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ORIGINAL ARTICLE

Temporal variation of β-diversity and assembly mechanisms in a bacterial metacommunity

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The turnover of community composition across space, β-diversity, is influenced by different assembly mechanisms, which place varying weight on local habitat factors, such as environmental conditions and species interactions, and regional factors such as dispersal and history. Several assembly mechanisms may function simultaneously; however, little is known about how their importance changes over time and why. Here, we implemented a field survey where we sampled a bacterial metacommunity consisting of 17 rock pools located at the Swedish Baltic Sea coast at 11 occasions during 1 year. We determined to which extent communities were structured by different assembly mechanisms using variation partitioning and studied changes in β-diversity across environmental gradients over time. β-Diversity was highest at times of high overall productivity and environmental heterogeneity in the metacommunity, at least partly due to species sorting, that is, selection of taxa by the prevailing environmental conditions. In contrast, dispersal-driven assembly mechanisms were primarily detected at times when β-diversity was relatively low. There were no indications for strong and persistent differences in community composition or β-diversity between permanent and temporary pools, indicating that the physical disturbance regime is of relatively minor importance. In summary, our study clearly suggests that there are temporal differences in the relative importance of different assembly mechanisms related to abiotic factors and shows that the temporal variability of those factors is important for a more complete understanding of bacterial metacommunity dynamics.
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Introduction

Understanding the distribution and abundance of species, how they vary across spatial and temporal scales and the factors that control them are fundamental objectives of ecological research. β-Diversity, that is, the turnover of community composition over space and time, varies along environmental gradients, such as productivity (Chase and Leibold, 2002; Chase and Ryberg, 2004), environmental heterogeneity (Chase, 2003; Mouquet *et al.*, 2006; Verleyen *et al.*, 2009), disturbance regime (Chase, 2007; Jiang and Patel, 2008; Vanschoenwinkel *et al.*, 2010) and depends on dispersal or connectivity among patches (Chase, 2003; Mouquet and Loreau, 2003; Verleyen *et al.*, 2009).In general, β-diversity can be influenced by local within-habitat factors, such as environmental conditions or species interactions, as well as regional factors that are related to dispersal from a regional species pool to the local community (Ricklefs, 1987). These factors are integrated into the metacommunity framework (Leibold *et al.*, 2004), which includes four perspectives that differ with regard to the importance that they allocate to the local environment, dispersal and stochasticity. First, the neutral perspective assumes that community assembly is stochastic and regulated by random dispersal, colonisation, speciation and extinction events that operate among functionally equivalent species (Hubbell, 2001). Second, the patch dynamics perspective presumes that community composition is a result of regional colonisation–extinction dynamics among homogeneous patches. Third, the species sorting perspective assumes that local environmental conditions primarily influence community composition, whereas, fourth, under the mass effect perspective, possible effects of local environmental conditions are outweighed by high dispersal rates so that even suboptimally adapted species can exist in local patches due to frequent and high dispersal rates.

Methodological advances during the last three decades have greatly increased our understanding of diversity and turnover of natural bacterial communities (Øvreas, 2000; Dorigo *et al.*, 2005) and also, more recently, about the underlying assembly

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mechanisms (Lindström and Langenheder, 2011). It has been shown that bacterial communities can be assembled by species sorting (Beisner *et al.*, 2006; Van der Gucht *et al.*, 2007; Logue and Lindström, 2010) as well as mass effects (Lindström *et al.*, 2006; Crump *et al.*, 2007). It has also been demonstrated that frequency and abundance distributions in bacterial communities are, and often to a considerable extend, consistent with the neutral model (Sloan *et al.*, 2006; Woodcock *et al.*, 2007; Drakare and Liess, 2010; Östman *et al.*, 2010). More recently, it has also become clear that several mechanisms co-occur and that communities are, for example, at the same time structured by species sorting and neutral processes (Ofiteru *et al.*, 2010; Langenheder and Szekely, 2011).

Even though the prevalence of different assembly mechanisms should result in differences in β-diversity along spatial, temporal and environmental gradients, this link has not been clearly established, in particular not in the case of bacterial communities. It is also not known how assembly mechanisms within the same region or metacommunity change over time and how this affects β-diversity. As there are temporal changes in bacterial communities, including patterns of seasonal reoccurrence and synchrony (Fuhrman *et al.*, 2006; Kent *et al.*, 2007; Crump *et al.*, 2009), it seems reasonable to presume that the same should also be the case for the actual mechanisms assembling communities.

