

Diversity patterns of Pampean stream vegetation at different spatial scales



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ABSTRACT

We examined diversity patterns at different spatial scales by observing the changes in the slopes of Species–Area relationships (SAR) and Local–Regional (L–R) relationships. Stream vegetation was sampled at four scales (reach ($N=50$), stream ($N=25$), watershed ($N=9$), and ecoregion ($N=2$)) in the Pampa Region (Buenos Aires, Argentina). The slopes of the SARs fitted to the logarithmic model increased significantly with scale from reach to ecoregion. For the L–R relationships, the slopes were significantly different from zero when analyzing stream richness in relation to reach richness, and undistinguishable from zero when analyzing watershed richness in relation to stream richness. The differences found in the slopes of the SAR mean that the scales proposed *a priori* are indeed different diversity scales. On the other hand, the linear relationship between reach and stream richness suggests that macrophyte assemblages in streams function as metacommunities, whose dynamics could be explained by the dispersal process. Thus, we propose that the metacommunities in streams and the assemblages in watersheds and ecoregions can be considered as the three diversity scales most relevant when attempting to understand macrophyte dynamics in Pampean streams. The increase in the species accumulation rate across all scales indicates that any actions for the conservation of macrophyte diversity in Pampean streams should be taken at the largest scale, that is, the ecoregion scale; on the other hand, the loss of species in the headwaters not only implies a decrease in local diversity, but also a loss of species downstream, that is why particular attention should be paid to the headwaters.

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1. Introduction

In nature, the ecosystems' diversity is determined by both local and regional processes. However, the relative importance assigned to either depends on the scales at which the processes generating the patterns of diversity occur. Therefore, to obtain a correct description of diversity patterns, different scales must be taken into account (Schmida & Wilson, 1985; Ricklefs, 2004).

The increase in the number of species with the size of the sampling area is a widely recognized pattern in ecology. In order to explain this pattern, the most frequently used models are: the one by Arrhenius (1921), which proposes a power relationship between species richness and area; and the one by Gleason (1922), which proposes a logarithmic relationship between the two. More

recently, several other models have also been proposed (for a review, see Tjørve, 2003). In species–area relationships (SAR), the slope of the curve indicates the rate of species turnover, focused on species net gain (Lennon et al., 2001), and according to some studies, the slope varies with the scale; for example, in vascular plants, the slope varies as the scale increases from cm^2 to km^2 , maximum value being reached at intermediate scales (1 ha–10 km^2) (Crawley & Harral, 2001), and in a meta-analysis of almost 800 SAR curves, applying both the power and logarithmic models, it was found that the slope of nested SARs varies as the scales increase from 10^{-8} to 10^{12} m^2 (Drakare et al., 2005).

The above-mentioned models are phenomenological, that is, they propose different shapes for the species–area relationship, but do not imply a single explanatory mechanism. In order to explain the observed patterns for SAR, several non-exclusive alternatives have been proposed (Connor & McCoy, 1979; Drakare et al., 2005). On one hand, there are explanations which consider the relationship to be dependent on the sampling design (Rosenzweig, 1995;

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Cam et al., 2002) and, on the other, the ones which attribute it to ecological causes. Among the latter, some consider that the relationship is due to an increase in habitat diversity resulting from the inclusion of a larger area (Kolasa et al., 2012), while some consider it to be due to demographic processes, such as dispersal, colonization, speciation and extinction (Connor & McCoy, 1979).

The changes in richness at different scales can also be approached from another perspective: the Local–Regional diversity relationship (L–R) (Cornell & Lawton, 1992). In this relationship, a high slope indicates a low rate of species turnover at the local scale, which could be explained either by the similar environmental conditions among the locations, or by a high propagule dispersal between sampling sites (Heino, 2011).

