

# Canopy cover as the key factor for occurrence and species richness of subtropical stream green algae (Chlorophyta)



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## ABSTRACT

Understanding how local and regional environmental factors influence species richness remains a key issue in ecology. Green algae (Chlorophyta) are a diverse and widely occurring group, which may be a good model for studying the factors that influence species richness at local and regional scales. Here, we tested the influence of local (water quality and structural complexity) and regional environmental factors (phyto-ecological regions) on the occurrence and species richness of macroscopic green algae (MGA) in subtropical streams. We sampled algae in 105 streams located in the four major phyto-ecological regions of the Brazilian subtropics. We used cross-transect technique in streams to sample algae and environmental variables. To determine the most important variables in species occurrence and richness, we used Hierarchical Partitioning analysis (HP). We found that canopy cover alone explained 34% of MGA occurrence, regardless of phyto-ecological region. At the sites where MGA occurred, the species richness was determined by both regional and local factors. The species richness was mainly influenced by phyto-ecological region, which explained 34% of the variation in species richness, along with canopy cover and pH which explaining 22% and 15% respectively. The highest richness was found in non-forested regions, in transects without canopy cover, and slightly acidic pH. Our results illustrate how the combination of regional and local factors can shape the spatial distribution of species richness and are pivotal to understanding richness patterns at broad spatial scales.

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## 1. Introduction

Hypotheses to explain species distribution in space usually involve local and regional scales (Shurin et al., 2000). The regional species pool is determined by biogeographic and evolutionary processes, such as speciation, extinction and migration (Ricklefs, 2004; Harrison and Cornell, 2008). Furthermore, these processes are influenced by geomorphological and environmental characteristics (Rahbek and Graves, 2001) and historical variations in climate of each region (Carnaval et al., 2009). Thus, species richness may vary between regions as a result of these factors. At the local scale, species composition is a result of species sorting from the regional species pool (Ricklefs, 2004; Vellend, 2010) influenced mainly by local environmental characteristics (Tuomisto et al., 2014) and biotic factors (Morin, 1999), with species tracking environmental variations.

Environmental gradients have been widely related to photosynthetic organisms in lotic habitats. For instance, nutrient (e.g., conductivity, nitrogen, phosphorus), light availability (e.g., canopy cover, turbidity), temperature, pH, hydraulic conditions (e.g., water velocity and depth), grazing rate, and stable substrate availability (Allan and Castillo, 2007) are the most important factors determining photosynthetic organisms distribution in stream realms. These factors exhibit a wide spatial variation, so their influence is related to spatial scale, ranging from microhabitat to regional scale (Frissell et al., 1986), what reflects in ecological patterns still not completely understood or fairly predictable. Hence, more effort is needed to uncover some neglected points regarding ecological distribution of stream dwellers. For example, determining how local and regional environmental factors influence species richness is a key issue in ecology (Ricklefs, 2004, 2008; Brooker et al., 2009), but this approach remains seldom applied for stream algae.

Green algae (division Chlorophyta) are important primary producers in streams (Stevenson, 1996), commonly having higher richness than other macroalgal groups. Thus, macroscopic green algae (MGA) are an interesting group of organisms to investigate

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factors related to richness variations at both local and regional scales. For example, a recent study (Branco et al., 2014) showed that the influence of spatial (e.g. related to dispersal process) and environmental processes (e.g. niche-based process) on the species composition of stream macroalgae varies among taxonomic groups (Cyanobacteria, Chlorophyta, and Rhodophyta). For instance, the taxonomic composition of green algae is influenced by both environment and space, while cyanobacteria only by environment and Rhodophyta only by space (Branco et al., 2014). Thus, local and regional factors may influence algal groups differently. Specifically for MGA, most studies have been conducted at small spatial scales or with limited number of species (Biggs and Price, 1987; Dodds and Gudder, 1992; Okada and Watanabe, 2002). Most of the ecological information about MGA comes from studies dealing with all groups of stream macroalgae. In these studies, some patterns are usually common, such as low endemism rate in each region (Borges and Necchi, 2006), occurrence in a few streams in a region (Branco et al., 2009), dominance by a few species (Necchi et al., 2000; Borges and Necchi, 2006), and local distribution in a mosaic (Necchi et al., 2000, 2003). Nevertheless, how environmental variables determine these distribution patterns is still poorly known (Branco et al., 2009).

