

Phytoplankton metacommunity structure in subarctic rock pools

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ABSTRACT: Rock pools are ephemeral aquatic systems that provide important ecosystem functions as stepping stones for sustaining aquatic biodiversity within an inhabitable terrestrial matrix. We investigated the fine-scale (<60 m) spatial variation of phytoplankton communities in 30 pristine subarctic rock pools in Finland within the metacommunity context. We differentiated between straight-line overland and watercourse distances among the rock pools, as the latter may reflect actual dispersal pathways more realistically. Environmental variables, such as total phosphorus, varied by an order of magnitude among the pools, but showed a rather random and patchy distribution instead of a distinct spatial gradient. Bray-Curtis dissimilarities and taxon-accumulation curves showed that the community composition differed considerably among the pools. Redundancy analysis suggested that such among-pool differences in communities may partly be driven by the variation in conductivity and water temperature. Variation partitioning further showed that the pure spatial component was considerably larger and residual variation lower when watercourse distances were used instead of overland distances. This indicates that watercourse distances better represented the spatial structure of the phytoplankton metacommunity than overland distances. These results further suggest that occasional flooding during snow melt or heavy rainfall as well as random faunal fertilization probably shaped the community composition and that phytoplankters were mainly dispersed via watercourses in this rock pool system.

KEY WORDS: Rock pools · Metacommunity · Watercourse distances · Mass effects

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INTRODUCTION

Ecological communities are structured at multiple spatial scales. A number of ecological processes, such as competition, predation, environmental filtering and dispersal processes, affect the local alpha diversity as well as the degree of beta diversity, i.e. the species turnover among local communities (Sepkoski 1988, Legendre et al. 2005, Beisner et al. 2006, Soininen et al. 2007, Vanschoenwinkel et al. 2007). These processes are addressed in the metacommunity framework, in which linkages between different spatial scales in ecology are examined (Leibold et al. 2004).

The metacommunity framework comprises 4 different paradigms that emphasize the different mecha-

nisms of community assembly and predict changes in local community composition based on habitat and species characteristics as well as the rate of dispersal (Holyoak et al. 2005, Logue et al. 2011). High dispersal rates and subsequent colonization may lead to mass effects (including source–sink dynamics or rescue effects) resulting in a homogenized metacommunity and relatively low beta diversity (Martiny et al. 2006). At intermediate dispersal rates, species can disperse to their most suitable patch, resulting in a conformance between environmental gradients and community composition (i.e. species sorting) (Van der Gucht et al. 2007). However, if habitat patches are isolated and dispersal is limited, a colonization–competition trade-off can be observed, indicating

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patch dynamics. In contrast, neutral theory presents a null model (Hubbell 2001), assuming that all species have equal fitness, movement and competitive abilities, leading to random community assembly generated by species losses and gains (Leibold et al. 2004).

The role of dispersal in shaping beta diversity patterns can be approximated indirectly with spatial predictors (Landeiro et al. 2011). For the aquatic community assembly, it is important to distinguish between straight-line overland and watercourse distances: watercourse distances are more likely to reflect the dispersal limitation experienced by aquatic organisms (Landeiro et al. 2011). Landeiro et al. (2011) and Liu et al. (2013) found that in dendritic river networks, spatial variables based on watercourse distances represented actual dispersal-related spatial patterns in community variation better than overland distances. Consequently, the usage of watercourse distances may be particularly important for detecting underlying metacommunity paradigms (Landeiro et al. 2011).

In freshwater ecosystems, organism dispersal and beta diversity depend on the spatial distribution of habitats (Soininen et al. 2007). Clear large-scale distribution patterns in freshwater phytoplankton communities have been revealed by some studies (e.g. Ptacnik et al. 2010, Soininen et al. 2011), whereas others have reported only weak relationships between phytoplankton distribution and environmental or spatial factors (Spencer et al. 2002, Beisner et al. 2006, Nabout et al. 2009). Yet, metacommunity studies have only rarely been conducted at fine spatial scales (here defined as <100 m). For example, in a review by Cottenie (2005), only 5 out of 158 studies examined metacommunities at a scale <100 m, while the majority investigated community variations at scales of several hundreds of kilometres. This is probably related to the assumption that habitat heterogeneity and dispersal limitation increase with increasing spatial scale, potentially resulting in higher community variation and thus clearer results and conclusions (Cottenie 2005). However, for understanding underlying coexistence mechanisms, it is important to identify the minimum spatial scales at which significant spatial patterns in community variation manifest (Lear et al. 2014).

At fine spatial scales, the relative influence of dispersal-related mechanisms and environmental factors seems to be highly variable for different habitats and organism groups. For example, zooplankters may not typically be dispersal limited at <60 m scales (Spencer et al. 2002, Havel & Shurin 2004, Van-

schoenwinkel et al. 2007), but rather are driven by local abiotic factors (Cottenie et al. 2003). In contrast, Lear et al. (2014) found distinct bacterial communities separated by distances as short as 20 m, presumably indicating dispersal limitation and strong environmental filtering at fine spatial scales, even within the continuous water column of a freshwater lake. Langenheder et al. (2012) revealed that a bacterial rock pool community structure was shaped by species-sorting and dispersal-related mechanisms in an area of ~600 m². Yet, it is still under discussion whether freshwater phytoplankton species are subject to dispersal limitation at fine spatial scales, particularly as they are able to form cysts, which may build up a permanent seed bank that potentially homogenizes their distribution (Litchman & Klausmeier 2008, DeBie et al. 2012).

