of vegetation also negatively influences the soil structure and fertility, including low levels of organic debris and exudates, which are very important for the development of microbial communities (Cifuentes-Croquevielle et al., 2020). On the other hand, plantations have not reached the level of soil quality observed in soil conserving native plant cover probably due to the effects of using monospecific tree plantations (Widyati et al., 2022). Higher plant diversity implies multiple plant-specific functional traits such as exudation and root architecture, as well as species specific organic matter inputs (Colin et al., 2019; Meng et al., 2019; Parhizkar et al., 2021; Xu et al., 2022) that can ultimately increase microbial diversity and activity and nutrient availability (Xu et al., 2022). The greater rates of enzyme activities measured in soils with high native
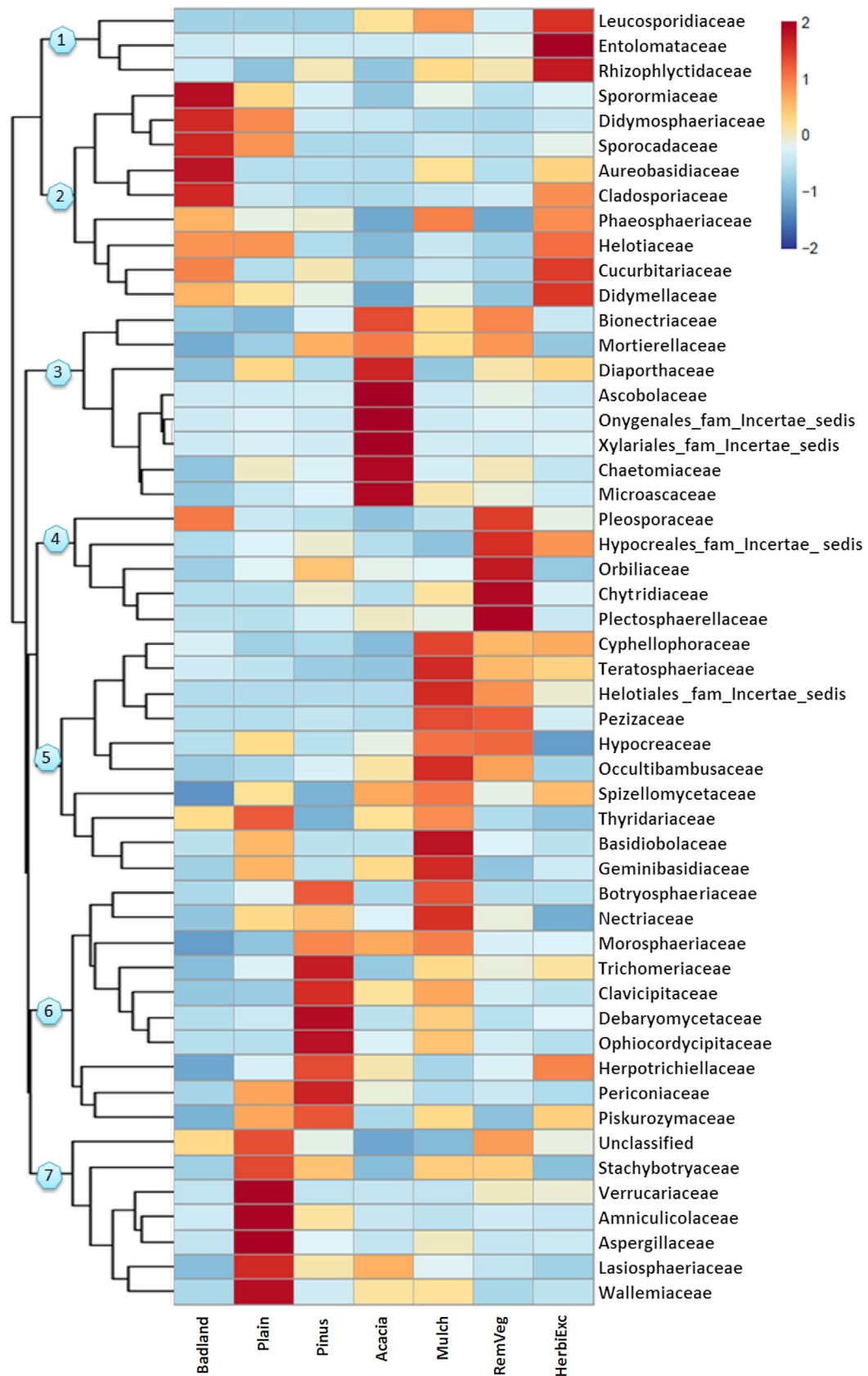
Fig. 7. Hierarchically clustered (using the standard Euclidean distance) heatmap displaying fungal families that exhibited biologically relevant changes in abundance, determined by low count filter (based on the prevalence of at least 30 counts on the 30 % of the plots) and low variance filter (using inter-quantile range: 30 % of the groups with lowest variance are excluded). The scale represents the positive or negative increase of the standard deviation with respect to the mean of the relative abundances of a taxon.

species cover, which are consistent with larger soil respiration rates (Zhou and Staver, 2019) agree with results reported by Wang et al. (2015), who found that exotic pine plantations depressed soil respiration compared to indigenous pines. Instead, they do not match with other research finding that revegetation with some exotic plants, particularly grass species, increased soil fertility and enzyme activities, mainly those involved in N and P cycles, with regard to native plants (Zhou and Staver, 2019; Xu et al., 2022).

