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ABSTRACT

Biodiversity surveys are a pre-requisite for efficient habitat conservation policies and actions, but surveys are mainly focusing on aboveground biodiversity whereas belowground biodiversity is a key component for aboveground functioning. The current study aims at identifying the belowground microbiota associated with major plant components of carob habitats sampled in the North and South Morocco. *Actinobacteria*, *Proteobacteria* and *Ascomycota* were the most predominant phyla, among which only a few microbial genera dominated, *i.e. Rubrobacter*, *Microvirga* (bacteria) and *Alternaria*, *Mortierealla* and *Fusarium* (fungi). Microbiota structure analyses revealed a significant North / South pattern for the bacterial and fungal communities, associated with specific subsets of soil properties (C / N ratio and N-P-K, CaCO3 contents, respectively). These difference are emphasized by microbial indicator taxa analysis showing contrasted significance at the kingdom level and functionality divergences characterized by fungal pathogens in the North and stress-tolerator plant-beneficial bacteria in the South. Nevertheless, a core microbiota of 138 OTUs were revealed for the association *Ceratonia-Pistacia*, an indicator of Mediterranean thermophilous woodlands.

INTRODUCTION

Carob trees (*Ceratonia siliqua* L., Leguminosae), an important component of Mediterranean thermophilous woodlands and traditional rural landscapes, are characterized by declining population levels (Rankou et al., 2017). The major causes are the high urbanization affecting the Mediterranean coasts where most carob populations are localized, and an abandon of traditional carob orchards in favor of other fruit sectors (Rankou et al., 2017; Talhouk et al., 2005). A phytosociological study of Mediterranean carob habitats highlighted their high floristic diversity, notably in the Western basin where the carob tree meets its maximum ecological gradient (Baumel et al., 2018). In addition to its ecological importance, carob habitat conservation could be of great importance for the future since carob tree is known for its tolerance to marginal soils (Correia and Martins-Loução, 2005; Ozturk et al., 2010) and for the nutritional quality of its fruits as functional food (Papaefstathiou et al., 2018; Stavrou et al., 2018).

The development of efficient habitat conservation policies and actions needs an integrative view of the biodiversity that sustains ecosystem functioning. However, shortfalls in knowledge are observed for belowground biodiversity in the Mediterranean basin (Cameron et al., 2019), whereas it constitutes, notably soil microbiota, the bedrock on which soil nutrient cycling, plant productivity and ecological succession are built (Bardgett and van der Putten, 2014; van der Heijden et al., 2008; Wagg et al., 2014). Moroccan semi-natural and traditional agrosystems have a pivotal role for the conservation of carob genetic ressources by sheltering the main evolutionary lineages found in this tree (Viruel et al., 2020). Moreover, Moroccan carob habitats are divided into two main floristic groups related to distinct edaphic parameters, climatic conditions and biogeographic history. The North group is close to South Iberian and North African vegetations and the South group is at the margin of the carob

59 geographic range with a vegetation composed of species found nowhere else on carob habitats
60 (Baumel et al., 2018).

61 The current study aims at identifying the belowground microbiota associated with carob trees
62 and major plant components of Moroccan carob habitats. Indicator plant taxa associated with
63 both the North and South habitats (*Pistacia lentiscus*), or mainly with North (*Cistus albidus*)
64 or South (*Vachellia gummifera*, *Globularia alypum*) (Baumel et al., 2018) were selected. In
65 addition, *Lavandula dentata* and *Retama monosperma* were selected for their known
66 beneficial properties on soil mycorrhizal potential (Hafidi et al., 2013; Manaut, 2015;
67 Ouahmane et al., 2006b).

MATERIALS AND METHODS

Study sites and soil sampling

Two carob habitats representative of the floristic group 1 (*Asparago albi-Rhamnion oleoidis*) and 4 (*Senecio anteuphorbii-Arganion spinosae*) as defined in Baumel et al. (2018) were selected, localized respectively in North Morocco (the Rif, 35°17'55.1"N, 5°13'40.0"W), and South Morocco (the Ourika valley, High Atlas, 31°17'45"N, 7°42′36"W). Soil samples were collected in April 2017 in close contact with the roots of carob trees (*C. siliqua*) or six other plant species (*Vachellia gummifera* (Willd.) Kyal. & Boatwr. 1806 ; *Cistus albidus* L. ; *Globularia alypum* L. ; *Lavandula dentata* L. ; *Pistacia lentiscus* L. ; *Retama monosperma* Boiss. 1840) localized 2 m around carob trunks. For each plant species, 3 to 5 kg of soil samples at 20 cm depth from five individuals, mixed and sieved through a 2 mm mesh sieve. The soil under *C. siliqua* and *P. lentiscus* were sampled in both sites, *L. dentata*, *C. albidus* in the North site, and *G. alypum, R. monosperma* and *V. gummifera* in the South site. All soil samples were stored at 4°C before processing. Soil properties were determined by the Laboratory of soil analysis (INRA, Arras, France) (Table S1).

DNA extraction, gene amplification and sequencing

Total DNA was extracted from 500 mg of soil using the FastDNA SPIN kit for soil (MP Biomedicals Europe, Illkirch, France) according to manufacturer's instructions. DNA purity was improved by adding 40 mg Polyvinylpolypyrrolidon (PVPP) during the first step of DNA extraction, and an additional washing step with 5.5 M guanidine thiocyanate before the use of the washing buffer SEWS-M. DNA extractions were done in duplicate and stored at -20°C for further analysis.

