RESEARCH ARTICLE

Potential for atmospheric deposition of bacteria to influence bacterioplankton communities

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Abstract

Biogeographic patterns in microbial communities are an exciting but controversial topic in microbial ecology. Advances in theory pertaining to assembly of microbial communities have made strong assumptions about dispersal of bacteria without exploration. For this reason, we investigated rates of atmospheric bacterial deposition and compared the taxonomic composition of bacteria in rain with that of common freshwater bacterial communities. Our findings suggest that it is not appropriate to take for granted that atmospheric deposition of bacteria is a significant vector of immigration to freshwater ecosystems.

Introduction

The field of microbial ecology is experiencing a period of rapid advancement in its ability to use theoretical frameworks to study and explain the distribution, abundance, and dynamics of microbial taxa. Microbial ecologists are successfully applying traditional ecological concepts to bacterial communities; examples include island biogeography (MacArthur & Wilson, 1967; Whitaker *et al.*, 2003; Horner-Devine *et al.*, 2004), the neutral theory of biodiversity (Bell, 2000; Hubbell, 2001; Sloan *et al.*, 2006; Woodcock *et al.*, 2007), and local-regional diversity scaling (Fenchel *et al.*, 1997; Fenchel & Finlay, 2004; He *et al.*, 2005). The application of these conceptual models is encouraging to those hoping to quantitatively predict or model bacterial community assembly. However, many of these open-system theories make assumptions about, or estimate parameters describing, immigration rates and the composition of the regional community (Martiny *et al.*, 2006; Sloan *et al.*, 2006; Woodcock *et al.*, 2007). For example, application of the neutral theory framework to bacterial communities (Sloan *et al.*, 2006) requires estimation of the relative composition of the 'source community' from observation and an immigration parameter (m). m is the probability that a death in the local community is replaced by an immigrant from the source community and therefore $1 - m$ is the probability that a death in the local community is replaced from within. In addition, very few efforts have been made to estimate the taxonomic composition of bacteria immigrating into ecosystems or the relative significance of immigration for community assembly processes.

Rates of immigration and the taxonomic identity of immigrants entering lakes by surface water flow have been reported previously (Lindstrom & Bergstrom, 2004; Lindstrom *et al.*, 2006). As might be expected, hydraulic residence time plays a key role in determining the similarity between the inlet and lake bacterial community composition and the relative contribution of the inlet to the cell concentration in the recipient lakes (Lindstrom & Bergstrom, 2004; Lindstrom *et al.*, 2006). Hydrology seems to play a similar role in determining bacterial abundance and composition in estuarine systems (Crump *et al.*, 2004). These studies indicate that connectivity between physically distinct aquatic environments can influence the bacterial community in the recipient ecosystem. However, the majority of bacterial taxa observed in these studies have been observed previously in aquatic environments (Crump *et al.*, 2004; Lindstrom & Bergstrom, 2004; Lindstrom *et al.*, 2006). We hypothesize that the number and composition of bacteria depositing into aquatic systems from the

atmosphere differs from the number and composition immigrating via surface water inflow.

Information about atmospheric transport of bacterial cells in the literature is derived mainly from research conducted in agricultural systems (Lindemann *et al.*, 1982; Lindemann & Upper, 1985; Lindow & Andersen, 1996). The majority of this research sought to understand the release mechanisms of bacterial and fungal plant pathogens to the atmosphere, and drivers of subsequent deposition on fields (Lindemann & Upper, 1985; Lindow & Andersen, 1996). All of this work relied on culture-dependent microbiological techniques, such as enumeration of CFUs. A few studies have since used molecular techniques to identify the taxonomic composition of bacteria in the lower atmosphere (Brodie *et al.*, 2007). In the studies that have used these techniques (Maron *et al.*, 2005; Ahern *et al.*, 2007; Brodie *et al.*, 2007), the fate of the atmospherically deposited organisms either were not considered or were primarily considered in relation to public health issues.

The current study represents an investigation of the potential for airborne bacteria to affect aquatic bacterial community composition. This question is also more broadly relevant to molecular, microbial ecologists who consider ecological questions such as those outlined above.

