

Bacterial diversity and composition during rain events with and without Saharan dust influence reaching a high mountain lake in the Alps

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Summary

The diversity of airborne microorganisms that potentially reach aquatic ecosystems during rain events is poorly explored. Here, we used a culture-independent approach to characterize bacterial assemblages during rain events with and without Saharan dust influence arriving to a high mountain lake in the Austrian Alps. Bacterial assemblage composition differed significantly between samples with and without Saharan dust influence. Although alpha diversity indices were within the same range in both sample categories, rain events with Atlantic or continental origins were dominated by Betaproteobacteria, whereas those with Saharan dust intrusions were dominated by Gammaproteobacteria. The high diversity and evenness observed in all samples suggests that different sources of bacteria contributed to the airborne assemblage collected at the lake shore. During experiments with bacterial assemblages collected during rain events with Saharan dust influence, cell numbers rapidly increased in sterile lake water from initially $\sim 3 \times 10^3$ cell ml⁻¹ to $3.6\text{--}11.1 \times 10^5$ cells ml⁻¹ within 4–5 days, and initially, rare taxa dominated at the end of the experiment. Our study documents the dispersal of viable bacteria associated to Saharan dust intrusions travelling northwards as far as 47° latitude.

Introduction

Because of their small size and large numbers, microbes can be easily dispersed among distant habitats, thus

potentially influencing local community composition in recipient ecosystems. Besides the transport of microbes by animals, aeolian dust particles act as a long-range vector for large numbers of microorganisms (Kellogg and Griffin, 2006; Hervas *et al.*, 2009; Yamaguchi *et al.*, 2012). Strong winds over arid lands can lift particles above the boundary layer and up to altitudes well above 7000 m (Kaspari *et al.*, 2009). Along with organic and inorganic nutrients bound to dust mineralogenic particles (Psenner, 1999), microorganisms are mobilized from the arid soils and transported over long distances (Griffin *et al.*, 2003; Prospero *et al.*, 2005; Mladenov *et al.*, 2011). One of the most important worldwide sources of dust is the Sahara–Sahel region in northern Africa (Moulin *et al.*, 1997).

The distance and trajectory of aeolian dust particles and associated microbes depend on factors such as wind speed and land topography (Womack *et al.*, 2010). During long-distance transport at high altitudes, microorganisms are potentially exposed to harsh conditions such as desiccation that may act as a strong selective force (Smith *et al.*, 2011). Soil-derived microbes might not be well adapted to such conditions, but spores (dormant cells with a minimum of metabolic activity) are the most likely survivors of long-distance transport in dust clouds. Interestingly, many bacterial species unknown to form spores have been observed to reach distant habitats in a viable stage (Griffin, 2007; Hervas *et al.*, 2009).

Precipitation facilitates the deposition of microbes into new habitats, as many cells from an air mass or cloud are probably washed out at the same time. Although the scavenging efficiency of aerosols by precipitation is size-dependent (Volken and Schumann, 1993), airborne bacteria are usually associated to particles of larger size (Shaffer and Lighthart, 1997; Polymenakou *et al.*, 2008) that facilitates their transport to the Earth's surface. Thus, during a rain event, microorganisms will be able to reach a recipient aquatic habitat. The long-distance atmospheric transport of bacteria and the ecological consequences for recipient aquatic ecosystems, particularly for freshwaters, have long been overlooked (Kellogg and Griffin, 2006). More recently, however, changes in bacterial community composition of the water surface microlayer of high mountain lakes during Saharan dust intrusion events have been documented (Hervas and Casamayor, 2009; Hervas

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et al., 2009; Hörtnagl *et al.*, 2010). Saharan dust intrusion events have also a strong effect on bacterial productivity via the deposition of inorganic nutrients and organic carbon (Aymoz *et al.*, 2004; Mladenov *et al.*, 2008; Pulido-Villena *et al.*, 2008; Reche *et al.*, 2009).

