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The power of species sorting: Local factors drive bacterial community composition over a wide range of spatial scales

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There is a vivid debate on the relative importance of local and regional factors in shaping microbial communities, and on whether microbial organisms show a biogeographic signature in their distribution. Taking a metacommunity approach, spatial factors can become important either through dispersal limitation (compare large spatial scales) or mass effects (in case of strongly connected systems). We here analyze two datasets on bacterial communities [characterized by community fingerprinting through denaturing gradient gel electrophoresis (DGGE)] in meso- to eutrophic shallow lakes to investigate the importance of spatial factors at three contrasting scales. Variation partitioning on datasets of both the bacterial communities of 11 shallow lakes that are part of a strongly interconnected and densely packed pond system <1 km apart, three groups of shallow lakes ≈100 km apart, as well as these three groups of shallow lakes combined that span a large part of a North-South gradient in Europe (>2,500 km) shows a strong impact of local environmental factors on bacterial community composition, with a marginal impact of spatial distance. Our results indicate that dispersal is not strongly limiting even at large spatial scales, and that mass effects do not have a strong impact on bacterial communities even in physically connected systems. We suggest that the fast population growth rates of bacteria facilitate efficient species sorting along environmental gradients in bacterial communities over a very broad range of dispersal rates.

dispersal limitation | metacommunity biology | microbial biogeography | microbial community | mass effects

Microbial communities may constitute the majority of the earth's biodiversity and catalyze processes that are critical to sustaining life on earth. Understanding the mechanisms that govern their distribution is thus of great interest. There is currently a vivid debate on whether microbial communities share patterns of distribution and diversity similar to those of macroscopic organisms (1–7). The traditional hypothesis among microbiologists, “everything is everywhere, but the environment selects” (8), presumes ubiquity based on the high dispersal rates for microorganisms. This hypothesis has been reinforced by a number of studies in pro- as well as eukaryotic microorganisms that showed the same species or lineage to be present in very different parts of the world (e.g., refs. 9 and 10). However, the results of these studies have been questioned by researchers who claim that insufficient ability to discriminate cryptic taxa may have led to the wrong conclusion that many taxa are cosmopolitan (e.g., ref. 11). In addition, a number of recent studies suggest that some microbial taxa can exhibit geographical isolation and marked biogeographical patterns (3, 12, 13).

Bacterial communities can be locally controlled by a multitude of factors, including habitat size and heterogeneity, ecosystem productivity, biological interactions (competition and predation), and human impact (14–18). If bacteria are ubiquitous because of high dispersal rates, then we expect no differences in community composition in different sites after eliminating the response to environmental variables. This scenario conforms to the model of strong species sorting in a metacommunity framework (19, 20). If, however, bacteria show some dispersal limitation, we expect in addition to the environmental signal a relationship between community composition and location, which may either be due to chance effects or to a biogeographical signal reflecting changes in the regional species pool with distance. Spatial factors may also interfere with the signal of local environmental conditions at the other extreme of the gradient in dispersal rates, however. In very strongly connected habitats, dispersal rates may be so high that they lead to homogenization through mass effects (19). In the metacommunity concept, species sorting results in a matching between the environmental gradients and taxon composition, and is impeded by either too low (dispersal limitation) or too high dispersal rates (mass effects; source-sink dynamics). It follows that it is important to quantify the relative contribution of regional factors (dispersal) and local environmental conditions (species sorting; we here use this term, commonly applied in metacommunity theory, also for bacterial communities, but acknowledge that species delimitation needs other criteria in asexually reproducing prokaryotes than in sexually reproducing taxa) to bacterial community composition over a wide range of spatial scales. To date, only a few studies have investigated the relative influence of geographic distance and habitat factors on bacterial community composition (BCC) (see refs. 6 and 22 for an overview), and none covered an extensive range of spatial scales (e.g., refs. 2, 16, 18, and 21).