The SAR for macrophytes has been explored in different ways. Some studies use the accumulation curve in order to estimate richness (Melo et al., 2007; Ferreira et al., 2011). In lakes, richness has been related to total water-body size, and the results were inconsistent, even yielding non-significant regressions (Heegaard, 2004; Chappuis et al., 2014). In wetlands, there are also no univoque relationships, either the habitat area had no effect on species richness (Rey Benyas et al., 1999), either it was the main determinant in macrophyte richness (Rolon et al., 2008), either the area in conjunction with environmental heterogeneity influenced species richness (Shi et al., 2010). Lastly, in lotic water bodies, the SAR has not been explored. Instead, great relevance has been given to hydrological connectivity for the explanation of macrophyte diversity (Bornette et al., 1998; Capers et al., 2010). Vegetative reproduction and hydrochory, as the hydrophytes' characteristic dispersal mechanisms (Barrat-Segretain, 1996; Santamaría, 2002) are key to explain species distribution among sites connected along lotic water bodies (Riis et al., 2001).

In this paper, SAR patterns at different scales and L–R diversity relationships will be studied regarding a particular kind of ecosystem and community: the Pampean streams and their vegetation assemblages. In Pampean streams, macrophytes reach significant growth as a result of the low current velocity, and the high availability of light and nutrients. The Pampa Region (Argentina) is a system highly modified by its use for agricultural and livestock purposes, which results in many types of stream disturbance. This could, in turn, lead to a decrease in macrophyte diversity and, subsequently, to a decrease in the diversity of other aquatic communities. Correctly identifying the macrophytes' diversity scales would aid in determining the spatial scale of the effects produced by these disturbances.

Our aim is to analyze the change in the slope of the SAR and in the L–R relationship with the increase in spatial scale for the vegetation found on Pampean streams at four scales: reach, stream, watershed, and ecoregion. We propose that, within the Pampean region, the most relevant processes that explain macrophyte diversity patterns are the dispersal processes. If this is the case, there will be more similarities between the assemblages of any two hydrologically connected sites than between the assemblages found in isolated sites and, therefore, the slope of the SARs will be lower for the connected sites than for the isolated sites, while the slope for the L–R relationship will be higher for connected sites than for isolated sites.

2. Experimental

2.1. Study sites

The Pampa ecoregion has a surface area of approximately 540,00 km², making it Argentina's most important prairie ecosystem. Its relief is relatively flat, with highest slopes towards the Atlantic Ocean and below 1%. The soils are suitable for

agriculture and livestock farming, though this suitability decreases with the decrease in annual rainfall, which varies from 400 mm in the south–west to 1000 mm in the north–east. The rain is distributed all along the year, with peaks in spring and summer. Mean annual temperatures fluctuate between 14 and 20 °C. The natural vegetation is composed of about a thousand species of vascular plants (León, 1991), where grasses are dominant. However, the prairie's original vegetation has mostly been replaced with exotic species introduced for agricultural and livestock activities. The Pampa region is quite homogeneous; nevertheless, upon geomorphologic characteristics it has been divided into four fluvial systems (Frenguelli, 1956) or ecoregions (Viglizzo et al., 2006), that are also differentiated by their hydrochemical characteristics (Feijóo & Lombardo, 2007). This study focuses on two out of those four: the Pampa Ondulada ecoregion (henceforth, ecoregion 1), and the Pampa Austral ecoregion (henceforth, ecoregion 2) (Fig. 1). Both ecoregions are gently sloped, and present slight morphological differences, i.e., the rivers in ecoregion 1 have well defined drainage networks and steeper banks, while those in ecoregion 2 are characterized by scarcely marked channels in the upper and middle reaches, that become deeper downstream forming steep banks close to the mouth. On the other hand, while the watersheds in ecoregion 1 are dendrite-like, most of the water courses in ecoregion 2 run parallel to each other. The ecoregions have slight differences in temperature and rainfall. In relation with the chemical characteristics of the water, the ecoregions differ the most in their nutrient content at certain times of the year (Table 1 in Feijóo & Lombardo, 2007). The streams range between 1st and 3rd order, with no cities or industries in the surrounding areas, watersheds predominantly used for agriculture and livestock grazing. Data summarizing the physical and chemical characteristics of the sampled streams are shown in Table 1.