Materials and methods

Sampling of atmospheric deposition

Dry and wet deposition of bacterial cells were sampled using 25-cm-diameter dust collectors containing 250 mL of 10% formaldehyde in glycerol (Segawa *et al.*, 2005). Four dust collectors were deployed on each of the surfaces of five northern Wisconsin lakes, two in littoral areas (near shore) and two in pelagic areas (near geographic center) for 8 days. All lakes were within 2 km of the University of Wisconsin's Trout Lake Field Station (46°01′N, 89°40′W); land use in this region is primarily national forest and seasonal residence. Subsamples (10 mL) were collected from dust collectors at *c.* 0, 48, 96, and 192 h after deployment (July 11, 2006 to July 19, 2006) using a sterile pipet and were stored in scintillation vials at room temperature until bacteria could be enumerated using 4′,6′-diamidino-2-phenylindole (DAPI). A small amount (3.3 mm) of precipitation occurred over the 8-day period. The first hour of precipitation (6.0 mm) during a rainstorm on July 23, 2006 was also collected using sterilized dust collectors, but the need for rapid deployment and retrieval necessitated deployment at Trout Lake Field Station. For collection of rainwater, two dust collectors were deployed at each of two sites, located *c.* 200 m apart. The forest canopy at one site was dominated by deciduous trees and the canopy at the second site was dominated by conifers. A sample of rain was also stored for subsequent enumeration of bacterial cells. The rain samples from July 23, 2006 and the contents of dust collectors following 192 h of dry deposition deployment were collected on 0.2 μm Supor-200 filters (Pall) and stored at $-80\,^{\circ}C$ until DNA extraction with a FastPrep Spin DNA purification kit (Qbiogene) and previously described modifications (Kent *et al.*, 2004).

Calculation of deposition rates

Dust collector subsamples were incubated with DAPI ($100\,ng\,mL^{-1}$, final concentration) and collected onto 0.2-μm polycarbonate filters (Millipore) (Porter & Feig, 1980). Ten digital pictures of each filter were taken using a Zeiss Axioplan 2 compound microscope equipped with an Olympus DP70 camera. Cells were enumerated using IP Lab v3.71 (Scanalytics Inc.) segment enumeration tools. Rates of deposition per square meter per hour were calculated as the change in concentration of cells in subsamples multiplied by the volume of the dust collector (measured after 192 h deployment) and divided by the time since last sampling and area of the dust collector.

Clone library construction, sequencing, and analysis

16S rRNA gene clone libraries were constructed from rain samples at the deciduous- and conifer-dominated sites. The fixative placed in dust collectors used to estimate dry deposition rates dramatically decreased the PCR detection limit (>3 orders of magnitude, data not shown), and therefore clone libraries could not be constructed from dry deposition samples. Methods used for clone library construction were published elsewhere (Newton *et al.*, 2006). Briefly, we amplified bacterial 16S rRNA genes and their corresponding 16S–23S internal transcribed spacer (ITS) region from DNA using a 20-cycle PCR reaction (Eppendorf Mastercycler) with previously described conditions (Newton *et al.*, 2006). Clone libraries were constructed for each of the rain samples using standard protocols from the Invitrogen Topo TA Cloning® system with TOP10 chemically competent cells and sequenced using the ABI Prism BigDye terminator sequencing kit (PE Applied Biosystems). A single sequencing pass using the 1492R primer (5′-GGTTACCTTGTTACGACTT-3′) was conducted to determine the approximate phylogenetic affiliation of each clone. Sequences were checked for putative chimeras using the program MALLARD (Ashelford *et al.*, 2006), but none were identified. Our rain library was appropriately sampled at *c.* 92% sequence identity based on the full bias corrected chao 1, ace, and bootstrap-based richness estimators (Schloss & Handelsman, 2005).

In order to compare bacterial taxonomic composition of aquatic systems, the atmosphere, and our rain samples, we

compiled previously published 16S rRNA gene sequences from freshwater (Zwart *et al.*, 2002; Newton *et al.*, 2006) and atmospheric samples collected at an urban site in Texas (Brodie *et al.*, 2007) and in rural France (Maron *et al.*, 2005). The review of freshwater bacterial diversity by Zwart *et al.* (2002) included all available 16S rRNA gene sequences from freshwater systems available at the time of publication and is the most current, published metaanalysis of freshwater bacterial 16S rRNA gene sequences. Newton *et al.* (2006) have since conducted a survey of bacterial 16S rRNA gene sequences across the 2002 ice off-season in one of the lakes included in this study (Crystal Bog). The Brodie *et al.* (2007) and Maron *et al.* (2005) 16S rRNA gene sequences were collected from a sample of air from San Antonio in July of 2003 and rural France in March and May of 2003, respectively. Although collected at disparate times and locations, this collection of sequences is expected to represent bacterial 16S rRNA gene sequences typically found in lakes and the atmosphere. All acquired sequences (319 rain, 296 freshwater, and 529 atmosphere) were initially aligned using the FAST_ALIGNER ARB tool (Ludwig *et al.*, 2004) before the alignment was heuristically adjusted using primary and secondary rRNA structure as a guide. The Classifier function of the Ribosomal Database Project II (RDP) (Cole *et al.*, 2007) was used to assign rain, freshwater, and air 16S rRNA gene sequences to the RDP taxonomical hierarchy at the phylum and class levels of resolution.

