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Soil bacterial and fungal biomass are independent of aboveground plant communities in a rocky island system

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ABSTRACT

Soil microbial communities and plants are intimately associated and each can regulate the growth and specific composition of the other through relationships such as competition and symbiosis. Such links between the above and belowground components of soil ecosystems are important as they determine the functioning of key ecosystem processes, including decomposition and nutrient cycling. In the present study, we used structural equation models to investigate the direct and indirect effects of plant community properties (richness, evenness and net primary productivity) and of soil nutrient pools (C, N and P) on the biomass of rhizosphere and non-rhizosphere bacteria and fungi. The biomass of rhizosphere and non-rhizosphere bacteria and fungi was mainly determined by the organic matter content. More importantly, nutrient pools were not modulated by plant communities and we did not find any evidence of a link between aboveground and belowground components of soil systems in this respect. The findings indicate that aboveground and belowground components of the soil system are not directly linked and that any potential relationships will be mediated by the effects of aboveground components in nutrient pools.

1. Introduction

In most terrestrial ecosystems, around 80–90% of the aboveground net primary production enters the soil food web as dead plant material (Cebrian, 1999). In addition, plants release up to 10% of the C that is fixed daily through their roots (Farrar et al., 2003). Thus, incoming resources from plants, either living or dead, are important factors governing the abundance of bacteria and fungi, which form up to 90% of the soil microbial biomass and are the primary litter decomposers (Wardle, 2002). Microorganisms can also control aboveground plant communities by immobilizing or mineralizing nutrients (van der Heijden et al., 2008). Hence, soil microorganisms are closely associated with plants at a local scale (Wardle, 2002), and such links drive ecosystem functioning (Wardle et al., 2004; Bardgett et al., 2005; De Deyn and Van der Putten, 2005).

Belowground productivity is related to the availability of dead organic matter, and as such, microbial biomass responds positively to increased net primary productivity. However, bacteria are mainly controlled by top-down forces and are more independent of resource availability than fungi, which are controlled by bottom-up forces (Wardle et al., 2004). Moreover, plants are known to exert strong control over microorganisms. Thus, microbial biomass varies greatly among different plant species, reflecting differences in the quality of nutrients released by plants, as well as in rooting strategies, thus creating new microhabitats that are readily exploited by microorganisms (Bardgett and Wardle, 2010). The space available for plant communities to grow and develop should modulate microbial growth, because plants use different rooting and nutrient allocation strategies when they grow separately than when they grow together (Dudley and File, 2007; Lamb and Cahill Jr, 2008; Cahill Jr et al., 2010).

As soil microorganisms control several key processes such as nutrient cycling, plant nutrient acquisition and soil formation, it is important to determine the strength of links between plant communities and soil microorganisms. In order to examine these links, we applied the island theory (MacArthur and Wilson, 1967) to a natural system comprised of rocky outcrops with holes where plants communities grow, referred to hereafter as “gaps” (Fig. 1). Island theory postulates that the richness of island species depends on island size and isolation from source regions. This theory has been tested in soil ecosystems; in this context, it has been predicted that diversity (plants and microorganisms) is related to island size (Bell et al., 2005; Wardle et al., 1997, 2003), productivity is related to diversity, and soil nutrient pools are related to productivity (reviewed

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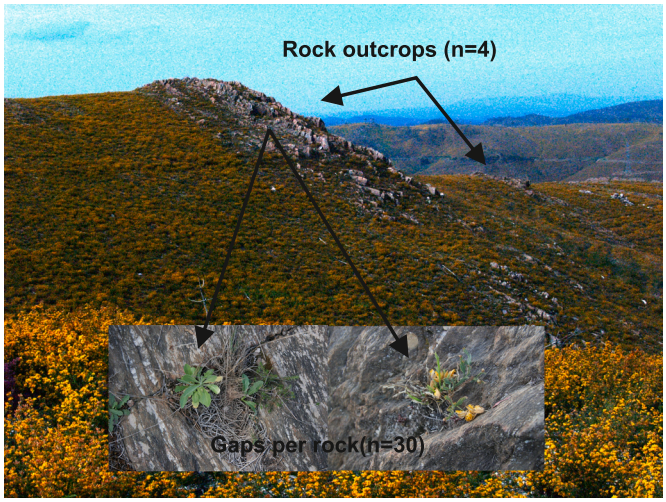