2.2. Sampling procedures

Five watersheds were selected for ecoregion 1, and four for ecoregion 2, their areas ranging between 3000 and 10,000 km². For ecoregion 1, 13 streams were selected; in 10 of them two reaches were sampled, in two of the streams only one reach was sampled and in the remaining stream, four reaches were sampled. For ecoregion 2, 12 streams were selected and in each of them, two reaches were sampled. At each reach six transects perpendicular to the water course were defined within a 40 m stretch. This sample size (six transects) covered a homogeneous area of the stream with regard to stream width and current velocity, based on personal observations. In each transect, 2500 cm² contiguous quadrats were placed, and the species present within each quadrat were identified (Makkay et al., 2008). Transects covered both the whole stream width and the 50 cm of the bank adjacent to the water, the latter being very dependent on water fluctuation. Thus, the transect is representative of the heterogeneity observed in the stream's cross section and, as such, it was considered the grain of scale.

At the reach scale, the distance between sampling units (transects) was always 8 m, and transect length varied according to stream width. At the stream scale, the distance between reaches was on average 5 km, and never less than 500 m. In 84% of the cases, reaches were in the same stream branch, whereas, in the other 16%, they were in independent branches. The streams from each watershed were not connected. The scales set *a priori* do not represent a systematic increase in the sampling area; rather, they describe frequently employed sampling units.

Data were gathered during the summer months (December, January and February) of 2010–2011, when most of the plant species are flowering. The plants collected were identified and specimens of each species were deposited at the Museo de La Plata herbarium (LP), and at the Departamento de Ciencias Básicas, Uni-

