RESEARCH ARTICLE

Active and total prokaryotic communities in dryland soils

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Received 3 October 2012; revised 24 May 2013; accepted 24 May 2013. Final version published online 26 June 2013.

DOI: 10.1111/1574-6941.12155

Editor: Christoph Tebbe

Keywords
biodiversity; biogeography; community fingerprinting; semi-arid; soil chemistry; statistical analysis of microbial communities.

Abstract

The relationship between total and metabolically active soil microbial communities can change drastically with environment. In dry lands, water availability is a key factor limiting cells’ activity. We surveyed the diversity of total and active Archaea and Bacteria in soils ranging from arid desert to Mediterranean forests. Thirty composited soil samples were retrieved from five sites along a precipitation gradient, collected from patches located between and under the dominant perennial plant at each site. Molecular fingerprinting was used to site-sort the communities according to their 16S rRNA genes (total community) and their rRNA (active community) amplified by PCR or RT-PCR from directly extracted soil nucleic acids. The differences between soil samples were much higher in total rather than active microbial communities: differences in DNA fingerprints between sites were 1.2 and 2.5 times higher than RNA differences (for Archaea and Bacteria, respectively). Patch-type discrepancies between DNA fingerprints were on average 2.7–19.7 times greater than RNA differences. Moreover, RNA-based community patterns were highly correlated with soil moisture but did not necessarily follow spatial distribution pattern. Our results suggest that in water-limited environments, the spatial patterns obtained by the analysis of active communities are not as robust as those drawn from total communities.

Introduction

Water-limited ecosystems (especially hot arid, semi-arid and dry subhumid regions, collectively termed dry lands) are of high importance as they span over a third of the world’s land surface and are home to about half of the global human population (Middleton & Thomas, 1997; Ffolliott et al., 2003). Dry lands are highly susceptible to the effects of global climate change; as a result, they expand rapidly through desertification and threaten to occupy larger portions of Earth’s terrestrial area in the near future (Reynolds et al., 2007). Despite the eminent threat desertification poses to the world’s food supply and to neighbouring ecosystems, dryland ecosystems are typically understudied compared with more humid ones. With respect to microbial diversity in dry lands, only a handful of studies were performed utilizing modern molecular techniques (Holmes et al., 2000; Nagy et al., 2005; Clark et al., 2009; Abed et al., 2012; Steven et al., 2012), yet fewer addressed the issue of microbial activity (e.g. community analysis on the RNA level). Microorganisms carry out myriad microscale processes that underlie many of the soil’s biogeochemical functions. In arid and semi-arid soils, microbial function may be associated with the sparse distribution of shrub vegetation (Bachar et al., 2012), occasional rain events (Clark et al., 2009), soil moisture (Angel et al., 2010) and human activity (Kuske et al., 2012). Studies on the microbial ecology of dryland soils have focused on bacterial abundance and community composition in shrub islands (Herman et al., 1995), desert crusts (Nagy et al., 2005; Gundlapally & Garcia-Pichel, 2006), endolithic communities (Wierzchos et al., 2006) and extreme hyperarid areas such as the Atacama Desert (Neilson et al., 2012).

In previous studies, we showed that the biogeographical patterns of the total communities of Bacteria and Archaea are similar. Both domains exhibited significant spatial clustering into distinct communities in arid,
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semi-arid and Mediterranean soils in Israel, although their abundance differed and was positively correlated with the soil’s water content (WC; Angel et al., 2010; Bachar et al., 2010). We also demonstrated that shrub ‘islands’ support different bacterial and archaeal communities than inter-shrub sites in arid and semi-arid soils, but not in moist Mediterranean soils (Angel et al., 2010; Bachar et al., 2012). However, as only DNA was used for analysis in these studies, we do not know what proportion of these characterized communities was viable or whether the patterns we have observed with respect to spatial distribution, effect of shrubs and soil moisture were also reflected in the metabolically active soil microbial communities.

