

Hydrological disturbance overrides the effect of substratum roughness on the resistance and resilience of stream benthic algae

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SUMMARY

1. Habitat heterogeneity in lotic systems is usually associated with the availability of refuges. Heterogeneous habitats (here, rough substrata) should mediate the effect of high-flow disturbances by protecting benthic algae, thus increasing the resistance and resilience of the system. Additionally, the ability of algae to resist a disturbance and recover after it should be dependent on biological traits that confer resistance and resilience.
2. We designed a field experiment, simulating a high-flow event with bed movement, to test the effect of substratum roughness on the resistance (assessed as the similarity between samples collected before and immediately after disturbance) and resilience (the similarity between samples collected before and 7 and 15 days after disturbance) of five algal life forms. We evaluated whether algal resistance and resilience were higher on rough than on smooth substrata, and whether the life forms differed in their ability to resist and recover from a disturbance.
3. Rough substrata had higher species richness than smooth substrata at all sampling periods, even immediately after the disturbance. There was no significant effect of substratum roughness on algal resistance and resilience, for both species richness and density of the total assemblage. Neither did roughness affect the resistance and resilience of the total algal assemblage or of the algal life forms separately, when evaluated using multivariate data sets (presence-absence and quantitative).
4. Algal life forms differed in resistance and resilience; adnate/prostrate and erect/stalked species were more resistant and resilient than the other life forms (filamentous, motile and metaphytic). Additionally, motile species resisted and recovered better than did species that are only loosely associated with the substratum (metaphytic species).
5. Substratum roughness had no pronounced effect on benthic algal resistance and resilience. The results of this and some other studies suggest that the intensity of disturbance determines the importance of habitat heterogeneity and flow refuges for benthic algae in streams.

Keywords: algal life form, floods, habitat heterogeneity, periphyton, refuges

Introduction

Natural physical disturbances are major components of many ecosystems and generate much of the spatial and temporal heterogeneity in the functioning of communities (Sousa, 1984; Townsend, 1989). In streams, disturbances caused by high-flow events play a key role, as they

rearrange the physical environment and reorganise the structure and dynamics of assemblages (Lake, 2000; Death, 2010). For example, hydrological disturbances can reduce algal biomass (Grimm & Fisher, 1989) and the abundance of invertebrates (Melo *et al.*, 2003) and macrophytes (Riis & Biggs, 2003), affect species richness (Melo *et al.*, 2003; Cardinale, Hillebrand & Charles, 2006)

and patchiness (Matthaei, Guggelberger & Huber, 2003; Melo *et al.*, 2003) and alter ecosystem metabolism (Bertrand *et al.*, 2009).

One factor likely to mediate the effects of hydrological disturbances is habitat heterogeneity (Lancaster & Hildrew, 1993; Brown, 2007), which can be recognised at different spatial scales, from catchments (Vannote *et al.*, 1980) to microhabitats (Bergey, 2005; Costa & Melo, 2008). Habitat heterogeneity generates distinct habitats that are affected to different degrees by high flows, so that more stable and sheltered patches may act as refuges, protecting organisms against hydraulic stress (Townsend, 1989; Palmer *et al.*, 1996). Similarly to habitat heterogeneity, flow refuges occur at many spatial scales. In large basins, side channels in floodplains can act as refuges (Sedell *et al.*, 1990), while at the scale of stream reaches, refuges may be provided by areas of reduced flow (Lancaster & Hildrew, 1993) and patches of stable streambed (Matthaei, Arbuckle & Townsend, 2000). At fine scales, rough substrata (Bergey & Resh, 2006) were found to protect organisms during high-flow events. Organisms protected within refuges are able to resist disturbances and to recolonise the habitat shortly after the disturbance (Lancaster & Hildrew, 1993). The availability of refuges may increase the resistance of the biota to flow disturbance and provide propagules to the affected patches, increasing the resilience of the system (Lake, 2000).

The surface roughness of substrata, formed of crevices, pits and small projections, plays an important role in regulating the structure of benthic algal assemblages in streams (Bergey, 2005; Schneck, Schwarzbald & Melo, 2011). Rough substrata influence algal colonisation (Bergey, Cooper & Phillips, 2010), support higher algal biomass (Bergey, 2005) and are more species-rich than smooth substrata (Schneck *et al.*, 2011). There is also strong evidence of the efficacy of crevices as refuges for algae (Dudley & D'Antonio, 1991; Bergey, 2005; Bergey & Resh, 2006). Therefore, we could expect assemblages on rough substrata to be more resistant to disturbances and to recover more quickly (i.e. show higher resilience) than assemblages on smooth substrata.