Particularly relevant is the case for lithic-mulched soils (*Mulch*), corresponding to agricultural soils abandoned about 50 years ago, that have been recolonised by native flora. In those soils, the pyroclastic mulch has improved the soil water balance with a strong increase in infiltration rates and reduction in evaporation, as it has been demonstrated in previous research (Díaz et al., 2004, 2013). Our results shown that these soils have a health status close to those with remnant vegetation (i.e., *RemVeg* and *HerbiExc*), suggesting the great potential that this traditional agricultural technique may represent for accelerating the recovery of degraded semiarid and arid land.

4.2. Influence in soil microbial diversity and community structure

Our findings suggest that soil microbial diversity was more influenced by the presence of vegetation cover, even when it is seasonal, than by plant species identity. Similar results have been found by Byers et al. (2020) who reported no differences in microbial α-diversity among exotic plantations and remnant forests, arguing that crucial soils characteristics for the establishment of microorganisms such as pH were the same in both situations. Oppositely, Li et al. (2015) demonstrated that during the early years of restoration, the soils associated with the native tree species had greater microbial biomass and diversity when compared with the exotic *Eucalyptus* trees, probably because the quantity and quality of litter inputs and root exudations were different among those two scenarios. In the present study, only highly eroded soils had a significantly lower diversity suggesting that the loss of top layer renders soils unable to support many types of organisms present in vegetated soils due to extreme physical and chemical conditions.

The ordering of fungal communities from soils with different vegetation cover allows separating the soils with exotic vegetation coverage from those with low and high native vegetation coverage (Fig. 3). For the bacterial communities, the separation between the soils with exotic species and those with a high cover of native species was less pronounced. Sample ordination was influenced by soil properties as it has been shown in other studies (Li et al., 2015; Bai et al., 2020; Wu et al., 2020; Parhizkar et al., 2021; Zhao et al., 2021; Xu et al., 2022). In our case a clear effect of physical degradation was observed for low native vegetation coverage, while differences between exotics and high native coverage responded to a concentration gradient in organic carbon pools, nutrients and biological activity. In a similar study conducted by Li et al. (2015), the composition of the soil microbial community was significantly related to the type of plant species (exotic or native), the depth of the litter layer and the concentrations of K in soil.

4.3. Influence in soil microbial community composition

The relative abundance of several taxa experienced differences across sites. While in most cases the increase or decrease in relative abundance of some taxa was indicative of a change away from the more degraded sites (*Badland*) towards vegetated sites independently if they are exotic or native plants, in a few cases abundance of some taxa was greatest or lowest in the exotic plantations. This could indicate that different components of the community may be affected negatively or positively by extreme conditions in bare soils while other are more plant type-specific (Fernández-González et al., 2020).

The most degraded soils were predominated by phototrophic (e.g., *Chloroflexi* and *Cyanobacteria*) and chemolithotrophic bacteria (e.g., *Acidimicrobiales*), as well as groups that are extremely tolerant to desiccation and UV radiation (e.g., *Rubrobacterales* and *Gemmatimonadetes*) or to salinity such as *Egibacterales* (Ward and Bora, 2008; Zhang et al., 2016;

Zeng et al., 2021). The families *Rubrobacteraceae* and *Blastocatellaceae* predominated in degraded soils, as they are frequently found in water-stressed and low nutrients and organic matter soils (Araujo et al., 2020; Cui et al., 2022). Maestre et al. (2015) found that with increasing aridity, *Acidobacteria* decreased and *Chloroflexi* increased, same trend that can be observed in this study for *Badland* soils with regards to vegetated soils. In soils with well-preserved native vegetation, increased eminently heterotrophic taxa which play a crucial role in carbon mineralization and nitrogen fixation (e.g., *Bacteroidetes*, *Rhizobiaceae*, *Sphaerobacteraceae*) (Fierer et al., 2007; Qi et al., 2020). *Reyranellaceae*, isolated from agricultural soils (Lee et al., 2017), and *Bradyrhizobiaceae*, that include diazotrophic members and establishes nitrogen-fixing symbioses with plants (Crisóstomo et al., 2013), were prominent in exotic species, curiously more in soils with *Pinus* than with the leguminous *Acacia*.

