RESEARCH PAPER

Partitioning multiple facets of beta diversity in a tropical stream macroalgal metacommunity

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Abstract

Aim: We evaluated different facets of beta diversity (taxonomic, phylogenetic and functional), and its components (spatial turnover and nestedness), of a stream macroalgal metacommunity, as well as the effect of local environmental variables, types of biome and spatial factors on these facets and components.

Location: Ten natural areas of southern Brazil, covering the main biomes represented in the region.

Taxon: Stream macroalgae.

Methods: We analysed a macroalgal data set collected in 105 stream segments using a dissimilarity partitioning approach to decompose total beta diversity into spatial turnover and nestedness components. Furthermore, we assessed the effects of local environmental variables, biome type and spatial factors on beta diversity components by performing distance-based redundancy analysis (db-RDA), and its partial version (db-pRDA). Taxonomic data were tabulated considering four different species incidence matrices: total macroalgae; only green algae; only red algae and only cyanobacteria.

Results: For taxonomic and phylogenetic facets, very high values of total beta diversity were found for all species incidence matrices, with spatial turnover (species replacement) accounting for almost all this diversity; nestedness had extremely low values. For functional diversity, total beta diversity was again high and spatial turnover was greater than nestedness, but nestedness (the tendency for less diverse locations to contain a subset of those in higher diversity locations) was considerably higher than that observed for taxonomic and phylogenetic facets. In regard to taxonomic and phylogenetic facets, total beta diversity and spatial turnover were, in general, significantly related to local environmental variables, biome type and spatial factors for total macroalgae and green algae, whereas they were significantly related to types of biome and space for red algae, and only to local environment for cyanobacteria.

Main conclusions: Our results showed that spatial turnover was the main component of beta diversity, regardless of the facet and macroalgal species incidence matrix, and that the relative influence of local environmental variables, types of biome and spatial factors on the total beta diversity and its spatial turnover component can vary according to the facet considered and by algal group.

1 | INTRODUCTION

The idea that regional diversity (gamma diversity) can be partitioned into two fundamental components—alpha diversity and beta diversity—has been established for a long time in community ecology (Magurran, 2004; Whittaker 1972). Until fairly recently, however, the main focus of community ecology studies was on the description of patterns and processes related to alpha diversity. This trend has changed in the last two decades, as investigations into the patterns, causes and consequences of beta diversity have become more prominent in the literature (Melo et al., 2011). Beta diversity expresses spatial variation in community composition, and an analysis of beta diversity is important both for understanding changes in the structure of communities driven by different factors, including those related to anthropogenic activities (Heino & Tolonen, 2017; Leibold & Chase, 2017) and for guiding conservation efforts.

Traditionally, studies of beta diversity in communities have focused on variation in taxonomic composition. In recent years, the number of studies considering other facets of beta diversity (e.g. phylogenetic and functional) has increased. This allows a more complete view of the processes that underlie beta diversity (e.g. Heino & Tolonen, 2017; Hill, Heino, White, Ryves, & Wood, 2019; Leão-Pires, Luiz, & Sawaya, 2018; Perez Rocha et al., 2018; Schneck, Lange, Melo, Townsend, & Matthaei, 2017; Swenson, 2014; Swenson et al., 2012). One reason for measuring phylogenetic and functional beta diversity, along with beta diversity based on taxonomic composition, is that these measures can provide functional and historical insights into the complementary ecological and/or evolutionary forces acting on communities (Nunes, Braga, Figueira, Neves, & Fernandes, 2016; Pavoine & Bonsall, 2011). These facets of beta diversity may also help shed light on the respective roles of environmental/spatial factors and evolutionary processes as filters of species and their traits (Heino & Tolonen, 2017; Nunes et al., 2016; Perez Rocha et al., 2018; Villéger, Miranda, Hernandez, & Mouillot, 2012).

Recent studies (Baselga, 2010, 2012), supported by pioneering works from the end of the last century (e.g. Harrison, Ross, & Lawton, 1992; Lennon, Koleff, Greenwood, & Gaston, 2001; Williams, 1996), have suggested that beta diversity reflects two distinct processes—spatial turnover and nestedness. Spatial turnover refers to species replacement (e.g. along ecological gradients). Spatial turnover therefore represents the exchange of some species for others due to sorting of species (environmental filtering), combined with dispersal constraints and historical factors. In contrast, nestedness represents situations where the species composition of less rich communities comprises subsets of the species composition of the richest community (Legendre, 2014). Therefore, nestedness reflects the gain or loss of species without replacement (Baselga, 2010; Melchior, Rossa-Feres, & Silva, 2017). Any analysis of beta diversity should thus consider both spatial turnover and nestedness, since differences between the compositions of different communities should reflect these two additive components, and/or combinations thereof (Baselga, 2007, 2010; Heino & Tolonen, 2017).

Tropical lotic ecosystems contain a rich biota composed of organisms with distinct ecological traits and strategies. Among these organisms are benthic algae with macroscopic growth (termed macroalgae, sensu Sheath & Cole, 1992), a functional group that is one of the most important primary producers in tropical streams, especially those of low orders (Strahler order ≤ 4—Audet et al., 2019; Branco, Riolfi, Crulhas, Tonetto, & Necchi Júnior, 2017; Dell'Uomo, 1991). Several previous studies have pointed to local environmental variables as principal structuring factors for macroalgal communities (see a synthesis in Branco, Krupek, & Peres, 2009). It is also to be expected that, in general, communities that inhabit low-order streams will experience isolation from each other imposed both by the terrestrial matrix and by the unfavourable conditions and resources of the larger rivers (creating dispersal challenges), suggesting that spatial factors must be involved in determining their diversity patterns (e.g. Clarke, MacNally, Bond, & Lake, 2008). Taking into account both predictors—local environmental variables and spatial factors—a more recent study (Branco, Bispo, Peres, Tonetto, & Branco, 2014) has challenged the general view that the local environment is inevitably the most important factor acting on the structure of lotic macroalgal communities. This study found that local environmental variables and spatial factors operate together, and that their relative influences may vary depending on the algal phylum examined. These results strongly suggested that a metacommunity approach can be used to understand the ecology of stream macroalgae, given that interactions between local environmental variables and spatial factors in the determination of community structure is a central tenet of metacommunity theory (Brown et al., 2011; Leibold & Chase, 2017; Logue et al., 2011). Branco et al. (2014) showed that red macroalgal (Rhodophyta) assemblages were significantly influenced by space, cyanobacteria (Cyanobacteria) assemblages by local environments, and green macroalgal (Chlorophyta) assemblages by both factors. The observed differences among these groups were ascribed to differences in dispersal mechanisms among the algal phyla, indicating that effects of local environmental variables and spatial filters on the structure of stream macroalgal metacommunities may be modulated by phylogeny and functional traits.

Some studies have also shown that the intrinsic landscape features of distinct types of biomes, mainly the vegetation structure, have a direct influence on determining the diversity and structure of macroalgal communities of tropical streams (Oliveira, Tonetto,

Peres, & Branco, 2013; Peres, Tonetto, Garey, & Branco, 2017). The biome type in which a given stream is located acts as a strong primary environmental filter, operating on a larger scale in determining distribution patterns of macroalgae in these freshwater ecosystems. These prior studies have reported that macroalgal communities from streams in a biome with a predominance of grasses on the landscape scale (highland grassland) had a high abundance and dominance of Chlorophyta, an algal group specifically adapted to high levels of light. By contrast, in a biome with a strong canopy development (seasonal semideciduous forest), macroalgal communities showed a low abundance and predominance of Rhodophyta, an algal group adapted to shady conditions. More broadly, these previous findings suggest that dissimilarity between stream macroalgal communities may be affected by factors operating on multiple spatial scales, as indeed has been observed for stream biodiversity in general (Perez Rocha et al., 2018). To the best of our knowledge, no studies to date have investigated beta diversity patterns of stream macroalgal communities simultaneously using local environmental variables, types of biome and spatial factors as predictors. Moreover, no studies have assessed other facets of beta diversity (such as phylogenetic and functional diversities), or the different components of beta diversity (spatial turnover and nestedness). In the current study of a macroalgal metacommunity in southern Brazil, we consider each of the three key facets of beta diversity (Leão-Pires et al., 2018)—taxonomic, phylogenetic, and functional—and analyse the relative contributions of spatial turnover and nestedness to the beta diversity of stream macroalgae (Baselga, 2010, 2012; Heino & Tolonen, 2017; Melchior et al., 2017). We also assessed the effect of local environmental variables (for brevity, called below 'local environment'), biome type ('biomes') and spatial factors ('space') on the beta diversity components for each of the taxonomic, phylogenetic and functional facets.