Fig. 1. A general view of the study area in Monte Carbelo, Melón, Ourense (Spain), showing two of the four rocky outcrops sampled and two of each of the 30 gaps sampled per rocky outcrop.

in Bardgett and Wardle, 2010). Consequently, larger islands should support higher plant diversity, which should result in increased productivity and soil nutrient pools supporting higher microbial biomass. To test this theory, we searched for gaps in rocky outcrops containing small plant communities. For each gap, we collected data on plant species, number and biomass, soil nutrient contents (C, N and P) and microbial biomass (determined using PLFAs). We fitted the data to structural equation models (SEM), including the effect of the gap area on plant communities, soil nutrients and microbial biomass. We then used SEM models to analyse the data, in order to test direct and indirect effects on bacterial and fungal biomass in relation to gap area, properties of aboveground plant communities (richness, evenness and net primary productivity) and soil nutrient pools.

2. Material and methods

2.1. Site description and sampling design

The experimental site is located at Mount Carvelo, Melón, Ourense (Spain). The elevation of the area is 550 m above sea level. The climate is temperate Mediterranean, with a mean annual precipitation of 950 mm (rank 759–818 mm) and mean annual temperature of 14.5 °C (rank −4.4 - 36.3 °C). The main tree species in the area were originally *Pinus pinaster* and *Eucalyptus globulus*, but these completely disappeared after a forest fire that burned the area in the summer of 2006. Two years after the fire, the vegetation cover was mainly composed of gorse (*Ulex europaeus*), broom (*Chamaespartium tridentatum*) and heather (*Erica umbellata*). In the site, we randomly selected four rocky outcrops with differently sized gaps colonized by plants (Fig. 1). The gaps thus resemble natural microcosms (Srivastava et al., 2004) or discrete islands within the surrounding environment. Island theory has similarly been applied to study the ecology of microorganisms, as in the following examples: soil suspended on tree canopies (Wardle et al., 2003); bacterial populations in tree hole habitats (Bell et al., 2005); unicellular fungi living in flowers (Belisle et al., 2012); archaea living in geothermal solfatara (Whitaker et al., 2003); and ectomycorrhizal fungal associations with host plants (Peay et al., 2007; Glassman et al., 2017). All of these different systems, as well as the gaps in our study system, can be considered isolated habitats surrounded by a common environment, and as such, they are isolated, controllable and replicable microcosms of biological communities.

We randomly selected and flagged, with epoxy putty (IVECOR), a total of 30 gaps per rocky outcrop (n=4). The gaps ranged in size from 17.1 to 2684.9 cm^2. We photographed (Canon Eos 20D) each gap along with an established scale and used AnalySIS software to measure the area occupied by each gap. We identified and counted the number of each plant species colonising each gap, and removed all aboveground standing plant biomass. We then sampled the soil. We collected all of soil contained within each of the smallest gaps. However, for the larger gaps, we collected five soil samples at random and then combined these to make a composite sample for each gap. By doing this, we tried to minimize the effects of uneven distribution of plant species and depth of gaps, which usually increased from the edges to the centre of gaps. The plant biomass was transported to the laboratory where it was dried (60 °C) to constant weight (plant biomass). The following 10 plant species were found in the gaps (percentage of presence in the gaps): *Erica umbellata* (80%), *Agrostis castellana* (73%), *Sedum anglicum* (51%), *Pinus pinaster* (22%) *Chamaespartium tridentatum* (15%), *Jasione montana* (10%), *Halimium lasianthum* (5%), *Simethis planifolia* (5%), *Pedicularis sylvatica* (2%) and *Eucalyptus globulus* (1%). After sampling the plants, we sampled the soil from each gap for chemical and microbial analysis. The fresh soil samples were chemically analysed the day after sampling, whereas the fraction of samples used to determine PLFAs was frozen at −80 °C until analysis.

