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Undervalued Ecosystems: Ponds Boost Regional Macrophyte Diversity

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Received: 6 October 2025 | **Revised:** 4 December 2025 | **Accepted:** 14 January 2026

Keywords: beta diversity | depressional wetlands | gamma diversity | legislation | policy frameworks | pond conservation | riparian wetlands | species turnover | wetland networks | wetland plants

ABSTRACT

Ponds—depressional wetlands with ≤ 2 ha—are largely undervalued worldwide, despite serving as crucial diversity reservoirs. However, the extent to which ponds support diversity at the landscape scale is still underappreciated. Here, we investigate the contributions of ponds to macrophyte beta and gamma diversity in a subtropical wetland network where streambanks, riverbanks and ponds are the predominant wetland types. To this end, the diversity of riparian areas (streambanks and riverbanks [SR]) was compared to that of the global wetland set (streambanks, riverbanks and ponds [SRP]) so that only ponds could account for increases in diversity from SR to SRP. Three species groups were considered in the analyses: herbaceous, woody and the global pool. Total beta diversity increased significantly from SR to SRP for all plant groups, a pattern driven by the turnover component, not by the nestedness-resultant component. Gamma diversity also increased for all plant groups as a result of increased species turnover, except for the woody component when indices that assign successively greater weights to frequent species were used. Our results demonstrate that ponds make pivotal contributions to macrophyte conservation at the regional level, which is why their inclusion in policy frameworks and legislation that ensure their safeguarding is essential.

1 | Introduction

Ponds, defined as depressional wetlands with ≤ 2 ha (Biggs et al. 2005), are neglected in most regions of the globe (e.g., Williams et al. 2004; Biggs et al. 2005; Calhoun et al. 2017; Grasel et al. 2018; Hill et al. 2018). Except for a few cases, legislative or policy frameworks generally lack management strategies aimed specifically at these ecosystems (Davies et al. 2008; Hill et al. 2018). When ponds are protected, this usually happens indirectly, for example, through action plans of individual species associated with them (e.g., threatened migratory waterbirds) or because they are inside conservation units (Biggs et al. 2005; Hill et al. 2018), the latter commonly biased towards terrestrial ecosystems (e.g., Azevedo-Santos et al. 2019). The explanation for such carelessness may be linked in part to the fact that, until a few years ago, ponds were treated merely as small versions of lakes and largely ignored by scientists (Céréghino et al. 2008; Boix et al. 2012; Coccia and Scalici 2025). Regardless of this, the practical result is that ponds suffered high rates of degradation and/or conversion and are under continuous human pressure in many landscapes around the world (e.g., Calhoun et al. 2017; Serran et al. 2018; Grasel et al. 2019a, 2019b; Zuquette et al. 2020). In short, pond conservation is largely a matter of chance (Biggs et al. 2005).

Although overlooked, a growing body of evidence demonstrates that ponds are irreplaceable ecosystems for the conservation of macrophytes from a landscape perspective. Particularly relevant support in this regard comes from studies that contrasted plant community patterns in ponds with those in other wetland types. For example, when compared to streambanks, riverbanks, streams, rivers, ditches and lakes, ponds often ranked among the environments with the highest numbers of beta diversity, gamma diversity, floristic singularity, as well as unique, rare and endangered species (e.g., Williams et al. 2004; Biggs et al. 2005; Davies et al. 2008; Bubíková and Hrivnák 2018; Grasel et al. 2021; Sun et al. 2022; Svitok et al. 2025). Furthermore, ponds benefit regional wetland flora by increasing connectivity among diverse wet habitats through their role as 'stepping stones' (Oertli and Parris 2019), providing refuges from disturbances (Chester and Robson 2013) and catalysing unique ecological interfaces (Grasel et al. 2020; Cawood et al. 2025).

The high conservation value of ponds, especially concerning macrophyte diversity at the landscape scale, is attributed to factors essentially determined by their relatively small sizes and their insular nature (Williams et al. 2004; Scheffer et al. 2006; Davies et al. 2008). These include high inter-site environmental heterogeneity, notable environmental unicity, varying levels of connectivity with other wetland ecosystems and susceptibility to stochastic events (Williams et al. 2004; Scheffer et al. 2006; Davies et al. 2008). Combined, these characteristics contribute to a unique floristic composition in individual ponds, which in turn underlies both high beta and gamma diversity (Williams et al. 2004; Davies et al. 2008; Grasel et al. 2021).

Although the relevance of ponds for macrophyte conservation is undeniable, the extent to which these ecosystems support wetlands' plant diversity in a regional context remains largely unknown. For instance, we are unaware of studies that have directly and statistically assessed the magnitude of the increase in regional macrophyte diversity that ponds provide relative to other wetland types considered together. Here, our main objective was to examine the contribution of ponds to beta and gamma plant diversity of a wetland network in the upper Uruguay River basin, Southern Brazil. For this, we used data previously explored by us (Grasel et al. 2021) on the following three wetland types widely prevalent in the region: ponds, streambanks and riverbanks. We then compared the diversity of riparian areas (streambanks and riverbanks [SR]) with that of the global set of wetlands (streambanks, riverbanks and ponds [SRP]) so that increases from SR to SRP estimates could only be attributed to ponds. Such analyses were made considering herbaceous and woody (shrub to tree) species separately and together, as the diversity patterns of these plant groups can vary (Grasel et al. 2021). We hypothesized that (1) total beta diversity is greater in SRP than in SR, and this difference is primarily driven by the turnover component rather than by the nestedness-resultant component; and (2) SRP holds higher gamma diversity than SR as a direct result of the higher contribution of the turnover component to beta diversity.

