

Distribution of Microbial Generalists and Habitat Specialists in Soils Along a Climate Gradient in the Chilean Coastal Cordillera

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Research

Keywords: Biogeography, Community composition, Illumina HiSeq, Bacteria, Archaea, Niche breadth, Environmental gradient, EarthShape

Posted Date: July 16th, 2020

DOI: <https://doi.org/10.21203/rs.3.rs-41494/v1>

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Abstract

Background: Recent studies have made significant progress in understanding how microbial composition varies across the major terrestrial biomes. However, they neglected large-scale environmental gradients and a defined set of global environmental predictors, which are applicable within biomes and across gradients, are elusive. We identified the soil microbial community composition on a broad continental scale along the Chilean Coastal Cordillera based on the generalist-specialist concept. Thereby, encompassing surface and subsurface soils from arid, semi-arid, mediterranean, and humid-temperate climate conditions.

Results: Our results showed that soil communities from different climate regions are composed of the same subset of taxonomic groups. We further identified generalists, comprising taxa that predominated in all four regions, and habitat specialists that predominated in one or two regions only. We obtained higher proportions of habitat specialists (34 groups) than generalists (22 groups) with an increase of the generalist-to-specialist index along our gradient from North to South. The arid climate region revealed a unique hotspot of microbial specialization (60.1%). Contrary, the mediterranean and semi-arid regions featured mainly boundary-crossing specialists (35.5%).

Conclusions: Our study supports that species sorting in response to local environmental factors is a key determinant of microbial community composition and further, the degree of microbial specialization can potentially be linked to the overall ecosystem stability.

Introduction

Soil represents the most diverse and species-rich environment on Earth, thereby inhabiting members of all three domains of life [1]. According to the species sorting model, the environment forms a natural gradient of various prevailing conditions, in which microbial species sort themselves according to their potentially favored conditions [2, 3]. This natural selection is directly linked to niche-based mechanisms [4] and reflects the individual affinity of species for particular habitats. Hence, the overall classification of microorganisms can be separated in generalists, which exhibit broad environmental tolerances with even distributions across many habitats, and specialists, which are strongly restricted to one specific habitat due to narrow tolerances [5–7].

The process of microbial specialization is evolutionary based and mainly triggered by relatively stable rather than perturbed environmental conditions [8, 9]. In general, microorganisms have tremendous capacities to adapt and survive in all kinds of environments, thereby evolving elaborate mechanisms. For instance, members within the phyla *Actinobacteria*, *Firmicutes*, and *Cyanobacteria* produce dormant stages to resist typical terrestrial stress conditions such as desiccation and ultraviolet radiation [10]. In addition to *Deinococcus*, which represents the most prominent radiation-resistant organism, also *Chloroflexi*, *Alpha*-, and *Gammaproteobacteria* (e.g. *Pseudomonas*, *Enterobacter*) have been shown to resist ionizing radiation by containing photoreactive pigments [11, 12]. In extreme desert ecosystems,

microbial specialists are capable to survive in mineral substrates such as natural porous salt rocks [13, 14]. Here, especially the archaeal class *Halobacteria* and the bacterial phylum *Bacteroidetes* contain extremely specialized members to persist high-salt conditions by accumulating potassium ions to balance the external salt concentration [15].

The distribution and co-occurrence of microorganisms and their differences in community composition across different habitats provide evidence of biogeographical patterns [16, 17]. The most prominent pattern observed in microbial communities states that the overall microbial similarity decreases with increasing geographic distance [18], but little is known about the mechanisms controlling this transfer across biome gradients. Due to niche adaptations, which are directly linked to environmental conditions, it could be assumed to find similar microorganisms in similar habitats [16].

Previous work has made significant progress in understanding how microbial composition varies across the major terrestrial biomes (i.e. desert, forest, grassland). Several global cross-biome studies mapped dominant bacterial [1, 19, 20] and archaeal phyla [21–23] in dependence to their environmental requirements. Overall, global communities contain the same bacterial phyla (*Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Proteobacteria*, *Verrucomicrobia*, *Planctomycetes*) with only minor differences at finer taxonomic scales [19, 24]. In contrast, archaea have been shown to comprise especially members of *Thaumarchaeota* in various terrestrial habitats, especially dominating in deserts and tropical forests [1]. Based on correlative relationships, several edaphic parameters like salinity [25], temperature [26, 27], rainfall amount [28], vegetation type, organic carbon, and nutrient content [22, 29–31] have been shown to significantly shape a microbial community. Besides the environmental impact mentioned above, communities can also be controlled on a local-scale by habitat size, ecosystem productivity [32], and trophic interactions [33]. However, the soil pH turned out to be the only consistent global predictor and has the strongest effect on the community composition on a local [30, 34], regional [35, 36], and continental scale [37]. Generally near-neutral soil pH was shown to be more advantageous for bacteria and contains higher diversities in comparison to acidic or basic soils [37]. However, a defined set of global environmental predictors, which are applicable within biomes and across gradients, are elusive. This is largely because most of the studies, focusing on the biogeography of microorganisms, are highly specific and centered either on single groups or biomes only [1, 28, 38, 39]. Thereby, these studies neglected large environmental gradients covering hundreds of kilometers [31, 40].

The most intensely researched habitat in Chile has been the Atacama Desert by far [41, 42]. Recently, this research area has been augmented by the Chilean Coastal Cordillera which offers a unique natural gradient including various large-scale factors such as biome types, climatic patterns, or latitude [43, 44]. This is the first study focusing on this gradient microbiologically, thereby complimenting previous work on the distribution of microorganisms on a broad continental scale. Here, we investigated the soil bacterial and archaeal abundances and community composition in four different study sites along a broad climate gradient along the Chilean Coastal Cordillera. Thereby, encompassing arid, semi-arid, mediterranean, and humid-temperate climate conditions. In order to characterize overall generalists, comprising taxa that predominated in all four regions, and habitat specialists that predominated in one or

two regions only, we performed Illumina HiSeq amplicon sequencing of 16S rRNA genes. Selected soil physico-chemical parameters were included from previous work for statistical correlation. Thereby, we aimed to determine whether soil communities exhibit clear climate-specific patterns, which are also manifested in the distribution of globally widespread generalists and unique habitat specialists.

Material And Methods

Field site description and sampling

In the frame of the EarthShape project (German Science Foundation SPP 1803), soil samples were collected along a natural climate gradient in the Coastal Cordillera of Chile. This gradient encompasses a great variation in vegetation, which is controlled by climates ranging from arid to humid-temperate. Fieldwork was conducted from March to April 2016 in the four study sites (from North to South) Pan de Azúcar National Park (~ 26°S), Santa Gracia Nature Reserve (~ 30°S), La Campana National Park (~ 33°S), and Nahuelbuta National Park (~ 38°S) (Fig. 1). According to the climate classification [45, 46], the study sites range from arid (Pan de Azúcar), semi-arid (Santa Gracia), mediterranean (La Campana), to humid-temperate climate conditions (Nahuelbuta). Mean annual temperatures decrease from North (18.1 °C) to South (14.1 °C), whereas the mean annual precipitation increases and ranges from 10 mm yr⁻¹ in Pan de Azúcar, 89 mm yr⁻¹ in Santa Gracia, 436 mm yr⁻¹ in La Campana, and 1084 mm yr⁻¹ in Nahuelbuta [44]. For detailed site-specific descriptions as well as soil classifications, we refer to the baseline publications from Bernhard et al. [43] and Oeser et al. [44].

