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High assemblage persistence in heterogeneous habitats: an experimental test with stream benthic algae

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SUMMARY

1. The persistence of biological assemblages is positively affected by spatial heterogeneity. This influence may be indirect, through increased species richness. Another possibility is the increased availability of refuges from disturbances, which would prevent local loss.
2. We conducted a field experiment to test the hypothesis that greater roughness (a form of spatial heterogeneity) on the surface of substrata allows higher persistence of assemblages of stream benthic algae and that this relationship does not depend on species richness. Samples were taken on six occasions from smooth and rough artificial substrata used for algal colonisation. We calculated the persistence of assemblages using two analytical approaches: the mean distance to group centroid and the sum of the Euclidean distances between consecutive sampling occasions, both in a multivariate space. We also subsampled the data to take into account differences in species richness between treatments and thus to evaluate the effect of species richness on persistence.
3. Assemblages on rough substrata were more persistent than assemblages on smooth substrata. The effects detected were not due to the greater species richness on rough substrata, since a higher persistence of the assemblages on rough substrata remained after the subsampling procedures.
4. Our results indicate a strong positive relationship between substratum roughness and the persistence of stream benthic algal assemblages. We suggest that this is due to the presence of physical refuges in heterogeneous habitats.

Keywords: periphyton, refuges, spatial heterogeneity, substratum roughness, temporal variability

Introduction

Assemblages vary in space and time, and it is of major importance to identify the mechanisms responsible for this variability, as this information may provide insights into the processes governing the assembly of communities and the functioning of ecosystems. For instance, understanding the temporal variability of assemblages is important for both basic and applied ecology, since it may enhance our ability to detect and predict impacts and thus improve management and conservation efforts (Cottingham, Brown & Lennon, 2001).

The temporal variability of assemblages is profoundly influenced by the physical environment, particularly its temporal stability, and by biotic interactions (Bengtsson, Baillie & Lawton, 1997). In aquatic ecosystems, some studies suggest that the persistence of assemblages [i.e. '…constancy in absolute abundance, abundance ranking, or the presence or absence of species over time', accordingly to Rahel (1990)] is shaped by interspecific interactions, while others show that the persistence of assemblages is most likely to be affected by environmental factors. For example, Hildrew & Townsend (1982) suggested that the dynamics of a stream insect community is dominated by predation, in which predatory insects determine the temporal variability of prey. On the other hand, Oberdorff, Hugueny & Vigneron (2001) found that the variability of stream fish assemblages decreased with

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environmental stability (i.e. less discharge variability), and Schneck *et al.* (2011a) showed the occurrence of patterns of increased persistence of phytoplankton assemblages with environmental stability in a subtropical reservoir. The relative role of biotic interactions and environmental factors in shaping the temporal variability of assemblages may be related to the harshness of the environment, with biotic interactions being more important in more stable environments, as suggested by Townsend, Hildrew & Schofield (1987).

Recently, physical spatial heterogeneity has been suggested to play a prominent role in the temporal variability of stream assemblages (Brown, 2003; Mykrä *et al.*, 2011). Although the increase in species richness as a result of spatial or habitat heterogeneity is widely recognised in ecology and has been documented for many taxa in a variety of environments (e.g. MacArthur & MacArthur, 1961; Taniguchi & Tokeshi, 2004; Thomaz *et al.*, 2008), the effect of spatial heterogeneity on the persistence of assemblages remains unclear (Kovalenko, Thomaz & Warfe, 2012). According to Brown (2003), two mechanisms inherent to spatial heterogeneity may affect the persistence of assemblages, either indirectly, through an increase in species richness, or directly, through an increase in the number of refuges. The first mechanism is related to the fact that heterogeneous habitats provide large quantities and wide varieties of resources and may allow resource partitioning and promote diversity (MacArthur & MacArthur, 1961). An increased diversity may increase the persistence of assemblages by reducing local extinction and/or colonisation rates, and thus preventing large population variability in assemblages with mostly weak interspecific interactions (McCann, Hastings & Huxel, 1998; Shurin *et al.*, 2007). Additionally, species richness may enhance the persistence of assemblages through statistical averaging, in which the fluctuation of individual species in species-rich assemblages will cause proportionally less temporal variability than in species-poor assemblages (Doak *et al.*, 1998).