Dolan (22), in his review on microbial biogeography, stated that the contrasting patterns and trends observed in different

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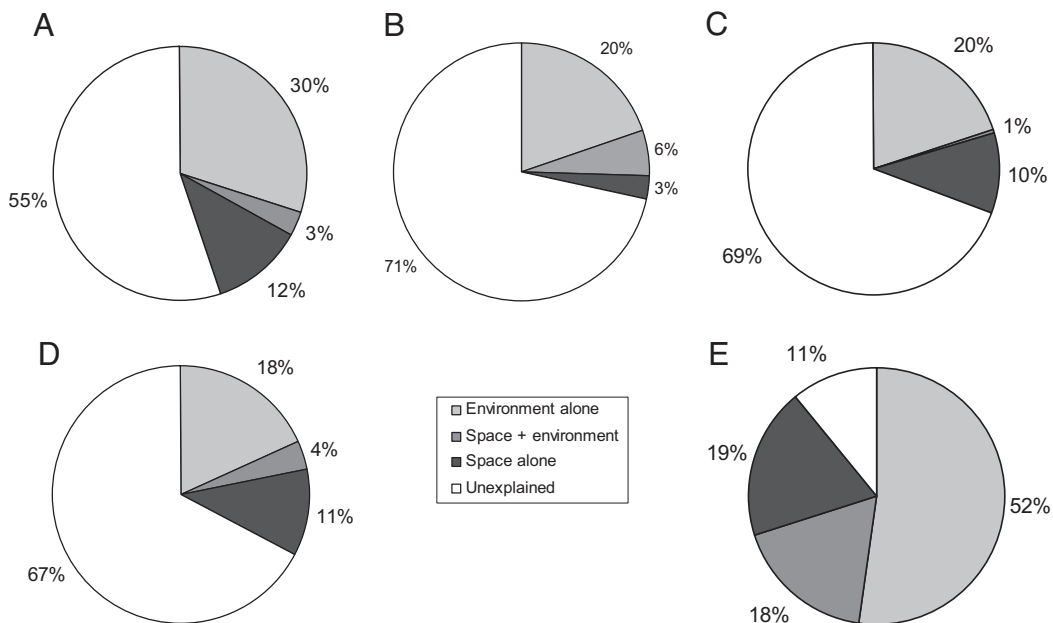


Fig. 1. Variation partitioning of the BCC. Shown are the three regions together (A), Denmark (B), Belgium and the Netherlands (C), Spain (D), and "De Maten" (E).

studies may reflect differences in temporal and spatial scales. He concluded that patterns of biogeography are more likely to emerge in studies that focus on similar habitats across different spatial scales. In the present study, we therefore set out to quantify the relative importance of local environmental factors and spatial distance in two datasets on BCCs of the same habitat type, shallow meso- to eutrophic lakes, collected at widely different spatial scales. A first dataset consists of bacterial communities of 98 lakes located in three geographic regions separated by several hundreds to >2,500 km: 32 lakes in Denmark (DK), 34 in The Netherlands and Belgium (BNL), and 32 in southern Spain (SP) [supporting information (SI) Fig. 2]. This dataset is analyzed at both the regional and the near-continental level. At the regional scale, lakes were on average in DK 23 km separated from each other (range 1–78 km distance among individual lakes), in BNL 97 km (range 0.1–250 km), and in SP 185 km (range 0.2–430 km). The most distant lakes in the combined area DK and BNL are separated 1,060 km; the most distant lakes in the total dataset are separated by 3,100 km. The second dataset consists of bacterial communities of 11 lakes in a strongly interconnected pond system that encompasses 34 small shallow lakes on a total area of <300 ha (SI Fig. 3) (23). We used a 16S rRNA gene-based fingerprinting technique, denaturing gradient gel electrophoresis (DGGE), to determine BCC. The fingerprints consisted of banding patterns, where each band was translated to one operational taxonomic unit (OTU) that was considered as a surrogate of the predominant bacterial "species" present. Our specific goals were to (i) test to which degree geographic distance has an influence on BCC in these two widely contrasting datasets focusing on the same and common habitat category, and (ii) identify the (environmental; spatial) factors that best explain variation in BCC. We take a metacommunity approach (19) as a logical framework to study the impact of local and regional factors.