A suitable study system to address these questions, in particular for organisms with short generation times, are small island-like habitats (Srivastava *et al.*, 2004), as they combine the advantages of small sizes and clear boundaries but are still exposed to natural environmental variance, openness and realistic species combinations. Here, we work with rock pools, that is, water-filled bedrock depressions, which constitute small, semipermanent, discrete entities embedded in a landscape of rocks close to the sea. They show high levels of environmental heterogeneity, both temporally and spatially due to weather conditions, distance to the sea and distance to other rock pools. A total of 17 pools in a small area of $\sim 600\,m^2$ (Figure 1) were sampled 11 times during 1 year, and for each occasion we studied local environmental variables, the degree of β-diversity in the bacterial metacommunity and tested the significance of species sorting versus spatial effects using variation partitioning (Borcard *et al.*, 1992; Legendre, 2008).

The major aim of this study was to investigate whether bacterial communities may be structured by different assembly mechanisms over time and to what extent three factors, productivity, environmental heterogeneity and disturbance regime, which have been shown to be important regulating factors of β-diversity and assembly mechanisms in larger organisms (Chase, 2007, 2010; Verleyen *et al.*, 2009; Vanschoenwinkel *et al.*, 2010), drive temporal dynamics in β-diversity and assembly mechanisms. More specifically, we investigate (1) whether β-diversity changes over time along gradients of productivity and environmental heterogeneity, (2) whether these changes can be linked to differences in the underlying assembly mechanisms, in particular species sorting compared with dispersal-driven mechanisms, and (3) whether β-diversity will be lower in systems frequently exposed to physical disturbances such as droughts.

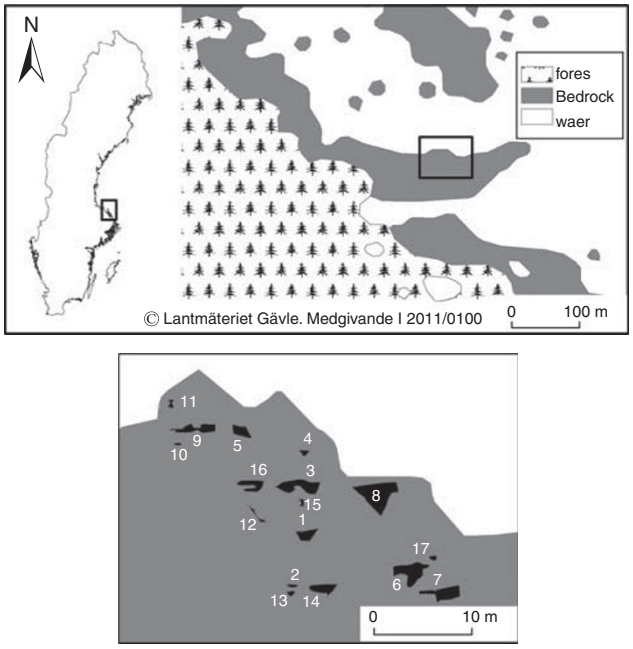

Figure 1 Maps of the sampling area.

Materials and methods

Field sampling

The sampling site was located on the island of Gräsö close to the Baltic Sea Coast in Uppland, Sweden (60°29.910′N, 18°25.768′E). All pools were located within an area of $600\,m^2$ (Figure 1). The average elevation above sea level was 0.81 m (range: 0.2–1.35 m) and the distance to the coast ranged between 1 and 20 m. During the period between June 2008 and June 2009, 17 rock pools were sampled at 15 occasions out of which 11 were selected for this study to avoid time points at which approximately half of the pools had dried out (see below). We refer to this set of pools as the metacommunity or region and each of the individual pools as localities or habitats in the manuscript. Sampling points (as shown in Supplementary Figure S1) were selected to reflect seasonal differences, starting in summer 2008 when pools had been refilled after a prolonged drought period and proceeded during summer and autumn until the pools froze rock-solid for ~4 months. In 2009, sampling covered the period from ice break-up in early spring to mid-summer. Sampling was

conducted more frequently during summer 2008 to cover large environmental fluctuations occurring as a result of two drought periods. At some sampling occasions, a few pools were dried up or partly frozen and snow covered, but at all selected sampling points at least 75% of all pools were filled with water (Supplementary Table S1). Eight of the pools (pools 1–8) were permanent and never dried out during the entire sampling period, whereas the remaining nine pools (pools 9–17) were temporary and dried at least once. At each sampling occasion, we measured a number of environmental parameters and determined bacterial community composition (see below).

Salinity was measured using a WTW Conductometer (Cond 3210) with a TetraCon 325/C measuring cell (WTW, Weilheim, Germany), and temperature, maximum length, width and depth were recorded for each pool. A 2-l water sample was collected in a rinsed polyethylene bottle and transported back to the laboratory in cool boxes at approximately *in situ* water temperatures. Upon return, samples were immediately processed further for subsequent analysis of chemical parameters and bacterial community composition. Zooplankton ($>250\,\mu m$), derived from volumes ranging between 0.3 and 6 l depending on pool size and zooplankton density were preserved with 70% ethanol. Subsequently, the samples were counted under a dissecting microscope. Total phosphorus, chlorophyll a and absorbance were analysed as described earlier (Langenheder and Ragnarsson, 2007). Additionally, samples of up to 500 ml water were filtered onto 0.2 μm Polysulfone filters and stored at $-80\,^{\circ}C$ until subsequent nucleic acid extraction. The geographic position of the pools was recorded using a geographic positioning system unit and a total station (Geodimeter 600, Trimble, Sunnyvale, CA, USA).