The relationship between total and metabolically active soil microbial communities can change drastically with environmental conditions, with water availability being a key factor in the resuscitation of dormant cells. As such, precipitation in dryland environments should be reflected by changes in the ratio between active and dormant cells. The dynamics of total and active microbial communities in arid soil may also reflect other environmental conditions such as desiccation, radiation and temperature (Kendrick & Kral, 2006; Clark et al., 2009; Angel et al., 2010; Bachar et al., 2010; Neilson et al., 2012). Nevertheless, little attention has been paid to the active microbial communities and the spatial, temporal and physico-chemical parameters that affect them. Specifically, no study has yet compared the total and active microbial communities in arid environments or attempted to link microbial communities to the factors that may mediate their diversity.

Surveys of microbial diversity in soils based on directly extracted nucleic acids generally employ analysis of part of the bacterial genomes through the gene encoding the small subunit (16S) ribosomal RNA (rRNA), some functional gene or the environmental metagenome. However, DNA-based analyses describe both the active and inactive communities. Microbial community analysis through environmental DNA is potentially biased because it might not report on the viable community but rather originate from contamination by free DNA (Romanowski et al., 1992), structural exopolysaccharide DNA (Seper et al., 2011) or DNA from dead or dormant cells (Hansen et al., 2007). RNA-based analyses could better reflect the active members of the soil microbial community, but the method has its own pitfalls linked to a more laborious extraction procedures, RNA degradation, multiple copies of the ribosome (Wang et al., 2012) and dormant cells containing rRNA reserves (Sukenik et al., 2012).

In this study, we examined the spatial diversity of total and active bacterial and archaeal communities in dryland environments based on their rRNA and comparing the patterns to our previously generated data based on DNA (Angel et al., 2010). We used the soil samples collected from five long-term ecological research sites distributed along a steep precipitation gradient ranging from 100 to almost 900 mm annual rainfall, from barren sites and from under the canopy of the dominant perennial shrub at each site (Angel et al., 2010). This scheme enabled us to compare and contrast the active and total microbial communities in the water-limited ecosystems.

Materials and methods

Soil sampling and characterization

Sampling was performed in May and June of 2007 at five long-term ecological research sites in Israel (www.hamaarag.org.il/) located along a steep precipitation gradient ranging from arid (c. 100 mm annual precipitation) to semi-arid (c. 300 mm annual precipitation), to dry Mediterranean (c. 450 mm annual precipitation), to Mediterranean (c. 600 mm annual precipitation) and meso-Mediterranean (c. 900 mm annual precipitation) climates; for more details, see Angel et al. (2010) and Table 1. The sites are otherwise similar in their physical properties: they are located away from the sea, at similar altitudes and slopes and lie on similar bedrocks. Sampling was performed after winter rains had stopped, to avoid ephemeral influences of hydration pulses on the community (Placella et al., 2012). At each site, sampling was performed in triplicate plots of 40 × 25 m, all fenced and thus protected from grazing livestock and human activity. In each plot, eight random subsamples were taken from the soil in the spaces between the dominant perennial plants (inter-shrub soil patch) and under the canopy of the dominant perennial plant (under-shrub soil patch). The eight subsamples taken from each patch type in each plot were composited to better represent each patch at any given site. Overall, a total of six composite soil samples were obtained from each site. After litter and crust removal, the top 5 cm of the soil was collected into sterile bags and placed in a cooler. The samples were transported to the laboratory and homogenized within 24 h of sampling. A 50-g subsample of each composite sample was stored at −80 °C for molecular analysis, and the rest was used for physico-chemical analyses.

Soil physico-chemical analyses

Soil chemical analyses were performed according to standard methods (Page et al., 1986): soil WC by gravimetric method, percentage organic matter by dichromate oxidation method, pH and electrical conductivity in saturated soil extract (SSE), sodium, calcium and magnesium in
Table 1. Characteristics of the sites and values of major physico-chemical parameters of the sampled soils. For each site, mean values are separated by dash for inter- and under-shrub soil patches.