Rock pools are an ideal system for studying the fine-scale spatial distribution of phytoplankton metacommunities, since they are locally numerous, vary in size and connectivity, and thus in the degree of dispersal limitation (Cottenie 2005). Rock pools are ephemeral aquatic systems (Urban 2004) that provide important ecosystem functions as stepping stones for sustaining aquatic biodiversity within an inhabitable terrestrial matrix (De Meester et al. 2005). Rock pools are shaped by precipitation, thawing snow and evaporation, resulting in high temporal variation in size (volume) and connectivity among the pools (Pellowe-Wagstaff & Simonis 2014). Consequently, the rock pool community structure is largely determined by the disturbance regime (e.g. freezing, draining), local nutrient enrichment, temporal permanence and dispersal processes (Spencer et al. 2002, Urban 2004, Vanschoenwinkel et al. 2013). Yet, so far mostly macroinvertebrate and zooplankton rock pool communities have been investigated (Spencer et al. 2002, Ilmari Pajunen & Pajunen 2003, De Meester et al. 2005, Kolasa & Romanuk 2005, Vanschoenwinkel et al. 2007, Jocque et al. 2010, Vanschoenwinkel et al. 2010, Vanschoenwinkel et al. 2013), but see Pellowe-Wagstaff & Simonis (2014) for a study on phytoplankton and Langenheder et al. (2012) for a study on bacterial communities. Further, studies on rock pool communities have not yet used different connectivity pathways (i.e. watercourse vs. overland distances) among the pools, even though this may provide insight into prevalent dispersal routes and thus mechanisms of community assembly.

Here, we investigated the fine-scale spatial variation of phytoplankton communities in 30 pristine dendritically connected rock pools in subarctic Finnish Lapland. The first objective was to assess whether there is a spatial imprint in the phytoplank-

ton community structure at fine spatial scales. Differences in local diversity were characterized by investigating Shannon diversity and evenness. We also investigated the relative influence of local environmental factors and spatial variables on the phytoplankton community structure using direct ordination with variation partitioning to identify underlying metacommunity dynamics (Cottenie 2005, Oksanen et al. 2012). A significant spatial signal in the data would imply dispersal-driven processes (patch dynamics, neutral model, mass effects) or spatially structured environmental variation (Peres-Neto and Legendre 2010, Langenheder et al. 2012, Lear et al. 2014). In contrast, a high environmental influence on the community variation would indicate species-sorting mechanisms (Langenheder et al. 2012, Lear et al. 2014).

We also examined whether overland or watercourse distances provide a better representation of the spatial structure of phytoplankton communities (Spencer et al. 2002, Beisner et al. 2006, Landeiro et

al. 2011). We expected that watercourse distances would better represent major dispersal pathways among the rock pools than overland distances (wind or faunal vectors) (Liu et al. 2013).

MATERIALS AND METHODS

The sampling area comprised 30 pristine rock pools located within a 55×30 m grid in close proximity to a subarctic lake (located at 796 m above sea level) southeast of Kilpisjärvi, Finland (coordinates of rock pool 1: $68^\circ 58.897' N$, $21^\circ 01.515' E$) (Fig. 1). Sizes of the rock pools as well as watercourse distances between the pools were measured in the field with a yardstick. The pool volumes ranged from 0.075 to 11.7 m^3 . As pools were not influenced by anthropogenic activities, most of the nutrients in these pools seemed to originate from terrestrial vegetation and faunal sources, such as frogs, water birds, decaying moths and reindeer faeces.