Here, we used a cultivation-independent approach to characterize bacterial assemblages deposited during rain events at a high mountain lake located in the Austrian Alps. We used satellite-based tracking of air masses to verify that three rain events were influenced by Saharan dust intrusions, whereas three other events had continental or oceanic origins. We hypothesized that the different origins and the conditions during transport are reflected in composition and diversity of airborne bacteria, and that harsh environmental conditions during high-altitude, long-range dispersal will act as a selective force. We further anticipated that particle-associated airborne bacteria represent a significant source of microbes for high mountain lakes. To assess viability, we conducted experiments where dust-associated bacteria were allowed to grow in sterilized lake water, and then assessed changes within the assemblage.

Results and discussion

Source of air masses and chemical characterization of rainwater

Backwards modelled trajectories of the air masses contributing to wet deposition at the high mountain (2417 m above sea level) lake Gossenköllesee (Supporting Information Fig. S1) revealed that three events originated either from oceanic or continental sources and were unaffected by Saharan dust plumes, whereas three other events can be traced back to northern Africa. Saharan dust plumes typically arrived within 3–4 days to the Austrian Alps, most of the time residing between 500 and 2000 m above ground level. In some cases, lower air masses (500 m above ground level) had followed different trajectories as compared with higher air masses (2000 m above ground level). Anyway, rain water chemistry clearly indicated the Sahar dust influence in three events (e.g. the high concentration of major ions such as Ca^{2+} , Mg^{2+} and K^+ (Supporting Information Table S1, Morales-Baquero *et al.*, 2013). However, one needs to keep in mind that the rainwater integrated over different airmasses and hence reflects a mixture of different source locations.

The dust events differed in dust loads, as can be seen from the Absorbing Aerosol Index (Supporting Information Fig. S1) and from the dust concentration measured in rainwater samples (Supporting Information Table S1). During Saharan dust intrusions, between 0.014 and 0.146 g dust $\text{m}^{-2} \text{day}^{-1}$ were deposited, whereas no

measurable dust was deposited during rain events with continental or marine origin. In addition to the different concentration of major ions, rainwater of Atlantic or European origin typically had slightly acidic pH values ranging between 5.79 and 6.05, whereas rainwater collected during Saharan dust intrusions was less acidic with pH ranging between 6.15 and 6.83 (Supporting Information Table S1). The concentration of water-soluble organic carbon (WSOC) in rainwater was usually higher (range 1.82–5.43 $\mu\text{g C m}^{-2} \text{day}^{-1}$) during Saharan dust intrusions than during rain events from other origins (range 1.71–3.71 $\mu\text{g C m}^{-2} \text{d}^{-1}$). Absorbance slope ratios of WSOC, used as proxy for the dominant molecular weight, were higher in samples collected during Saharan dust intrusions than in those collected without dust influence; the differences, however, were not statistically significant (Supporting Information Fig. S2, *t*-test, $P = 0.25$). Nevertheless, a shift towards greater molecular masses in rainwater with Saharan dust influence suggests the terrestrial origin of this carbon (Supporting Information Fig. S2). Using optical properties of water-soluble organic compounds, Mladenov and colleagues (2009) could trace organic carbon associated to Saharan dust in high mountain lakes in southern Spain. The chemical characterization of rainwater enriched with Saharan dust also revealed a substantial load of inorganic nutrients such as N and P (Supporting Information Table S1, Supporting Information Fig. S2), which, together with organic carbon, might foster bacterial growth in the recipient ecosystem. For example, rainfall during a Saharan dust event delivered up to 10-fold more phosphorus than rain without Saharan dust influence (range 32.6 to 141.0 $\mu\text{g P m}^{-2} \text{day}^{-1}$ as compared with 4.3–8.8 $\mu\text{g P m}^{-2} \text{day}^{-1}$). High mountain lakes are typically oligotrophic ecosystems and receive little nutrients from sparsely vegetated catchments with thin soil cover (Sommaruga, 2001). Hence, Saharan dust might act as a 'fertilizer' in high mountain lakes (Psenner, 1999) and can also support the accompanying bacterial community (Reche *et al.*, 2009).