<table>
<thead>
<tr>
<th>Climate</th>
<th>Location (coordinates, elevation)</th>
<th>Average precipitation (mm yr(^{-1}))</th>
<th>WC(^1) (%)</th>
<th>pH</th>
<th>NO(_3)-N (mg kg(^{-1}))</th>
<th>NH(_4)-N (mg kg(^{-1}))</th>
<th>P(_{tot}) (mg kg(^{-1}))</th>
<th>Calcium carbonate (%)</th>
<th>OM(^2) (%)</th>
<th>Predominant perennials(^3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arid</td>
<td>Avdat (30°47' N’34°46' E, 600–700 m)</td>
<td>100</td>
<td>1.9/1.8</td>
<td>7.9/8.0</td>
<td>4.0/9.4</td>
<td>3.4/6.3</td>
<td>0.03/0.04</td>
<td>33.0/33.7</td>
<td>0.6/0.8</td>
<td><em>Hammada scoparia and Zygophyllum dumosum</em></td>
</tr>
<tr>
<td>Semi-arid</td>
<td>Lehavim (31°20’ N’34°45’ E, 350–500 m)</td>
<td>300</td>
<td>2.6/3.8</td>
<td>7.2/7.0</td>
<td>2.8/3.5</td>
<td>49.0/62.5</td>
<td>0.07/0.09</td>
<td>17.0/16.3</td>
<td>2.0/3.4</td>
<td><em>Sarcopoterium spinosum</em> and <em>Thymelaea hirsuta</em></td>
</tr>
<tr>
<td>Dry-Mediterranean</td>
<td>Adulam (31°40’ N’34°50’ E, 200–300 m)</td>
<td>400</td>
<td>6.0/20.4</td>
<td>7.3/7.2</td>
<td>5.9/3.7</td>
<td>21.0/27.5</td>
<td>0.09/0.02</td>
<td>14.0/6.7</td>
<td>6.1/9.9</td>
<td>*Quercus calliprinos and <em>Pistacia palestina</em></td>
</tr>
<tr>
<td>Mediterranean</td>
<td>Ramat Hanadiv (32°30’ N’34°55’ E, 100–200 m)</td>
<td>600</td>
<td>9.6/14.7</td>
<td>7.0/7.1</td>
<td>6.7/6.5</td>
<td>40.8/51.0</td>
<td>0.09/0.02</td>
<td>1.7/1.7</td>
<td>4.9/10.5</td>
<td>*Phillyrea latifolia and <em>Quercus calliprinos</em></td>
</tr>
<tr>
<td>Meso-Mediterranean</td>
<td>Mt. Meron (32°00’ N’35° 20’E, 700–900 m)</td>
<td>900</td>
<td>12.1/23.6</td>
<td>7.0/6.9</td>
<td>8.2/2.7</td>
<td>54.6/98.6</td>
<td>0.09/0.13</td>
<td>1.7/2.3</td>
<td>7.3/10.9</td>
<td>*Quercus calliprinos and <em>Quercus boissii</em></td>
</tr>
</tbody>
</table>

*Table adopted from Angel et al. (2010).  
†Water content [g water (100 g dry soil)]\(^{-1}\).  
‡Organic matter.  
§The under-shrub patch samples were taken from under the canopy of the underlined plant species.  