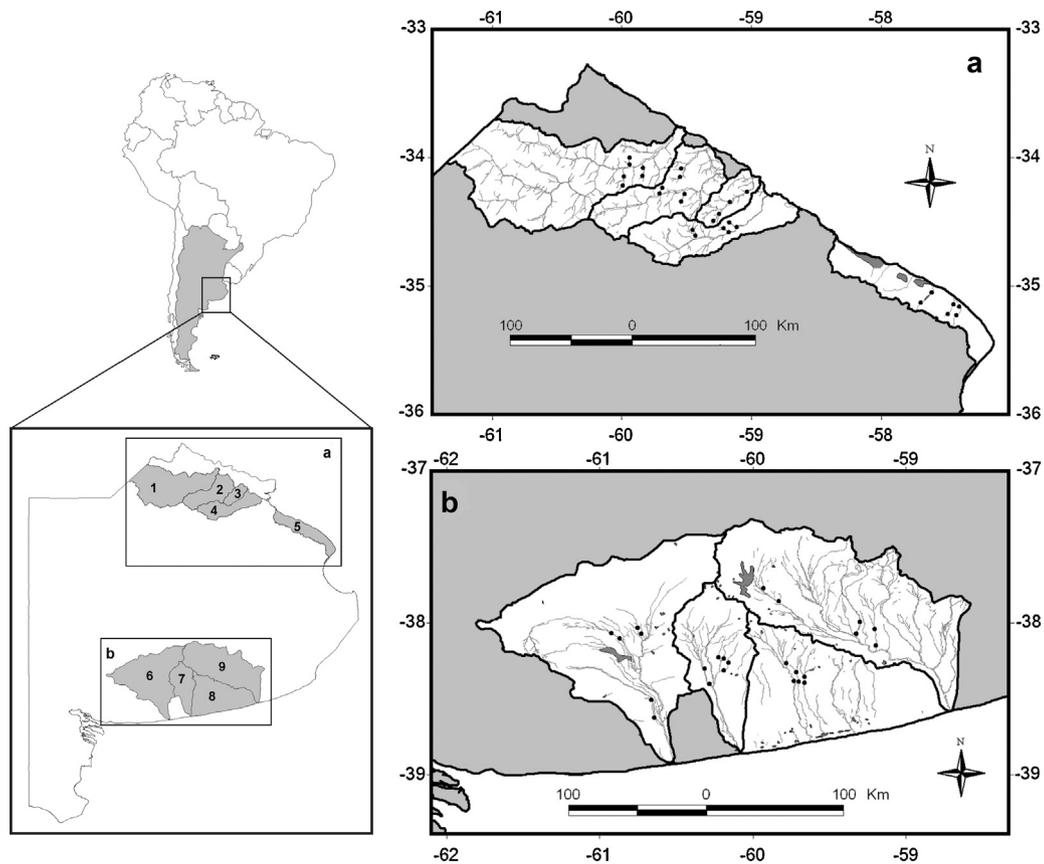


Fig. 1. Location of sampling sites marked with ●. (a) Pampa Ondulada ecoregion; (b) Pampa Austral ecoregion; 1: Arrecifes watershed; 2: Areco watershed; 3: de la Cruz watershed; 4: Luján watershed; 5: Río de la Plata watershed; 6: Quequén Salado watershed; 7: Claromecó watershed; 8: Atlantic tributaries watershed; 9: Quequén Grande watershed.

Table 1
Water characteristics in the sampled streams (medians, minimum, maximum and methods).

Variable	Median	Min	Max	Method
Channel width (m)	5.200	1.387	36.000	
Depth (m)	0.406	0.010	0.871	
Current velocity (m/s)	0.083	0	1.200	Propeller flowmeter (Mini-Air 20)
Discharge (m ³ /s)	0.160	0	1.444	
Transmitted light (%)	51.283	1.036	86.868	light meter (LI-250 LI-COR)
Ultra-fine particulate matter (mg/l)	26.800	0.720	171.200	Drying and combustion
Ultra-fine particulate organic matter (mg/l)	11.600	0	332.400	Drying and combustion
Temperature (°C)	27.500	19.400	37.500	Field sensors (HANNA equipment)
pH	8.360	7.410	9.350	Field sensors (HANNA equipment)
Conductivity (μS/cm)	194.000 ^a	474.000	6 300.000	Field sensors (HANNA equipment)
Dissolved oxygen concentration (mg/l)	7.300	4.000	18.700	Field sensors (HANNA equipment)
Alkalinity (mg/l)	17.000	2.800	28.400	titration APHA (1992)
Soluble reactive phosphorus (SRP) (mg/l)	0.634	0.234	3.408	Ascorbic acid method APHA (1992)
Ammonia concentration (μg/l)	252.886	5.974	1 247.300	phenol-hypochlorite method Wetzel and Likens (1991)
Nitrate concentration (mg/l)	3.901	0.835	32.192	nitratometer (OAKTON)

^a 22 400 μS/cm at one sample site.

versidad Nacional de Luján. The nomenclature follows Zuloaga et al. (2008). The species were assigned to different life forms according to Tur & Lavigne (1992).

3. Data analysis

Species–area curves based on accumulated transects were constructed for each scale: 50 curves for the reach scale, 25 for the stream scale, 9 for the watershed scale, and 2 for the ecoregion scale. From one scale to the next, the extent (number of transects) was increased, but the grain (stream-width sized transects) was kept constant. Each of the curves was smoothed by 50 randomiza-

tions, in order to nullify the effect produced by the order in which the samples were taken. The randomizations were performed using the software EstimateS (V. 8.2.0, Colwell, 2006). The curves for the two ecoregions were fitted to the logarithmic model:

$$S = a + b \times \log A$$

and to the power model:

$$S = a \times A^b$$

where S: species richness, and A: number of transects. Among the two proposed models, the one which presented a better fit to the data was selected. To do this, the Akaike Information Criteria