Bacterial community composition was determined by using terminal-restriction fragment length polymorphism analysis. DNA was extracted using the Power Soil DNA Isolation Kit (MO BIO, Carlsbad, CA, USA) and the *16S rRNA* gene amplified by PCR using the HEX-labelled bacterial forward primer 341f and the reverse universal primer 805R and the PCR conditions described in Langenheder and Szekely (2011), with the exception that we used the Biotaq DNA polymerase (Bioline, London, UK) for this study. Approximately 40 ng of PCR products was then digested with the restriction enzyme *Hae*III as described earlier (Langenheder and Ragnarsson, 2007). Terminal-restriction fragment length polymorphism electropherograms were analysed using GeneMarker v1.70 (Soft Genetics, State College, PA, USA) using the settings described by Logue and Lindström (2010). Peaks that were not detected in each of two replicate samples were deleted and the data were normalised for differences in total signal intensity between different samples by including only peaks that accounted for $\geqslant 0.5\%$ of total signal intensity. This made sure that the results were not biased by differences in peak number related to variations in total signal intensity between samples. After this procedure, the number of operational taxonomic units varied between 7 and 22 (average: 13 ± 3.5) between individual samples and 32 and 62 (average: 47 ± 8.4) between sampling points, respectively. The produced list of operational taxonomic units and their relative abundances was used for the statistical analyses described below.

Statistical analyses

For each sampling point, we calculated β-diversity as the mean of all pairwise Bray–Curtis dissimilarities, based on the relative abundances of operational taxonomic units obtained by terminal-restriction fragment length polymorphism. β-Diversity was calculated for the entire metacommunity, as well as separately for permanent and temporary pools at each sampling point. To estimate differences in environmental heterogeneity at the different sampling points, we first calculated the coefficients of variation (CVs) of several environmental parameters, that is, determined the extent to which values measured in individual pools deviated from the mean at a given sampling point. This was done for five environmental parameters (total phosphorus concentration, absorbance, chlorophyll a concentration, salinity and *Daphnia* concentration), which were selected based on results from a previous study (Langenheder and Ragnarsson, 2007). Then, we used the CVs in a principal component analysis to obtain one composite number that reflects the total environmental heterogeneity in the metacommunity at each sampling point. For this, we used the scores of the first principal component (PC1), which explained 88% of the total variation. *Daphnia* concentration was the variable that was most strongly correlated to PC1.

To test our hypotheses with regard to how β-diversity varied over time, in particular seasonally, and with productivity and environmental heterogeneity, Spearman's rank order correlations were performed between β-diversity and temperature, total phosphorus concentrations (which we use as an estimator of productivity) and environmental heterogeneity (calculated as described above), respectively. Pairwise correlations between the three environmental factors were in all cases positive, but not significant. Moreover, we calculated correlations between β-diversity and the mean and CVs of all other environmental parameters mentioned earlier, that is, salinity, absorbance, chlorophyll a and *Daphnia* abundance. Finally, we implemented non-metric multidimensional scaling analysis and analysis of similarities based on Bray–Curtis similarities using the PAST software package (Hammer *et al.*, 2001) to investigate whether there were differences in community similarity among permanent and temporary pools, respectively.

To study more specifically which assembly mechanisms determine community composition at

