Science of the Total Environment 487 (2014) 187–195

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Structure, inter-annual recurrence, and global-scale connectivity of airborne microbial communities

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HIGHLIGHTS

- We analyzed the composition of microbial communities in airborne dust deposition collected in a high altitude area.
- Additional analysis of lake surface waters and Mauritanian soils indicate very different microbial composition in the three habitats.
- Communities in aerosol deposition varied in time with a strong seasonal component of interannual similarity.
- Communities immediately following dust deposition were closer to Saharan soils than those found when dust inputs receded.
- A high microbial biodiversity was found in the aerosol deposition

ARTICLE INFO

Article history:
Received 23 November 2013
Received in revised form 21 March 2014
Accepted 8 April 2014
Available online 3 May 2014

Editor: Lidia Morawska

Keywords:
Aerosols
Saharan dust outbreaks
Airborne bacteria
Temporal pattern
16S rRNA gene
Diversity

ABSTRACT

Dust coming from the large deserts on Earth, such as the Sahara, can travel long distances and be dispersed over thousands of square kilometers. Remote dust deposition rates are increasing as a consequence of global change and may represent a mechanism for intercontinental microbial dispersal. Remote oligotrophic alpine lakes are particularly sensitive to dust inputs and can serve as sentinels of airborne microbial transport and the ecological consequences of accelerated intercontinental microbial migration. In this study, we applied high-throughput sequencing techniques (16S rRNA amplicon pyrosequencing) to characterize the microbial communities of atmospheric deposition collected in the Central Pyrenees (NE Spain) along three years. Additionally, bacteria from soils in Mauritania and from the air-water interface of high altitude Pyrenean lakes were also examined. Communities in aerosol deposition varied in time with a strong seasonal component of interannual similarity. Communities from the same season tended to resemble more each other than those from different seasons. Samples from disparate dates, in turn, slightly tended to have more dissimilar microbial assemblages (i.e., temporal distance decay), overall suggesting that atmospheric deposition may influence sink habitats in a temporally predictable manner. The three habitats examined (soil, deposition, and air-water interface) harbored distinct microbial communities, although airborne samples collected in the Pyrenees during Saharan dust outbreaks were closer to Mauritian soil samples than those collected during no Saharan dust episodes. The three habitats shared c.a. 1.4% of the total number of microbial sequences in the dataset. Such successful immigrants were spread in different bacterial classes. Overall, this study suggests that local and regional features may generate global trends in the dynamics and distribution of airborne microbial assemblages, and that the diversity of viable cells in the high atmosphere is likely higher than previously expected.

1. Introduction

The Saharan desert in Africa is the largest source of aerosolized soil dust on Earth (50 to 75% of the global dust production), contributing as much as one billion metric tons of dust per year to the atmosphere (Kellogg and Griffin, 2006). The global atmospheric mobilization of dust has likely increased in recent decades due to persistent drought in the Sahara-Sahel region over the past 40 years, the onset of commercial agriculture, and an increase in land-use practices (such as livestock grazing) that have desiccated large aquatic regions such as the Chad lake, decreasing vegetation cover and increasing the frequency and intensity of dust storms (Mulitza et al., 2010; Hulme, 2001). Dust storms can transport microscopic particles thousands of kilometers away from the source, a phenomenon that was noted more than 160 years ago by Charles Darwin (Darwin, 1846). Airborne dust may particularly

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http://dx.doi.org/10.1016/j.scitotenv.2014.04.030
0048-9697/

mobilize microscopic organisms (Bovallius et al., 1978; Prospero et al., 2005; Yamaguchi et al., 2012). It is well known that bacteria and fungi are commonly found associated with dust (even at altitudes of 20,000 m; Griffin, 2004) and many of these microbes can survive prolonged transport in the atmosphere and may even be metabolically active while aloft (Sattler et al., 2001; Amato et al., 2005). The topic of microbial dispersal via dust events has generated general interest due to concerns about health effects of allergens and the possible long-distance transport of pathogens (Kellogg and Griffin, 2006; Hervàs et al., 2009). In addition, ecologists are interested in understanding the role of these transoceanic and transcontinental dust events in injecting large pulses of viable microorganisms into the atmosphere, thereby expanding the geographical range of some organisms and possibly altering microbial community composition in sink environments by facilitating long-distance dispersal events.

Microorganisms enter the atmosphere as aerosol particles, can remain in the atmosphere for many days and can be transported by wind over long distances before being washed out by precipitation (rain and snow) or dry deposition (Burrows et al., 2009a). The general assumption of the atmosphere as a mere conduit for the dispersal of microorganisms rather than a dynamic habitat itself has been recently questioned (Womack et al., 2010). Although the impact of microbial atmospheric deposition on sink environments is a poorly studied issue of unpredicted consequences, very few efforts have been addressed to estimate the composition of extraneous microorganisms, their temporal dynamics, and the significance of immigration for community assembly (Hervàs et al., 2009; Jones et al., 2008). To gain knowledge on the ecology of these processes field studies should ideally combine in addition to state-of-the-art molecular methods (i) long-term temporal tracking of atmospheric depositions, (ii) careful selection of pristine and distant sink environments connected to the source, and (iii) these environments should experience frequent and intense atmospheric deposition episodes.