Additionally, the ability of benthic algae to resist and to recover after a disturbance depends on their biological characteristics (Peterson, 1996). For instance, algal assemblages usually shift from dominance by upright species to dominance by tightly attached species after disturbances (Peterson & Stevenson, 1992; Francoeur, Biggs & Lowe, 1998). Adnate species with prostrate growth forms have tight adhesion structures and live on the understory layer of the biofilm, features that render them resistant to disturbance (Steinman & McIntire, 1990; Peterson &

Stevenson, 1992). Other algae, such as motile and metaphytic species, are less resistant and may benefit mostly from the presence of refuges (Murdock & Dodds, 2007; Schneck *et al.*, 2011).

We evaluated experimentally the effect of substratum roughness on the resistance and resilience of five algal life forms following a hydrological disturbance. Specifically, we tested the hypotheses that (i) resistance and resilience of algal assemblages would be higher on rough than on smooth substrata and (ii) the five algal life forms would differ in their ability to resist and recover after a hydrological disturbance. For this last hypothesis, we predicted that the adnate/prostrate life form would be more resistant and resilient than the other life forms and that the metaphytic life form would be the least resistant and resilient.

Methods

Study site

We conducted the experiment in the Marco stream (28°36'S; 49°51'W), São José dos Ausentes, state of Rio Grande do Sul, southern Brazil. The vegetation is *Campos* grassland with patches of Araucaria Forest, and the climate is high-altitude subtropical (Cfb), with uniform precipitation throughout the year (Behling, 2002). The stream is fourth order at an altitude of approximately 1100 m asl, and the water is oligotrophic (Buckup *et al.*, 2007), well oxygenated (10 mg L⁻¹), slightly acidic (pH 6.6) and with low electrical conductivity (22 µS cm⁻¹). The mean current velocity is 0.26 m s⁻¹. Stream width varies from 2 to 5 m, and the depth varies from 0.2 to 0.4 m in the reaches studied. The streambed is composed mostly of basaltic stones, boulders and bedrock.

Experimental design and biological analyses

We evaluated the effects of substratum roughness on the resistance and resilience of algal life forms through a field repeated-measures experiment designed in blocks (11 reaches that were at least 100 m apart from each other in the stream). We used smooth and rough substrata as the two levels of substratum roughness and took samples on four occasions: immediately before, immediately after, 7 days after and 15 days after the experimental disturbance. We sampled two artificial substrata of each type per block at each sampling occasion, giving a total of 176 sampling units. Each pair of sampling units was pooled to produce one experimental unit so that the experiment consisted of 88 experimental units (two substratum

types \times four sampling occasions \times 11 blocks). Samples collected immediately before the experimental disturbance were considered as the control. Samples collected immediately after the disturbance were used to measure resistance, while samples collected 7 and 15 days after the disturbance measured the resilience of assemblages.

We used acrylic substrata (5 \times 5 cm) as sampling units for algal colonisation. The smooth substrata had an even surface, and the rough substrata had a surface with nine longitudinal crevices. All crevices had the same width (1 mm) and depth (1 mm). The size of the crevices was defined during pilot experiments and following the study of Bergey & Weaver (2004), who found that crevices with openings smaller than 2 mm protected algal assemblages. We glued the substrata on 50 \times 50 \times 8 cm flat basalt pavers and placed one paver in each of the 11 stream reaches with the substratum crevices aligned across the current. We glued the substrata in a non-random manner by alternating smooth and rough surfaces, and arrayed them in six rows of six substrata each, giving 36 substrata per paver (16 of these were used in this study). On each paver, we removed the substrata in an upstream direction. That is, we first removed the substrata glued on the last row, followed by the penultimate row and so on. Our intention was thus to avoid disturbing the remaining substrata as much as possible and also to avoid changing the local hydraulic environment formed by the arrangement of substrata since the beginning of algal colonisation. We placed the basalt pavers with the artificial substrata in the stream in April 2009 for algal colonisation and conducted the study during July and August 2009.

We used a water compressor and a hose to simulate a high-flow event (mean current velocity 2.08 m s⁻¹, a velocity eight times higher than the mean current velocity at base flow). While the water flowed from the hose, we continuously added 2 L of sediment to the section of the stream that was being disturbed to simulate the movement of suspended sediment caused by floods. The sediment was removed from the stream bank and sieved through a 1 mm mesh. The experimental disturbance was applied for 10 min in each of the 11 blocks. The disturbance was enough to suspend sediments from the bottom and to move small stones (the streambed is mainly composed of boulders and bedrock, so only small stones were moved). A similar experimental disturbance was employed by Melo *et al.* (2003) and significantly reduced species richness and abundance of stream invertebrates.

We scraped the upper surfaces of the substrata with a toothbrush to remove the biofilm and preserved the samples with 4% formaldehyde (Lowe & LaLiberte, 2007). We counted 500 cells or units (each unit corresponded to

10- μ m-long cyanobacterial filaments with fine cells that are difficult to discern) from each experimental unit within a known number of fields (with a known area), using an inverted microscope at 400 \times magnification. We calculated the number of cells per unit area (cm²) to estimate the cell density of each species and total cell density of each experimental unit. We used additional subsamples to mount glass slides, using standard techniques to identify diatoms to species (Lowe & LaLiberte, 2007).