The major capability of green algae to grow in habitats with higher irradiance is well accepted and recognized among specialists (Hill, 1996; and references therein). Indeed, previous studies showed that unshaded environments support higher primary production and abundance of green algae. However, the role of irradiance as a key factor on MGA occurrence and species richness is not clear at either regional or local scale. For example, open stream segments do not ensure the presence or high species richness of MGA (Branco and Necchi, 1996; Necchi et al., 2000) and the landscape could be exhibiting an important contribution (Oliveira et al., 2013). Hence, we expect that equally opened stream segments, but from distinct phyto-ecological regions, can exhibit different species richness. This logic led us to assess the species richness and occurrence of MGA regarding environmental factors at local and regional scales in order to check how environmental variables are determining the distribution pattern of MGA.

Herein, we tested the influence of local (water quality and stream structural complexity) and regional factors (phyto-ecological regions) on the occurrence and species richness of MGA in subtropical streams. We first assessed the occurrence (presence in stream segment) of MGA among all studied streams, regardless of species identity, abundance or species number. After that, we analyzed which factors are determining the MGA species richness in the streams. For this, we sampled MGA in four phyto-ecological regions that encompass very different climatic conditions and vegetation structure (mainly related to light availability). Thus, we predict that MGA species richness will be higher in phyto-ecological regions dominated by herbaceous vegetation (steppe) due to higher light incidence in the whole stream determined by a lower canopy cover. This condition could possibly increase the number of species in the regional pool because MGA have higher photosynthetic capability in places with high light availability (Wetzel, 2001). Furthermore, at local scale (e.g., within stream), other factors could regulate the MGA species richness and, hence, we predict that such factors (e.g., water quality, water flow, stable substrate, and canopy cover) could be influencing the species occurrence and richness of MGA in streams. As a final point, these factors are really important for algal distribution (Stevenson, 1996), and to the best of our knowledge, this is the first study evaluating the relationship of regional and local factors in determining geographical patterns in MGA species richness.

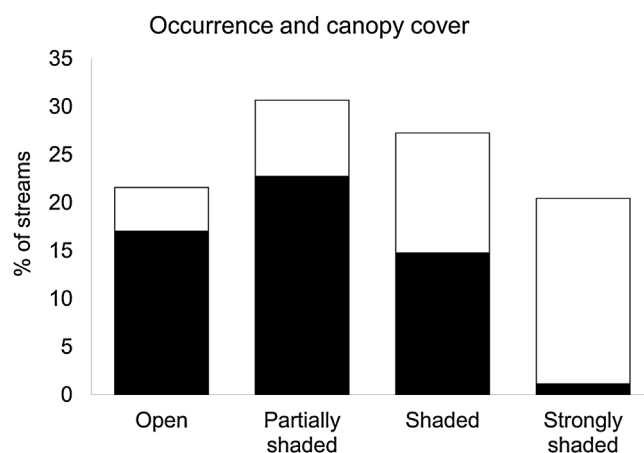


Fig. 1. Percentage of stream transects sampled in each canopy cover class (total bars) and percentage of streams with green algae species occurrence in each canopy cover class (black bars).

## 2. Material and methods

### 2.1. Study region

The sampled area comprises the Brazilian subtropical region (33° 44' 59" S; 48° 01' 08" W and 22° 31' 10" S; 57° 36' 05" W; Branco et al., 2014; see their Fig. 1), and is included in the states of Paraná, Santa Catarina and Rio Grande do Sul, located in southern Brazil. The region belongs to humid subtropical zone of oceanic climate, without a defined dry season (Alvares et al., 2013). The Brazilian subtropical area is dominated basically by four phyto-ecological regions (IBGE, 1992) arranged in a mosaic: Seasonal Forest (SF); Mixed Ombrophilous Forest (MOF); Dense Ombrophilous Forest (DOF), and Steppe (ST). These formations were formed and shaped by fire during the quaternary climate changes (Behling and Pillar, 2007). Climatic conditions determine these four phyto-ecological regions (IBGE, 1992). DOF has stable climate defined by high and regular rainfall throughout the year, while in SF, MOF and ST the precipitation is sparsely distributed along the year. Regarding temperature, ST exhibit the highest annual amplitude (winter with frost) and DOF exhibit the lowest temperature variation, while SF and MOF exhibit an intermediate variation. MOF cover higher altitude areas (more than 700 m a.s.l.) than SF.

We sampled 105 streams in 10 protected areas distributed in four vegetation formations of southern Brazil (Table 1). The region and stream segments are the same used by Branco et al. (2014) see their Fig. 1). The sampled streams were all inside protected areas to avoid the effect of anthropogenic disturbances.