different time points, we applied redundancy analysis to determine the amount of variation in community composition among pools that can be explained by local environmental and spatial variables. If communities are solely significantly shaped by environmental factors, but not spatial factors, this will indicate species sorting. If, on the contrary, only spatial but not environmental factors are significant, this indicates that dispersal driven mechanisms, such as neutral processes, patch dynamics or mass effects, are important. Initially, the relative operational taxonomic unit abundance data were Hellinger transformed (Legendre and Gallagher, 2001). Environmental parameters that were included in the model were also here salinity, total phosphorus concentration, absorbance, chlorophyll a and *Daphnia* abundance, and they were normalised by log transformation and standardised by *Z*-score transformations (Leps and Smilauer, 2003). Spatial variables were derived from XY co-ordinates using the principal coordinates of neighbour matrices procedure (Griffith and Peres-Neto, 2006) to ensure that we included all spatial scales that can be detected in the data set as predictor variables in the statistical models (Borcard and Legendre, 2002). Four eigenvectors with positive eigenvalues could be extracted and were used together with elevation as spatial predictors. Redundancy analyses were implemented using CANOCO 4.5 (Biometrics, Wageningen, The Netherlands) and the settings described earlier (Langenheder and Ragnarsson, 2007). We implemented a forward selection procedure according to Blanchet *et al*. (2008) to select a sub-set of environmental [E] and spatial [S] variables out of the entire set of available predictors. We further used variation partitioning (Borcard *et al*., 1992) to determine how much of the variation in bacterial community composition could be attributed to [E] and [S]. In all models, significance testing was done with 999 Monte Carlo permutations under the reduced model and all $\bar{R}^2$ values were calculated and adjusted as described by Peres-Neto *et al*. (2006). We started by testing whether [E] and [S] contributed significantly to the explanation of variation in community composition among local communities. In cases where both, [E] and [S], were significant, the variation was further partitioned using partial redundancy analysis to account for possible co-variation between environmental and spatial variables (Peres-Neto *et al*., 2006; Langenheder and Ragnarsson, 2007). For this, we calculated the fractions [E|S](pure environmental variation), [S|E](pure spatial variation) and [S∩E] (shared variation).

Results

β-Diversity was relatively high during summer 2008 and declined during autumn and early spring 2009, before it increased to similar values as during summer 2008 (Figure 2). This temporal pattern was reflected in positive Spearman's rank correlations between β-diversity and phosphorus concentration ($\rho_s = 0.745$, $P = 0.0068$), temperature ($\rho_s = 0.636$, $P = 0.0321$) and environmental heterogeneity ($\rho_s = 0.554$, $P = 0.065$), with the latter not being significant. With the exception of a significant positive correlation between β-diversity and chlorophyll a concentrations ($\rho_s = 0.745$, $P = 0.0068$), correlations to average values of other environmental parameters (absorbance, *Daphnia* concentration and salinity) were much weaker and not significant. Moreover, there were no significant correlations between β-diversity and the variability, that is CVs, of any of the environmental variables.

Redundancy analysis revealed that environmental variables had significant effects on bacterial community composition at 7 out of the 11 investigated time points (Supplementary Table S2) and they explained 7–22% of the total variation in community composition. In all these cases, only environmental effects but not spatial effects were significant, identifying species sorting as the predominant assembly mechanism (Figure 4, Supplementary Table S2). Species sorting was frequently found during summer 2008 when β-diversity was high but less common during the remaining study period (Figures 2 and 4). Spatial factors were significant and explained variation in community composition at two sampling points in autumn 2008 (11–18%), one in spring 2009 (20%) and one in summer 2009 (7%). Interestingly, β-diversity was comparably low at these occasions (Figures 2 and 3). At the sampling point during ice break-up in spring 2009, neither environmental nor

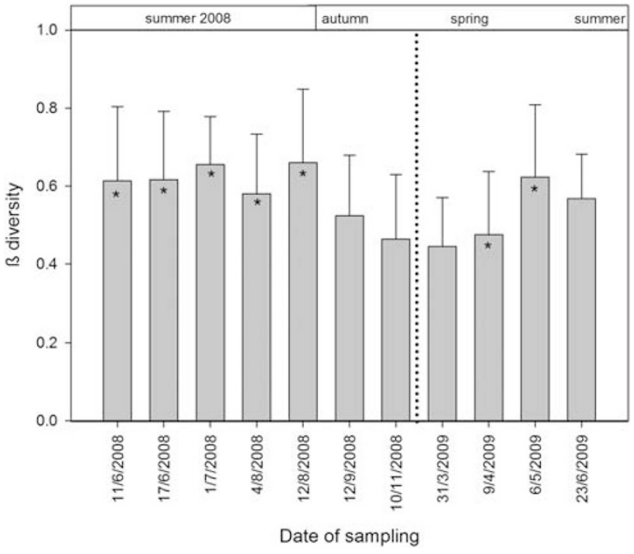

Figure 2 β-Diversity (mean ± s.d.) in the rock pool metacommunity at different sampling points. The dashed vertical line indicates that there was a winter break in the sampling scheme when pools froze rock-solid approximately between December 2008 and the end of March 2009. The symbol '*' indicates time points at which significant species-sorting processes were observed.