2.2. Chemical and microbiological analysis

The moisture content of the soil samples was determined after drying at 105 °C for 24 h, and the organic matter content was determined after heating at 550 °C for 4 h. The soil pH was recorded in a suspension of the samples in distilled water at a sample to extractant ratio of 1:20 (weight/volume). Total extractable N (TEN) was determined in 0.5 M K_2SO_4 extracts after oxidation with $K_2S_2O_8$, as described by Cabrera and Beare (1993). Dissolved organic C (DOC) was determined colorimetrically after moist digestion ($K_2Cr_2O_7$ and H_2SO_4) of aliquots of 0.5 M K_2SO_4 extracts of the samples. Phosphate was extracted from the soil samples (2 g dw) with acetic acid (2.5%), and the absorbance of the filtered extracts was read at 700 nm after the addition of ammonium molybdate (0.1 M) and tin chloride (Allen et al., 1986).

Microbial communities were examined by phospholipid fatty acid (PLFA) analysis. Total lipids were extracted from 2 g of freeze-dried soil samples with methanol and chloroform (1:2, v:v). The mixture was then filtered and evaporated under a stream of N_2 gas. The total lipidic extract was then dissolved with chloroform (3 × 1 mL). Lipids were separated into neutral, glyco- and phospholipids in silicic acid columns (Strata SI-1 Silica (55 μm, 70 A), 500 mg/6 mL), with chloroform, acetone and methanol respectively. The fraction containing phospholipids was evaporated under a stream of N_2 and redissolved in 500 L of methyl-*tert*-butyl ether. One hundred microliters of this solution was placed in a 1.5 mL vial with 50 μL of the derivatizating agent (trimethylsulfonium hydroxide, TMSH). The mixture was then vortexed for 30 s and allowed to react for 30 min before the addition of 10 μL of nonadecanoic acid methyl ester as an internal standard. The chromatographic conditions used to identify and quantify the fatty acid methyl esters, retention times and mass spectra were compared with those obtained for known standard mixtures or pure PLFAs (Gómez-Brandón et al., 2008).

The PLFAs used as biomarkers have been described in the relevant literature (Frostegård and Bååth, 1996). Total microbial biomass was determined as the sum of all extracted PLFAs expressed as μg g^{-1} dry weight. The abundance of each of the different microbial groups (bacteria and fungi) was determined by the abundance of specific biomarkers commonly used for these groups. PLFAs considered to be predominantly of bacterial origin were summed in order to estimate bacterial biomass (15:0, 17:0, i14:0, i15:0, a15:0, i16:0, i17:0, a17:0, 16:1c, cy17:0, 17:1c, 18:1ω7c and cy19:0) (Frostegård and Bååth, 1996). Fungal biomass was determined from the relative concentration of 18:2ω6c PLFA (Frostegård and Bååth, 1996). The biomass of rhizosphere bacteria was estimated as the sum of PLFAs cy17:0 and cy19:0 (Drigo et al., 2010). The biomass of non rhizosphere bacteria was

estimated as the difference between overall bacterial biomass and the biomass of rhizosphere bacteria.

