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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.

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 km^2, 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 (Frengüelli, 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 km^2. 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 cm^2 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-