A suite of phylogenetic analysis tools developed by Schloss and colleagues (Schloss & Handelsman, 2005; Schloss & Handelsman, 2006a, b) was used to make comparisons at finer scales of taxonomic resolution. These tools (DOTUR, SONS, and TREECLIMBER) are based on a pairwise genetic distance matrix. In order to maximize the number of alignment positions used when calculating genetic distances, short and nonoverlapping sequences were removed from the original alignment. The reduced data set was comprised of an alignment that was 562 bp in length (*Escherichia coli* positions 831–1393) containing 310 rain-derived sequences (from this study), 144 freshwater-derived sequences (Zwart *et al.*, 2002; Newton *et al.*, 2006), and 415 atmosphere-derived sequences all from Brodie *et al.* (2007). All characters in the reduced alignment were used to calculate a distance matrix for input into distance-based operational taxonomic units (OTU) and richness determination (DOTUR, Schloss & Handelsman, 2005). DOTUR uses a distance matrix to estimate the number of OTUs corresponding to different levels of sequence identity. The number of OTUs containing rain, freshwater, or both rain and freshwater sequences were recorded from DOTUR output at a broad range of sequence identities. SONS (Schloss & Handelsman, 2006a, b) was used to compare overlap between freshwater, rain, and atmosphere communities using DOTUR output. SONS uses collector's curve extrapolation methods similar to Ace and Chao's richness estimators to predict the proportion of overlap between two or more communities (Schloss & Handelsman, 2006a, b). An additional distance matrix was constructed using the reduced alignment, but was subjected to a 50% base frequency filter with columns containing gaps removed (*c.* 439 resultant positions) in ARB (Ludwig *et al.*, 2004). The filtered distance matrix was used along with TREECLIMBER to determine whether the rain, freshwater, and air sequence libraries share an ancestral community structure (Schloss & Handelsman, 2006a, b). TREECLIMBER estimates a parsimony score from a phylogenetic reconstruction with the tips labeled with their source. How this parsimony score differs from the parsimony scores calculated with randomly assigned sources for each phylogenetic tree tip determines the statistical significance of differences between sampled communities.

Nucleotide sequence accession numbers

16S rRNA gene sequence fragments generated in the current study have been submitted to GenBank under accession numbers EU136733–EU137051.

Results and discussion

Temporal variability in deposition rates may be driven by precipitation

The estimated rates of deposition were two orders of magnitude higher during the first hour of precipitation (*c.* 5.7×10^8 cells $m^{-2} h^{-1}$) than during relatively dry conditions (*c.* 7.3×10^6 cells $m^{-2} h^{-1}$). Our estimates of deposition were significantly higher than previous estimates: dry, 5×10^3 to 2×10^4 CFU $m^{-2} h^{-1}$ (Lindow & Andersen, 1996); and wet, 2.5×10^6 CFU $m^{-2} h^{-1}$ (Lindemann & Upper, 1985). However, the discrepancies are likely because of the underestimation of bacterial cell density from CFU counts. Finally, we found no difference in dry deposition rates between littoral and pelagic sites (*T*-test, $P = 0.24$, $N = 20$) or across lakes (ANOVA, $P = 0.54$, $N = 20$).