Molecular fingerprinting of soil microbial communities

RNA was extracted by bead beating the soil samples in the presence of 10% (v/v) CTAB and phenol according to Angel et al. (2012). Terminal restriction fragment length polymorphism (T-RFLP) fingerprints of the active bacterial and archaeal soil communities were generated following Angel et al. (2010). Terminal restriction fragment size was rounded to the nearest integer, and fragment heights were expressed in percentage. Multivariate analysis was performed using PC-ORD v5.32 (M.J.M Software; Glen, NH) with Sorensen distances. Ordinations were generated with nonmetric multidimensional scaling (NMDs) with Spearman's distances. The samples were then mixed with HiDi (Applied Biosystems) and analysed on a 3100 genetic analyser (Applied Biosystems). Peak heights were expressed in percentage. Multivariate analysis was performed using PC-ORD v5.32 (M.J.M Software; Glen, NH) with Sorensen distances. Ordinations were generated with nonmetric multidimensional scaling (NMDs) with Spearman's distances. The samples were then mixed with HiDi (Applied Biosystems) and analysed on a 3100 genetic analyser (Applied Biosystems).
Taguchi & Oono, 2004) using 500 iterations. Differences between sample groups were calculated by multiresponse permutation procedure (MRPP; Mielke et al., 1981), a test based on the assumption that if two groups are different from each other, the average within-group difference will be smaller than the average between-group distance. The ‘effect size’ of the difference between data groups was represented by the A-statistic of the MRPP test (MRPP-A), while its significance was identified by the MRPP’s P-value. MRPP-A ranges from zero, meaning that data points are randomly distributed (i.e. the two tested groups are homogenous), to one, meaning that data point distribution is wholly determinate (i.e. the two groups are completely separate); therefore, we are able to compare MRPP-A values obtained from different MRPP tests conducted with different data sets.

Results

T-RFLP profiling of the soil samples on the DNA level revealed, on average, 10–20 and 30–40 T-RFs per sample for Archaea and Bacteria, respectively, with no apparent trend with respect to the precipitation gradient (Supporting Information, Table S1). The numbers of T-RFs in the RNA profiles were somewhat lower and averaged 6–12 and 20–25 T-RFs per sample for Archaea and Bacteria, respectively, again with no apparent trend. The T-RF sets from DNA and RNA showed a 39 ± 31% overlap, meaning that, averaged over restriction enzymes and prokaryotic kingdoms, 39% of the T-RFs from a soil sample appeared in both DNA and RNA profiles. When considering only the abundant T-RFs that accounted each for > 1% of the total T-RF abundance in that sample, the overlap percentage increased to 64 ± 45%.

DNA- and RNA-based archaeal (Fig. 1a and b) and the DNA-based bacterial (Fig. 1c) community compositions were sorted into three distinct groups based on multiple pairwise MRPP tests (A > 0.07, P < 0.05): (1) the arid site (c. 100 mm annual precipitation); (2) the semi-arid site (c. 300 mm annual precipitation); and (3) the three Mediterranean sites (c. 450–800 mm annual precipitation). RNA-based bacterial communities could not be site-sorted according to their T-RFLP fingerprints (MRPP tests, P > 0.05; Fig. 1d). Of the tested environmental parameters (Table 1), WC was best correlated with microbial community structure (R^2 > 0.6 and P < 0.05 between WC and the 1st NMDS ordination axis for all restriction enzymes). Organic matter also correlated but to a lesser degree (0.4 < R^2 < 0.6 and P < 0.05 between organic matter and the 1st NMDS ordination axis for all restriction enzymes). DNA-based archaeal (Fig. 1a and b) and bacterial (Fig. 1c and d) communities better discriminated between soil samples taken from the five long-term ecological research sites than the RNA-based communities.

Figure 2 depicts the measured differences between RNA- and DNA-based patterns for both bacterial (Fig. 2a) and archaeal (Fig. 2b) communities and their correlation with soil moisture differences (shown as the ratio of soil WC between each two sites: the nominator always being the more humid of the two). The DNA-based patterns showed a weaker correlation with the local soil WC compared with the RNA-based differences (MRPP-A value ratios) for both Bacteria (τ = 0.36, P = 0.17 and τ = 0.54, P = 0.04, respectively) and Archaea (τ = 0.47, P = 0.07 and τ = 0.56, P = 0.03, respectively). In fact, the difference between DNA-based bacterial communities in soil sampled from inter-shrub patches at different sites (including all possible combinations among sites, i.e. 10 MRPP-A tests) were on average 2.5 ± 0.7 times greater than the RNA-based differences (average difference in the A-statistic; Fig. 2a). The archaeal patterns were less distinct (Fig. 2b), but again the divergence of the DNA-based bacterial community was on average 1.2 ± 0.9 times greater than the differences depicted by the RNA-based communities (average difference in the A-statistic; Fig. 2b).