Bacteria in rain events

Several recent publications have shown that Saharan dust particles act as vectors for viable bacterial cells and might constitute an immigration source to high mountain lakes in the Sierra Nevada (Spain) (Reche *et al.*, 2009), the Spanish Pyrenees (Hervas *et al.*, 2009; Vila-Costa *et al.*, 2013) and the French Alps (Chuvochina *et al.*, 2011). Our study expands the maximum distance that bacteria associated to Saharan dust particles can travel northwards to high mountain lakes located as far as 47° latitude, covering a distance of roughly 2500 km.

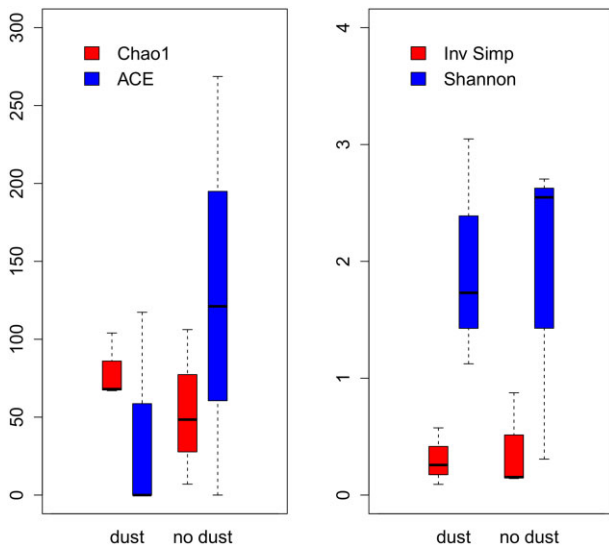


Fig. 1. Box and whiskers representation of indices used to describe bacterial community diversity in samples with and without Sahara dust influence. The box indicates median and quartile values, and the whiskers indicate the range (minima and maxima).

Bacterial cell deposition rates varied substantially between individual sampling occasions, with no significant difference between samples with and without Sahara dust influence (t -test, $P = 0.43$, Supporting Information Table S1). We obtained 573 good quality 16S rRNA sequences from clone libraries, which clustered into 136 operational taxonomic units (OTUs) at a 97% sequence similarity level, comprising 37 taxa in 16 different classes of bacteria. The absence of saturation in rarefaction curves (Supporting Information Fig. S3) indicated that not the entire diversity in rainwater samples was sampled. Conservative estimates of bacterial OTU numbers resulted in most cases in ca. 100 OTUs per sample, maximum values exceeded 200 OTUs in rain samples without Saharan dust influence. This is within the same range as next-generation sequencing-based estimates from airborne bacterial communities in Denver, CO, USA (Bowers *et al.*, 2013) and cultivation-dependent estimates

of bacterial diversity on African dust (see table 1 in Kellogg and Griffin, 2006).

Estimators of alpha diversity were used to assess differences in bacterial community structure between rain events with and without Saharan dust influence. Chao1 and ACE (abundance-based coverage estimator), which are particularly useful in comparing communities with skewed abundance distributions, were within the same range in both rain event categories (Fig. 1). Inverse Simpson and Shannon diversity indices, which both consider evenness within communities, were within similar ranges, however with generally lower values in rain events with Saharan dust influence. Such evenness is rather untypical for microbial communities, which are usually dominated by a few abundant taxa and otherwise comprised by many rare taxa. In combination, the high diversity and high evenness might reflect a rather stochastic long-distance transport of bacteria with rain and dust clouds, suggesting that bacteria from different sources such as arid soils in northern Africa, Mediterranean surface seawater, and local soils or freshwaters might contribute to the airborne community. These different source communities might mix in the air masses and hence form a diverse source community for recipient ecosystems. This contrasts with near-surface airborne bacterial communities that represent the local terrestrial environment even at high altitudes (Bowers *et al.*, 2012). Nevertheless, because of the remote location of the alpine lake, samples were collected for several days with rain events. Therefore, dry deposition of local airborne bacteria can also be assumed to have contributed to the collected bacterial diversity.