Results

European Dataset. A total of 107 different operational taxonomic units (OTUs) were detected from the 98 study lakes. Eighty-eight OTUs were recorded in DK, 86 in BNL, and 98 in Spain. The total number of OTUs found in one lake ranged from 11 to 37. Although 85% of the OTUs (94 of 107) were detected in all

three geographic regions, there was a clear overall differentiation in BCC between these regions, confirmed by an analysis of similarities (ANOSIM) test ($r = 0.18$, $P < 0.001$). Pairwise tests revealed significant differences between DK and SP ($r = 0.22$, $P < 0.001$), between BNL and SP ($r = 0.24$, $P < 0.001$), and between DK and BNL ($r = 0.12$, $P < 0.001$). The dissimilarity in BCC tended to be lower between DK and BNL (average dissimilarity: 50%) than between DK and SP (60%), or between BNL and SP (59%).

The results of the similarity percentage (SIMPER) analyses of the transformed abundance identifying the OTUs that contribute most strongly to the dissimilarity between geographic regions are given in SI Table 1; parts of these bands were excised and sequenced. The Spanish samples show a higher average abundance of a member of the Actinomycetes, subgroup *Agrococcus jenesis* (DGGE 67.4), a member of the Bacteroidetes subgroup CL500-6 (DGGE 51.1), and an *Aeromonas* like organism (DGGE 65.8). Conversely, in the DK and BNL lakes, we found a higher average abundance of members of the Actinomycetes subgroup ACK-M1 (DGGE 79.4, 59.8, 52.5, 63.2), Bacteroidetes Cytophaga subgroup (DGGE 39.2), *Phormidium limnetica* (DGGE 37.3), and Alphaproteobacteria LD12 (DGGE 32.9). Bacterioplankton communities in BNL differed from DK mainly because of higher abundance of a member of the alpha-proteobacteria (DGGE: 32.9) and a member of the CFB-group (DGGE: 42.2), and a lower abundance of a member of the genus *Synechococcus* (DGGE: 41.5). Some OTUs showed an abundance gradient from North to South (increasing: DGGE 79.4, 52.5, 39.2, 20.3, 58.0; decreasing: DGGE 50.1, 20.3, 47.8, 65.8, 67.4).

Considering the three regions together in one analysis, variation partitioning between significant environmental variables and spatial location (here limited to a grouping variable indicating what region the lake belongs to) yielded 3% (1% unbiased) of total variance explained by region, 20% (8%) by environmental variables, and 6% (6%) by a common environment-region effect (Fig. 1A and SI Table 2). A large amount of variation (71%, 85% unbiased) remains unexplained in this dataset. The environmental variables that significantly contributed to explain the overall BCC patterns after removal of the region effect were: depth of the lake, pH, total nitrogen concentration (TN), bacterial densities, % *Bosmina*, densities of

heterotrophic nanoflagellates (HNFDENS), biomass of ciliates, % grassland, and % forest (SI Fig. 4A).

Restricting our analysis to DK only, environmental and spatial variables (third order polynomials of projected longitudes and latitudes) explained 31% (10% unbiased) of the total variance. Twenty percent (9% unbiased) of the total variance was explained by pure environmental variables. After removal of environment-related variation, space did no longer significantly explain any variation in the data collected in DK (Fig. 1B and SI Table 2). The environmental variables that significantly explained BCC patterns in the DK lakes were as follows: lake area, TN, biomass of *Bosmina*, total zooplankton (ZOOPTOT) and *Ceriodaphnia*, % Cyanobacteria, and % ultraphytoplankton (SI Fig. 4B).

