UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

Daniel Grasel

Conservação de áreas úmidas no âmbito da Lei de Proteção da Vegetação Nativa do Brasil

Porto Alegre

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Tese apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul como parte dos requisitos para a obtenção do título de Doutor em Ciências: Botânica.

Orientador: Prof. Dr. João André Jarenkow

Porto Alegre

2020

Agradecimentos

Agradeço imensamente:

Ao Prof. Dr. João André Jarenkow, pela valiosa orientação.

Aos coautores dos manuscritos desta Tese, pelos inúmeros ensinamentos transmitidos. São eles: Florian Wittmann, Eduardo Luís Hettwer Giehl, Philip Martin Fearnside, Roger Paulo Mormul, Reinaldo Luiz Bozelli, Ricardo Ribeiro Rodrigues, André Scarlate Rovai, Sidinei Magela Thomaz, Jean Ricardo Simões Vitule, Flávia Duarte Ferraz Sampaio e Angelo Antonio Agostinho.

Aos seguintes pesquisadores, pelo auxílio na identificação de espécies e/ou na resolução de questões nomenclaturais: André Luís de Gasper, Ilsi Iob Boldrini, Marco Octávio de Oliveira Pellegrini, Maria Salete Marchioretto, Sérgio Augusto de Loreto Bordignon, Monica Gomes Buchoski, Silviane Cocco Pesamosca, Danilo Soares Gissi, João Marcelo Alvarenga Braga, Martin Molz, Carlos Alberto Ferreira Júnior, Emerson Ricardo Pansarin, Jefferson Prado, Luis Adriano Funez, Maria de Fátima Freitas, Regina Celis Lopes Affonso e Marília Cristina Duarte.

Ao Luíz Fernando Esser, pela produção dos mapas das áreas de estudo.

Aos proprietários das terras onde se localizam as áreas de estudo, por autorizarem a realização das pesquisas. São eles: Alberto Knorst, Alceu Fransozi, Alcindo Ritter, Avelino Miguel Penso, Blásio Kroetz, Cláudia Maria Costa Eidt, Claudir Luiz Salerno, Clenor Bisolo, Cristiano Ertel, Enio Raimundo Griebeler, Eusébio Antônio Dill, Evandro Rambo, Flávio Rauber, Francisco Klunk, Helmut Swab, Idone Luiz Kreling, Inácio Kroetz, Anselmo José Rambo, Herbert Knorr, Milton Heck, Nativo José Keil, Nestor Sehn, Pedro Canísio Sidegum e Roque de Souza.

Ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul (UFRGS), pelo acolhimento institucional.

A Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), pela concessão da bolsa de Doutorado.

Aos membros do Laboratório de Fitoecologia e Fitogeografia, pelas inúmeras conversas e discussões. São eles: Edilvane Inês Zonta, Guilherme Krahl de Vargas, Alessandro Abreu Fávero, Ronaldo dos Santos Júnior, Edilaine Andrade Melo, Luíz Fernando Esser e Daniel Dutra Saraiva.

A minha esposa, Manueli Blatt Spezia, por ter sido meu porto seguro durante esse período turbulento.

Aos meus pais, Denilson João Grasel e Lúcia Meurer Grasel, e aos meus irmãos, Lucas Grasel e Indira Grasel, pelo incentivo e pelo apoio logístico.

À família Rodrigues, a saber, Alisson Samoel Rodrigues, José Odenir Rodrigues e Maria Sonia Samoel Rodrigues, por terem me acolhido caridosamente em seus lares e prestado auxílio logístico imensurável durante minhas viagens para Porto Alegre – RS.