2 | Material and Methods

2.1 | Study Areas

The study was conducted in a transition zone between the semideciduous seasonal forest and the evergreen seasonal *Araucaria* forest in the upper Uruguay River basin, western Santa Catarina State, Southern Brazil (Oliveira-Filho et al. 2015; Figure 1). This region is in a globally recognized hotspot of diversity, endemicity and rarity of macrophytes (Murphy et al. 2019; Lobato-de Magalhães et al. 2024). The regional climate is subtropical humid without a pronounced dry season (Alvares et al. 2014); the annual averages of temperature and precipitation are 18°C–20°C and 1900–2000 mm, respectively (Wrege et al. 2012). The bedrock is basalt and most upland and wetland soils are eutrophic (IBGE 1990; Cunha et al. 2006; Giehl and Jarenkow 2008), but areas such as ponds and adjacent sites show predominantly dystrophic substrates or soils (Grasel et al. 2020).

In this region, based on operational criteria, we first distinguished three widely prevalent natural wetland types: streambanks, riverbanks (both locally known as *matas ciliares*) and ponds (locally known as *banhados*). Streambanks and riverbanks are both lotic wetlands and are here defined as riparian areas alongside streams and rivers (Junk et al. 2014) that are ≤ 7 m and > 7 m wide, respectively (Bubíková and Hrivnák 2018; see similar criteria in Williams et al. 2004 and Svitok et al. 2025). Ponds, the unique lentic wetland type we found within the study region, are here defined as temporary or permanent depressional wetlands with ≤ 2 ha (Biggs et al. 2005). For each wetland ecosystem, we chose eight study areas based on the following four criteria: (1) no clear sign of human-induced environmental change; (2) no evidence of recent natural resource extraction; (3) relatively large percentage of natural habitats within a 100-m radius; and (4) distance of at least 1500 m between the study sites.

All chosen riparian areas occur in slopes and are subjected to temporary, polymodal and unpredictable flood pulses of short duration, thus remaining well-drained for most of the year. Previous field observations (e.g., litter and sediment removal or deposition after floods in elevated areas) and landowner interviews were used to estimate the flood extents and so establish the width of the riparian areas. These data revealed that the selected streambanks and riverbanks are at least 1 and 4 m wide, respectively. All these areas are forested and their vegetation is physiognomically little variable within and among sites. Differences in habitat features between the two lotic wetland types include higher elevation ranges (primarily due to variation in wetlands' width) and slightly higher light availability in the understory (due to differential canopy openness, which is mainly determined by watercourses' width) in riverbanks than in streambanks. Watercourses adjacent to the studied streambanks and riverbanks are intermittent or permanent and permanent, 1st–3rd and 3rd–5th order (mean = 1.8 and 4.3) and 1.8–5 m and 7.6–14.1 m wide (mean = 3.3 m and 10.3 m), respectively.

Among the selected ponds, all are subjected to polymodal and unpredictable flood pulses of short duration; one is permanently flooded (at least in most patches; otherwise

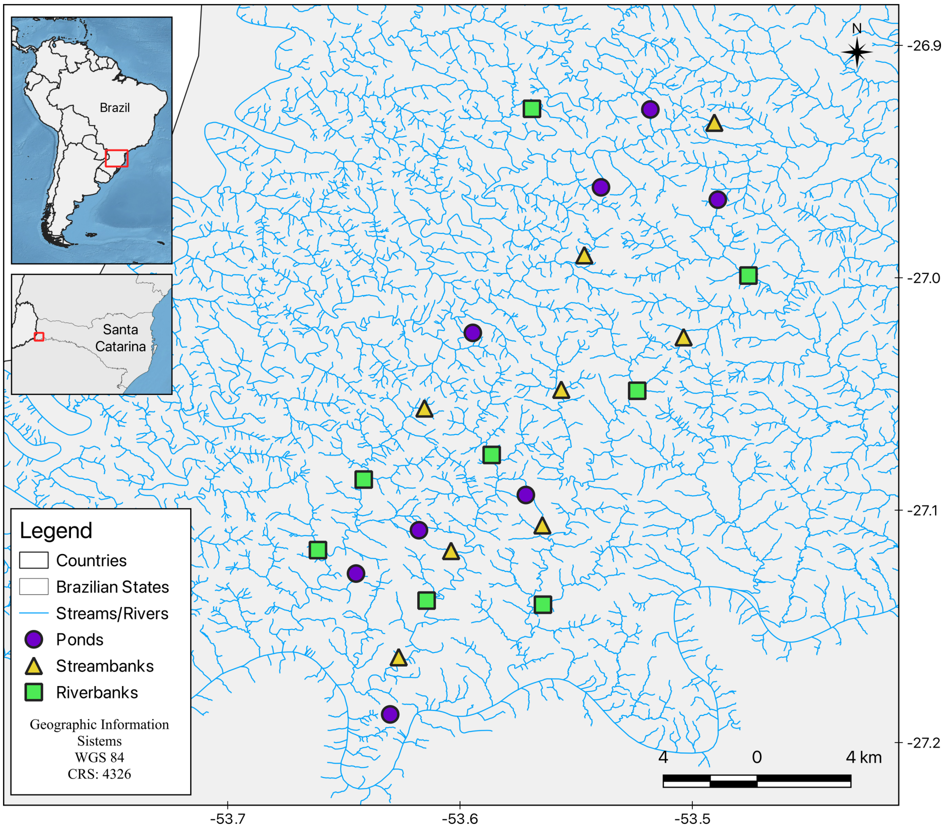

FIGURE 1 | Location of the study areas in the upper Uruguay River Basin, Southern Brazil.

permanently saturated), and seven are permanently saturated (at least in most patches; otherwise relatively well-drained). The vegetation physiognomies of these ecosystems are highly variable within and/or among sites, varying from marshes to swamps (sensu Keddy 2010). All ponds are at least partially hummocked, especially in swampy areas. Ponds range from 0.01 to 0.98 ha (mean = 0.30 ha) and are all fed only by local rainwater and located in interfluvial areas (i.e., all are upland-embedded) close to the water divisors of watercourses' watersheds.

