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Explanatory variables associated with diversity and composition of aquatic macrophytes in a large subtropical river floodplain

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ABSTRACT

The structure of aquatic macrophyte assemblages can be affected by myriad factors, including physical, chemical and morphometric characteristics. We describe the patterns of plant species diversity and composition and vegetation height in aquatic ecosystems and their potential determinants at a regional scale in the Middle Paraná River floodplain. Sampling was conducted in twenty-three water bodies, including secondary channels, connected lakes and disconnected lakes. We compared the macrophyte species richness, composition and vegetation height in water bodies with different degrees of connectivity with the river and assessed the most important abiotic explanatory variables (morphometric, physical and chemical) associated with these assemblage attributes. Species accumulation curves showed that species richness did not differ between water bodies with different degrees of connectivity, although it tended to be lowest in secondary channels. Species richness was specifically associated with depth, conductivity, percent of solar radiation reaching the bottom and nitrate. Macrophyte assemblage composition was related primarily to the degree of connectivity, as rare species mostly occurred in disconnected lakes. Composition was also related to the degree of wind exposure (fetch), distance to shoreline and depth. Finally, vegetation height (a surrogate for biomass) was associated with the ammonium and sediment organic matter. Thus, a combination of morphometric and abiotic factors explained species richness, while degree of connectivity and morphometry explained assemblage composition. Vegetation height was explained by nutrients. These results suggest that a single set of variables is not sufficient to explain different aspects of macrophyte assemblages.

1. Introduction

Aquatic macrophytes comprise a variety of species belonging to different life forms that colonize almost all types of shallow waters (Sculthorpe, 1967). The richness and composition of macrophyte assemblages are affected by a myriad of factors, which include physical and chemical characteristics and morphometry of the water body (Murphy et al., 2003; Johnston and Brown, 2013; Kisson et al., 2013; Steffen et al., 2014; Azzella et al., 2014). At fine spatial scales, macrophytes are likely to be sensitive to the physical and chemical characteristics of the water and sediment, generating patterns which are also mirrored at broader scales (Bornette and Puijalon, 2011; Neiff et al., 2014). For example, while free-floating species usually thrive in water with high nutrient concentrations, submerged plants are mainly associated with light availability (Chambers and Kalff, 1985). Alternativelly, morphometric characteristics especialy affect macrophytes on broader spatial scales. Wave disturbance, measured indirectly by degree of wind exposure (fetch), for instance, can influence macrophytes by changing the rates of sedimentation and the resuspension process or by causing direct damage to these plants (Madsen et al., 2001; Zhang et al., 2014). The littoral slope is another important morphometric variable that influences the establishment of rooted macrophytes, determining the biomass of submerged plants (Duarte and Kalff, 1986) and affecting the dissipation pattern of wave energy and sediment dynamics (Azza et al., 2007).

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Particularly in river floodplain systems, patterns of richness and composition of macrophytes species are also affected by the degree of connectivity between the water body and river (Neiff, 1979; Junk et al., 1989; Monção et al., 2012; Rooney et al., 2013). In more connected water bodies floating species are usually removed by flushing and submerged species are commonly limited by increase in water column turbidity, both caused by disturbance events of strong floods (e.g., Madsen et al., 2001; Zhang et al., 2014). In contrast, macrophyte assemblages colonizing disconnected lakes, which are more stable, may be structured by biotic interactions, such as interspecific competition (Grime, 1974; Thomaz et al., 2007). As the degree of connectivity with the river regulates the magnitude of disturbance caused by floods (Monção et al., 2012; Rooney et al., 2013), intermediate disturbance hypothesis (Grime, 1974; Ward and Tockner, 2001) is quite probable to be supported by macrophytes assemblages colonizing these ecosystems.

Many studies using morphometric and limnological variables to explain macrophyte richness and composition have been conducted in rivers and lakes in temperate regions (e.g., Rooney et al., 2013). In large subtropical river-floodplain systems, several studies explored the effects of flood pulse on macrophytes (Thomaz et al., 2007; Neiff et al., 2011), while others tested the correlation between macrophyte assemblage attributes and the degree of connectivity with the river, lake morphometry, and physical and chemical factors (e.g., Murphy et al., 2003; Neiff and Poi de Neiff, 2003). However, morphometric and abiotic variables are usually not studied in combination. Therefore, it is necessary to test the combined importance of the degree of connectivity with the river, lake morphometry and water physic-chemistry for macrophyte assemblage attributes in large river-floodplain ecosystems, especially in Neotropical regions where these ecosystems are highly representative.