2.3. Statistical analysis

The following data were obtained for the gaps: plant species richness, PIE Hurlbert's (as a measure of plant community evenness, calculated as $PIE = \left(\frac{N}{N-1}\right)\left(1 - \sum_{i=1}^{S}(p_i^2)\right)$, where N is equal to the total number of species in the assemblage, and p_i represents the proportion of the entire sample represented by species *i*), and plant biomass (as a measure of net primary productivity: NPP). The nitrogen contents determined by chemical analysis were expressed as TEN (total extractable nitrogen, the sum of mineral and dissolved organic N). Organic matter content and pH were included in the model as separate variables. These variables were arranged in a network and analysed by structural equation modelling (SEM) to explore how plant communities and soil nutrient pools influence bacterial (rhizosphere and non-rhizosphere bacteria) and fungal biomass in the soil. We fitted three SEM models, one for each of the microbial variables (Fig. 2). The SEM models were analysed with the "piecewiseSEM" (Lefcheck, 2016) and "nlme" packages. The piecewiseSEM may also account for random effects of sampling sites (to account for having more than one gap per rock outcrop), by providing "marginal" and "conditional" contributions of environmental predictors in driving microbial diversity. Fisher's C test was used to confirm the goodness of the modelling results. Double headed arrows were used to represent covariance between variables included in all three models to achieve adequate model fits. Relationships between variables were established using current scientific knowledge on soil ecosystems (Bardgett and Wardle, 2010). Thus, plant diversity is expected to increase with the gap area (Wardle et al., 1997, 2003), plant richness should increase productivity, and plant productivity should promote increased soil nutrient pools (reviewed in Bardgett and Wardle, 2010). Consequently, larger gaps should support higher plant diversity, which should result in increased productivity and soil nutrient pools supporting higher microbial biomass. As we were not able to obtain large enough soil samples for all analyses in each gap, we only used data from 91 gaps. We analysed the effect of gap area on soil nutrient pools by fitting linear mixed models with rock outcrop and island identity nested within rock as random effects by using the nlme library (Pinheiro et al., 2009). We analysed the effect of gap isolation on plant richness and microbial variables using mixed models. We did not find any effect of isolation, i.e. plant richness and microbial biomass were not lower in the islands/gaps further from the main soil (Supplementary Fig. 1). The Pearson's correlations between the study variables are included in Supplementary Table 1.

All analyses were performed with R Development Core Team (2010).

3. Results

Microbial communities in the soil system under study were dominated by bacteria, and the bacterial biomass was greater (mean: 20.98, range: 6.39–73.46 and 95% CI: 18.81, 23.15 μg g^{-1} dw) than the fungal biomass (mean: 0.68, range: 0.09–13.03 and 95% CI: 18.81, 23.15 μg g^{-1} dw). The models describing the biomass of rhizosphere and non-rhizosphere bacteria and fungi are shown in Fig. 3. All three SEM models provided a good fit to the data (Fisher's C = 19.007; $P = 0.165$.) All three models showed that the gap area directly affected plant richness and evenness and indirectly affected NPP through the effects on plant richness (Fig. 3abc). Only organic matter content directly affected the biomass of rhizosphere and non-rhizosphere bacteria and fungi (Fig. 3abc, Table 1). The DOC content marginally and negatively affected non-rhizosphere bacteria. No effect of gap area on the four nutrient pools analysed was observed (Fig. 4)."

4. Discussion

The study findings showed that aboveground components matched island theory predictions. Thus, plant diversity increased with gap size and productivity was consequently also higher in larger islands. However, this did not result in increased soil nutrient pools. The findings also indicate that the bacterial (rhizosphere and non-rhizosphere bacteria)