Given that the regional species pool and dispersal limitation increase as spatial extent increases (Harrison & Cornell, 2008), that low-order stream communities present a certain degree of isolation (Clarke et al., 2008) and that stream macroalgae may be significantly influenced by environmental variation on both local (Branco et al., 2009) and larger scales (e.g. biome type, as shown by Oliveira et al., 2013), we hypothesized that (a) spatial turnover should be the main driver of dissimilarity in the composition of beta diversity for the stream macroalgal metacommunity, regardless of the facet investigated (i.e. taxonomic, phylogenetic or functional) and (b) local environment and biomes should have a relatively higher influence on beta diversity than does space. We hypothesized that the magnitude of this trend may be influenced by which algal phylum is considered, as previously suggested by Branco et al. (2014). In particular, Rhodophyta are expected to be more influenced by space and/or biomes since red algae (a) have no efficient adaptation for long-distance transport, resulting in a lower dispersal ability than is likely for other algal phyla (Branco et al., 2014; Sheath & Hambrook, 1990) and (b) are better adapted to shady conditions than other algal groups, to the point that they are often reported as dominant in low light (Branco & Necchi Júnior, 1996; Necchi Júnior, 2004; Oliveira et al., 2013; Sheath & Cole, 1992; Tonetto, Branco, & Peres, 2012).

Given that organisms occupying similar niches (as inferred from their traits) are lumped into functional groups/guilds (Tapolczai, Bouchez, Stenger-Kovács, Padisák, & Rimet, 2016) and that generalist taxa can be found in most streams, we hypothesized that the magnitude of functional beta diversity should be relatively lower than that for beta diversity based on both phylogeny and taxonomy, as well as being more influenced by nestedness. As sorting of taxa in a community is mediated by trait–environment relationships (Heino & Tolonen, 2017), we expected that functional and phylogenetic beta diversities would be more affected by environment (local environment and biomes) than space.

2 | MATERIALS AND METHODS

2.1 | Study area, macroalgal data, local environmental variables, types of biome and spatial factors

A stream macroalgal metacommunity was sampled in 105 stream segments located in 10 natural protected areas of southern Brazil (Figure 1). The study area is part of the Brazilian subtropical region, which is dominated by four main biomes: Dense Ombrophylous Forest (DOF); Mixed Ombrophylous Forest (MOF); Seasonal Forest (SF) and Steppe (S) (IBGE, 1992; Peres et al., 2017). The vegetation structure of these biomes is ultimately determined by their climatic conditions (IBGE, 1992; Peres et al., 2017). DOF exhibits high and regular annual precipitation, while MOF, SF and S have less intense and irregularly distributed precipitation throughout the year (Peres et al., 2017). S is the biome with the highest annual temperature variation (ranging from very hot summers to frosty winters), while DOF is the one with the lowest annual thermal range; MOF and SF, in turn, present an intermediate annual temperature variation (Peres et al., 2017).

Following the Strahler stream classification system (Strahler, 1957), all stream segments sampled in this study are of low order (first to third orders and, only occasionally, fourth order). Low-order streams are characterized, in a simplified way, as those of small size with reduced width and depth and low water volume. These lotic systems are spread across the terrestrial landscape, representing an active zone of exchange of materials between the land and the water (Graça et al., 2015). With regard to their locations, all sampled stream segments were inside protected areas to avoid the effect of anthropogenic disturbance. Macroalgae are primary benthic producers that usually occur in lotic environments where the water column is shallower, allowing enough solar radiation to reach the bottom to maintain photosynthesis (Rott & Wehr, 2016). Each stream segment consisted of a 10 m cross transect, which was thoroughly surveyed for the presence of macroalgal taxa (sensu Sheath & Cole, 1992). Among the 105 streams segments sampled, 93 (89% of total) recorded the presence of at least one species of macroalgae. Specimens of each macroalgal taxa were collected in the field, preserved and taken

FIGURE 1 Southern Brazil showing its main biomes and the protected areas (with respective number of sampled streams) investigated in the present study

to the laboratory for identification. Specimen identification, based on morphometric features, was conducted under microscope (a Leica, DM 100, equipped for capture and analysing images, Leica DFC 280) to the species level whenever possible, using taxonomic references specific to Brazilian material (e.g. Branco, Krupek, & Peres, 2008, 2009; Branco & Necchi Júnior, 1996; Necchi Júnior, Branco, & Branco, 2000; Necchi Júnior, Branco, Simões, & Branco, 1995).

The following predictors of beta diversity of stream macroalgae were evaluated: local environment, biome and space. In each stream segment, a set of local environmental variables were measured, including water temperature, conductivity, pH, turbidity, dissolved oxygen, current velocity, depth, total phosphorus and total nitrogen. In addition, substrate types were quantified by the percentage of stream bed coverage, following the categories proposed by Gordon, McMahon, and Finlayson (1992: continuous rock, boulders, pebbles, gravel and sand), as well as by shading level, as proposed by DeNicola, Hoagland, and Roemer (1996: open, partially shaded, shaded and heavily shaded). All local environmental variables were log-transformed, except for pH.

The biome in which the macroalgae were collected was determined based on regional maps (IBGE, 1992) and confirmed directly in the field (see Figure 1). In the current study, we considered biome to be a proxy for variation of a set of environmental variables at a larger spatial scale (e.g., vegetation, climate, altitude and soil type).

Spatial factors were obtained following the method of principal coordinates of neighbour matrices (PCNM). PCNM were represented by *eigenvectors* with positive *eigenvalues* extracted from a distance matrix, which describes significant spatial autocorrelation using the Moran Index (Borcard & Legendre, 2002). Additional information about the study area, macroalgal data, and the environmental and spatial variables has been previously described by Branco et al. (2014) and Peres et al. (2017), utilizing the same data sets (or part of them) as in the current study.

2.2 | Taxonomic and phylogenetic information

The familiar term 'algae' refers to an artificial group including prokaryotic and eukaryotic organisms that can be best defined as 'oxygenic photosynthesizers other than embryophytes' (Cavalier-Smith, 2007). Thus, there is ambiguity and difficulty in ascribing a reliable phylogeny to this group as a whole. There does not yet exist a comprehensive well-established phylogeny encompassing the main algal groups. But there is available a widely accepted online database of information on marine, freshwater and terrestrial algae with taxonomic and nomenclatural data (i.e. AlgaeBase—Guiry & Guiry, 2018; Guiry et al., 2014), so we chose to use taxonomic distances, represented by the length of the path connecting pairs of species through a Linnaean taxonomic classification (Clarke & Warwick, 1998), as a

proxy for stream macroalgal phylogeny, a protocol used in other comparable studies (e.g. Heino & Tolonen, 2017). AlgaeBase provided the primary source of data to establish the taxonomic arrangement that generated a matrix with eight taxonomic levels—species, genus, family, order, class, phylum, kingdom and empire. In addition to this matrix, three other matrices were built, representing the currently accepted taxonomic arrangements for Chlorophyta, Cyanobacteria and Rhodophyta (Branco et al., 2014).

