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Habitat conditions drive phylogenetic structure of dominant bacterial phyla of microbialite communities from several locations in Mexico

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Abstract: Community structure and composition are dictated by evolutionary and ecological assembly processes which are manifested in signals of, species diversity, species abundance and species relatedness. Analysis of species coexisting relatedness, has received attention as a tool to identify the processes that influence the composition of a community within a particular habitat. In this study, we tested if microbialite genetic composition is dependent on random events versus biological/abiotical factors. This study was based on a large genetic data set of two hypervariable regions (V5 and V6) from previously generated barcoded 16S rRNA amplicons from nine microbialite communities distributed in Northeastern, Central and Southeastern Mexico collected in May and June of 2009. Genetic data of the most abundant phyla (Proteobacteria, Planctomycetes, Verrucomicrobia, Bacteroidetes, and Cyanobacteria) were investigated in order to state the phylogenetic structure of the complete communities as well as each phylum. For the complete dataset, Webb NTI index showed positive and significant values in the nine communities analysed, where values ranged from 31.5 in Pozas Azules I to 57.2 in Bacalar Pirate Channel; meanwhile, NRI index were positive and significant in six of the nine communities analysed with values ranging from 18.1 in Pozas Azules I to 45.1 in Río Mesquites. On the other hand, when comparing each individual phylum, NTI index were positive and significant in all groups, except in Cyanobacteria for which positive and significant values were only found in three localities; finally, NRI index was significant in only a few of the comparisons performed. The results suggest that habitat filtering is the main process that drives phylogenetic structure in bacterial communities associated to microbialites with the exception of Cyanobacteria where different lineages can contribute to microbialite formation and growth. Rev. Biol. Trop. 64 (3): 1057-1065. Epub 2016 September 01.

Key words: community assembly, community composition, Cyanobacteria, heterotrophic bacteria, microbialites, NRI, NTI.

Microbialites are organo-sedimentary structures formed by the interaction of resident benthic microorganisms (bacteria, archaea and a few eukaryotes) (Burne & Moore, 1987) and surrounding environmental factors (Foster et al., 2009; Westphal, Heindel, Brandano, & Peckman, 2010), which allow the precipitation of carbonates and / or *in situ* calcification, with the subsequent formation of lithified horizons that shape microbialite fabric (Dupraz & Vischer, 2005). Microbialites are considered living representatives of ancient stromatolites, which first appeared during the Archaean eon (Allwood, Walter, Kamber, Marshall, & Burch, 2006). Nowadays, these biogenic fabrics develop in different kinds of aquatic systems worldwide, from fully marine conditions (Reid et al., 2000) to freshwater desert ponds (Dinger, Hendrickson, Winsborough, & Marks, 2006). The active growing microbial-portion is vertically stratified and represents diverse (Bolhuis & Stal, 2011; Centeno et al., 2012; Mobberley, Ortega, & Foster, 2012) and highly productive multi-trophic microbial self-controlling

ecosystems (Pringault, De Wit, & Camoin, 2005; Schneider, Arp, Reimer, Reitner, & Daniel, 2013), where slight changes in depth correspond to marked niche boundaries (Armitage, Gallagher, Youngblut, Buckley, & Zinder, 2012). To date, it is well known that microbial communities associated to microbialites are dominated by bacterial phyla including: Proteobacteria, Bacteroidetes, Cyanobacteria, Planctomycetes, Verrucomicrobia and Actinobacteria, among others (Papineau, Walker, Mojzsis, & Pace, 2005; Baumgartner et al., 2009, Foster et al., 2009; Centeno et al., 2012; Saghaï et al., 2015). Nevertheless, it is unclear if these bacterial assemblages differ between locations (Martiny et al., 2006), as well as the factors that are responsible for their community structure and composition (Fierer & Lennon, 2011; Chong, Pearce, Convey, Yew, & Tan, 2012).