For the BNL data, variance partitioning between significant environmental variables and spatial variables yielded 12% (6% unbiased) of total variance explained by pure spatial variables, 30% (15%) by environmental variables and 3% (1%) by common effects (Fig. 1C and SI Table 2). The amount of variation not explained by the environmental and spatial variables was 55% (79%). The environmental variables that significantly explained BCC patterns were as follows: lake area, TN, biomass of *Bosmina*, ZOOPTOT, and *Ceriodaphnia*, % Cyanobacteria, and % ultraphytoplankton (SI Fig. 4C). This list of environmental variables that significantly explain variance in BCC in the BNL lakes is identical to that of the DK lakes.

For SP, variance partitioning between significant environmental variables and spatial variables yielded 11% (3% unbiased) of total variance explained by pure spatial variables, 18% (8%) by environmental variables, and 4% (2%) by common effects (Fig. 1D and SI Table 2). A large amount of variation (67%, 87% unbiased) was not explained by the environmental and spatial variables. The environmental variables that significantly explained the BCC patterns were as follows: depth, temperature, HNFDENS, and total coverage of submerged macrophytes (SMTOT) (SI Fig. 4D).

Because of the overlap in environmental variables explaining BCC in BNL and DK, we explored this similarity in detail. First, we calculated Pearson correlations between the relative abundance of taxa and all environmental factors. We observed that for 10 of the 55 taxa (18%), significant correlations were observed with the same environmental variables or combination of environmental variables (SI Table 3). This number increased to 17 (31%) when we relaxed significance criteria of the correlations to 0.1. This pattern was confirmed by our observation that similarity matrices among taxa for their correlations with environmental variables were significantly related between the two regions (Relate function in Primer; $\rho = 0.082$; $P = 0.005$).

De Maten Dataset. A total of 42 different OTUs were detected in the 11 lakes of the strongly connected De Maten system. The number of OTUs per lake varied from 16 to 23. Seven OTUs occurred in all lakes, and represented on average 47% (33–68%) of the relative band intensity in the lakes. The average dissimilarity between the lakes was relatively low (40.7%) and varied between 56% (between lakes 12 and 17) and 11% (between lakes 9 and 10). The turbid lakes 9, 10, 11, and 12 had a similarity in BCC exceeding 80%; their high similarity was mainly due to the presence of the same dominant OTU that made up 21–30% of the relative band intensity and was much less intense in the other lakes (< 6% relative band intensity).

Variance partitioning on this dataset revealed that environmental and spatial variables explained 89% (46% unbiased) of the total variance. Fifty-two percent (36%) of the total variance was explained by pure environmental variables. After removal of environment-related variation, spatial configuration did no longer significantly explain any variation (Fig. 1E and SI Table 2). The environmental variables that significantly explained the

BCC pattern in the De Maten lakes were transparency (Sneller depth), pH, conductivity, biomass of dinoflagellates, and biomass of calanoid copepods (SI Fig. 4E).

Discussion

At the largest spatial scale, we observed a differentiation in BCC among geographic regions. This differentiation is strongest between the Spanish lakes and the lakes of the more northern regions (DK and BNL). There are several factors that may account for this among-region effect. One possible explanation is that regional differences in BCC reflect the biogeography of bacteria, implying that there would be a certain amount of historical contingency impacting bacterial distribution patterns, similar to the patterns observed for multicellular organisms. Rather than every species potentially being everywhere, the array of taxa that may colonize a given patch would then be confined to a more regional taxon pool. Alternatively, the patterns observed in our study may reflect regional differences in environmental conditions, either not measured in our study or confounded in spatial differences. Several lines of evidence suggest that the latter explanation is more likely than a biogeography mediated by dispersal limitation. First, as >85% of the detected bacterial OTUs were found in all three studied regions, we can conclude that the majority of freshwater bacterial taxa are not confined to a subset of regions at this geographical scale (<3,000 km). It is therefore unlikely that a strong biogeography effect plays an important role in determining the BCC at a given location. Second, when environmental variables were taken into account, geographic distance alone explained only a very low percentage of the total variation (3%). Our data thus suggest that lakes with similar environmental characteristics have similar bacterial communities regardless of geographic distance. This observation is strongly supported when we focus on BNL and DK only, two regions for which the lakes in general are ecologically more similar than when the Spanish lakes are included (24). For the datasets of DK and BNL, the same set of environmental variables is selected as significantly impacting BCC in local lakes. Our observation that the pattern of correlations of the relative abundance of almost 20% of the taxa is significantly related among these two regions suggests that a significant part of the BCC of lakes in the combined area (covering a distance of >1,000 km) is structured in a similar way by the environment. Given that our analysis captures only part of the relevant environmental factors (e.g., not including sources of DOM, the major food source of the bacteria), this observation is striking. Overall, our data thus suggest that the two regions basically share the same regional taxon pool. The BCC of the lakes in SP did show appreciable differentiation from that of DK and BNL, but the same holds for the ecology of the lakes (24).