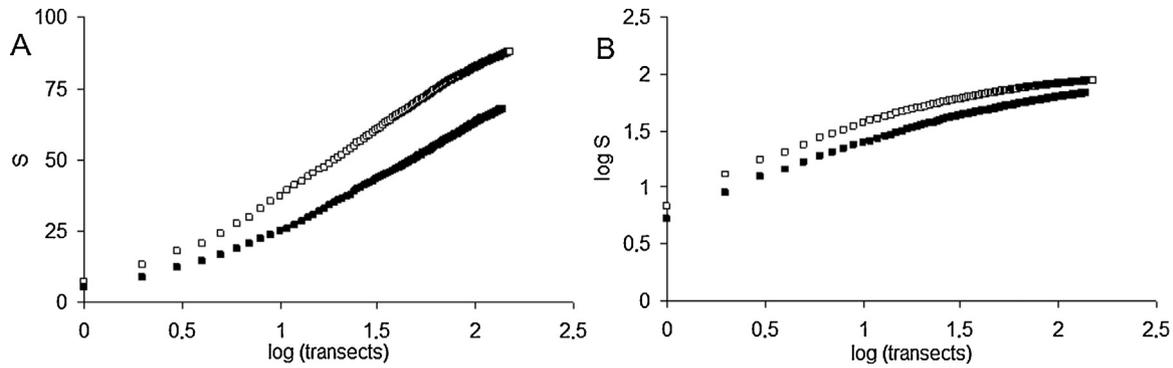


Fig. 2. Species richness at ecoregion scale, logarithmic (A) and power models (B). Smoothed curves from 50 randomizations. Each data point represents one transect of Pampa Ondulada (ecoregion 1) □ and Pampa Austral (ecoregion 2) ■. (A) The curves were fit to $S = a + b \times \log A$, where S : number of species and A : number of transects. $N = 150$; $b = 42.53$; $F = 23443$ and $R^2 = 0.994$ for the ecoregion 1 data set; and $N = 137$; $b = 35.44$; $F = 9201$ and $R^2 = 0.985$ for the ecoregion 2 data set. (B) The curves were fit to $\log S = a + b \times \log A$. $N = 150$; $b = 0.382$; $F = 1767$ and $R^2 = 0.923$ for the ecoregion 1 data; and $N = 137$; $b = 0.433$; $F = 3597$ and $R^2 = 0.964$ for the ecoregion 2 data set.

(AIC) is usually recommended; the AIC compares model fittings, but penalizes the number of parameters according to the following formula:

$$AIC = \text{Log}(L) - 2K$$

where L is a maximum likelihood estimation, and K is the number of model parameters (Oksanen et al., 2008). However, when the compared models have the same number of parameters, the AIC is equivalent to the R-squared estimation for linear models (McCullum, 2000). Since we are using two models that have the same number of parameters, and we made the fit for the linearized data, the model with the best fit (higher R^2) was chosen to be applied to all scales and to obtain the slope for each of them. A total of 86 slopes were compared. The slopes for the reaches ($N = 50$), streams ($N = 25$), watersheds ($N = 9$) and ecoregions ($N = 2$) were compared, after being logarithmically transformed, using a one-factor ANOVA and a Tukey test. The relationship between local and regional diversity was analyzed at two levels: between reaches and streams, and between streams and watersheds. In both cases, linear regressions using Infostat (Di Rienzo et al., 2008) were performed in order to test for relationships between reach and stream richness in ecoregion 1 ($N = 27$) and in ecoregion 2 ($N = 24$), and between stream and watershed richness in both ecoregions (ecoregion 1: $N = 13$; ecoregion 2: $N = 12$). Except for the watershed richness in ecoregion 2, the other seven variables met the normality assumption.