### 2.2. Sampling

We sampled 105 stream segments (selected by convenience) in the dry periods between 2007 and 2008. The segments were sampled once. To sample the algae, we used 10-m transects, which were further divided into 10 1-m cross-sections (Sheath and Burkholder, 1985; Necchi et al., 1995, 2000). In each stream transect we analyzed all streambed looking for macroscopic green algae (presence/absence of species). In order to standardize the sampling procedure all transects were sampled for at least 30 min by the same collectors (CKP, CCZB and AFT). When benthic green algae occurred they were scraped off the substrate *in loco* using small knives or spatulas. After we have checked all specimens present in the stream segment, we transferred manually small parts of them into plastic flasks containing 4% formaldehyde. Thereafter,

**Table 1**  
Protected Areas along phyto-ecological regions (SF = Seasonal Forest; MOF = Mixed Ombrophilous Forest; DOF = Dense Ombrophilous Forest and; ST = Steppe).

Phyto-ecological region	Protected area	Sampled streams	Streams with MGA	Open canopy streams	Location in map <sup>a</sup>
MOF	Irati National Forest, Paraná State	11	1	0	A
	Araucárias State Park, Santa Catarina State	11	5	0	E
	Caracol State Park, Rio Grande do Sul State	10	6	0	I
DOF	Saint-Hilaire/Lange National Park, Paraná State	14	2	0	D
	Serra do Itajaí National Park, Santa Catarina State	10	3	1	F
	Iguaçu National Park, Paraná State	10	3	0	C
SF	Fritz Plaumann State Park, Santa Catarina State	9	4	1	H
	Turvo State Park, Rio Grande do Sul State	10	8	2	G
ST	Vila Velha State Park, Paraná State	10	8	6	B
	Aparados da Serra National Park, Rio Grande do Sul State	10	8	9	J

<sup>a</sup> In accordance with Fig. 1 of Branco et al. (2014).

we took these samples to laboratory for taxonomic identification under microscopy (Leica DM 1000) by using specialized literature.

We classified each stream according to a phyto-ecological region (following IBGE, 1992). Environmental variables were measured on each transect (Table 2). Turbidity, conductivity, and pH, were measured at the midpoint of the stream segment using a water analyser with water quality checker Horiba U-10 (a portable electronic device with probes). The percentage of stable substrate was visually estimated (following Gordon et al., 1992). Stable substrates were those larger than 25 mm (e.g., pebbles, boulder, and solid rock). Canopy cover was estimated in the field into four classes, following DeNicola et al. (1992): open (A), partially shaded (B), shaded (C), and heavily shaded (D). Average water flow and depth of the transect were obtained by averaging the values measured in each section. Water flow was measured using mechanical flowmeter (General Oceanics 2030R) positioned just below the surface for 20 s. Water depth was measured with a vertically positioned ruler. Total dissolved inorganic nitrogen and orthophosphate were measured from a frozen water sample using a spectrophotometer (Spectroquant Nova 60).

### 2.3. Data analysis

We tested for spatial autocorrelation in macroalgal richness using Moran's I correlograms with ten distance classes (Legendre and Legendre, 2012). Moran's I measures the spatial autocorrelation calculated as the product of deviations from the mean (Legendre and Legendre, 2012). Spatial autocorrelation in a given variable can affect the results of linear models, increasing the probability type 1 error (Diniz-Filho et al., 2003). A high positive spatial autocorrelation in the first distance classes for richness means that closer areas have similar richness (Diniz-Filho et al., 2003). Likewise, a high positive autocorrelation in the first distance classes for abundance may suggest that biotic or abiotic variables that determine abundance are spatially structured and should be considered in the analysis, or point to dispersal limitation (Peres et al., 2010). We found a weak positive autocorrelation in macroalgae richness

**Table 2**  
Independent quantitative variables used in the study with range, mean and standard deviation (SD) (N = 105).

Variables	Range	Mean + SD
Specific conductance (Cond)	1–63 $\mu$ S/cm	27 + 15
pH (pH)	4.6–7.3	6.2 + 0.7
Turbidity (Turb)	0–86 NTU	10 + 13
Average current velocity (Veloc)	5–233 cm/s	53 + 39
Average depth (Depth)	3–42 cm	16 + 9
Orthophosphate (PO4)	0.01–0.46 mg/L	0.09 + 0.06
Total Nitrogen (N)	0.1–4.6 mg/L	0.7 + 0.8
Stable substrate (Ssub)	0–100%	68 + 30

Note: Canopy cover (Canopy) and Phyto-ecological region (Phyto) were registered as categorical variables.

only for the first distance class (Fig. S1). However, we found no spatial autocorrelation in the residuals of multiple regression analysis (Fig. S2). This suggest a low Type I error (Peres et al., 2010). Analyses were performed with a SAM software (Rangel et al., 2010).