2.2 | Species Survey

Using the line intercept method (Canfield 1941), we inventoried plants that approximately constitute the component commonly termed 'ground flora' or 'herb layer': herbaceous species and ≥0.3- to ≤1-m high plants of woody species—except bryophyte, climber and epiphyte species (Goebel et al. 2012; Santos-Junior et al. 2018). In each study site, we sampled species in 40 linear meters using a specific sampling protocol for each wetland type due to their abiotic and biotic particularities (Supplementary Material Figure A1). In streambanks and riverbanks, we established 40 and 10 linear transects of 1 and 4 m in length, respectively, oriented perpendicular to the watercourses (to their left or right) and distributed equidistantly in 30-m long stretches—as streams and rivers lacked plants that met the inclusion criteria, inventories were not extended to their 'regular beds.' In ponds, we adopted the same transect length and organization used in riverbanks, but the sampling effort was equally divided into two areas that best represented the variation in plant communities' composition and structure (e.g., patches dominated by herbaceous or woody species). All sampling designs were based on Junk et al.'s (2014) wetland delineation proposal. Species survey was carried out in summer 2016–2017 (December–March) and their identification was made by consulting specialized bibliography, taxonomists and exsiccates of the ICN Herbarium of the Universidade Federal do Rio Grande do Sul. The species data presented in Grasel et al. (2021) have been updated here because of a few corrections and nomenclatural updates. Taxa names are based on Flora e Funga do Brasil (2024) and Flora Argentina (2024).

Considering that we sampled wetlands, all sampled plants were treated here as macrophytes (vascular hydrophytes/wetland plants), regardless of their frequency and abundance in aquatic, wetland or terrestrial environments and their growth form, following the proposal of Cronk and Fennessy (2001). The same proposal was used for the classification of macrophytes into the following life forms: emergent, submerged, floating-leaved and floating.

2.3 | Data Analysis

Data were explored considering native herbaceous and woody (shrub to tree) species separately and pooled—woody species groups (e.g., shrub or tree species) were not analyzed separately because few or no species with specific habits were sampled in ponds. We previously showed that the data used here had no spatial structure using spline correlograms (see Grasel et al. 2021), so all sampling units were also treated here as true replicates.

For brevity and because some adopted gamma diversity analyses (see below), when individual-based, ideally require the number of plants as a measure of abundance (to estimate diversity based on singletons and doubletons), a condition not met by our original database where coverage is the measure of abundance (see Grasel et al. 2021), all analyses were based on binary data or incidence-based frequency counts.

For the objectives of this manuscript, the beta diversity of a certain group of sites is defined as the mean of the pairwise dissimilarities within the group (Whittaker 1972; Bacaro et al. 2012). Based on this definition, we compared wetland groups' beta diversity using the method proposed by Bacaro et al. (2012, 2013), which consists in creating a dissimilarity matrix among all pairs of sites, comparing the mean values of the within-group dissimilarities through ANOVA and calculating a *p* value by randomly permuting within-group dissimilarities between groups without replacement and ignoring between group dissimilarities (Bacaro et al. 2013). This method allows testing the null hypothesis of no differences in the mean plot-to-plot dissimilarities within groups, ensures the selection of the correct null model and overcomes problems in other methods (see details in Bacaro et al. 2012, 2013). Overall beta diversity was compared using dissimilarity matrices based on the Jaccard index, and dissimilarity matrices based on Baselga-family decompositions of the Jaccard coefficients into turnover (dissimilarity due to species replacement) and nestedness-resultant (dissimilarity due to nestedness; hereafter simply nestedness) components were used to explore the underlying processes driving differences in total beta diversity between wetland groups (Baselga 2012). *P* values were obtained using 9999 permutations. To visually assess beta diversity patterns, we used violin/box plots based on the within-group dissimilarities and nonmetric multidimensional scaling (NMDS; McCune and Grace 2002) ordinations (optimized for two dimensions) based on the same dissimilarity matrices described above.

Additionally, to assess if mean pairwise dissimilarities captured the underlying patterns in compositional heterogeneity, we also calculated the Baselga-family multiple-site Jaccard dissimilarities and their turnover and nestedness components (Baselga 2013) (Appendix B).

To initially explore and interpret gamma diversity patterns, we employed Chao et al.'s (2020) analyses routine, which includes the following: (1) sample completeness profiles; (2) size-based interpolation (rarefaction) and extrapolation curves; (3) empirical (observed) and asymptotic (estimated) diversity profiles; (4) coverage-based interpolation and extrapolation curves; and (5) observed and estimated evenness profiles (Appendix C). The sample completeness profiles showed that sampling was incomplete (Supplementary Material Table C1 and Figure C1). In this case, the use of coverage-based interpolation and extrapolation curves with associated 95% confidence intervals is an appropriate alternative to make fair diversity comparisons, since it is based on equally complete samples, where the measure of sampling completeness is sample coverage (Turing's sample coverage or simply coverage); for the data type used here, sample coverage is the proportion of the total number of incidences that belong to detected species (Chao et al. 2020). However, for woody species, coverage-based curves (and size-based curves and diversity profiles) showed overlapping confidence intervals, which requires additional and rigorous statistical tests to verify whether the differences are significant—unlike the nonoverlapping confidence intervals, which guarantee significant differences at the 5% level (Colwell et al. 2012; Chao et al. 2020).