4. Results

4.1. Floristic data

A total of 110 plant species was recorded, of which 103 were identified to species level (Appendix 1). All growth forms were found in the sample sites. Amphibious plants were the most represented, comprising 35% of the total number of species; mesophytic species following with 32%; submerged with 23%; floating rooted with 7%, and lastly, free floating with 3%. The most frequent species were *Stuckenia striata* (28.56%), *Eleocharis bonariensis* (7.49%), and *Elodea callitrichoides* (5.27%). All the other species had less than 5% of frequency.

4.2. Diversity results

The SARs in both ecoregions fitted significantly to the logarithmic and power models. Yet, SARs fitted to the logarithmic model yielded higher R^2 values ($F = 23,443$, $R^2 = 0.994$, $p < 0.001$ for ecoregion 1; and $F = 9201$, $R^2 = 0.985$, $p < 0.001$ for ecoregion 2) (Fig. 2a) than for the power model ($F = 1767$, $R^2 = 0.923$, $p < 0.001$

Table 2

Slopes of the logarithmic model at four scales (reach; stream; watershed and ecoregion). Means values (± 1 SD). One factor ANOVA and Tukey test ($F = 14.613$, $p < 0.001$). Letters indicate different slopes for the different scales ($p < 0.001$).

Scale	Mean (± 1 SD)
Reach ^A	10.019 (± 1.358)
Stream ^B	14.552 (± 2.002)
Watershed ^C	23.277 (± 3.200)
Ecoregion ^D	38.985 (± 6.790)

for ecoregion 1, and $F = 3597$, $p < 0.001$, $R^2 = 0.964$ for ecoregion 2) (Fig. 2b). Thus, the logarithmic model was applied to all scales to obtain the slope for each scale. The SARs fitted significantly to the logarithmic model at all scales (Appendix 2) and the slopes for reaches, streams, watersheds and ecoregions increased significantly ($F = 39.36$, $df = 85$, $p < 0.001$) with scale (Table 2).

For the L–R relationship, when analyzing stream richness in relation to reach richness, the regression slopes found for each ecoregion were 0.36 ($R^2 = 0.21$, 26 reaches, 13 streams, $p < 0.01$) for ecoregion 1 and 0.70 ($R^2 = 0.49$, 24 reaches, 12 streams, $p < 0.01$) for ecoregion 2 (Fig. 3a and b); and when analyzing watershed richness in relation to stream richness, no significant relationship was found (Fig. 3c and d).

5. Discussion

In our study, the differences found in the slopes of the SAR for the stream’s macrophytes mean that the scales proposed *a priori* are indeed different diversity scales. In previous investigations, the change in the slope of the SAR with the change in scale has been considered in relation to much bigger spatial scales (even inter-continental), and at those scales the changes in the slopes were interpreted as changes in the kind of process generating diversity patterns (Rosenzweig, 1995; Schmid & Wilson, 1985). We work on considerably smaller scales and, thus, understand that a single process can account for the changes in the slopes of the SAR. Attempts to interpret SARs have generally been based on two different ecological hypotheses: the habitat diversity hypothesis and the demographic processes hypothesis. According to the habitat diversity hypothesis, larger areas have higher environmental heterogeneity, leading to an increase in the number of species (Shi et al., 2010; Kolasa et al., 2012). The differences found in our research between the slopes of the SAR for each scale could be interpreted so that each new scale has a higher level of heterogeneity. On the other hand, according to the demographic process hypothesis, the increase in the number of species is due to the fact that, in larger areas, there is a greater probability of colonization and a smaller of extinction; furthermore, it has been