Independent quantitative variables were standardized to zero mean unit standard deviation prior to analysis. Multicollinearity was assessed using the Variation Inflation Factor (VIF) in the R (R Core Team, 2012) package car (Fox and Weisberg, 2011). VIF > 3 indicates high multicollinearity, but the VIF of all variables was below that value.

We used all sampling points (n = 105) to test the influence of local environmental variables and regional factors on the occurrence (presence or absence in stream segments) of MGA. However, we only included sampling points with at least one species (n = 48) to test the influence of environmental variables (local and regional) on the species richness. To test the influence of environmental variables (independent variables) on the occurrence and richness (dependent variables) we used a Hierarchical Partitioning analysis (HP; Chevan and Sutherland, 1991). The HP separates independent variables of a multiple regression model (local or regional) that better explain species occurrence and the distribution of MGA richness. The HP determines the independent effects of predictor variables on the dependent variable (Chevan and Sutherland, 1991). Thus, the independent explanatory power ("I") of each environmental variable on the dependent variable (occurrence and species richness) represents the independent contribution of an environmental variable to the variance explained by the model (Mac Nally, 2002). A second parameter "J" measures the interaction between each environmental variable and the others (Mac Nally, 2002). The results of HP are expressed as Z-score for each independent variable. The Z-score is obtained by conducting 1000 randomizations to generate 95% confidence intervals. Values of Z greater than 1.65 were considered significant (Mac Nally, 2002).

### 3. Results

We identified 32 species of macroscopic green algae from 11 families (Table S1). The most speciose family was Zygnemataceae with 10 species, followed by Chaetophoraceae with six, and Microsporaceae and Oedogoniaceae with three species each. Only *Bacilladiala emedii* Peres & Branco is an endemic species, restricted to Seasonal Forest.

Approximately half (n = 48) of the sampled stream segments had MGA. Species occurrence was higher in transects with higher light intensity. Canopy cover alone explained 34% of the total variance (Table 3; Fig. 1). Neither other local environmental variable nor vegetation formations explained significantly species occurrence.

Conversely, both local and regional variables influenced species richness. Species richness (mean = 2.2, standard deviation + 1.6, range = 1–8, only in stream segments with MGA) was mainly influenced by phyto-ecological region, which explained 34% of the

**Table 3**

Results of Hierarchical Partitioning analysis (HP) showing only the significant for the occurrence and species richness (as number of taxa) of green algae. Significance values are showed (Z-score), along with the effect of the variable alone *I*, interaction of this variable with other independent variables *J*, and totals (occurrence *N* = 105, species richness *N* = 48).

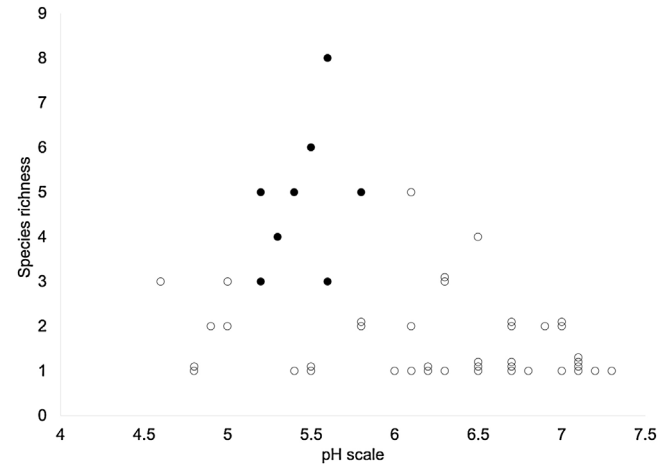
Dependent variables	Significant independent variables	Z-score	Hierarchical Partitioning		
			I	J	Total
Species occurrence	Canopy cover	11.47	0.1751	0.1694	0.3445
Species	Phyto-ecological region	2.55	0.1851	0.1583	0.3434
rich-	Canopy cover	3.08	0.0794	0.1396	0.2190
ness	pH	2.82	0.0491	0.0966	0.1457