To appropriately address these particularities and limitations, we compared gamma diversity using coverage-based rarefaction curves and Cayuela et al.'s (2015) BiogTest and maintained Chao et al.'s (2020) analyses routine as a complement. The BiogTest consists in calculating the observed Z statistic (Z_{obs})—the sum of the area between all pairs of possible i individual curves—generating the null distribution of Z (Z_{sim}) through random sampling of different simulated communities using alternative abundance distributions and in the comparison of Z_{obs} with Z_{sim} to estimate *P*. This method allows testing the biogeographic null hypothesis (H_{0biog}), which states that the i samples were drawn from communities with similar richness and relative abundance profiles, regardless of species composition (Cayuela et al. 2015). The above-mentioned rarefaction curves were constructed based on the following diversity parameters (Hill numbers; Hill 1973): richness ($q = 0$); exponential of Shannon's index ($q = 1$); and Simpson's inverse index ($q = 2$) (see Roswell et al. 2021 for the advantages of using sample coverage with Hill diversity). To generate Z_{sim}, we used 9999 randomizations and the log-normal series to create the abundance distributions (Cayuela et al. 2015). The observed coverage-based rarefaction curves based on Cayuela et al. (2015) differed slightly from those based on Chao et al. (2020) due to methodological updates. Additionally, Cayuela et al. (2015) implemented a graphical demarcation adjustment (verticalization) before the curve's ends, which subtly reduced the total sample coverage.

All analyses were performed in R (R Core Team 2025) using function BetaDispersion 2.0 (Bacaro et al. 2013) and packages vegan (Oksanen et al. 2025), betapart (Baselga et al. 2025), and rareNMtests (Cayuela and Gotelli 2022)—packages cited in the Supplementary Material are referenced there.

3 | Results

In total, we sampled 178 species distributed across 128 genera and 60 families (Supplementary Material Table A1). Of these species, —34 shrubby and 51 arboreal (Supplementary Material Table A1). The most diverse genera were *Eugenia* (5 species), *Cyperus*, *Justicia* (4), *Asplenium*, *Carex*, *Eleocharis*, *Ludwigia*, *Piper*, *Polygonum*, *Rhynchospora*, *Tradescantia* and *Trichilia* (3) and the most diverse families were Poaceae (16), Cyperaceae (14), Acanthaceae, Fabaceae, Myrtaceae (8), Commelinaceae, Euphorbiaceae, Lamiaceae, Meliaceae, Pteridaceae, Rubiaceae and Thelypteridaceae (5) (Supplementary Material Table A1). The most frequent species were *Anemia phyllitidis*, *Hildaea pallens* (16 sites), *Diplazium cristatum*, *Ctenitis submarginalis* (15), *Ruellia angustiflora*, *Piper gaudichaudianum* (14), *Tradescantia fluminensis* (13), *Hydrocotyle leucocephala*, *Ctenanthe muelleri*, *Acalypha gracilis* (12), *Pombalia bigibbosa*, *Nectandra megapotamica* and *Cupania vernalis* (11) (Supplementary Material Table A1). Among the sampled species, only *Lemna valdiviana* is floating, while the others are emergent—some species can fit into more than one life form, for example, *Alternanthera reineckii*, *Heteranthera zosterifolia* and *Micranthemum* *umbrosum* can also be submerged, but were predominantly observed as emergent, especially due to the predominantly shallow and temporary water columns. See Grasel et al. (2021) for more details on the data explored here, including coverage data and importance value of species and patterns of alpha, beta and gamma diversity and floristic uniqueness of each of the three wetland types studied.

3.1 | Beta Diversity

For all plant groups, mean pairwise dissimilarity was greater in SRP than in SR considering total beta diversity and the turnover component, while no difference was observed for the nestedness component (Figure 2; Supplementary Material Table A2). From SR to SRP, pairwise dissimilarities increased by 11.7%–22.6%