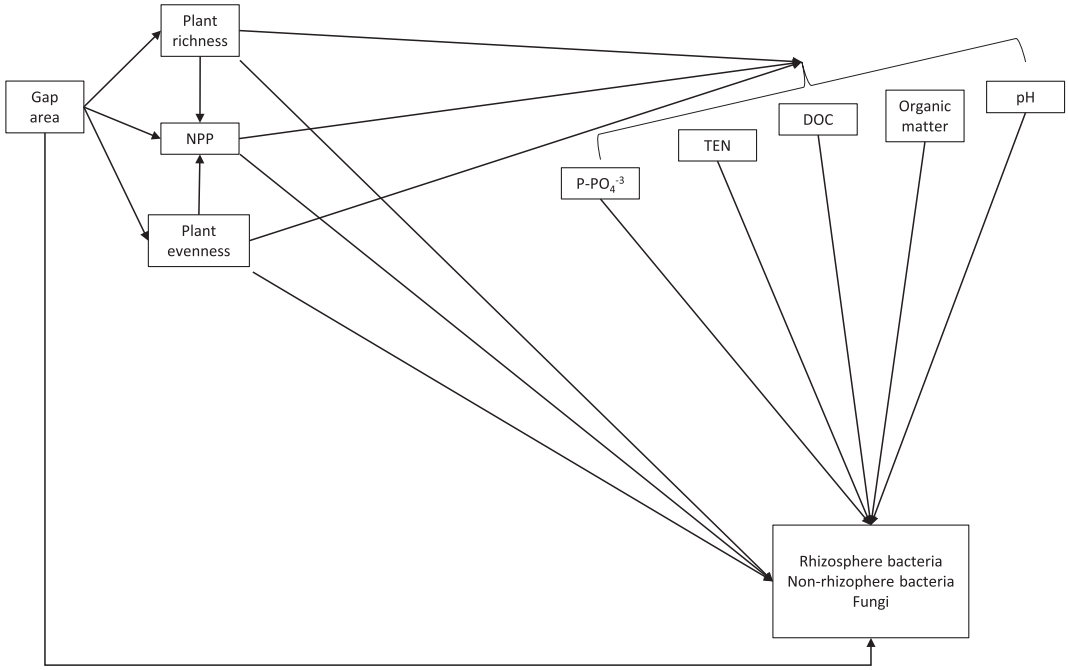

Fig. 2. Conceptual model of the biomass of rhizosphere, non-rhizosphere bacteria and fungi. The plant community variables (plant richness, net primary productivity [NPP] and plant evenness) were each related to all variables grouped in brackets (organic matter, dissolved organic carbon [DOC], total extractable nitrogen [TEN], phosphate content and pH). The relationships between variables were established on the basis of current scientific knowledge about soil ecosystems (Bardgett and Wardle, 2010).