We classified algae into five life forms: (i) adnate and/or prostrate (species of *Achnanthes*, *Achnantheidium*, *Cocconeis*, *Coleochaete*, *Epithemia*, *Psammothidium* and *Rhopalodia*), (ii) erect or with mucilage stalks or tubes (species of *Cymbella*, *Encyonema*, *Eunotia*, *Fragilaria*, *Gomphonema*, *Meridion*, *Synedra* and *Ulnaria*), (iii) motile algae (species of *Frustulia*, *Hantzschia*, *Luticola*, *Navicula*, *Neidium*, *Nitzschia*, *Pinnularia*, *Sellaphora*, *Stauroneis* and *Surirella*), (iv) filamentous (species of *Aulacoseira*, *Bulbochaete*, *Heteroleibleinia*, *Melosira*, *Oedogonium*, *Stigeoclonium*, an unidentified filamentous green alga and an unidentified filamentous desmid) and (v) metaphyton (species of *Cosmarium*, *Euastrum*, *Pleurotaenium*, *Scenedesmus*, *Staurastrum* and unidentified Chlorococcales). Some genera could fit in more than one life form group, such as *Epithemia* and *Rhopalodia*. Although they may be motile, these genera are commonly described as adnate or prostrate (Biggs, Stevenson & Lowe, 1998; Lowe, 2003), and therefore, we opted to assign them to the latter life form. Other genera, such as the diatoms *Aulacoseira* and *Melosira* or some green algae, are filamentous algae that are not attached to substratum, but live entangled with other algae or substrata (Stevenson, 1996; Biggs *et al.*, 1998). We based our classification on algal physiognomies, personal observations and information provided by Lowe, Golladay & Webster (1986), Round, Crawford & Mann (1990), Biggs *et al.* (1998), Wehr & Sheath (2003), Bixby *et al.* (2009), Spaulding, Lubinski & Potapova (2010) and Lange *et al.* (2011).

Data analysis

We used a two-factor analysis of variance with repeated-measures in both factors (i.e. substratum roughness and time; RM-ANOVA) to test for the effect of substratum roughness on species richness and log (density +1) of algae after the experimental disturbance. In this analysis, pavers containing the artificial substrata represented the unit in which the trials were obtained, also termed the 'subject'. We corrected *P*-values using the Huynh-Feldt method for RM-ANOVA (Looney & Stanley, 1989). In case of significant time effects, we made *post hoc* pairwise

comparisons based on estimated marginal means between the sampling occasions, and *P*-values were adjusted for multiple comparisons (Bonferroni correction). We used the Bray–Curtis similarity index on log (density + 1) and its qualitative version, the Sørensen index (presence–absence data; Legendre & Legendre, 1998), to calculate the resistance and resilience of each algal life form on smooth and rough substrata. We defined a resistance index as the similarity between the control samples and the samples collected immediately after the disturbance. A resilience index was obtained separately for 7 and 15 days after the disturbance, using the similarity values between the control samples and the samples from each date. We excluded from analysis one experimental unit of the metaphytic life form on the smooth substratum because no cells of this group were found in the control sample, and only two cells were found in each of the post-disturbance samples, preventing the calculation of reliable values for the indices. We carried out an analysis of variance (ANOVA) for each index, using the values obtained for each algal life form in each treatment per block (for both qualitative and quantitative data). The models in the ANOVAs included life form and substratum type as factors, plus their interaction and the block factor. In all cases, we used the logarithm of the indices to meet the assumption of normality and homoscedasticity. If the results of life forms were significant, we performed Tukey HSD *post hoc* tests for pairwise comparisons. We present the results of ANOVAs using the original values of *P* and discuss them based on the adjusted α value after the conservative Bonferroni correction ($\alpha' = 0.008$). We also performed analyses after subdividing the filamentous group (heterotrichous growth form and long filaments) and the erect/stalked group, but we found similar results as the ones presented here. We conducted the analyses in the R environment (The R Development Core Team, 2009).

Results

We found 81 taxa of algae. The adnate/prostrate life form was dominant, comprising on average more than 45% of the total density on smooth and rough substrata on each sampling occasion (Fig. 1a). The relative density of this group also increased immediately after the disturbance, while that of all other life form groups decreased (Fig. 1). The erect/stalked life form was the second most common group, with an average relative density ranging from 28 to 42% (Fig. 1b).

