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Reports

The spatial structure of bacterial communities is influenced by historical environmental conditions

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Abstract. The spatial structure of ecological communities, including that of bacteria, is often influenced by species sorting by contemporary environmental conditions. Moreover, historical processes, i.e., ecological and evolutionary events that have occurred at some point in the past, such as dispersal limitation, drift, priority effects, or selection by past environmental conditions, can be important, but are generally investigated much less. Here, we conducted a field study using 16 rock pools, where we specifically compared the importance of past vs. contemporary environmental conditions for bacterial community structure by correlating present differences in bacterial community composition among pools to environmental conditions measured on the same day, as well as to those measured 2, 4, 6, and 8 d earlier. The results prove that selection by past environmental conditions exists, since we were able to show that bacterial communities are, to a greater extent, an imprint of past compared to contemporary environmental conditions. We suggest that this is the result of a combination of different mechanisms, including priority effects that cause rapid adaptation to new environmental conditions of taxa that have been initially selected by past environmental conditions, and slower rates of turnover in community composition compared to environmental conditions.

Key words: assembly mechanisms; bacteria; beta diversity; biogeography; historical processes; metacommunities.

Introduction

One of the fundamental questions in ecology is to understand why species occur in one location while they are absent in another, i.e., to understand the mechanisms behind patterns in beta diversity. While several key mechanisms in the assembly processes of communities have been identified and integrated into the metacommunity framework (Leibold et al. 2004), knowledge about the circumstances in which a particular mechanism prevails and how different mechanisms interact with each other is still limited (Logue et al. 2011).

A number of studies have shown that species sorting by contemporary environmental conditions is important for structuring community composition across space (Cottenie 2005, Logue et al. 2011), including bacterial communities in freshwater ecosystems (Logue and Lindström 2008, Lindström and Langenheder 2012). Hence, differences in the distribution of bacterial taxa among local communities derive primarily from the reality that species have different niche requirements, can thrive under different abiotic and biotic conditions, and are rapidly sorted among sites according to these requirements and conditions. There are, however, also studies that have found effects of spatial distance, which may reflect the importance of historical processes, e.g., evolutionary as well as ecological events that have occurred at some point in the past, such as dispersal limitation, drift, priority effects, or adaption to past environmental conditions, and that are generally poorly understood (Martiny et al. 2006, Leibold et al. 2010, Hanson et al. 2012).

Dispersal limitation has been shown to occur in bacterial communities (e.g., Declerck et al. 2013), and can cause spatial differences in community composition, because dispersal rates are too low for a taxon to spread sufficiently from one site to another. The result of this is that communities in locations with similar environmental conditions may differ in species composition. Priority effects, on the other hand, can arise when earlier colonizers or resistant local populations monopolize empty patches or niche space that becomes available, for example, as a result of changes in environmental conditions or disturbances. The colonizers or resistant populations may then, via a range of potential mechanisms (including microevolution, phenotypic plasticity, and resource depletion), alter the establishment success of late-coming species (e.g., Shulman et al. 1983, Drake 1991, Urban and De Meester 2009). Priority effects occur under certain circumstances in simple microbial model communities (e.g., Jiang and Patel 2008, Tan et al. 2012), but their importance during the

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assembly of natural bacterial communities is currently unknown. The spatial distribution patterns of communities may also be influenced by delayed response times of communities towards environmental changes or perturbations. In bacterial communities, for example, it has been shown that the strongest alterations in community composition in response to a salinity pulse occurred with a delay of several days, i.e., at time points when salinity was already reset to initial conditions (Berga et al. 2012). This demonstrates that the potential gap between the initial and final response can be significant, and can persist for a considerable time after the actual perturbation.

Importantly, historical processes may result in a situation where variation in present-day community composition is explained to a greater extent by past conditions, compared to contemporary environmental conditions. This can be due to (1) the fact that dispersal limitation, in combination with a certain degree of adaptation to past conditions, prevents rapid species sorting by contemporary conditions, (2) the fact that priority effects cause rapid adaptation to new environmental conditions by taxa that have been initially selected by past environmental conditions, and (3) slower rates of turnover in community composition compared to environmental conditions. Since the importance of historical factors is difficult to derive from the snapshot studies that have dominated the literature thus far (Logue et al. 2011), we conducted a field study focusing on bacterial communities in rock pools in order to specifically compare the influence of contemporary vs. past environmental conditions on the composition of present-day bacterial communities among pools.