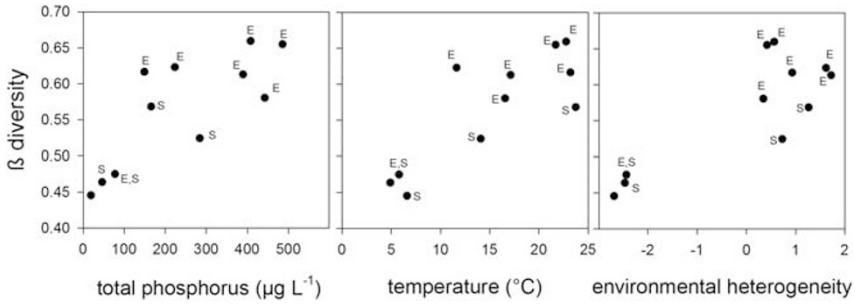

Figure 3 Changes in β-diversity in relation to total phosphorus concentration, temperature and environmental heterogeneity at different sampling points. For each sampling point, β-diversity was calculated as the average Bray–Curtis dissimilarity of pairwise comparisons of all pools in the metacommunity. Environmental variability refers to the PC1 scores of a principal component analysis using the CVs of five environmental parameters (see Material and methods for details). Each point represents 1 out of 11 sampling points. 'E' and 'S' indicate significant effects of environmental and spatial factors in the redundancy analysis, respectively. 'E' indicates that communities are structured by species sorting and 'S' indicates that they are structured by dispersal-related assembly mechanisms. Note that pairwise correlations between the three environmental factors were generally positive, but not significant.

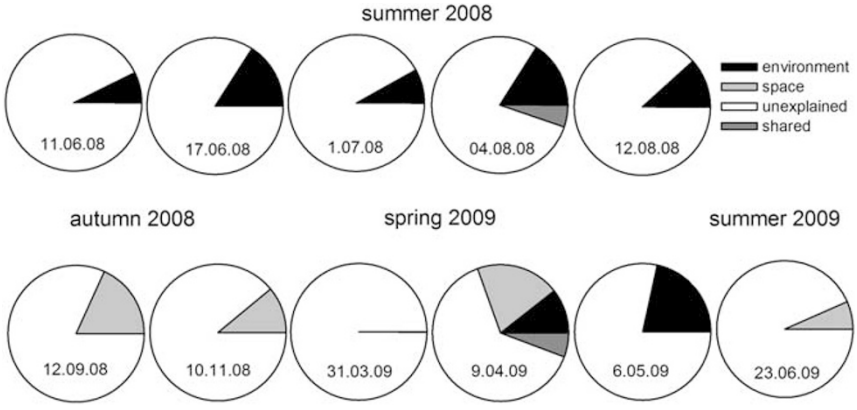

Figure 4 Fractions of the total variation in community composition at the different sampling points that could be explained by environmental and spatial factors as determined by redundancy analysis. The prevalence of significant environmental factors indicates that communities are structured by species-sorting processes.

spatial factors could significantly explain any of the variations in community composition between pools (Figure 4).

There were no apparent differences in community composition between permanent and temporary pools at the majority of sampling occasions (Supplementary Figure S2). Significant differences were, however, found at the first sampling point in June 2008 (analysis of similarities, $R = 0.512$, $P = 0.0001$) and at two sampling occasions in spring 2009 (analysis of similarities, 9 April 2009: $R = 0.1814$, $P = 0.04$; 6 May 2009: $R = 0.194$, $P = 0.035$). β-Diversity among permanent and temporary pools was similar at all time points.

DISCUSSION

This study shows that there are temporal differences in β-diversity as well as the underlying assembly mechanisms in a bacterial metacommunity. At sampling occasions with the highest β-diversity (Bray–Curtis dissimilarities ~0.6), a significant amount of variation in community composition among pools was explained by environmental factors, hence indicating that species-sorting processes were important. In contrast, significant effects of spatial factors, which may indicate a stronger importance of dispersal-driven community assembly mechanisms, such as neutral processes, patch dynamics or mass effects (Cottenie, 2005), were mostly detected at sampling points when β-diversity was relatively low. This suggests that species sorting and/or the absence of strong dispersal-driven assembly mechanisms often lead to high levels of β-diversity in the metacommunity.

We found that β-diversity was positively related to average phosphorus concentration, temperature and environmental heterogeneity in the metacommunity at the time of sampling, reflecting the congruent temporal dynamics of these environmental variables and their simultaneous effects on β-diversity. However, significant correlations were only observed between β-diversity and total phosphorus