Community structure and composition are driven by ecological and evolutionary processes (Hanson, Fuhrman, Horner-Devine, & Martiny, 2012; Pontarp, Ripa, & Lundberg, 2012) that can either facilitate or inhibit that a particular taxon colonizes a local habitat; and can be manifested in signals of species relatedness, species diversity and species abundance (Pontarp, Sjöstedt, & Lundberg, 2013). Species relatedness has received attention to try to identify the processes that influence the composition of a biological ensemble. Hanson et al., (2012) proposed that selection, drift, dispersal and mutation, are the main processes that rule microbial biogeographic patterns. In this phylogenetic context, the use of net relatedness index (NRI) and nearest taxon index (NTI) (Webb, 2000) has proven useful for the analysis of microbial phylogenetic structure within different communities and environments. NRI measures the overall phylogenetic distance between paired taxa of a particular location relative to the total gene pool (Chong et al., 2012), whereas NTI is based on the average phylogenetic distance to the nearest neighbor, and it is used to determine whether closely related taxa in a community are more related than expected by chance (Horner-Devine & Bohannan, 2006). In other words, both indices tend to reveal phylogenetic clustering in two levels, NTI at the tips of the branches in a lower taxonomical resolution, and NRI to the base of the tree at a deep taxonomical level (Letcher, 2010).

The degree of phylogenetic relatedness computed by NRI and NTI allows the understanding of the processes (biotic or abiotic) that determine community composition (Bryant et al., 2008). Hence, the goal of this study was to evaluate if dominant bacterial phyla that form and maintain microbialites in different geographic locations exhibit patterns of phylogenetic structure and if so, to elucidate if biotic or abiotic factors are their main causal factors. To test this, we considered a large genetic data set of two hypervariable regions (V5 and V6), from previously generated barcoded 16S ribosomal (rDNA) amplicons from microbialite communities distributed in different geographical regions of Mexico. It has been suggested that environment drives biogeographic patterns at a large scale, whereas competition determines diversity in small neighbourhoods (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012), thus we hypothesize that biological ensembles present in each location will be driven by abiotic factors, due that each environment has different conditions of pH, temperature, conductivity and available nutrients (Centeno et al., 2012).

MATERIAL AND METHODS

The abundance of each microbialite phyla in each locality has been previously described in Centeno et al. (2012).

Microbialites 16S rDNA sequence selection: Sequences of nine localities from different geographical regions of Mexico where microbialites develop were included. A permanent stream (RM) and two freshwater ponds (PI and PII) in Cuatro Cienegas basin, Northeastern Mexico; Alchichica crater-lake, an athalosaline soda-lake in Central Mexico, where two microbialite morphotypes develop: a spongy type (AS) that is widely distributed, and a columnar

type (AC) with a restricted distribution in the lake; and two costal lagoons sites, Sian Ka´an (S) and Bacalar (BP, BM and BR), Southeastern Mexico (Fig. 1). In each locality, a total of six microbialites were sampled manually in May and June (summer) of 2009. In order to obtain a homogeneous mixture for each of the ten localities, approximately 5 g of each microbialite were grind with 30 mL of liquid nitrogen and 10 mL of extraction buffer (100 mM Tris-HCl, 20 mM NaCl, 100 mM EDTA pH 8); total environmental DNA was extracted according with the protocol of Zhou, Bruns and Tiedje (1996). Microbialites sequences (~250 bp length) covering the V5-V6 hypervariable region of the 16S rDNA gene were generated using a parallel massive sequencing approach as described in Centeno et al. (2012). The genetic affiliation of each sequence was determined according to the Ribosomal Data Project, RDP-classifier (http://rdp.cme.msu.edu) with a cutoff of 80% of similarity. After it, only the sequences of the five most abundant phyla were used in the analysis. All sequences used in this study were deposited in Bioproject SRX095440 of NCBI GeneBank.

Sequence alignment and phylogenetic reconstruction: A total of 3 171 sequences were obtained and aligned with Clustal X v.2.1 (Thompson, Gibson, Plewniak, Jeanmougin, Higgins, 1997) using default parameters. Maximum likelihood phylogenetic reconstructions were analyzed for different datasets: the first contained all phyla, and the rest was constructed for each separate phylum, using RAxML T-REX web server (http://www.trex.uqam.ca) (model GTR+GAMMA and Hill-climbing) (Boc, Diallo, & Makarenkov, 2012). The phylogenetic reconstructions obtained were exported into Newick format (Olsen, 1990) for subsequent analyses.