Materials and Methods

Samples were taken from 16 rock pools located along the Baltic Sea coast in the province of Uppland, in central Sweden (60°29′54″ N, 18°25′45″ E). Each rock pool was sampled five times, starting on 3 August 2011 and ending on 11 August 2011, with a 48-h interval between each sampling occasion (days 1, 3, 5, 7, and 9). At each sampling occasion, the following factors were measured in the field: pool width, length, depth, salinity (as parts per thousand), conductivity, and temperature. Water samples were collected for measurements of total phosphorus concentration (μg/L), chlorophyll *a* concentration (μg/L), absorbance, and abundances of *Daphnia* (individuals/L) and flagellates (10^3/mL; see Appendix A for a summary of measured environmental parameters). Additionally, weather data (precipitation and air temperature) was obtained from a local weather station belonging to the Swedish Meteorological and Hydrological Institute (SMHI). Bacterial community composition (BCC) was determined at the initial and final sampling dates (days 1 and 9). Chlorophyll *a* concentration, *Daphnia* abundance, and pool volume were determined as described in Langenheder et al. (2012). To determine flagellate abundance, 2 mL of formaldehyde-preserved water was stained with 4′, 6-diamidino-2-phenylindole (DAPI) at a final concentration of 100 μg/mL, filtered onto 0.8-μm polycarbonate filters, and then counted using an epifluoresence microscope.

BCC was analyzed by terminal restriction fragment length polymorphism (T-RFLP), as described in Langenheder et al. (2012). Briefly, the 16S rRNA gene was amplified by polymerase chain reaction (PCR) using the bacterial forward primer 341f and the universal reverse primer 805, and the amplicons were subsequently digested using the restriction enzyme *HaeIII*.

The T-RFLP data was analyzed using GeneMarker (Version 1.95, SoftGenetics, State College, Pennsylvania, USA). All peaks smaller than 50 base pairs and less than 0.5% of the total signal were removed from the analysis. Peaks closer than 0.5 base pairs were merged in order to account for the differences in running time between the different samples. Each peak that remained after these modifications was considered an operational taxonomical unit (OTU).

Locations and distances between the pools were calculated in ArcGIS 9.2 (ESRI, Redlands, California, USA), based on GPS coordinates obtained on day 1. As pool volume and flow connections between pools changed as a result of rainfall during the sampling period, we calculated for each pool at each subsequent sampling point (days 3 through 9) the changes in distance to the closest neighbor that resulted from increasing pool volumes/areas.

Statistical analyses

To determine correlations between BCC and spatial and environmental factors, partial redundancy analysis (pRDA) was used. The pRDA procedure enables the determination of the independent effects of each explanatory factor on BCC, as well as shared effects due to covariation. RDAs were run with CANOCO 4.5 (Microcomputer Power, Ithaca, New York, USA), using chord transformations of the OTU data to make it conform to a linear gradient (Legendre and Birks 2012), and environmental variables that were transformed to a logarithmic scale ($\log(x + 1)$) in order to achieve a normal distribution and standardized-by *z*-score transformations. In all models, significance testing was done using Monte Carlo permutation tests with 999 permutations.

The statistical analysis was done in the following steps:

First, standard RDAs were performed to test the correlations between six environmental factors (salinity, water color, *Daphnia* abundance, flagellate [HNF] abundance, total phosphorus concentration, and chlorophyll *a* concentration) on all five sampling days, and BCC at day 9. The same procedure was performed with the spatial factors, where we used the same 10 positive eigenvectors obtained from the principal coordinates of