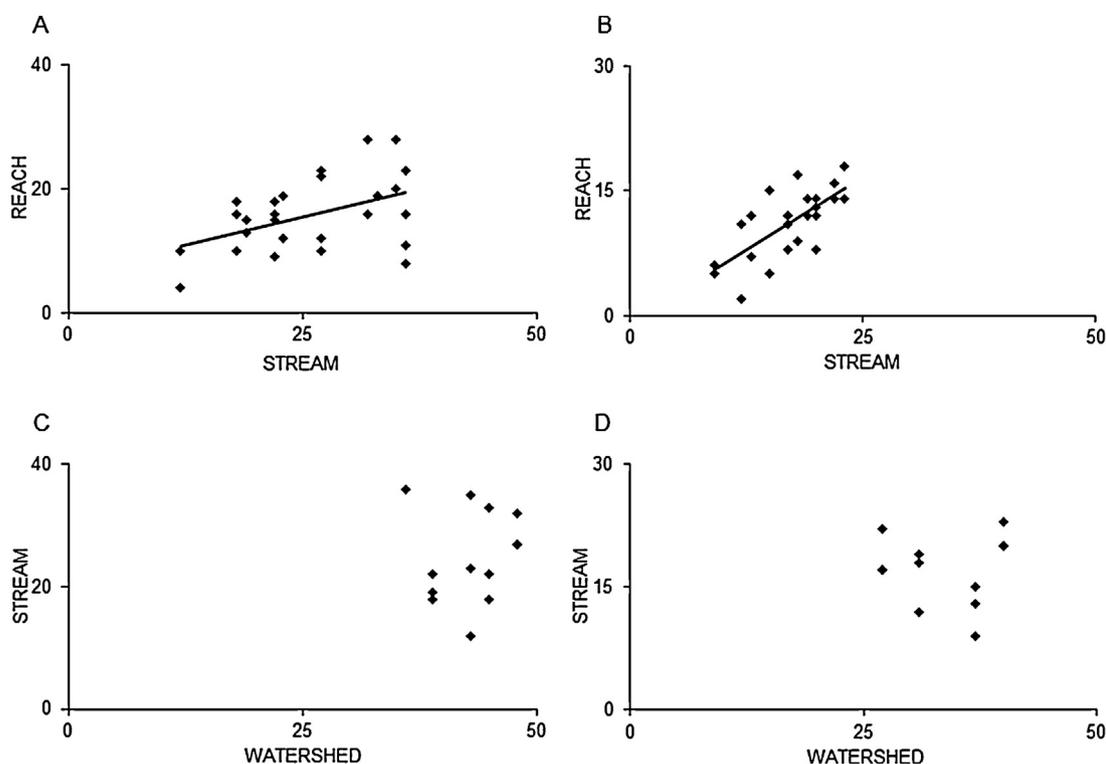


Fig. 3. Local-Regional species richness relationships. A and B: Relationships between reach and stream species richness. Each point represents one reach's species richness. (A) $y = 0.36x + 6.5659$; $F = 6.831$; $R^2 = 0.21$, $p = 0.015$ for the Pampa Ondulada (ecoregion 1) data set: 26 reaches, 13 streams; and (B) $y = 0.6991x + 0.8186$; $F = 20.95$; $R^2 = 0.49$, $p = 0.0001$ for the Pampa Austral (ecoregion 2) data: 24 reaches, 12 streams. C and D: Relationships between stream and watershed species richness. Each data point represents one stream's species richness. (C) $y = 0.2077x + 15.96$, $R^2 = 0.01$, $p > 0.05$, for ecoregion 1 data: 13 streams, 5 watersheds; and $y = 0.0041x + 16.46$, $R^2 = 3E-05$, $p > 0.05$, for ecoregion 2 data: 12 streams, 4 watersheds.

