

# The influence of landscape on the spatial and temporal distribution of stream macroalgal communities of two types of subtropical biomes

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## ABSTRACT

### The influence of landscape on the spatial and temporal distribution of stream macroalgal communities of two types of subtropical biomes

Landscape properties must be considered in the interpretation of ecological patterns of stream macroalgal communities. In this study, we sampled streams with different types of riparian cover from two biomes (highland grassland, HG, and seasonal semideciduous forest, SSF) for a period of one year. Each stream was visited four times, once in each season, during which we observed the algal growth and recorded measurements of a set of physical and chemical properties. Nineteen macroalgal taxa were recorded for HG, while 21 were recorded for SSF, but only three species were common to both biomes. Student's t-test results showed that significant differences existed between HG and SSF only for stream depth for abiotic variables and for abundance for biotic variables, while the results of a detrended correspondence analysis (DCA) revealed that the taxonomic compositions were sharply different at the landscape level. In addition, the DCA results showed that when each landscape was considered individually, the HG macroalgal communities had a clear spatial structure, while for SSF macroalgal communities no spatial structure was detected. These results suggest that although the taxonomic richness of HG and SSF are relatively similar, the landscape conditions of each biome, mainly riparian cover types, could be relevant in the determination of quantitative and qualitative differences in the stream macroalgal communities both between and within biomes.

**Key words:** Aquatic vegetation, subtropical biome, lotic systems, stream algae, South America.

## RESUMEN

### La influencia del paisaje en la distribución espacial y temporal de las comunidades de macroalgas en arroyos de dos tipos de biomas subtropicales

Las propiedades del paisaje deben ser consideradas en la interpretación de los patrones ecológicos de las comunidades de macroalgas en arroyos. En este estudio, se tomaron muestras de arroyos con una cobertura de ribera diferente situados en dos biomas (campos de montaña, HG y el bosque semidecíduo estacional, SSF) por un periodo de un año. Cada arroyo fue visitado cuatro veces, una vez en cada estación del año, cuando se observó el crecimiento de las algas, y se registraron una serie de datos sobre sus características físicas y químicas. Diecinueve taxones de macroalgas fueron registrados para HG, mientras que 21 para SSF, pero sólo tres especies fueron comunes a ambos paisajes. La prueba t de Student mostró diferencias entre HG y SSF sólo en la profundidad de los ríos, para las variables abióticas, y en la abundancia para las variables bióticas, mientras DCA reveló que la composición taxonómica fue marcadamente diferente en función del paisaje. Además, la DCA demostró que, cuando se considera individualmente cada paisaje, las comunidades de macroalgas de HG tienen una estructura espacial clara, mientras que para SSF no se observó ninguna estructura espacial. Estos resultados sugieren que a pesar de que la riqueza taxonómica de HG y SSF sea relativamente similar, las condiciones paisajísticas de cada bioma, principalmente el tipo de cobertura de ribera, podrían ser relevantes en la determinación de las diferencias cuantitativas y cualitativas de las comunidades de macroalgas corriente inter y entre los biomas.

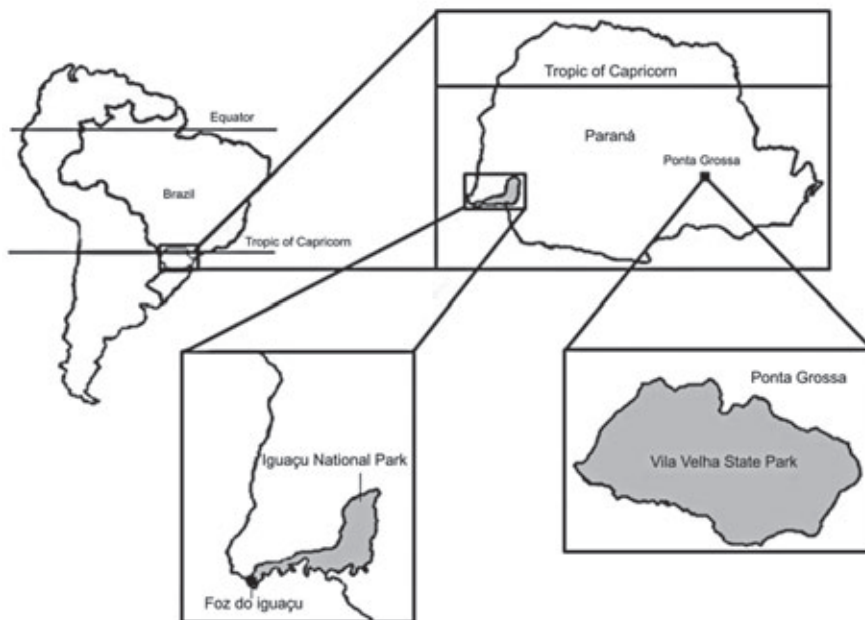
**Palabras clave:** Vegetación acuática, bioma subtropical, sistemas lóticos, macroalgas fluviales, Sudamérica.

## INTRODUCTION

Lotic macroalgae have been widely described as being among the major primary producers that support higher trophic levels in rivers and streams (Stevenson *et al.*, 1996). Important studies of stream macroalgal communities have been conducted in boreal, temperate, and tropical regions of various continents (e.g., Bojorge-García *et al.*, 2010; Branco *et al.*, 2009; Branco & Necchi, 1996; Hu & Xie, 2006; Krupek *et al.*, 2007; McClintic *et al.*, 2003; Necchi *et al.*, 1995; 2000; Peres *et al.*, 2009; Sherwood *et al.*, 2000). The results of these studies have suggested that the structure of stream macroalgal communities may change in response to the spatial and temporal variations of local environmental factors (e.g., temperature, dissolved oxygen, and current velocity). However, properties that determine the heterogeneity and dynamics of streams can be strongly influenced by many landscape factors (Hughes & Hunsaker, 2002; Wang *et al.*, 2003; 2006; Allan, 2004), highlighting the importance of these attributes in ecological studies on lotic organisms. The landscape approach allows an ecological evaluation, from a truly holistic per-

spective, of the relationships between organisms and their environment on multiple scales in space and time (Tockner *et al.*, 2002; Wiens, 2002). This approach, although traditionally applied to land, can be very useful in the evaluation of aquatic systems.