There was no significant interaction between substratum type and time, either for species richness ($P = 0.201$) or density ($P = 0.096$) (Table 1), indicating that assem-

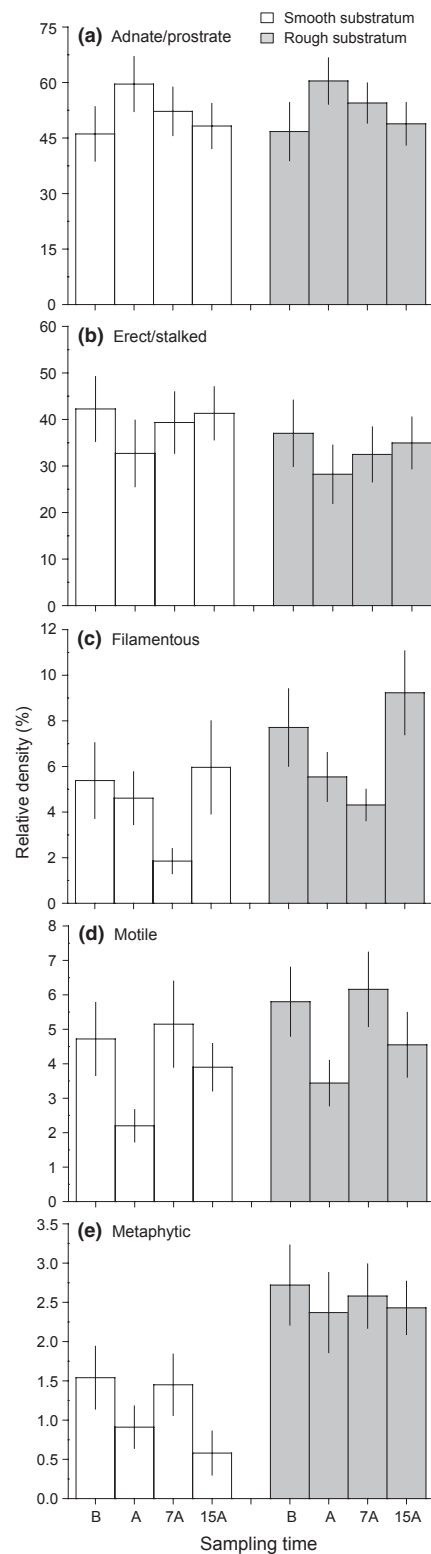


Fig. 1 Relative cell densities (mean \pm standard error) of adnate/prostrate (a), erect/stalked (b), filamentous (c), motile (d) and metaphytic (e) algal life forms on smooth and rough substrata at four sampling times during an experimental hydrological disturbance (B, before; A, immediately after; 7A, 7 days after; 15A, 15 days after the disturbance).

Table 1 Summary of the results of repeated-measures ANOVA for the effects of substratum roughness on species richness (a) and log (density +1) (b) of stream benthic algae after an experimental hydrological disturbance

| | df | MS | F | P | Pairwise comparisons |
|-----------------------|----|---------|---------|------------------|----------------------|
| (a) Richness | | | | | |
| Subject (Sj) | 10 | 31.420 | | | |
| Within-subjects | | | | | |
| Substrata (S) | 1 | 585.557 | 144.339 | <0.001 | Rough > Smooth |
| Sj × S | 10 | 4.057 | | | |
| Time (T) | 3 | 140.830 | 15.426 | <0.001 | (B, 7A, 15A) > A |
| Sj × T | 30 | 9.130 | | | |
| S × T | 3 | 12.890 | 1.641 | 0.201 | |
| Sj × S × T | 30 | 7.857 | | | |
| (b) Log (density + 1) | | | | | |
| Subject (Sj) | 10 | 15.961 | | | |
| Within-subjects | | | | | |
| Substrata (S) | 1 | 0.444 | 1.233 | 0.293 | |
| Sj × S | 10 | 0.360 | | | |
| Time (T) | 3 | 3.873 | 7.518 | 0.003 | B > A |
| Sj × T | 30 | 0.515 | | | |
| S × T | 3 | 0.214 | 2.313 | 0.096 | |
| Sj × S × T | 30 | 0.093 | | | |

The pavers containing the artificial substrata represented the unit in which the trials were obtained, also termed the 'subject'.

P-values were corrected using the Huynh-Feldt method for repeated-measures ANOVA. Significant *post hoc* pairwise comparisons are shown. B, before; A, immediately after; 7A, 7 days after; 15A, 15 days after the disturbance. P-values = <0.05 are in bold.

blages on smooth and rough substrata did not differ in their response to the disturbance with respect to resistance and resilience. Species richness and density differed significantly among sampling times (richness: $P < 0.001$, density: $P = 0.003$; Table 1), and this was mostly attributed to the differences between samples obtained before vs. immediately after the disturbance (*post hoc* pairwise comparisons; richness: $P = 0.004$, density: $P = 0.002$). Both species richness and density recovered after 7 days, showing similar values to those observed for samples collected before the disturbance (*post hoc* pairwise comparison of before versus 7 days after, richness: $P = 0.999$, density: $P = 0.137$; *post hoc* pairwise comparison of before versus 15 days after, richness: $P = 0.999$, density: $P = 0.999$). Species richness was significantly higher on rough than on smooth substrata ($P < 0.001$), whereas density did not differ ($P = 0.293$) (Table 1; Fig. 2).