2.3 | Functional descriptors

Functional descriptors used to evaluate the functional beta diversity of the stream macroalgal metacommunity were chosen from the conceptual framework presented by Lange, Townsend, and Matthaei (2016). In Lange et al. (2016), morphological, physiological, behavioural and life-history information (distributed in 7 traits with 23 trait categories) was used to assess relationships between multiple anthropogenic stressors and algal traits. We utilized the trait categories proposed by Lange et al. (2016), with some modifications to better represent functional characteristics of our metacommunity. For instance, we excluded categories related to motility ('behavioural trait'), since stream macroalgae as mature thallus are by definition sessile organisms ('sensu' Sheath & Cole, 1992). The following species traits (and respective categories) were obtained from the literature and direct observation: life form (colony, mats, tufts, crusts, free filaments and gelatinous filaments); attachment to substrate (loosely attached and strongly attached); attachment system (rhizoids, entangled filaments and prostrate filaments); organism size (1.0–3.0 cm; 3.1–5.0 cm and >5.0 cm); nitrogen fixation (homocyted cyanobacterium, heterocyst-forming cyanobacterium and eukaryotic algae); main reproductive mechanism (fission and fragmentation); resistant spore formation (presence or absence) and sexual reproduction (presence or absence). These functional traits have been tested and well supported in addressing hypotheses in previous studies (e.g. Lange et al., 2016), suggesting that they should well describe the life-history strategies of stream benthic algae, as required for a good trait-based ecological classification (Tapolczai et al., 2016).

Given that the diversity of functional traits is closely related to phylogenetic/taxonomic diversity, and that functional traits can be phylogenetically conserved (Weiher, 2011, in algae this can clearly be seen at the phylum level), analyses of functional diversity were carried out only for the full set of macroalgae.

2.4 | Statistical analyses

First, effects of biome on the local environment were tested using Permutation Analysis of Variance (PERMANOVA; Anderson, 2001), based on a matrix of environmental dissimilarity between streams (using the Euclidian distance index, after standardization). Additionally, a PERMANOVA was also applied to evaluate the effects of biome on the composition of macroalgal communities, which, in turn, were ordinated using a three-dimensional Nonmetric Multidimensional Scaling (NMDS). The PERMANOVA and NMDS applied to the composition of macroalgal communities were based on the Sørensen dissimilarity index. The PERMANOVA, with 999 permutations, and the NMDS were run using, respectively, the functions *adonis* and *metaMDS*, both from the R package *vegan*.

Analyses of beta diversity were performed using three distinct facets of community composition: (a) species incidence or taxonomy (hereinafter referred to as 'taxonomic beta diversity'); (b) phylogeny (phylogenetic beta diversity) and (c) functional traits (functional beta diversity). For each of these facets, total beta diversity was partitioned into spatial turnover and nestedness.

We used the multisite dissimilarity and pairwise dissimilarity partitioning approaches proposed by Baselga (2010, 2012) to decompose total beta diversity into spatial turnover and nestedness components. Following these approaches, the Sørensen dissimilarity index (beta.SOR for multisite dissimilarity; beta.sor for pairwise dissimilarity), a measure of overall species replacement, was decomposed into two additive components: (a) a measure of dissimilarity related to spatial turnover, without the effect of species richness variation, obtained by applying the Simpson dissimilarity index (beta.SIM; beta.sim) and (b) the fraction of the dissimilarity due to a nested pattern (beta.SNE; beta.sne), calculated by the difference between beta.SOR/beta.sor and beta.SIM/beta.sim. For the calculation of beta diversity components (beta.SOR/beta.sor, beta.SIM/beta.sim and beta.SNE/beta.sne), we used the functions *beta.multi* and *beta.pair* available in the R package *betapart* (Baselga, Orme, Villeger, Bortoli, & Leprieur, 2018). Sørensen, Simpson and Nestedness dissimilarity indices for both multisite and pairwise dissimilarity were calculated based on formulae presented by Baselga (2010).

These procedures were repeated for each of four different types of macroalgal species incidence matrices, which were constructed (following Branco, Bispo, Peres, Tonetto, & Branco, 2014) using (a) all taxa recorded (hereinafter referred to as 'macroalgae matrix'); (b) only representatives of Chlorophyta (green algae matrix); (c) only Rhodophyta (red algae matrix) and (d) only Cyanobacteria (cyanobacteria matrix). As pointed out by Branco et al. (2014), individual analyses with these phyla are justified because they have marked differences with respect to their physiological and ecological characteristics, including dispersal abilities (Kristiansen, 1996;Sheath & Hambrook, 1990), and also because they are the main macroalgal groups in lotic habitats worldwide (Sheath & Cole, 1992). After completion of these procedures, 12 dissimilarity matrices were produced, that is, three dissimilarity matrices (pairwise beta.sor, beta.sim and beta.sne) for each species incidence matrix (macroalgae, green algae, red algae and cyanobacteria).

We assessed the unique effects of local environment, biome and space on the pairwise beta diversity components (beta.sor, beta.sim and beta.sne) obtained from macroalgae, green algal, red algal and cyanobacteria matrices using distance-based redundancy analysis (db-RDA) and its partial version (db-pRDA). db-RDA, which was

developed by Legendre and Anderson (1999), is a means to conduct RDA using pairwise beta diversity matrices, while db-pRDA allows the partitioning of specific effects of two or more sets of predictors (i.e. local environment, biome and space) on the beta diversity matrices (Beisner, Peres-Neto, Lindstrom, Barnett, & Longhi, 2006; Borcard, Legendre, & Drapeau, 1992; Legendre & Legendre, 2012).

Effects of the local environmental, biome and spatial predictors on beta diversity were gauged in two steps. First, a global db-RDA was performed considering each of these predictors separately and including all variables. After that, given that in all cases at least two individual sets of predictors were significant (local environment, biome, and space or biome, and local environment or biome and space), we carried out a selection of variables for the significant components, and then a db-pRDA using the selected variables was performed. In the case of biome, as we use only one variable to represent this component (i.e. type of biome), the selection of variables was not necessary. Selection of variables was done using the forward selection method considering two stopping criteria, namely (a) the significance level and (b) an R^2 not exceeding the global R^2 (considering all variables) (following Blanchet, Legendre, & Bocard, 2008).

In the db-pRDA, the following fractions were evaluated: (a) pure local environment, that is, the local environmental component without space and biome; (b) pure biome, that is, the biome component without local environment and space and (c) pure space, that is, the spatial component without local environment and biome. The importance of each fraction was identified considering the adjusted R^2 (Beisner et al., 2006; Peres-Neto, Legendre, Dray, & Borcard, 2006), since the variance partition is influenced both by the number of variables and by sample size (Peres-Neto et al., 2006). The significance of each component was tested using 999 permutations (Peres-Neto et al., 2006).

To run db-RDA and db-pRDA, we used the functions *ordiR2step* (forward selection), *capscale* (db-RDA), *varpart* (db-pRDA) and *RsquareAdj* (adjusted R^2 calculation), all from the R package *vegan* (Oksanen et al., 2018).

Additionally, we produced two other sets of dissimilarity matrices representing the two other complementary facets of beta diversity: (a) phylogenetic data and (b) functional traits (Heino & Tolonen, 2017). The procedures we used to perform these analyses were basically the same as those for taxonomic beta diversity, but some specific procedures used to construct dissimilarity matrices and calculate beta diversity need to be highlighted. For the phylogenetic beta diversity, three matrices of dissimilarity (based on Sørensen, Simpson and Nestedness indexes) were produced, considering taxonomic information as proxies for phylogenetic data (see Section 2.2). In the same way as for taxonomic data, phylogenetic dissimilarity matrices were also generated considering the data sets for total macroalgae species, for green algae species, for red algae species and for cyanobacteria species. We utilized a three-step procedure: (a) tables containing the taxonomic arrangements were used to calculate the taxonomic distances between species using the function *taxa2dist* from the R package *vegan* (Oksanen etal.,2018); (b) matrices of taxonomic distances were then used to construct a representation of the phylogenetic relationships

between taxa using the function *upgma* from the R package *phangorn* (Schliep,2011) and finally, (c) each phylogenetic relationship representation, saved in Newick format using the function *write.tree* from the R package APE (Paradis, Claude, & Strimmer,2004), was utilized in association with the respective incidence matrix (i.e. site-by-species matrix) to calculate each phylogenetic beta diversity component (based on Sørensen, Simpson and Nestedness indexes), using the functions *phylo.beta.multi* and *phylo.beta.pair* from the R package *betapart* (Baselga etal.,2018).