Differences in the structures of macroalgae communities among streams with distinct levels of riparian vegetation in tropical regions have been previously suggested. Riparian vegetation is important in the regulation of several stream characteristics (e.g., light availability and water temperature) and processes (e.g., seasonal habitats) that can influence the spatial and temporal distribution of macroalgae (Wang *et al.*, 2006). For instance, Necchi *et al.* (2008) showed that in open streams, macroalgal communities have higher richness and abundance than in shaded ones. However, ecological studies of macroalgal communities in streams with different types of riparian vegetation have not been carried out using the landscape approach. This approach differs from that taken in previous studies that have focused on the ecological distribution of stream macroalgal communities in that it allows the evaluation of the effect of the environment



**Figure 1.** Locations of biomes studied. *Ubicación de los biomas estudiados.*

as a whole, as opposed to consideration of particular local abiotic factors only.

In this context, landscape features (riparian vegetation cover) were used in this study to compare taxonomic composition, species richness and abundance of macroalgal communities in streams with different types of riparian cover located in two distinct biomes, highland grassland (HG) and seasonal semideciduous forest (SSF), by season. As previous studies have found differences in the distribution of macroalgal communities in streams with different riparian vegetation (e.g., Branco *et al.*, 2009; Necchi, 2004; Sheath & Burkholder, 1985), our hypotheses were that richness, abundance and diversity should be higher in the non-forested biome (HG) than in streams from the forested one (SSF) and that the taxonomic composition should be different between these distinct landscapes.

## MATERIALS AND METHODS

### Study areas

The highland grassland area (HG), a non-forested biome, sampled during the study period was the Vila Velha State Park (VVSP), a protected unit located in Paraná State in southern Brazil, covering an area of 31.22 km<sup>2</sup> (Fig. 1). The region has a humid subtropical climate, characterised by well-distributed rainfall, a moderate summer and a severe winter (IAP, 2004). The VVSP is located in a sedimentary basin in the second plateau of Paraná, in a region strongly affected by faults, fractures and dikes related to Mesozoic activity (Melo *et al.*, 2004). The geological units present in the VVSP are the Furnas and Ponta Grossa formations (Devonian), the Itararé Group (Carboniferous–Permian), Serra Geral diabase dikes (Lower Cretaceous) and Quaternary alluvial and colluvial sediments (Melo *et al.*, 2004). The topography of the region is formed by rolling hills, alternating peaks with valley floors, without tabular features. The shading level in the VVSP sampling sites was estimated using the procedures described by Denicola *et al.* (1992), and they all fit within the categories “open” or

“partly shaded,” which means that the sparse riparian vegetation allows total availability of sunlight to organisms at the bottoms of streams. The forested biome sampled was a seasonal semideciduous forest (SSF) in the Iguacu National Park (INP), a protected unit located in Paraná State in southern Brazil, covering an area of approximately 1,850 km<sup>2</sup> (Fig. 1). The region has a mild mesothermal humid climate without a defined dry season (Salamuni *et al.*, 2002). The INP is situated in the third plateau of Paraná, a volcanic basaltic region, and the topography is formed by gently rolling hills with a predominance of tabular forms. The shading levels of the INP sampling sites were categorised as “shaded” or “heavily shaded.” This means that the strong arboreal riparian vegetation limits the availability of light to organisms at the bottoms of streams.

A previous study (Branco *et al.*, unpublished data) reported very low concentration of total nitrogen and total phosphorus in streams in the VVSP and INP, indicating that these environments are oligotrophic. In addition, the headwaters of all streams in both landscapes sampled in the present study are located within protected units, so that very little anthropic impact was observed.

### Sampling procedures

We sampled five streams in each landscape, totalling 10 sampling sites. At all of the sampling sites, the only macroscopic primary producer found was macroalgae, despite some macrophytes (mainly aquatic bryophytes) being observed in occasional samplings. The investigation was conducted in 2009. When each stream was visited four times, once in each season (fall, winter, spring and summer). We analysed the growth of macroalgae and collected physical and chemical characteristics of each stream. During each sampling visit, 10 m of a stream segment was checked for the richness and abundance (per cent cover) of macroalgal species, following the cross-transect technique (Branco *et al.*, 2008). The specimens collected were preserved in a 4 % formaldehyde solution (Branco *et al.*, 2008). We

adopted the concept of macroalgae defined by Sheath & Cole (1992).

In addition to the macroalgal data, water temperature, turbidity, specific conductance, pH and dissolved oxygen were measured at the midpoint of the stream segment using a water analyser (HORIBA U-10). The current velocity and depth were measured using a mechanical flow meter (General Oceanics 2030R) and a ruler, respectively.

In the laboratory, we identified the species by microscopic observations and morphometric analysis of the collected specimens using a Leica DM1000 trinocular microscope and a Leica DFC 280 image capture digital camera system coupled to a computer. The morphometric analyses required for species identifications were made using the image analysis software Leica IM-50. The macroalgal specimens were identified to the species level whenever possible, using taxonomic references specific to Brazilian material (e.g., Branco *et al.*, 2008, 2009; Necchi *et al.*, 1995, 2000, 2008). The classification of taxa into divisions and families followed Hoek *et al.* (1995), except for Cyanobacteria (Anag-

nostidis & Komárek, 1988, 1990; Komárek & Anagnostidis, 1986, 1989, 2005).