There were no significant interactions between algal life forms and substrata in terms of similarity, for resistance or resilience (Table 2). The effect of substratum roughness on resistance and resilience was statistically non-significant (Bonferroni correction, all $P > 0.008$; Table 2). However, there was a tendency towards higher resilience on rough substrata, for both the qualitative and quantitative indices (all P -values between 0.013 and 0.050; Table 2), especially for the filamentous life form (Fig. 3). Algal life forms differed in their resistance and resilience. The adnate/prostrate and the erect/stalked life forms were

more resistant and resilient than the other groups in most of the comparisons (Table 2; Fig. 3). Further, the motile life form was more resistant and resilient than the metaphyton (Table 2; Fig. 3).

Discussion

Effects of substratum roughness

Our hypothesis of higher resistance and resilience of benthic algal assemblages on rough substrata than on smooth was not supported, as shown by the non-significant interaction terms for species richness and density in the RM-ANOVAs and by the non-significant differences of substratum roughness when using the indices based on similarity. However, we cannot completely exclude the protective effect of rough surfaces, and the evidence is threefold. First, there was a (non-significant) tendency towards higher resilience on rough substrata, especially for the filamentous life form. While this result, if valid, cannot be explained by the occurrence of relict algae protected in crevices (because in this case we also should have found higher resistance on rough substrata), it could be explained if new colonisers settle more easily on rough than on smooth substrata during base flow (e.g. Dudley & D'Antonio, 1991). Second, rough substrata harboured more species-rich assemblages than smooth substrata on all sampling occasions, a pattern previously observed for

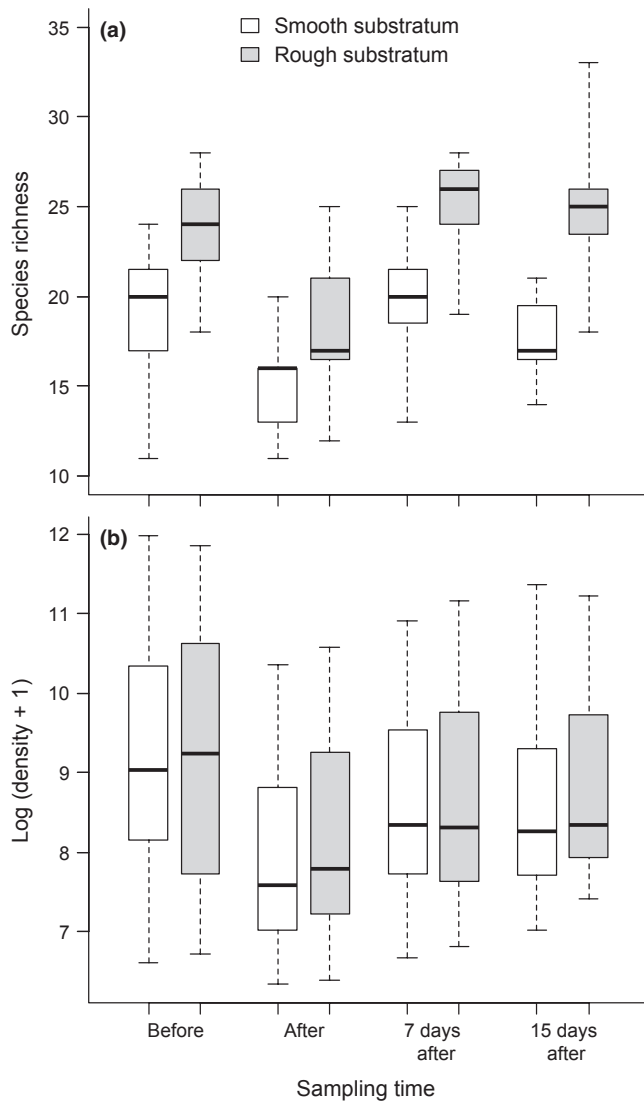


Fig. 2 Boxplots of species richness (a) and log (density + 1) (b) of stream benthic algae on smooth and rough substrata for four sampling times before and after an experimental hydrological disturbance. The heavy line represents the median, box ends are the first and third quartiles, and whiskers are the minimum and maximum values.

algae and attributed to the high availability of resources and refuges on rough substrata (Schneck *et al.*, 2011). Third, the metaphytic life form, the least resistant and resilient group, had higher relative density on rough than on smooth substrata (Fig. 1e). This life form has been shown to benefit from the occurrence of crevices, with increased species richness and density on rough surfaces (Schneck *et al.*, 2011). This evidence suggests that habitat heterogeneity affected the benthic algae to some extent, probably by protecting at least part of the assemblage in crevices and by facilitating recolonisation after disturbance.