For the functional traits approach, three matrices of dissimilarity (based on Sørensen, Simpson and Nestedness indexes) were produced considering functional traits. Because functional data tend to be conserved at phylum level, beta diversity analyses considering this kind of information were only performed using the total macroalgal species incidence matrix (see Section 2.3). To perform the functional beta diversity analyses themselves, we constructed a table of functional descriptors per species based on the trait categories proposed by Lange et al. (2016) (see Section 2.3). The original table containing the functional traits was utilized to calculate the functional distances between species using the function *taxa2dist* from the R package *vegan* (Oksanen et al., 2018), and then, the functional distance matrix was summarized by principal coordinates analysis (PCoA) using the function *cmdscale* from the R package *stats*. The PCoA was performed to reduce the dimensionality of the original functional matrix (Heino & Tolonen, 2017). The first two PCoA axes (which accounted for 65.6% of all functional variability) and the macroalgal species incidence table (i.e. site-by-species matrix) were, finally, used to produce the three functional matrices of dissimilarity. Due to computational limitations, we used 10 random sites to calculate functional beta diversity for multiple sites. The calculation of functional beta diversity for multiple sites was performed using *functional.beta.multi*, while the paired functional beta diversity was performed using *functional.beta.pair*, both functions of the R *betapart* package (Baselga et al., 2018). As for taxonomic data, we examined the unique effects of local environment, biome and space on the pairwise phylogenetic and functional beta diversity components (beta.sor, beta.sim and beta.sne) using db-RDA and db-pRDA.

Finally, based on the pairwise dissimilarity data, we applied a Mantel correlation test to compare the degree of congruence between the dissimilarity matrices using *mantel.rtest* from the R *ade4* package.

3 | RESULTS

The PERMANOVA revealed that biome affected both local environment ($F = 6.41$, $P > 0.001$) and macroalgal community compositions ($F = 2.67$, $P > 0.001$). NMDS ordination of the macroalgal communities according to their composition is presented in Figures S1–S3.

Local environmental variables revealed considerable variation over the study area (Branco et al., 2014). In the 105 sampling sites, we identified a total of 83 taxa, among which 67 belong to the three

main algal phyla represented in tropical stream macroalgal communities, namely Chlorophyta (25 species), Cyanobacteria (30) and Rhodophyta (12; Branco et al., 2014).

The total multisite taxonomic beta diversity (Figure 2a) showed very high values for all macroalgal groups, with a Sørensen dissimilarity index (beta.SOR) value of 0.98 for total macroalgae, 0.97 for green algae and cyanobacteria and 0.96 for red algae. The species Simpson dissimilarity index (beta.SIM) showed strong congruence with beta.SOR, since the difference between the values of these two indices was less than 0.02, as follows: beta.SIM was 0.97 for macroalgae, 0.95 for green algae, 0.96 for cyanobacteria and 0.94 for red algae (Figure 2a). Complementarily, the values of nestedness (beta.SNE) were very low for all types of macroalgal species incidence matrices (total macroalgae = 0.01, green algae = 0.02, cyanobacteria = 0.01 and red algae = 0.02; Figure 2a).

The three components of multisite phylogenetic beta diversity (beta.SOR, beta.SIM and beta.SNE) showed strong parallels with those observed for taxonomic beta diversity for all algal groups investigated (Figure 2b). Total macroalgae, green algae, cyanobacteria and red algae showed very high values for beta.SOR (at least 0.94) and beta.SIM (at least 0.91) and very low values for beta.SNE (at most 0.04). These results indicate a high degree of variation in phylogenetic community structure among the sampling sites and suggest that this variation is related to spatial turnover.

For multisite functional beta diversity for total macroalgae, a high value for beta.SOR (0.73) was found with a predominance of beta.SIM (0.53) over beta.SNE (0.20; Figure 2c). The difference between the values of the spatial turnover and nestedness components was, however, much lower than that observed for the other two facets of beta diversity (taxonomy and phylogeny).

Pairwise beta diversity showed similar patterns to those observed for multi-site beta diversity, such that the values of the spatial turnover component (beta.sim) were higher than those recorded for the nestedness component (beta.sne), regardless of the beta diversity facet or the algal phylum considered (Figure 3). The Mantel correlation test for the different facets and components of pairwise beta diversity calculated for total macroalgae showed that taxonomic, phylogenetic and functional dissimilarities were all significantly correlated (Table 1). The highest correlation coefficients were found among the beta.sor, beta.sim and beta.sne of the taxonomic and phylogenetic facets of beta diversity (r values of 0.64, 0.65 and 0.37, respectively). Furthermore, moderate correlation coefficients were also found between the beta.sor and beta.sim of the functional and phylogenetic beta diversity (0.34 and 0.33, respectively). The other correlations, although significant, showed relatively low values (r < 0.30).

The relationships between taxonomic, phylogenetic and functional beta diversity, and local environment, biome and space showed specific patterns for each macroalgal group investigated (Figures 4–6; Table 2), with total macroalgae often having a pattern relatively similar to that of green algae. Sørensen and Simpson dissimilarities for taxonomy and phylogeny were significantly related to local environment for total macroalgae, green algae and cyanobacteria, but
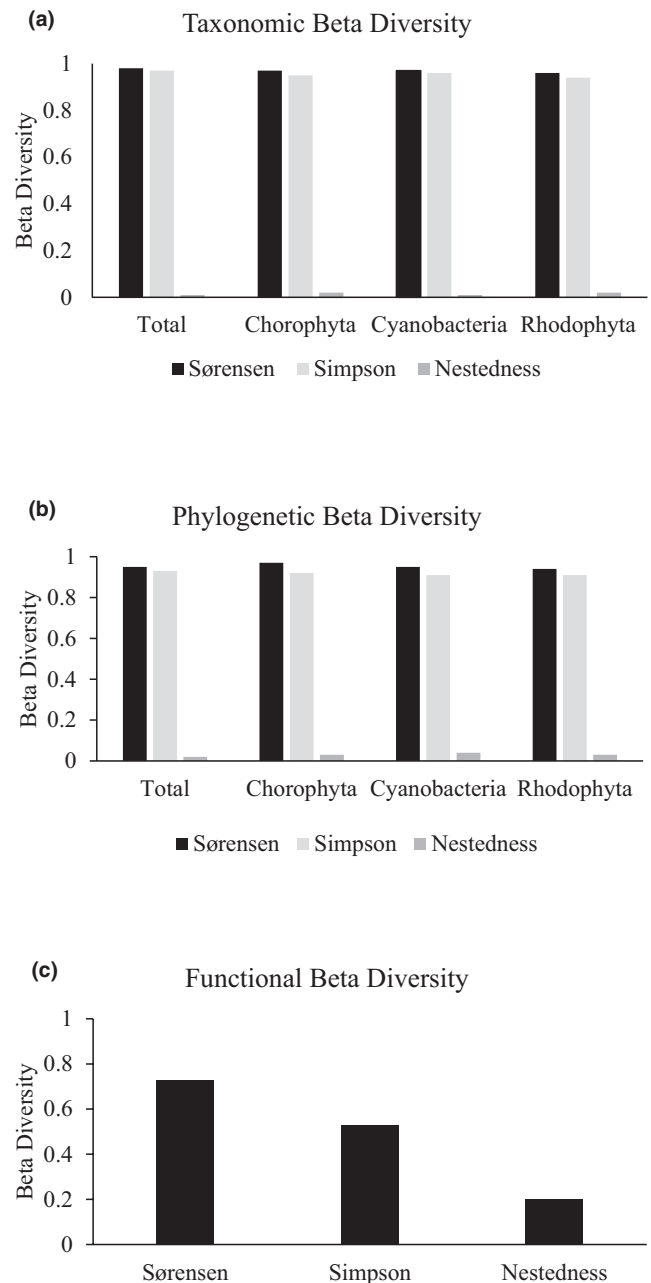