Saprotrophs were the most abundant fungi in all soils analyzed. Compared to *Ascomycota*, *Basidiomycota* were scarce (79 % vs. 7 % in average), coinciding with previous studies in other arid territories (Maestre et al., 2015; Zeng et al., 2021). In the most degraded soils, xerotolerant and halotolerant organisms (e.g., *Wallemiomycetes)* and some parasites (e.g., *Ustilaginomycetes*) stood out (Bauer et al., 1997; Zalar et al., 2005; Jančič et al., 2015). In soils with greater vegetation cover, saprotrophic fungi of the phylum *Mortierellomycota* increased. *Pezizomycetes*, which includes some plant parasites and bryophytes (Pfister and Healy, 2021), showed a preference for soils with exotic species. Specifically, Chaetomiaceae and Clavicipitaceae were prominent in soils planted with Acacia and Pinus, respectively. Chaetomiaceae has been cited as a biomarker in amended soils and during the composting process (Dang et al., 2021), while Clavicipitaceae range from free-living soil saprotrophs to endophytes (Singh and Mazumdar, 2022). In soils with greater native species diversity, Rhizophlyctidaceae, which have been associated with high respiration rate aggregates (Yang et al., 2019), stood out. Both in Badlands and HerbiExc soils highlighted *Lecanoromycetes*, that represent the largest class of lichenized fungi and has been described as N-fixers in limiting environments (Miadlikowska et al., 2014; Deng et al., 2020; Canini et al., 2021).

5. Conclusions

Opposite to the initial hypothesis, the assessment of soil properties, including bacterial and fungal diversity, revealed that reforestation with exotic plants (*Acacia cyclops* and *Pinus halepensis*) has prevented a progressive degradation of the soil ecosystem in this extremely arid insular territory. However, the planting of exotic species has shaped a particular composition of the soil microbiome with unknown potential effects for ecosystem stability. The better conservation status observed in soils with exotic plantation compared to highly eroded soils where no restoration activity has been carried out, indicates that in arid areas subject to intense desertification processes, keeping the soil covered seems to be a key factor in order to avoid a significant decline in soil quality. Therefore, the policies and projects that advise the elimination of these plantations with the aim of conserving native biodiversity, should take these aspects into account. In any case, the transformation to native vegetation communities should be done progressively, avoiding leaving bare soil areas, and focusing the restoration not only on the aboveground elements of the system but also on those belowground like soil biological communities through techniques based on soil inoculation using isolated and amplified microorganisms from the target soil ecosystems.

Information gained in this research could be useful for environmental agencies and decision makers for identifying potential tradeoffs associated with replacement of exotic plantations in insular arid territories, also contributing to establishing the reference ecosystems that must be targeted in future restoration projects.

CRediT authorship contribution statement

Adolfo Perdomo-González: Methodology; Validation; Formal analysis; Investigation; Data Curation; Writing - Original Draft; Writing - Review &

Data availability

Data will be made available on request.

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.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.163030.

References

Araujo, R., Gupta, V.V.S.R., Reith, F., Bissett, A., Mele, P., Franco, C.M.M., 2020. Biogeography and emerging significance of actinobacteria in Australia and northern Antarctica soils. Soil Biol. Biochem. 146, 107805. https://doi.org/10.1016/j.soilbio.2020.107805.

Arévalo, J.R., Tejedor, M., Jiménez, C., Reyes-Betancort, J.A., Díaz, F.J., 2016. Plant species composition and richness along abandoned agricultural terraces vs. natural soils on Lanzarote (Canary Islands). J. Arid Environ. 124, 165–171. https://doi.org/10.1016/j.jaridenv.2015.08.012.

Arteaga, M.A., Delgado, J.D., Otto, R., Fernández-Palacios, J.M., Arévalo, J.R., 2009. How do alien plants distribute along roads on oceanic islands? A case study in Tenerife, Canary Islands. Biol. Invasions 11 (4), 1071–1086. https://doi.org/10.1007/s10530-008-9329-8.

Bai, Y., Zha, X., Chen, S., 2020. Effects of the vegetation restoration years on soil microbial community composition and biomass in degraded lands in Changting County, China. J. For. Res. 31 (4), 1295–1308. https://doi.org/10.1007/s11676-019-00879-z.

Bello-Rodríguez, V., Cubas, J., Fernández, Á.B., Del Arco Aguilar, M.J., González-Mancebo, J.M., 2020. Expansion dynamics of introduced Pinus halepensis miller plantations in an oceanic island (La Gomera, Canary Islands). For. Ecol. Manag. 474, 118374. https://doi.org/10.1016/j.foreco.2020.118374.

BIOTA, 2022. Gobierno de Canarias. Banco de Datos de Biodiversidad de Canarias (http://biodiversidadcanarias.es\biota) [accessed: 20/09/2022].

Boudiaf, I., Baudoin, E., Sanguin, H., Beddiar, A., Thioulouse, J., Galiana, A., Prin, Y., Le Roux, C., Lebrun, M., Duponnois, R., 2013. The exotic legume tree species, Acacia mearnsii, alters microbial soil functionalities and the early development of a native tree species, Quercus suber, in North Africa. Soil Biol. Biochem. 65, 172–179. https://doi.org/10.1016/j.soilbio.2013.05.003.