concentration and temperature, that is, parameters that can be related to productivity, but not between β-diversity and environmental heterogeneity, indicating that the latter was relatively less important. Further to this, a significant positive correlation was also found between β-diversity and chlorophyll a concentration, that is, an estimator of the biomass of primary producers, further supporting that the positive β-diversity—productivity relationship was the most prevailing pattern in our study. An increase in β-diversity with increasing productivity is frequently observed in nature as well as in experiments (Chase and Leibold, 2002; Chalcraft *et al.*, 2008; Ptacnik *et al.*, 2010), and previous studies have also shown that regions or metacommunities with higher environmental variability have higher β-diversity (Verleyen *et al.*, 2009) and lower degrees of regional invariance (Östman *et al.*, 2010). Here, we show that similar patterns are found within a single bacterial metacommunity over time. Significant species sorting was observed at all sampling points with the highest productivities (Figure 3), suggesting that it contributed to the high levels of β-diversity (but see discussion below). The relationship between β-diversity and environmental heterogeneity was rather multifaceted. β-Diversity was lowest at the lowest end of the environmental heterogeneity gradient; however, at the high end of the gradient, β-diversity varied considerably (Figure 3). Interestingly, significant species-sorting processes could be detected at high environmental heterogeneity only when β-diversity was relatively high, whereas spatial factors were significant when it was comparably low. This indicates that not only species sorting but also dispersal-driven assembly mechanisms can be found during times when the environmental variability in a metacommunity is high. Moreover, species sorting was not limited to periods of high environmental heterogeneity and productivity, but also found when those factors were relatively low. Thus, an important conclusion from this study is that species sorting is an important assembly mechanism frequently, but not always and not exclusively, found at high productivity and environmental heterogeneity.

Several mechanisms have been suggested to explain positive relationships between productivity and β-diversity. One possibility is that a region with an on average higher productivity could have a higher variation in productivity among locations, which in turn might lead to stronger species-sorting processes in relation to differences in productivity among sites (Chase and Leibold, 2002). However, in congruence with previous studies on larger organisms (Chase and Leibold, 2002; Harrison *et al.*, 2006), we found only limited support for that increased variability in phosphorus concentration increased species sorting in relation to phosphorus *per se*. Despite the fact that communities were structured by species sorting at occasions with in average high phosphorus concentrations (Figure 3), phosphorus concentration directly explained parts of the variation in community composition at only three of the sampling occasions (Supplementary Table S2). Moreover, the variability in phosphorus concentration (CV) among sites was not significantly correlated to β-diversity ($\rho_s = 0.036$, $P = 0.903$). This might suggest that phosphorus rather 'fuels' the effect of other factors. For example, phosphorus concentration was positively and significantly correlated to salinity ($\rho_s = 0.691$, $P = 0.01$), the variability of salinity ($\rho_s = 0.618$, $P = 0.039$), the mean and variability of chlorophyll a concentration ($\rho_s = 0.709$, $P = 0.013$ and $\rho_s = 0.691$, $P = 0.017$) and *Daphnia* abundance ($\rho_s = 0.624$, $P = 0.035$). Phosphorus levels are important for the population growth rates of phytoplankton (Reynolds, 2009) and *Daphnia* (Anderson and Hessen, 2005) and might therefore have fostered differences in phytoplankton and *Daphnia* abundance among pools with increasing productivity and, together with stronger salinity effects at high productivity, caused the positive β-diversity—productivity relationship. On the contrary, Chase (2010) provided an alternative explanation by demonstrating that an increased productivity led to an increased role of stochastic assembly and multiple stable states in an experimental pond study using communities of primary producers and animals. Thus, further experimental studies are also needed to address the mechanisms behind the temporal β-diversity—productivity relationship that we found in the present bacterial metacommunity.

We found no indications that the disturbance regime, more specifically droughts that affected some of the rock pools, translated into differences in β-diversity or strong and persistent differences in community composition compared with permanent pools. This was surprising as several previous studies with larger organisms have shown that physical harshness, including droughts and differences in habitat permanency, decreases β-diversity and leads to strong species sorting in the sense that only a fraction of the predisturbance communities can survive the disturbance event (Chase, 2007; Lepori and Malmqvist, 2009; Vanschoenwinkel *et al.*, 2010). Possible reasons for the absence of a similar pattern in the studied bacterial metacommunity might be related to rapid recolonisation of rewettened patches after drought events from presumably large seed banks of dormant cells (Lennon and Jones, 2011), rain or adjacent permanent pools. In addition, rapid recolonisation of keystone predators such as *Daphnia magna* (the dominant *Daphnia* species in our system), which is known to have strong direct and indirect structuring effects on bacterial communities (for example, Jürgens, 1994; Langenheder and Jürgens, 2001), occurred as well and may 'blur' possible initial differences between permanent and temporary pools. Moreover, even permanent pools are heavily perturbed systems that frequently experience extreme environmental

conditions, such as heavy phytoplankton blooms or strong salinity changes, and it might be possible that rock pools in the general are inhabited by a bacterial community of generalists that is adapted to several forms of environmental extremes. This is supported by in general high share of community composition between rock pools, with average Bray–Curtis similarities ranging between 0.35 and 0.55, despite the often quite pronounced differences in environmental conditions among them.