(a) Taxonomic Beta Diversity

(b) Phylogenetic Beta Diversity

(c) Functional Beta Diversity

FIGURE 2 Bar plots of multiple-site beta diversity components (Sørensen dissimilarity; Simpson dissimilarity; Nestedness) of a stream macroalgal metacommunity from Southern Brazil. A = Taxonomic beta diversity; B = Phylogenetic beta diversity and C = Functional beta diversity. Taxonomic and phylogenetic beta diversities were calculated considering the occurrence of (a) total macroalgal species, (b) only Chlorophyta species, (c) only Cyanobacteria species and (d) only Rhodophyta species, while functional beta diversity was calculated considering exclusively the occurrence of total macroalgal species. Legends for bar colours: black bar = Sørensen dissimilarity; light grey bar = Simpson dissimilarity and dark grey bar = Nestedness

not for red algae. Space and biome were also significantly related to these dissimilarity matrices for total macroalgae, green algae (except for the effect of space on phylogenetic beta.sim) and red algae, but not for cyanobacteria (Figures 4–6).
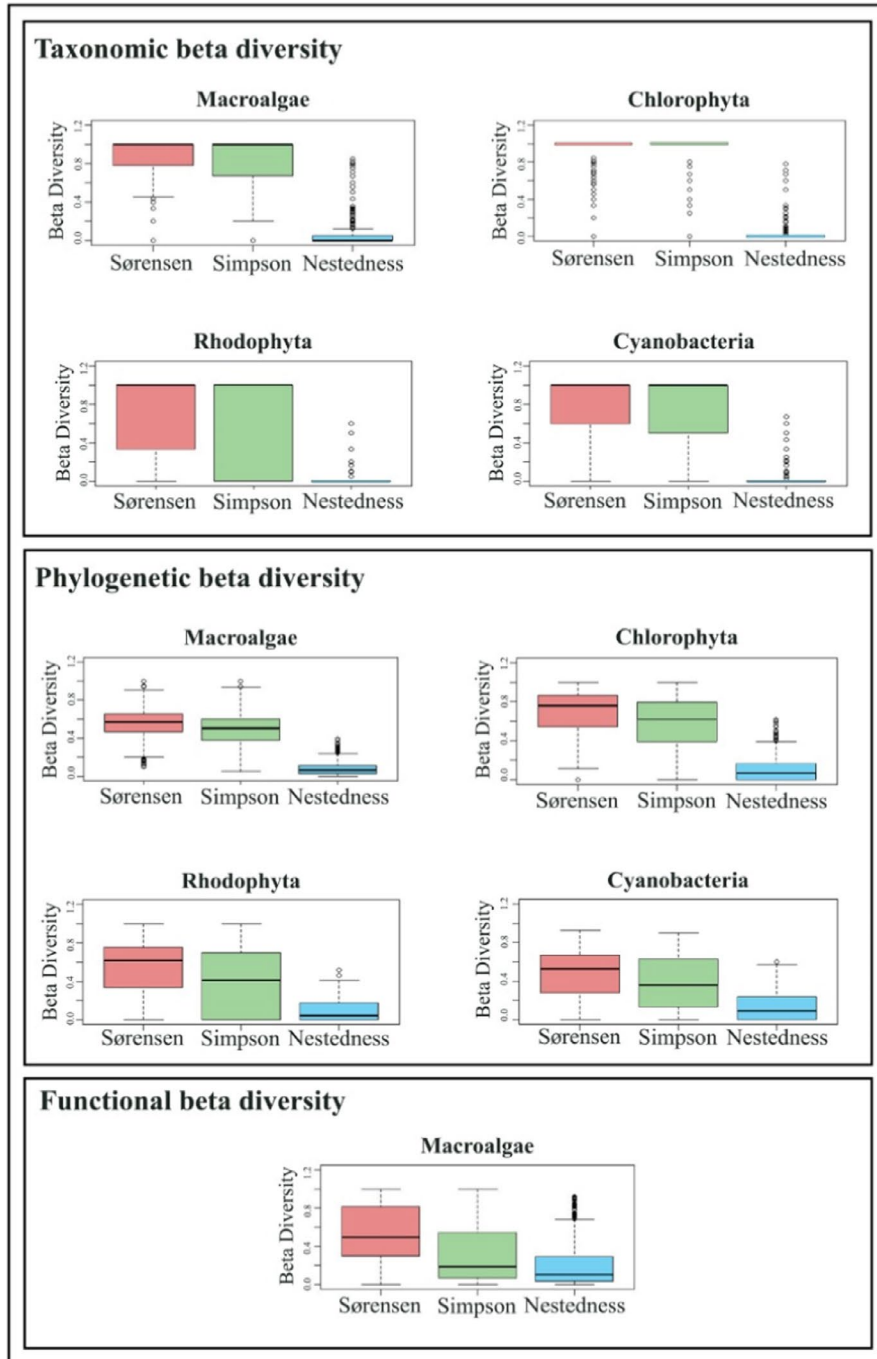
FIGURE 3 Boxplots of the pairwise taxonomic, phylogenetic and functional beta diversities of the components (beta.sor = Sørensen dissimilarity; beta.sim = Simpson dissimilarity; beta.sne = Nestedness) of a stream macroalgal metacommunity from southern Brazil. Taxonomic and phylogenetic beta diversities were calculated using the occurrence of (a) total macroalgal species, (b) only Chlorophyta species, (c) only Rhodophyta species and (d) only Cyanobacteria species. The horizontal line represents the median, while the lower and upper limits of the box are the 25th and 75th percentiles. Whiskers above and below the box indicate 1.5 time the interquartile range (IQR) 'above' and 'below' the limits of the box, respectively, and points indicate outliers [Colour figure can be viewed at wileyonlinelibrary.com]

For taxonomic and phylogenetic beta diversity, local environment was, in general, the most important predictor for macroalgae and green algae. This explained by itself the highest amount of beta.sor and beta.sim variations (as observed for phylogenetic beta.sor for macroalgae and for taxonomic beta.sim for green algae) or, more commonly, shared the highest explicability value with one of the other two predictor variables (biome or space) (Figures 4–6). On the other hand, beta.sor and beta.sim for the functional component were not significantly correlated to any predictor assessed, that is, local environment, biome and space for total macroalgae (Figure 4). The nestedness component considering all beta diversity facets was not significantly correlated with

local environment, biome and space for any of the macroalgal species incidence matrices.