A matrix of unique sequences including abundance data was generated for each phylum and for the dataset containing all phyla. These matrices and their corresponding newick format tree were imported into phylocom 4.1 (Webb, Ackerley, & Kembel, 2008) to calculate the NRI and NTI indexes using the command *comstruct (community structure)* and model 2. This model assumes the null hypothesis that microorganisms are randomly distributed over space. Statistical significance was compared against the hypothesis of null structure derived from 999 randomized matrices. High and positive values of both metrics indicate phylogenetic clustering, where taxa coexisting in a local assemblage are more closely related

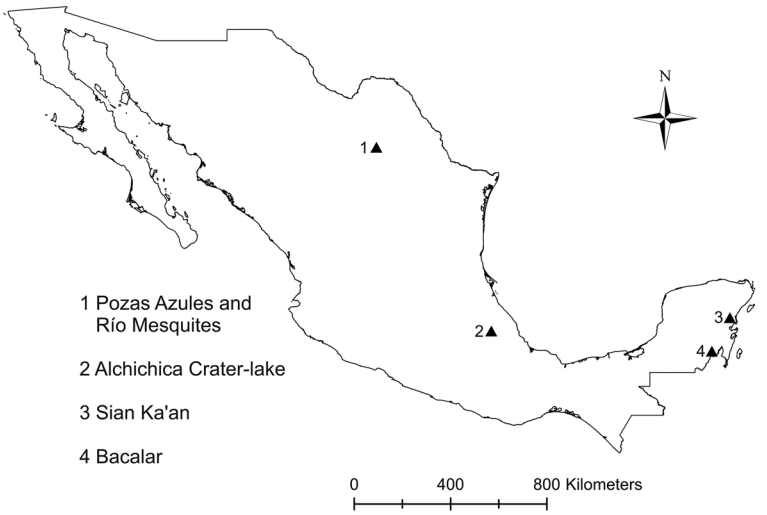

Fig. 1. Geographic location of the samples analyzed in this study.

to each other than expected by chance (Pontarp, Canbäck, Tunlid, & Lundberg, 2012), which is consistent with the hypothesis that selective filters such as environmental conditions are responsible for community composition (Pérez-Gutiérrez et al., 2013). Negative values of NRI and NTI indicate overdispersion (Horner-Devine & Bohannan, 2006; Webb, Ackerly, McPeeek, & Donoghue, 2002), in other words, that the taxa present in a community are less related to each other than expected by chance, as expected if biological interactions including parasitism, competition, predation and facilitation are the main factors controlling community structure.

RESULTS

All microbialites communities shared the most abundant bacterial phyla, Proteobacteria, Planctomycetes, Verrucomicrobia, Bacteroidetes, and Cyanobacteria, that together represented ~ 70 % of the original dataset. The phylogenetic analysis of the most abundant phyla identified in microbialites showed that the net relatedness index (NRI) yielded positive and significant values in six of the nine localities. Further, the nearest taxon index (NTI), showed positive and significant results for all sites. The results of both metrics suggested that closely related taxa in a community were more related than expected by chance (Table 1). Consequently, a majority of the communities that form microbialites analyzed in this study tend to be phylogenetically clustered. On the other hand, there were no significant negative values for NRI or NTI, and thus overdispersion was not suggested as a relevant feature in any of the assemblages studied (Table 1).

In contrast, when we tested the phylogenetic structure of each individual phylum within the different localities we observed particular differences (Table 2). A significant clustering pattern was observed in Bacteroidetes and Planctomycetes measured by NTI and NRI, whereas Proteobacteria and Verrucomicrobia yielded positive and significant values only for NTI in the nine study localities. Finally, Cyanobacteria differed considerably from all other phyla since only three of the nine communities analyzed (S, AC and AS) showed phylogenetic clustering, while the rest were randomly structured. There was no evidence of overdispersion in none of the phyla analyzed (Table 2).