Soil samples along a depth profile were collected on the mid slope position of the South-facing hillslopes in each study site. These depth profiles covered all soil horizons (A, B, C) and were separated into surface (0 to 40 cm) and subsurface (saprolite) soils. The border between each varied and started in 50 cm depth in Pan de Azúcar and Santa Gracia, in 110 cm in La Campana, and 100 cm in Nahuelbuta. In addition, shallow replicate profiles, comprising the upper 40 cm only, were excavated. Soil samples were collected from bottom to top per depth increments (0–5, 5–10, 10–20, 20–40 cm, down to 260 cm) and stored at – 20 °C until further processing.

Soil characterization and DNA extraction

A detailed characterization of the soil profiles was published in Bernhard et al. [43, 47] and Oeser et al. [44, 48]. In this study, we used selected soil physico-chemical parameters (Table S1) for statistical correlation with relative abundances of the bacterial and archaeal communities. A detailed description of all analytical methods (clay-, sand-, silt content, pH, C/N ratio, plant-available phosphorus, total nitrogen) is described in Bernhard et al. [43]. In addition, the total organic carbon (TOC) of all samples was determined by Potsdamer Wasser- und Umweltlabor GmbH (PWU, Potsdam, Germany) according to DIN EN ISO/IEC 17025:2005. Total genomic DNA was extracted using the PowerSoil® (for Santa Gracia, La Campana, Nahuelbuta soil samples) and the PowerMax® (for Pan de Azúcar soil samples) DNA Isolation

Kit (both MoBio Laboratories, CA, USA) following the manufacturer's instructions. Samples from Pan de Azúcar and saprolites from Santa Gracia were crushed before processing.

Illumina HiSeq amplicon sequencing of bacteria and archaea

PCR products were prepared for Illumina HiSeq high-throughput sequencing of bacterial and archaeal 16S rRNA genes. Unique primer combinations of barcode-tagged 515F (5' – GTG CCA GCM GCC GCG GTA A – 3') and 806R (5' – GGA CTA CGV GGG TWT CTA AT – 3') primers were assigned to each sample [49]. Surface samples (0 to 40 cm) were prepared in biological duplicates containing two pooled technical replicates. Saprolite samples were prepared as technical replicates. The amplification assay was carried out in a total reaction volume of 25 µL, containing 0.25 µL Opti *Taq* DNA Polymerase (Roboklon, Germany), 2.5 µL 10x Pol Buffer C, 0.75 µL forward and reverse primer, 1.5 µL MgCl₂, 0.25 µL BSA, 1 µL dNTP mix, 16 µL PCR-grade water, and 2 µL genomic DNA. PCR amplification was performed in a T100™ Thermal Cycler (Bio-Rad Laboratories, CA, USA) with the following cycling program: initial denaturation at 95 °C for 5 min, followed by 10 cycles of denaturation at 95 °C for 30 sec, annealing for 45 sec with decreasing temperatures from 65–55 °C (-0.2 °C/ cycle), elongation at 72 °C for 1 min, followed by 30 cycles of denaturation at 95 °C for 1 min, annealing at 55 °C for 30 sec, elongation at 72 °C for 1 min, followed by a final elongation step for 7 min at 72 °C. PCR products were afterwards purified using carboxyl-coated magnetic beads (SPRI beads, Agencourt® AMPure® XP-Kit, Beckman Coulter, Brea CA, USA) following the manufacturer's protocol. DNA concentrations were measured with a Qubit® 2.0 Fluorometer using the Qubit™ dsDNA HS Assay Kit (both Invitrogen Life Technologies, Thermo Fisher Scientific, Carlsbad CA, USA). All PCR products were pooled equally with final concentrations of 30 ng DNA per sample. In total, two libraries were prepared.

Classification of generalists and specialists

The overall identification of generalists and habitat specialists was done based on total amplicon sequence variant (ASV) proportions. Here, all detected ASVs were included and evaluated based on the presence-absence method, thereby, focusing on the distribution of the ASVs in the different climate regions and along the depth profiles. Habitat generalist were defined as taxa that predominated in all four climates, thus, also including natural variations in abundance along the depth profiles. Habitat specialists dominated in only one climate region, whereas taxa that were obtained in two climates were considered as boundary-crossing specialists. In general, these specialist-related ASVs could possibly also be present in other regions but at significantly lower abundances (< 0.1%), thereby escaping our detection assay. In a second step, we used Levins' approach [5] to calculate the niche breadth (*B*) for each identified taxonomic group to support our findings. This was done by using the following formula;

$$B = 1 / \sum P_j^2$$

with B as the niche breadth and P as the proportion of individual taxa (based on total ASVs) found in a resource state j . The calculated niche breadths are not directly related to the environmental factors as we defined the resource state as habitats. Based on the indices, which ranged from 1.07 to 29.13, taxa with higher values used a potentially broader niche breadth and were considered as generalists (10.23–29.13), respectively. Contrary, taxa with low values were considered as specialists (1.07–7.83). Detailed niche breadths are provided in the data publication (Table S4, S5, S6).

Bioinformatics and statistical analysis

Sequencing was carried out by Eurofins GATC Biotech (Eurofins Scientific, Constance, Germany), on an Illumina HiSeq (2×250 bp). Raw sequence data was filtered and quality-controlled by using the tool FastQC (Quality Control tool for High Throughput Sequence Data; <http://www.bioinformatics.babraham.ac.uk/projects/fastqc/>). Demultiplexing of the reads according to their barcodes was done by using CutAdapt [50]. PEAR [51] was used to merge the forward and reverse read pairs. ASVs from 16S amplicons were identified by using dada2 (Diversity Amplicon Denoising Algorithm) [52]. ASVs which were not classified as bacteria or archaea, as well as chloroplast- and mitochondria-related classifications were removed prior to statistical analysis. Absolute ASVs were transformed to relative abundances.

Statistical analyses were performed with the PAST3 software [54] and visualization with Sigmaplot (Version 12.0, Systat Software). The taxonomical data was discussed on a genus level and above. The biological duplicates were analyzed as independent samples. In order to examine trends between specific bacterial as well as archaeal taxa and soil characteristics, parametric Pearson's correlation coefficients including Bonferroni correction were calculated. Further, Mantel tests (Permutation $N = 9999$) were conducted to study the potential relationship between soil parameters and community structure. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis distance was carried out to visualize general patterns of bacterial and archaeal communities across all samples. Furthermore, soil physico-chemical properties were included to identify possible associations between patterns of community structure and environmental variables.

Results

Soil characteristics

The well-studied soil profiles along the climate gradient from North (26°) to South (38°) featured distinct environmental conditions. In the following, we provide a brief summary of previously published baseline data from Bernhard et al. [43, 47] and Oeser et al. [44, 48] regarding physical and chemical characteristics (selected parameters are shown in the Additional file 1: Figure S1, Table S1).

Soils from the arid desert contained 69.2% sand, 19.7% silt, and 11% clay with highest compositional variations in the uppermost 5 cm. By comparison, soils from the semi-arid and mediterranean regions were similarly composed of 75.1–78% sand, 14.7–15.2% silt, and 7.3–9.7% clay. Surface soils from the

humid-temperate forests were composed of 50.2% sand, 27.8% clay, and 22.0% silt content, whereas in the saprolite a distinct increase in sand but decrease in clay content was observed. Moreover, the soil pH decreased from alkaline to strongly acidic along the climate gradient and varied from 8.1 in arid, 6.3 in semi-arid, 5.5 in mediterranean, to 4.2 in humid-temperate conditions. The two southernmost regions Nahuelbuta and La Campana contained the highest TOC (mean 9.6 and 5.9%) and total nitrogen (mean 0.3 and 0.2%), both parameters were drastically decreasing with depth. Plant-available P was highest in surface soils of the semi-arid (33.1 mg kg⁻¹) and saprolites of the humid-temperate climate (32.7 mg kg⁻¹). The carbon-to-nitrogen (C/N) ratio increased from North to South with mean values ranging from 12.1 in Santa Gracia, 14.3 in La Campana, to 20.8 in Nahuelbuta.