Byers, A.-K., Condron, L., Donavan, T., O'Callaghan, M., Patuawa, T., Waipara, N., Black, A., 2020. Soil microbial diversity in adjacent forest systems – contrasting native, old growth kauri (Agathis australis) forest with exotic pine (Pinus radiata) plantation forest. FEMS Microbiol. Ecol. 96 (5). https://doi.org/10.1093/femsec/fiaa047.

Canini, F., Geml, J., D'Acqui, L.P., Buzzini, P., Turchetti, B., Onofri, S., Ventura, S., Zucconi, L., 2021. Fungal diversity and functionality are driven by soil texture in Taylor Valley, Antarctica. Fungal Ecol. 50, 101041. https://doi.org/10.1016/j.funeco.2021.101041.

Chen, F., Zheng, H., Zhang, K., Ouyang, Z., Lan, J., Li, H., Shi, Q., 2013. Changes in soil microbial community structure and metabolic activity following conversion from native Pinus massoniana plantations to exotic eucalyptus plantations. For. Ecol. Manag. 291, 65–72. https://doi.org/10.1016/j.foreco.2012.11.016.

Cherlet, M., Hutchinson, C., Reynolds, J., Hill, J., Sommer, S., von Maltitz, G., 2018. World Atlas of Desertification: Rethinking Land Degradation and Sustainable Land Management. Publication Office of the European Union, Luxembourg.

Chong, J., Liu, P., Zhou, G., Xia, J., 2020. Using MicrobiomeAnalyst for comprehensive statistical, functional, and meta-analysis of microbiome data". Nat. Protoc. 15, 799–821. https://doi.org/10.1038/s41596-019-0264-1.

Cifuentes-Croquevielle, C., Stanton, D.E., Armesto, J.J., 2020. Soil invertebrate diversity loss and functional changes in temperate forest soils replaced by exotic pine plantations. Sci. Rep. 10 (1), 7762. https://doi.org/10.1038/s41598-020-64453-y.

Colin, Y., Goberna, M., Verdú, M., Navarro-Cano, J.A., 2019. Successional trajectories of soil bacterial communities in mine tailings: the role of plant functional traits. J. Environ. Manag. 241, 284–292. https://doi.org/10.1016/j.jenvman.2019.04.023.

Crisóstomo, J.A., Rodríguez-Echeverría, S., Freitas, H., 2013. Co-introduction of exotic rhizobia to the rhizosphere of the invasive legume Acacia saligna, an intercontinental study. Appl. Soil Ecol. 64, 118–126. https://doi.org/10.1016/j.apsoil.2012.10.005.

Cross, A.T., Krueger, T.A., Gonella, P.M., Robinson, A.S., Fleischmann, A.S., 2020. Conservation of carnivorous plants in the age of extinction. Glob. Ecol. Conserv. 24, e01272. https://doi.org/10.1016/j.gecco.2020.e01272.

Cui, J., Zhu, R., Wang, X., Xu, X., Ai, C., He, P., Liang, G., Zhou, W., Zhu, P., 2022. Effect of high soil C/N ratio and nitrogen limitation caused by the long-term combined organic-inorganic fertilization on the soil microbial community structure and its dominated SOC decomposition. J. Environ. Manag. 303, 114155. https://doi.org/10.1016/j.jenvman.2021.114155.

Custer, G.F., van Diepen, L.T.A., 2020. Plant invasion has limited impact on soil microbial α-diversity: a meta-analysis. Diversity 12 (3). https://doi.org/10.3390/d12030112.

Dang, Q., Wang, Y., Xiong, S., Yu, H., Zhao, X., Tan, W., Cui, D., Xi, B., 2021. Untangling the response of fungal community structure, composition and function in soil aggregate fractions to food waste compost addition. Sci. Total Environ. 769, 145248. https://doi.org/10.1016/j.scitotenv.2021.145248.

del Arco Aguilar, M.-J., González-González, R., Garzón-Machado, V., Pizarro-Hernández, B., 2010. Actual and potential natural vegetation on the Canary Islands and its conservation status. Biodivers. Conserv. 19 (11), 3089–3140. https://doi.org/10.1007/s10531-010-9881-2.

Deng, S., Zhang, D., Wang, G., Zhou, X., Ye, C., Fu, T., Ke, T., Zhang, Y., Liu, Y., Chen, L., 2020. Biological soil crust succession in deserts through a 59-year-long case study in China: how induced biological soil crust strategy accelerates desertification reversal from decades to years. Soil Biol. Biochem. 141, 107665. https://doi.org/10.1016/j.soilbio.2019.107665.

Derbel, S., Cortina, J., Chaieb, M., 2009. Acacia saligna plantation impact on soil surface properties and vascular plant species composition in Central Tunisia. Arid Land Res. Manag. 23 (1), 28–46. https://doi.org/10.1080/15324980802599209.

Dhariwal, A., Chong, J., Habib, S., King, I.L., Agellon, L.B., Xia, J., 2017. MicrobiomeAnalyst: a web-based tool for comprehensive statistical, visual and meta-analysis of microbiome data. Nucleic Acids Res. 45 (W1), W180–W188. https://doi.org/10.1093/nar/gkx295.