Amplification of a 16S rRNA gene sub-region and the internal transcribed spacer ITS2 were performed for bacterial and fungal communities, respectively. All amplification products were

analyzed using paired-end Illumina MiSeq sequencing (2×300 bp) performed by Get-PlaGe (Genotoul, Castanet-Tolosan, France). The 16S was amplified by polymerase chain reaction (PCR) using the primers V3F (5'-TACGGRAGGCAGCAG-3') and V4R (5'-GGACTACCAGGGTATCTAAT-3') (Alm et al., 1996) , and ITS2 with the primers ITS86F (5'-GTGAATCATCGAATCTTTGAA-3') (Turenne et al., 1999) and ITS4 (5'-TCCTCCGCTTATTGATATGC-3') (White et al., 1990). Details of the amplification and sequencing steps are provided in Appendix S1.

Data processing

Illumina sequencing, base calling and demultiplexing were carried out using RTA v1.18.54, MCS 2.6 and bcl2fastq2.17. Paired reads were assembled with vsearch v2.11.0 (Rognes et al., 2016), and primer clipping was performed with cutadapt v1.9 (Martin 2011). Clustering with swarm v2.2.2 (Mahé et al., 2015), chimera detection and taxonomic assigment were performed as detailed in Maghnia et al. (2017). The ribosomal database SILVA v132 (Quast et al., 2012) and a custom version of the ITS database UNITE v7 (Koljalg et al., 2013) were used for the bacteria and fungi, respectively. Details of data processing steps are provided in Appendix S1. The raw data are available under the bioproject PRJEB36517 (https://www.ebi.ac.uk/ena/data/view/PRJEB36517).

Statistics

Tables were transformed using the R tidyverse package version 1.2.1 (Wickham, 2017) and the plots were generated using the R ggplot2 package version 3.0.0 (Wickham, 2016). Global rarefaction (based on the samples with the smallest sizes), diversity (Shannon, inverse Simpson [1/D]) and richness (number of OTUs) analyses of microbiota were performed with the R vegan package version 2.5-2 (Oksanen et al., 2016). Microbiota structure analysis was performed either by hierarchical clustering (HC) with the stat package (R Core Team, 2017)

or nonmetric multi-dimensional scaling (NMDS) with the R package vegan, and significance of differences was assessed using PERMANOVA and HOMOVA from the R package vegan. The variability of soil properties, the correlation between them and with the components of principal component analysis (PCA) were estimated with the R package ade4 (Chessel et al., 2004). The best subset of soil properties with maximum (rank) correlation with the microbiota structure was estimated with the R vegan package. Community membership among plant species and between habitats were assessed with the R package VennDiagram version 1.6.20 (Chen, 2016), and because of their importance in plant ecology, the specificity of interactions between *Glomeromycota* taxa and plant species was evaluated and visualized using the R package bipartite version 2.11 (Dormann et al., 2009). The significance of microbial taxa association with respect to habitat types (North and South), defined as microbial indicator, was based on the indicator value (IndVal) index from the R package indicspecies version 1.7.6 (De Cáceres and Legendre, 2009). Details of R functions used for statistics are provided in Appendix S1.

RESULTS

Global composition of belowground microbiota

Higher ranges of bacterial community richness (2,080 ± 188 OTUs) and diversity (shannon index 6.7 ± 0.2) were observed compared to the fungal community (richness 647 ± 209 OTUs; shannon index 4.1 ± 0.9) (**Table S1**). Lower levels were obtained for the fungal community in the South (richness 557 ± 169 OTUs; shannon diversity 3.7 ± 0.3) compared to the North (richness 760 ± 218 OTUs; shannon diversity 4.8 ± 1.0), but not for the bacteria (**Table S1**). The bacterial community was dominated by *Actinobacteria* (52 % of sequences) and *Proteobacteria* (32 %) (**Figure 1A; Table S2)**, and the fungal community by *Ascomycota* (71 %), except for *C. albidus* (*Basidiomycota*, 69 %) (**Figure 1B; Table S3**). Only 1 % of microbial OTUs were found in all samples, and 60 % only in one sample.

The most dominant bacterial OTUs (top 10 % of most abundant; present in 2/3 of samples) belonged for 62 % to *Actinobacteria* and 28 % to *Proteobacteria* (**Table S2**) whereas the remaining 10 % were split among seven other phyla. The most dominant fungal OTUs belonged mostly to *Ascomycota* (89 %), then *Mortierellomycota* (8 %) and *Basidiomycota* (2 %) (**Table S3**). The top genera (> 5 %) were *Rubrobacter* and *Microvirga* for bacteria and *Mortierella*, *Alternaria* and *Fusarium* for fungi, but a large part of sequences were not identified, 36 % and 54 %, respectively.

Habitat-related microbiota taxa

Microbiota structure analysis revealed a significant North / South pattern for the bacterial (**Figure 2B**, $P < 0.0202$) and fungal (**Figure 2D**, $P < 0.0345$) communities, with only 3 % of bacterial OTUs and 20 % of fungal OTUs shared between both habitats (**Figure S1**). However, HC and NMDS analyses revealed a higher similarity of bacterial community associated with *C. albidus* in the North **(Figure 2A, B)** with those associated with plant

154 species in the South. In a lesser extent, the fungal community of *P. lentiscus* in the South was
155 strongly dissimilar from those associated with the other plant species of the same habitat
156 (**Figure 2C, D**). Indicator species analyses revealed significant contrasted results between the
157 North / South habitats and bacterial / fungal microbial taxa (Table 1). The North was
158 characterized by 17 fungal indicator taxa, notably *Pestalotiopsis*, *Pleurostoma, Spirosphaera*,
159 and one bacterial taxa, whereas the South was characterized by 11 bacterial indicator taxa,
160 notably *Kocuria* and *Naasia,* and no fungal indicator taxa (**Table 1**). The functional
161 assignment of the microbial indicators also showed functionnal divergences with a
162 predominance of fungal pathogens in the North and stress-tolerant plant-beneficial bacteria in
163 the South.