Overall community structure on a phylum along the Chilean climate gradient

The composition of the microbial communities was assessed by HiSeq amplicon sequencing resulting in 14.4 million ASVs in the 40 samples, respectively (Table S2). After merging, orientation correction, and the deletion of chimeric sequences 12.1 million reads remained in the final dataset (82.1% mean ASVs kept). From this 95.3% of the ASVs were assigned to bacteria, 4.7% to archaea, and 0.1% could not be assigned to any domain. After taxonomic classification, 1,467 putative genera (1,417 for bacteria, 50 for archaea) were obtained.

The four climate regions featured a diverse soil bacterial and archaeal community composition, which was composed of eight dominant phyla, thereby explained 81.5% of the total ASV reads determined in the arid, 86.2% in the semi-arid, 88.6% in the mediterranean, and 93.6% in the humid-temperate climate. Based on phylogenetic classification, ASVs could be assigned to the six bacterial phyla *Actinobacteria* (28.7%), *Proteobacteria* (24.7%), *Acidobacteria* (15.3%), *Chloroflexi* (7.6%), *Verrucomicrobia* (5.8%), *Planctomycetes* (5.6%) and the two archaeal phyla *Euryarchaeota* (59.3% of Archaea-related ASVs) and *Thaumarchaeota* (35.9%; Fig. 3, Table S3). In contrast, *Bacteroidetes*, *Firmicutes*, *Gemmatimonadetes*, and *Crenarchaeota* represented only minor proportions of the microbial community. All dominant phyla, excepting *Actinobacteria* and *Euryarchaeota*, followed the climate gradient from North to South and increased in relative abundances. Soils from the arid climate turned out to contain the majority of shifts, which were strongly depth-dependent. Here, *Actinobacteria* (41.8%), *Proteobacteria* (25.4%), and *Euryarchaeota* (64.4%) clearly dominated, whereas lowest abundant phyla were *Acidobacteria* (0.9%) and *Verrucomicrobia* (0.4%). The semi-arid and mediterranean climate regions were mainly dominated by *Actinobacteria* (28.2–37.9%), *Proteobacteria* (~ 19%), and *Acidobacteria* (13.6–17.2%). In the humid-temperate climate, proportions of *Proteobacteria* (35.7%), *Acidobacteria* (22.4%), and *Chloroflexi* (10.2%) dominated and showed constant abundances between 0–40 cm, followed by slight shifts in the saprolite (e.g. decrease of *Planctomycetes* and *Verrucomicrobia*). Based on Pearson correlations, *Acidobacteria* and *Planctomycetes* revealed a positive correlation with TOC, the latter additionally correlated positively with total N content ($p < 0.05$). *Proteobacteria* correlated positively with the C/N ratio but negatively with the pH ($p < 0.05$).

Bacterial community composition

Bacterial generalists

Bacterial generalists comprised 8 phyla, which were assigned to *Proteobacteria* (31.3% of total ASVs), *Actinobacteria* (22.2%), *Acidobacteria* (19.7%), *Planctomycetes* (11.4%), *Verrucomicrobia* (9.9%), *Bacteroidetes* (5.4%) and *Firmicutes* (1.5%), thereby comprising 22 different taxonomic groups (Fig. 3a, Table S4). Calculated niche breadths are listed in Table S4 and plotted in the Additional file 3: Figure S3. They varied mainly between 10.23 to 29.13, whereas three outliers (*Staphylococcaceae*, *Ralstonia*, *Pelomonas*) showed significantly lower values (< 5).

In the most dominant phylum, six *Proteobacteria*-related groups were identified (*Rhizobiales*, *Elsterales*, *Sphingomonadaceae*, *Myxococcales*, *Ralstonia*, *Pelomonas*). While the proportions of the major groups remained constant along the climate gradient, the genera *Ralstonia* and *Pelomonas* varied more drastically and dominated in saprolites of the arid, semi-arid, and humid-temperate climates. Three taxa affiliated within the *Actinobacteria* (*Acidimicrobiia*, *Solirubrobacterales*, *Pseudonocardiaceae*) showed an overall slight decrease with depth. Especially *Solirubrobacterales* predominated between 0–10 cm in the arid climate followed by a massive decrease. Within the phylum *Acidobacteria*, four generalists were identified (*Acidobacteriales*, Subgroup 6, *Solibacteraceae*, Subgroup 7). While the proportion of *Acidobacteriales* showed an even distribution in the humid-temperate soils (mean 6.8%), Subgroup 6 predominated in the mediterranean climate (mean 6.3%). The proportion of *Planctomycetes*-related generalists (*Phycisphaerae*, *Gemmatales*, *Pirellulales*, *Isosphaerales*) decreased with depth in all four climates, especially in the saprolites. Generalists affiliated within the *Verrucomicrobia* revealed a dominance of the group *Candidatus Udaeobacter* in the semi-arid and mediterranean climates, while the proportion of *Pedosphaeraceae* was evenly distributed. The group *Chitinophagales* was the only generalist identified within the *Bacteroidetes* and showed a slight decrease with depth, which was most pronounced under semi-arid conditions. The overall lowest proportions accounted to the *Firmicutes* (*Bacillus*, *Staphylococcaceae*) and featured *Staphylococcaceae* as dominant member in arid subsurface soils (20–140 cm).

Distinct shifts in relative abundances were observed in the saprolites of the semi-arid, mediterranean, and humid-temperate climates, whereas the arid climate featured a high variability and unique relative abundances in each depth increment. Mantel tests revealed that the distribution of all generalists on a continental-scale was significantly shaped by the soil texture (clay-, sand-, and silt content), pH and the C/N ratio ($p < 0.05$, Table S7). Moreover, the generalists of the humid-temperate climate were significantly shaped by the soil texture, TOC, C/N ratio, total N and plant-available P ($p < 0.05$).

Bacterial habitat specialists

In total, 35 taxa were identified as habitat specialists, with 20 distributed in the arid, 6 in the semi-arid, and 8 in the humid-temperate climate (colored boxes in Fig. 3b; Table S5). Those groups were characterized to predominate in only one climate and showed narrow niche breadths varying from 1.05 to 7.83 (Additional file 3: Figure S3, Table S5). The mediterranean climate turned out to contain no habitat specialists, only boundary-crossing specialists (c.f. 3.3.3).

Highest proportions of specialists were detected under arid climate conditions and could be affiliated within a broad spectrum of phyla (5 *Actinobacteria*, 5 *Bacteroidetes*, 2 *Chloroflexi*, 1 *Planctomycetes*, 1 *Gemmatimonadetes*, 2 *Firmicutes*, 4 *Proteobacteria* and 1 *Deinococcus-Thermus*; yellow boxes in Fig. 3b). The *Actinobacteria*-related groups (*Euzebyaceae*, *Nitriliruptoraceae*, *Rubroacter*, *Thermomonosporaceae*) accounted for 53.2% of all specialists-related ASVs obtained in this climate. Similar to the generalists, the habitat specialists featured distinct shifts in community composition in the surface (0–5 cm) and subsurface soils (20–140 cm). Habitat specialists identified in the semi-arid climate could be assigned to *Actinobacteria* (*Micrococcales*), *Chloroflexi* (*Chloroflexales*, *Kallotenuales*, *C0119*), *Verrucomicrobia* (*Chthoniobacter*), and *Proteobacteria* (*Skermanella*) and revealed only minor variations with depth (orange boxes in Fig. 3b). The humid-temperate climate contained habitat specialists related to *Actinobacteria* (*Acidothermus*), *Bacteroidetes* (*Flavobacteriales*), *Chloroflexi* (*Ktedonobacteraceae*), *Verrucomicrobia* (*Candidatus Xiphinematobacter*), *Proteobacteria* (*Burkholderia–Caballeronia–Paraburkholderia*, *Acidibacter*, *RCP2-54*) and *Acidobacteria* (Subgroup 2) (blue boxes in Fig. 3b). Here, a strong differentiation in proportions between the uppermost 40 cm and the saprolite was obtained, especially of the groups *Acidothermus*, *Ktedonobacteraceae*, and *Candidatus Xiphinematobacter*.