4 | DISCUSSION

Total beta diversity (i.e. beta.SOR/beta.sor) for a stream macroalgal metacommunity from southern Brazil showed high values for taxonomy, phylogeny and functional traits (Figures 2 and 3). This clearly demonstrates the dominance of between-community turnover in influencing the composition of the regional biodiversity pattern for this group of primary producers. High values of beta diversity have
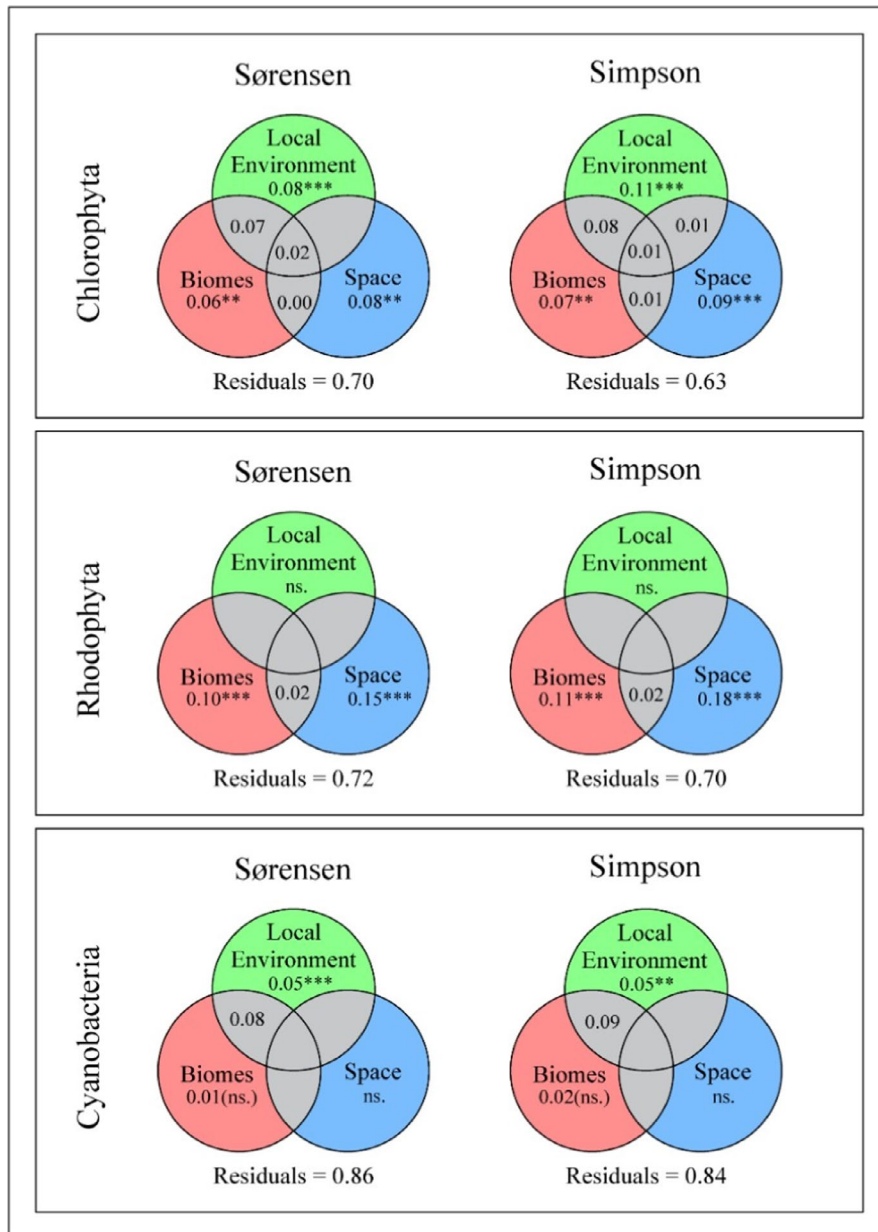
TABLE 1 Mantel correlation among different components (Sørensen dissimilarity, .sor; Simpson dissimilarity, .sim; Nestedness, .sne) and dimensions of beta diversity (taxonomic; phylogenetic; functional) of stream macroalgae from southern Brazil

Beta diversity components/facets	Correlation coefficient
functional.sor versus phylogenetic.sor***	0.34
functional.sor versus taxonomic.sor***	0.22
taxonomic.sor versus phylogenetic.sor***	0.64
functional.sim versus phylogenetic.sim***	0.33
functional.sim versus taxonomic.sim***	0.24
taxonomic.sim versus phylogenetic.sim***	0.65
functional.sne versus phylogenetic.sne**	0.19
functional.sne versus taxonomic.sne***	0.28
taxonomic.sne versus phylogenetic.sne***	0.37

**P < 0.01.

***P < 0.01.

often been reported for aquatic and terrestrial organisms, but there are almost no reported values as high as those observed for the stream macroalgae in our study (e.g. Heino & Tolonen, 2017; Villéger et al., 2012; Zbinden & Matthews, 2017; Zellweger, Roth, Bugmann, & Bollmann, 2017), especially for taxonomic and phylogenetic data. Beta diversity should be scale-dependent. Our study spans a large area (see Figure 1) in Brazil, and a range of elevation and geological substrate, as well as a variety of biomes, factors which likely would boost beta diversity.

As other researchers have argued (e.g. Heino et al., 2015; Podani & Schmera, 2011), a combination of a high contribution of rare species and a high number of absences in a species-by-site matrix can produce, in general, an increase in the values of beta diversity. The high values of beta diversity observed in the current study match this suggestion, since the combination of a high occurrence of species with restricted distributions and a low relative richness of species per site is perhaps the most general structural feature that describes the stream macroalgal metacommunity we have analysed.

Our results also agree with previous studies that suggested that, as a rule, the diversity patterns of tropical stream macroalgal communities are closely related to processes of species sorting along spatial/environmental gradients (Branco et al., 2009; Oliveira et al., 2013). This pattern has been consistently noted in other systems. For instance, a comparison between the species composition of stream macroalgal communities from two different regions of southern Brazil, one with a predominance of highland grassland and the other with a predominance of seasonal semideciduous forest, showed that given the same sample size, these communities registered very similar species richness (19 versus 21 species, respectively), with a very low magnitude of shared species (only 3 species, or 7.5% of the total species; Oliveira et al., 2013). Similarly, a more detailed analysis of several comprehensive floristic studies carried out around the world, including tropical, subtropical, temperate and boreal regions (e.g. Branco & Necchi Júnior, 1996; Necchi Júnior et al., 2000, 1995; Sheath & Burkholder, 1985; Sheath, Hamilton, Hambrook, & Cole, 1989; Sheath, Morison, Korch, Kaczmarczyk, & Cole, 1986), indicated that spatial variation in the species composition of stream macroalgae communities can be strongly influenced by species with a low frequency of occurrence (less than 5% of the sampling sites; Branco et al., 2009). In general, these studies revealed that species with restricted occurrence contributed more than 50% of the total macroalgal community (Branco et al., 2009), and such species drive patterns of beta diversity.

FIGURE 4 Venn diagrams showing explained variation (based on *adjusted R²*) of distance matrices representing the effects, unique and joint, of local environment, space and biomes on the different components (Sørensen and Simpson) of the taxonomic, phylogenetic and functional beta diversity in the stream macroalgae from southern Brazil. Taxonomic, phylogenetic and functional beta diversity were calculated considering exclusively the occurrence of total macroalgal species. No significant value was found for the Nestedness component. Local environment = local environmental variables; space = spatial factors (db-MEM); biome = type of biome (representing larger-scale environmental variables). *P < 0.05; **P < 0.01; ***P < 0.001 [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 5 Venn diagrams showing explained variation (based on *adjusted R²*) of distance matrices representing the effects, unique and joint, of local environment, space and biomes on the different components (Sørensen and Simpson) of taxonomic beta diversity in the stream macroalgae from southern Brazil. Taxonomic beta diversity was calculated considering exclusively the occurrence of (a) only Chlorophyta, (b) only Rhodophyta and (c) only Cyanobacteria species. No significant value was found for the Nestedness component. Local environment = local environmental variables; space = spatial factors (db-MEM); biome = type of biome (representing larger-scale environmental variables). *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$ [Colour figure can be viewed at wileyonlinelibrary.com]