Díaz, F.J., Tejedor, M., Jiménez, C., Grattan, S.R., Dorta, M., Hernández, J.M., 2013. The imprint of desalinated seawater on recycled wastewater: consequences for irrigation in Lanzarote Island, Spain. Agric. Water Manag. 116, 62–72. https://doi.org/10.1016/j.agwat.2012.10.011.

Díaz, F., Jiménez, C., Tejedor, M., Mejías, G., 2004. The use of Tephra Mulch Increases Soil Fertility (Lanzarote, Spain).

FAO, 2020. Global forest resources assessment, key findings. Glob. for. resour. assessment, key find. http://www.fao.org/3/ca8753en/CA8753EN.pdf.

Fernández-González, A.J., Villadas, P.J., Gómez-Lama Cabanás, C., Valverde-Corredor, A., Belaj, A., Mercado-Blanco, J., Fernández-López, M., 2019. Defining the root endosphere and rhizosphere microbiomes from the world olive germplasm collection. Sci. Rep. 9 (1), 20423. https://doi.org/10.1038/s41598-019-56977-9.

Fernández-González, A.J., Wentzien, N.M., Villadas, P.J., Valverde-Corredor, A., Lasa, A.V., Cabanás, C.G.L., Mercado-Blanco, J., Fernández-López, M., 2020. Comparative study of neighboring holm oak and olive trees-belowground microbial communities subjected to different soil management. PLoS One 15, 1–21. https://doi.org/10.1371/journal.pone.0236796.

Fierer, N., 2017. Embracing the unknown: disentangling the complexities of the soil microbiome. Nat. Rev. Microbiol. 15 (10), 579–590. https://doi.org/10.1038/nrmicro.2017.87.

Fierer, N., Bradford, M.A., Jackson, R.B., 2007. Toward an ecological classification of soil bacteriA. Ecology 88 (6), 1354–1364. https://doi.org/10.1890/05-1839.

Gatiboni, L., 2018. Soils and plant nutrients, chapter 1. In: Moore, K.A., Bradley, L.K. (Eds.), North Carolina Extension Gardener Handbook. NC State Extension, Raleigh, NC.

Goberna, M., Sánchez, J., Pascual, J.A., García, C., 2007. Pinus halepensis mill. Plantations did not restore organic carbon, microbial biomass and activity levels in a semi-arid Mediterranean soil. Appl. Soil Ecol. 36 (2–3), 107–115. https://doi.org/10.1016/j.apsoil.2006.12.003.

Gómez-Aparicio, L., Domínguez-Begines, J., Villa-Sanabria, E., García, L.V., Muñoz-Pajares, A.J., 2022. Tree decline and mortality following pathogen invasion alters the diversity, composition and network structure of the soil microbiome. Soil Biol. Biochem. 166, 108560. https://doi.org/10.1016/j.soilbio.2022.108560.

Hassani, M.A., Durán, P., Hacquard, S., 2018. Microbial interactions within the plant holobiont. Microbiome. 6 (1), 58. https://doi.org/10.1186/s40168-018-0445-0.

IPBES, 2018. Land Degradation and Restoration.

Jančič, S., Nguyen, H.D.T., Frisvad, J.C., Zalar, P., Schroers, H.-J., Seifert, K.A., 2015. A taxonomic revision of the wallemia sebi species complex. PLoS ONE 10 (5), e0125933. https://doi.org/10.1371/journal.pone.0125933.

Kandeler, E., Gerber, H., 1988. Short-term assay of soil urease activity using colorimetric determination of ammonium. Biol. Fertil. Soils 6 (1), 68–72. https://doi.org/10.1007/BF00257924.

Kelt, D.A., Meserve, P.L., 2016. To what extent can and should revegetation serve as restoration? Restor. Ecol. 24 (4), 441–448. https://doi.org/10.1111/rec.12371.

Kier, G., Kreft, H., Tien, M.L., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J., Barthlott, W., 2009. A global assessment of endemism and species richness across island and mainland regions. Proc. Natl. Acad. Sci. U. S. A. 106 (23), 9322–9327. https://doi.org/10.1073/pnas.0810306106.

Lee, H., Kim, D.-U., Lee, S., Park, S., Yoon, J.-H., Seong, C.N., Ka, J.-O., 2017. Reyranella terrae sp. Nov., isolated from an agricultural soil, and emended description of the genus reyranella. Int. J. Syst. Evol. Microbiol. 67 (6), 2031–2035. https://doi.org/10.1099/ijsem.0.001913.

Legendre, P., Legendre, L., 2012. Chapter 9 - ordination in reduced space. In: Legendre, P., Legendre, L. (Eds.), Numerical EcologyVol. 24. Elsevier, pp. 425–520. https://doi.org/10.1016/B978-0-444-53868-0.50009-5.

Li, C., Bo, H., Song, B., Chen, X., Cao, Q., Yang, R., Ji, S., Wang, L., Liu, J., 2022. Reshaping of the soil microbiome by the expansion of invasive plants: shifts in structure, diversity, co-occurrence, niche breadth, and assembly processes. Plant Soil 477 (1), 629–646. https://doi.org/10.1007/s11104-022-05445-x.