Resumo

Em 2012, retrocessos na legislação ambiental mais importante sobre terras privadas brasileiras, renomeada como “Lei de Proteção da Vegetação Nativa” (LPVN), colocaram uma série de áreas úmidas sob risco de degradação e/ou conversão. Dentre as áreas úmidas mais afetadas estão as lagoas, que praticamente perderam sua proteção legal. As alterações legislativas na LPVN colocaram em risco não apenas a grande biodiversidade das áreas úmidas, mas também a provisão de importantes serviços ecossistêmicos por elas prestados. Aqui, contribuí com a identificação e divulgação de retrocessos e inadequações na LPVN e chamei a atenção para a necessidade da regulamentação sustentável dela nos estados. Além disso, conduzi investigações sobre a diversidade (alfa, beta e gama) e composição florística em áreas úmidas na bacia do alto Rio Uruguai, Sul do Brasil, que contemplaram três tipos de áreas úmidas amplamente predominantes na região: lagoas e áreas ripárias adjacente a córregos e rios. Esses estudos objetivaram a geração de subsídios para a gestão sustentável de áreas úmidas e a detecção de potenciais efeitos negativos decorrentes de medidas na LPVN. Os resultados mostraram que cada tipo de área úmida apresenta padrões de biodiversidade únicos e contribui de forma categórica para a conservação, evidenciando que a adequada proteção do contínuo de conectividade das áreas úmidas é essencial para a sua gestão sustentável. Além disso, mostrei que lagoas apresentam a maior singularidade florística, um número muito maior de espécies herbáceas exclusivas e níveis de diversidade vegetal até maiores do que os exibidos por áreas ripárias, que apresentam um *status* legal muito menos desfavorável, evidenciando que a remoção da proteção legal de lagoas é inadequada. Eu argumento que a legislação ambiental do Brasil precisa passar por mudanças drásticas se o objetivo for assegurar a conservação da biodiversidade nas áreas úmidas e a manutenção de importantes serviços provisionados por esses ecossistemas. A criação de uma política nacional focada na gestão de áreas úmidas e baseada no conhecimento científico é provavelmente a melhor maneira de alcançar esse propósito.

Palavras-chave legislação ambiental; políticas públicas; lagoas; áreas ripárias; diversidade vegetal; composição florística.

Abstract

In 2012, setbacks in the most important environmental legislation on Brazilian private lands, renamed the “Native Vegetation Protection Law” (NVPL), have placed a number of wetlands at risk of degradation and/or conversion. Among the most affected wetlands are ponds, which have virtually lost their legal protection. The legislative changes in the NVPL put at risk not only the great biodiversity of wetlands, but also the provision of important ecosystem services they provide. Here, I contributed to the identification and divulgation of setbacks and inadequacies in the NVPL and drew attention to the need for its sustainable regulation in the states. In addition, I conducted investigations on diversity (alpha, beta and gamma) and floristic composition in wetlands in the upper Uruguay River basin, southern Brazil, which contemplated three wetland types widely prevalent in the region: ponds and riparian areas adjacent to streams and rivers. These studies aimed to generate subsidies for the sustainable management of wetlands and the detection of potential negative effects resulting from measures in the NVPL. The results showed that each wetland type has unique biodiversity patterns and contributes categorically to conservation, showing that the adequate protection of the wetland connectivity continuum is essential for its sustainable management. In addition, I showed that ponds have the greatest floristic uniqueness, a much greater number of exclusive herbaceous species and even greater levels of plant diversity than those displayed by riparian areas, which have a much less unfavorable legal status, showing that the removal of the protection of ponds is inadequate. I argue that Brazil’s environmental legislation needs to undergo drastic changes if the objective is to ensure the conservation of biodiversity in wetlands and the maintenance of important services provided by these ecosystems. The creation of a national policy focused on wetland management and based on scientific knowledge is probably the best way to achieve this purpose.

Keywords environmental legislation; public policy; ponds; riparian areas; plant diversity; floristic composition.