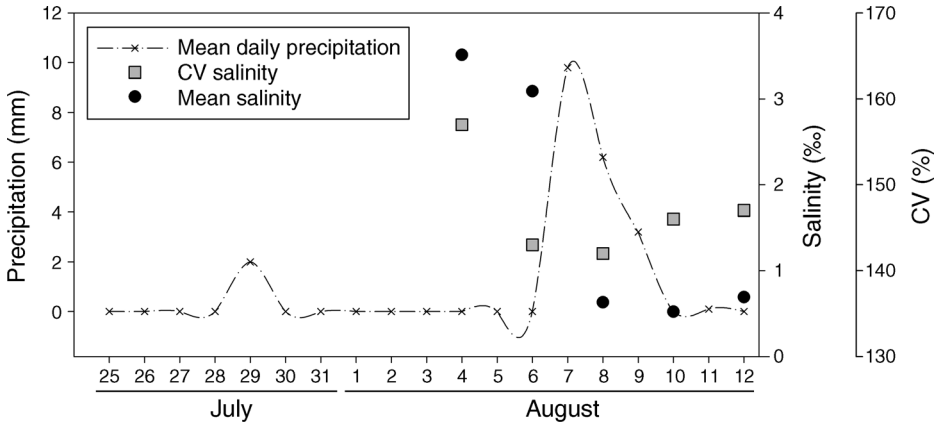

FIG. 1. Mean daily precipitation during and prior to the sampling period (3 August –11 August 2011). Values for mean salinity (measured in parts per thousand) and the coefficient of variation (CV) in salinity among rock pools at the different sampling points are also shown.

neighbor matrices analyses (PCNM; see Langenheder et al. 2012 for details) for all sampling dates and estimates for pool volume and distance to closest neighbor, which varied between days, as explanatory variables. The reason for including volume in the spatial model was that, to some extent, it reflects the increasing likelihood that close pools can merge during periods with high precipitation. It also reflects the likelihood of overall decreases in distance and increases of water movement between pools. Environmental factors were significantly correlated with BCC at day 9 on all sampling occasions, while none of the spatial factors gave a significant result at any sampling point (Appendix B). Hence, no further calculations were performed with the spatial data, and we could specifically focus on the comparison on the effect of contemporary vs. past environmental conditions on the composition of bacterial communities at day 9.

Second, forward selection with all measured environmental variables was done as described in Blanchet et al. (2008), in order to determine whether or not each of them made a significant contribution to explaining variation in BCC. This procedure selected only one significant environmental factor, namely salinity, at all sampling dates. For that reason, the following analyses were implemented using salinity as the only environmental variable.

Third, pRDAs were performed using salinities at each sampling day to test to what extent they significantly affected BCC at day 9, independent of salinity levels on the respective other sampling days. For example, the effect of salinity at day 1 was first tested with salinity at day 3 as a covariable, next with salinity at day 5 as a covariable and so on, with all 20 possible combinations being tested.

Finally, correlations between salinity levels at the different sampling dates and BCC were tested with partial Mantel tests (two-tailed, based on Pearson correlations), using an Excel add-on, XLSTAT (Addinsoft, New York, New York, USA), in a similar fashion as described above for the pRDAs and with 10.000 permutations in the significance test. Dissimilarity matrices based on Euclidean distances were created for salinity after log-transformation, and Bray-Curtis dissimilarities were used for the OTU matrix. RDA and Mantel tests provide complementary approaches to study correlations between environmental variables and community composition, and both were used to check the robustness of the results, irrespective of the statistical method used to analyze the data.

Overall differences in community composition among pools at days 1 and 9 were analyzed using nonmetric multidimensional scaling analysis (NMDS), based on Bray-Curtis dissimilarities. To specifically compare differences in beta diversity among pools at days 1 and 9, we used multivariate dispersion analysis (Anderson et al. 2006), based on Bray-Curtis distances, using the vegan package in R (Oksanen et al. 2012). For each pool, the similarity in community composition between days 1 and 9 was calculated based on Bray-Curtis similarities, and the proportion of shared OTUs between both days was determined based on presence-absence data. Finally, we tested (1) how much of the variation in BCC at day 1 could be explained by differences in salinity at day 1 using RDA, and (2) correlations between BCC and salinities at day 1 using a Mantel test.