Regarding Pearson correlations, the soil pH turned out to be the major parameter in the arid region and correlated positively with *Actinobacteria* (*Euzebyaceae*, *Nitriliruptoraceae*, *Rubroacter*) and *Bacteroidetes* (*Rhodothermaceae*) ($p < 0.05$). In the humid-temperate climate, the clay content and TOC showed a positive correlation (*Candidatus Xiphinematobacter*, Subgroup 2, *Burkholderia–Caballeronia–Paraburkholderia*, *Acidibacter*; *RCP2-54*, *Ktedonobacteraceae*, *Acidothermus*). In addition, a negative correlation with the sand content was detected with *Acidothermus*, *Candidatus Xiphinematobacter*, *Burkholderia–Caballeronia–Paraburkholderia* and *RCP2-54*. Performed Mantel tests revealed that the specialists identified in the semi-arid climate were directly shaped by clay content, pH, TOC, C/N ratio and total N ($p < 0.05$). Moreover, specialists of the humid-temperate climate were shaped by the soil texture (clay-, sand-, and silt content), TOC, total N, and plant-available P ($p < 0.05$; Table S7).

Bacterial boundary–crossing specialists

Besides identified extreme habitat-specific specialists, we also detected specialists that are potentially capable of crossing a climate boundary. In total, 14 boundary-crossing specialists were identified in all four climates and could be assigned to *Actinobacteria* (13.9% of total ASVs), *Chloroflexi* (8.3%), *Gemmatimonadetes* (7%), *Firmicutes* (1.2%), *Proteobacteria* (0.9%), *Acidobacteria* (11.1%) and *Rokubacteria* (2.9%) (grey boxes in Fig. 3b; Table S5). Niche breadths ranged from 5.93 to 17.2 (Additional file 3: Figure S3, Table S5).

Only two boundary-crossing specialists were identified under arid conditions (2.06% of specialist-related ASVs) and could be assigned to *Firmicutes* (*Paenibacillus*), thereby shared with the adjacent semi-arid climate, and *Proteobacteria* (*Rhodobacteraceae*), thereby shared with the humid-temperate climate. In addition to *Rhodobacteraceae*, two more specialists were identified in the humid-temperate climate (8.4%), which were affiliated within *Chloroflexi* (*SBR1031*, *AD3*), crossing the humid-temperate

mediterranean climates. Especially *AD3* peaked in relative abundances between 5 to 40 cm (5.2%) in comparison to the surface soils and saprolite. Overall highest proportions of boundary-crossing specialists were identified in the semi-arid and mediterranean climates with 35.5% of all specialist-related ASVs. Those ASVs could be affiliated within *Actinobacteria* (*Micromonosporaceae*, *Streptomyces*, *Gaiella*, *MB-A2-108*, *Geodermatophilaceae*), *Chloroflexi* (*S085*), *Gemmatimonadetes* (*Gemmatimonadaceae*), *Proteobacteria* (*Nitrosomonadaceae*), and *Acidobacteria* (*Pyrinomonadales*). Interestingly, the bacterial community of the mediterranean climate contained only boundary-crossing specialists, shared mainly with the adjacent semi-arid climate. Here, the most dominant boundary-crossing specialist was *Pyrinomonadales*, which was evenly distributed between 0 to 40 cm (mean 6.1%), followed by a drop in the saprolite (2.5%).

Performed Mantel tests revealed that boundary-crossing specialists obtained in the humid-temperate climate were significantly shaped by the soil texture (clay-, sand-, and silt content), TOC, C/N ratio, total N, and plant-available P ($p < 0.05$, Table S7). Under mediterranean climate conditions, soil texture and C/N ratio significantly shaped the specialists. The pH was the only environmental parameter, which had a significant influence in the semi-arid climate region ($p < 0.05$).

The generalist-to-specialist ratio

NMDS analysis of bacterial ASVs revealed clear differences between abundances of generalists and specialists (including habitat and boundary-crossing specialists) in each climate (Additional file 3: Figure S2a). Overall, the proportion of generalists increased along the gradient from North to South, whereas specialists decreased in the same manner (Table 1). Accordingly, the calculated generalist-to-specialist index increased from 0.66 to 2.57. The semi-arid and mediterranean climates featured similar proportions of generalists and specialists.

Table 1

Distribution of generalists versus specialists identified in the climate regions based on ASV proportions.

Climate	Generalists [%]	Specialists [%]	Index
Arid	39.9	60.1	0.66
Semi-arid	65	35	1.86
Mediterranean	66.8	33.2	2.01
Humid-temperate	72	28	2.57

Specialists contain the sum of bacterial extreme habitat-specialists and boundary-crossing specialists. The generalist-to-specialist ratio is given as index.

Each climate featured distinct shifts along the depth profile, especially between surface (0–40 cm) and subsurface soils (Additional file 2: Figure S2b). Specialists in the arid climate clearly dominated the uppermost 20 cm with overall highest abundances between 10–20 cm (75.8%). In the semi-arid climate, the proportion of specialists drastically dropped in the saprolite (50–200 cm) from 24.3–14.3%,

respectively. The opposite trend was observed in the mediterranean climate where specialists clearly dominated the saprolite (32.8%). In the humid-temperate climate, especially the depth ranging from 5 to 40 cm was dominated by specialists (23.3%), whereas the surface samples (15.3%) as well as the saprolite (7.1%) contained significantly lower proportions.

Archaeal community composition

Archaeal generalists

Archaeal generalists comprised six taxonomic groups within *Thaumarchaeota* (33.4% of total ASVs), *Euryarchaeota* (62%), and *Crenarchaeota* (4.5%; Fig. 4, Table S6) with niche breadths ranging from 2.89 to 24.2 (Additional file 3: Figure S3, Table S6). The family *Nitrososphaeraceae* turned out to be the major component along the climate gradient throughout the depth profiles (mean 31% in arid, 74% in semi-arid, 70.6% in mediterranean, 20.3% in humid-temperate). Further, the class *Thermoplasmata* dominated in all four climates, respectively and showed an increasing trend with increasing soil depth (mean 9–12.5% in arid, 2.1–44% in semi-arid, 4–31% in mediterranean, 10–19% in humid-temperate). In addition, *Group 1.1c*, which showed highest proportions in the humid-temperate and the saprolite (110–160 cm) of the mediterranean climate, *Halobacteriales*, *Bathyarchaeia* and *Thermoprotei* were identified as generalists. Interestingly, both *Crenarchaeota*-related classes dominated especially in the deeper soil depths (20–260 cm) in the mediterranean and humid-temperate climates. Performed Mantel tests revealed that the distribution of generalists along the climate gradient was directly shaped by the clay and sand content, pH, and the C/N ratio ($p < 0.05$, Table S7). Additionally, generalists obtained in the humid-temperate climate were directly shaped by TOC and total N ($p < 0.05$).