164 ***Soil properties-related microbial taxa***

165 The North / South pattern observed for belowground microbiota is supported by the soil
166 properties (**Table S4**), for which the main component of variance was organized between
167 North and South (**Figure 3A**) (Axis 1, 61% of total inertia; Axis 2, 15 %). The differences
168 was mainly explained by a higher global nutrient status in the North, with notably higher
169 amount of organic matter and organic C (> 95% of relative contribution along axis 1). The
170 South was, on the contrary, characterized by lower levels of all parameters measured, except
171 for total K (> 80% of relative contribution along axis 1) (**Figure 3B**). High pH levels were
172 observed in both habitats, but intra-habitat variability was observed (> 75 % of relative
173 contribution along axis 2) (**Figure 3B**). The analysis of the best correlation between a subset
174 of soil properties and the microbiota structure highlighted the C / N ratio (r = 0.61) for the
175 bacterial community and the association of Total N, $CaCO_3$, Olsen-P, K^+ and Total K (r =
176 0.52) for the fungal community.

177 ***Plant-related microbiota taxa***

178 In the North, the belowground microbiota associated with *P. lentiscus* and *L. dentata* showed
179 the strongest similarity with *C. siliqua* (**Figure 2B, D**). By contrast, the South was marked by
180 divergences regarding the closest microbiota components between C. siliqua and the other
181 plant species. The fungal community associated with *R. monosperma* in the South showed the
182 strongest similarity with that of *C. siliqua* (**Figure 2D**), whereas the most similar bacterial
183 community of that of *C. siliqua* were *P. lentiscus* and *V. gummifera* (**Figure 2B**). The *C.*
184 *siliqua* - *P. lentiscus* association, one of the most frequent plant association in Moroccan
185 carob habitats was more precisely analyzed, revealing a core microbiota of *c.a.* 25 % and 20
186 % of the total bacterial and fungal OTUs, respectively (**Figure 4**). The most dominant
187 bacterial OTUs (top 10 % of most abundant; present in all samples) constituting the core
188 microbiota belonged mainly to deep-branching actinobacterial taxa, *Rubrobacter*
189 (*Rubrobacteriales*), *Solirubrobacter* (*Solirubrobacter*), and one alphaproteobacterial taxa,
190 *Microvirga* (*Rhizobiales*) (**Figure 4A**). For the fungi, the most dominant OTUs were mainly
191 assigned to *Fusarium* (*Hypocreales*), *Mortierella* (*Mortierellales*), *Chrysosporium*
192 (*Onygenales*), *Alternaria* (*Pleosporales*), *Chaetomium* (*Sordariales*) (**Figure 4B**). *Gaiellales*
193 and *Capnodiales* were composed of unidentified taxa at the genus level.

194 ***Characteristics of Glomeromycota community***

195 The estimation of *Glomeromycota* abundance (read numbers) showed higher levels in the
196 North (**Figure 5**), notably for *L. dentata* (> 250 sequences), but no significant North / South
197 pattern (PERMANOVA, R^2 = 019362, P = 0.1217) was obverved *Glomeromycota* accounted
198 for 0.03 % to 2.61 % of the total soil fungal community depending on the habitat. The
199 analysis of potential mycorrhizal networks at the habitat level between *Glomeromycota*
200 (genus level) and plant species (**Figure 6**) revealed a higher level of nestedness (weigthed
201 NODF-based index) in the North (49.6) compared to the South (29.3), but low levels of
202 specialisation (H2 index), 0.14 and 0.20, respectively. In the North, three genera were

associated with only one plant species, *Domonikia* with *P. lentiscus* and *Rhizophagus* / *Funnelifomis* with *L. dentata*. In the South, *Domonikia* and *Rhizophagus* was not detected, and *Funneliformis* was associated with *R. monosperma*. *Ceratonia siliqua* was associated with the same *Glomeromycota* genera (i.e. *Claroideoglomus*, *Diversispora*, *Glomus*, and *Septoglomus*), except for *Kamienskia* only in the North.

DISCUSSION

Belowground microbiota is a major driver of plant diversity and ecosystem functioning (Graham et al., 2016; van der Heijden et al., 2008). Recent worldwide surveys revealed their tremendous diversity (Davison et al., 2015; Delgado-Baquerizo et al., 2018a; Egidi et al., 2019; Tedersoo et al., 2014), but also pinpointed the lack of data in some part of the world, e.g. Southern Mediterranean regions like Morocco. The current study focused on the belowground microbiota associated with several plant species representative of Mediterranean thermophilous carob woodlands in Morocco. The plant species investigated had been mainly assessed for their mycorrhizal community (Alguacil et al., 2011; Azcon-Aguilar et al., 2003; Ferrol et al., 2004; Manaut et al., 2015; Ouahmane et al., 2012; Torrecillas et al., 2014; Turrini et al., 2010) notably because of the role of mycorrhiza in ecosystem functioning (Banerjee et al., 2018; Gianinazzi et al., 2010; Qin et al., 2019; Rillig, 2004). The *Glomeromycota* are more particularly well known for their benefits (i) on plant productivity, (ii) on tolerance to drought stress and resistance to pathogens, as well as (iii) in the process of plant succession (Smith and Read, 2009). In contrast, only fragmentary data were available for the other belowground microbiota compartments.