RESULTS

Sampling days 1 and 3 and days 7 and 9 were separated by a 3-d period during days 4 through 6 with frequent and intense rainfall (Fig. 1), which increased the average volume of the pools by more than 100%. This triggered a number of environmental responses, including a decrease in mean salinity, accompanied by a slight reduction in variability (Fig. 1), the latter indicating that the environment became more homogenous among pools. This was not only observed for salinity, but also for other environmental variables (e.g.,

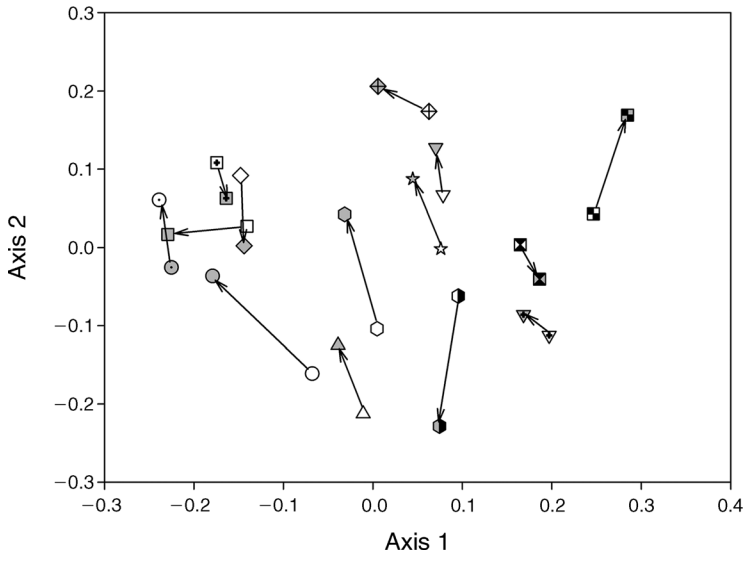

FIG. 2. Nonmetric multidimensional scaling (NMDS) plot showing differences in bacterial community composition among rock pools at day 1 (white symbols) and day 9 (gray symbols). The different symbol shapes and color patterns refer to different rock pools, and arrows mark the changes in conditions in each pool between days 1 and 9. Stress = 0.22.

total phosphorus and chlorophyll *a* concentrations, and water color; Appendix A: Table A1).

Spatial differences in BCC among rock pools at days 1 and 9 were weakly, but significantly, correlated (Mantel test, $r_M = 0.28$, $P < 0.01$). On the level of individual pools, Bray-Curtis similarities were on average 0.45 ± 0.08 (mean ± SD, range: 0.29–0.58) between communities found on days 1 and 9, whereas values calculated based on the number of shared OTUs were on average 0.37 ± 0.13 (mean ± SD, range: 0.15–0.58). Hence, there were clear changes in BCC between days 1 and 9 in the individual pools, even though the overall differences in community composition, i.e., the spatial variability among pools, remained (Fig. 2). There was also no indication that beta diversity among pools differed strongly between sampling days, since the multivariate dispersion analysis showed that the average distances from the centroids at day 1 (0.5744) and day 9 (0.5617) did not differ significantly from each other ($F_{1,13} = 0.286$, $P = 0.62$).

Environmental conditions (e.g., salinity) at early sampling points, in particular those found at days 1 and 3, often explained more of the variation in (or were more strongly correlated to) BCC at day 9 than more recent environmental conditions, i.e., those observed at days 7 or 9. Without accounting for covariation, salinity at days 1 and 3 showed a stronger correlation to BCC at day 9 than salinity at days 7 and 9, both in Mantel and RDA tests, whereas day 5 was intermediate (Fig. 3). Effects of salinity levels at early sampling days (days 1 and 3) remained significant when days 5, 7, and 9 were included as covariables when tested with both partial Mantel tests and pRDAs (Table 1). Results from Mantel tests also showed that correlations were strongest when day seven was used as a covariable (Table 1). Further correlations between salinities at day 7 and BCC at day 9 were generally the weakest (Fig. 3). Effects of salinities at later sampling days, in particular days 7 and 9, were in most cases not significant when salinities at earlier sampling days were included as covariables, whereas day 5 took an intermediate position (Table 1). Notably, salinity levels were never significant when salinities at days 1 and 3 were included as covariables. Differences in salinities among pools at day 1 explained 8.3 % of the variation in BCC at day 1 ($P = 0.003$), which was generally lower than the fraction that could be explained at day 9 (12.0–15.3%; Fig. 3). Correlations between