Archaeal habitat specialists

Only ASVs within the phyla *Thaumarchaeota* and *Euryarchaeota* were identified as habitat specialists, being distributed in the arid and humid-temperate climate (highlighted boxes in Fig. 4; Table S7). Niche breadths varied from 3.51 to 6.84 (Additional file 3: Figure S3, Table S7).

Even though the class *Halobacteriales* was infrequently detected throughout the depth profiles in all four climates, only under arid conditions five unique orders were detected (yellow-marked boxes in Fig. 4), which could be assigned to *Halococcaceae* (genus *Halococcus*, 6–22%), *Halobacteriaceae* (7–22%), *Halomicrobiaceae* (genus *Natronomonas*, 0.5–34%), *Haloadaptaceae* (genus *Haladaptatus*, 1–15%), and *Haloferacaceae* (genus *Halolamina*, 1–43%). Interestingly, only *Halomicrobiaceae*-like sequences were obtained between 0–5 cm. Moreover, the 10–20 cm depth increment harbored almost 100% of habitat specialists (< 0.2% affiliated to generalists). The humid-temperate climate featured *Nitrosotaleaceae* as habitat specialist and was detected in the uppermost 40 cm (2–6%; blue-marked box in Fig. 4). The family showed a positive correlation with the clay content, TOC, and C/N ratio but negative correlation with the sand content (Pearson correlation, $p < 0.05$).

Discussion

Exploring general patterns in soil microbial community composition and expanding these findings on a global scale to challenge the complex organization of microorganisms on Earth is of current research interest. The present study evaluated the microbial community composition along the Chilean Coastal Cordillera based on the generalist-specialist concept, which reflects natural tolerances of microbial species in dependence to their environment [6, 7].

Generalists

The distribution of generalists along the Chilean Coastal Cordillera in comparison to global patterns

Overall detected microbial community composition along the Chilean Coastal Cordillera perfectly support global estimations, highlighting that soil communities are composed of the same seven bacterial phyla with highest abundances of *Proteobacteria*, *Actinobacteria*, and *Acidobacteria*, whereas *Bacteroidetes*, *Firmicutes*, *Verrucomicrobia*, and *Planctomycetes* are less abundant [1, 19, 24]. In total, we identified 22 generalists within 8 dominant phyla (Fig. 3a, 4) with archaea representing only a minor fraction of the community (4.7% of total ASVs). This is in concordance with the fact that archaea lack diversity and abundance in the same environment co-occurring with bacteria [55]. With the exception of *Actinobacteria* and *Euryarchaeota*, all phyla followed the climate gradient from arid to humid-temperate and increased in relative abundances (Fig. 2).

We identified *Proteobacteria*-related groups as the majority of generalists (31.3%) as this phylum features mainly copiotrophic life strategies, including fast growth rates [56]. *Acidobacteria* also represented a high abundance (22.4%), especially in the humid-temperate climate which is in line with their clear preference for soils with lowest pH [36]. We detected *Acidobacteriales*, Subgroup 3, 6 and 7 as frequent soil colonizers with a preference for grasslands and forests [24, 57]. The dominance of Subgroup 6 in the semi-arid and mediterranean climate is potentially related to the positive effect of grazing animals [58]. Abundances of *Planctomycetes* (11.4%) increased with decreasing salinity, as already demonstrated by Chen et al. [59], and are widespread soil-key players involved in carbon and nitrogen cycles [60]. *Verrucomicrobia* (9.9%) are ubiquitous in soils but in minor proportions only [61] due to their slowly growing members [62]. High abundances of *Verrucomicrobia* in grasslands were previously linked to the amount of nematode biomass due to their ability to associate with eukaryotic hosts [19]. The arid climate turned out to feature highest variations in overall proportions and showed a dominance of *Actinobacteria* (*Solirubrobacterales*) and *Proteobacteria* (*Ralstonia*, *Pelomonas*), but minor abundances of *Verrucomicrobia* and *Acidobacteria*. The significantly lower proportions of *Acidobacteria* can be explained by the fact that *Actinobacteria* can outcompete this group in deserts [63]. However, observed shifts are in line with previous studies [1, 28] and correspond with data from the Yungay region [64].

Archaeal generalists were overwhelmingly dominated by *Nitrososphaeraceae* (formerly described as Group 1.1b; Fig. 4), which is consistent with several studies [65, 66]. We could further approve the well-known pH preference of Group 1.1c for acidic forest soils [67]. The *Euryarchaeota*-related

Thermoplasmata showed a distinct depth-dependent trend with highest abundances in the C horizons. *Crenarchaeota* comprised the lowest fraction (4.5%) with a clear preference for subsurface soils of the mediterranean and humid-temperate climates. Previous studies already demonstrated the absence of this group in high salinity environments [68, 69] and suggested the distribution as clumps within soil, which could also explain the observed depth distribution [70].

Soil pH and C/N ratio as key predictors on a continental-scale

Numerous continental-scale [1, 37] studies highlighted soil pH as the only consistent predictor for overall community variations. We indeed support this global trend ($R_{\text{Bac}} = 0.48$, $p = 0.0001$; $R_{\text{Arch}} = 0.2016$, $p = 0.0026$) but could additionally declare the C/N ratio ($R_{\text{Bac}} = 0.45$, $p = 0.0001$; $R_{\text{Arch}} = 0.21$, $p = 0.0004$) as predictor for the distribution of generalists along the Chilean climate gradient (Table S7). Relative abundances of dominant taxa changed in a consistent manner in dependence to both environmental parameters (Fig. 2). Already Lauber et al. [37] mentioned that variations in microbial communities cannot be explained singly by the impact of only one environmental condition. As many soil properties such as salinity, nutrient availability, or soil moisture are directly and indirectly linked to soil pH, it rather functions as an integrating variable, thereby promoting other soil conditions (e.g. C/N).

Overall, our results confirm that soil communities from different climate regions are composed of the same subset of taxonomic groups (generalists) even though each region features distinct environmental conditions. Hence, we have strong evidence that the Chilean climate gradient supports the species sorting model in dependence to the prevailing environmental conditions.

Specialists

Survival of the fittest in the arid desert

The Chilean arid region in Pan de Azúcar featured a unique hotspot of microbial specialization with overall highest proportions of habitat specialists (Fig. 3b, 4). The selection of highly competitive and adaptive species is an important prerequisite in extreme deserts, as only the fittest microorganisms survive by evolving elaborate life strategies. Although we were unable to identify a strong ecological preference, despite the availability of a comprehensive dataset of environmental variables, our results underline the importance of salinity as already discussed in recent studies [25, 71]. Besides typical colonizers of global deserts (e.g. *Delftia*, *Caulobacteraceae*, *Thermomicrobiales*, *Caldilineaceae*) and the Atacama Desert (e.g. *Cytophagales*, *Balneolaceae*, *Rhodothermaceae*, *Halomonas*, *Rubrobacter*), we could identify specialists attributed to the most essential survival strategies needed in deserts.

The first survival mechanism involves the resistance against high salinity conditions, which is generally explained as salt-in strategy, and is driven by the accumulation of potassium ions to balance the external salt concentration [72, 73]. In the archaeal domain we detected numerous salt-loving specialists assigned to *Halobacteriales* (*Halococcaceae*, *Halobacteriaceae*, *Halomicrobiaceae*, *Haloadaptaceae*,

Haloferacaceae; Fig. 4), which feature an extremely halophilic lifestyle with requirements of $\sim 150 \text{ g L}^{-1}$ salt for growth and structural stability [74]. Several ecological studies highlighted their widespread distribution [75, 76], for instance *Haladaptatus* was already found in Atacama salt lakes [77], sulfur-rich springs in the USA [78], as well as *Halolamina* in marine and sediment salterns in Korea [79], China [80], Turkey [81], and India [82]. Moreover, previous studies already mentioned that although the overall community diversity is limited, only a few archaeal phylotypes can dominate [83, 84].