The artificial substrata used here did not mimic completely natural smooth and rough stream substrata, but were smoother and structurally simpler. However, there is strong evidence for the efficacy of our artificial rough substrata in protecting algae (Schneck *et al.*, 2011; F. Schneck & A. S. Melo, unpublished data), and the simple design of the artificial substrata allowed us to test the specific effect of crevices as refuges by excluding other factors that could confound the results (e.g. the size or stability of substrata). It is worth mentioning, however, that the nature of substratum roughness and the type of disturbance may influence the resistance and resilience of benthic organisms. For instance, it has been shown that larger amounts of algal biomass remained, after experimental scrubbing, in crevices of naturally rough pumice, while moderate amounts remained on schistous stones and smaller amounts on smooth greywacke (Bergey, 2005). Further, crevices between sand grains of caddisfly cases protect more algae from high-flow events than natural streambed stones (Bergey & Resh, 2006) and substratum texture influences the effects of grazing on algae (Dudley & D'Antonio, 1991). In this sense, substrata with distinct degrees of roughness, and thus with variable size and number of crevices, may vary in their ability to protect benthic organisms (Bergey & Resh, 2006).

As here, the absence of a significant relationship between habitat heterogeneity and high-flow disturbance has also been observed in other studies, for both natural and experimental disturbances. For example, Grimm & Fisher (1989) found low and similar algal resistance (measured as chlorophyll *a*) to natural floods between cobble–boulder riffles and sand–gravel runs, two habitats with different degrees of heterogeneity and substratum stability. An experimental study found that invertebrate assemblages inhabiting streams with greater habitat heterogeneity, and thus with more flow refuges (natural tussock streams), did not differ in resistance and resilience from invertebrate assemblages in less heterogeneous streams (pasture streams) (Melo *et al.*, 2003).

In a previous experiment using the same type of artificial substrata and number and size of crevices, we found low temporal variability of algal assemblages on rough substrata than on smooth substrata during a period without high-flow events and suggested that a plausible mechanism was the high availability of refuges on rough substrata (F. Schneck & A. S. Melo, unpublished data). In this study, the effect of substratum roughness was less pronounced than found previously. This suggests that crevice refuges were effective in buffering against less-severe hydraulic disturbances and grazing, but were inefficient in protecting against a disturbance of high

Table 2 Summary of the results of ANOVAs comparing resistance and resilience among algal life forms and substratum type (smooth \times rough) after an experimental hydrological disturbance

| | df | MS | F | P | Pairwise comparisons |
|--------------------------|----|-------|--------|-------------------|---------------------------------|
| Qualitative data | | | | | |
| Resistance | | | | | |
| Algal life forms (Al) | 4 | 0.448 | 17.546 | < 0.001 | (Ad, E) > (Mo, Me, F); Mo > Me |
| Substrata (S) | 1 | 0.022 | 0.877 | 0.352 | |
| Block | 10 | 0.022 | | | |
| Al \times S | 4 | 0.024 | 0.948 | 0.440 | |
| Residuals | 89 | 0.026 | | | |
| Resilience after 7 days | | | | | |
| Algal life forms (Al) | 4 | 0.295 | 13.503 | <0.001 | (Ad, E) > (Mo, Me, F) |
| Substrata (S) | 1 | 0.086 | 3.938 | 0.050 | Rough > Smooth |
| Block | 10 | 0.029 | | | |
| Al \times S | 4 | 0.044 | 2.031 | 0.097 | |
| Residuals | 89 | 0.022 | | | |
| Resilience after 15 days | | | | | |
| Algal life forms (Al) | 4 | 0.401 | 17.052 | <0.001 | (Ad, E) > (F, Me); Ad > Mo > Me |
| Substrata (S) | 1 | 0.099 | 4.205 | 0.043 | Rough > Smooth |
| Block | 10 | 0.024 | | | |
| Al \times S | 4 | 0.028 | 1.189 | 0.321 | |
| Residuals | 89 | 0.024 | | | |
| Quantitative data | | | | | |
| Resistance | | | | | |
| Algal life forms (Al) | 4 | 0.533 | 26.075 | <0.001 | (Ad, E) > (Mo, Me, F); Mo > Me |
| Substrata (S) | 1 | 0.048 | 2.330 | 0.131 | |
| Block | 10 | 0.019 | | | |
| Al \times S | 4 | 0.012 | 0.599 | 0.664 | |
| Residuals | 89 | 0.020 | | | |
| Resilience after 7 days | | | | | |
| Algal life forms (Al) | 4 | 0.353 | 21.370 | <0.001 | (Ad, E) > (Mo, Me, F); Mo > Me |
| Substrata (S) | 1 | 0.105 | 6.372 | 0.013 | Rough > Smooth |
| Block | 10 | 0.016 | | | |
| Al \times S | 4 | 0.040 | 2.407 | 0.055 | |
| Residuals | 89 | 0.017 | | | |
| Resilience after 15 days | | | | | |
| Algal life forms (Al) | 4 | 0.392 | 17.911 | <0.001 | (Ad, E) > (F, Me); Ad > Mo > Me |
| Substrata (S) | 1 | 0.097 | 4.447 | 0.038 | Rough > Smooth |
| Block | 10 | 0.019 | | | |
| Al \times S | 4 | 0.028 | 1.271 | 0.287 | |
| Residuals | 89 | 0.022 | | | |