DISCUSSION

Explaining the distribution of free-living microorganisms as well as understanding the forces that structure community composition is a central issue in Microbial Ecology (Hanson et al., 2012; Stegen, Lin, Konopka, & Fredickson, 2012; Stomeo et al., 2013). It is generally

TABLE 1
NRI and NTI of microbialite forming communities from different geographic locations

	Locality	Key	OTUs	NRI	NTI
Southeastern Mexico	Sian Ka'an Biosphere Reserve	S	1 400	-29.207	41.400*
	Bacalar "Rapids"	BR	1 553	-0.8992	52.131*
	Bacalar "Pirate Channel"	BP	1 305	21.660*	57.257*
	Bacalar "Medio"	BM	1 167	0.9290	56.194*
Northeastern Mexico	Río Mesquites	RM	937	45.140*	56.202*
	Pozas Azules II	PII	1 052	23.382*	56.679*
	Pozas Azules I	PI	1 278	18.566*	31.550*
Central Mexico	Alchichica crater-lake spongy morphotype	AS	721	28.606*	50.376*
	Alchichica crater-lake columnar morphotype	AC	728	27.386*	47.196*

NRI = net relatedness index, NTI = nearest taxa index, OTU = operational taxonomic unit.
Stars indicate statistically significant values ($P < 0.05$).

TABLE 2
NRI and NTI of major phyla in microbialite communities from different locations

Phylum	Bacteroidetes			Cyanobacteria			Plactomycetes			Proteobacteria			Verrucomicrobia		
Locality	OTUs	NRI	NTI	OTUs	NRI	NTI	OTUs	NRI	NTI	OTUs	NRI	NTI	OTUs	NRI	NTI
S	122	2.94*	1.65*	73	2.60*	1.53*	231	2.77*	2.27*	820	-0.53	2.88*	154	1.04	1.41*
BP	124	3.41*	3.05*	61	0.64	0.77	210	1.65	2.29*	770	-0.58	3.70*	140	1.18	1.46*
BR	119	3.13*	2.24*	97	0.66	0.86	245	2.03*	1.65*	928	0.50	3.66*	164	1.07	1.49*
BM	119	-1.14	2.36*	53	0.69	1.18	153	1.93*	2.72*	696	-1.50	3.69*	146	0.14	1.43*
RM	57	0.61	1.35	17	0.23	0.34	158	3.51*	1.72*	625	-0.04	3.83*	80	1.23	1.77*
PI	106	3.22*	2.54*	40	-0.81	1.43	216	1.71	2.91*	803	1.21	2.14*	113	1.69	1.50*
PII	108	2.94*	2.79*	54	0.42	0.47	241	2.35*	3.45*	819	0.83	4.12*	125	1.71*	1.53*
AS	67	0.51	2.08*	137	0.36	2.01*	80	4.46*	3.82*	417	3.95*	5.49*	29	-1.81	1.61*
AC	57	1.37	1.91*	140	0.71	1.90*	73	2.53*	3.06*	916	7.99*	3.48*	158	-1.69	0.92

OTU = operational taxonomic unit, NRI = net relatedness index, NTI = nearest taxa index. Stars indicate statistically significant values ($P < 0.05$).
S = Sian Ka'an Biosphere Reserve, BP = Bacalar "Pirate Channel", BR = Bacalar "Rapids", BM = Bacalar "Medio", RM = Río Mesquites.
PI = Pozas Azules I, PII = Posas Azules II, AS = Alchichica crater-lake spongy morphotype, AC = Alchichica crater-lake columnar morphotype.

assumed that community membership is generated through a mixture of stochastic processes and micro-evolutionary processes (mutation, selection, gene flow and genetic drift) (Hanson et al., 2012; Stegen et al., 2013) that include both environmental filtering and biotic interactions (Pérez-Gutiérrez et al., 2013). In this sense, the analysis of the phylogenetic community structure through NTI and NRI metrics, has been an excellent tool to understand the composition of communities in relation to ecological interactions, especially for large data sets generated through next generation sequencing approaches (Jones et al., 2009).