The second mechanism through which spatial heterogeneity may affect persistence is by generating a high availability of physical refuges (Brown, 2003). Refuges may protect organisms against predation, disturbance and other adverse abiotic factors (Townsend & Hildrew, 1994; Bergey, 2005). This may prevent local losses that could occur as a result of increased population variability of one or more species in the face of disturbance (Pimm, 1991). Consequently, refuges tend to reduce the variability of assemblages. Additionally, the organisms protected within refuges can rapidly recolonise the habitat after an adverse condition ceases (e.g. Bergey, 2004).

The study conducted by Brown (2003) was the first to disentangle the effects of high species diversity and habitat heterogeneity on the persistence of assemblages. He took into account the effect of statistical averaging caused by increased species richness and found an increased persistence in stream invertebrate assemblages along a gradient of spatial heterogeneity. Accordingly, he concluded that the increased persistence was probably due to the larger number of refuges. However, Brown's (2003) study could have been partially confounded by the correlation between spatial heterogeneity and physical stability of the substratum. For instance, his three measures of spatial heterogeneity, the Simpson index, contagion and evenness, were correlated with the mean particle size of the substrata in each plot along the gradient of heterogeneity (0.75, −0.70 and 0.58, respectively; data from his Table 1), and coarse substrata lead to high assemblage persistence (Gurtz & Wallace, 1984). Accordingly, his observational study did not allow unequivocal conclusions as to whether the effect of habitat heterogeneity leads to high persistence of assemblages. We avoided this pitfall and reevaluated the hypothesis raised by Brown (2003), by conducting a field experiment in which we set up two treatments composed by smooth and rough artificial substrata for algal colonisation. The roughness of substrata (e.g. crevices, small projections), a type of small-scale spatial heterogeneity (Bergey, 2006), plays an important role in regulating the composition and structure of benthic algal assemblages in aquatic ecosystems such as marine intertidal rocky shores (Harlin & Lindbergh, 1977; Hutchinson *et al.*, 2006) and streams (Dudley & D'Antonio, 1991; Bergey, 2005), including increased species richness (Schneck, Schwarzbold & Melo, 2011b). We tested the hypothesis that small-scale spatial heterogeneity increases the persistence (or conversely, decreases the temporal variability) of stream benthic algae and that this relation does not depend on species richness.

Methods

Study area

We conducted the experiment in the Marco stream (28°36'S; 49°51'W), a fourth-order stream at an altitude of *c.* 1100 m asl, in the state of Rio Grande do Sul, southern Brazil. The regional climate is high-altitude subtropical, with uniform precipitation throughout the year. Annual mean rainfall ranges from 1400 to 2200 mm, and annual mean temperature ranges from 12 to 18 °C (Behling, 2002). The vegetation is *Campos* grassland with patches of Araucaria Forest. The stream drains a

catchment with low local human impact. The water is oligotrophic (Buckup *et al.*, 2007) and well oxygenated (10 mg L^{-1}), with a mean pH of *c.* 6.6, low conductivity (22 μS cm^{-1}) and a mean current velocity of 0.26 m s^{-1} during baseflow. The streambed is composed mainly of basaltic stones, boulders and bedrock. The stream width varies from 2 to 5 m, and the depth varies from 0.2 to 0.4 m in the reaches studied. In addition, the reaches studied are characterised by the absence of canopy cover, as the stream flows along a grassland plateau.

Experimental design

We designed a field experiment in which we used smooth and rough substrata as the two levels of substratum roughness. Samples were obtained every 15 days on six sampling occasions from May to July 2009 (austral autumn and winter) in 11 stream reaches that were at least 100 m apart from each other. On each sampling occasion, we sampled two substrata of each treatment per stream reach. Each pair of substrata collected under the same conditions was pooled for analysis and constituted one experimental unit (n = 132).