Considering the components of beta diversity, we found that the main cause of dissimilarities among stream macroalgal communities was spatial turnover, regardless of the beta diversity facet or type of macroalgae included in the particular incidence matrix analysed. For taxonomic and phylogenetic data, spatial turnover represented almost all of total beta diversity (Figure 2a,b; including all sorts of macroalgal matrices). A single exception in this pattern was observed for functional beta diversity, in which the contribution of nestedness to total beta diversity, although still much smaller than spatial turnover, was much higher than observed for the other facets (Figure 2c). Higher contributions of spatial turnover along with low values of nestedness have been repeatedly reported across many different kinds of organisms, habitat types and geographical regions (e.g. Boschilia, Oliveira, & Schwarzbold, 2016; Heino & Tolonen, 2017; Hill, Heino, Thornhill, Ryves, & Wood, 2017; Soininen, Heino, & Wang, 2018; Zbinden & Matthews, 2017). Our finding may thus

exemplify a typical pattern in the relationship between the additive components of beta diversity. Soininen et al. (2018) found, from a meta-analysis involving several studies with different groups of organisms, spatial and latitudinal positions, and habitat types, that spatial turnover was consistently larger than nestedness (5.7 times on average). Considering studies of freshwater algae, the combination of high spatial turnover and low nestedness has been repeatedly found (e.g. Dunck, Schneck, & Rodrigues, 2016; Jamoneau, Passy, Soininen, Leboucher, & Tison_Rosebery, 2018; Maloufi et al., 2016; Yang et al., 2018). However, except for functional beta diversity, the differences between the relative contributions of the turnover and nestedness components observed for stream macroalgae seem overall to be higher than observed for other groups (Figure 2a,b).

High values of species replacement among communities may reflect species selection by environmental or spatial filters (Boschilia et al., 2016; Soininen et al., 2018). With regard to environmental

FIGURE 6 Venn diagrams showing explained variation (based on *adjusted R²*) of distance matrices representing the effects, unique and joint, of local environment, space and biomes on the different components (Sørensen and Simpson) of phylogenetic beta diversity in the stream macroalgae from southern Brazil. Phylogenetic beta diversity was calculated considering exclusively the occurrence of (a) only Chlorophyta, (b) only Rhodophyta and (c) only Cyanobacteria species. No significant value was found for the Nestedness component. Local environment = local environmental variables; space = spatial factors (db-MEM); biome = type of biome (representing larger-scale environmental variables). *P < 0.05; **P < 0.01; ***P < 0.001 [Colour figure can be viewed at wileyonlinelibrary.com]
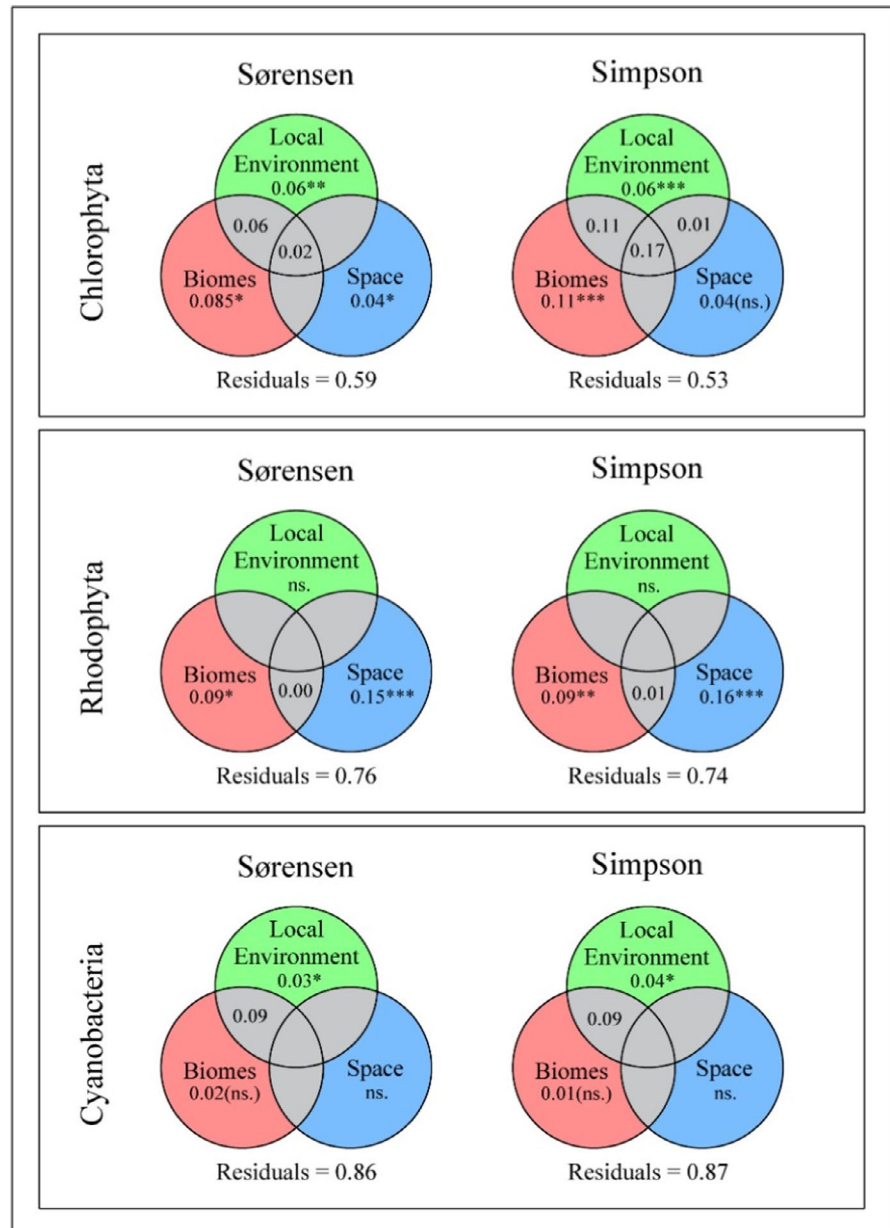
filters, it is important to emphasize that these kinds of filters can operate on different scales, ranging from local (e.g. microhabitat, mesohabitat or stream segment) to larger (e.g. catchment, biome or biogeographical region) scales. Our results showed that the relative influence of environmental variables at different scales (local and biome) and spatial filters on spatial turnover may vary according to the beta diversity facet, and also with the type of macroalgal incidence matrix analysed. For total macroalgal and Chlorophyta matrices, in general, the effects of local environment, biome and space were significant for beta.sim when considering taxonomic and phylogenetic beta diversity (Figures 4–6). However, although all predictors proved to be significant, greater proportions of taxonomic and phylogenetic compositional changes were due to environmental variables, considering both scales, local and biome. For Cyanobacteria, spatial turnover considering taxonomic and phylogenetic matrices was significantly related only to local environment,

while for Rhodophyta, this beta diversity component was significantly related to spatial factors and biome (Figures 5 and 6).

Essentially, our results concord with our earlier findings (Branco et al., 2014), which showed that differences in the relative effects of space and local environment on the structure of a given metacommunity may be closely related to ecological differences among the algal groups present in the community. Branco et al. (2014) suggested that algal groups with a lower dispersal capacity (e.g. Rhodophyta) may be more influenced by spatial processes than those with greater dispersal ability (e.g. Cyanobacteria), which, in turn, may be more affected by local environmental variables (suggesting the dominance of the species sorting process; Leibold & Chase, 2017). In the current study, this same pattern of relative influence of local environment and space was recorded not only for total beta diversity but also for spatial turnover. We also found that the influence of local environment and space observed for the taxonomic facet was repeated