Sumário

Introdução geral

Áreas úmidas podem ser genericamente definidas como sítios com substratos/solos hidromórficos submetidos temporária ou permanentemente ao encharcamento ou a inundações rasas, apresentando, portanto, uma biota adaptada aos seus regimes hídricos, especialmente a de hidrófitas – terras firmes internas, quando existentes, fazem parte do conceito (Junk et al., 2014; Mitsch e Gosselink, 2015). Tais ecossistemas são cruciais para a conservação da biodiversidade, uma vez que abrigam parcela substancial da biota, comunidades com composição muito particular e um sem-número de espécies exclusivas, raras e ameaçadas de extinção (Williams et al., 2004; MA, 2005; Davies et al., 2008a,b; Pitman et al., 2014; Draper et al., 2018). Além disso, áreas úmidas provisionam um portfólio de serviços ecossistêmicos essenciais ao bem-estar humano, incluindo o sequestro de carbono, a transformação de materiais, a melhoria da qualidade da água e a regulação hidrológica (MA, 2005; Marton et al., 2015; Rains et al., 2016; Craft et al., 2017; Hansen et al., 2018). O Brasil, por ser o país mais biodiverso do mundo, tanto em números gerais (Brandon et al., 2005) como em termos de espécies aquáticas (Padial et al. 2017), e por apresentar a maior área úmida e o maior volume de turfa nos trópicos e subtrópicos (Gumbricht et al., 2017), ocupa uma posição estratégica para a conservação de áreas úmidas no âmbito internacional.

Apesar do exposto, as áreas úmidas brasileiras em propriedades privadas passaram a estar sob grande risco depois da promulgação da Lei de Proteção da Vegetação Nativa (LPVN; Brasil, 2012), que substituiu o antigo “Código Florestal” (Brasil, 1965) – embora Maltchik et al. (2018) tenham concluído, inadvertidamente, que a LPVN assegura a proteção de todos esses habitats. Exemplos de retrocessos ambientais que colocaram tais ecossistemas sob risco de degradação e/ou conversão incluem:

- Remoção da proteção conferida – por meio de Áreas de Preservação Permanente (APPs) – às lagoas com < 1 ha e áreas úmidas associadas a nascentes e córregos efêmeros;
- Grande redução na largura de inúmeras APPs convertidas antes de 22 de julho de 2008, cujas larguras agora são determinadas com base no tamanho das propriedades rurais, independentemente do tamanho ou largura das áreas úmidas ou dos corpos d'água;
- Alteração da base para a delimitação das APPs adjacentes a córregos e rios, que passou do nível máximo do espelho d'água para o nível do leito regular dos cursos d'água;
- Autorização para a prática da aquicultura (incluindo a de espécies exóticas e invasoras) em APPs convertidas no entorno de lagoas e lagos e adjacentes a cursos d'água intermitentes ou permanentes em propriedades rurais com ≤ 15 módulos fiscais; e
- Permissão para a utilização de espécies lenhosas exóticas para a "restauração" de APPs no entorno de lagoas, lagos e nascentes e adjacentes a cursos d'água temporários ou permanentes e veredas em pequenas propriedades, mesmo que tais áreas estejam em ambientes campestres ou savânicos (Brasil, 1965, 2012; Brancalion et al., 2016; Garcia et al., 2016).

Essas e outras inadequações foram adicionadas a problemas já existentes no antigo "Código Florestal" e, em grande parte, retidos pela LPVN, como a provisão de mecanismos parcos para o monitoramento da conformidade ambiental das propriedades privadas (e.g., Taniwaki et al., 2018), e o emprego de termos e definições (quando existentes) pobres relacionadas com áreas úmidas, que geram grandes incertezas sobre o escopo da lei (Maltchik et al., 2018). As inadequações e retrocessos legislativos acima mencionados são especialmente preocupantes diante das já altas taxas de conversão de áreas úmidas na América do Sul (89% após 1900; Creed et al., 2017) e ao fato de a rede de unidades de conservação no Brasil ser enviesada para a gestão de terras firmes, fornecendo, portanto, eficiência apenas limitada para a conservação de áreas úmidas (Azevedo-Santos et al., 2019). Diante desse cenário, uma das opções mais viáveis para a reversão dos retrocessos na LPVN, ao menos no curto prazo, é a sua regulamentação sustentável nos estados, uma vez que estes podem adotar medidas mais restritivas, porém nunca mais permissivas, do que as da lei federal. Nesse contexto, a academia cumpre papel fundamental no sentido de tentar reduzir a lacuna entre a ciência e a política (Brancalion et al., 2016).