Li, C., Shi, L.L., Ostermann, A., Xu, J., Li, Y., Mortimer, P.E., 2015. Indigenous trees restore soil microbial biomass at faster rates than exotic species. Plant Soil 396, 151–161. https://doi.org/10.1007/s11104-015-2570-x.

Liu, X., Lu, Y., Xue, Y., Zhang, X., 2014. Testing the importance of native plants in facilitation the restoration of coastal plant communities dominated by exotics. For. Ecol. Manag. 322, 19–26. https://doi.org/10.1016/j.foreco.2014.03.020.

Maestre, F.T., Delgado-Baquerizo, M., Jeffries, T.C., Eldridge, D.J., Ochoa, V., Gozalo, B., Quero, J.L., García-Gómez, M., Gallardo, A., Ulrich, W., Bowker, M.A., Arredondo, T., Barraza-Zepeda, C., Bran, D., Florentino, A., Gaitán, J., Gutiérrez, J.R., Huber-Sannwald, E., Jankju, M., Mau, R.L., Miriti, M., Naseri, K., Ospina, A., Stavi, I., Wang, D., Woods, N.N., Yuan, X., Zaady, E., Singh, B.K., 2015. Increasing aridity reduces soil microbial diversity and abundance in global drylands. Proc. Natl. Acad. Sci. U. S. A. 112 (51), 15684–15689. https://doi.org/10.1073/pnas.1516684112.

McCool, D.K., Williams, J.D., 2008. Soil erosion by water. In: Jorgensen, Sven Erik, Fath, Brian D. (Eds.), Ecological Processes. Vol. [4] of Encyclopedia of Ecology, 1st edition 5. Elsevier B.V, pp. 3284–3290.

McLeod, M.L., Bullington, L., Cleveland, C.C., Rousk, J., Lekberg, Y., 2021. Invasive plant-derived dissolved organic matter alters microbial communities and carbon cycling in soils. Soil Biol. Biochem. 156, 108191. https://doi.org/10.1016/j.soilbio.2021.108191.

Meng, M., Lin, J., Guo, X., Liu, X., Wu, J., Zhao, Y., Zhang, J., 2019. Impacts of forest conversion on soil bacterial community composition and diversity in subtropical forests. Catena 175, 167–173. https://doi.org/10.1016/j.catena.2018.12.017.

Miadlikowska, J., Kauff, F., Högnabba, F., Oliver, J.C., Molnár, K., Fraker, E., Gaya, E., Hafellner, J., Hofstetter, V., Gueidan, C., Otálora, M.A.G., Hodkinson, B., Kukwa, M., Lücking, R., Björk, C., Sipman, H.J.M., Burgaz, A.R., Thell, A., Passo, A., Stenroos, S., 2014. A multigene phylogenetic synthesis for the class lecanoromycetes (Ascomycota): 1307 fungi representing 1139 infrageneric taxa, 317 genera and 66 families. Mol. Phylogenet. Evol. 79, 132–168. https://doi.org/10.1016/j.ympev.2014.04.003.

Mologni, F., Bellingham, P.J., Tjørve, E., Cameron, E.K., Wright, A.E., Burns, K.C., 2021. Similar yet distinct distributional patterns characterize native and exotic plant species richness across northern New Zealand islands. J. Biogeogr. 48 (7), 1731–1745. https://doi.org/10.1111/jbi.14110.

Navarrete, A.A., Aburto, F., González-Rocha, G., Guzmán, C.M., Schmidt, R., Scow, K., 2023. Anthropogenic degradation alter surface soil biogeochemical pools and microbial communities in an andean temperate forest. Sci. Total Environ. 854, 158508. https://doi.org/10.1016/j.scitotenv.2022.158508.

Navarro-Cano, J.A., Verdú, M., Goberna, M., 2018. Trait-based selection of nurse plants to restore ecosystem functions in mine tailings. J. Appl. Ecol. 55 (3), 1195–1206. https://doi.org/10.1111/1365-2664.13094.

Nkonya, E., Mirzabaev, A., 2016. Economics of Land Degradation and Improvement – A Global Assessment for Sustainable Development.

Öhlinger, R., 1993. Bestimmung des Biomasse-Kohlenstoffs mittels Fumigation-Exstraktion. In: Schinner, F., Ö̈hlinger, R., Kandeler, E., Margesin, R. (Eds.), Bodenbiologische arbeitsmethoden. Springer, New York, pp. 60–62.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P., O'Hara, R.B., Simpson, G., Solymos, P., Stevens, M.H.H, Szöcs, E., Wagner, H., 2020. vegan community ecology package version 2.5-7.. (Accessed November 2020). .

Olson, K.R., Al-Kaisi, M., Lal, R., Cihacek, L., 2016. Impact of soil erosion on soil organic carbon stocks. J. Soil Water Conserv. 71 (3), 61A–67A. https://doi.org/10.2489/jswc.71.3.61A.