The global composition of belowground microbiota revealed in this study was congruent with worldwide surveys at the phylum levels (Delgado-Baquerizo et al., 2018a; Tedersoo et al.,

227 2014), with *Actinobacteria*, *Ascomycota*, *Basidiomycota*, *Proteobacteria* and
228 *Mortierellomycota* as the most dominant taxa. The rhizosphere of *C. albidus* was remarkably
229 dominated by *Basidiomycota* compared to other plant rhizospheres, probably due to its
230 preferential association with ectomycorrhizal basidiomycota (Comandini et al., 2006).
231 Similarly to the patterns observed in worldwide surveys (Delgado-Baquerizo et al., 2018a;
232 Egidi et al., 2019), only few OTUs were dominant, mostly belonging to *Ascomycota*
233 (*Sordariomycetes* and *Dothideomycetes*), *Actinobacteria* (*Actinobacteria*, *Thermoleophilia*
234 and *Rubrobacteria*) and *Proteobacteria* (*Alphaproteobacteria*). Amongst the plant species
235 investigated in the current study, the two trees (*C. siliqua* and *P. lentiscus*) the most
236 frequently associated in Mediterranean thermophilous woodlands (Baumel et al., 2018) shared
237 24 % of OTUs, whose only 7 % were dominant. *Rhizobiales*, a main keystone
238 alphaproteobacterial taxa in forest and woodland ecosystems (Banerjee et al., 2018), was the
239 second most represented bacterial order among the dominant OTUs, as well as in the core
240 microbiota between *C. siliqua* and *P. lentiscus*. The importance of *Rhizobiales* in carob
241 funtionning remains controversial. Indeed, evidence of N-fixing bacteria in carob roots (El
242 Idrissi et al., 1996) has been strongly questionned (Konate et al., 2007), and neither nodules or
243 N-fixation were observed for field-grown carob trees (La Malfa et al., 2010). Nevertheless,
244 potential N-fixing *Rhizobiales* belonging to *Microvirga* (Andrews and Andrews, 2017)
245 appeared as predominant taxa in both carob habitats.

246 A significant North / South pattern was observed for the belowground microbiota, supported
247 bydifferences in the soil properties. The soil properties are known as a major driver of
248 belowground microbiota (Bastida et al., 2019; Delgado-Baquerizo et al., 2018b; Tedersoo et
249 al., 2014), but specific soil properties differently affects bacterial and fungal communities.
250 Soil pH has been described as shaping mostly the bacterial community structure, whereas soil
251 nutrient status (C / N ratio, total N, total P) was more correlated with the fungal community

structure (Lauber et al., 2008; Rousk et al., 2010). Soil pH is undoubtedly the best predictor of bacterial diversity and biomass (Griffiths et al., 2011; Karimi et al., 2018; Lauber et al., 2009), but it weakly contributed to the North / South pattern observed in the current study, due probably to a narrow pH range among soil samples, and rather explaining intra-habitat variabilities potentially related to differences in plant root exudates (Herz et al., 2018; Wang et al., 2016). In the current study, C / N ratio was the best predictor of bacterial community structure, whereas the highest correlation with the fungal community was obtained for N-P-K and $CaCO_3$ contents. The soil C / N ratio is rather highly correlated with fungal community structure (Lauber et al., 2008; Thomson et al., 2015), and has been previously described as one of the best predictors of fungal community structure in the Northern Moroccan forest (Maghnia et al., 2017). Nevertheless, the soil C / N ratio has been also reported as an important driver, though less significant than pH, of bacterial community structure (Griffiths et al., 2011), with an increasing significance for specific bacterial taxa (Karimi et al., 2018; Thomson et al., 2015). P content is generally one of the most significant soil nutrient paramaters, though less significant than C / N ratio, correlated with fungal community structure (Lauber et al., 2008; Maghnia et al., 2017). At contrary, few data are provided regarding the contribution of calcium carbonate ($CaCO_3$) content in the structure of fungal communities, but soil calcium content has been shown as a strong predictor at the global scale (Tedersoo et al., 2014).

A subset of habitat-related microbial indicators were characterized, emphasizing differences at the kingdom level, with a higher significance of fungal taxa to characterize the North habitat and bacterial taxa for the South habitat. In addition, functional divergences highlighted habitat-related microbial traits with mainly fungal plant/animal pathogens in the North, which may be related to more favorable climatic (higher humidity) and soil nutrient (Higher C-N-P) conditions in the North, as suggested in Tedersoo et al. (2014). The South was on the contrary

277 characterized by bacterial taxa with the ability to both resist to harsh conditions and promote
278 plant growth, highlighting the importance to consider semi-arid environments as a reservoir of
279 stress-tolerant plant-beneficial microorganims in futher studies of Mediterrean belowground
280 microbiota. The use of microbiota as species / compositional indicators of environmental
281 factors have shown its reliability in various environmental and spatial scales (Bouffaud et al.,
282 2016; Fortunato et al., 2013; Maghnia et al., 2017; Ritz et al., 2009; Stone et al., 2016) but
283 remains one of the least studied indicator groups (Gao et al., 2015; Schloter et al., 2017).

284 Plant host species weakly contributed to microbiota structure compared to the soil properties,
285 which is in accordance with previous observation in woodlands and grasslands (Bonito et al.,
286 2014; Kuramae et al., 2011), but plant host effect appeared more important on the
287 *Glomeromycota* community. Differences in the composition of *Glomeromycota* community
288 related to plant host species as been widely shown in semi-arid ecosystems (Alguacil et al.,
289 2011; Martinez-Garcia et al., 2011; Sanchez-Castro et al., 2012). Nevertheless, the lack of
290 North / South pattern could be explained by the low number of *Glomeromycota* sequences
291 retrieved, due, among other things, to the molecular approach used, *i.e.* a general fungal ITS
292 marker sequencing rather than a Glomeromycota-specific 18S marker sequencing, known as
293 potential biase affecting the *Glomeromycota* abundance, diversity and composition (Berruti et
294 al., 2017; Lekberg et al., 2018). *Glomeromycota* was abundant mostly in the rhizosphere of
295 *L. dentata*, reaching 3 % of the total fungal community, which supports the promoting effect
296 of *L. dentata* on the soil mycorrhizal potential (Hafidi et al., 2013; Ouahmane et al., 2006a).
297 The abundance of *Glomeromycota* in lavandula-associated soils corresponded to the top
298 levels observed in soils using general fungal ITS marker sequencing (Clemmensen et al.,
299 2015; Guo et al., 2019; Leff et al., 2015; Orgiazzi et al., 2012; Tedersoo et al., 2014). Benefits
300 of mycorrhizal symbiosis were demonstrated on carob growth and drought stress tolerance
301 (Essahibi et al., 2017; Manaut et al., 2015; Ouahmane et al., 2012), but different effects