### Data analyses

The data on physical and chemical features and macroalgal species (richness and abundance) were subjected to a one-way analysis of variance (ANOVA) to identify possible spatial and temporal differences among the streams in each landscape. Student's t-test was applied to compare the biomes analysed. Both tests were carried out using BioEstat 5.0 (Ayres *et al.*, 2007). For each sampling site, we calculated the Shannon–Wiener diversity index using the equation  $H' = \Sigma(p_i * \log_{10} p_i)$ , where  $p_i$  = proportion (abundance = per cent cover) of species  $i$  within a community. The species per cent cover was used to create dominance–diversity curves to compare the dominant species among the sites and seasons for both landscapes (Wilson, 1991). For HG and SSF together, a detrended correspondence analysis (DCA) based on the species composition was used. These analyses were per-

**Table 1.** Values of the physical and chemical variables measured (minimum, maximum, mean and standard deviation) for each biome sampled (highland grassland = HG and seasonal semideciduous forest = SSF). *Valores de las variables físicas y químicas (mínimo, máxima, media y desviación estándar) para cada bioma muestreado (campos de montaña/HG y bosque semideciduo estacional/SSF).*

	Fall		Winter		Spring		Summer	
	HG	SSF	HG	SSF	HG	SSF	HG	SSF
Temperature (°C)	16.5-18.5 17.4 ± 0.7	19.2-20.7 19.7 ± 0.6	15.2-19.4 17.1 ± 1.6	17-20.2 19.0 ± 1.2	21-25.1 22.5 ± 1.7	21-22.5 21.8 ± 0.7	18.5-21.3 19.8 ± 1.0	17.5-21.3 19.3 ± 1.8
Dissolved oxygen (mg · L <sup>-1</sup> )	4.4-6.7 5.9 ± 0.9	5.6-6.9 6.2 ± 0.5	5-7.6 6.6 ± 1.0	6.7-7.6 7.0 ± 0.3	4.9-6.2 5.8 ± 0.5	4.5-6.3 5.4 ± 0.8	4.7-5.9 5.5 ± 0.5	5.7-6.4 5.9 ± 0.3
pH	5.1-7.1 6 ± 0.7	3.2-7.8 6.4 ± 1.9	4.8-6.8 5.4 ± 0.8	6.8-7.2 6.9 ± 0.2	6.4-7.8 6.9 ± 0.5	5.2-6.9 6.1 ± 0.6	5.9-7.8 6.6 ± 0.7	6.2-7.8 7.2 ± 0.6
Specific conductance (μS · cm <sup>-1</sup> )	5-49 20.8 ± 19.9	13-43 29.4 ± 11.8	5-68 23.2 ± 26.5	20-36 28.8 ± 6.6	3-46 13.4 ± 18.3	13-250 99.4 ± 116.0	3-59 16.2 ± 24.0	15-37 28 ± 8.3
Turbidity (NTU)	2-13 6.6 ± 5.0	5-11 6.8 ± 2.4	1-9 5.2 ± 3.2	2-13 6.4 ± 4.0	7-30 14.2 ± 9.0	43-246 112.8 ± 82.4	5-12 7.0 ± 2.9	2-14 6.4 ± 4.9
Depth (cm)	7.8-24.1 17.8 ± 6.5	11.7-45.4 26.0 ± 14.3	3.5-12.4 9 ± 3.3	11-27.8 18.3 ± 8.1	6.9-18.1 12.8 ± 5.0	24.4-60.9 43.8 ± 18.3	10.3-24 15.6 ± 6.0	7.5-29.4 16.7 ± 9.5
Current velocity (cm · s <sup>-1</sup> )	38.9-112.8 70.6 ± 28.8	34.5-106.9 57.1 ± 29.7	15.2-89.4 39.3 ± 29.6	24.3-106.5 51.8 ± 37.7	44.5-106.4 78.7 ± 25.7	82.5-157.4 108.1 ± 30.0	37.6-91.1 63.7 ± 20.1	14.9-83.8 39.5 ± 31.1

formed using the software PC-ORD for Windows version 4.1 (McCune & Mefford 1999).

## RESULTS

### Environmental variables

The abiotic data from both landscapes are summarised in Table 1. The comparison of environmental variables between the two landscapes showed a significant difference only for stream depth ( $t = -24.718$ ,  $p < 0.05$ ), with higher values in SSF than in HG. There were no notable differences in any of the environmental characteristics between the two landscapes.

For the HG streams, we recorded moderate water temperatures (15.2–25.1 °C) and dissolved oxygen values (4.9–7.6 mg L<sup>-1</sup>), acid to slightly basic pH (5.8–7.3), variable current velocity (15.2–106.4 cm·s<sup>-1</sup>), low specific conductance (3–68 µS·cm<sup>-1</sup>), low turbidity (1–30 NTU) and shallow depths (3.5–24 cm). The ANOVA results for the five sites in HG indicated that significant differences existed between sites 1 and 2, 1 and 3, and 1 and 5 with respect to dissolved oxygen ( $F = 6.54$ ,  $p < 0.001$ ), between site 5 and all other sites with respect to specific conductance ( $F = 29.99$ ,  $p < 0.001$ ), between sites 3 and 1 and 3 and 4 with respect to depth ( $F = 4.81$ ,  $p < 0.05$ ), and between sites 4 and 5 with respect to current velocity ( $F = 3.61$ ,  $p < 0.05$ ). Significant differences by season were detected for temperature ( $F = 17.26$ ,  $p < 0.001$ ) and pH ( $F = 4.78$ ,  $p < 0.05$ ), with higher values observed in the spring and lower values observed in the winter for both variables.

For the SSF streams, we recorded moderate water temperatures (17–22.5 °C), moderate values of dissolved oxygen (4.5–7.6 mg·l<sup>-1</sup>), moderate pH (5.2–7.8), moderate to high values of specific conductance (13–250 µS·cm<sup>-1</sup>), and variable levels of turbidity (2–246 NTU), depth (7.5–60.9 cm), and current velocity (14.9–157.4 cm·s<sup>-1</sup>). The only significant difference detected was between the current velocities of sites 1 and 5 ( $F = 3.39$ ,  $p < 0.05$ ). The comparisons of seasonal values found the following significant

differences: the highest temperature ( $F = 5.28$ ,  $p < 0.01$ ), turbidity ( $F = 8.24$ ,  $p < 0.001$ ) and depth ( $F = 5.63$ ,  $p < 0.001$ ) were registered in the spring, the highest dissolved oxygen value was registered in the winter ( $F = 7.74$ ,  $p < 0.001$ ), and the lowest current velocity was registered in the summer ( $F = 4.37$ ,  $p < 0.05$ ).