Otto, R., Barone, R., Delgado, J.D., Arévalo, J.R., Garzón-Machado, V., Cabrera-Rodríguez, F., Fernández-Palacios, J.M., 2012. Diversity and distribution of the last remnants of endemic juniper woodlands on Tenerife, Canary Islands. Biodivers. Conserv. 21 (7), 1811–1834. https://doi.org/10.1007/s10531-012-0278-2.

Parhizkar, M., Shabanpour, M., Miralles, I., Zema, D.A., Lucas-Borja, M.E., 2021. Effects of plant species on soil quality in natural and planted areas of a forest park in northern Iran. Sci. Total Environ. 778, 146310. https://doi.org/10.1016/j.scitotenv.2021.146310.

Pfister, D.H., Healy, R., 2021. Pezizomycetes. Encyclopedia of Mycology. Volume 1. Elsevier, Amsterdam, The Netherlands, pp. 295–309. https://doi.org/10.1016/B978-0-12-819990-9.00054-8.

Qi, G., Chen, S., Ke, L., Ma, G., Zhao, X., 2020. Cover crops restore declining soil properties and suppress bacterial wilt by regulating rhizosphere bacterial communities and improving soil nutrient contents. Microbiol. Res. 238, 126505. https://doi.org/10.1016/j.micres.2020.126505.

R Core Team, .. R: A language and environment for statistical computing https://www.r-project.org/.

Raposeiro, P.M., Martins, G.M., Moniz, I., Cunha, A., Costa, A.C., Gonçalves, V., 2014. Leaf litter decomposition in remote oceanic islands: the role of macroinvertebrates vs. microbial decomposition of native vs. exotic plant species. Limnologica 45, 80–87. https://doi.org/10.1016/j.limno.2013.10.006.

Bauer, R., Oberwinkler, F., Vánky, K., 1997. Ultrastructural markers and systematics in smut fungi and allied taxa. Can. J. Bot. 75 (8), 1273–1314. https://doi.org/10.1139/b97-842.

Singh, P., Mazumdar, P., 2022. Chapter 5 - microbial pesticides: trends, scope and adoption for plant and soil improvement. In: Rakshit, A., Meena, V.S., Abhilash, P.C., Sarma, B.K., Singh, H.B., Fraceto, L., Parihar, M., Singh, A.K. (Eds.), Biopesticides. Woodhead Publishing, pp. 37–71 https://doi.org/10.1016/B978-0-12-823355-9.00023-7.

Soil Survey Staff, 1996. Soil Survey Laboratory Methods Manual. Procedures for Collecting Soil Samples and Methods of Analysis for Soil Survey, Soil Survey Investigation Report No. 42, Version 3.0. USDA, Washington DC.

Soil Survey Staff, 2014. Keys to Soil Taxonomy. 12th ed. USDA-Nat.Resource Conservation Service, Washington DC, USA.

Stanek, M., Piechnik, Ł., Stefanowicz, A.M., 2020. Invasive red oak (Quercus rubra L.) modifies soil physicochemical properties and forest understory vegetation. For. Ecol. Manag. 472, 118253. https://doi.org/10.1016/j.foreco.2020.118253.

Stefanowicz, A.M., Stanek, M., Majewska, M.L., Nobis, M., Zubek, S., 2019. Invasive plant species identity affects soil microbial communities in a mesocosm experiment. Appl. Soil Ecol. 136, 168–177. https://doi.org/10.1016/j.apsoil.2019.01.004.

Stefanowicz, A.M., Stanek, M., Nobis, M., Zubek, S., 2016. Species-specific effects of plant invasions on activity, biomass, and composition of soil microbial communities. Biol. Fertil. Soils 52 (6), 841–852. https://doi.org/10.1007/s00374-016-1122-8.

Stevenson, C.M., Naranjo-Cigala, A., Ladefoged, T.N., Díaz, F.J., 2021. Colonial rainfed farming strategies in an extremely arid insular environment: niche construction on Lanzarote, Canary Islands, Spain. J. Isl. Coast. Archaeol. 0 (0), 1–29. https://doi.org/10.1080/15564894.2021.1924898.

Strobl, W., Traunmüller, M., 1993. Bestimmung der β-glucosidase-Aktivität. Bodenbiologische Arbeitsmethoden, 2nd edn. Springer, Berlin Heidelberg New York, pp. 128–130.

Tabatabai, M.A., Bremner, J.M., 1969. Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. Soil Biol. Biochem. 1 (4), 301–307. https://doi.org/10.1016/0038-0717(69)90012-1.

Tatoni, T., Médail, F., Roche, P., Barbero, M., 2005. The impact of changes in land use on ecological patterns in provence (Mediterranean France). Recent Dyn. Mediterr. Veg. Landsc., 107–120 https://doi.org/10.1002/0470093714.ch10.

Tejedor, M., Jiménez, C., Dıaz, F., 2003. Volcanic materials as mulches for water conservation. Geoderma 117 (3–4), 283–295. https://doi.org/10.1016/S0016-7061(03)00129-0.