proposed that high levels of colonization, resulting from propagule mobility between connected or nearby habitats, may lead to a flattening of the SARs' slopes (Drakare et al., 2005). This is particularly relevant in the case of macrophytes, given their high dispersal rate (Santamaría, 2002). In some cases, and even between isolated bodies of water such as lakes, the spatial processes explain an important part of the macrophyte communities' structure (Capers et al., 2010; Alahuhta & Heino, 2013). However, in some other cases, community composition is explained by environmental factors and not by dispersal limitations (Sarnecki et al., 2011). The fundamental difference between these other studies and ours is that we have analyzed qualitatively different scales: connected (reaches of a stream) and isolated (streams of a watershed and watersheds of an ecoregion). In this context, dispersal becomes a relevant mechanism for explaining diversity patterns. In the case of our research, as the scale increases, the distance between sites also increases and hydrological connectivity between sites decreases differentially: the transects in each reach were contiguous and separated by a small distance (8 m); and reaches from the same stream were also connected but separated by a greater distance (average of 5 km). Meanwhile, watersheds and ecoregions represented isolated habitats. Furthermore, the distance between streams from each watershed was smaller than the distance between one watershed and another, and between one ecoregion and another (an average of 11.73 km and 436 km, respectively). Given that distances increased with scale, the slopes of the SARs increased from one scale to the following one, at all scales.

Regarding the L–R relationship, we found a linear relationship between reach and stream scales, but not between stream and watershed scales (Fig. 3). The L–R relationship can also be interpreted under the two hypotheses proposed for explaining the SAR. Under the habitat hypothesis, if the different components of a single

scale (for example, the reaches of a stream) had different habitats, the species richness of the stream would be close to the sum of the species richness of its reaches. Then, if richness increased at the regional scale (e.g. in streams), one would not expect to find a linear increase in richness at the local scale (e.g. in reaches) and, therefore, the L–R relationship might be expected to have a slope not different from zero. The same would occur at any of the scales, for example between the stream and watershed scales. If, on the contrary, the components of a single scale (e.g. reaches) had similar habitats, their species would be similar, and the species richness in the stream would be similar to that of the reaches; therefore, one would expect the L–R relationship to have a slope different from zero. This would apply at any of the scales. Under the demographic hypothesis, on the other hand, the L–R relationship would have a slope different from zero (low beta diversity) (Heino, 2011) between the more connected or spatially closer sampling sites which, in our case, would apply to the data of reaches and streams, and a slope undistinguishable from zero for the isolated sites, (in our case, between streams and watersheds).

Thus, our findings regarding SARs, -an increase in slope at all scales-, can successfully be explained by both hypotheses, while the differences observed in the L–R relationship can only be explained by the demographic processes hypothesis.

The differences found between the slopes of the SAR mean that the scales proposed *a priori* may be considered different diversity scales and, thus, represent differences in the way the systems function at every scale. On the other hand, the linear relationship between reach and stream richness indicates that, in streams, the dispersal process is of great importance. The results support the idea that a metacommunity dynamics exists at the stream scale, and also show the actual spatial scale of the dispersal processes of the aquatic macrophytes under study. Thus, we propose that,

instead of considering the reach and stream scales as independent in relation to their ecological processes, the streams' assemblages could be considered metacommunities (Leibold et al., 2004), and that the streams' metacommunities and the watersheds' and ecoregions' assemblages could be considered as the three most relevant diversity scales.

In a highly modified environment such as the Pampean region, where streams are affected by several kinds of disturbances, knowing the factors which determine diversity patterns is crucial for the conservation of the stream ecosystems. The differences found in the rate of species accumulation for reaches, streams, watersheds and ecoregions, and the linear relationship between reach and stream scales, can reasonably be interpreted as the effect of a metacommunity dynamics. This perspective leads to understand that the effects of the disturbances are not restricted to the local scale, but rather extend downstream. That is, the loss of species in the headwaters not only implies a local decrease in diversity, but also a decrease in propagule dispersal, which leads to a loss of species downstream as well. This interpretation highlights the need to conserve the headwater reaches. On the other hand, the differences between the assemblages of streams and watersheds, which function as isolated patches, indicate that the conservation of this community should be considered on a large scale. That is, the geographical extension of any measure aiming to conserve diversity should be applied at the regional scale, and whenever possible take into special account the headwaters.

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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.2015.05.007>

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