302 depending on *Glomeromycota* taxa was observed (Essahibi et al., 2017), highlighting the need
303 to better characterize mycorrhizal partners of carob trees. The current results extended the
304 range of *Glomeromycota* taxa previously described as associated with carob trees using older
305 methodologies (Manaut et al., 2015), with notably the detection of *Diversispora* spp.,
306 expanding the potentialities of carob habitats as reservoir of mycorrhizal ressources to
307 improve carob afforestation strategies (Manaut et al., 2015). Nevertheless, a deeper
308 investigation of carob habitats and cross-compartment surveys (soils vs roots; Berruti et al.,
309 2017; Varela-Cervero et al., 2015) are necessary to fully decipher the mycorrhiza community
310 associated with carob trees.

311

312 **CONCLUSION**

313 The current work provided new insights on rarely assessed belowground biodiversity of
314 Moroccan carob habitats. Microbiota community structure appeared as a relevant variable to
315 characterize carob habitat heterogeneity in addition to floristic diversity and soil properties.
316 Taxonomy and function of bacteria and fungi differed in their significance to define the type
317 of habitat, strenghtening the need to survey both bacterial and fungal communities in
318 biodiversity surveys, and highliting different microbial reservoirs with functionalities of
319 interest (PGPR, stress-tolerant bacteria, Mycorrhiza) for biotechnology developments.

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622 **Table 1.** List of microbial indicator taxa associated with the North or South habitats.

Locality	Taxonomic (genus) assigment	Functional assigment [(1)]	Probability [(2)] (A ; B)	Indicator value [(3)] (Indval.g)	p-value [(4)]
North Morocco	**Bacteria**				
	Parafilimonas	nd	1.00 ; 1.00	0.95	*
	Fungi				
	Pestalotiopsis	Plant pathogen / Endophyte	1.00 ; 1.00	1.00	**
	Pleurostoma, Spirosphaera	Undefined Saprotroph	1.00 ; 1.00	1.00	**
	Purpureocillium	Fungal parasite	0.97 ; 1.00	1.00	*
	Cylindrosympodium	Plant pathogen / Endophyte	0.97 ; 1.00	1.00	*
	Geosmithia	nd	0.97 ; 1.00	1.00	**
	Dothiorella	Plant pathogen / Endophyte	0.95 ; 1.00	0.97	*
	Macrophomina	Plant pathogen / Endophyte	0.93 ; 1.00	0.97	*
	Exophiala	Animal pathogen	0.93 ; 1.00	0.97	*
	Lecanicillium	Animal pathogen	0.87 ; 1.00	0.94	*

	Calonectria, Kellermania	Plant pathogen	1.00 ; 0.75	0.87	*
	Malassezia, Phaeoacremonium	Animal pathogen	1.00 ; 0.75	0.87	*
	Ophionectria, Quadricrura	Undefined Saprotroph	1.00 ; 0.75	0.87	*
	Guttulispora	nd	1.00 ; 0.75	0.87	*
	Bacteria				
	Kocuria	PGPR, metal resistant, halotolerant	1.00 ; 1.00	1.00	**
	Naasia	nd	1.00 ; 1.00	1.00	**
	Cellulomonas	PGPR, nitrogen fixer, lignin degrading, halotolerant	0.98 ; 1.00	0.99	**
	Rhodocytophaga	nd	0.94 ; 1.00	0.97	*
	Rubellimicrobium, Geminicoccus	Potential global stress tolerant	0.92 ; 1.00	0.96	**
	Segetibacter	nd	0.90 ; 1.00	0.95	*
	Rhodococcus	PGPR, metal resistant, hydrocarbon degrading	0.88 ; 1.00	0.94	**
South Morocco	*Lautropia*	Potential hydrocarbon degrading	0.87 ; 1.00	0.93	*
	Myxococcus	Plant pathogen antagonist, insoluble	0.87 ; 1.00	0.93	*

		organic compound degrading			
	Uncharacterized Beijerinckiaceae	nd	0.86 ; 1.00	0.93	*
	No significant fungal indicator				ns

(1) For fungi, functional assignment was based on FUNGuild database (http://www.funguild.org/). For bacteria, traits related to plant pathogeny, plant-promoting effect, soil cycling or stress tolerance based on literrature were indicated (Web of Science, TOPIC:*genus name* AND TOPIC:*soil*). nd, not defined. PGPR, Plant growth promoting rhizobacteria

(2) Probablility A indicates the specificity, *i.e.* the probability that a soil sample belongs to a given habitat given the fact that the taxa has been found. Probablity B indicates the fidelity, *i.e.* the probability of finding the species in a soil sample belonging to a given habitat

(3) Indval.g indicates the model of association used for the association test

(4) Significance code. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, $P > 0.05$