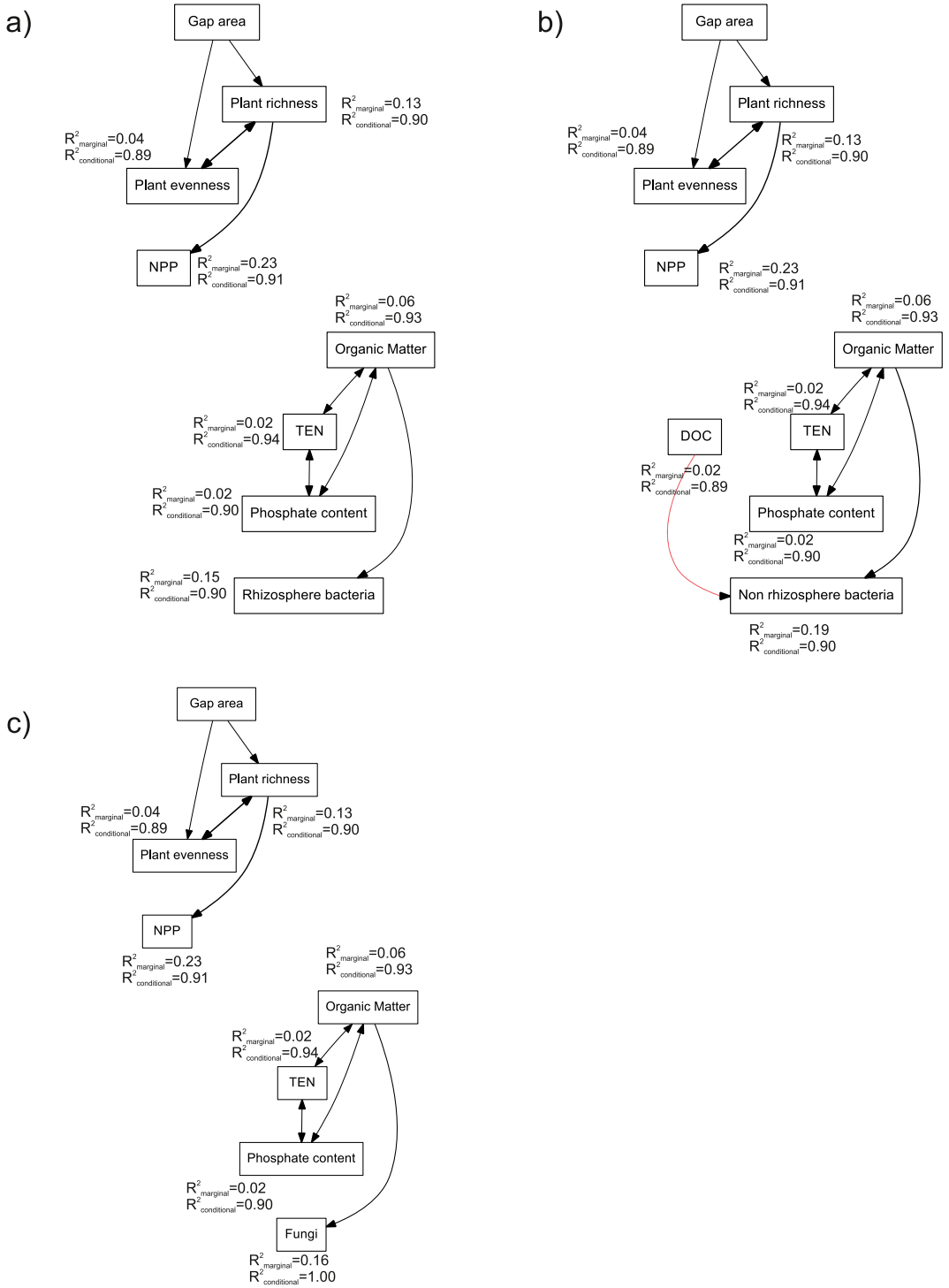

Fig. 3. Structural equation models for (a) rhizosphere biomass, (b) non-rhizosphere bacterial biomass and (c) fungal biomass. Only significant ($P < 0.05$, solid lines) and marginally significant relationships ($0.1 < P < 0.05$, dashed lines) are shown. Positive and negative relationships between pairwise predictors are shown in black and red, respectively. The width of the lines is proportional to the value of the standardized coefficients of SEM models. DOC (dissolved organic carbon), TEN (total extractable nitrogen) and NPP (net primary productivity). Marginal and conditional R^2 denote the proportion of variance explained by the predictors included that do or do not account for random effects of sampling site respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and fungal biomass were mainly directly and positively related to soil organic matter content. More importantly, organic matter content was completely independent of aboveground components. In addition, other nutrient pools such as DOC also negatively affected the biomass of non-rhizosphere bacteria.

The lack of any effects of plant community on microbial biomass is not consistent with the findings of previous studies relating increases in microbial biomass in the laboratory (Bardgett and Shine, 1999) and in experimental grassland communities (Zack et al., 2003; De Deyn et al., 2011). However, Zack et al. (2003) showed that the effects of plant richness disappeared when the NPP of plots was taken into account. More recently, De Deyn et al. (2011) reported that fungi did not respond

Table 1
Output from piecewiseSEM analysis using the full models depicted in Fig. 2. For each rhizosphere, non-rhizosphere bacteria and fungi models (microbes in the table), we provide the estimates and their associated *P* values for only significant relationships. DOC: dissolved organic carbon, TEN: total extractable nitrogen, NPP: net primary productivity.