Dentre a grande diversidade de áreas úmidas brasileiras (Junk et al., 2014), lagoas foram provavelmente as que sofreram o maior impacto em seu *status* legal após a promulgação da LPVN. Esses ecossistemas são amplamente definidos como áreas úmidas com ≤ 2 ha e completamente circundadas por terras firmes (Biggs et al., 2005; Hamerlík et al., 2014). A grande maioria e, em algumas regiões, a quase totalidade das lagoas apresenta < 1 ha – e.g., 76-99% (Martin et al., 2012; Williams et al., 2010). Um único retrocesso ambiental na LVPN, i.e., a remoção da proteção de lagoas com < 1 ha, tem, portanto, o potencial de permitir o colapso regional desses ecossistemas – vale lembrar que lagoas também foram afetadas por outras políticas e medidas insustentáveis com potenciais efeitos negativos adicionais (veja acima).

As inadequações e retrocessos ambientais relacionados às lagoas estão em profunda dissonância com importantes contribuições acadêmicas, embora muito escassas, que apontaram para a crucial relevância desses ecossistemas para a conservação da biodiversidade de ambientes aquáticos numa perspectiva de paisagem. Por exemplo, em comparação com outros ecossistemas como lagos, córregos, rios e valas, lagoas foram mostradas para exibir grande singularidade florística, a maior diversidade vegetal beta e gama, bem como um número muito maior de espécies exclusivas e raras (Williams et al., 2004; Davies et al., 2008a,b). Contudo, a contribuição de lagoas para a biodiversidade vegetal de redes de áreas úmidas é ainda amplamente desconhecida. Logo, estudos comparativos que abordem a diversidade e composição de plantas em lagoas e nas demais áreas úmidas em escala regional são fundamentais para reduzir essa lacuna de conhecimento e subsidiar a gestão sustentável desses ecossistemas como um todo.

Apesar da extrema carência de estudos voltados à avaliação da diversidade e composição de plantas em redes de áreas úmidas, cada um de seus tipos tem potencial para apresentar padrões de biodiversidade únicos, já que os mesmos tendem a exibir características particulares relacionadas, por exemplo, com a hidrologia, a geomorfologia, as propriedades físico-químicas da água e do substrato/solo, a organização espacial e a luminosidade (Keddy, 2010; Junk et al., 2014; Mitsch e Gosselink, 2015). Logo, tanto lagoas como as demais áreas úmidas das paisagens tendem a contribuir de forma singular para a manutenção das funções e serviços ecossistêmicos, necessitando, portanto, de proteção legislativa adequada.

Os principais propósitos dessa Tese foram: (1) identificar e divulgar medidas insustentáveis na LPVN relacionadas à gestão de áreas úmidas e propor ajustes; (2) chamar a atenção para a necessidade da regulamentação sustentável da LPVN nos estados; (3) corrigir interpretações infundadas sobre a proteção que a LPVN confere às áreas úmidas; (4) realizar estudos sobre a diversidade (alfa, beta e gama) e composição florística de diferentes tipos de áreas úmidas, a saber, lagoas e áreas ripárias adjacentes a córregos e rios, numa paisagem na bacia do alto Rio Uruguai, Sul do Brasil, para subsidiar a gestão sustentável desses ecossistemas e possibilitar a identificação de potenciais efeitos negativos das inconsistências na LPVN. Dados os excepcionais riscos enfrentados por lagoas nas propriedades privadas brasileiras e a sua grande relevância para a conservação, esta Tese foca principalmente nesses ecossistemas. Com relação ao item (4), as hipóteses levantadas foram: (1) cada tipo de área úmida apresenta padrões de diversidade e composição únicos e, portanto, contribuições singulares para a conservação; e (2) lagoas fazem contribuições essenciais para a diversidade beta e gama de redes de áreas úmidas.