Post hoc pairwise comparisons are shown for results with $P \leq 0.05$. Ad, adnate/prostrate; E, erect/stalked; F, filamentous; Me, metaphytic; Mo, motile life form. P -values = <0.008 (α' for Bonferroni correction) are in bold.

magnitude, indicating that the efficacy of refuges depends on the type and severity of disturbance (Sedell *et al.*, 1990). Indeed, previous evidence has shown that the efficacy of refuges for invertebrate assemblages depends on the severity of disturbance events. For instance, Brown (2007) observed that habitat heterogeneity decreased the temporal variability of stream invertebrates during base flow, while it had no influence on assemblage variability during high-flow and drought events. As suggested by Brown (2007) for stream invertebrates, it is likely that intensity of disturbance may also regulate the effectiveness of habitat heterogeneity and flow refuges to benthic algae.

Resistance and resilience of algal life forms

We found a clear pattern of differences in resistance and resilience among the five algal life forms. The ability of benthic algal species to resist and/or recover from a high-flow disturbance varies markedly (Peterson & Stevenson, 1992) and is mostly related to the differences in biological traits, such as adhesion structures, growth rates, body size and adaptation to live in resource-stressed environments (Grimm & Fisher, 1989; Steinman & McIntire, 1990; Townsend & Hildrew, 1994). In our study, the two most resistant and resilient life forms, adnate/prostrate and erect/stalked, together with the motile group (which was