We used acrylic substrata (5 × 5 cm) with either a smooth surface or a surface with longitudinal crevices for algal colonisation. All rough surfaces had nine crevices, and all crevices were 1 mm in width and 1 mm in depth. We conducted pilot experiments to define the size of the crevices based on the study of Bergey & Weaver (2004), who found that algal assemblages remained protected within crevices with openings smaller than 2 mm. We glued the substrata on 50 × 50 × 8 cm flat pavers and placed one paver in each of the 11 stream reaches. On each paver, we arranged the substrata by alternating smooth and rough surfaces within six rows and six columns, in a manner that if the first substratum in a row had a smooth surface, the first substratum in the next row would have a rough surface. We removed the substrata in an upstream direction by first removing the first four substrata glued on the last row and leaving the last two substrata of this row to be removed at the second sampling occasion with the first two substrata of the penultimate row and so on. By doing so, we avoided changing the local hydraulic environment formed by the arrangement of substrata since the beginning of algal colonisation. It is worth noting that at each sampling occasion, one sampled substratum in each treatment was positioned at the edge, while the other was not. Since each paver had all substrata necessary for the six sampling occasions, we were able to minimise the variation of physical variables, such as current velocity and water depth, between treatments. The substrata had their crevices aligned perpendicular to the flow, and we left them in place to be colonised during a period of 45 days. We carried out the first sampling at the end of the 45-day colonisation period and subsequent samplings every 15 days, totalling six sampling occasions. Reaches (or pavers) were considered blocks in statistical analyses.

Sampling and laboratory analyses

We scraped the upper surfaces of the substrata with a toothbrush to remove the biofilm, adjusted the samples to a defined volume and preserved them with 4% formaldehyde (Lowe & LaLiberte, 2007). For each experimental unit, 500 cells or units (each unit corresponded to 10-μm-long fine-celled filaments of Cyanobacteria, hereafter referred to as cells for simplicity) were counted and identified, using an inverted microscope at 400× magnification. For the taxonomic identification of diatoms, additional subsamples were acid-cleaned using standard techniques (Lowe & LaLiberte, 2007) and examined at 1000× through a light microscope. We counted a standardised number of cells in each experimental unit to avoid the possible effects of higher abundance and area of the rough substratum on species richness. We calculated the number of cells per unit area (cm^2) to estimate cell density of each taxon and total cell density of each experimental unit. We identified 92 taxa of benthic algae. The benthic algal assemblage was composed mostly of diatoms, which comprised 56 species and 85% of the total cell density in both treatments. The dominant species in both treatments were the diatoms *Achnanthidium minutissimum*, *Cocconeis placentula* and *Ulnaria ulna*. Species richness on smooth substrata ranged from 10 to 26 taxa (mean 18) and on rough substrata from 15 to 38 taxa (mean 26). Additional details on the experiment and on the composition of the assemblage can be found in Schneck *et al.* (2011b).

Data analyses

To ensure that our results were not dependent on the method, we used two approaches to test for differences in the persistence of assemblages between smooth and rough substrata. In the first, the distances from individual experimental units to their group centroid (the point that minimises the sum of distances to points within a group, also known as the spatial median) in multi-dimensional space obtained in a principal coordinates analysis (PCoA) were used as a measure of the variability of assemblages (Anderson, 2006). These distances should be small when assemblage composition or structure does not experience