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Manuscrito I

Brazil’s Native Vegetation Protection Law threatens to collapse pond functions[I]

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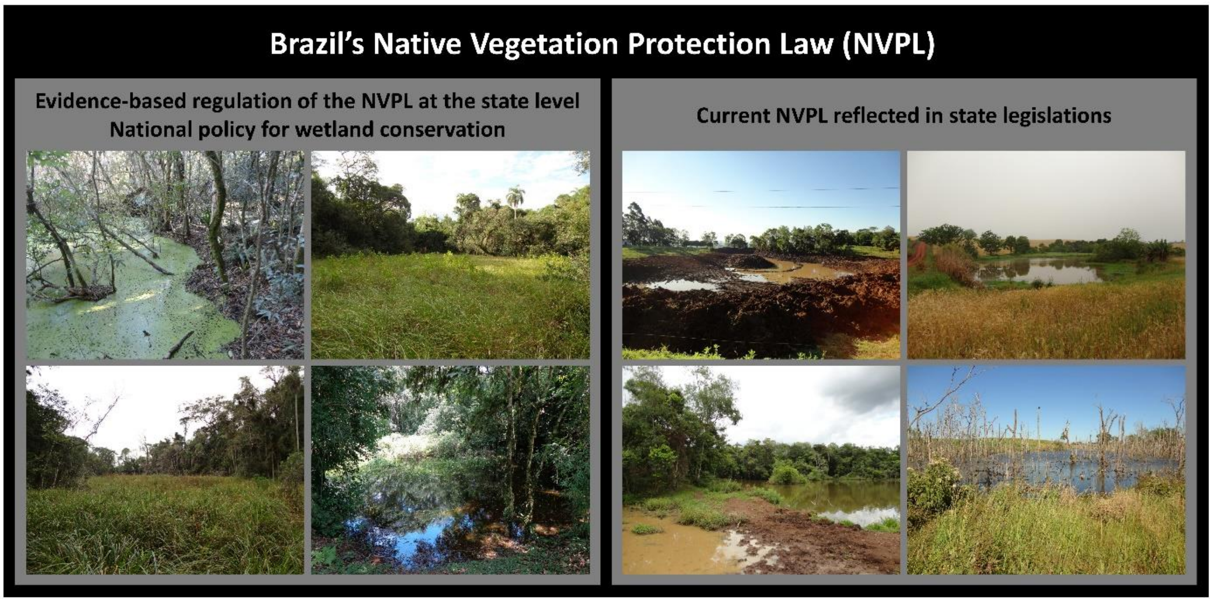
[I] *Perspectives in Ecology and Conservation* 16, 234–237, 2018. https://doi.org/10.1016/j.pecon.2018.08.003. Redigido nas normas do referido periódico.

Highlights

- Pond systems provide essential and unique landscape functions.
- Unsustainable policies threaten to collapse pond functions in Brazil.
- Emergency measures are necessary to prevent pond extirpation.
- Brazil needs a national policy for wetland conservation.

Graphical abstract



Abstract

Pond systems perform a myriad of ecosystem services and make unique contributions to aquatic biodiversity conservation at the landscape scale. Despite their high conservation value, in Brazil, natural ponds have been lost and degraded at alarming rates. The remaining have become exceptionally vulnerable after the enactment of the recent Native Vegetation Protection Law (NVPL), whose unsustainable policies threatens to collapse these ecosystems. Although in force since 2012, the regulation of the NVPL is still in course at the state level, offering a unique opportunity to reduce the gap between science and policy. Here, we show why the NVPL threatens ponds and how its inadequacies can be overcome. Finally, we emphasize the need to create a national policy specifically focusing on wetland conservation.