variation in species richness, along with canopy cover explaining 22%, and pH which predicted 15% of the variation (Table 3). The most speciose phyto-ecological region was Steppe (Fig. 2A), while the other three (SF, MOF and DOF) exhibited lower and similar values among them. The highest number of exclusive species (i.e., those species found exclusively in one phyto-ecological region) were found in the steppe (Fig. S3). The relative number of MGA species (i.e., total species number per sampling point, including all studied streams, even those without MGA) was low in rain forests (0.21 species per point in DOF and 0.38 in MOF), intermediate in seasonal forest (0.52), and high in steppe (0.80). The greatest species richness was found in stream segments with high light incidence (Fig. 2B). Another key variable was pH and the highest richness (more than three species per sampling segment) occurred in stream segments with pH ranging from 5.2 to 6.5 (Fig. 3).

#### 4. Discussion

Our results showed that both local and regional factors influence the distribution of green algae in subtropical streams. However, light incidence stood out as the most important local variable influencing both species occurrence and richness. These results concur with previous studies showing that green algae have a higher photosynthetic efficiency in places with lower canopy cover (Hill, 1996; Necchi, 2004). Thus, the green algae occurrence increases due to the high energy input (Okada and Watanabe, 2002).

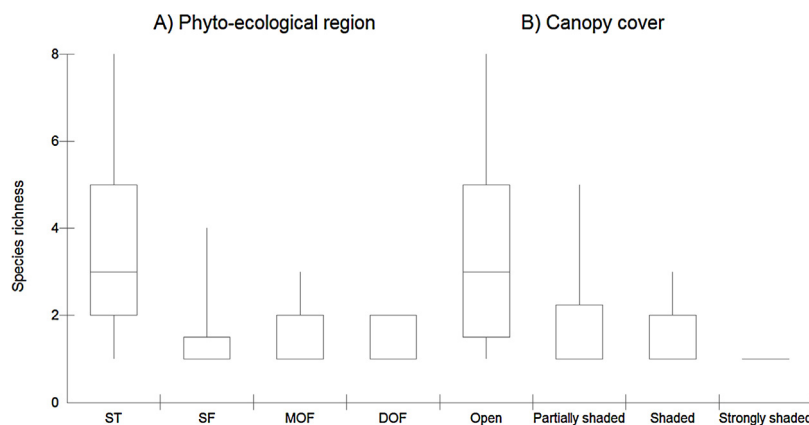
Green algae physiological features can explain partly the preference to stream segments with lower canopy cover and consequently more light incidence. This algal group contain a peculiar pigment represented mainly by chlorophyll *a*, *b* and carotenoids (Lee, 2008). For instance, carotenoids protect the photosynthetic apparatus against high light intensities and, hence, photoinhibition is low or absent in green algae from well-lit streams (Hill, 1996; Necchi, 2004). Furthermore, differently from any other algal group, green algae exhibit high amounts of chlorophyll *b* that



**Fig. 3.** Species richness of macroscopic green algae in relation to stream pH. Filled circles represent streams without shading from canopy in Steppe regions, and with pH between 5.2 and 5.8 (*N* = 48).

capture other portions of the PAR spectrum (blue and red), enhancing the light absorption (Wetzel, 2001; Necchi, 2004). Thus, the transfer light energy mediated by carotenoids and chlorophyll *b* to chlorophyll *a* could explain the higher presence of MGA in open-canopy streams.

Canopy cover has been related not only to the seasonal variation in richness of green algae (Sheath and Burkholder, 1985), but also its local abundance (e.g., Sheath et al., 1996; Tonetto et al., 2012) and species distribution (e.g., Everitt and Burkholder, 1991; Peres et al., 2009). Other studies regarding tropical and subtropical stream macroalgae assessment have not directly addressed the relationship between stream green algae and light incidence (e.g., Necchi et al., 1995; Branco and Necchi, 1996; Krupek et al., 2007; Branco et al., 2009). However, by looking carefully at their data it is



**Fig. 2.** Box plot (median and interquartile range) of species richness values of macroscopic green algae (MGA) per stream sampled A) in each phyto-ecological region. (SF = Seasonal Forest; MOF = Mixed Ombrophilous Forest; DOF = Dense Forest and Ombrophilous; ST = Steppe). B) in each canopy cover class. Only stream segments with MGA occurrence were considered (*N* = 48).

possible to notice a trend of green algae occurrence in stream segments with high light availability. Hence, our study is the first one that directly links the influence of canopy cover on the occurrence and richness of green algae at a regional spatial scale.