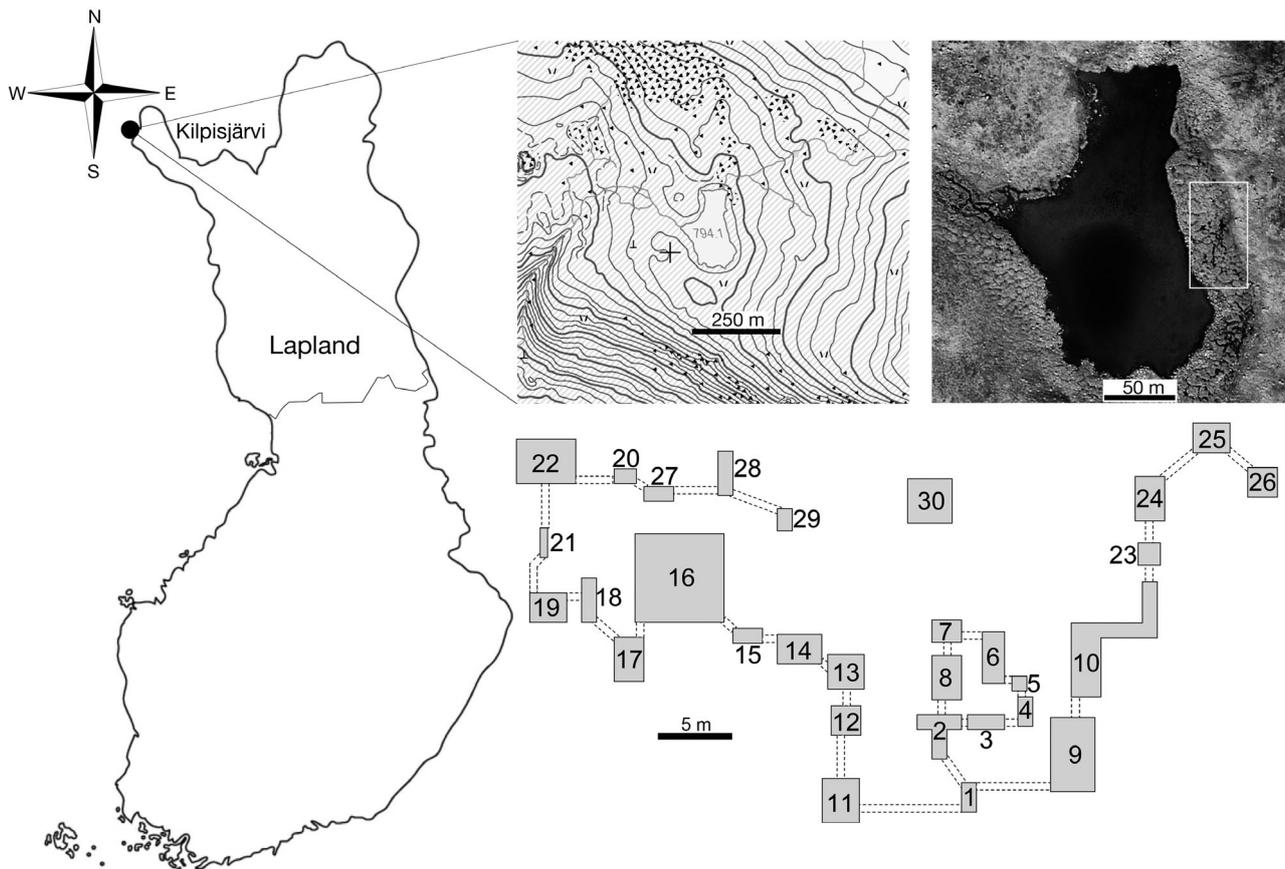


Fig. 1. Map of Finland with a schematic map of the rock pool distribution. The investigated rock pools were located near Kilpisjärvi (Lapland) in close proximity to a tarn (coordinates of rock pool 1: $68^\circ 58.897' N$, $21^\circ 01.515' E$). The white box marks the study area (maps were taken from <http://kansalaisen.karttaipaikka.fi>). Pools 1 to 30 are shaded grey and watercourse connections are indicated by dashed lines

Sampling and laboratory analyses

Samples of rock pools 1 to 10 were taken on 24 August 2013 and samples of rock pools 11 to 30 on 26 August 2013. We could not control for the possible variation in community composition between sampling dates, which may have caused additional residual variation in the data. The maximum depth, length and width of the rock pools were measured. Conductivity and water temperature were measured in the field. Water samples were taken in the middle of each rock pool with a beaker (1.7 l) mounted on a stick. For photometrical (Spectrophotometer DR5000, Hach Lange) water chemistry analyses (total N according to European standard EN ISO 11905-1:1997 and total P according to Finnish standard association SFS-EN 1189), 100 ml subsamples were stored at 4°C. For microscopical analyses, 250 ml subsamples were preserved with acidic Lugol's iodine solution in the field and also stored at 4°C.

Microscopical analyses

Depending on cell number, subsamples of either 50 or 100 ml were sedimented in Utermöhl chambers (Utermöhl 1958) and analyzed microscopically using an inverted Nikon Eclipse TS100 microscope (Nikon, Japan). Cells were identified to the lowest possible taxonomic level at 200- and 400-fold magnification following Tikkanen (1986), John et al. (2002) and von Berg et al. (2012). At least 600 cells (combined at both magnifications) were counted in randomly chosen grids. Biovolume means for the cells were taken from the literature (Naulapää 1972, Olenina et al. 2006). Biovolumes were used as they better represent the ecological importance of the respective species (e.g. abundant but small-sized species contribute only a minor fraction to the total biovolume) (Hillebrand et al. 1999).

Statistical analysis

All analyses were conducted in R, version 3.0.2 (R Development Core Team, 2013) using packages betapart (Baselga & Orme 2012), MASS (Venables & Ripley 2002), PCNM (Legendre et al. 2009), pgirmess (Giraudoux & Giraudoux 2013), spdep (Bivand et al. 2009) and vegan (Oksanen et al. 2012). Prior to analyses, we square-root transformed environmental variables (conductivity, temperature, P, pool

volume) and Hellinger-transformed phytoplankton biovolumes to better approximate normal distribution. We also tested whether explanatory variables showed multicollinearity. Total P and total N concentrations were strongly correlated ($r^2 = 0.908$), and we thus excluded total N from further analyses as total P would likely be a more influential explanatory variable for freshwater phytoplankton than total N (Wetzel 2001).