Our observations on the wide distribution of bacterial taxa are in agreement with the finding of Yannarell and Triplett (16), who observed differences in bacterial communities between northern and southern Wisconsin lakes, but also found that most of the bacterial taxa were distributed state-wide. Fierer and Jackson (25) came to the same conclusion in their study on the biogeography of soil bacterial communities, covering 98 soil samples from across North and South America. These studies and our study suggest that the distribution of bacterial taxa is not strongly limited by dispersal even at relatively large spatial scales [up to several thousands of km, i.e., spatial scales at which the influence of both historical contingencies and contemporary ecological factors on microbial biogeography are most likely to be detected (6)]. Our results further agree with Horner-Devine *et al.* (2), who found that the taxa-area relationship for bacteria in salt marsh sediments was driven primarily by environmental heterogeneity, which increased with increased area considered, rather than by geographic distance itself.

Dolan (22) suggested that a signature of biogeography would more likely emerge in studies that focus on similar habitats across space. A key feature of our study is that similar lake types were selected across all spatial scales. All studied lakes were shallow and meso- to eutrophic, and they were selected to fit into 16 categories comprising all combinations of large/small, connected/isolated, relatively low versus relatively high potential productivity, and absence/presence of macrophytes in the three regions studied. This sampling design ensured that very similar lakes were selected in the different regions, although this strategy worked better for BNL and DK than for SP (24). Even though this sampling design made our study ideally suited to detect a signature of biogeography (22), no strong effect of geographic distance was detected. Although there are some recent reports demonstrating that dispersal limitation may occur at large spatial scales for some microbial organisms (12), the environments involved were extreme and isolated, and may thus perhaps not be representative of typical and common surface water categories (rivers and rivulets, ditches, ponds, and lakes). In rare and more isolated habitat types, one is more likely to detect dispersal limitation, as dispersal rates are also a function of the amount and size of source populations. Our results are indeed not incompatible with the idea that a subset of bacterial taxa may be more strongly dispersal limited. Rather, they suggest that the majority of taxa present in natural bacterial communities seem to be very widely distributed.

At the other extreme of the spatial spectrum, we show a much higher association of BCCs with environmental factors in the studied interconnected pond system than with spatial factors. These results are in contrast with Reche *et al.* (21), who found that the location of water bodies in the Sierra Nevada influenced bacterial communities and that BCCs of nearby lakes showed more similar OTU compositions. They argued that this pattern is due to recolonization of a lake by microorganisms from adjacent lakes being more frequent than from more remote lakes. Similarly, Lindström *et al.* (18) showed that BCC of lakes with a residence time <100 days showed a signature of mass effects, reflected by similarity of BCC of the lake community with that of the inlet. The discrepancy between these studies and ours may lie in the fact that we studied meso- to eutrophic systems, in which species replacements are expected to occur faster (i.e., more efficient species sorting) than in oligotrophic systems.