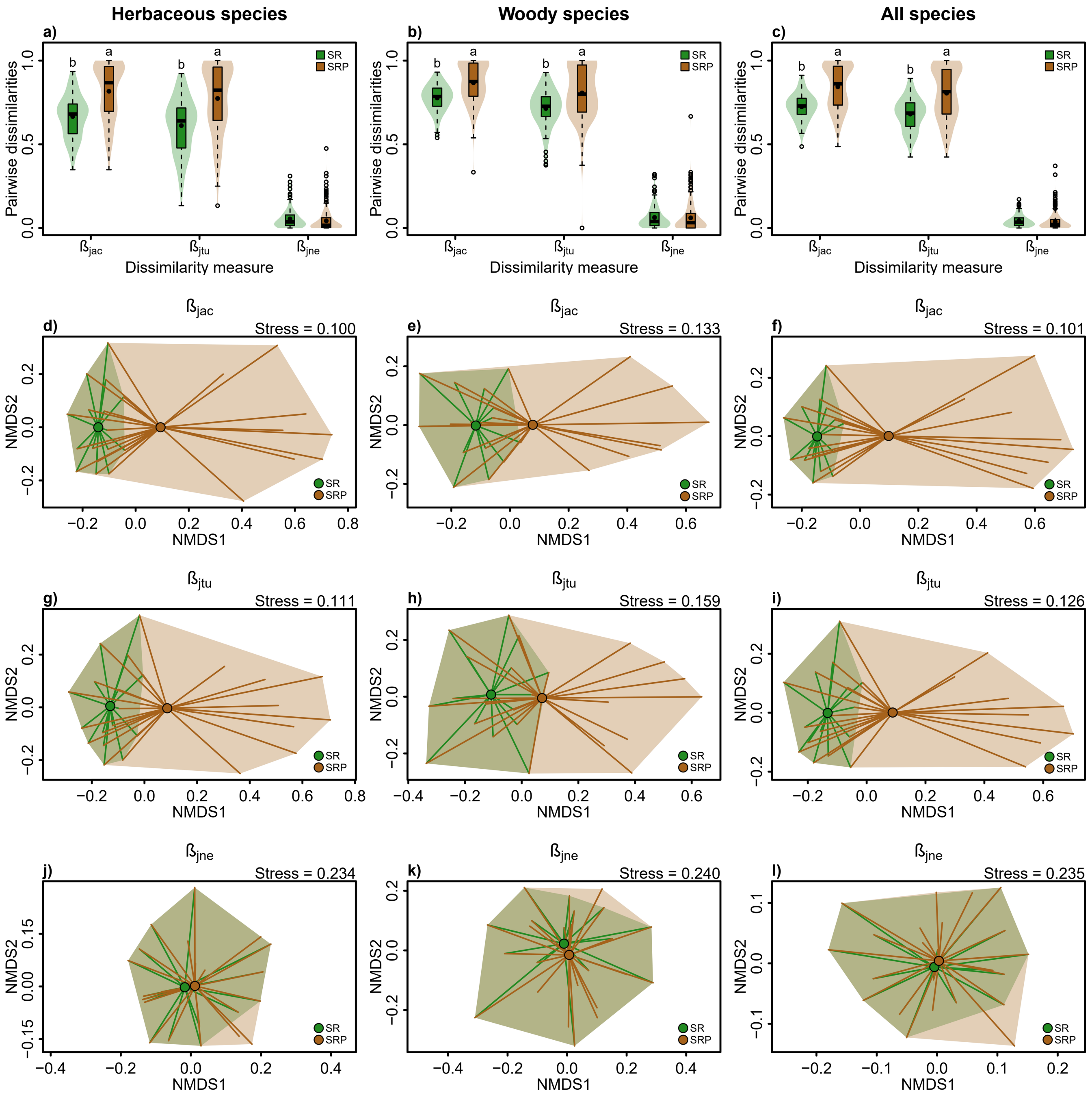

FIGURE 2 | Results of beta diversity analyses comparing riparian areas (streambanks and riverbanks [SR]) with the global set of wetlands (riparian areas and ponds [SRP]) sampled in the upper Uruguay River basin, Southern Brazil. (a–c) Violin (shaded areas) and box plots displaying within-group pairwise dissimilarities. Boxes show the 25th and 75th percentiles, medians (thick lines) and means (black dots), while staples indicate the smallest and highest values (excluding outliers, shown as hollow circles). Different letters above the top staples indicate significant differences ($p \leq 0.05$) in beta diversity (see Supplementary Material Table A2). (d–l) Nonmetric multidimensional scaling (NMDS) ordinations. Spider diagrams connect sites to their sample groups' centroids represented by circles. $ß_{jac}$, Jaccard dissimilarities; $ß_{jtu}$, turnover component of Jaccard dissimilarities; $ß_{jne}$, nestedness-resultant component of Jaccard dissimilarities. Note that the overlap of SR and SRP in the NMDSs is due exclusively (d–i) or in part (j–l) to the fact that the same riparian areas constitute both wetland groups.

on average for total beta diversity and 13.1%–26.5% for the turnover component, whereas the nestedness component decreased by 3.7%–21.0% (Supplementary Material Table A2). In all cases, total beta diversity was predominantly explained by the turnover component (91.9%–95.5%) rather than by the nestedness component (4.5%–8.1%) (Figure 2; Supplementary Material Table A2).

Under the multiple-site approach, the turnover component explained an even larger proportion of overall beta diversity when compared to the results obtained under the pairwise approach (96.3%–98.4%) (Supplementary Material Table B1).

3.2 | Gamma Diversity

The gamma diversity of the herbaceous component and the overall species pool was higher in SRP than in SR considering all diversity parameters (Figure 3; Supplementary Material Tables A3 and C1 and Figures C2–C4). Regarding the woody component, gamma diversity was higher in SRP than in SR only for $q=0$, although the difference for $q=1$ was marginally significant (Figure 3; Supplementary Material Table A3). From SR to SRP, empirical and asymptotic gamma diversity increased by 47.3%–60.3% and 52.2%–78.3% for herbaceous species, 12.1%–14.9% and 13.3%–14.1% for woody species and 29.3%–34.8% and 32.7%–40.8% for the global species set, respectively (Supplementary Material Table C1).

Total observed sample coverage was lower for SRP than for SR in all cases (Figure 3 and Supplementary Material Tables A3 and C2 and Figure C4). The same was true for total extrapolated sample coverage, except for the woody component (Supplementary Material Table C2 and Figure C4). Total sample coverage simulated through Cayuela et al.'s (2015) method was higher for SRP than for SR for all plant groups, except for $q=0$ of the woody component (Figure 3; Supplementary Material Table A3).

Sample completeness ranged from 78.1% to 89.0% for $q=0$, 91.2%–96.0% for $q=1$ and 98.2%–99.2% for $q=2$ (Supplementary