The bacterial assemblage composition differed significantly between rain events with and without Saharan dust influence (Libshuff scores: 0.0026 and 0.0037, $P < 0.001$). Rain events with Atlantic or central European origin were dominated by Betaproteobacteria of the genera *Massilia* and Sphingobacteria of the genera *Hymenobacter* (Fig. 2). Moreover, *Sphingomonas*, *Acidisphaera* and *Oxalicibacterium* were mainly found in

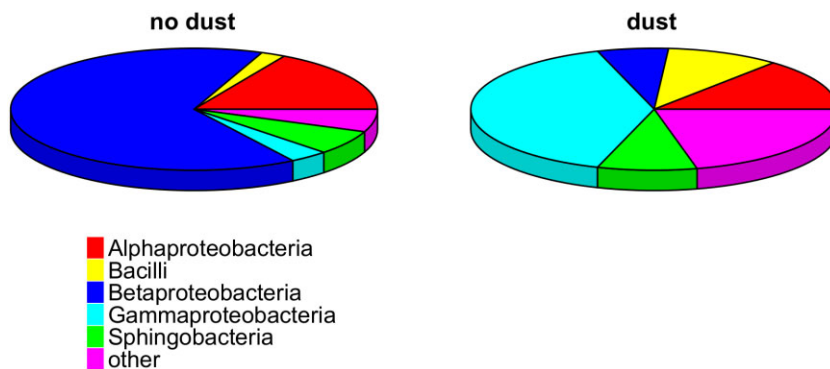


Fig. 2. Pie charts showing the relative contribution of common bacterial classes to overall diversity in rain samples with and without Saharan dust influence. Colours indicate operational taxonomic unit class affiliation.

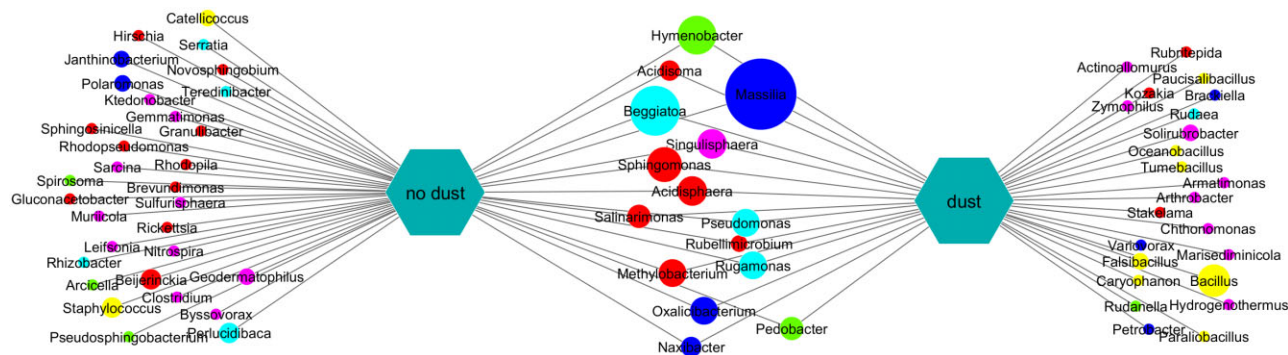


Fig. 3. Operational taxonomic unit (OTU) level representation of bacterial sequences retrieved from samples collected during rain events with and without Saharan dust intrusions. Circles represent OTUs, and lines indicate the occurrence of an OTU in the respective samples. Circle size reflects log-transformed sequence abundance, while colour indicates taxonomic affiliation (see Fig. 2 for key). While several abundant sequences were found in samples with and without Saharan dust influence, *Bacillus*, *Falsibacillus* and *Solorubrobacter* were exclusively found during Saharan dust intrusions and dominated these samples. The diversity of OTUs retrieved exclusively during rain events without dust appears larger, and no taxon was distinctively dominant in those samples.