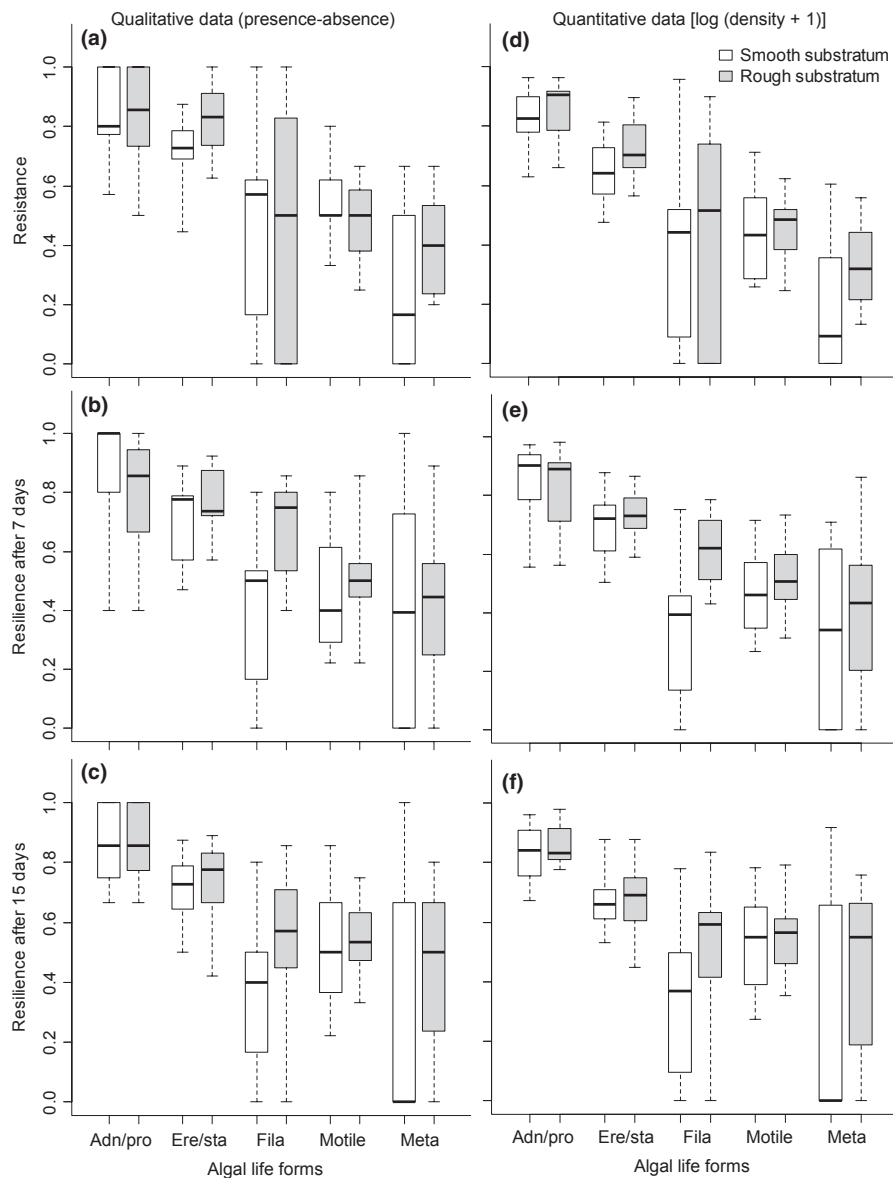


Fig. 3 Boxplots of the resistance and resilience of each algal life form on smooth and rough substrata. The indices were calculated for qualitative (presence-absence; a, b, c) and quantitative data (log [density + 1]; d, e, f). The heavy line represents the median, box ends are the first and third quartiles, and whiskers are the minimum and maximum values. Adn/pro, adnate/prostrate; Ere/sta, erect/stalked; Fila, filamentous; Meta, metaphytic life form.

more resistant and resilient than metaphytic species), were composed mainly of diatoms. Diatoms usually resist disturbances better than other groups and are almost always the first algal colonisers of denuded substrata (e.g. Grimm & Fisher, 1989; Peterson & Stevenson, 1992). These attributes are probably related to their ability to secrete mucilage, their rapid growth and their high species diversity (Steinman & McIntire, 1990). For instance, diatoms were more resistant and recovered faster than other groups of algae after several floods and were followed by filamentous green algae and mats of cyano-

bacteria (Grimm & Fisher, 1989). Grimm & Fisher (1989) also observed that diatoms rapidly recolonised substrata after the flood ceased.

The adnate/prostrate life form primarily includes small and tightly attached resource-stressed species that live in the understory, with limited light and nutrients (Passy, 2007). Living in the understory enables them to avoid the shear stress of high-flow events and resist scour (Stevenson, 1996). Species of this group, such as *Achnanthes minutissimum* (Kützinger) Czarnecki and *Cocconeis placentula* Ehrenberg are fast growing and early colonisers of open

spaces (Steinman & McIntire, 1990). In addition to their high resistance and resilience, the dominance of the adnate/prostrate life form at the four sampling times is expected in nutrient-poor and rapid streams, such as the one studied here, in which pioneer fast-growing species are not likely to be replaced by competitively dominant species, such as filamentous algae (Townsend & Hildrew, 1994).

Erect/stalked species are usually the second group in the succession, growing faster than filamentous species (which have higher light and nutrient requirements and are late colonists) (Steinman & McIntire, 1990; Peterson & Stevenson, 1992). The high resistance of the erect/stalked group is probably related to the ability of all these species to live attached to the substratum, while the filamentous group includes attached and unattached species that may differ in resistance (Power & Stewart, 1987). Filamentous species may also have long filaments growing out of the boundaries of the biofilm, increasing their susceptibility to shear stress of floods (Grimm & Fisher, 1989; Steinman & McIntire, 1990). Finally, the difference in resistance and resilience between motile and metaphytic species can be explained by the ability of motile species to move through the biofilm and select habitats relatively free from disturbance but with sufficient resources (Passy, 2007). In contrast, metaphytic algae in our study occurred as detached single cells or small colonies that are easily carried away from the biofilm matrix by high flow.

In conclusion, we observed that the interplay between habitat heterogeneity and hydrological disturbance is not as simple and clear as expected. While there is much evidence that flow refuges protect organisms and that the occurrence of refuges is related to habitat heterogeneity, we showed that more heterogeneous habitats are not always effective in protecting organisms. Our study, in addition to some others, showed that severe disturbances may negatively affect benthic assemblages, independently of habitat heterogeneity. Although in this study we did not evaluate the effects of different intensities of disturbance, such as grazing, subtle hydraulic disturbances and high-flow events, evidence from this study, and others of benthic algae and invertebrates, allows us to infer that habitat heterogeneity may have a positive effect on the resistance and resilience of benthic assemblages during less-severe disturbances. We also observed a clear pattern of differences in the resistance and resilience of algal life forms, mostly related to biological traits that confer an ability to overcome disturbance. Further studies on habitat heterogeneity and disturbance should take into account the interaction among different intensities of disturbance and algal life forms, to disentangle the effects of habitat heterogeneity on benthic assemblages.

Acknowledgments

We thank Albano Schwarzbald for contributions to this study; Ana Pressi, Flávia Montagner, Geraldo Schneck and Marcelo Saraiva for field assistance; Daniela Bes for help in the preparation of permanent diatom slides; Sidinei Magela Thomaz, Leandro da Silva Duarte, Luciane Crossetti and two anonymous reviewers for suggestions that improved the manuscript. Alan Hildrew carefully edited our manuscript. Janet Reid reviewed the English. FS received a student fellowship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). ASM received research grants (476304/2007-5; 474560/2009-0) and a research fellowship (302482/2008-3) from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

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(Manuscript accepted 15 May 2012)