### Macroalgal communities

#### *Highland Grassland*

Nineteen taxa were recorded in the HG streams (Table 2). Chlorophyta was the highest represented algal division (42 %), followed by Cyanobacteria (37 %) and Rhodophyta (21 %). *Zygonium* sp. showed the highest frequency of occurrence among all taxa (45 % of the total samples), while nine other species (47 % of the total species) were found at only one sampling site (Table 2). With respect to the occurrence of species by season, seven species (37 %) were found in all seasons; six species (31.5 %) were found in three seasons, two species (10.5 %) were found in two seasons, and four species (21 %) were found in only one season. The abundance of macroalgal communities was relatively similar in all seasons, ranging from 3 to 25 % in the fall, 3 to 21 % in the winter, 2 to 28 % in the spring and 7 to 16 % in the summer. The richness of the macroalgal communities was relatively similar in all seasons, with 1 to 7 species recorded in the fall, 2 to 8 recorded in the winter and spring, and 2 to 5 recorded in the summer, although the highest richness at two of the five sites was recorded in the winter (Table 2). The ANOVA revealed no significant differences ( $p > 0.05$ ) among the streams or the seasons with respect to richness ( $F = 0.09$ ) or abundance ( $F = 0.22$ ). In general, the Shannon–Wiener diversity index showed relatively low variation among the seasons (Table 2). The highest diversity values were observed in the fall and winter (with mean values of 0.33 and 0.32, respectively), and the lowest values were observed in the spring and summer (with mean values of 0.25 and 0.28, respectively) (Table 2).

**Table 2.** Richness and abundance of species and diversity index ( $H'$ ) distributed seasonally in the highland grassland (HG). *Riqueza y abundancia de especies e índice de diversidad ( $H'$ ) distribuidos por estaciones en campos de montaña (HG).*

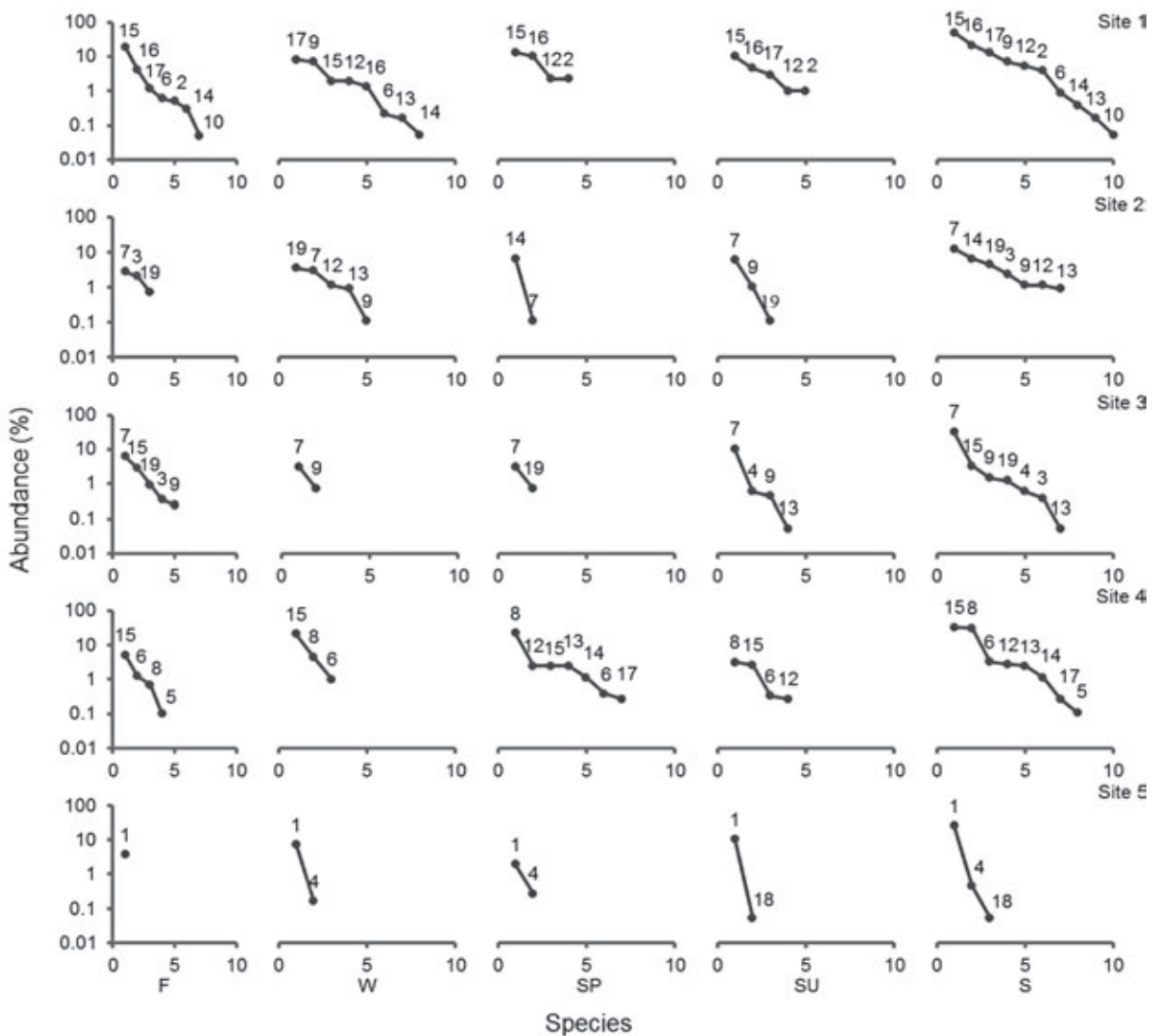
Taxa	Fall					Winter					Spring					Summer				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Cyanobacteria																				
1. <i>Blennothrix komarekii</i> Branco et Montejano				3.8						6.1					1.7				0.9	
2. <i>Nostoc verrucosum</i> Vaucher ex Bornet et Flahault	0.5											2								
3. <i>Phormidium aerugineo-caeruleum</i> (Gomont) Agnostidis et Komárek				2.1	0.4															
4. <i>Phormidium retzii</i> (C. Agardh) Gomont ex Gomont					0.1					0.2					0.3					0.6
5. <i>Symplocastrum friesii</i> (C. Agardh) Forti				1.3																
6. <i>Scytonema arcangeli</i> Bornet et Flahault	0.6					0.2			0.9					0.4						0.3
7. <i>Stigonema robustum</i> Gardner			2.7	6.3		2.5	2.7				5.5	8.7						8.5	8.5	
Chlorophyta																				
8. <i>Closterium pusillum</i> Hantzsch var. <i>pusillum</i>				0.7					3.8					18						2.7
9. <i>Cylindrocapsa brevissonii</i> Meneghini ex De Bary				0.3		6	0.1	0.7										0.9	0.4	
10. <i>Desmidiium swartzii</i> (C. Agardh) C. Agardh ex Ralfs var. <i>swartzii</i> f. <i>punctata</i> Irénée – Marie, Flor	0.1																			
11. <i>Geminella interrupta</i>														2.2						
12. <i>Microspora tumidula</i> Hazen						1.7	1				2				0.9					0.3
13. <i>Mougeotia</i> sp.						0.2	0.8							2.2						0.1
14. <i>Nitella leptostachys</i> (A. Braun) R.D. Wood var. <i>leptostachys</i>	0.3					0.1					0.1			1						
15. <i>Zygonium</i> sp.	19		2.9	5.1		1.7		17			11.2			2.2				8.6		2.3
Rhodophyta																				
16. <i>Batrachospermum kerathophyllum</i> Bory emend. Sheath, Vis et Cole	4.1					1.2					8.4				4					
17. <i>Batrachospermum puiggarianum</i> Grunow in Wittrock et Nordstedt	1.2					6.9									2.6					
18. <i>Batrachospermum</i> sp.																				0.1
19. <i>Hildenbrandia angolensis</i> Welwitsch ex W. West et G.S. West						0.7	1			3				0.2				0.1		
Species richness	7	3	5	4	1	8	5	2	3	2	4	2	2	7	2	5	3	4	4	2
Seasonal diversity index ( $H' \log_{10}$ )	0.38	0.42	0.46	0.36	0	0.63	0.45	0.21	0.27	0.04	0.49	0.03	0.03	0.51	0.16	0.55	0.21	0.18	0.44	0.01
Mean value of diversity index			0.33				0.32					0.25								0.28