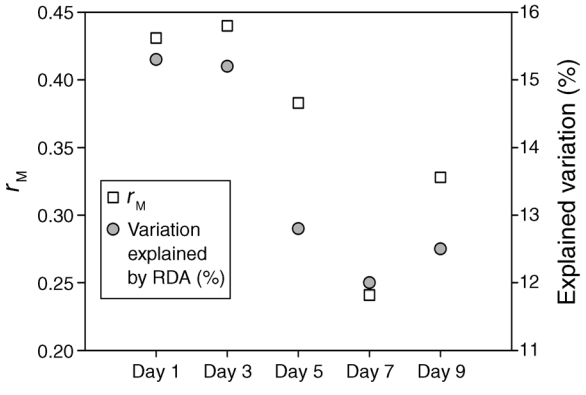

FIG. 3. Results from Mantel tests and RDA analyses comparing the effect of salinities at the different sampling days on bacterial community composition at day 9. The r_M values from Mantel test and the amount of variation explained by RDA (adjusted R^2 values) are shown. All cases were significant at $P < 0.05$.

TABLE 1. Influence of past and present environmental conditions on bacterial community structure.

Covariable	Explanatory variable				
	Day 1	Day 3	Day 5	Day 7	Day 9
r_M values					
Day 1		ns	ns	ns	ns
Day 3	ns		ns	ns	ns
Day 5	0.315	0.330		ns	ns
Day 7	0.402	0.414	0.368		ns
Day 9	0.316	0.332	0.210	ns	
Adjusted R^2					
Day 1		ns	ns	ns	ns
Day 3	ns		ns	ns	ns
Day 5	0.025	0.036		0.036	ns
Day 7	0.046	0.057	0.036		ns
Day 9	0.036	0.048	0.048	ns	

Notes: The r_M values are from partial Mantel correlation tests, and show correlations between bacterial community composition (BCC) at day 9 and the explanatory variable (salinity, measured in parts per thousand) at days 1 through 9 (shown in columns). Adjusted R^2 values are from partial redundancy analyses (pRDA) showing the amount of variation in BCC among rock pools at day 9 that could be explained by differences in salinity at the different time points (days 1–9, shown in columns). In both cases, salinity values from a second sampling occasion were used as covariates (shown in rows). Cells marked ns show a non-significant correlation.

salinity and BCC at day 1 were also significant when tested with a Mantel test ($r_M = 0.233$, $P = 0.035$).

DISCUSSION

This study shows that past environmental conditions can be better predictors of present spatial differences in BCC among locations when compared to contemporary environmental conditions. More specifically, we found that BCC was to a greater extent determined by past, rather than contemporary, differences in salinity between the studied rock pools. This shows that attributes that characterize bacterial communities, such as short generation times and great dispersal abilities, are not sufficient to exclude effects of historical factors.

Our study enabled us to specifically address the effect of past environmental conditions, since the rainfall in the middle of the sampling period had a strong diluting effect on measured environmental parameters, leading to decreases in the mean and variability of salinity in the pools. This allowed us to separate effects of pre- and post-rainfall environmental conditions on spatial differences in BCC. The decrease in the mean value and variability of salinity after the rainfall event did not, however, result in more similar communities, since beta diversity among pools remained approximately the same at day 9 as at day 1. Instead, differences in salinity prior to the rainfall events explained more of the variation in BCC among pools (or were more strongly correlated to it), compared to differences in salinity on the day where the samples for BCC analyses were taken. This result is surprising, given that salinity is generally a strong structuring factor for BCC (Lozupone and Knight 2007, Tamames et al. 2010), where even relatively minor changes in salinity can induce clear and rapid changes in community composition (e.g., del Giorgio and Bouvier 2002, Szekely et al. 2013).

There are several possible explanations for the observation that past environmental conditions explained a larger fraction of the variation in BCC than contemporary conditions.

First, the consistently dry and warm weather prior to the rainfall (Fig. 1) could have resulted in a high level of adaptation of the bacterial community to relatively stable environmental conditions. In the case of dispersal limitation, this may have maintained spatial differences in community composition among pools, despite the relatively strong changes in salinity following the rainfall, simply because species adapted to the new salinities had not yet reached the respective local communities. The fact that we generally did not observe an effect of spatial distance suggests that dispersal limitation did not occur (Cottenie 2005), however, we can still not preclude this possibility entirely, since we lack direct measurements of dispersal among pools.