In this study, we applied high-throughput sequencing techniques (16S rRNA amplicon pyrosequencing) to characterize the microbial communities of the atmospheric deposition on the Central Pyrenees (NE Spain) along a period of three years. In this area, higher frequency of African dust outbreaks is observed during late spring and summer. High mountain lakes are remote and often considered pristine ecosystems largely unaffected by local anthropogenic factors due to their inaccessibility. For this reason, it has been proposed that high mountain lakes can serve as sentinels of global change (Catalan et al., 2006). The first natural collector/interceptor of these atmospheric depositions is the neuston, the biological community inhabiting the hydrophobic surface microlayer located within the first millimeter of the air-water interface (Hervàs and Casamayor, 2009). Thus, ideally the neuston should capture the remote effects that long-distance dust deposition may have on the composition of microbial communities. Our objectives were (i) to describe the microbial structure and dynamics of atmospheric deposition in the long-term, (ii) to assess the temporal pattern structuring the deposition-associated microbial communities along a inter-annual survey, and (iii) to explore the potential biological connectivity lithosphere (bacteria of soils in Mauritania)-atmosphere (airborne bacteria)-hydrosphere (neuston of high altitude lakes) by global-scale transport of microorganisms.

2. Materials and methods

2.1. Study site and sampling

The atmospheric deposition was obtained from an automatic dry/wet passive collector MTX ARS 1010 equipped with two 667 cm2 area polyethylene containers and a hygroscopic sensor cell, placed at c.a. 1,800 m altitude on a rocky landscape within the protected area of Aigüestortes National Park (Pyrenees, NE Spain). Samples were collected approximately twice per month during three years (from 15th May 2007 to 26th May 2010; Table 1 and Fig. 1). Particles deposited in the wet container (i.e. those washed from the atmosphere by rain or snow precipitation) were collected onto precombusted (450 °C, 4 hours) Whatman GF/F filters and then, were dried in a laboratory heater for 4 hours and kept in the dark (Hervàs et al., 2009). The wet container remained covered and isolated from the atmosphere but during the rain/snow precipitation intervals when the hygroscopic sensor remained activated. Thus, we were mostly targeting viable airborne microbes with the potential to develop in highly diluted waters (e.g., rain, oligotrophic lakes) and, therefore, the initial relative proportions of the different airborne populations may have been changed. The timing of Saharan dust events was determined by TOMS (Total Ozone Mapping Spectrometer) which provides a measure of the atmospheric loading of UV-absorbing aerosols (i.e., mineral dust and soot from anthropogenic and natural combustion sources; Herman et al., 1997). Saharan dust intrusion data were obtained from www.calima.ws. The temporal trend of Saharan dust intrusion to the Pyrenees region (NE Spain) showed the highest frequency during late spring and summer (from May to September) for the period 2004-2012 (Fig. 1).

Different samples from Mauritanian sandy soils located within the Sahel region, 40 km SE of Boûmdeid, from 4 different locations in the Karakoro river basin (c.a. 3,000 km distant from the Pyrenees), were pooled together for each location to characterize the composition and heterogeneity of soil samples in the area. This area is subjected to frequent dust storms and is potential source of dust plumes (Kellogg and Griffin, 2006). The soil was treated to obtain soil particles of size < 0.63 μm as reported in Hervàs et al. (2009).

Finally, the lakes sampled belong to the Limnological Observatory of the Pyrenees (LOOP; Spanish Pyrenees; 42°33 N, 00°53 E) within the protected area of the Aigüestortes National Park (Table 2). The air-water surface microlayer was collected from the upper c.a. 400 μm of the surface film with a nylon screen sampler as previously reported (Auguet and Casamayor, 2008). The lakes were sampled during 14-24 July 2008 within a 10-days interval, to minimize temporal variability, and covered a Saharan dust intrusion episode of several days. Water samples were pre-filtered in situ through a 40-μm pore-size net to retain large zooplankton and algae, and 300-500 mL were subsequently filtered on 0.2 μm pore-size polycarbonate filters. The filters were stored in lysis buffer (40 mM EDTA, 50 mM Tris pH 8.3, 0.75 M sucrose) and enzymatically digested as reported in Ferrera et al., 2004.

2.2. Molecular methods and sequence processing

DNA was extracted using the Mobio PowerSoil DNA Isolation Kit (Mobio Laboratories). Preparation of extracted DNA for pyrosequencing followed the protocol described in detail in Fierer et al., 2008a, 2008b. In brief, the variable V4 and V5 regions of the 16S rRNA gene (c.a. 250 nucleotides) were amplified with the primers F515 (5 -GTGCCAGC MGCCGCGGTAA-3) and R806 (5 -GGACTACVSGGGTATCTAAT-3). The 515 F primer included the Roche 454-B pyrosequencing adapter and a GT linker, while 806R included the Roche 454-A sequencing adapter, a 12-bp barcode (unique to each sample), and a GG linker. The region amplified by this primer set is well suited for accurate phylogenetic placement of bacterial sequences (Liu et al., 2007) and should amplify nearly all bacteria and archaea with a few biases against particular groups (Bates et al., 2011). The resulting barcoded PCR product was normalized

Table 1
Summary of the atmospheric deposition samples analyzed in this study. Mean and standard deviation are indicated for the number of sequences and number of OTUs at 97% identity.

Year	Number of samples	Number of sequences	Number of OTUs (97%)
2007	10	4,080 ± 1,435	328 ± 126
2008	14	3,256 ± 1,281	371 ± 209
2009	15	4,194 ± 1,103	334 ± 135
2010	10	3,324 ± 680	361 ± 206