Species number corresponds to the figures. *El número de las especies corresponde a las figuras.*

**Table 3.** Richness and abundance of species and diversity index ( $H'$ ) distributed seasonally in the semideciduous season forest (SSF). *Riqueza y abundancia de especies e índice de diversidad ( $H'$ ) distribuidos por estaciones en el bosque semideciduo estacional (SSF).*

Taxa	Fall	Winter	Spring	Summer
Cyanobacteria				
1. <i>Chroococcopsis fluviantilis</i> (Lagerheim) Komárek & Anagnostidis			0.1	0.1
2. <i>Geitlerinema splendidum</i> (Gomont) Anagnostidis	0.2			
3. <i>Microcoleus subtorulosus</i> Gomont	0.2			
4. <i>Phormidium retzii</i> (C. Agardh) Gomont ex Gomont	0.1	1.6	0.1	1.4
Chlorophyta				
5. <i>Basycladia emedii</i> Peres & Branco		0.1	0.2	
6. <i>Chaetophora pisiformis</i> (Roth) C.A. Agardh		0.1	0.2	0.7
7. <i>Cladophora glomerata</i> (Linnaeus) Kützing		0.5	0.2	
8. <i>Ecballocystis pulvinata</i> var. <i>pulvinata</i> Bohlin		0.4	0.1	0.3
9. <i>Microspora stagnorum</i> (Kützing) Lagerheim		0.1		0.2
10. <i>Oedogonium</i> sp.		0.1		0.1
11. <i>Spirogyra</i> sp.		0.1		0.1
Heterokontophyta				
12. <i>Terpsinoë musica</i> Ehrenberg var. <i>musica</i>	0.1		0.1	0.1
13. <i>Vaucheria</i> sp.	0.2	0.1	0.1	8.6
Rhodophyta				
14. <i>Batrachospermum helminthosum</i> Bory			0.4	
15. <i>Batrachospermum puiggarrianum</i> Grunow in Wittrock et Nordstedt		4.8		
16. <i>Batrachospermum</i> sp.1	0.3			
17. <i>Batrachospermum</i> sp. 2		2		0.3
18. <i>Kumanoa abiliti</i> (Reis) Necchi Júnior & Vis		1.6	0.1	
19. <i>Kumanoa ambigua</i> (Montagne) Entwistle M.L. Vis, W.B. Chiasson, Necchi Júnior & A. R. Sherwood				
20. <i>Hildenbrandia angolensis</i> Welwitsch ex W. West et G.S. West	1.5		0.1	0.1
21. "Chantransia" <i>pygmaea</i>	1.6	0.1	1.3	0.5
Species richness	3	1	5	2
Seasonal diversity index ( $H'$ log <sub>10</sub> )	0.38	0	0.64	0.07
Mean value of diversity index	0.26	0.33	0.27	0.29

Species number corresponds to the figures. *El número de las especies corresponde a las figuras.*



**Figure 2.** Dominance–diversity curves for HG, based on the percentage abundance of macroalgae by site (S) and season (F = fall, W = winter, SP = spring, SU = summer). The numbers presented in the graphs correspond to the species reported in table 2. *Curvas dominancia-diversidad de HG basado en el porcentaje de abundancia de macroalgas en los lugares de muestreo (S) y las estaciones (F = otoño, W = invierno, SP = primavera, SU = verano). Los números del gráfico corresponden a las especies de la tabla 2.*