In this study, the global analysis of dominant bacterial phyla recovered from complex communities forming microbialites showed phylogenetic structuring and clustering of taxa that are more closely related to co-occurring nearest relatives than expected by chance. This pattern can be explained by habitat filtering as the main factor that drives community structure, where a group of closely related taxa share a trait or set of traits, which allow them to persist in a given habitat, making them suitable for those particular environmental conditions at specific localities (Horner-Devine & Bohannan, 2006). In other words, this supports the hypothesis that habitat characteristics or environmental stress can filter a community, so that only closely related species can persist (Pontarp et al., 2013). In a previous published paper, Centeno et al. (2012) found that abiotical factors such as pH and conductivity explained 33 % of the differences in community composition in microbialites from the same study sites here included. In spite of such low value it was higher than the 25 % of the variance explained by the same variables in prokaryotic communities isolated from water columns in the same localities (Centeno, unpublished data) and higher than the variation explained by environmental variables (26 %) in other microbial studies (Hanson et al., 2012). The low percentage of explained variance in genetic composition could be attributed to the comparision of samples from a wide geographic gradient and not from a single locality. For example, Mobberley et al. (2012) compared four types of thrombolitic mats from a single locality in Bahamas, and found that 67 % of the variance is explained by the two first principal coordinates. Similar results were found by Schneider et al. (2013) analyzing genetic composition of

bacteria in a hypersaline lake at Kiritimati atoll Central Pacific, where almost 91 % of the variance was explained by pH and depth; however, this value drops to 63 % when they compared their results with a similar hypersaline system in Guerrero Negro, Mexico. The clustering pattern observed in microbialites considered in this study, would be related to micro-environmental heterogeneity as proposed by Horner-Devine and Bohannan (2006), since these are complex biofabrics, where biogeochemical and physicochemical gradients promote niche availability in a few millimeters, mimicking what has been described in microbial mat systems (Ley et al., 2006; Harris et al., 2013). Similar clustering patterns have been found in other microbial assemblages. For example, Bryant et al. (2008) found that Acidobacteria were phylogenetically clustered in soils along an elevation gradient. Jones et al. (2009) found that acidobacterial communities collected throughout North and South America, were more phylogenetically clustered as soil pH departed from neutrality, thus suggesting that pH is an effective habitat filter that restricts community membership to progressively more narrowly defined lineages, as pH deviates from neutrality. Barberán and Casamayor (2010) used the NRI and NTI metrics to evaluate processes that lead to the phylogenetic structuring of bacterioplankton, and reported significant phylogenetic clustering related to salinity and ionic composition. Amaral-Zettler et al. (2011) reported phylogenetic clustering in microbial taxa inhabiting the aquatic systems of Rio Tinto, Spain, indicating that abiotic factors are primarily responsible for shaping community structure. Chong et al. (2012) found phylogenetic clustering in soil bacterial assemblages in different sites of Antarctica. Finally, Pontarp et al. (2012) analyzed the phylogenetic structure of marine bacterioplankton in coastal regions from nine sampling points around the world, and also suggested that marine bacterioplankton were strongly structured by habitat filtering, where water temperature was the main factor.

When we analyzed each bacterial phylum separately (Proteobacteria, Planctomycetes, Bacteroidetes, Verrucomicrobia and Cyanobacteria) we observed that phylogenetic structure measured by NTI and NRI was variable. We found that Proteobacteria, Planctomycetes, Bacteroidetes and Verrucomicrobia were phylogenetically clustered in specific sites, whereas Cyanobacteria showed a tendency to be randomly structured. Since Cyanobacteria were amongst the main biological drivers of microbialite formation (Reid et al., 2000), different species will be randomly associated to microbialitic fabrics, depending on the environment (Pholchan, Baptista, Davenport, Sloan, & Curtis, 2013). Similar results were found in a salt marsh microbial mat, where Armitage et al. (2012) detected phylogenetic clustering of bacteria in deeper layers of the mat structure, while the clustering signal was lost in the top layers where oxygenic phototrophs including cyanobacteria reside. Chase (2010) argued that this tendency could be related to the function of the trophic consortia, where stochastic processes predominate in highly productive systems (in this case represented by the phototrophic surface layer of the microbialites where resident cyanobacteria are located), whereas deterministic processes predominate in lower-productive systems (in this case the portion below the surface layer in the microbialites structures). The same trend has been observed in terrestrial systems dominated by cyanobacteria. For example, Stomeo et al. (2013) mentioned that heterotrophic assemblages could be explained partially by environmental factors, whereas the phototrophic bacterial assemblages exhibited strong signals related to stochasticity. Makhalanyane et al. (2013) found evidence of random phylogenetic structure in desert hypolithic communities when cyanobacteria and heterotrophic bacteria were analyzed separately, whereas species co-occurrence was non-random when bacterial groups were analyzed together. We hypothesize that the three cyanobacterial ensembles that showed phylogenetic clustering in this study, including both microbialite types from Alchichica crater-lake and Sian Ka'an coastal lagoon, develop in stressful environments that filter specific taxa, sharing