We calculated Shannon diversity indices and Pielou's evenness for each pool to display the phytoplankton distribution among the rock pools. We also examined whether the community structure of neighbouring rock pools was more similar to the focal community than communities of more distant rock pools (Bray-Curtis dissimilarities calculated with the bray.part function) due to the assumed more similar environmental conditions in neighbouring pools and short-distance dispersal processes (Spencer et al. 2002). Moreover, we computed a taxon accumulation curve, illustrating the cumulative number of taxa with increasing sampling effort (pools 1 to 30). The higher the slope of the taxon accumulation curve, the more pronounced is the spatial turnover of the community composition.

To evaluate the dispersal pathway (overland vs. watercourse dispersal) predominantly shaping the regional community composition in this dendritically connected rock pool system, we created matrices of pairwise overland and watercourse distances between the rock pools. Watercourse distance between unconnected pools was set to 100 to strengthen the differences between physically connected and unconnected pools. We assessed the correlation between these 2 distance matrices using a Mantel test (Landeiro et al. 2011). We then modelled spatial variables using principal coordinates of neighbour matrices (PCNM) (Ptacnik et al. 2010, Liu et al. 2013). PCNM derives a series of spatial eigenvectors from the matrix of Euclidean distances between all pairs of sampling sites. Using principal coordinate analysis (PCA), we determined the eigenvectors with positive eigenvalues which were used as spatial explanatory variables in the following multivariate analyses (Borcard et al. 2011). We conducted this procedure for a matrix of overland and watercourse distances, of which the latter may reflect dispersal pathways of aquatic organisms more realistically (Landeiro et al. 2011). We retained only PCNM variables showing significant ($p < 0.05$) positive spatial autocorrelation (based on Moran's I autocorrelation, obtained using the correlog function in package pgirmess) in the analyses.

We conducted 2 separate redundancy analyses (RDA) to assess the importance of environmental variables combined with overland or watercourse distances (implemented as PCNM variables) on the phytoplankton community structure. Significant ($p < 0.05$) variables were determined using the function `anova.cca` with 1000 permutations. We decided to include all variables in the subsequent variation partitioning, as in the permutation analysis and in a preliminary test using Akaike's information criterion-based forward selection procedures (Akaike 1973) too many ecologically meaningful variables were excluded.

We ran 2 separate variation partitioning analyses (Borcard et al. 1992) to estimate the fractions of community variation that could be ascribed to pure effects of environmental variables, pure effects of overland or watercourse spatial distances (implemented as PCNM variables) and their shared variance (Beisner et al. 2006). The variation partitioning methodology may lead to negative adjusted R^2 values for any unique or shared fraction, indicating non-linear dependencies or opposing effects between the groups of variables (Peres-Neto et al. 2006, Oksanen et al. 2012). As these negative fractions are not ecologically meaningful, we did not report them in the results.

RESULTS

We did not find a consistent trend in Shannon indices and Pielou's evenness of the phytoplankton communities among the rock pools, although Shannon diversity tended to be slightly higher in the pools furthest from the lake (Fig. 2). We also found particularly low evenness in 3 pools (pool 9 = 0.25; pool 15 = 0.29; pool 23 = 0.23) along with high total biovolumes (pool 9 and 23 = $1.9 \times 10^7 \mu\text{m}^3 \text{ml}^{-1}$ each and pool 15 = $4.4 \times 10^7 \mu\text{m}^3 \text{ml}^{-1}$), indicating monospecific blooms of *Hyalotheca dissiliens* in pools 9 and 15 and blooms of *Tabellaria flocculosa* in pools 9 and 23 (Fig. 2). These blooms appeared in pools having intermediate (10 to $19 \mu\text{g l}^{-1}$) P concentrations.

Total P concentrations varied by an order of magnitude among the pools. The highest total p-values ($>40 \mu\text{g l}^{-1}$) were found in pools 18, 22 and 25. Total P concentrations and total biovolumes showed patchy distributions, yet slightly increasing with increasing distance from the lake (Fig. 3).

Average Bray-Curtis dissimilarities among the pools were overall high (0.70) (Fig. 4a). However, we did not find a distinct spatial trend in the phytoplankton communities: neighbouring communities were not more similar in terms of Bray-Curtis dissimilarities to each other than communities further apart

