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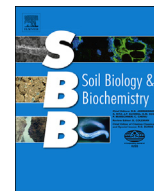

Environmental conditions shape soil bacterial community structure in a fragmented landscape

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ABSTRACT

Several biogeographical hypotheses have been proposed to explain microbial distribution, but there is ongoing debate about the magnitude of the contribution of niche–based processes and historical contingencies in determining patterns of microbial structure. In this context, currently fragmented relict forests of olivillo (*Aextoxicon punctatum* Ruiz et. Pav.), which belonged to a continuous community along the coast of Chile during the Pleistocene, and their surrounding scrublands are ideally–suited for testing these hypotheses, since they remain as patches located at the northern tip of the distribution of the relicts. In each study site, edaphic and geographic variables were determined, and the bacterial structures were evaluated at the genetic and metabolic levels through fingerprint approaches along with multivariate analytical methods including redundancy (RDA) and variance partitioning (VPA) analyses. Forests possessed lower pH, and higher contents of moisture and organic matter. In addition, bacterial communities from both habitats differed, whereas the bacterial communities of the forests in different regions were very similar to each other. Our conclusion is that current abiotic soil factors, but not past events due to the historical connection of the forests, account for the variance in the structure of these soil bacterial communities.

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1. Introduction

Processes underlying the generation and maintenance of microbial diversity have been widely–studied during recent decades (Fierer and Lennon, 2011). Currently, it is known that patterns in microbial biogeography exist; even so, the processes involved in shaping such arrangements are poorly understood (Hanson et al., 2012). However, unraveling them is critical for furthering our understanding of the factors that contribute to soil microbial diversity (Monroy et al., 2012). One hypothesis that has been put forward is that a structurally more complex and heterogeneous habitat is capable of sustaining a greater number of species (Bowman and McCuaig, 2003), demonstrating that the sorting of species by contemporary environmental conditions is important for shaping the community composition across space (Andersson et al., 2014). However, it has also been proposed that the distribution of microorganisms responds to historical events as a consequence of their limited dispersion and colonization capabilities (Fierer, 2008). The soil matrix thus acts as a physical barrier which limits passive dispersal of soil organisms and enhances the separation between communities (Vos and Velicer, 2008). In this context, it has been documented that spatial–distance effects related with past evolutionary events and adaption to past environmental conditions, among others, reflect the importance of historical processes (reviewed by Hanson et al., 2012). Furthermore, other researchers have proposed that both spatial heterogeneity and dispersion limitations explain the patterns of geographic diversity of the microbiota, suggesting that both historical and contemporary environmental factors are responsible for current bacterial distribution (reviewed by Hanson et al., 2012).

Consequently, there is substantial ongoing debate about the relative contribution of niche–based processes and historical contingencies in determining patterns of microbial structure. Interestingly, in Chile the existence of historically connected but currently fragmented olivillo (*Aextoxicon punctatum* Ruiz et. Pav.) forests that maintain today similar vegetational and climatic characteristics, allow the structure of their bacterial communities to be analyzed, and the various biogeographical hypotheses to be examined.

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The differences produced naturally in these fragmented areas of forest and the surrounding scrublands, with contrasting climate and soil properties as well as unique floral compositions, could create conditions that impact directly on soil microbiota (Reyes et al., 2011). The current communities of fragmented forests of olivillo belong to a community which continuously extended along the coast of central Chile (30°S – 42°S) during the last ice age of the Pleistocene (2.6 million years ago) (Villagrán et al., 2004). Discontinuous relict forests of northern and southern Chile currently maintain very similar climatic features and vegetation. In the Chilean semiarid region (Fray Jorge National Park, 30°S; and Santa Inés Hill, 32°S), these ecosystems are generally characterized by having hygrophilous forest areas present on top of the hills of the Cordillera de la Costa, with high relative humidity and low thermal oscillation, whilst the surrounding matrices have xerophytic scrubland with less influence of fog, greater diurnal temperature ranges and lower relative humidity (Pérez, 1994; Francois, 2004).

Therefore, our main aim is to understand the balance between long–term historical legacies versus more recent climate and vegetation patterns in structuring the assembly of bacterial communities. Considering the conditions found in the aforementioned sites, as a case study, we examined the bacterial communities in the soil of relict inner olivillo forests and the adjacent scrublands (habitats) in both Fray Jorge National Park and Santa Inés Hill (regions), locations separated by 200 km, which correspond to soils that have retained unique features over the years.

2. Materials and methods

2.1. Sampling sites and experimental design

In August 2013, soil samples from relict inner olivillo forests and from the surrounding scrublands in which they are immersed, were collected in Fray Jorge National Park and Santa Inés Hill (Table 1). Each sampling site is represented by the corresponding initials: FJF, Fray Jorge forest; FJS, Fray Jorge scrubland; SIF, Santa Inés forest; SIS, Santa Inés scrubland. In each of the four sites, 3 plots of 10 m × 10 m, separated by 20–25 m were defined. In each plot, 10 simple soil samples were collected from the top layer (0–10 cm) with 6 cm diameter corers. Subsequently, the 10 samples were sieved through a 2–mm mesh and pooled to form one composite soil sample per plot, thus obtaining 3 composite soil samples per site which were considered biological replicates. Samples were stored at 4 °C for bacterial metabolic profiling and edaphic physicochemical analyses, and frozen at −20 °C for bacterial genetic profiling.