When comparing the microbial communities sampled in inter- and under-shrub soil patches along the precipitation gradient, DNA-based fingerprints could discriminate between patch types (Angel et al., 2010). In contrast, RNA-based fingerprints of either the archaeal or bacterial communities did not discriminate between patches in almost any of the five sites tested in this study. The bacterial DNA-based differences, as depicted by the MRPP-A values of patch types, were on average 19.7 ± 26.9 times greater than the RNA-based differences (Fig. 2a). Figure 3b illustrates the DNA- and RNA-based differences in the composition of archaeal communities between patches, with the latter being slightly higher (2.7 ± 2.2) than the DNA-based differences. On the other hand, soil moisture ratios between patches (shown as the ratio of soil WC between each two sites: under-shrub values divided by inter-shrub values) were not correlated with differences between microbial communities from the inter- and under-shrub patches (τ < 0.60, P > 0.22; Fig. 3).

Discussion

Analysis of microbial communities through their RNA rather than DNA has the potential to provide a more accurate image of their active members. Nevertheless, the suitability of microbial RNA analysis for answering such ecological questions has rarely if ever been explicitly addressed. We contrasted inter- and under-shrub soils
along a precipitation gradient ranging from desert (< 100 mm annual precipitation) to meso-Mediterranean forests (> 800 mm annual precipitation). The sampling scheme included a composite of eight soil subsamples in each patch in triplicate plots at each site along the precipitation gradient. This scheme was designed to assure that each sample indeed represented the microbial community of an entire plot while still providing replicates for statistical analysis. Moreover, the use of three restriction enzymes to generate the T-RFLPs for each microbial domain and the concomitant analysis of each T-RFLP batch further increased the reliability of the emerging spatial patterns of soil microbial communities. We are aware that T-RFLP fingerprinting accounts mainly for relatively abundant microbial groups, while rare groups, comprising the majority of the population, are unaccounted for; nevertheless, it has been shown that T-RFLP fingerprinting is a robust method capable of revealing spatial patterns of microbial communities, reflecting reproducible biogeographical patterns (Fierer & Jackson, 2006; Lauber et al., 2009).

We previously showed that the microbial community compositions as well as the biomass in Israeli arid, semi-arid and Mediterranean long-term ecological research sites are significantly different, but that the microbial communities within the three Mediterranean sites, ranging in annual precipitation from 400 to above 800 mm, were generally similar (Angel et al., 2010; Bachar et al., 2010). Moreover, we previously suggested that the community patterns are governed mainly by precipitation rate and vegetation cover (Angel et al., 2010). In the current study, we analysed the bacterial and archaeal communities...
in the same samples along Israel’s precipitation gradient on the rRNA level. As expected, we recovered less T-RFs compared with the DNA-based profiles, as the RNA-based communities are presumably active and thus represent a subset of the total, DNA-based communities. However, this does not necessarily mean that the T-RFs that are missing in the RNA-based profiles are of dead cells as it is likely that different microorganisms are active at different times, while our sampling represented only a single time point. Many of the T-RFs in each soil sample were not shared between the DNA- and RNA-based profiles. Of all the noncommon peaks, about half were ‘DNA-only’ and half were ‘RNA-only’ peaks. This discrepancy is likely to have originated, at least partially,
from some method biases, that is, different extraction techniques for RNA and DNA (see Pasternak et al., 2013) but most of it is probably real. The appearance of 'DNA-only' peaks is expected because the RNA profile should represent the active subset of the community and these peaks probably originated from species that are dormant or otherwise nonactive at the time of sampling. On the other hand, the 'RNA-only' peaks could have originated from rare species, which are highly active and create large amounts of rRNA, because T-RFLP profiling has a rather low detection threshold.