considerable change in time. That is, according to the hypothesis under test, the mean distance to the group centroid should be smaller for rough than for smooth substrata. PCoAs were generated for both qualitative (presence–absence; Sørensen dissimilarity index) and two forms of quantitative data (density; Bray–Curtis index). The first form consisted of log-transformed data, and the second of standardisation by the species maximum. In the qualitative analysis, rarity is not taken into account, and all species have the same importance in the analysis. Using the data standardised by the maximum, species still retain the same overall importance, but relative densities are maintained within species. Log-transformed data maintain part of the original relative densities and importance of each species. The use of presence–absence and log-transformed data and the cited dissimilarity indices is equivalent to the use of the NESS index with different weights given to rare species (Trueblood, Gallagher & Gould, 1994). Since the use of non-metric dissimilarity coefficients may produce principal coordinate axes with negative eigenvalues, we computed the square root of distances before the analyses (Legendre & Legendre, 1998). We conducted separate PCoAs for each stream reach (block) and used the mean multivariate distances to the group centroid of each treatment per block to perform a one-tailed paired *t*-test for each type of data. The option to use a one-tailed test is in accordance with the hypothesis of Brown (2003) that spatial heterogeneity should increase persistence.

In the second approach, we conducted a procedure similar to that employed by Brown (2003) and Brown & Lawson (2010), which calculates the distance in the multivariate taxa space that an assemblage moved between sampling occasions (hereafter referred to as EDCA, i.e. Euclidean distance in a correspondence analysis space; Brown, 2003). For each type of data (presence–absence, log-transformed and standardised by species maximum), we first conducted separate correspondence analyses (CA) of the experimental units for each of the 11 blocks. Next, using the scores of experimental units in the first 11 CA axes, we calculated the Euclidean distance in the ordination space between experimental units of a given treatment on two consecutive sampling occasions. The distance between the experimental units for each interval is a direct measure of temporal variability, and the greater the Euclidean distance, the greater the variability of the assemblage (Brown, 2003). Since there were six sampling occasions, five intervals were calculated and summed to generate a total Euclidean distance for each treatment per block. We used these total Euclidean distances for the two treatments to perform a one-tailed paired *t*-test for each type of data.

We conducted subsampling procedures to investigate the effect of increased species richness on the persistence of assemblages, since rough substrata were more species-rich than smooth substrata (Schneck *et al.*, 2011b). The procedure was conducted for each of the two approaches and for all three types of data (presence–absence, log-transformed and standardised by species maximum). First, we randomly subsampled the species on the richest treatment of each of the 11 blocks to contain the same number of species of the poorest treatment in the block. For the first approach, we conducted a separate PCoA for each of the 11 blocks using the subsampled data of the richest treatment and the observed data of the poorest treatment, followed by calculation of the mean distance to the group centroid in each block. For the EDCA approach, we conducted a CA for each block (also with the subsampled data of the richest treatment and the observed data of the poorest treatment), followed by calculation of the total Euclidean distance for each treatment. The procedure was repeated 100 times. Next, using all 100 subsamples, we calculated the mean distance to the centroid for each treatment per block (first approach) and the mean total Euclidean distances for each treatment per block (EDCA approach). Finally, we used the two sets of 11 pairs of values (rough and smooth treatments) to perform one-tailed paired *t*-tests. We conducted all analyses in the R environment (R Development Core Team, 2009) using functions in the *vegan* package (Oksanen *et al.*, 2010), and routines that we wrote for the subsampling procedures.

Results

Assemblages on rough substrata were less dispersed in the multivariate space of the PCoA (i.e. were more persistent) than assemblages on smooth substrata, for presence–absence ($F_{1,10} = 44.27$; $P < 0.001$), log-transformed ($F_{1,10} = 37.00$; $P < 0.001$) and standardised by species maximum data ($F_{1,10} = 28.67$; $P < 0.001$) (Fig. 1a). The subsampling procedures indicated that the persistence of assemblages on rough substrata remained higher than the persistence on smooth substrata for all types of data, even after taking into account differences in species richness between treatments ($F_{1,10} = 43.91$; $F_{1,10} = 36.22$; $F_{1,10} = 24.74$, respectively, for presence–absence, log-transformed and standardised data; in all cases $P < 0.001$; Fig. 1a).