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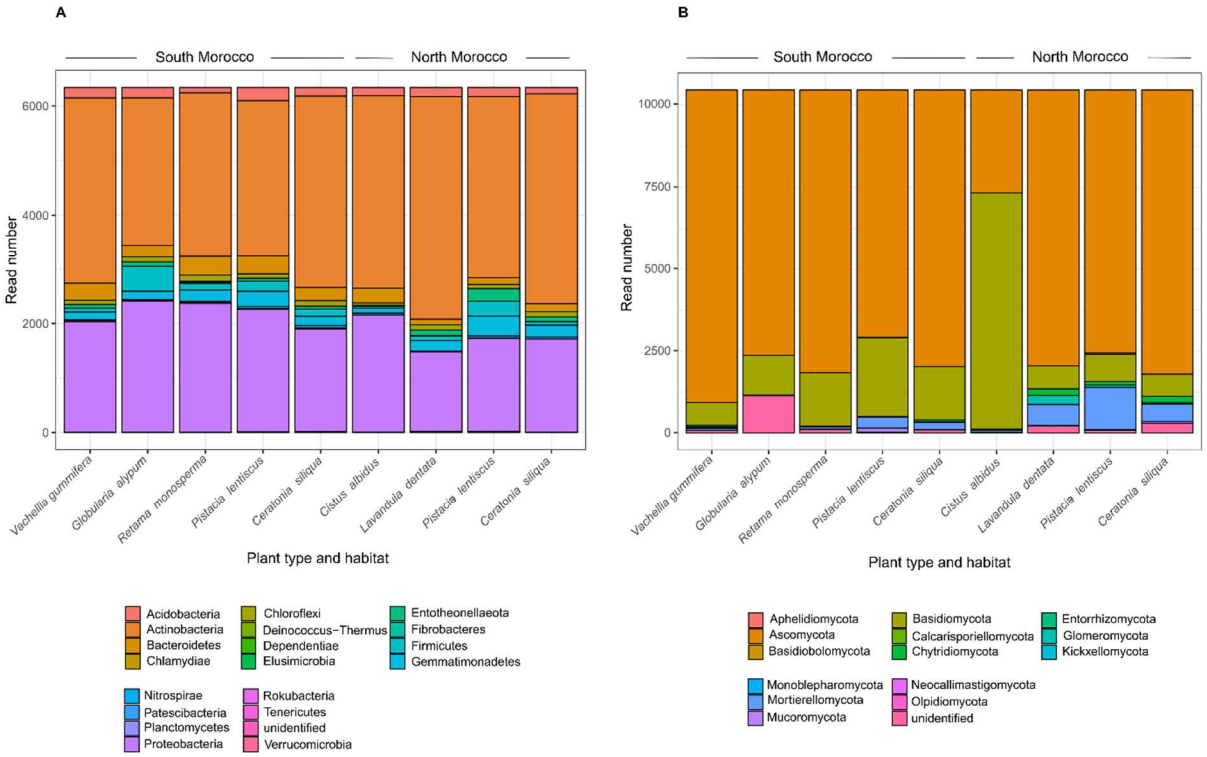

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632

633 **Figure 1.** Phylum level distribution of (A) bacterial and (B) fungal communities among plant

634 species from the South and North habitats.

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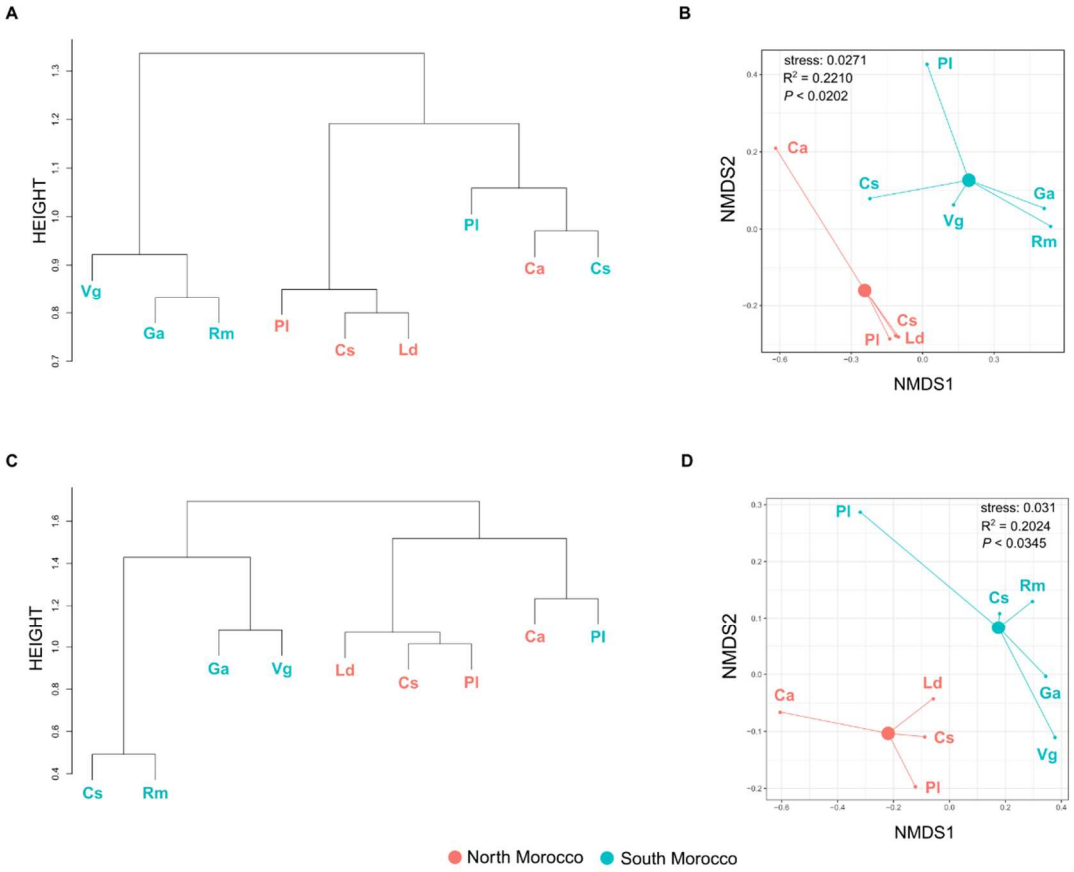
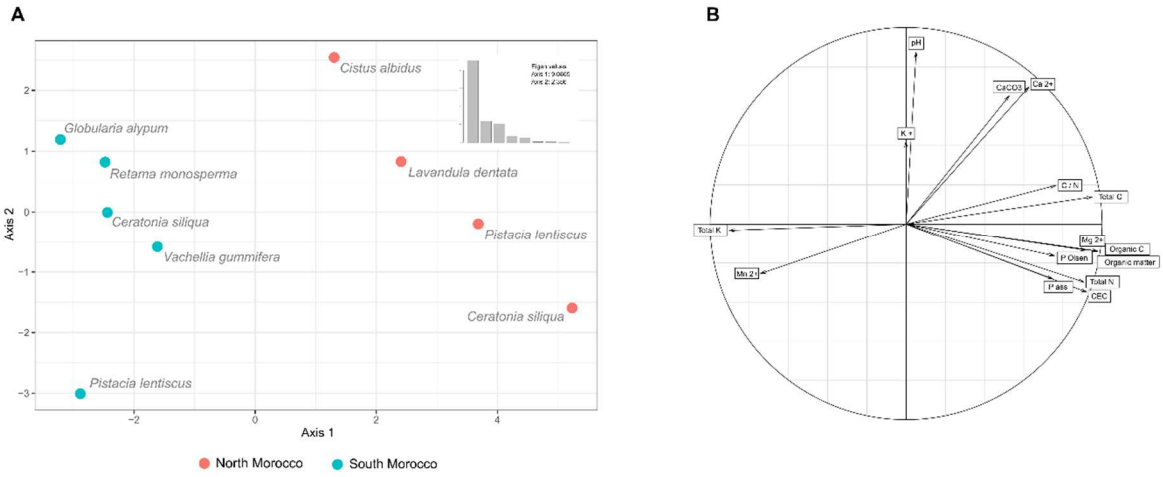