At first glance, atmospheric deposition of bacterial cells (wet *c.* 5.7×10^8 cells $m^{-2} h^{-1}$ and dry *c.* 7.3×10^6 cells $m^{-2} h^{-1}$) seems large and would seem to be a significant contribution to bacterial numbers in lakes. However, if we consider our rates of deposition in a mass balance context, atmospheric deposition over a day only represents 0.0001–0.1% of typical planktonic bacterial stock in a lake (*c.* 1×10^{12} cells m^{-3}), depending on lake bathymetry and weather conditions. In addition, bacterial production estimates range from 0.1 to 50 μgC $L^{-1} h^{-1}$ (del Giorgio & Cole, 1998). Using an estimate of bacterial cell carbon content from Bratbak (1985), this corresponds to roughly 8×10^8–4×10^{12} cells m^{-2} day^{-1} (assuming a 1-m-deep epilimnion, Fig. 1). This range encompasses and significantly

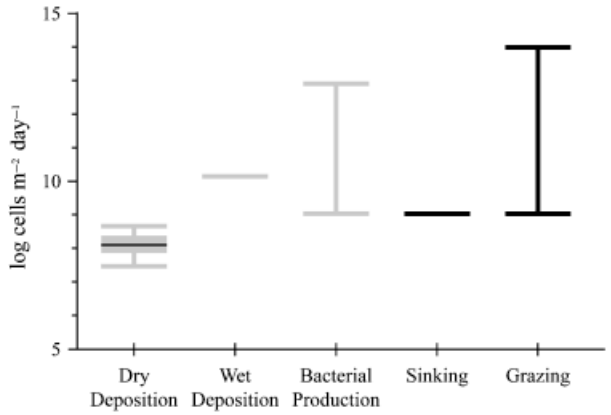

Fig. 1. Potential magnitudes of cell loss and gain to a lake epilimnion. Gray bars indicate gains and black bars indicate cellular losses. Grazing and production are based upon literature values, although reported volumetrically we assume a epilimnetic depth of 1 m for these calculations (Vaque *et al.*, 1994; del Giorgio & Cole, 1998); sinking is an estimate based upon Stokes' law (Nazaroff & Alvarez-Cohen, 2001), and atmospheric deposition rates are from this study. Both sinking and atmospheric deposition are calculated on an areal basis (m^{-2}).

surpasses our estimates of bacterial deposition from the atmosphere, even during rain events. These estimates also approach estimates of contribution from surface water inlet in lakes with theoretical retention times >1 year (Lindstrom *et al.*, 2006). Both estimates of particle sinking flux from the epilimnion of a lake using Stokes' law (*c.* 8×10^8 cells m^{-2} day^{-1}) and empirically determined grazing rates (*c.* 1×10^9 to 1×10^{14} cells m^{-2} day^{-1}, again assuming a 1-m-deep epilimnion) (Vaque *et al.*, 1994) remove equal or greater numbers of cells than we estimate to be deposited from the atmosphere. These data suggest that atmospheric deposition does not represent a significant contribution to bacterial cell concentrations in temperate lakes (Fig. 1), and it is unlikely that bacterial immigration can be conceptualized using a mass-effect perspective (Leibold *et al.*, 2004).

Taxonomic affiliation of bacterial cells deposited in rain

The RDP-defined taxonomic composition of each set of sequences is presented in Fig. 2. *Proteobacteria* dominated the freshwater and rain libraries, whereas the remaining