Second, there might be a time lag in the compositional response of bacterial communities to the salinity change because of the time needed by the taxa selected by the new environment to grow to become detectable among the dominant members of the bacterial communities. Similarly, in an earlier experimental study, we observed a delay of several days in the change in BCC in response to a salinity pulse (Berga et al. 2012). A slow response time of several weeks was also found in a transplant experiment with bacterial communities in sediments (Reed and Martiny 2013). In our case, such a growth lag may not only have been due to changes in salinity, but also to decreases in the availability and composition of substrates available for bacterial growth after the rainfall event. Hence, even though we found clear

changes in community composition before and after the rainfall, with a taxa turnover that exceeded 50% in most pools, it is still possible that community composition was not at equilibrium with the contemporary environmental conditions. The existence of a mismatch between changes in environmental conditions and community composition is further supported by the observation that community composition at day 1 was also not well explained by contemporary environmental conditions, i.e., salinity at day 1.

The third possible explanation to why past environmental conditions explained a larger fraction of the variation in BCC than contemporary conditions is priority effects related to the arrival history of species during community assembly. Here, early immigrants or resistant taxa that are already present in the community take advantage of empty niche space becoming available when environmental conditions change, because they have the ability to adapt rapidly (Mergeay et al. 2011). This could, in our case, lead to less pronounced changes in community composition than what we would expect, based on changes in environmental conditions. Rock pools are systems that fluctuate strongly in environmental conditions over time, and it is therefore likely that there is a considerable number of bacterial populations that are able to cope with or rapidly adapt to environmental fluctuations, which might foster priority effects. Moreover, priority effects could be due to rain bacteria that have the ability to rapidly colonize empty niche space (Langenheder and Szekely 2011), however, their importance as an immigration source is relatively minor, since we typically find that similarities between rock pool, air, and rain communities are low, even in situations where pools receive large inputs of rainwater (M. Berga, *unpublished data*).

Finally, even though the fraction of shared OTUs between days 1 and 9 was on average less than 40%, which shows the suitability of our approach to detect differences in bacterial communities, there are methodological biases that might have dampened changes in community composition in relation to those in environmental conditions. These are related to the low taxonomic resolution of T-RFLP, which only detects the most abundant bacterial taxa, or the fact that we analyzed the composition of the *total* community, i.e., active as well as inactive taxa, and were not able to differentiate between taxa that entered dormancy or were resurrected from it in response to salinity changes. Another limitation is that the degree of variation between communities that could be explained by the measured environmental factors was rather low. This is a commonly observed pattern (e.g., Lindström and Langenheder 2012), and it remains unresolved whether this is a consequence of neglecting important factors, or reflects the importance of stochastic processes during community assembly.

It is likely that processes related to the selection by contemporary and past environment conditions overlap, in the sense that some taxa that are found to be present in a community are there because they were selected by present conditions, whereas others are there because they were selected by past conditions. One indication that this might have been the case in our study was that we observed that correlations were lowest to salinity levels at a lag of −2 d (day 7; Fig. 3, Table 1), but higher before and afterwards, which might indicate that there was a turning point or transition zone during and directly after the rainfall, where salinities changed rapidly (Fig. 1). This turning point may have separated the two processes, i.e., effect of past differences in salinities found at days 1 and 3 from those induced by present-day differences at day 9.

To conclude, we show that, to our knowledge for the first time, historical environmental conditions need to be considered to explain spatial differences in community composition. Hence, our study shows that to fully describe patterns in beta diversity across sites, we need to apply and develop sampling designs, as well as statistical tools that enable measurements of time delayed interactions (ideally at various time gaps) in a spatial context. Our study also demonstrates that our study system of bacterial communities in rock pools provides a very useful and short-term complement to other studies that have previously been used to study historical processes in larger organisms (Leibold et al. 2010, Mergeay et al. 2011, Rader et al. 2012). Future studies are, however, now needed to test how far back in time we can detect structuring by past environmental conditions, whether it is a process that also occurs in communities of other organisms and in other types of ecosystems, and to determine the underlying mechanisms.

Acknowledgments

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Supplemental Material

Appendix A

Environmental parameters in the rock pools (*Ecological Archives* E095-097-A1).

Appendix B

Adjusted R^2 values and P values from RDA analyses testing the overall effects of environmental and spatial factors measured at different sampling days on bacterial composition at day 9 (*Ecological Archives* E095-097-A2).