Finding appropriate methods to measure community assembly in observational studies is a major challenge in contemporary community ecology. Variation partitioning is a commonly applied and useful tool (Legendre, 2008); however, the separation of environmental and spatial effects is far from clear cut, and hence results have to be interpreted with care. For example, the indirect measurement of dispersal, derived from spatial distances among locations, is problematic as spatial effects might mask unmeasured environmental factors that are spatially autocorrelated or historical effects, such as past dispersal events or past environmental conditions (Lindström and Langenheder, 2011). Thus, we cannot be certain that significant spatial effects observed in this study were only caused by dispersal-related mechanisms. Moreover, as typical for this type of studies, only a relatively small fraction of the total variation in community composition could be explained by the measured variables, pointing to the fact that we neglected important factors. Thus, one of the major future challenges will be to include a comprehensive set of environmental variables, direct measurements of dispersal, as wells as to develop a unified statistical framework that enables us to directly detect and quantify various assembly mechanisms at the same time.

In conclusion, our study demonstrates that there are temporal differences in β-diversity as well as the underlying assembly mechanisms in a bacterial metacommunity. Variation in local environmental factors seemed to be the main cause for differences in β-diversity over time, suggesting species sorting to be the main assembly process during most of the year. However, at some occasions, there was an evident effect of spatial factors on community composition, which shows that dispersal-related assembly mechanisms were also important. Thus, our study clearly shows the need to move away from the snapshot studies that have dominated so far to achieve a more comprehensive understanding of microbial metacommunity dynamics.

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References

Anderson TR, Hessen DO. (2005). Threshold elemental ratios for carbon versus phosphorus limitation in Daphnia. *Freshwater Biol* **50**: 2063–2075.

Beisner BE, Peres PR, Lindstrom ES, Barnett A, Longhi ML. (2006). The role of environmental and spatial processes in structuring lake communities from bacteria to fish. *Ecology* **87**: 2985–2991.

Blanchet FG, Legendre P, Borcard D. (2008). Forward selection of explanatory variables. *Ecology* **89**: 2623–2632.

Borcard D, Legendre P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol Model* **153**: 51–68.

Borcard D, Legrende P, Drapeau P. (1992). Partialling out the spatial component of ecological variation. *Ecology* **73**: 1045–1055.

Chalcraft DR, Cox SB, Clark C, Cleland EE, Suding KN, Weiher E *et al.* (2008). Scale-dependent responses of plant biodiversity to nitrogen enrichment. *Ecology* **89**: 2165–2171.

Chase JM. (2003). Community assembly: when should history matter? *Oecologia* **136**: 489–498.

Chase JM. (2007). Drought mediates the importance of stochastic community assembly. *Proc Natl Acad Sci* **104**: 17430–17434.

Chase JM. (2010). Stochastic community assembly causes higher biodiversity in more productive environments. *Science* **328**: 1388–1391.

Chase JM, Leibold MA. (2002). Spatial scale dictates the productivity-biodiversity relationship. *Nature* **416**: 427–430.

Chase JM, Ryberg WA. (2004). Connectivity, scale-dependence, and the productivity-diversity relationship. *Ecol Lett* **7**: 676–683.

Cottenie K. (2005). Integrating environmental and spatial processes in ecological community dynamics. *Ecol Lett* **8**: 1175–1182.

Crump BC, Adams HE, Hobbie JE, Kling GW. (2007). Biogeography of bacterioplankton in lakes and streams of an arctic tundra catchment. *Ecology* **88**: 1365–1378.

Crump BC, Peterson BJ, Raymond PA, Amon RMW, Rinehart A, McClelland JW *et al.* (2009). Circumpolar synchrony in big river bacterioplankton. *Proc Natl Acad Sci* **106**: 21208–21212.

Dorigo U, Volatier L, Humbert JF. (2005). Molecular approaches to the assessment of biodiversity in aquatic microbial communities. *Water Res* **39**: 2207–2218.

Drakare S, Liess A. (2010). Local factors control the community composition of cyanobacteria in lakes while heterotrophic bacteria follow a neutral model. *Freshwater Biol* **55**: 2447–2457.

Fuhrman JA, Hewson I, Schwalbach MS, Steele JA, Brown MV, Naeem S. (2006). Annually reoccurring bacterial communities are predictable from ocean conditions. *PNAS* **103**: 13104–13109.

Griffith DA, Peres-Neto PR. (2006). Spatial modeling in ecology: The flexibility of eigen function spatial analyses. *Ecology* **87**: 2603–2613.

Hammer O, Harper T, Ryan PD. (2001). PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4**: 9pp.