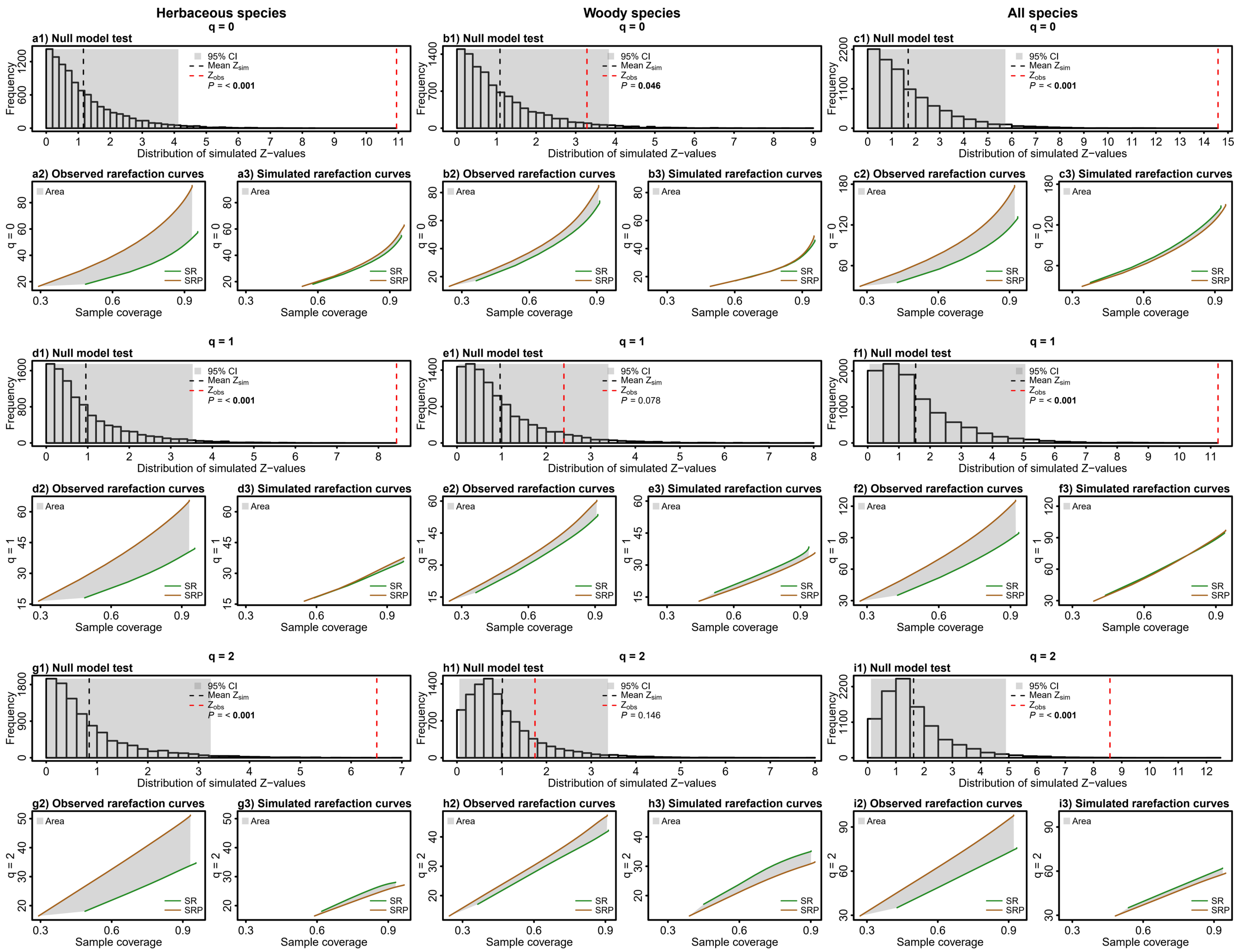

FIGURE 3 | Results of gamma diversity analyses comparing riparian areas (streambanks and riverbanks [SR]) with the global set of wetlands (riparian areas and ponds [SRP]) sampled in the upper Uruguay River basin, Southern Brazil. The shaded areas between the rarefaction curves represent the difference in area between the curves up to the horizontal limit of the curve with the lowest total sample coverage (C_{max}). Significant p values ($p \leq 0.05$) are shown in bold type. $q=0$, richness; $q=1$, exponential of Shannon's index; $q=2$, Simpson's inverse index; CI, confidence interval; Z_{sim}, simulated Z values; Z_{obs}, observed z value.

Material Table C1 and Figure C1). Generally, SR showed higher sample completeness than SRP, except for $q = 0$ of the woody component (Supplementary Material Table C1 and Figure C1). In all cases, the confidence intervals overlapped (Supplementary material Figure C1).

Observed and estimated evenness ($q > 0$) was lower in SRP than in SR for all plant groups, despite the overlap in confidence intervals (Supplementary Material Table C1 and Figure C5).

4 | Discussion

4.1 | Beta Diversity

As predicted, total beta diversity increased significantly from SR to SRP, and this increase was driven by the turnover component rather than by the nestedness component. The absence of spatial correlation in our data (Grasel et al. 2021) suggests spatial variables had little or no influence on the observed patterns, despite, for example, the contrasting levels of hydrological connectivity shown by the studied ponds (without surface flow connectivity or temporarily connected) and riparian areas (highly connected through drainage networks). This lack of structure can be attributed to the high dispersal capacity of macrophytes (Santamaría 2002; Soons 2006), the absence of geographic barriers, the small spatial scale (Fernández-Aláez et al. 2020), the relatively small anthropogenic influence on the sampled wetlands (Alahuhta et al. 2021) and the uniform distribution of the study areas. Therefore, as has been observed in most related works carried out at even broader spatial scales (Alahuhta et al. 2014, 2015; Viana et al. 2016; Fernández-Aláez et al. 2020), species sorting (Leibold et al. 2004), mediated by niche processes (environmental filters and/or species interactions), was probably the predominant mechanism responsible for the increase in floristic heterogeneity from SR to SRP.

Of particular relevance to this increase must have been ponds' environmental uniqueness. For example, in the study region, riparian areas typically have well-drained eutrophic soils and are predominantly forested, while ponds generally have dystrophic substrates subjected to at least prolonged periods of waterlogging and/or flooding and exhibit rich intra- or inter-site physiognomic diversity, ranging from marshes to swamps (Giehl and Jarenkow 2008; Grasel et al. 2020, 2021). Consequently, ponds differ markedly from riparian areas in a number of variables well known to drive floristic variation, including the tendency to have longer duration and frequency of flooding, lower fertility (e.g., base saturation) and higher phytotoxin concentrations (e.g., aluminium saturation) in the soil or substrate, and greater light availability (Budke et al. 2007; Giehl and Jarenkow 2008; Bando et al. 2015; Grasel et al. 2020, 2021). This sharp environmental difference between riparian areas and ponds is paralleled by their floristic distinction (Grasel et al. 2021), which was also observed in similar studies, but conducted in larger lotic and lentic systems—temporarily flooded and predominantly well-drained floodplains and permanently waterlogged and temporarily or permanently flooded swamps, respectively (Pitman et al. 2014; Draper et al. 2018).

The high environmental uniqueness may have been added to the great inter-site environmental heterogeneity generally presented by ponds. While riparian areas tend to have spatial variation in their physico-chemical characteristics reduced by the homogenizing action of flooding (Thomaz et al. 2007), ponds, because they generally reflect the specific conditions of their micro-catchments, tend to present greater environmental heterogeneity among sites (Williams et al. 2004; Svitok et al. 2025). This variation in ponds' abiotic properties may have favoured the establishment of species with varied environmental requirements and, consequently, boosted total beta diversity.