The second survival mechanism involves the resistance against high ultraviolet radiation and is broadly based on complex DNA repair networks and metabolic processes, the use of photoreactive pigments, sporulation, and dormancy. We detected the most radiation-resistant specialist *Deinococci*, which was already isolated from global deserts, including Gobi [85], Kalahari [25], Sonoran [11], Sahara [86], and the Tataouine Desert [87]. Ogwu et al. [12] impressively demonstrated the positive feedback of *Deinococcus* in relation to increasing radiation due to its perfect adaptations by using specific DNA repair mechanisms. Members of *Chloroflexi* (*Caldilineaceae*, *Thermomicrobiales*) respond similar although they lack this specific strategy, thus, suggesting the use of photoreactive pigments [12]. Additionally, several spore-forming groups (*Tepidimonas*, *Anoxybacillus*, *Clostridiales*, *Thermomonosporaceae*) were obtained, as dormancy and sporulation avoid radiation damage, which actively dividing cells are prone to [88].

Combined parameters trigger the specialization in the humid-temperate forest

The humid-temperate forests of Nahuelbuta comprised nine habitat specialists (blue boxes in Fig. 3b, 4), all of which have been shown to colonize forest soils worldwide. Mantel correlations revealed that the distribution of these specialists is shaped by their requirements for TOC ($R = 0.49$, $p = 0.012$), total N ($R = 0.57$, $p = 0.01$), and plant-available P ($R = 0.61$, $p = 0.02$), suggesting that multiple environmental factors or the combination trigger microbial specialization (Table S7). The most prominent combination in forest soils is described for high C/N ratio coupled with low pH, which was shown to promote various processes based on the specialization for decomposing recalcitrant organic matter through lignocellulose breakdown [89], denitrification [90], and nitrogen fixation [91]. We identified typical representatives of these strategies such as *Ktedonobacteraceae*, *Flavobacteriales* [90, 92], *Acidibacter*, and *Paraburkholderia*. Moreover, we also suggest the distribution of *Acidotherrmus* and the *Thaumarchaeota*-related *Nitrosotaleaceae* to be dependent on the above-mentioned combination of environmental properties. Both have recently been shown to inhabit diverse forest and rainforest ecosystems in Germany [90], Korea [93], and Brazil [94], thereby functioning as ammonia oxidizer [67]. The distribution of Subgroup 2 in global forest soils is well documented [90, 95], but little is known about the metabolic potential. De Chaves et al. [96] recently discussed that the occurrence of this group is not triggered by N fertilization, as this is a common feature of *Acidobacteria*, but obtained a positive correlation with aluminium. Furthermore, we obtained an endosymbiotic representative of nematodes (*Candidatus Xiphinematobacter*) [97], which is a well-known inhabitant of Chilean soils [98].

The potential of crossing a climate boundary and the fault in the climate gradient along the Coastal Cordillera

Besides extreme habitat specialists, we also identified boundary-crossing specialists that co-occurred in two climate regions. This was most strikingly revealed in the semi-arid and mediterranean climate with highest proportions of specialists that are capable to exist in both regions (35.5%), even though they are characterized by different climate and vegetation conditions. We identified *Pyrinomonadales* (RB41) as most dominant boundary-crossing specialist, which was recently shown to endure low-nutrient stress conditions, thereby playing an important role in maintaining the soil metabolic functions [99]. We further obtained several groups (*Gemmatimonadaceae*, *Nitrosomonadaceae*, *Rokubacterales*, *Gaiella*) with previously described potential affinities for soil nitrate [100, 101] and *Streptomyces*, which was recently correlated with their plant-growth promoting abilities by stimulating the mycorrhiza formation, thereby also improving the drought tolerance of plants [102].

Both climates, the semi-arid and mediterranean, turned out to be more similar with respect to humidity conditions than expected and represent a fault in the overall Chilean gradient. With reference to Gajardo [103], the Chilean semi-arid region is directly influenced by a mediterranean climate with highest precipitation during winter seasons and on a daily interval due to the coastal fog. Data received from on-site weather stations confirm corresponding air relative humidity values (mean 65.15% in mediterranean, 66.45% in semi-arid [104]. Hence, the adjacent regions experience the same intervals of moisture changes on a daily and seasonal basis, thus, offer similar ecological niches and favor the specialization for moisture-fluctuating groups.

The generalist-to-specialist index and the role of ecosystem stability

Our study confirms that generalists can cope with a wide range of environmental conditions and occur in various habitats, whereas habitat specialists need specific environmental conditions and are limited to few habitats only [105]. This distinct classification is further reflected in Levins niche breadth [5] indicating lower niche breadths as a result of higher microbial specialization (Additional file 3: Figure S3, Table S4, S5, S6). Even though we obtained outliers regarding the generalist classification, which resulted in narrow niche breadths (e.g. *Ralstonia*, *Pelomonas*, *Thermoprotei*), they are explained by strong depth-dependent peaks.

Overall, soils from the Chilean climate gradient are comprised of higher proportions of habitat specialists (34 groups) than generalists (22 groups) with an increase of the generalist-to-specialist index from North to South (Table 1). The most striking difference was revealed in the arid climate regarding the ratio between habitat specialists (60.1%) compared to generalists (39.9%), whereas all other climates contained more generalists. The extreme ecosystem of Pan de Azúcar impressively demonstrates that even though habitat specialists are known to have a limited niche, they show the highest fitness in their optimal habitat [106]. However, due to habitat specialization, specialists are much more susceptible to changes in environmental conditions and extinction, thus, favor rather stable ecosystems [6, 8, 9]. This

evolutionary response may explain the significantly higher proportions of habitat specialists found in the arid region in contrast to the non-desert climates. Although the Atacama Desert is the oldest and driest desert worldwide and prevails harsh temperature and radiation conditions, environmental variables remain overall rather constant [107]. In comparison, Central Chile (30–38° S) is prone to naturally occurring intense 1 to 2 yearlong droughts and experienced the so-called megadrought from 2010–2015 with rainfall deficits of up to 75%, thus, involving sustainable changes in the regional vegetation and microbial composition [108]. For instance, grassland and meadow communities have been shown to oscillate for 9 and 12 years after drought events [109, 110]. As a result, these fluctuating conditions lead to a natural extinction of habitat specialists in central Chile due to their smaller niche breadth and explains the increased emphasis on generalists in these regions.

Our findings therefore raise the question if the degree of microbial specialization based on the generalist-to-specialist index could directly be correlated with the overall ecosystem stability or resilience? Hence, higher proportions of generalists in an ecosystem would directly be related to an unstable ecosystem due to their broader possibilities for niche adaptations. Contrary, higher specialist proportions would directly be related to rather stable conditions due to their narrow and highly specific adaptations. Nonetheless, we point out that additional studies and datasets are needed to verify this hypothesis and define specific ranges in relation to ecosystem resilience.