Dominance–diversity curves showed that *Zygonium* sp. was the dominant species at sites 1 and 4, *Stigonema robustum* was the dominant species at sites 2 and 3, and *Blennothrix komarekii* was the dominant species at site 5 (Fig. 2). The dominant species at each site were relatively consistent throughout the samplings, with minor changes from season to season (Fig. 2). According to the dominance–diversity

curves, the highest evenness was found at site 2, and the lowest was found at site 5 (Fig. 2). For the individual sampling sites, no consistent pattern was observed for evenness in all seasons; however, the dominance–diversity curves showed higher dominance in the fall and lower dominance in the spring and summer at sites 1, 4 and 5 (Fig. 2). At site 1, the lowest evenness and the highest total richness were found in the fall

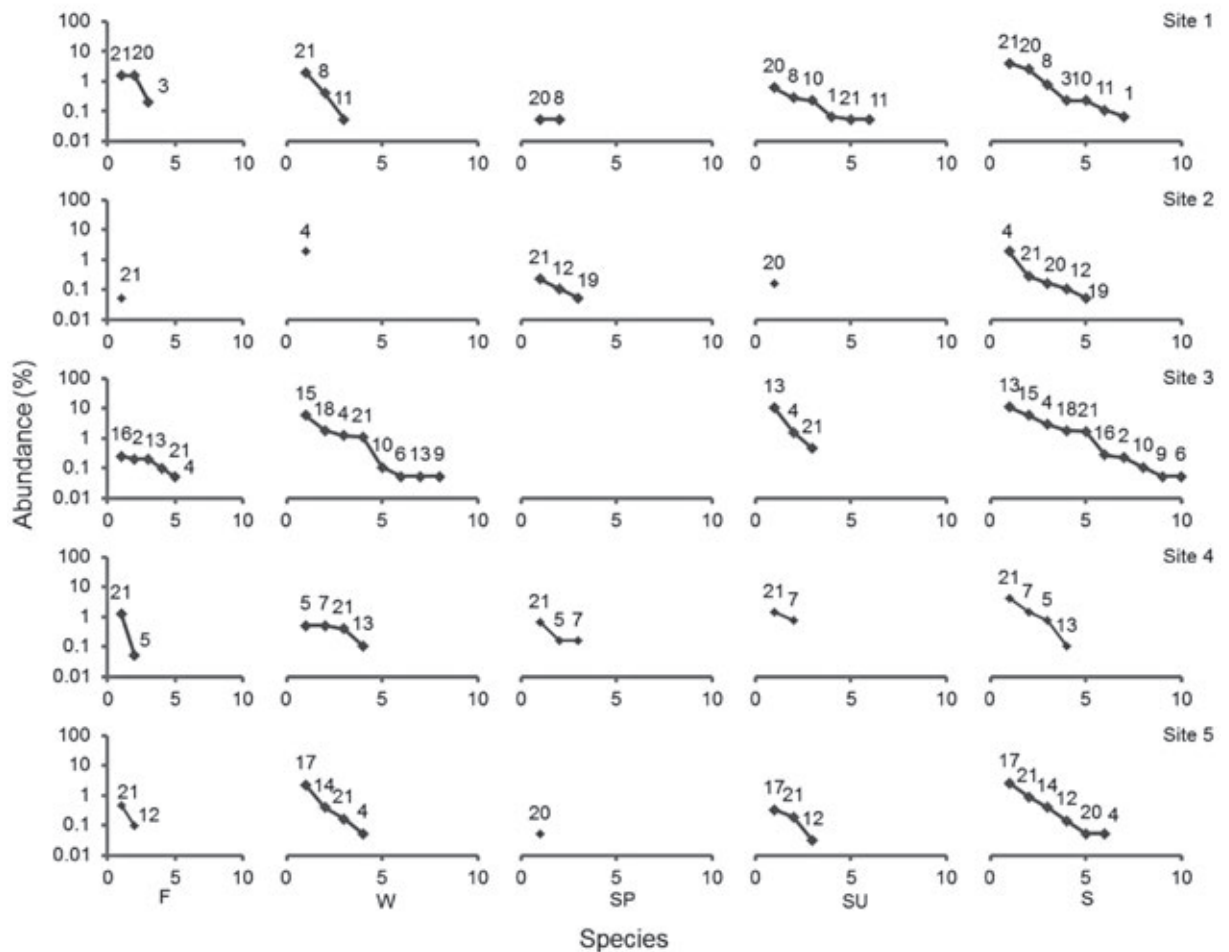


and winter, respectively. *Zygonium* sp. was dominant in all seasons, except in the winter, when the dominant species was *Batrachospermum puiggarianum*. Site 2 had higher richness and evenness during the winter. *Stigonema robustum* was the only species found in all samples and was dominant in the fall and summer. At site 3, the highest richness and evenness were observed in the fall. *Stigonema robustum* was the dominant species in all seasons. Site 4 had the highest richness and evenness in the spring, with *Zygonium* sp. being dominant in the fall and winter and *Closterium pusillum* being dominant in the spring and summer. At site 5, only two

species were found, with *Blennothrix komarekii* being dominant in all seasons and the highest evenness occurring in the summer.

*Seasonal Semideciduous Forest*

Twenty-one taxa were found in the SSF streams (Table 3), including representatives of Rhodophyta (38.1 %), Chlorophyta (33.3 %), Cyanobacteria (19.1 %), and Heterokonthophyta (9.5 %). The stage “Chantransia” *pygmaea* of *Batrachospermum* (Pueschel *et al.*, 2000) was the taxon with the highest frequency of occurrence (75 % of the total samples) and was the only