a common ancestry and common traits that allow them to adapt to these systems (Pontarp et al., 2013). The samples included in this study comprised a limited latitudinal gradient of approximately 8º in latitude (from 18º 35' N - 26º 55' N), nevertheless, they were consistent with those of Caruso et al. (2011), who evaluated desert microbial communities worldwide. In both analyses, cyanobacteria showed evidence of random colonization, while dominant heterotrophic bacteria showed a tendency to phylogenetic clustering.

The major bacterial phyla here analyzed represent high diverse groups in terms of genetic variation and metabolic functionality, the sequences proportions found were similar to data generated with more recent high-throughput sequencing technologies (e.g,. Illumina) (Saghaï et al., 2015), supporting the importance of these taxa as members of microbialites communities. We suggested that environmental factors are more important in limiting bacterial structure and composition than biological factors in the microbialites of study, and microbialite communities in other regions of the world must follow a similar phylogenetic pattern, although further studies are necessary to validate this hypothesis.

In conclusion, our results suggest that habitat filtering acts as the main structuring process determining genetic composition of communities forming microbialites. However, Cyanobacteria, which are key species in microbialite fabric formation (where they act as the main photoautotrophs and diazotrophs), are the only lineage that did not show a phylogenetic structure, suggesting that different cyanobacterial lineages can contribute to microbialite formation and growth.

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RESUMEN

Las condiciones del hábitat determinan la estructura filogenética de filos (phyla) bacterianos dominantes de comunidades de microbialitos de diferentes regiones en México. La estructura y composición de las comunidades son determinadas por procesos evolutivos y ecológicos que se manifiestan en señales de diversidad, abundancia y la relación de especies. El análisis de la relación de especies que coexisten ha recibido atención como una herramienta para identificar los procesos que influyen en la composición de una comunidad dentro de un hábitat particular. En este estudio, evaluamos si la composición genética de bacterias microbialíticas depende de acontecimientos al azar vs factores biológicos/ abióticos. Este estudio se basa en un conjunto de datos genéticos de dos regiones hipervariables (V5 y V6) de gen 16S rRNA generados previamente de nueve comunidades de microbialitos distribuidos en el Noreste, Centro y Sureste de México, recolectados en mayo y junio 2009. Los datos genéticos de los filos más abundantes (Proteobacteria, Planctomycetes, Verrucomicrobia, Bacteroidetes y Cyanobacteria) fueron analizados para determinar la estructura filogenética de la comunidad y de cada filo por separado. Para el análisis conjunto, el índice NTI de Webb mostró valores positivos y significativos en las nueve comunidades analizadas, en donde los valores oscilaron entre 31.5 en Pozas Azules I y 57.2 en el Canal Pirata en Bacalar; en contraste, los valores del índice NRI fueron positivos y significativos en seis de las nueve comunidades analizadas con valores oscilando desde 18.1 en Pozas Azules I hasta 45.1 en Río Mezquites. Por otro lado, en la comparación de cada filo individual, el índice NTI fue positivo y significativo en todos los grupos excepto en Cyanobacteria, en donde valores positivos y significativos fueron encontrados sólo en tres localidades; finalmente, el índice NRI fue significativo sólo en unas cuantas de las comparaciones realizadas. Los resultados sugieren que el filtrado del hábitat es el proceso principal que determina la estructura filogenética de las comunidades bacterianas asociadas a microbialitos con la excepción de las cianobacterias en donde diferentes linajes pueden contribuir a la formación y crecimiento del microbialito.

Palabras clave: ensamble comunitario, composición comunitaria, cianobacterias, bacterias heterotróficas, microbialitos, NRI y NTI.

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