Figure 2. Microbiota structure analysis from plant species of the North (red) and South (blue) habitats. Two methods were used to visualize the bacterial (A, B) and fungal OTU (C, D) community structures, hierarchical clustering (A, C) and non-metric multidimensional scaling (B, D). Vg, *Vachellia gummifera*; Ca, *Cistus* albidus; Cs, *Ceratonia siliqua*; Ga, *Globularia alypum*; Ld, *Lavandula dentata*; Pl, *Pistacia lentiscus*; Rm, *Retama monosperma*. Differences in community structure between the North and South habitats were assesed by PERMANOVA. R^2 and P-values from PERMANOVA are indicated on non-metric multidimensional scaling (B, D). Heterogenity of data dispersion (HOMOVA) between North and South habitats were non significant.



647

648 **Figure 3**. Principal component analysis of soils collected under different plant species from
649 North and South habitats based on soil properties. (A) Structuration of soil samples according
650 their physico-chemical characteristics. (B) Correlation circle indicating the contribution of
651 each soil property in the structuration of soil samples.

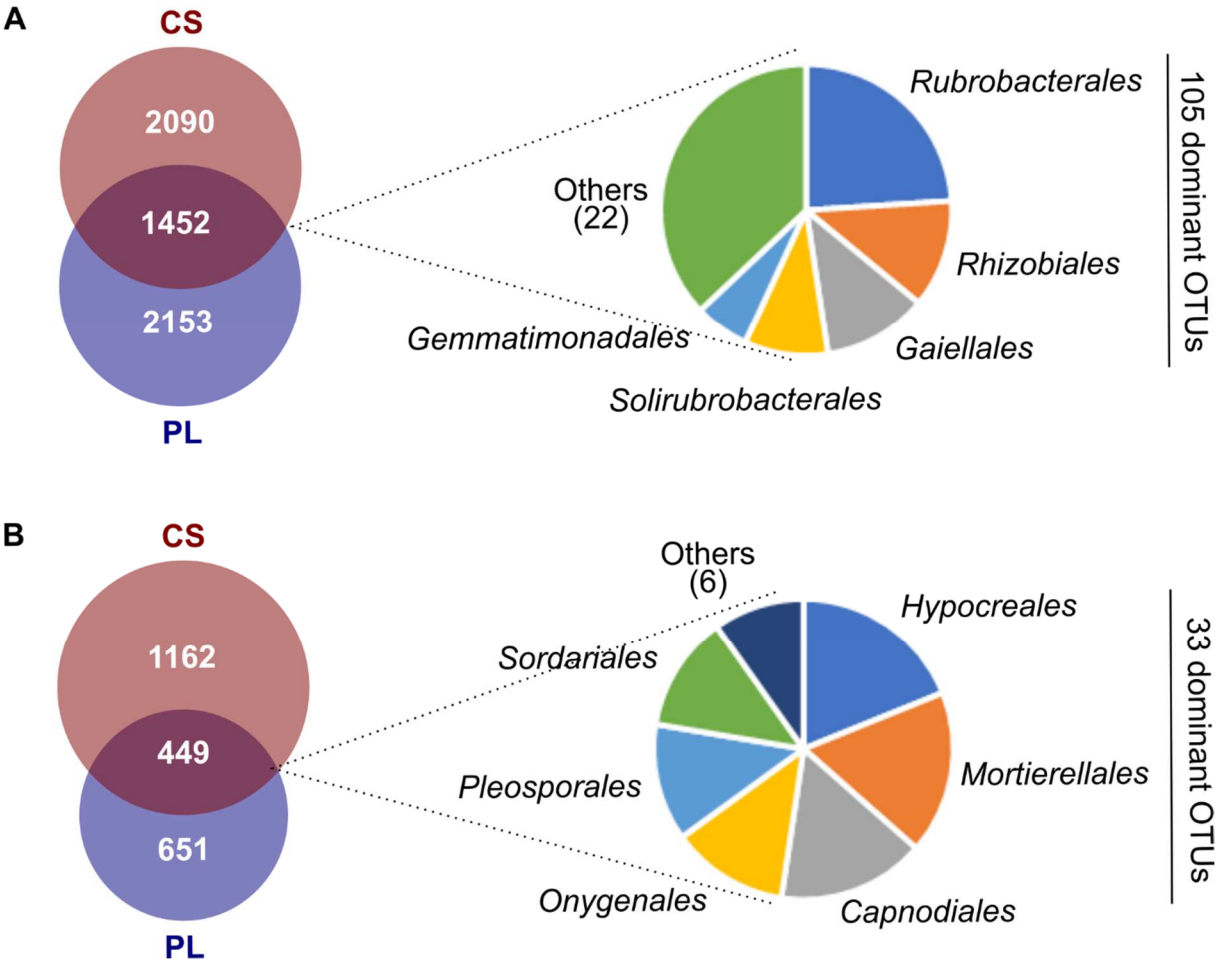


Figure 4. Comparison of (A) bacterial and (B) fungal community membership (Venn diagram analysis) among *C. siliqua* and *P. lentiscus* from both the North and South habitats. For each venn category, the number of OTUs is indicated. Color pie charts represents the taxonomic distribution (order) of the most dominant OTUs (top 10 % of most abundant; present in all samples) shared between the two plants. The category "Others" combines taxa representing less than 5%. Cs, *Ceratonia siliqua*; Pl, *Pistacia lentiscus*.

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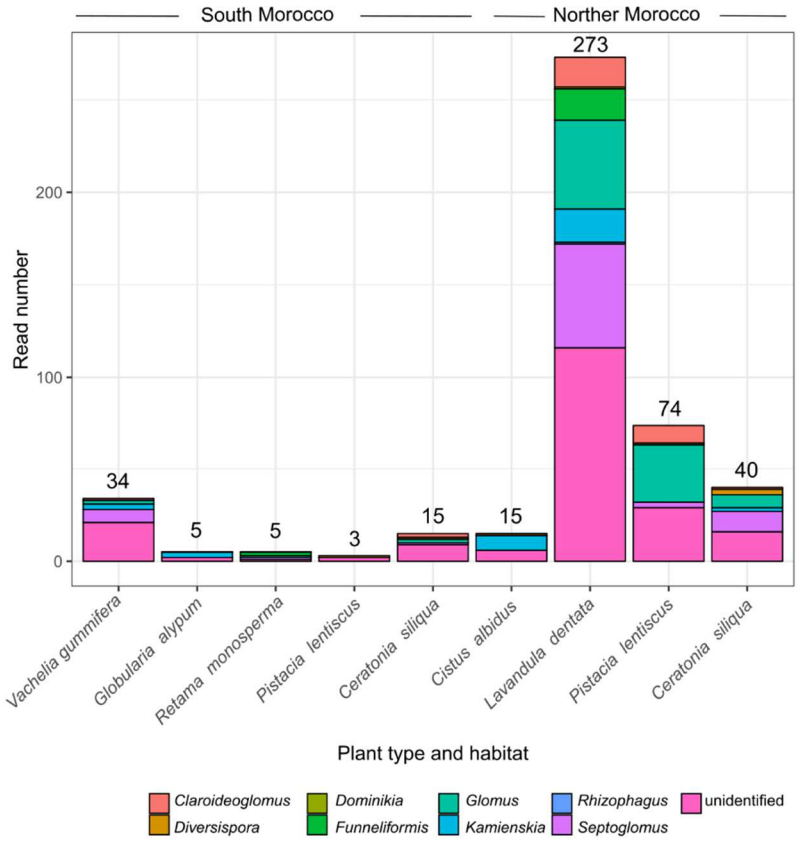

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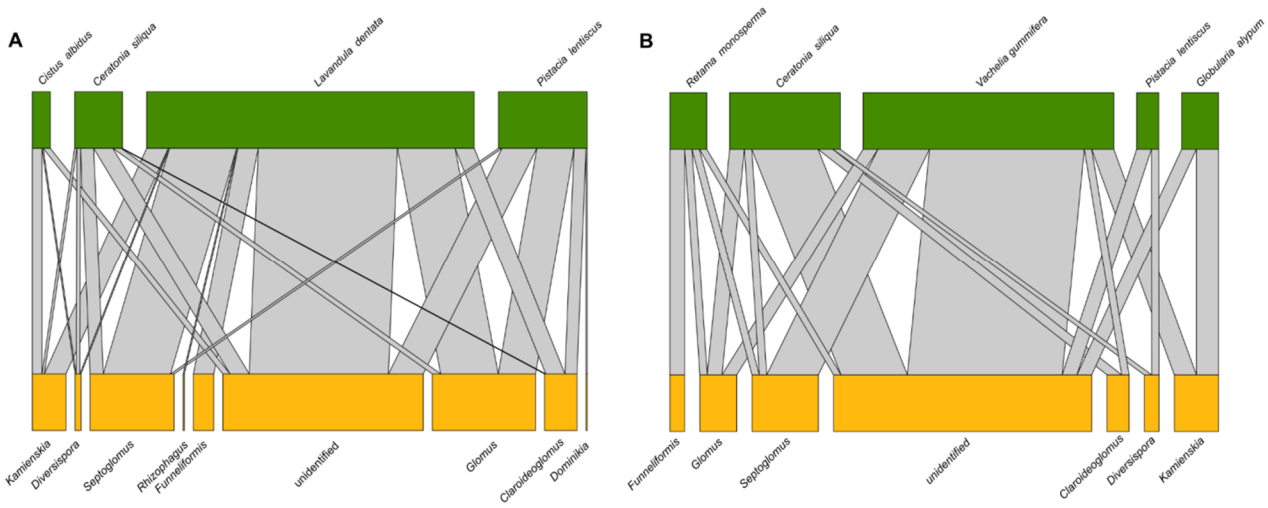
662 **Figure 5.** *Glomeromycota* genus distribution among plant species from the North and South

663 habitats. The total number of sequences is indicated above each barplot.

664



665

666 **Figure 6**. Bipartite interaction network formed by *Glomeromycota* (genus taxonomic level;

667 lower boxes) and major plants species (upper boxes) in the North (A) and South (B) habitats.