	Rhizosphere bacteria		Non rhizosphere bacteria		Fungi	
	Estimate	*P*	Estimate	*P*	Estimate	*P*
Area→plant richness	0.371	0.0002	0.371	0.0002	0.371	0.0002
Area→plant evenness	0.214	0.032	0.214	0.032	0.214	0.032
Plant richness→NPP	0.521	0.0004	0.521	0.0004	0.521	0.0004
Organic matter→microbes	0.334	0.0031	0.462	0.0001	0.419	0.0005
DOC→microbes	0.105	0.317	−0.183	0.089	−0.149	0.172
Plant richness↔plant evenness	0.690	<0.0001	0.690	<0.0001	0.690	<0.0001
TEN ↔PO_4^{-3}	0.196	0.032	0.196	0.032	0.196	0.032
Organic matter↔PO_4^{-3}	0.366	0.0002	0.366	0.0002	0.366	0.0002
Organic matter↔TEN	0.195	0.032	0.195	0.032	0.195	0.032

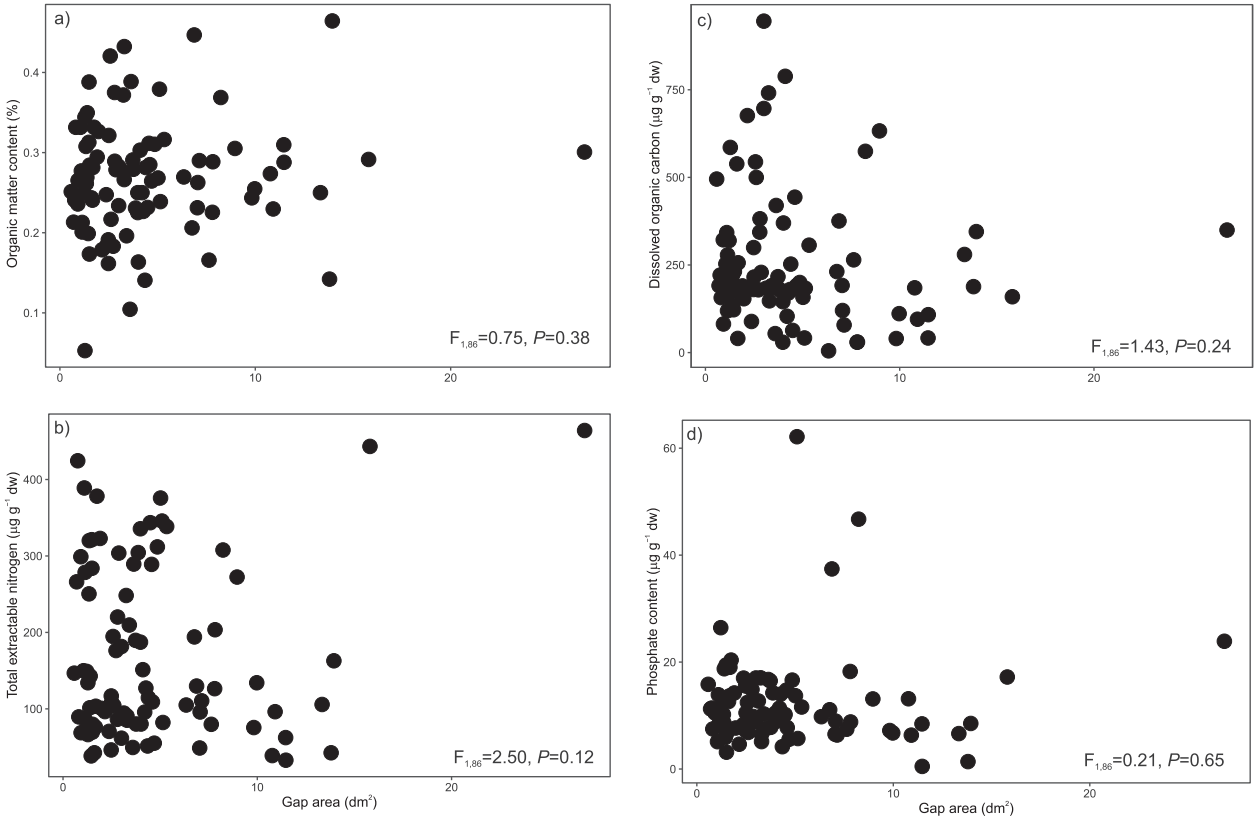

Fig. 4. Effect of island area on soil nutrient pools: a) organic matter content, b) total extractable nitrogen, c) dissolved organic content and d) phosphate content.