Harrison S, Davies KF, Safford HD, Viers JH. (2006). Beta diversity and the scale-dependence of the

productivity-diversity relationship: a test in the Californian serpentine flora. *J Ecol* **94**: 110–117.
Hubbell SP. (2001). *A unified neutral theory of biodiversity and biogeography*. Princeton University Press: Princeton, NJ.
Jiang L, Patel SN. (2008). Community assembly in the presence of disturbance: a microcosm experiment. *Ecology* **89**: 1931–1940.
Jürgens K. (1994). Impact of Daphnia on planktonic microbial food webs—a review. *Mar Microb Food Webs*, 1994 **8**: 295–324.
Kent AD, Yannarell AC, Rusak JA, Triplett EW, McMahon KD. (2007). Synchrony in aquatic microbial community dynamics. *ISME J* **1**: 38–47.
Langenheder S, Jürgens K. (2001). Regulation of bacterial biomass and community structure by metazoan and protozoan predation. *Limnol Oceanogr* **46**: 121–134.
Langenheder S, Ragnarsson H. (2007). The role of environmental and spatial factors for the composition of aquatic bacterial communities. *Ecology* **88**: 2154–2161.
Langenheder S, Szekely A. (2011). Species sorting and neutral processes are both important during the initial assembly of bacterial communities. *ISME J* **5**: 1086–1094.
Legendre P. (2008). Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *J Plant Ecol-Uk* **1**: 3–8.
Legendre P, Gallagher ED. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia* **129**: 271–280.
Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF *et al.* (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* **7**: 601–613.
Lennon JT, Jones SE. (2011). Microbial seed banks: the ecological and evolutionary implications of dormancy. *Nat Rev Microbiol* **9**: 119–130.
Lepori F, Malmqvist B. (2009). Deterministic control on community assembly peaks at intermediate levels of disturbance. *Oikos* **118**: 471–479.
Leps J, Smilauer P. (2003). *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press: Cambridge.
Lindström ES, Forslund M, Algesten G, Bergström AK. (2006). External control of bacterial community structure in lakes. *Limnol Oceanogr* **51**: 339–342.
Lindström ES, Langenheder S. (2011). Minireview: local and regional factors influencing bacterial community assembly. *Environ Microbiol Reports*; doi:10.1111/j.1758-2229.2011.00257.x.
Logue JB, Lindström ES. (2010). Species sorting affects bacterioplankton community composition as determined by 16S rDNA and 16S rRNA fingerprints. *ISME J* **4**: 729–738.
Mouquet N, Loreau M. (2003). Community patterns in source-sink metacommunities. *Am Nat* **162**: 544–557.
Mouquet N, Miller TE, Daufresne T, Kneitel JM. (2006). Consequences of varying regional heterogeneity in source-sink metacommunities. *Oikos* **113**: 481–488.
Ofiteru ID, Lunn M, Curtis TP, Wells GF, Criddle CS, Francis CA *et al.* (2010). Combined niche and neutral effects in a microbial wastewater treatment community. *Proc Natl Acad Sci* **107**: 15345–15350.
Östman O, Drakare S, Kritzberg ES, Langenheder S, Logue JB, Lindström ES. (2010). Regional invariance among microbial communities. *Ecol Lett* **13**: 118–127.
Ovreas L. (2000). Population and community level approaches for analysing microbial diversity in natural environments. *Ecol Lett* **3**: 236–251.
Peres-Neto PR, Legendre P, Dray S, Borcard D. (2006). Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* **87**: 2614–2625.
Ptacnik R, Andersen T, Brettum P, Lepisto L, Willen E. (2010). Regional species pools control community saturation in lake phytoplankton. *P R Soc B* **277**: 3755–3764.
Reynolds CS. (2009). Phytoplankton population dynamics in natural environments. In: Likens GE (ed.), *Encyclopedia of Inland Waters*. Elsevier: Amsterdam, pp 197–203.
Ricklefs RE. (1987). Community diversity—relative roles of local and regional processes. *Science* **235**: 167–171.
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.
Srivastava DS, Kolasa J, Bengtsson J, Gonzalez A, Lawler SP, Miller TE *et al.* (2004). Are natural microcosms useful model systems for ecology? *Trends Ecol Evol* **19**: 379–384.
Van der Gucht K, Cottenie K, Muylaert K, Vloemans N, Cousin S, Declerck S *et al.* (2007). The power of species sorting: local factors drive bacterial community composition over a wide range of spatial scales. *Proc Natl Acad Sci* **104**: 20404–20409.
Vanschoenwinkel B, Waterkeyn A, Jocque M, Boven L, Seaman M, Brendonck L. (2010). Species sorting in space and time-the impact of disturbance regime on community assembly in a temporary pool metacommunity. *J N Am Benthol Soc* **29**: 1267–1278.
Verleyen E, Vyverman W, Sterken M, Hodgson DA, De Wever A, Juggins S *et al.* (2009). The importance of dispersal related and local factors in shaping the taxonomic structure of diatom metacommunities. *Oikos* **118**: 1239–1249.
Woodcock S, van der Gast CJ, Bell T, Lunn M, Curtis TP, Head IM *et al.* (2007). Neutral assembly of bacterial communities. *FEMS Microbiol Ecol* **62**: 171–180.

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