those samples. One sample collected during Saharan intrusions (11 September) was dominated surprisingly by the gammaproteobacterial taxa *Beggiatoa*. *Massilia* dominated also in two out of three rain events with Saharan dust influence. At the OTU level (Fig. 3), alphaproteobacterial and gammaproteobacterial taxa were either present in both assemblages or exclusively found in rainwater samples without Saharan dust influence, whereas several different taxa of Bacilli were exclusively retrieved from rainwater samples influenced by Saharan dust. Gammaproteobacteria and a relative smaller contribution of Betaproteobacteria characterized Saharan dust samples. Gammaproteobacteria are generally more abundant in saline environments and soils than in freshwaters. Newton and colleagues (2011) pointed out that Gammaproteobacteria found in freshwater lake ecosystems appear to be transient 'tourists'. Betaproteobacteria have been reported to be particle-associated in limnetic environments (Weiss *et al.*, 1996; Lemarchand *et al.*, 2006) and efficient attachment to particles might also play an important role in their transport.

Owing to the small cell size and ability to form spores of Actinobacteria (Warnecke *et al.*, 2005), they might be expected to be effectively dispersed with rain and dust clouds. Newton and colleagues (2011) suggested that aerial dispersal could explain their ubiquitous occurrence in lake ecosystems. Indeed, we identified eight actinobacterial sequences in our clone library, three in rain samples without and five in samples collected during Saharan dust influence. In addition, one actinobacterial sequence was retrieved from the growth experiment. Spore-forming Bacilli of terrestrial origin have also been detected in the upper atmosphere (Griffin, 2004; Kellogg and Griffin, 2006), and different *Bacillus* taxa were retrieved mainly in dust-influenced samples.

During the transport in the atmosphere, the predominantly soil-derived bacteria are exposed to harsh environmental conditions that might act as an efficient dispersal barrier (Smith *et al.*, 2011). How well microbial cells are protected, for example, from UV radiation, desiccation or freezing within clouds is not yet explored, although desert dust has been shown to reduce UV irradiance by more than 50% (Herman *et al.*, 1999). The molecular mechanisms that enable bacterial populations to withstand the conditions during transport, as well as the ecological and evolutionary benefits of such mechanisms for soil-derived bacteria, also remain to be explored. However, the accumulation of photoprotecting pigments (Tong and Lighthart, 1997) and variations in the GC content of DNA have been proposed as mechanisms to minimize UV damage in bacteria (Singer and Ames, 1970; Matallana-Surget *et al.*, 2008). In fact, approximately 20% of the particles in the diameter range between 0.25 and 1 μm have been identified as viable bacterial cells in the upper troposphere (DeLeon-Rodriguez *et al.*, 2013). Spore formation in soil-derived bacteria, a microbial bet-hedging strategy (Jones and Lennon, 2010), might be another way to cope with harsh conditions during airborne long-distance dispersal. Therefore, different strategies might favour the growth of certain bacterial taxa as compared with more sensitive ones.

Anyway, the harsh environmental conditions during transport likely act as an environmental filter, and many cells might not arrive at the recipient ecosystem in a viable state. Therefore, even though the diversity in samples with and without Saharan dust was surprisingly high, only few specialized taxa are potentially able to grow in high mountain lakes. In our experiments, we found that several taxa were viable in lake water after being transported in Saharan dust plumes. Cell numbers during the two experiments with rainwater collected during Saharan dust