RNA-based profiles of the microbial communities largely followed the same patterns as the DNA-based one, with two major differences: (1) the discrepancies among sites were better illustrated by the DNA-based analysis; and (2) the spatial distribution as elucidated using rRNA better reflected the soil's transient local conditions (WC). Consequently, RNA-based analysis only found differences between patches that differed in their soil WCs (Fig. 3; Table 1), while DNA-based analyses also differed according to patch type, regardless of soil moisture. As mentioned above, significant variations in bacterial composition and abundance in patch communities were inversely related to the precipitation gradient, and in the arid site, each patch type was characterized by a distinct bacterial community (Bachar et al., 2012) although, as seen in Table 1, both patches had similar soil WCs. Moreover, the differences between patches in the semi-arid site were less pronounced, whereas in the dry Mediterranean site, the diverse moisture contents in the soils were not reflected in the bacterial community compositions (Bachar et al., 2012).

Actinobacteria and Proteobacteria (specifically Alphaproteobacteria) have been previously shown to dominate soil patches at all sites, yet their diversity was associated with patch type in arid and semi-arid sites (Bachar et al., 2010, 2012). We suggested in those studies that members of both the Actinobacteria and Proteobacteria were inactive at the time of sampling, particularly in the arid and semi-arid environments, and thus, it is likely that their rRNA was not detected. DNA-based patterns may also reflect past metabolic activity of the Bacteria and Archaea, perhaps during periods when the soil was moister. The recorded dynamics are thus no longer occurring at the time of sampling, perhaps, due to heat or osmotic stress cells have become dormant, but the fingerprints of the formerly active communities are still found in the DNA. Therefore, rRNA-based analyses of microbial communities in arid environments are likely to not reflect the total diversity, as stress conditions are common and trigger members of the microbial community to substantially reduce their metabolism and ribosome synthesis. In contrast, a study analysing the rRNA- and DNA-based bacterial and archaeal communities in a tropical forest soil in Puerto Rico, with no water or nutrient restrictions, found that the communities' richness and diversity values were similar (DeAngelis & Firestone, 2012). A comparison of total and active bacterial populations in a moist and nutrient-rich forest soil in Bohemia also revealed similar DNA- and RNA-based diversity patterns (Baldrian et al., 2012).

The discrepancy between DNA- and RNA-based community fingerprints is shown here to be less pronounced in Archaea than in Bacteria. Members within the archaeal community have been found to be more resilient to energy starvation and extreme conditions (Macario et al., 1999; Valentine, 2007; Maupin-Furlow et al., 2012), including high temperatures (Bowers & Wiegel, 2011) and desiccation (Kendrick & Kral, 2006). This might explain the similarities between active and total archaeal diversity along the precipitation gradient and between patch types. Likewise, ammonia-oxidizing archaeal and bacterial diversity was tested following desiccation and heat shock: the extreme conditions mainly affected the Bacteria, while the Archaea were more durable (Zeng et al., 2011; Vasiliev et al., 2012). This observation was reported not only in water- and heat-stressed environments but also in tropical forest soil, where Bacteria yielded more exclusive 'RNA-only' detected populations than Archaea (DeAngelis & Firestone, 2012).

Conclusions

This study shows that while the community compositions of total soil Bacteria and Archaea follow large-scale and long-term pattern (e.g. geographical site, patch type), the composition of the active communities is less discriminated by site and is more correlated with transient local variables, such as soil moisture. This tended to be more pronounced in Bacteria than in Archaea, probably because the latter are less susceptible to changes in the tested environmental conditions.

Authors' contribution

R.A. and Z.P. contributed equally to this work.

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**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Average number of T-RFs detected in the samples from each site along the precipitation gradient ($n = 6$; mean ± 1 SE).