2.2. Soil analyses

For each composite soil sample, we measured the soil parameters that are normally described as the most influential in determining soil bacterial community diversity (Lauber et al., 2008; Docherty et al., 2015; Cao et al., 2016): pH, moisture content (MC), organic matter (OM), nitrogen from ammonium ($[N{-}NH_4^+]$) and nitrate ($[N{-}NO_3^-]$) content. Briefly, pH was measured using potentiometry; MC and OM were calculated gravimetrically before and after desiccation and calcination, respectively; $[N{-}NH_4^+]$ was measured using an ion selective electrode and $[N{-}NO_3^-]$ was determined by colorimetry (Sadzawka et al., 2006).

2.3. DNA extractions and PCR amplification

From each composite sample, 0.25 g of soil were extracted using the MoBio PowerSoil DNA isolation kit (MoBio Laboratories, CA, USA), according to the manufacturer's instructions. The quality and integrity of the extracted DNA were visualized in 0.8% (w/v) agarose gels in TAE 1X buffer (40 mM Tris–acetate, 1 mM EDTA [pH 8.0]) stained with GelRed™ (Biotium, CA, USA). The primers used for amplification of the bacterial 16S rRNA gene were fD1 labeled with 6–carboxyfluorescein (6–FAM) at the 5′ end, and rP2 (Weisburg et al., 1991). All the amplifications were performed according to the cited literature recommendations, using the GoTaq® Green Master Mix (GoTaq® DNA polymerase in 1× Green GoTaq® Reaction Buffer [pH 8.5], 200 μM of each dNTP and 1.5 mM $MgCl_2$) (Promega, WI, USA) in a Maxygene thermocycler (Axygen, CA, USA). The quality of amplicons was determined by electrophoresis in 1.2% (w/v) agarose gels in 1× TAE buffer stained with GelRed™. PCR products were then purified using the Wizard SV PCR Clean–Up System (Promega, WI, USA) and spectrophotometrically quantified.

2.4. Terminal restriction fragment length polymorphism (TRFLP)

TRFLPs were used to evaluate the genetic structure of microbial communities in each composite soil sample. The amplicons from PCR products of the 16S rRNA marker were hydrolyzed independently with the restriction enzymes *Hae*III and *Alu*I (Fermentas, NY, USA), according to the manufacturer's specifications, and then digestion fragments were purified by ethanol precipitation. Terminal restriction fragments (TRFs) were separated on an automated Genetic Analyzer ABI3730XL (Applied Biosystems; Macrogen Inc., Seoul, S. Korea). The length of the fluorescently labeled TRFs was determined by comparison with the GeneScan™1200 LIZ® size–-standard using the GeneMapper 3.7 software (Applied Biosystems, CA, USA). Patterns from different samples were normalized to identical total fluorescence units by an iterative standardization procedure (Dunbar et al., 2001). The relative abundance of TRFs, as percentage, was determined by calculating the ratio between the height of a given peak and the normalized total peak height of each sample (Yeager et al., 2004). Peaks with a relative abundance of less than 2% were discarded. The communities were characterized by

Table 1
Explanatory spatial (geographic) and environmental (edaphic) variables of each site (± standard error). The same lowercase letters in a row represent no significant differences ($p < 0.05$).

Explanatory variables		Fray Jorge		Santa Inés	
		Forest	Scrubland	Forest	Scrubland
		FJF	FJS	SIF	SIS
Geographic data	Latitude	30°40′14.5″S	30°40′08.4″S	32°09′47.5″S	32°09′41.8″S
	Longitude	71°40′36.8″W	71°40′22.8″W	71°29′41.6″W	71°29′44.9″W
Edaphic data	pH	5.2 ± 0,1 (a)	6.0 ± 0.1 (b)	5.2 ± 0.1 (a)	5.6 ± 0.1 (c)
	Moisture Content (g H_2O/100g_{dw})	39.2 ± 1.6 (a)	3.8 ± 0.5 (b)	61.4 ± 12.5 (c)	2.9 ± 0.9 (b)
	Organic Matter (g/100g_{dw})	24.8 ± 1.7 (a)	7.5 ± 1.0 (b)	23.5 ± 1.4 (a)	5.3 ± 0.9 (b)
	Nitrate Content (μg N/g_{dw})	33.1 ± 2.7 (ac)	43.8 ± 1.9 (a)	59.3 ± 6.2 (b)	21.9 ± 0.8 (c)
	Ammonium Content (μg N/g_{dw})	0.6 ± 0.1 (ac)	1.2 ± 0.1 (b)	0.9 ± 0.1 (a)	0.4 ± 0.1 (c)

dw: dry weight.

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