In addition to environmental properties, biotic interactions may also be among the factors that contributed to determining the observed beta diversity patterns. For example, the occupation of vacant habitat patches by specific species in different wetlands can result in the rapid monopolization of spaces and the inhibition of the establishment of immigrant species with similar environmental requirements, leading to multiple stable equilibria, i.e., divergences in species composition among communities (Chase 2003). The chance of multiple stable states occurring, for instance, decreases with increasing levels of disturbance, because (1) few species tolerate such conditions, (2) species are less likely to quickly dominate vacant spaces and (3) species that establish and survive well in such environments are generally weak competitors (Tilman 1994; Chase 2003). Ponds, being lentic ecosystems, are not subject to the currents that frequently occur in riparian areas and which can cause physical damage to plants or even their uprooting. Because they are environmentally more stable, ponds may have favoured the domination of spaces by specific species, which is hindered in riparian areas due to frequent and intense disturbances, which tend to favour species coexistence—particularly in locations with intermediate disturbances (Connell 1978; Pollock et al. 1998; Arias et al. 2018). Therefore, presumably more pronounced priority effects in ponds than in riparian areas may have contributed to the observed increase in beta diversity from SR to SRP.

Regardless of the determinants of macrophyte beta diversity, most studies, particularly those conducted in diversity hotspots (Alahuhta et al. 2021) such as the study region (Murphy et al. 2019), have shown that the turnover component predominates over the nestedness component—as also observed in relation to their abundance-based analogues (Viana et al. 2016; Fernández-Aláez et al. 2020; Grasel et al. 2021; Manzo et al. 2022; Svitok et al. 2025). However, such patterns have generally been explored separately for specific ecosystems (e.g., streambanks, riverbanks, streams, rivers, ditches, lakes and ponds). The isolated analysis of the underlying mechanisms of beta diversity in a given wetland type disallows a full verification of the degree of regional exclusivity of its communities, since this requires the inclusion of other ecosystem types. Here, we show that, when wetlands of different types are treated collectively, inter-site dissimilarities remain almost exclusively explained by the turnover component (under both pairwise and multisite approaches). This finding presents important conservation implications as it reinforces that integral wetland conservation is essential for the protection of macrophytes across landscapes—in other words, protecting only specific types of wetlands and/or sites with certain properties (e.g., size or diversity) is insufficient due to the high intersite species turnover (Oertli et al. 2002; Socolar et al. 2016; Hill et al. 2018; Grasel et al. 2021). Obviously, ponds are no exception, especially given the significant increase in beta diversity (determined by the turnover component) observed from SR to SRP. This pattern cannot simply be attributed to an increase in the sampling intensity from SR to SRP, as we previously demonstrated, using the metric 'local contributions to beta diversity' (Legendre and De Cáceres 2013), that ponds had the highest floristic uniqueness among the studied wetland types (Grasel et al. 2021).

4.2 | Gamma Diversity

As expected, ponds contributed significantly to the increase in gamma diversity, which is mainly explained by the notorious rise in species turnover observed from SR to SRP. The only exceptions were the values of $q=1$ and $q=2$ of the woody component. These results are due to the lower evenness presented by SRP, as, unlike the diversity of order $q=0$, which is sensitive only to species richness, diversities of orders $q>0$ are influenced by both richness and evenness (Chao et al. 2020).

Our findings regarding the woody component, however, should be interpreted with caution. Because the sampling design adopted in ponds aimed at global species detection by including the sampling of areas with different ecological characteristics, for example, forested (which generally feature herbaceous, shrub and tree species) and nonforested areas (generally dominated by herbaceous and shrub species), the diversity of the woody component—particularly that of tree species—may have been underestimated at the local level, which may have impacted both richness and evenness regionally. Furthermore, young individuals of tree species, such as those sampled, are generally the most sensitive to prolonged flooding events, such as those that occur in ponds (Kozlowski 1984), which may have further reduced the detection of species belonging to this group.

Nevertheless, the more modest contributions of ponds may be expected specifically regarding the tree component. Grasel et al. (2020) demonstrated that no tree species sampled in ponds in the study region are regionally restricted to them. In addition, none of the tree species sampled here occur exclusively in ponds (Giehl and Jarenkow 2008; Grasel et al. 2017, 2020, 2021). The same is not true for shrub species, which can be regionally restricted to ponds or very rare in other ecosystems, as is the case for *Boehmeria cylindrica*, *Hibiscus striatus*, *Hydrolea spinosa*, *Ludwigia sericea* and others. Indeed, when the gamma diversity of shrub and tree species was assessed separately, the diversity of the shrub component was significantly higher in SRP than in SR for the values of $q=0$ and $q=1$ and marginally significant for $q=2$, whereas differences for the tree component were far from significant (results not shown).

In summary, our findings show that the contributions of ponds to macrophyte gamma diversity follow the following pattern: herbaceous > woody or, in a more detailed analysis, herbaceous > shrubby > arboreal.

The root cause of pond contributions to macrophyte gamma diversity, given that all macrophytes have terrestrial ancestors (Sculthorpe 1985; Cronk and Fennessy 2001), may be a combination of the environmental harshness and the speed at which the assessed plant groups reproduce. Ponds (and other wetland ecosystems) exhibit a series of environmental filters that prevent the establishment, development and reproduction of a large portion of the regional plant species pool, including anoxic, phytotoxic, unstable and nutrient-poor substrates (Blom and Voesenek 1996; Pezeshki and DeLaune 2012; Grasel et al. 2020). Species with successively smaller sizes may have had greater opportunities to adapt to such conditions—meaning greater selective pressures to specialize in them—because they reproduce more quickly than larger species and, consequently, exhibit higher rates of molecular evolution (Smith and Donoghue 2008; Lanfear et al. 2013). Furthermore, it is likely that the greater evolutionary potential of small species was enhanced by multiple demographic, ecological, evolutionary, historical, morphological and physiological factors. For instance, the development of aerenchyma requires the phenotypic plasticity of herbaceous or slightly lignified tissues, which is why it is much more frequent in herbaceous species than in woody ones (Jackson and Drew 1984; Kozlowski 1984).