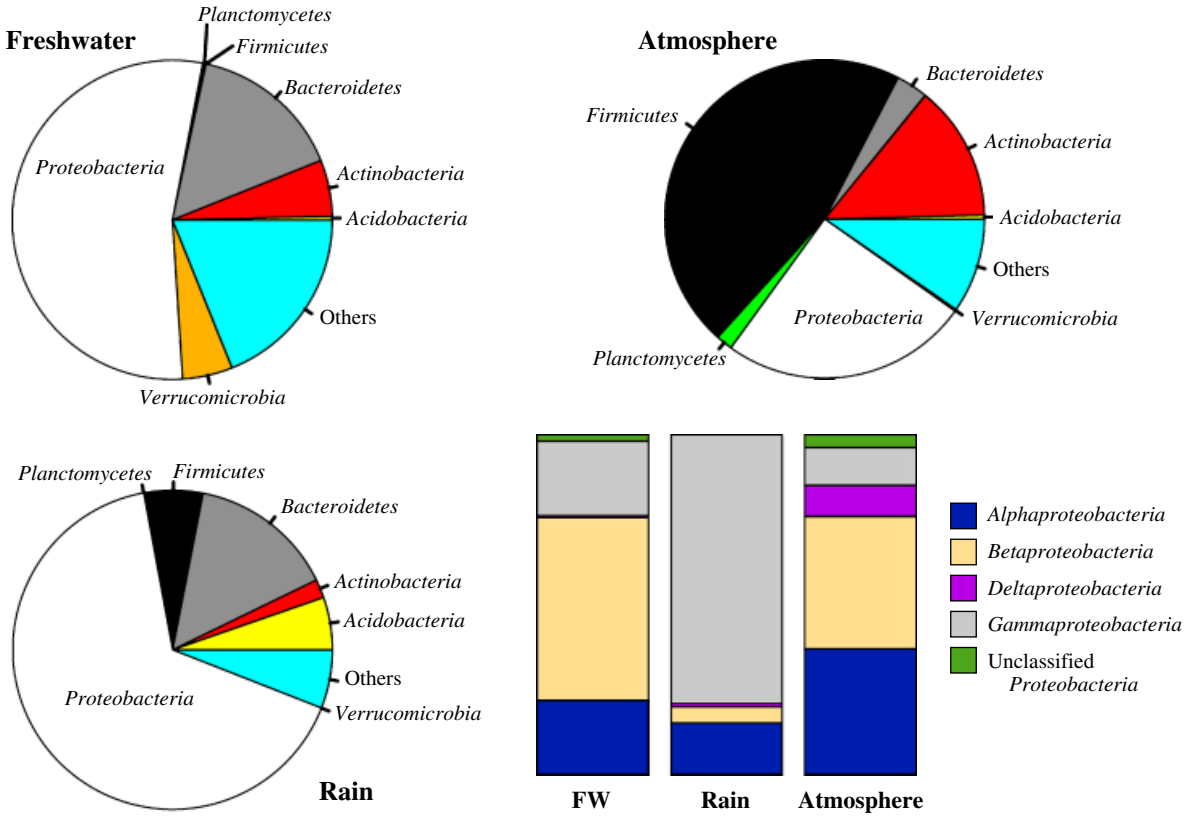

Fig. 2. Taxonomic proportions of clone libraries from published freshwater sequences (Zwart *et al.*, 2002; Newton *et al.*, 2006), published sequences from air in San Antonio, TX (Brodie *et al.*, 2007), and rain at two sites (deciduous-dominated canopy and conifer-dominated canopy). Bars represent proportions of only *Proteobacteria* sequences and colors correspond to the *Proteobacteria* key. All taxonomic definitions are based on the Ribosomal Database Project II (Cole *et al.*, 2007).

Table 1. Output from DOTUR analysis (Schloss & Handelsman, 2005)

DOTUR % identity	Rain OTUs	Atmosphere OTUs	Rain OTUs w/FW	Rain OTUs w/atmosphere	Atmosphere OTUs w/FW
100	213	387	0.00	0.00	0.00
99.5	150	343	0.00	0.00	0.00
99	104	293	0.02	0.01	0.00
97	71	227	0.13	0.02	0.01
95	57	181	0.18	0.03	0.03
90	38	90	0.37	0.15	0.13
85	26	50	0.42	0.29	0.24
80	17	23	0.76	0.54	0.61
70	3	5	1.00	0.60	0.80
67	1	2	1.00	0.50	0.50
61	1	1	1.00	1.00	1.00

The number of OTUs containing rain or atmosphere (Brodie *et al.*, 2007) sequences are reported. The proportion of rain OTUs containing sequences from our freshwater sequence database (FW) (Zwart *et al.*, 2002; Newton *et al.*, 2006) or sequences from the Brodie *et al.* study are also reported. Finally, overlap of the atmosphere and FW OTUs is presented.

sequences were variable in their phylogenetic affiliation, across libraries. The atmosphere library contained a large number of sequences derived from *Firmicute*-related taxa (primarily from the urban site) and *Proteobacteria*-related taxa (mostly from the rural site). Closer inspection of the *Proteobacteria* sequences in each data set revealed strong distinctions in *Proteobacteria* composition across libraries (Fig. 2). The freshwater data set (Zwart *et al.*, 2002; Newton *et al.*, 2006) was dominated by *Betaproteobacteria*, whereas the rain libraries were dominated by *Gammaproteobacteria* and the atmosphere libraries were relatively balanced in their proteobacterial class composition (Fig. 2 and Supplementary Table 1).