Conclusion

The Chilean climate gradient represents a strong environmental filter. Our results provide strong evidence that species sorting in response to local environmental factors is a key determinant of the bacterial and archaeal community composition also over a broad continental scale. This study contradicts with the theory of typical climate-specific specialists that can be correlated to distinct climates or biomes worldwide. We rather underline findings from previous broad-scale studies [30, 37, 111], which highlight that typical biome definitions are not reliable for predicting variability in communities as too many parameters have to be considered. Whereas soil pH and the C/N ratio explained the distribution of generalists, distinct as well as combined environmental variables affected the distribution of specialists, thereby reflecting their different abilities to adapt to the environment.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and material

Raw Illumina sequencing data was submitted to the European Nucleotide Archive (<http://www.ebi.ac.uk/ena>) with the BioProject ID PRJEB38745 under the accession numbers ERS4643350-ERS4643389 and ERS4652898-ERS4652900 (SequencingRuns: ERR4234140-ERR4234182). All data used in this study are freely available under the Creative Commons Attribution 4.0 International (CC BY 4.0) open access license at GFZ data services. All samples are identified via unique IGSN (international geo sample number). These data are available as a supplementary dataset [112], containing the tables S1-S7 with the following DOI:10.5880/GFZ.3.7.2020.001. When using the data please cite: Dataset for evaluating soil microbial generalists and specialists along the EarthShape climate and vegetation gradient. GFZ data services.

Competing interests

The authors declare that they have no competing interests.

Funding

This study was funded by the German Science Foundation DFG in the framework of the priority program “EarthShape: Earth Surface Shaping by Biota” by a grant to DW (WA 1554/17).

Author’s contributions

DW, LMM, and RO designed the study. LMM collected the soil samples with on-site support of RO, further performed all laboratory steps, analyzed, and illustrated the data. LMM and DW substantially wrote the manuscript. All authors contributed to the discussion.

Acknowledgements

The authors wish to thank all partners involved in the field campaign in Chile 2016, especially the Chilean colleagues for their scientific and logistical support on site. The authors also would like to thank Fabian Horn for the initial processing of the raw sequence data and for uploading the sequence data to the NCBI platform (GFZ German Research Centre for Geosciences). Special thanks to the Chilean National Park Service (CONAF) for giving us the opportunity to work in the national parks of Pan de Azúcar, La Campana, and Nahuelbuta as well as on-site support of our research. We also thank CEAZA for facilitating access to the Reserva Natural Santa Gracia.

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Figures



Figure 1

Study site. Location of the field sites along the Chilean Coastal Cordillera, encompassing climate conditions varying from North to South from arid in Pan de Azúcar, semi-arid in Santa Gracia, mediterranean in La Campana, to humid-temperate in Nahuelbuta. This map was constructed with Map Creator Version 2.2.1.

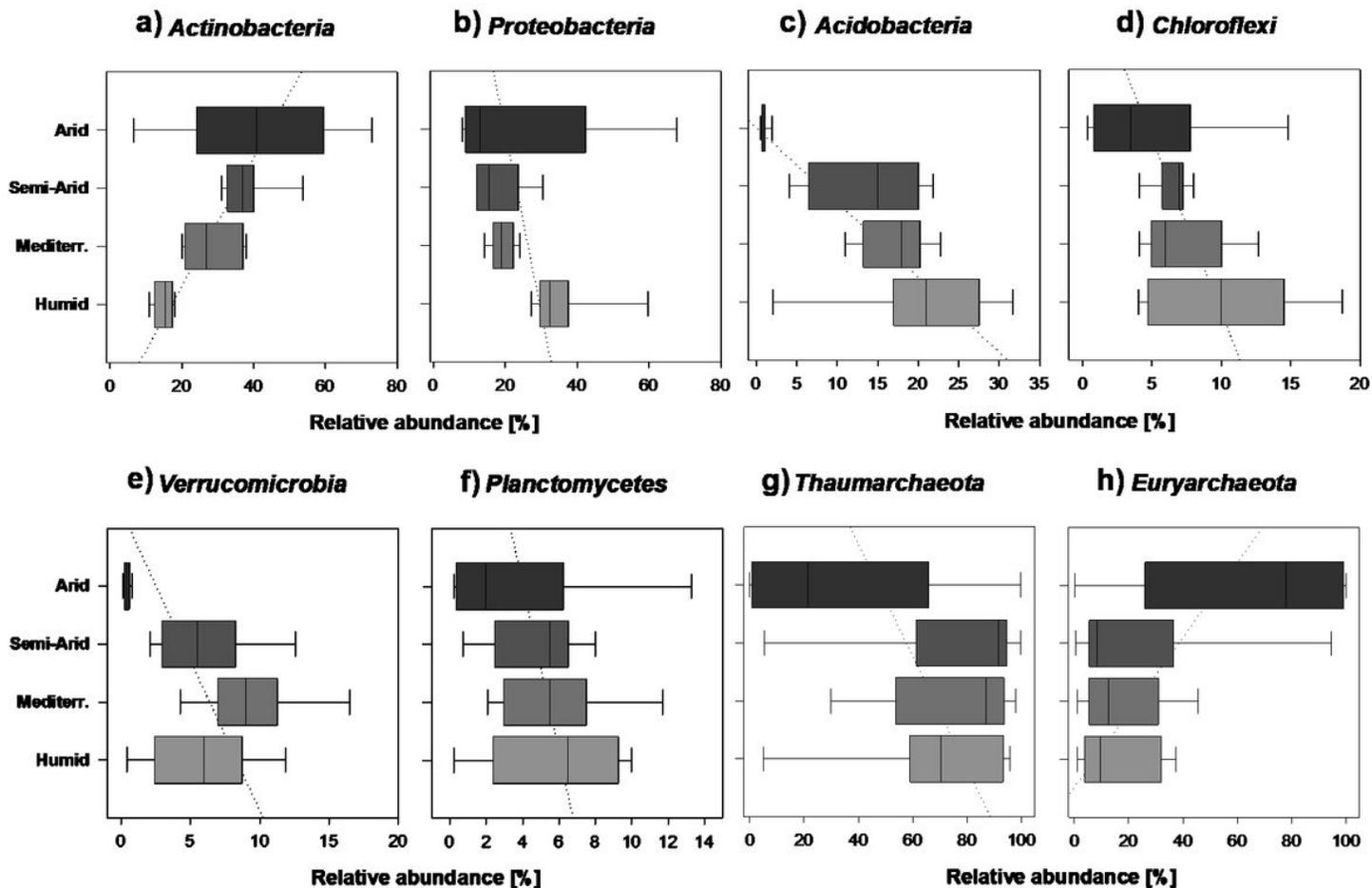


Figure 2

Relative abundances in % of dominant bacterial (a-f) and archaeal (g-h) phyla. Box plots represent the sum of all depth increments and replicates. Mean lines are indicated within the boxes of which the size corresponds to $\pm 25\%$ of the data, whereas the whiskery shows ± 1 Std of all data. Regression lines are indicated.