In the framework of metacommunity theory (19), dispersal rates play a key role in determining patterns of community similarities among habitat patches. Very low dispersal rates can lead to dispersal limitation, resulting in purely spatial biogeography patterns. Very high dispersal rates can lead to mass effects, with taxa also occurring in less suitable habitats because of continuous supply. Mass effects thus also lead to purely spatial effects and a reduction of the match between the occurrence of specific OTUs and environmental conditions. Intermediate dispersal rates provide the best conditions for environmental factors to determine community composition, as there is a sufficient supply of taxa from the regional species pool to fuel species sorting, whereas there is no blurring of the resulting differences in community composition by mass effects. In this gradient of environmental connectedness, the impact of environment is thus highest at intermediate dispersal levels. In the case of mass effects, one may anticipate that the impact of spatial factors is more pronounced at relatively small spatial scales, whereas the impact of spatial factors is expected to increase with geographical scale in the case of dispersal limitation. Our data suggest that BCCs comply to the scenario of species sorting, suggesting intermediate dispersal rates when scaled to the efficiency of species sorting along environmental gradients. Intriguingly, our data suggest that this strong species sorting occurs at the near-continental (European) scale as well as at the

within-regional and local scale. This finding suggests that dispersal rates at a scale of >1,000 km are still for most taxa high enough to allow species sorting to lead to a good association between BCC and environmental variation, while at the same time dispersal rates at a local scale of interconnected systems are not so high as to result in strong mass effects. At the intermediate scale, a very high impact of species sorting is observed. In the region with the smallest inter-lake distances (DK), the impact of spatial factors was indeed not significant when environmental differences are taken into consideration. Importantly, in the above, the dispersal gradient has to be viewed relative to the strength and rates of species sorting. Indeed, if species sorting is very efficient and rapid, dispersal rates must be very high to result in mass effects (e.g., ref. 26). It follows that our data strongly suggest that species sorting in bacterial communities is very efficient, at least in the meso- to eutrophic systems studied, so that bacterial communities track environmental conditions even in the presence of very high immigration rates of bacterial taxa from other sources. Similarly, their very high population growth rates make BCCs largely independent of the amount of propagules that arrive in the focal habitat, extending the range of actual dispersal rates over which species sorting can strongly impact BCC to the lower end of the spectrum. Our results thus suggest that species sorting in BCCs is very efficient at both very low and very high dispersal rates. This efficiency of space sorting is most likely due to the extremely high population growth rates of bacteria. Several studies that focused on the dynamics of BCCs in local habitats have indeed reported that bacterial communities can rapidly track changes in the environment (14, 27–31).

Conclusion

Our results provide strong evidence that species sorting in response to local environmental factors is a key determinant of the taxon composition of aquatic bacterial communities over a very broad range of spatial scales (<100 m to >1,000 km). The main factors controlling bacterial community composition were resources (TN) and grazing-related factors (e.g., zooplankton biomass). We argue that species sorting is so important in bacterial communities because the high population growth rates of bacteria largely uncouple local population dynamics and relative abundances of taxa from dispersal rates. In combination with sufficiently high dispersal rates to allow colonization of distant habitats, these high population growth rates lead to a weak biogeographical signal. Bacterial taxa need not be everywhere at all times to yield the observed pattern: it is sufficient that low but sustained or regular dispersal is coupled with very efficient tracking of environmental conditions through local population dynamics. The high population growth rates of microbial organisms in this way result in a much broader range of spatial scales over which species sorting plays a predominant role in shaping community structure than in many macroorganisms. The power of species sorting in microbial communities thus does not only reflect high dispersal rates, but rather the interplay of sufficiently high dispersal rates (caused by small size, production of resistant stages, and vast population sizes) and efficient tracking of environmental changes due to fast population growth rates. This framework explains metacommunity structure of microorganisms using the same mechanisms as in macroorganisms, and has in our opinion the potential to reconcile the two opposing viewpoints on the occurrence of biogeographical signals in microbial communities. It predicts that the biogeographical signal for many microorganisms is much weaker than for most macroorganisms because of the fact that long distance dispersal is more likely combined with a strong capacity to establish viable populations when environmental conditions allow. It also predicts that biogeographical signal is likely to be stronger in microorganisms inhabiting rare habitats. Both predictions are in line with current observations (e.g., ref. 12).

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