Our analysis conducted at a finer taxonomic resolution revealed that the composition of both rain libraries did not contain a large number of sequences traditionally seen in freshwater systems or in the urban atmosphere clone library (Supplementary Table 1). DOTUR revealed that at 99% and 97% identity only *c.* 2% and *c.* 13%, respectively, of the defined rain OTUs contained sequences from our freshwater sequence database (Zwart *et al.*, 2002; Newton *et al.*, 2006). SONS estimated that only *c.* 1% and *c.* 6% of rain OTUs (at 99% and 97%, respectively) would overlap with these freshwater sequences.

TREECLIMBER confirmed the strong distinctions between the rain libraries and the previously published freshwater sequences or atmospheric sequences. It is highly unlikely that the rain libraries and either the freshwater sequences or the San Antonio air sequences came from the same source community ($P < 0.0001$). Estimated parsimony scores well below the random distribution suggested that as yet unidentified factors have differentially structured the freshwater, air, and rain bacterial communities, as characterized in this study. Notably, it is also highly improbable that the two rain libraries (deciduous vs. conifer canopy) came from the same metacommunity ($P < 0.0001$).

The striking differences in the composition of the libraries constructed from bacterial cells deposited during a rain event and previously observed freshwater libraries suggest that atmospheric dispersal of common freshwater bacterial groups may be more limited than perceived previously (Fenchel, 2003; Sloan *et al.*, 2006). This is not to say that freshwater bacterial taxa are precluded from atmospheric transport. However, our comparison does imply that the majority of cells delivered to freshwater bodies via rain are not typically found in the freshwater body itself. This observation was confirmed by Maron *et al.* (2005), who observed bacterial 16S rRNA gene sequences, in their atmosphere samples, that are traditionally associated with soil and plants. The strong differences between the two rain libraries and the San Antonio air sequences also suggest that the taxonomic composition of bacteria deposited from the atmosphere is heterogeneous in space, although this is not surprising. This heterogeneity is likely driven by many factors including land cover differences, regional land use patterns, and weather patterns. Further characterization of bacteria dispersed via the atmosphere and their influence on dynamics in recipient environments is necessary. Our findings suggest that deposition could also vary in magnitude temporally in response to meteorological conditions.

The perception that microorganisms are not limited by dispersal and that immigration is a key component of bacterial population dynamics and distribution is widespread in microbial ecology (Baas Becking, 1934; Fenchel, 2003; Fenchel & Finlay, 2004; Sloan *et al.*, 2006). This perception is based on the small cell size, large population sizes, and apparent ubiquity of bacteria (Fenchel & Finlay, 2004); however, little effort has been made to characterize potential routes of immigration by bacteria. Our initial attempt to quantify rates of bacteria cell deposition and characterize the taxonomic composition of bacteria

deposited in rain suggests that it is unlikely that atmospheric deposition of bacteria strongly influences aquatic bacterial community dynamics. This is not surprising when one considers the success that researchers have had in explaining patterns of change in bacterial communities with chemical, physical, and biological drivers (Simek *et al.*, 2003; Kent *et al.*, 2004; Jones *et al.*, 2008; Shade *et al.*, 2007).

Our study does not disprove the species sorting (Baas Becking, 1934; Leibold *et al.*, 2004) or neutral (Bell, 2000; Hubbell, 2001; Sloan *et al.*, 2006) perspectives of metacommunity theory, but it does suggest that the influence of atmospheric deposition of bacteria relative to within-system interactions is quite small. The relatively small magnitude of cellular deposition and apparent lack of overlap in composition between freshwater bacterial communities and rain-derived bacteria suggest that immigration via the atmosphere may only represent low-level, stochastic variability that is independent of within-system dynamics. We estimated the contribution of wet and dry deposition relative to the growth rate of bacteria in a lake as (deposition rate/growth rate) $\times$ proportion of atmospheric immigrants that are traditionally aquatic. Based on our estimates in this study the relative contribution of atmospheric deposition would range from 4×10^{-8} to 0.09. The low end of this range corresponds to immigration rates during periods with no or low precipitation, high within-system bacterial production, and a stringent definition of bacterial 'species'; the high end represents extreme levels of precipitation with 'species' definitions at low percent identity cutoffs (*c.* 95–97%). Similar estimates for the relative contribution of inlet streams to the bacterial community of lakes in Sweden would range from 0.02 to 0.81 (Lindstrom *et al.*, 2006). These numbers are roughly analogous to the Neutral Theory's m (Hubbell, 2001; Sloan *et al.*, 2006; Woodcock *et al.*, 2007). Woodcock *et al.* (2007) recently estimated m to be 10^{-6} by fitting denaturing gradient gel electrophoresis-based estimates of bacterial community composition in water-filled tree holes to a parameterized version of the neutral model. Although the majority of the assumptions made by the Neutral Theory of Biodiversity are quite controversial, we believe that the immigration term (m) is a useful method for conceptualization of the influence of immigration on recipient bacterial communities. In addition, long-term monitoring of immigrating bacteria via all avenues and within-system bacterial dynamics should be conducted to accurately quantify the relative role of immigration in shaping aquatic bacterial communities.