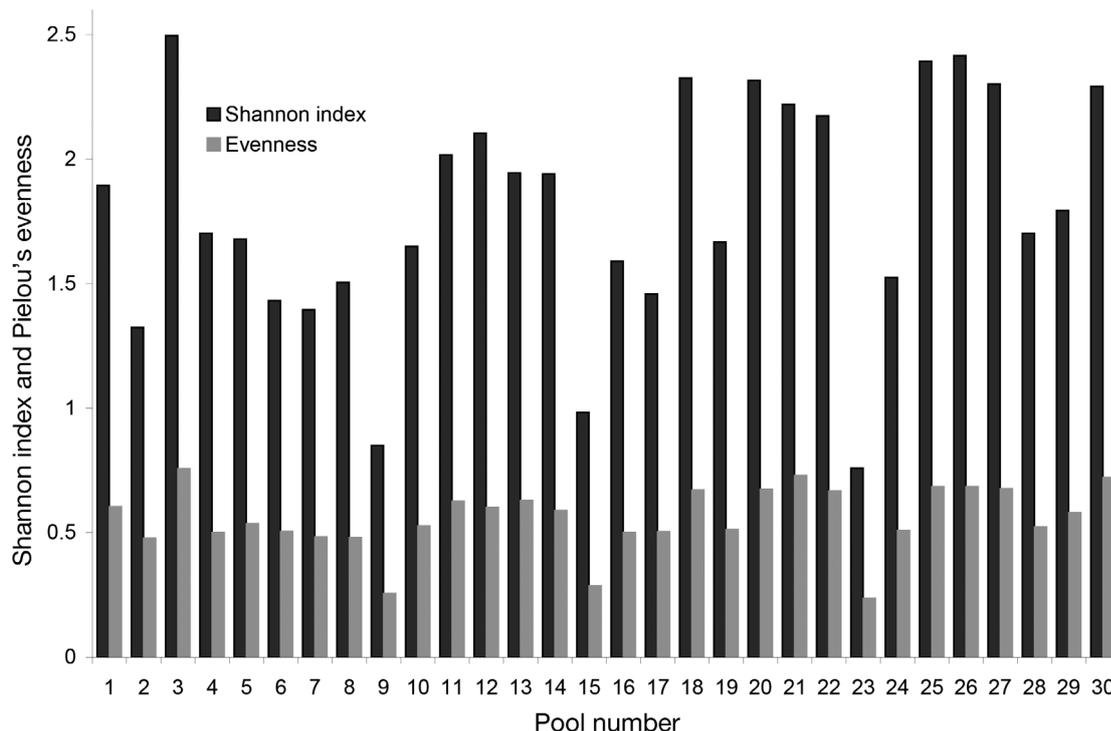


Fig. 2. The values of Shannon diversity and Pielou's evenness of the phytoplankton communities in the 30 rock pools

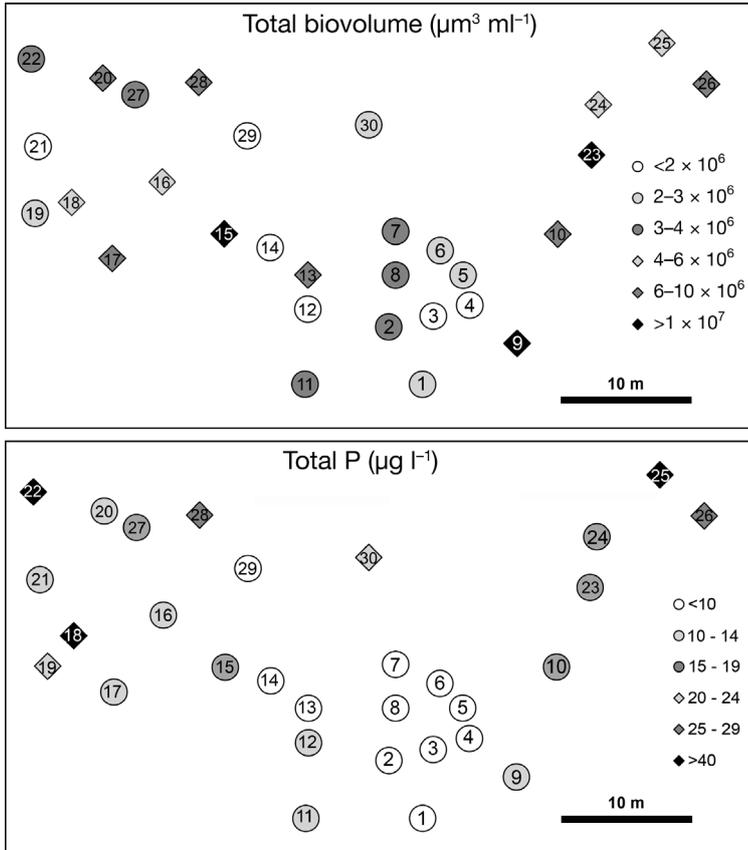


Fig. 3. The values of total algal biovolumes ($\mu\text{m}^3 \text{ml}^{-1}$) and total P ($\mu\text{g l}^{-1}$) concentrations. The positions of the data points reflect the actual locations of the rock pools (see Fig. 1)

(Fig 4a). The taxa-accumulation curve also showed that with increasing sampling effort, more taxa were found (Fig. 4b), indicating differences in the taxon composition of communities among the pools. In total 79 taxa were recorded.

Redundancy analyses

The Mantel test revealed a correlation between overland and watercourse distances of $r_M = 0.65$ ($p = 0.001$). Moran's I was significant ($p < 0.05$) for PCNM 1 to 5 constructed with overland distances and it was significant for PCNM 2 to 4 constructed with watercourse distances.