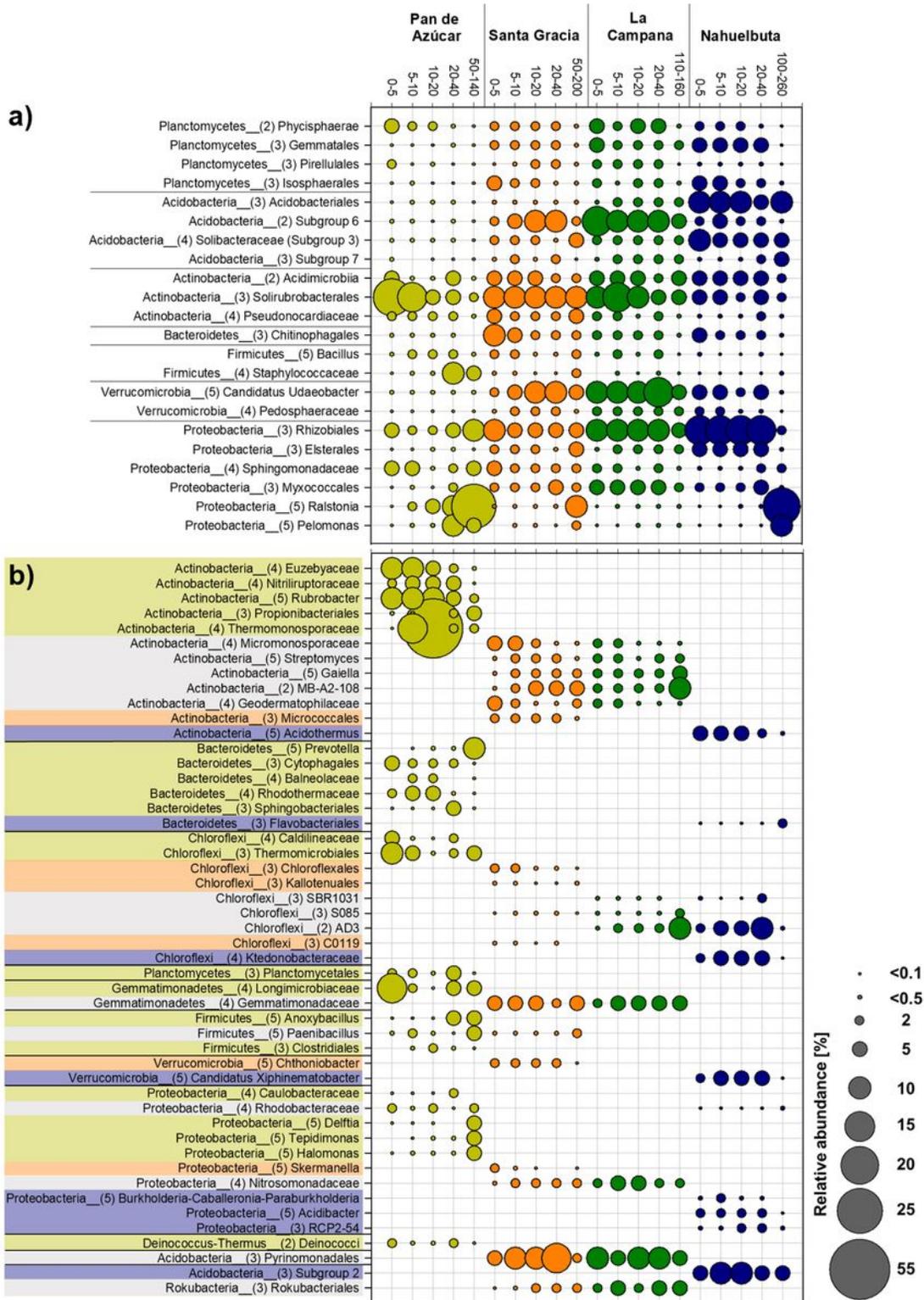


Figure 3

Bubble plot of a) bacterial generalists and b) specialists. Depth profiles along the climate gradient range from arid (Pan de Azúcar, yellow), semi-arid (Santa Gracia, orange), mediterranean (La Campana, green) to humid-temperate (Nahuelbuta, blue) climate conditions. Color-coded taxa, according to the study regions, in b represent habitat specialists detected in only one study site, whereas grey marks represent

boundary-crossing specialists found in two climate regions. Taxa are shown on a (2) class-; (3) order-; (4) family- or (5) genus level.

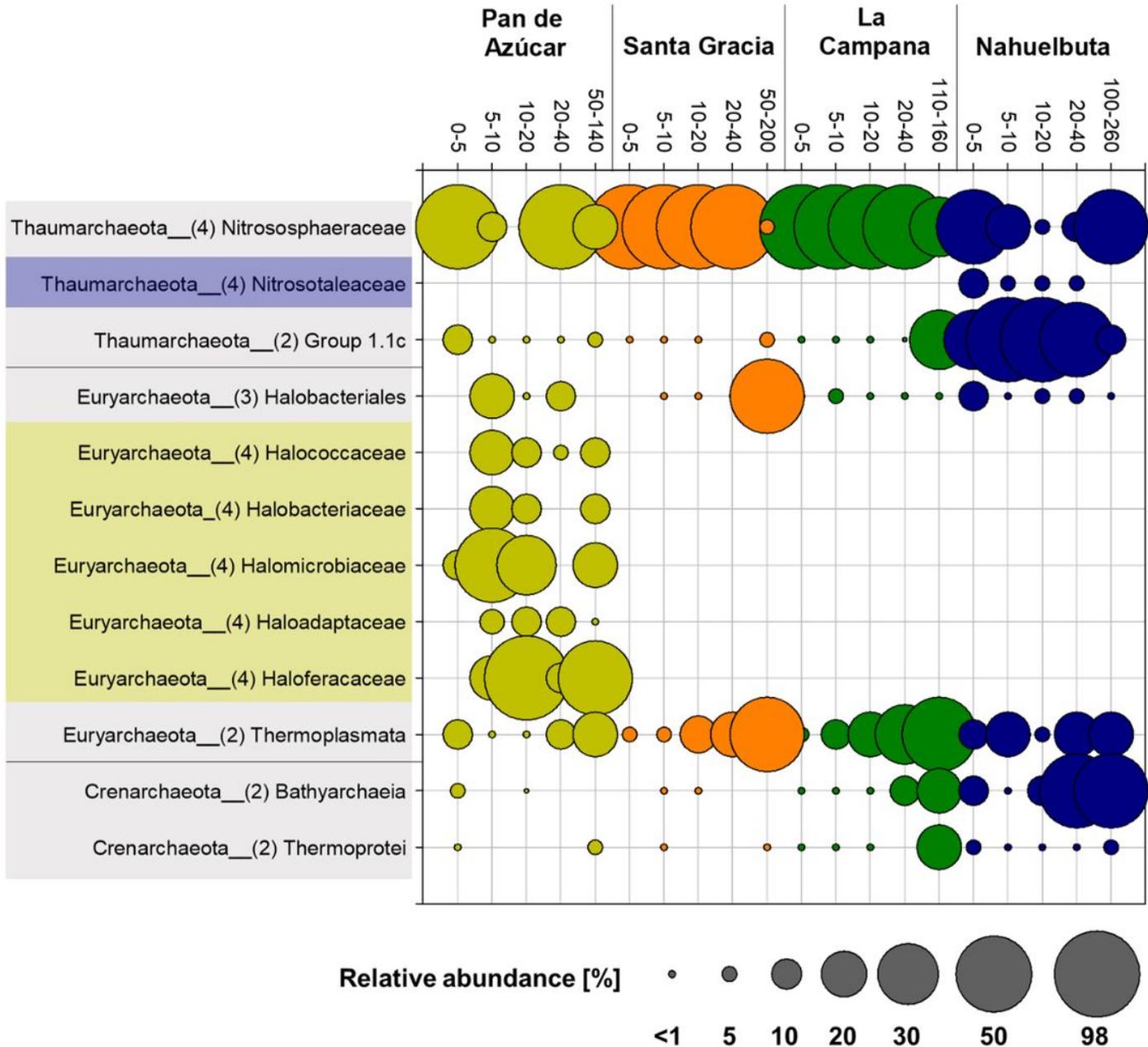


Figure 4

Bubble plot of archaeal community composition in the depth profiles along the climate gradient. Climates encompass from arid (yellow), semi-arid (orange), mediterranean (green) to humid-temperate (blue) conditions. Grey-coded taxa represent archaeal generalists. Color-coded taxa represent habitat specialists detected in only one study site. Taxa are shown on a (2) class-; (3) order- or (4) family level.

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