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References

Ahern HE, Walsh KA, Hill TCJ & Moffett BF (2007) Fluorescent pseudomonads isolated from Hebridean cloud and rain water produce biosurfactants but do not cause ice nucleation. *Biogeosciences* **4**: 115–124.

Ashelford KE, Chuzhanova NA, Fry JC, Jones AJ & Weightman AJ (2006) New screening software shows that most recent large 16S rRNA gene clone libraries contain chimeras. *Appl Environ Microbiol* **72**: 5734–5741.

Baas Becking LGM (1934) *Beobiologie of Inleiding Tot de Milleukunde*. W.P. Van Stockum & Zoon (in Dutch), The Hague, the Netherlands.

Bell G (2000) The distribution of abundance in neutral communities. *Am Nat* **155**: 606–617.

Bratbak G (1985) Bacterial biovolume and biomass estimations. *Appl Environ Microbiol* **49**: 1488–1493.

Brodie EL, DeSantis TZ, Parker JPM, Zubietta IX, Piceno YM & Andersen GL (2007) Urban aerosols harbor diverse and dynamic bacterial populations. *Proc Natl Acad Sci USA* **104**: 299–304.

Cole JR, Chai B, Farris RJ, Wang Q, Kulam-Syed-Mohideen AS, McGarrell DM, Bandela AM, Cardenas E, Garrity GM & Tiedje JM (2007) The ribosomal database project (RDP-II): introducing myRDP space and quality controlled public data. *Nucl Acids Res* **35**: D169–D172.

Crump BC, Hopkinson CS, Sogin ML & Hobbie JE (2004) Microbial biogeography along an estuarine salinity gradient: combined influences of bacterial growth and residence time. *Appl Environ Microbiol* **70**: 1494–1505.

del Giorgio PA & Cole JJ (1998) Bacterial growth efficiency in natural aquatic systems. *Annu Rev Ecol Syst* **29**: 503–541.

Fenchel T (2003) Biogeography for bacteria. *Science* **301**: 925–926.

Fenchel T & Finlay BJ (2004) The ubiquity of small species: patterns of local and global diversity. *Bioscience* **54**: 777–784.

Fenchel T, Esteban GF & Finlay BJ (1997) Local versus global diversity of microorganisms: cryptic diversity of ciliated protozoa. *Oikos* **80**: 220–225.

He FL, Gaston KJ, Connor EF & Srivastava DS (2005) The local-regional relationship: immigration, extinction, and scale. *Ecology* **86**: 360–365.

Horner-Devine MC, Lage M, Hughes JB & Bohannan BJM (2004) A taxa–area relationship for bacteria. *Nature* **432**: 750–753.

Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.

Jones SE, Chiu CY, Kratz TK, Wu JT, Shade A & McMahon KD (2008) Typhoons initiate predictable change in aquatic bacterial communities. *Limnol Oceanogr*, in press.

Kent AD, Jones SE, Yannarell AC, Graham JM, Lauster GH, Kratz TK & Triplett EW (2004) Annual patterns in bacterioplankton community variability in a humic lake. *Microb Ecol* **48**: 550–560.

Kent AD, Yannarell AC, Rusak JA, Triplett EW & McMahon KD (2007) Synchrony in aquatic microbial community dynamics. *ISME J*, In press.

Leibold Ma, Holyoak M, Mouquet N *et al.* (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* **7**: 601–613.

Lindemann J & Upper CD (1985) Aerial dispersal of epiphytic bacteria over bean-plants. *Appl Environ Microbiol* **50**: 1229–1232.

Lindemann J, Constantinidou Ha, Barchet WR & Upper CD (1982) Plants as sources of airborne bacteria, including ice nucleation-active bacteria. **44**: 1059–1063.

Lindow SE & Andersen GL (1996) Influence of immigration on epiphytic bacterial populations on navel orange leaves. *Appl Environ Microbiol* **62**: 2978–2987.