Finally, it is important to emphasize that, although they probably lack exclusive tree species, ponds can harbour communities with unique arrangements, which contributes to the complexity and resilience of landscapes as a whole (Previant and Nagel 2014; Grasel et al. 2020).

5 | Conclusions

This study demonstrates that ponds make critical contributions to macrophyte diversity at the landscape scale, boosting both beta and gamma diversity. This role derives primarily from the turnover component of beta diversity, not from the nestedness component. Contributions to gamma diversity are particularly notable for herbaceous species, although they are also relevant for woody species. Our findings indicate that including ponds in conservation strategies is pivotal if the goal is to maintain regional wetland plant diversity.

Author Contributions

Daniel Grasel: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing – review and editing, writing – original draft. **Florian Wittmann:** conceptualization, writing – review and editing. **Eduardo Luís Hettwer Giehl:** conceptualization, writing – review and editing. **João André Jarenkow:** conceptualization, funding acquisition, project administration, resources, supervision, writing – review and editing.

Acknowledgements

We thank Manueli Blatt Spezia for fieldwork assistance, Luíz Fernando Esser for producing Figure 1, two anonymous reviewers for constructive suggestions on the first version of the manuscript and the landowners for allowing this study to be conducted.

Funding

Daniel Grasel was supported by field per diem from the Programa de Pós-Graduação em Botânica at the Universidade Federal do Rio Grande do Sul and a PhD fellowship (Grant Number 1601741) from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES)—Finance Code 001.

Ethics Statement

Ethical review and specific permits were not required for this study.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data can be shared upon reasonable request by contacting the corresponding author.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **FIGURE A1** Schematic diagram showing the specific sampling designs for each of the three wetland types (ponds, streambanks and riverbanks) sampled in the upper Uruguay River basin, Southern Brazil, considering their abiotic and biotic particularities. Transects 1 m (for streambanks) or 4 m (for ponds and riverbanks) long used for plant inventory through the line intercept method are shown as black lines. **TABLE A1** Species sampled in riparian areas (streambanks and riverbanks [SR]; $n = 16$) and in the global set of wetlands (streambanks, riverbanks and ponds [SRP]; $n = 24$) located in the upper Uruguay River basin, Southern Brazil, with their respective frequencies. **TABLE A2** Results of beta diversity analyses—outputs of 'BetaDispersion 2.0' function—comparing riparian areas (streambanks and riverbanks [SR]) with the global set of wetlands (streambanks, riverbanks and ponds [SRP]) sampled in the upper Uruguay River basin, Southern Brazil. **TABLE A3** Results of gamma diversity analyses (outputs of BiogTest) comparing riparian areas (streambanks and riverbanks [SR]) with the global set of wetlands (streambanks, riverbanks and ponds [SRP]) sampled in the upper Uruguay River basin, Southern Brazil. **TABLE B1** Multiple-site Jaccard dissimilarities ($\beta._{JAC}$) and their turnover ($\beta._{JTU}$) and nestedness-resultant components ($\beta._{JNE}$) per plant group in riparian areas (streambanks and riverbanks [SR]) and in the global set of wetlands (streambanks, riverbanks and ponds [SRP]) sampled in the upper Uruguay River basin, Southern Brazil. **TABLE C1** Results of sample completeness, gamma diversity, and evenness analyses - Chao et al.'s (2020) routine - comparing riparian areas (streambanks and riverbanks [SR]) with the global set of wetlands (streambanks, riverbanks and ponds [SRP]) sampled in the upper Uruguay River basin, Southern Brazil. **TABLE C2** Observed and estimated (to double the reference sample size) total sample coverage for riparian areas (streambanks and riverbanks [SR]) and the global set of wetlands (streambanks, riverbanks and ponds [SRP]) sampled in the upper Uruguay River basin, Southern Brazil. **FIGURE C1** Sample completeness profiles for riparian areas (streambanks and riverbanks [SR]) and the global set of wetlands (streambanks, riverbanks and ponds [SRP]) sampled in the upper Uruguay River basin, Southern Brazil. Shaded areas indicate the 95% confidence intervals. The meaning of the *q*-values is given in the text above. **FIGURE C2** Size-based interpolation (rarefaction) and extrapolation curves for riparian areas (streambanks and riverbanks [SR]) and the global set of wetlands (streambanks, riverbanks and ponds [SRP]) sampled in the upper Uruguay River basin, Southern Brazil. Shaded areas indicate the 95% confidence intervals. The meaning of the *q*-values is given in the text above. **FIGURE C3** Observed (empirical) and estimated (asymptotic) diversity profiles for riparian areas (streambanks and riverbanks [SR]) and the global set of wetlands (streambanks, riverbanks and ponds [SRP]) sampled in the upper Uruguay River basin, Southern Brazil. Shaded areas indicate the 95% confidence intervals. The observed and estimated diversity profiles were plotted separately and together for better visualization. The meaning of the *q*-values is given in the text above. **FIGURE C4** Coverage-based interpolation (rarefaction) and extrapolation curves for riparian areas (streambanks and riverbanks [SR]) and the global set of wetlands (streambanks, riverbanks and ponds [SRP]) sampled in the upper Uruguay River basin, Southern Brazil. Shaded areas indicate the 95% confidence intervals. The meaning of the *q*-values is given in the text above. **FIGURE C5** Observed and estimated evenness profiles for riparian areas (streambanks and riverbanks [SR]) and the global set of wetlands (streambanks, riverbanks and ponds [SRP]) sampled in the upper Uruguay River basin, Southern Brazil. Shaded areas indicate the 95% confidence intervals. The observed and estimated evenness profiles were plotted separately and together for better visualization. The meaning of the *q*-values is given in the text above.