Environmental variables and overland distances

Local environmental variables and overland distances explained in total 40% (R^2) of the phytoplankton community variation; 16.7% was explained by RDA axis 1 and 9.4% by RDA axis 2 (Table 1). The most important environmental variables for phytoplankton com-

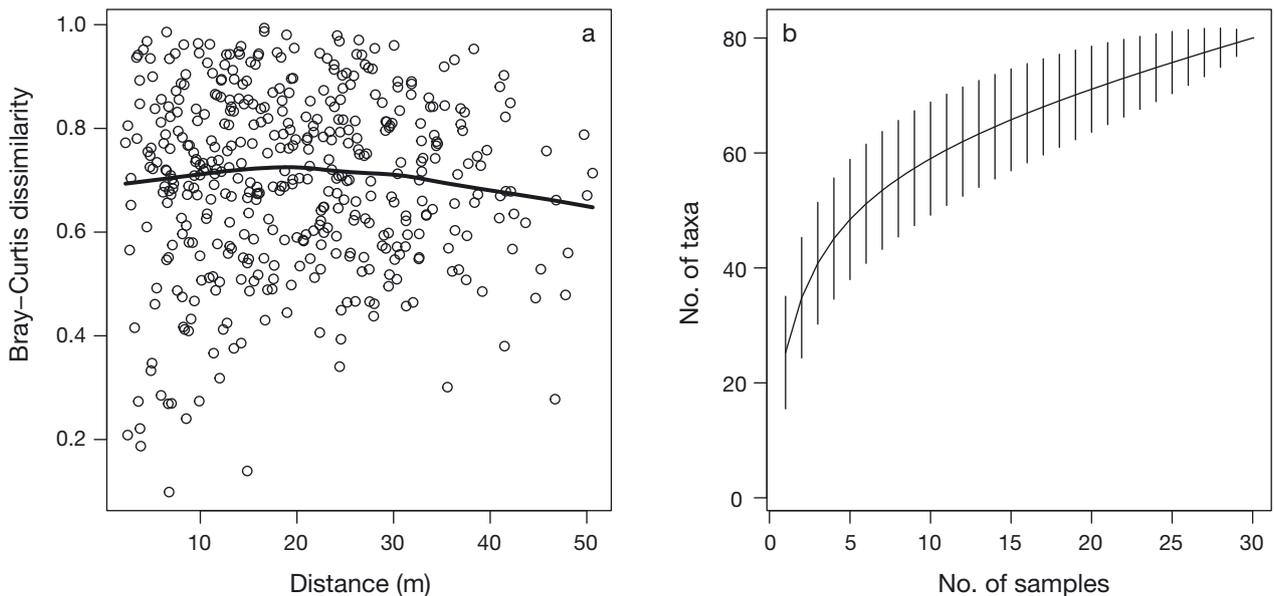


Fig. 4. (a) Beta diversity of phytoplankton communities presented as Bray-Curtis dissimilarities (based on species abundance data) in relation to spatial distance. Each data point represents the Bray-Curtis dissimilarity score for pairwise samples and the corresponding overland distance. The lowest curve was calculated with the lowest function (Cleveland 1981) in R, using locally-weighted polynomial regression. (b) Taxa-accumulation curve for phytoplankton samples illustrating the cumulative number of taxa with increasing sampling effort (pools 1 to 30). Error bars are SD

Table 1. Results of redundancy analyses (RDA), which were conducted separately for overland and watercourse distances (variables of principal coordinates of neighbour matrices (PCNM))

| Analysis | Proportion of the all constrained axes (variance explained by spatial and environmental variables) (%) | Proportion explained by RDA axis 1 (%) | Proportion explained by RDA axis 2 (%) |
|--|--|--|--|
| Overland PCNM + environmental variables | 40.41 | 16.72 | 9.42 |
| Watercourse PCNM + environmental variables | 42.16 | 20.60 | 10.11 |

position were conductivity, depth and pool volume (Fig. 5). The subsequent permutation analysis revealed that none of the effects of the overland distances were significant, while the effects of temperature and conductivity on phytoplankton were significant ($p < 0.05$) (Table 2).

Environmental variables and watercourse distances

Local environmental variables and watercourse distances explained 42% (R^2) of the phytoplankton community variation; 20.6% were explained by axis 1 and 10.1% by axis 2 (Table 1, Fig. 5). According to permutation analysis, the most influential variables were conductivity ($p < 0.05$), temperature ($p < 0.05$) and PCNM2 ($p < 0.1$) (Table 2).

Variation partitioning

Environmental variables and overland distances

Local environmental variables and overland distances explained together only 13.5% (adjusted R^2) of the phytoplankton community variation (Fig. 6) with a high residual variation (91%). The shared variation of environment and space had the largest influence on the community variation (12.3%), while pure overland distances did not show any influence on community variation (negative fraction).

Environmental variables and watercourse distances

The phytoplankton community composition was better explained (adjusted R^2 20.1%) when the com-