Tejedor, M., Jiménez, C., Díaz, F., 2004. Dry farming with soils under natural tephra cover in Lanzarote, Spain. Soil Use Manag. 20 (3), 360–362. https://doi.org/10.1111/j.1475-2743.2004.tb00382.x.

Trentini, C.P., Campanello, P.I., Villagra, M., Ferreras, J., Hartmann, M., 2020. Thinning partially mitigates the impact of Atlantic Forest replacement by pine monocultures on the soil microbiome. Front. Microbiol. 11. https://doi.org/10.3389/fmicb.2020.01491.

U.S. Salinity Laboratory Staff, 1969. In: Richards, L.A. (Ed.), Diagnosis and Improvement of Saline and Alkali Soils. USDA, Washington, DC.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. Microbial biomass measurements in forest soils: determination of kc values and test of hypotheses to explain the failure of the chloroform fumigation-incubation method in acid soils. Wilderness 19 (6).

Vieira, C.K., dos Anjos Borges, L.G., Bortolini, J.G., Soares, C.R.F.S., Giongo, A., Stürmer, S.L., 2022. Does a decrease in microbial biomass alter mycorrhizal attributes and soil quality indicators in coal mining areas under revegetation process? Sci. Total Environ. 802, 149843. https://doi.org/10.1016/j.scitotenv.2021.149843.

Wang, Y., Wang, H., Xu, M., Ma, Z., Wang, Z.-L., 2015. Soil organic carbon stocks and CO2 effluxes of native and exotic pine plantations in subtropical China. Catena 128, 167–173. https://doi.org/10.1016/j.catena.2015.02.003.

Ward, A.C., Bora, N., 2008. The actinobacteria. Practical Handbook of Microbiology. CRC Press, pp. 395–464.

Weil, R., Islam, K., Stine, M., Gruver, J., Samson-Liebig, S., 2003. Estimating active carbon for soil quality assessment: a simplified method for laboratory and field use. Am. J. Altern. Agric. 18 (1), 3–17. https://doi.org/10.1079/AJAA200228.

Wentzien, N.M., 2021. Micro4all workflow. https://nuriamw.github.io/micro4all/tutorial/package_workflow.html.

Widyati, E., Nuroniah, H.S., Tata, H.L., Mindawati, N., Lisnawati, Y., Abdulah, L., van Noordwijk, M., 2022. Soil degradation due to conversion from natural to plantation forests in Indonesia. Forests 13 (11), 1913. https://doi.org/10.3390/f13111913.

Wu, Z., Sun, L., Li, Y., Sun, Q., 2020. Shifts in vegetation-associated microbial Community in the Reclamation of coal mining subsidence land. Environ. Eng. Sci. 37 (12), 838–848. https://doi.org/10.1089/ees.2019.0491.

Xu, H., Liu, Q., Wang, S., Yang, G., Xue, S., 2022. A global meta-analysis of the impacts of exotic plant species invasion on plant diversity and soil properties. Sci. Total Environ. 810, 152286. https://doi.org/10.1016/j.scitotenv.2021.152286.

Yang, C., Liu, N., Zhang, Y., 2019. Soil aggregates regulate the impact of soil bacterial and fungal communities on soil respiration. Geoderma 337, 444–452. https://doi.org/10.1016/j.geoderma.2018.10.002.

Zalar, P., Sybren de Hoog, G., Schroers, H.J., et al., 2005. Taxonomy and phylogeny of the xerophilic genus wallemia (Wallemiomycetes and wallemiales, cl. Et Ord. Nov.). Anton Leeuw. Int. J. G. 87, 311–328. https://doi.org/10.1007/s10482-004-6783-x.

Zeng, Q., Liu, D., An, S., 2021. Decoupled diversity patterns in microbial geographic distributions on the arid area (the loess Plateau). Catena 196, 104922. https://doi.org/10.1016/j.catena.2020.104922.

Zhang, Y.G., Wang, H.F., Yang, L.L., Zhou, X.K., Zhi, X.Y., Duan, Y.Q., Xiao, M., Zhang, Y.M., Li, W.J., 2016. Egibacter rhizosphaerae gen. Nov., sp. nov., an obligately halophilic, facultatively alkaliphilic actinobacterium and proposal of Egibaceraceae fam. nov. and Egibacterales ord. nov. Int. J. Syst. Evol. Microbiol. 66 (1), 271–275. https://doi.org/10.1099/ijsem.0.000713.

Zhao, J., Ma, J., Yang, Y., Yu, H., Zhang, S., Chen, F., 2021. Response of soil microbial community to vegetation reconstruction modes in mining areas of the Loess Plateau, China. Front. Microbiol., 12 https://doi.org/10.3389/fmicb.2021.714967.

Zhou, Y., Staver, A.C., 2019. Enhanced activity of soil nutrient-releasing enzymes after plant invasion: a meta-analysis. Ecology 100 (11). https://doi.org/10.1002/ecy.2830.