Lindstrom ES & Bergstrom AK (2004) Influence of inlet bacteria on bacterioplankton assemblage composition in lakes of different hydraulic retention time. *Limnol Oceanogr* **49**: 125–136.

Lindstrom ES, Forslund M, Algesten G & Bergstrom AK (2006) External control of bacterial community structure in lakes. *Limnol Oceanogr* **51**: 339–342.

Ludwig W, Strunk O, Westram R *et al.* (2004) ARB: a software environment for sequence data. *Nucl Acids Res* **32**: 1363–1371.

MacArthur RH & Wilson EO (1967) *The Theory of Island Biography*. Princeton University Press, Princeton, NJ.

Maron PA, Lejon DPH, Carvalho E, Bizet K, Lemanceau P, Ranjard L & Mougel C (2005) Assessing genetic structure and diversity of airborne bacterial communities by DNA fingerprinting and 16S rDNA clone library. *Atmos Environ* **39**: 3687–3695.

Martiny JBH, Bohannan BJM, Brown JH *et al.* (2006) Microbial biogeography: putting microorganisms on the map. *Nat Rev Microbiol* **4**: 102–112.

Nazaroff WW & Alvarez-Cohen L (2001) *Environmental Engineering Science*. John Wiley and Sons Inc., New York.

Newton RJ, Kent AD, Triplett EW & McMahon KD (2006) Microbial community dynamics in a humic lake: differential persistence of common freshwater phylotypes. *Environ Microbiol* **8**: 956–970.

Porter KG & Feig YS (1980) The use of dapi for identifying and counting aquatic microflora. *Limnol Oceanogr* **25**: 943–948.

Schloss PD & Handelsman J (2005) Introducing DOTUR, a computer program for defining operational taxonomic units and estimating species richness. *Appl Environ Microbiol* **71**: 1501–1506.

Schloss PD & Handelsman J (2006a) Introducing TreeClimber, a test to compare microbial community structures. *Appl Environ Microbiol* **72**: 2379–2384.

Schloss PD & Handelsman J (2006b) Introducing SONS, a tool for operational taxonomic unit-based comparisons of microbial community memberships and structures. *Appl Environ Microbiol* **72**: 6773–6779.

Segawa T, Miyamoto K, Ushida K, Agata K, Okada N & Kohshima S (2005) Seasonal change in bacterial flora and biomass in mountain snow from the Tateyama Mountains, Japan, analyzed by 16S rRNA gene sequencing and real-time PCR. *Appl Environ Microbiol* **71**: 123–130.

Shade A, Kent AD, Jones SE, Newton RJ, Triplett EW & McMahon KD (2007) Interannual dynamics and phenology of bacterial communities in a eutrophic lake. *Limnol Oceanogr* **52**: 487–494.

Simek K, Hornak K, Masin M, Christaki U, Nedoma J, Weinbauer MG & Dolan JR (2003) Comparing the effects of resource enrichment and grazing on a bacterioplankton community of a meso-eutrophic reservoir. *Aquat Microb Ecol* **31**: 123–135.

Sloan WT, Lunn M, Woodcock S, Head IM, Nee S & Curtis TP (2006) Quantifying the roles of immigration and chance in shaping prokaryote community structure. *Environ Microbiol* **8**: 732–740.

Vaque D, Gasol JM & Marrase C (1994) Grazing rates on bacteria – the significance of methodology and ecological factors. *Mar Ecol Prog Ser* **109**: 263–274.

Whitaker RJ, Grogan DW & Taylor JW (2003) Geographic barriers isolate endemic populations of hyperthermophilic *Archaea*. *Science* **301**: 976–978.

Woodcock S, van der Gast CJ, Bell T, Lunn M, Curtis TP, Head IM & Sloan WT (2007) Neutral assembly of bacterial communities. *FEMS Microbiol Ecol* **62**: 171–180.

Zwart G, Crump BC, Agterveld MPKV, Hagen F & Han SK (2002) Typical freshwater bacteria: an analysis of available 16S rRNA gene sequences from plankton of lakes and rivers. *Aquat Microb Ecol* **28**: 141–155.

Supplementary material

The following material is available for this article online:

Table S1. Operational taxonomic units (OTUs) determined by DOTUR at 97% identity, their Ribosomal Database Project II taxonomic classifications, and relative contributions to both rain clone libraries.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1574-6941.2008.00476.x (This link will take you to the article abstract).

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