**Figure 3.** Dominance–diversity curves for SSF, based on the percentage abundance of macroalgae by site (S) and season (F = fall, W = winter, SP = spring, SU = summer). The numbers presented in the graphs correspond to the species reported in table 3. *Curvas dominancia-diversidad de SSF basado en el porcentaje de abundancia de macroalgas en los lugares de muestreo (S) y las estaciones (F = otoño, W = invierno, SP = primavera, SU = verano). Los números del gráfico corresponden a las especies de la tabla 3.*

taxon found in all seasons and at all sites. The majority of the species were restricted in their occurrence, with fifteen species (72 % of the total species) registered at a single sampling site. In relation to the seasonal occurrence, 10 species (48 %) were found in only one season (Table 3). In general, the abundance of macroalgal communities was low at all sites and in all seasons, ranging from 0 to 4 % in the fall, 1 to 9 % in the winter, 0 to 1 % in the spring and 0 to 10 % in the summer. The richness of macroalgal communities ranged from 1 to 5 species in the fall, 1 to 8 species in the winter, 0 to 3 species in the spring and 1 to 6 species in the summer, but the highest values for three of the five sites were recorded in the winter (Table 3). The ANOVA results revealed no significant differences ( $p > 0.05$ ) by season for richness ( $F = 1.195$ ) or abundance ( $F = 1.291$ ). In general, the Shannon–Wiener diversity index values varied relatively little from season to season. The highest seasonal diversity index corresponded to the winter and the lowest corresponded to the fall (mean values of 0.33 and 0.26, respectively; see Table 3).

The dominance–diversity curves showed that “*Chantransia*” *pygmaea* was dominant at sites 1 and 4, *Phormidium retzii* was dominant at site 2, *Vaucheria* sp. was dominant at site 3, and *Batrachospermum* sp. was dominant at site 5. In general, the dominant species at each site varied by season (Fig. 3). The evenness, indicated by the slope of the dominance–diversity curve, was relatively high in all sites. We observed a seasonal tendency for higher evenness in the spring (at sites 1, 2 and 4). Site 1 had the highest evenness and richness in the spring and winter, respectively. “*Chantransia*” *pygmaea* was dominant in the fall and winter, while *Hildenbrandia angolensis* was dominant in the spring and summer. At site 2, we observed the occurrence of a few species in all seasons, and more than one taxon was recorded only in spring (three taxa). Site 3 had higher evenness and richness in the fall and winter than in the spring and summer. In addition, site 3 had a distinct dominant taxon in each season. At site 4, the evenness was similar for all seasons except fall, when the dominance of “*Chantransia*” *pygmaea* was observed. Site 5

had similar evenness in all seasons except the spring, when only one species was recorded.

### Comparative Analyses

Among the 37 macroalgal species identified during the study, 21 (56.8 %) were found in SSF, 19 (51.4 %) in HG and only three (8.1 %) in both landscapes (Tables 2-3). Despite the similarity of richness values in HG and SSF, the average value of per cent cover was higher in HG than in SSF ( $\bar{x} = 11.2 \pm 8.1$  % and  $\bar{x} = 1.8$  %  $\pm$  2.8, respectively) (Tables 2-3). The maximum value of per cent cover observed in HG was 28.2 %, while in SSF, it was 10.4 %. The average diversity index of macroalgal communities from HG ( $\bar{x} = 0.29 \pm 0.2$ ) was very similar to that calculated for SSF ( $\bar{x} = 0.28 \pm 0.21$ ) (Tables 2-3). Student’s t-test comparisons of richness, per cent cover, and diversity index between the landscapes revealed a significant difference ( $t = 4.905$ ,  $p < 0.001$ ) only for per cent cover.

The seasonal analysis showed similar variations in richness throughout the seasons for both landscapes, with higher values in the winter for SSF ( $\bar{x} = 4 \pm 2.5$ ) and in the winter and fall for HG ( $\bar{x} = 4 \pm 2.5$  and  $\bar{x} = 4 \pm 2.3$ , respectively) (Tables 2-3). With respect to abundance, the mean values of per cent cover were much higher for HG than for SSF in all seasons (Tables 2-3). For HG, higher per cent cover values of macroalgal communities were observed in the spring ( $\bar{x} = 13.6 \pm 11.6$ ) and winter ( $\bar{x} = 11.3 \pm 8$ ), while for SSF, higher values were observed in the winter ( $\bar{x} = 3.2 \pm 3$ ). The seasonal variation in the diversity index values followed the same pattern as richness in both landscapes, with higher values in the winter for SSF ( $\bar{x} = 0.33 \pm 0.2$ ) and higher values in the fall and winter for HG ( $\bar{x} = 0.33 \pm 0.2$  and  $\bar{x} = 0.32 \pm 0.2$ , respectively) (Tables 2-3). Comparisons of richness, per cent cover, and diversity index between the two landscapes by season revealed significant differences ( $p < 0.05$ ) for per cent cover in all seasons (fall- $t = 2.34$ ; winter- $t = 2.13$ ; spring- $t = 2.58$ ; summer- $t = 2.34$ ).

The two first DCA axes accounted for 43.4 % of the variation in the macroalgal community

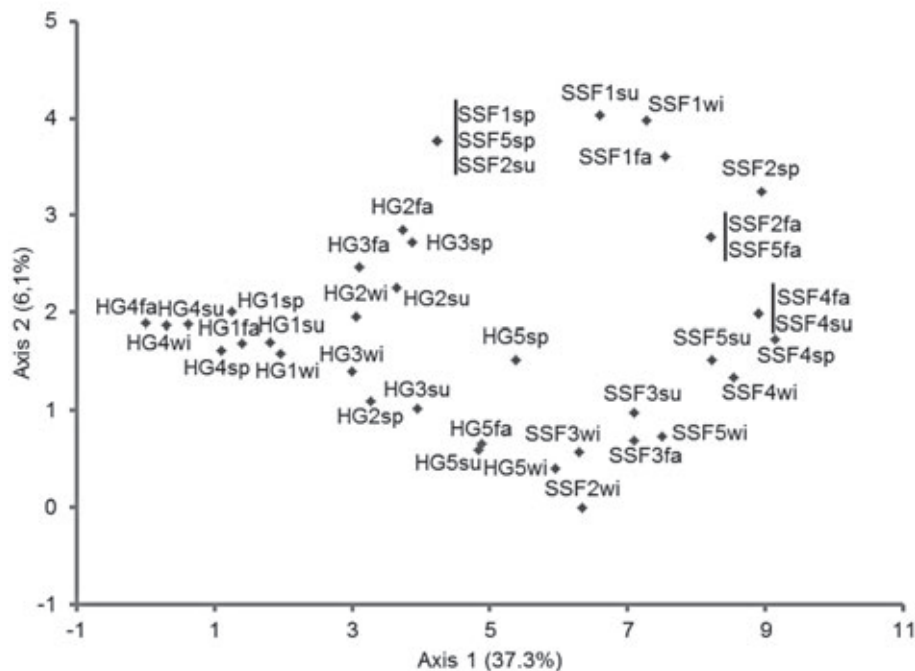
composition, considering both the HG and SSF sampling sites. The DCA showed a clear separation between the HG sampling sites and the SSF sampling sites, confirming that the species compositions of these two landscapes are distinct (Fig. 4). In addition, the DCA results revealed that the HG sampling sites exhibited a tendency to be spatially grouped, while no clear spatial grouping trend was observed for SSF, either by sampling site or by season.