Similarly, the EDCA approach indicated that the assemblages on rough substrata were more persistent than the assemblages on smooth substrata, for presence–absence, log-transformed and standardised by species

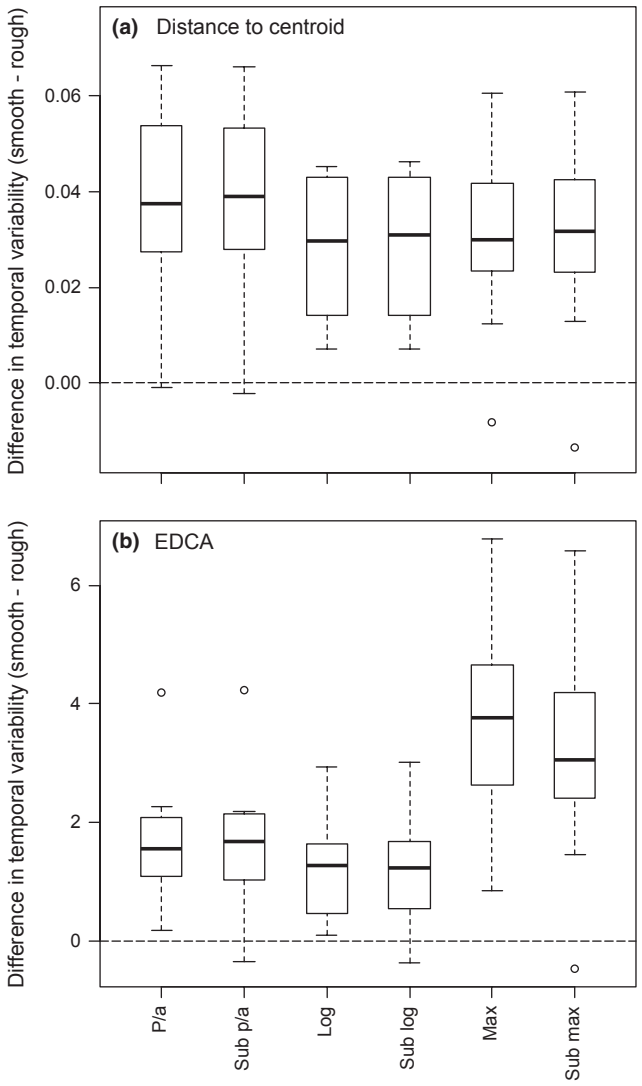

Fig. 1 Box-and-whisker plot of difference in the temporal variability of stream benthic algal assemblages on smooth and rough substrata (distances smooth – distances rough) for (a) mean distances to the group centroid in the multi-dimensional space obtained in a principal coordinates analysis (PCoA) and (b) total Euclidean distance of the assemblage along the six sampling occasions in the space obtained by a multivariate correspondence analysis (EDCA). The experiment was carried out in 11 blocks, and the hypothesis of differences in temporal variability (or persistence) between assemblages was tested using paired *t*-tests. Therefore, differences between treatments are presented rather than mean values. The dashed horizontal lines indicate the case of no difference between smooth and rough substrata. The minimum and maximum (whiskers), the lower and upper quartiles (box ends), the median (heavy line) and the outliers (open circles) for each type of data are shown. P/a, presence–absence data; Sub p/a, subsampled presence–absence; Log, log-transformed; Sub log, subsampled log-transformed; Max, standardised by the species maximum; Sub max, subsampled standardised by the species maximum.

maximum data ($F_{1,10}$ = 24.67; $F_{1,10}$ = 20.71; $F_{1,10}$ = 51.46, respectively; in all cases $P < 0.001$; Fig. 1b). These results persisted after the subsampling procedure ($F_{1,10}$ = 20.35; $F_{1,10}$ = 18.31; $F_{1,10}$ = 32.12, respectively, for presence–absence, log-transformed and standardised data; in all cases $P < 0.001$; Fig. 1b).