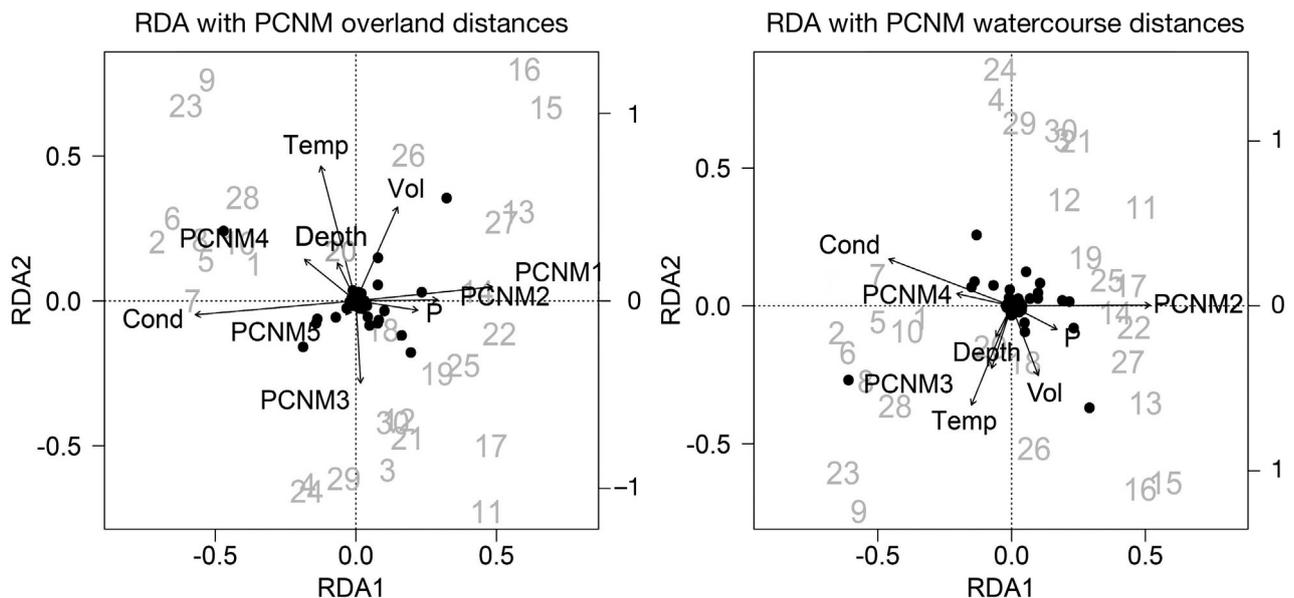


Fig. 5. Redundancy analyses (RDA) showing the importance of environmental and spatial variables (left: overland distances; right: watercourse distances) on the phytoplankton community composition. Abbreviations: Cond = conductivity ($\mu\text{S cm}^{-3}$); P = total P ($\mu\text{g l}^{-1}$); depth = pool depths (cm); Vol = pool volume (cm^3); Temp = water temperature ($^{\circ}\text{C}$). PCNM 1 to 5 (left) = significant PCNM variables constructed for overland distances; PCNM 2 to 4 (right) = significant PCNM variables constructed for watercourse distances. Phytoplankton taxa are represented as black dots and numbers of the rock pools are shown in grey

Table 2. Results of the permutation analysis (anova.cca) with 1000 permutations for evaluation of the significance of each variable in the redundancy analysis. The analysis was conducted separately for overland and watercourse distance matrices using principal coordinates of neighbour matrices (PCNM). *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$

| Analysis | Variables | p-value |
|--|--------------|----------|
| Overland PCNM + environmental variables | PCNM 1 | 0.90 |
| | PCNM 2 | 0.54 |
| | PCNM 3 | 0.82 |
| | PCNM 4 | 0.24 |
| | PCNM 5 | 0.50 |
| | Temperature | 0.03* |
| | Conductivity | 0.01** |
| | P | 0.41 |
| | Depth | 0.56 |
| | Volume | 0.23 |
| Watercourse PCNM + environmental variables | PCNM 2 | 0.058 |
| | PCNM 3 | 0.165 |
| | PCNM 4 | 0.194 |
| | Temperature | 0.042* |
| | Conductivity | 0.001*** |
| | P | 0.267 |
| | Depth | 0.460 |
| | Volume | 0.233 |

combination of watercourse distances and local environmental variables was used (Fig. 6). Local environmental variables explained 5.1% of variation, watercourse distances explained 6.6% and the shared variation was 8.4%.

DISCUSSION

The degree of beta diversity of the phytoplankton communities among the rock pools was relatively high in spite of the fine spatial scale of the study, as revealed by overall high Bray-Curtis dissimilarities

among the communities and the taxon-accumulation curve. This indicates that either mechanisms such as competition or drift took place or that local communities were shaped by environmental variation among pools (species sorting) or dispersal-related processes. Most importantly, models based on watercourse distances better represented the spatial structure of the phytoplankton metacommunity than overland distances, even though watercourse and overland distances were positively correlated. This indicates that phytoplankters were probably predominantly dispersed via watercourses among the pools. Consequently, random dispersal and subsequent community assembly via wind or animal vectors may have been less important in this system (Liu et al. 2013). This outcome is contrary to findings by Beisner et al. (2006), who reported that overland and watercourse distances were equally related to the phytoplankton community structure in 18 lakes, while covering a larger spatial scale than was considered here. However, our results are in line with the studies of Landeiro et al. (2011) and Liu et al. (2013), who documented that in riverine systems, watercourse distances provided a better representation of the spatial structure of benthic diatom communities. Thus, considering among-site connectivity via actual watercourses is essential for better understanding spatial coexistence mechanisms for phytoplankton communities as well. The present results further highlight that the usage of different distance matrices may largely influence the outcome of spatial analyses and their interpretations within the metacommunity context.