	Selected environmental variables	Selected spatial variables
Taxonomic beta diversity		
Sørensen index		
Macroalgae	pH; shading level; gravel; temperature; total nitrogen	V3; V1; V2; V4
Chlorophyta	pH; shading level; temperature; total nitrogen; current velocity	V1; V4; V2
Cyanobacteria	pH; shading level; gravel	—
Rhodophyta	—	V2; V3; V4; V1
Simpson index		
Macroalgae	pH; shading level; pebbles; temperature; total nitrogen	V3; V1; V2; V4; V9
Chlorophyta	pH; temperature; total nitrogen; shading level; current velocity	V1; V4; V2
Cyanobacteria	pH; shading level; pebbles	—
Rhodophyta	—	V2; V3; V4; V1
Phylogenetic beta diversity		
Sørensen index		
Macroalgae	Specific conductance; shading level; temperature; depth; total nitrogen	V1; V2
Chlorophyta	pH; current velocity; total nitrogen; temperature; pebble	V1; V3; V2; V5
Cyanobacteria	pH; shading level	—
Rhodophyta	—	V1; V2; V5
Simpson index		
Macroalgae	Specific conductance; shading level; temperature; depth	V2; V1
Chlorophyta	pH; current velocity; total nitrogen; pebble; dissolved oxygen	V1; V3; V5
Cyanobacteria	pH; shading level	—
Rhodophyta	—	V3; V4; V2

TABLE 2 Selected local environmental variables and spatial factors, according to forward selection, when the values of *adjusted R*^{2} of the global dbRDAs were significant. For non-significant values of *adjusted R*^{2} of the global dbRDAs (including nestedness component for taxonomic and phylogenetic beta diversity, and all components—Søresen, Simpson and Nestedness—for functional beta diversity), forward selection was not performed

for the phylogenetic facet. Hence, the results of the current study confirm the conclusions presented earlier by Branco et al. (2014). We here have extended that previous work by showing that the same pattern observed for total taxonomic beta diversity also emerges for the spatial turnover component and for the phylogenetic facet.

However, in the current study, we also found a significant relation between taxonomic and phylogenetic beta diversity and biome for macroalgae, Rhodophyta and Chlorophyta, but not for Cyanobacteria (Figures 4–6). Therefore, our results suggest biome as a large-scale environmental filter that affects different facets of macroalgal beta diversity. A similar effect of the biome on stream macroalgal algal diversity has been reported elsewhere (Peres et al., 2017). The vegetation types of the four biomes in our study ranged from grassland (e.g. Steppe), through deciduous seasonal forest (e.g. Seasonal Forest) and evergreen seasonal conifer forest (e.g. Mixed Ombrophylous Forest), to perennial forest formations with a highly developed canopy (e.g. Dense Ombrophylous Forest; see Figure 1). These biomes encompass a wide variation of other large-scale variables than vegetation, such as climate, altitude range and

soil type. Species selection by such large-scale environmental variables could explain the strong effect of the biome on stream macroalgal beta diversity reported in the current study. 'Biome' could be a proxy for other variables we have not measured on a larger scale. It is possible that other variables not congruent with biome type also operate at such broader scales level. Along with the effects of unmeasured local environmental variables (e.g. biological interactions), stochastic factors and noise related to the effects of time and space scales, this could explain, at least in part, the high fraction of the unexplained variation often observed in analyses of beta diversity (Branco et al., 2014; Pandit, Kolasa, & Cottenie, 2009; Schulz, Siqueira, Stefan, & Roque, 2012).

When considering the effect of the biome on macroalgae diversity, it is important to note that differences in the degree of vegetation development are closely related to the quality (i.e. spectral composition—Tonetto et al., 2012) and quantity (i.e. amount of light—Tonetto et al., 2012) of the photosynthetically active radiation (PAR) available to the algae. Variation in the availability and composition of PAR from biome to biome may,

ultimately, explain the significant effects of biome on beta diversity observed in the current study, since the presence/absence of a given species and/or an algal group depends primarily on the adjustment between its photosynthetic characteristics and features of the light environment (Peres et al., 2017; Tonetto et al., 2012). Many studies have shown that green algae often dominate in regions with high light intensity (Necchi Júnior, 2004; Oliveira et al., 2013; Peres et al., 2017; Tonetto et al., 2012), while red algae tend to dominate in regions with moderate to low light intensity (Necchi Júnior, 2004; Necchi Júnior & Zucchi, 2001 Oliveira et al., 2013; Tonetto et al., 2012); cyanobacteria have no strong preference for one or other light condition, revealing a weak influence of this variable on the ecological distribution of this group (Branco et al., 2017; Necchi Júnior, 2017). Ultimately, the relationship between variation in the availability of PAR in different biomes and the composition of macroalgae communities, mediated by the typical photosynthetic characteristics of the different species/algal groups, could explain significant effects of biome type on the beta diversity of macroalgae, green algae and red algae, and the absence of such effects in cyanobacteria.

With respect to functional beta diversity, although a predominance of spatial turnover was also found (this component accounted for almost two-thirds of the total beta diversity), the nestedness component was much higher than that observed for the other beta diversity facets analysed (Figure 2c). The difference between the contribution of nestedness to total functional beta diversity (27.4%) and to the other facets of beta diversity (1%–4.2%) was remarkable (Figure 2c). In addition, both components of functional beta diversity—spatial turnover and nestedness—showed no significant relationship with any predictor (i.e. local environment, biome, space; Figure 4). Although the main results of the functional beta diversity analyses (i.e. lower total beta diversity with higher values of nestedness) reported here match the findings of previous studies (e.g. Heino & Tolonen, 2017), some of our findings were unexpected.

We expected to observe even lower values of total functional beta diversity and its components, and some significant influences of environmental factors. There is a consensus that the ecological distribution of species can be affected by the degree of adaptation of each species to different habitats, which, in turn, is largely determined by the functional properties of those species (Lange et al., 2016; Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Tapolczai et al., 2016). Taking this premise into account and considering that stream environments are locally highly heterogeneous (Frissell, 1986), it was expected that such habitats could individually harbour a significant proportion of the total functional variability, resulting in considerable overlap of functional composition across communities and, consequently, low values for functional beta diversity. Limited number of functional attributes available to represent total functional variability seemed to us to make this hypothesis even more likely. Our unexpected finding may reflect substantial spatial heterogeneity in key environmental factors among our stream habitats (Bojorge-García, Carmona, Beltrán, & Cartajena, 2010; Branco

et al., 2009; Necchi Júnior et al., 2000; Sheath & Cole, 1992; Verb & Vis, 2001).

The patterns of taxonomic, phylogenetic and functional beta diversity observed for the stream macroalgal metacommunity in our study proved to be consistently related, showing significant correlations between each pair (Table 1). Some correlation among these facets of beta diversity was expected, since taxonomic-based and functional-based compositions can have a phylogenetic signal. However, although significant, the values of correlation coefficients were, in general, low to moderate (except for beta.sor and beta.sim for taxonomic and phylogenetic facets—Table 1). Similar results have been reported for other groups, including many diverse aquatic and terrestrial organisms (Heino & Tolonen, 2017; Leão-Pires et al., 2018; Villéger et al., 2012; Yang et al., 2015). Significant but weak correlations between dissimilarities measured on the basis of taxonomic, phylogenetic and functional data suggest that these three facets of beta diversity are complementary; the use of all together may be more informative than using just one for understanding beta diversity in macroalgae, a conclusion that has already been suggested for other groups (e.g. De Bello et al., 2015; Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011; Yang et al., 2015).

In the context of natural resource conservation management, high values of beta diversity and the predominance of spatial turnover over nestedness suggest that the contribution of each stream to the regional taxonomic, phylogenetic and functional diversity (i.e. gamma diversity) of a given macroalgal metacommunity can be very important. This means that the degradation of even a few streams may result in a marked reduction in the diversity of macroalgae at a regional scale. This suggests that conservation efforts encompassing stream macroalgae, as also suggested for other organisms (e.g. birds and lizards—Si, Baselga, & Ding, 2015, and Atlantic Forest trees—Bergamin et al., 2017), should focus on preserving the highest number of stream ecosystems covering large geographic areas. In the conservation literature, scant attention has been paid to the potential loss of macroalgal biodiversity due to processes like damming, pollution and land use change. Such losses could impact ecosystem services. We suggest that this is a largely unexplored yet potentially important frontier in stream conservation biology.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository (Branco et al., 2020, https://doi.org/10.5061/dryad.zgmsbcc73).

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BIOSKETCH

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SUPPORTING INFORMATION

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