Notably, the persistence was higher for assemblages on rough substrata in 31 of the 33 (11 blocks and three data types) pairs in the distance-to-centroid approach and in all 33 pairs in the EDCA approach for the observed data set. In the cases of subsample data, persistence on rough substrata was higher than on smooth substrata in 31 of the 33 pairs for the distance-to-centroid approach and in 30 of 33 pairs for the EDCA approach, indicating a strong effect of substratum roughness. Further, for the observed data set, the persistence increased on average 9.43, 6.90 and 5.45% in the distance-to-centroid approach (for presence–absence, log-transformed and standardised by species maximum data, respectively), and 18.30, 14.91 and 25.44% in the EDCA approach. For the subsampled data set, there was an increase of 9.43, 6.83 and 5.41% in the distance-to-centroid approach (for presence–absence, log-transformed and standardised by species maximum data, respectively), and of 17.54, 14.37 and 21.64% in the EDCA approach.

Discussion

The results agree with the hypothesis raised by Brown (2003) that spatial heterogeneity increases the persistence of assemblages. Our results also show that the increase in persistence was not influenced by the potential underlying mechanisms intrinsic to spatial heterogeneity that may affect the temporal variability of assemblages (e.g. physical stability and species richness). The experiment was carried out within blocks in which the substrata for both treatments were subjected to the same physical conditions, enabling an effective control of possible confounding factors and thus a response that is unequivocally attributed to spatial heterogeneity (i.e. substratum roughness).

The positive effect of substratum roughness on the persistence of stream benthic algal assemblages was irrespective of the role that rare and dominant species might play in affecting the temporal variability, as the data emphasising different aspects of the assemblage structure showed similar results. Accordingly, high persistence in spatially heterogeneous habitats should be valid for both rare and common species.

We suggested that the effects of spatial heterogeneity on the persistence of assemblages in the study of Brown (2003) may have been confounded by its correlation with the stability of the physical habitat. In his study, the size of the substrata and the bryophyte cover may have increased not only the spatial heterogeneity, but also the stability of the habitat for invertebrates (Gurtz & Wallace, 1984; Suren

et al., 2000). Similarly, Mykrä *et al*. (2011), in a study that involved multiple streams across a wide range of disturbance regimes, found a high persistence of stream invertebrates in heterogeneous habitats, defined as those with high bryophyte cover. They inferred that the bryophyte cover provides refuges and thus favours high persistence of assemblages. However, the authors recognised that bryophytes grow preferentially on stable substrata (Stream Bryophyte Group, 1999; Suren & Duncan, 1999) which, in turn, could have been the cause of the observed high persistence of invertebrate assemblages. Our experiment was set up to avoid this correlation, as both types of substrata were equally stable and subject to the same physical environment.

The subsampling procedures indicated that the higher persistence of the assemblages on rough substrata was related to the effect of substratum roughness *per se*, rather than to the increased species richness on these substrata. Since the substrata were very simple in design, and the only difference between the two treatments was the presence or absence of crevices, the most plausible mechanism that could mediate the higher persistence on rough substrata is the occurrence of refuges. The efficacy of refuges in protecting algae from disturbance has been shown by some studies. For instance, Bergey (2005) quantified the protection of algae within crevices after an experimental disturbance caused by scrubbing and found that the amount of total biomass that remained on stones increased with surface roughness, concluding that physical refuges (i.e. crevices) effectively protected the algae. Refuges have also been shown to be effective in protecting algae from grazers (Dudley & D'Antonio, 1991). Further, a study combined with the present experiment showed that the two types of substrata differed in the composition of assemblages (Schneck *et al*., 2011b). Motile, metaphytic and filamentous algal life forms were more species-rich and dense on the rough substrata, whereas adnately attached and prostrate algae did not differ in species richness and density between the substrata. Notably, the algal life forms that showed a positive response to substratum roughness are those most likely to benefit from the occurrence of refuges. For instance, crevices may enhance the protection of motile and metaphytic algae, which may also benefit from the availability of resources within crevices (Murdock & Dodds, 2007). Further, filamentous algae were shown to settle preferentially in crevices (Dudley & D'Antonio, 1991).

Our experiment provided clear-cut evidence of the major role that small-scale spatial heterogeneity plays in the persistence of stream benthic algal assemblages. The results also reinforce the hypothesis that the occurrence of physical refuges in heterogeneous habitats is an important ecological factor, especially in frequently disturbed ecosystems.

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