The phytoplankton community was predominantly patchily distributed, meaning that the community structure of neighbouring rock pools was only slightly more similar to the focal community than to the community of more distant rock pools (Pellowe-

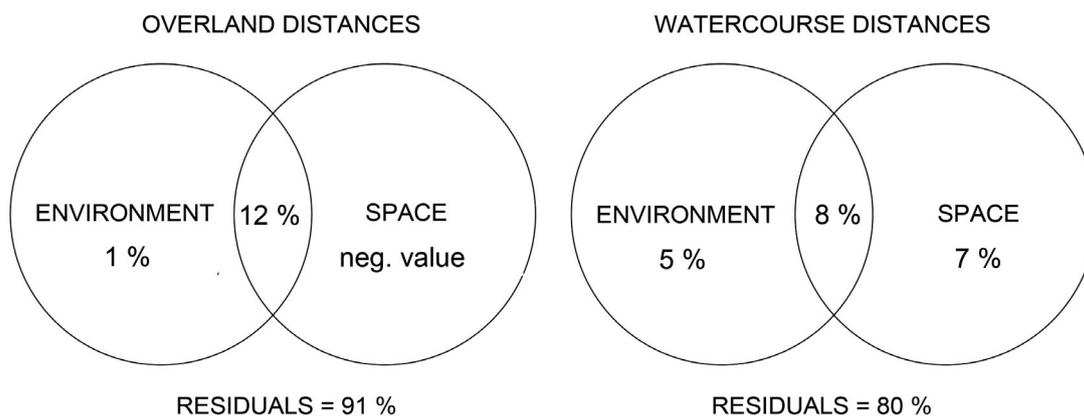


Fig. 6. Variation partitioning of phytoplankton communities using overland and watercourse distances

Wagstaff & Simonis 2014). This may be attributed to patchy local environmental conditions in the pools, as revealed by Soininen & Meier (2014) and also found by Östman & Langenheder (2013) for bacterial rock pool community composition. For example, total P varied by an order of magnitude among the pools and overall variation in water chemistry (especially in conductivity) affected the variation in community structure. Prominent examples of the patchy community structure were the occurrence of 3 distinct monospecific algal blooms, which were found at intermediate P levels. Both high biovolumes and nutrient concentrations were not mitigated by fluxes of organisms or nutrients among the well-connected pools.

The patchy metacommunity structure may result from occasional mass effects shaping the rock pool phytoplankton community structure when the entire system is overflowed during snow melt or heavy rainfall. Rather than homogenizing the phytoplankton across rock pools (Martiny et al. 2006), high turnover rates during mass effects may temporarily increase among-pool community variation (Pellowe-Wagstaff & Simonis 2014), which may be fostered by priority effects. Eventually, high levels of immigration may result in a mismatch of community similarity and fine-scale variability in environmental conditions, thus leading to purely spatial imprints (Van der Gucht et al. 2007, Lear et al. 2014), which we indeed found when watercourse distances were used. When connections dry out and watercourse dispersal becomes limiting, species are hindered from reaching suitable habitat patches and differences in community composition manifest—thereby further weakening the strength of species sorting (DeBie et al. 2012). Random terrestrial or faunal fertilization may then lead to rapid shifts in the phytoplankton community structure, further disassembling the communities and resulting in a patchy distribution.

The total explained community variation was relatively low, although we did find evidence that the community was shaped both by dispersal via watercourses and species-sorting mechanisms. At least 80% of the community variation remained unexplained in the variation partitioning, which may be attributed to our snapshot sampling strategy. With such sampling, we could not cover the high temporal variation in environmental conditions, in the disturbance (desiccation and overflow) regime and in the resulting community turnover (Korhonen et al. 2010, Langenheder et al. 2012, Liu et al. 2013, Pellowe-Wagstaff & Simonis 2014). However, this relatively high residual variation is in line with several other

studies. A meta-analysis by Cottenie (2005) showed that in systems with ≤ 30 sites, 20 to 80% of the community variation could be explained by spatial and environmental variables—even if wider spatial scales were considered. The high residual variation may result from unmeasured environmental variation, low taxonomic resolution, patch history, priority effects or intrinsic variability (demographic stochasticity) of the community assembly (Cottenie 2005, Vanschoenwinkel et al. 2007, Fox et al. 2010, DeBie et al. 2012, Liu et al. 2013). Alternatively, it could also be ascribed to grazing effects, which may cause shifts in the algal community composition (Pellowe-Wagstaff & Simonis 2014). Moreover, a permanent seed bank, from which rock pools may be colonized, could counterbalance directed species flows (colonization and competition) (Pellowe-Wagstaff & Simonis 2014).

CONCLUSIONS

We found that watercourse distances provided a better representation of the spatial structure in phytoplankton communities in this rock pool system. This may suggest that among-pool dispersal of the phytoplankton was mainly restricted to watercourses at fine spatial scales. Further, the fine-scale environmental variation was relatively high in this pristine ecosystem. Despite the fact that pools were well connected, this patchy structure was maintained and not mitigated by nutrient and organismal fluxes, presumably indicating dispersal limitation.

From the perspective of applied science, such a substantial fine-scale spatial variation in phytoplankton could have important implications for future sampling strategies in small lentic water bodies—researchers should be aware of the relatively large fine-scale variation in phytoplankton communities and environmental conditions. As the sampling scale is likely to determine the degree of environmental and spatial influence on biotic communities, appropriate scales for plankton sampling need to be further examined (Lear et al. 2014). Future metacommunity studies should thus focus more on the fine-scale variation in biotic communities and abiotic environment to reveal coexistence mechanisms that generate and maintain beta and gamma diversity (DeBie et al. 2012).

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