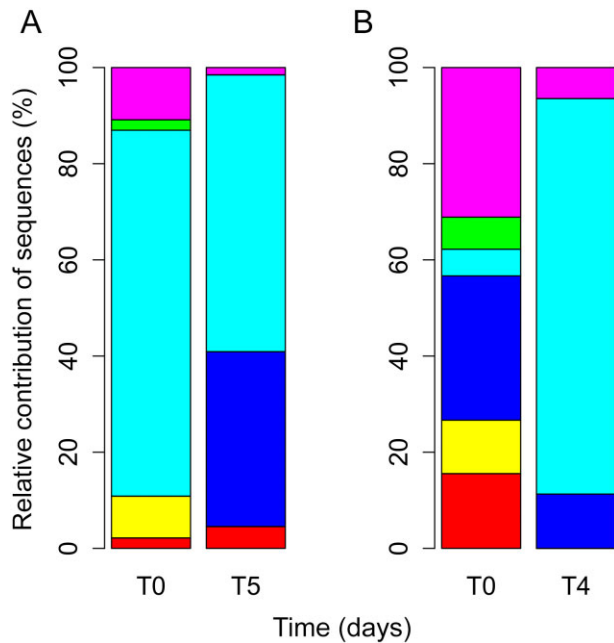


Fig. 4. Relative contribution of phylogenetic classes to bacterial diversity of samples prior (T0) and at the end (T4, T5, respectively) of the re-growth experiments conducted with Sahara dust influenced rainwater in September (A) and October (B) 2008. See Fig. 2 for colour key.

intrusions and inoculated into sterile lake water rapidly increased from initially $\sim 3 \times 10^3$ to $3.6\text{--}11.1 \times 10^5$ cells ml^{-1} within 4–5 days. Initially, abundant taxa such as the gammaproteobacteria *Beggiatoa*, *Massilia* and *Bacillus* were found only in low abundances in clone libraries at the end of the experiment. However, *Pseudomonas*-like OTUs were able to grow successfully under freshwater conditions in our experiments. Betaproteobacteria, in contrast, are common and abundant in many freshwater habitats, and the betaproteobacterial taxon *Janthinobacterium*, despite its absence from dust influenced samples, was able to increase in relative abundance when grown under freshwater conditions (Fig. 4). Hence, *Janthinobacterium* might be attributed to rainwater with rapid growth under freshwater conditions. On the other hand, the fact that taxa with low relative abundance in the original samples dominated the freshwater assemblages indicates the potential importance of rare taxa for long-distance dispersal.

In conclusion, we found that Saharan dust provide considerable concentrations of nutrients and organic carbon, which might support the growth of the transported microbial assemblage. Saharan dust plumes deliver significantly different bacterial assemblages to distant high mountain lakes than rain events with other origins. Our experiment indicated that certain taxa have the potential to establish viable populations in the recipient lake, and therefore, particle-associated airborne dis-

persal might be an important source for the rare freshwater bacterial biosphere. However, observations providing deeper insights in the diversity of rare and abundant taxa and experiments designed to address the competing role of established natural bacterial community remain to be conducted in order to assert positive colonization by airborne bacteria.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Fig. S1. Backwards modelled trajectories (lines) of the air masses contributing to wet deposition at Gossenköllesee (★) located in the Austrian Alps. Red lines depict the trajectories of air masses residing 500 m above ground level at the sampling site, while blue lines show the trajectories of air masses residing 2000 m above ground level. The panels on the right-hand side show air masses influenced by Saharan dust and the respective Absorbing Aerosol Index images as measured by the Ozone Monitoring Instrument (OMI, NASA). The left-hand side panels show air masses with Atlantic or central European origins. The altitudes in which air masses resided during transport are shown below each panel.

Fig. S2. Absorption slope ratios as proxy for DOC molecular weight distribution in rain samples collected in the absence and presence of Sahara dust influence.

Fig. S3. Rarefaction curves showing the number of OTUs retrieved from samples of rain events with and without Saharan dust influence. Saturation of the line indicates coverage of bacterial diversity in the samples.

Table S1. Physicochemical parameters of rainwater collected during summer 2007 and 2008 at the shore of the high mountain lake Gossenköllesee in Austria. Concentrations of dust, organic carbon and inorganic nutrients are given as deposition rates, i.e. units are adjusted for sampling area and duration of the rain event. The numbers of 16S rDNA clones used for microbial community analysis are indicated for the collected wet deposition samples and for the growth experiments at the beginning and end of the experiments. n.a., not available.

Appendix S1. Experimental procedures.