Along the Paraná River system, the middle course is the richest stretch in macrophyte diversity (Neiff et al., 2014). The middle Paraná course has been studied from different perspectives, and investigations related to the composition, the structure and successional dynamics have been conducted in this area (e.g., Neiff and Orellana, 1972; Neiff, 1975; Franceschi and Lewis, 1979; Lewis and Franceschi, 1979; Neiff, 1979; Sabattini et al., 1983). Nevertheless, despite having a high diversity of macrophytes, the morphometric and abiotic factors associated with macrophyte richness and composition are unknown in this part of the Paraná, as well as in other large subtropical rivers. Strong influences of physical and chemical factors on macrophyte assemblages are expected, especially during the dry season, when lakes and channels differ from one another with regards to morphometry and other physical and chemical features (Thomaz et al., 2007). Thus, the high environmental heterogeneity (in terms of abiotic factors) provided by the isolation of lakes during low water levels may be a key factor for the maintenance of high macrophyte diversity in river-floodplain systems.

Considering the assumptions of the intermediate disturbance hypothesis, we first tested the hypothesis that along a gradient of increasing connectivity, connected lakes (with intermediate disturbance) contain the highest species richness, followed by disconnected lakes and secondary channels (with lower and higher levels of disturbance, respectively). Second, we tested whether macrophyte composition differed between different degrees of connectivity. Finally, we used selected morphometric and abiotic environmental data to explore the likely determinants of macrophyte richness, composition and vegetation height. To reach our targets, we studied a wide variety of habitats within a large spatial scale (approximately 184 km^2) in the floodplain.

2. Methods

2.1. Study area

The Middle Paraná River (Fig. 1A–C) extends from its confluence with the Paraguay River (27°29′ S; 58°50′ W) to the city of Diamante (Argentina) (32°4′ S; 60°32′3″ W) and covers an area of 2,600,000–2,800,000 km^2 (Iriondo and Paira, 2007). Its main channel has a braided pattern with variable width (0.4–8 km) and several anabranches. Sediment deposition has almost filled the river valley, forming a complex floodplain with islands, bars, levees, secondary channels and shallow lakes (Paira and Drago, 2007). The dry season, when the water level is low and some lakes are isolated from one another (<10.5 m a.s.l.), usually occurs from July to December, while the flooding season (>13.2 m a.s.l) occurs between January and June (Drago, 2007). Due to its middle position along the river course, the Middle Paraná River serves as habitat for species common to both the Upper and the Lower Paraná River, establishing a continuum or biological corridor between them (Sabattini and Lallana, 2007).

2.2. Methods

Twenty-three water bodies (nine disconnected lakes, eight connected lakes and six secondary channels) distributed along the Middle Paraná River floodplain were sampled twice (from March to June 2012, and October 2012 to January 2013) during the dry seasons (Fig. 1C). We sampled during the dry season because, in general, individual habitats (see Thomaz et al., 2007) and macrophyte assemblages (Padial et al., 2009; Neiff et al., 2014) within a floodplain differ the most during this period (however, see Mayora et al. (2013)). Thus, a gradient of habitats with distinct connectivity to the main river could be used to assess the association of environmental variables and macrophyte assemblage attributes.

The macrophytes were sampled using quadrats (1 m × 1 m) that were placed along transects perpendicular to the shoreline. The number of transects in each lake ranged from one to five, according to the total area of the water body. Within each transect, the distance between successive quadrats was constant, and the number of quadrats per transect varied from one to sixteen according to the length of the macrophyte stand (3–50 m from the shoreline toward the limnetic zone). This procedure takes into account habitat area and the size of the macrophyte stands, ensuring a representative inventory of aquatic flora. In addition, this procedure accounts for the zonation along depth gradients and the variation of spatial distribution in the margins, allowing the investigation of associations between macrophyte assemblage attributes and environmental variables.

Inside each 1 m × 1 m quadrat, macrophyte species were visually scored for percent cover to provide an estimate of abundance. Rakes were used to sample the submersed macrophytes. We also measured the total height of the vegetation (a proxy for biomass) in each quadrat. The collected material was transported to the Instituto Nacional de Limnología (INALI-UNL-CONICET), and the plants were identified according to Cabrera (1968), Pott and Pott (2000) and others (complete list in Appendix S1). Despite some taxa were not identified to species level, for the sake of simplicity, we used the term species to represent taxonomic units.

Environmental parameters were characterized at different scales encompassing physical and chemical variables and morphometric features. In each transect, we measured the conductivity and pH with a portable water checker (Hanna®). The Secchi depth was determined in each transect and was used to estimate the light extinction coefficient (k) according to Padial and Thomaz (2008). We used k and the depth of the water column to calculate the mean