to plant richness and the bacterial biomass only increased in plant communities with more than 3 plant species. In addition, Lamb et al. (2011) reported that only plant evenness modulated bacterial abundance in experimental grassland communities. According to this, we expected NPP and plant evenness to have a positive influence on microbial biomass. However, the NPP did not affect the rhizosphere bacteria (the fraction of bacteria closely associated with plant roots), which strongly depend on plant exudates (Hartmann et al., 2009). A high NPP implies that more C enters the soil, via litter deposition and root exudates (Catovsky et al., 2002; Steinbeiss et al., 2008). In the present study system, root exudates probably comprise the largest fraction of C entering soil, as litter deposition was scarce. Moreover, a high NPP should thus enhance nutrient demands and the rate of photosynthesis, driving the release of plant root exudates. Rhizosphere microorganisms appear to be more limited by N than by C (Eisenhauer et al., 2010), and therefore plant root exudates may modify the abundance of soil microorganisms (Hartmann et al., 2009). Moreover, as each plant species has its own root exudate profile, plant communities should also have a standard root exudate profile (Bardgett and Wardle, 2010). According to this rationale, we expect microorganisms to respond positively to NPP, plant richness and evenness, directly or indirectly through the effects on soil nutrient pools. However, our data are not consistent with this rationale; this may be due to plant competition, which decreases with plant evenness and leads to different patterns of root production in response to non-kin, or to variable spatial resource availability (De Kroon, 2007; Dudley and File, 2007; Lamb and Cahill Jr, 2008; Cahill Jr et al., 2010). According to this, we found that plant evenness increased significantly with gap size.

The plant communities in our study system behaved as expected, i.e. larger gaps supported plant richness, resulting in higher NPP (MacArthur and Wilson, 1967; Loreau et al., 2001; Hooper et al., 2005). However, the plant communities scarcely affected microbial communities or even soil nutrient pools. This is surprising as each plant species utilizes a different strategy (rooting, release of exudates), which should

promote new microhabitats when plant richness increases; moreover, this effect will be enhanced by the evenness of plant communities (reviewed in Lamb et al., 2011). In addition, NPP did not determine soil organic matter content in the way expected (Hooper et al., 2005). These findings contradict previous observations relating increased nitrification rates to plant richness (Zack et al., 2003; Lamb et al., 2011), although they are consistent with the lack of any effects on DOC. Interestingly, phosphate content marginally depended on vegetation and it increased with plant evenness and thus indirectly with gap area. Although phosphorus limitation should appear at late stages of succession (Wardle, 2002), the fires that occurred two years previously in the study area may have altered the plant communities and reduced the organic matter content, so that these communities are at the initial stages of colonization, during which phosphorus is released to optimize growth (Wardle, 2002).

5. Conclusions

We conclude that there is no direct or indirect evidence of links between aboveground plant communities and soil bacterial and fungal biomass in the study system. Moreover, bacteria dominated microbial communities in the system, with fungi playing a minor role. This is consistent with top-down control of bacteria, which is strongly dependent on organic matter content (Wardle, 2002). The resulting food webs dominated by bacteria are characterized by rapid nutrient mineralization that favours plant growth.

Declaration of competing interest

All authors disclose any financial and personal relationships with other people or organizations that could inappropriately influence this work, In addition, all authors declare that there are no interests to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2020.103877.

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