## DISCUSSION

The hypothesis that richness, abundance, and diversity in HG streams would be higher than in SSF streams was partially corroborated by our analyses. The macroalgal species richness, species number per site and diversity index registered in HG were relatively similar to those recorded in SSF (Tables 2–3), but the t-test and DCA results revealed that the abundances and taxonomic compositions of the communities, respectively, of the two landscapes were sharply

different. Considering also that the t-test results only indicated a significant difference in stream depth between HG and SSF, the quantitative and qualitative differences observed for the macroalgal communities at the landscape level cannot be attributed to the physical and chemical characteristics of the streams. In this context, the results indicate that the intrinsic landscape features of the biomes, mainly the vegetation type, could be the environmental aspect most closely related to the observed differences in abundance and species composition between HG and SSF. The relationship between algal communities and landscape characteristics has been noted in other studies (McGregor *et al.* 2006).

The differences between HG and SSF in abundance and taxonomic composition detected in this study may be due to the presence of a specific vegetation type in each landscape that could determine the differential availability of a particular macroalgal species and their propagules (amount and dispersion). In HG, the predominance of grasses on the landscape scale, amplified by the lower depths observed in the



**Figure 4.** Detrended correspondence analysis (DCA) of the taxa sampled. Abbreviations are as defined for figures 2 and 3. *Análisis de Correspondencias Sin Tendencia (DCA), de los taxones muestreados. Abreviaciones como en la figura 3.*

streams of this biome, produced high availability of sunlight in stream bottoms in all catchment areas, allowing the establishment of macroalgal communities with higher abundance and with a dominance of algal groups specifically adapted to this light condition, particularly Chlorophyta (Denicola *et al.*, 1992; Necchi, 2004; Tonetto *et al.* 2012). Green algae are frequently reported as dominant in conditions of bright sunlight. In southern central Alaska, the high diversity of green algae has been reported to be related to poorly developed riparian canopies (Sheath *et al.*, 1986). The increase in irradiance caused by the falling leaves of riparian vegetation during the fall has been identified as one of the factors responsible for the high richness of macroalgae in woodland streams in temperate regions (Zalack *et al.*, 2006). In addition, it is possible that species that are well adapted to HG conditions were able to produce more dispersal propagules and thereby occupy more lotic habitats throughout the studied area. The effect of landscape features on dispersal efficiency has been described previously for other groups (Boström *et al.*, 2010; Veres *et al.*, 2013). In SSF, the stream macroalgal communities also responded to the landscape conditions. However, the limited light penetration permitted by the strong canopy development typically observed in the area resulted in a community with very low abundance and dominated by algal groups well adapted to shady conditions, particularly Rhodophyta (Branco & Necchi, 1996; Necchi, 2004; Tonetto *et al.*, 2012; Sheath & Cole, 1992).

For each landscape individually, the DCA showed that the macroalgal communities of HG had a tendency to exhibit a spatial structure, with grouping based on the sampling sites, while for SSF, no spatial structure was observed, with the sampling sites spread without a clear pattern (Fig. 4). Considering these results, we propose that in the absence of limiting irradiance (as occurs in HG streams), local abiotic characteristics may become relevant to the stream macroalgal distribution, producing more evident spatial patterns. On the other hand, in areas where the canopy cover is well developed (as in SSF streams), the limited irradiance acts as a strong

primary environmental filter, so that variations in the local abiotic characteristics are not able to influence the spatial distribution of stream macroalgae.

The seasonal variations in the richness, abundance and diversity index of the macroalgal communities in both landscapes were relatively similar, with higher values registered in the fall and winter than in the spring and summer. The only exception was for abundance in HG, with the highest value corresponding to the spring. These results are consistent with those of several studies that have shown a more pronounced development of macroalgal communities in the period from late fall to early spring (Branco & Necchi, 1997; Necchi & Pascoaloto, 1993).

Although the two biomes exhibited similar seasonal patterns with respect to some aspects of the community structure, the analysis of taxonomic composition and the dominance–diversity curves revealed different patterns between HG and SSF by season. In HG, 74 % of the macroalgal species were observed in three or four seasons, and few changes in the dominant species were observed throughout the seasons at almost all sampling sites. On the other hand, in SSF, 67 % of the macroalgal species were observed in only one or two seasons, and major differences in the dominant species by season was observed. These results suggest that the landscape works as a primary environmental filter in the temporal distribution patterns of macroalgal communities. In this context, the low seasonal variation in the landscape features in HG, mainly the constant high light availability, allows the establishment of more stable macroalgal communities, as demonstrated by the maintenance of a significant portion of the species and the consistency of the dominant species throughout the seasons (Kruppek *et al.*, 2012; Necchi *et al.*, 2008; Yang *et al.*, 2009). In SSF, the high seasonal variation in taxonomic composition and dominant species can be attributed to the seasonal loss of some tree leaves, which typically occurs in this biome, causing seasonal variation in the light availability in both time and space (Zalack *et al.*, 2006).

In summary, our results show that landscape features have an influence on the spatial and temporal distribution patterns of the stream macroal-

gal communities in highland grassland and seasonal semideciduous forest biomes. We recommend the consideration of the riparian landscape in future research to better understand the establishment, maintenance and distribution of stream macroalgae in tropical rivers.

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