Our study was carried out in both forested and non-forested regions. However, most species occurred in the Steppe, despite the predominance of streams in forested regions in our data set. Our results suggests that light incidence is key not only at local scales (i.e., transect), but also at regional scales, where stream segments in regions with herbaceous plants have higher species richness of green algae. Stream segments with higher local richness occurred in regions with also high richness. The influence of regional factors on green algae richness can be explained by the “species pool hypothesis”, in which local richness patterns vary as a result of large scale historical factors (Harrison and Cornell 2008; Zobel et al., 2011; Cornell and Harrison, 2014). According to this hypothesis, variation in species richness is explained by changes in extinction, colonization and speciation rates of each phyto-ecological region (Taylor et al., 1990; Schamp et al., 2002). For stream macroalgae in general, endemism is low (Borges and Necchi, 2006) so within a region the main richness increase occurs by colonization of species from other regions. Thus, the species pool of phyto-ecological region will influence the species richness in each stream segment.

Our work showed that phyto-ecological regions with more stable climate (with minimal seasonal variation in weather patterns), as dense ombrophilous forest, have a lower relative species richness of MGA than regions whose seasonal changes are more evident, as steppe. Studies conducted in other countries also showed similar results. For example, a study comprising 1000 stream segments in North America (Sheath and Cole, 1992) suggested that MGA richness among biomes was relatively similar. However, when we re-analyzed their data weighting the species richness by the number of sampling points, the highest species richness was in Chaparral (0.46 species per transect), while the lowest was found in Tropical Rain Forest (0.09 species per transect). Therefore, their data showed the same trend of our study. In both cases, streams from forested formations in areas with stable and warm climate have lower algae richness. Interestingly, a greater MGA diversity has been found in open vegetations, like Chaparral and Steppe, than tropical or temperate forests, even though the former are harsh environment for many plants and animals.

The pH along with canopy cover was a key local variable in determining MGA species richness patterns. There was a narrow variation in pH in the sampled stream segments, from neutral to slightly acidic, since we only sampled natural areas. However, the effect of this variable on the species richness was hump-shaped, with the greatest species richness in pH ranging between 5.2 and 6.5. The availability of inorganic carbon (essential for photosynthesis) in aquatic environments is usually regulated by pH (Allan and Castillo, 2007). Thus, different pH ranges determine the prevalence of various forms of carbon ( $\text{CO}_2$ ,  $\text{HCO}_3^-$ , and  $\text{CO}_3^{2-}$ ) that can be favorable to different photosynthetic organism groups (Maberly and Spence, 1983). The study by Sheath et al. (1989) found a negative correlation between Chlorophyta diversity and pH, arguing that many species of green algae are not able to use  $\text{HCO}_3^-$  as inorganic carbon source. The pH range (tending to slightly acid) where we found the greatest species richness corresponds to high  $\text{CO}_2$  availability (Allan and Castillo, 2007), being probably the optimum for many MGA species. Filamentous green algae (especially Zygnemataceae) can dominate aquatic ecosystems affected by acidification (Planas, 1996). Thus, the hump-shaped relationship between richness and pH reinforces the importance of local environmental factors on algal distribution. Then, most of the MGA in the study area seems to be adapted to the slightly acidic pH.

Our study showed the importance of both regional (i.e., phyto-ecological region) and local factors (i.e., canopy cover and pH) in

determining geographical patterns in green algae species richness. Previous studies have demonstrated that the relationship between local and regional factors are an important mechanism in determining the diversity patterns of other taxonomic groups in freshwater habitats (Heino, 2001; Passy, 2009; Lombardo et al., 2013). Both ecological and evolutionary processes affect the distribution of biodiversity (e.g., Harrison and Cornell, 2008), a claim that is supported by many empirical studies (e.g., Buckley and Jetz, 2007). Our results showed that phyto-ecological region, where the streams are inserted (i.e. regional factors), explained great part of the MGA richness variation among the streams (34% of total variation. See Table 3). Hence, after the influence of regional factors the local environmental factors begin to exert an essential influence on species richness variation of green algae in streams (mainly canopy cover and pH that explained 22% and 15% of the total variation, respectively. See Table 3).

In summary, we suggest that canopy cover is the main variable influencing the occurrence of MGA, regardless of phyto-ecological region. Furthermore, light availability and water pH seemed to be the key environmental filters influencing species richness. Thus, the greatest species richness were found in non-forest formations, in transects without shading from canopy, and slightly acidic pH. Taken together, our results show how local and regional factors can be integrated to understanding species richness patterns at large spatial scales.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.aquabot.2016.11.004>.

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