Keywords Biodiversity; Ecosystem services; Upland-embedded wetlands; Conservation; Environmental legislation; Unsustainable policies.

Introduction

Ponds – temporary or permanent upland-embedded wetlands (UEWs; sensu Calhoun et al., 2017a) with ≤ 2 ha (Biggs et al., 2005; Hamerlík et al., 2014) – are important landscape features, performing a portfolio of hydrological, biogeochemical, and biological functions crucial to maintaining the ecological integrity of watersheds and the provision of ecosystem services (Cohen et al., 2016; Evenson et al., 2018). Benefits provided by pond systems include carbon sequestration (Craft et al., 2017), material transformation (Marton et al., 2015), water quality improvement (Hansen et al., 2018), hydrologic regulation (Rains et al., 2016), and biodiversity support (Schofield et al., 2018). Particularly noteworthy are the contributions of ponds to the protection and management of the aquatic biota at the regional scale. Compared with lakes, rivers, streams, and ditches, ponds present the highest gamma diversity and support a disproportionately larger number of unique and rare species, in addition to having the smallest average catchment size, what makes them to be amongst the most valuable, easiest, and cheapest waterbody types to conserve (Davies et al., 2008a,b).

Despite their high conservation value, ponds have been historically neglected in Brazil, leading to the alteration or destruction of their majority in anthropized landscapes, caused mainly by agricultural expansion, urban development, combating mosquito-borne diseases, and road constructions (e.g., Macedo-Soares et al., 2010; Moraes et al., 2014; Setubal et al., 2016, personal observations). Although there are no estimates of the former and current distribution, number, and size of UEWs for any region of the Brazilian territory, a recent paper reported that 89% of wetland area in South America was lost after 1900 (Creed et al., 2017), which may mean that Brazil is inserted in the region with the highest conversion rate of ponds in the world.

Regardless of their conservation status, all the remaining ponds outside conservation units become exceptionally vulnerable after the enactment of the recent Native Vegetation Protection Law (NVPL; Law nº 12,651 from May 25, 2012; http://www.planalto.gov.br/ccivil_03/_ato2011-2014/2012/lei/l12651.htm), which replaced the 1965 "Forest Code". The NVPL is the primary environmental legislation on private land, regulating, in the case of UEWs, the conservation and restoration of "buffer zones" (legally considered Permanent Preservation Areas – PPAs) in their surroundings. In practical terms, however, the NVPL does not present clear elements that ensure the protection of ponds, besides establishing a series of unsustainable policies that put their ecosystem functions and structure at risk.

Although in force since 2012, the regulation of the NVPL at the state level is still in course, offering a unique opportunity to reduce the gap between science and policy. In this context, we have expanded the debate around the NVPL (e.g., Brancalion et al., 2016) and pointed out potential solutions to overcome the inadequacies that threaten to extirpate the natural ponds in the most biodiverse country of the planet (Brandon et al., 2005).

Inadequacies of the NVPL

One of the main inadequacies of the NVPL, which turns all ponds vulnerable, is the dissociation of the indissociable, i.e., the untying of the concept of “wetlands” from the term “ponds” (not conceptualized in the law). As the NVPL does not directly protect wetlands (the term is not used in any public policy) through PPAs, but supposedly contemplates ponds (which are wetlands), what should be considered a pond is unclear, making conservation strategies impractical.

Equally comprehensive and potentially catastrophic threats stem from the fact that the NVPL does not provide protection for ponds with < 1 ha and does not mention UEWs that hold surface water or near-surface groundwater temporarily. This means that virtually all ponds are at risk, once the large majority generally have less than one hectare (e.g., ca. 76% and 99%; Martin et al., 2012 and Williams et al., 2010, respectively) and, depending on the climatic characteristics in certain regions (e.g., in the semi-arid Northeast Brazil), the totality can be temporary (Junk et al., 2014; Lane and D’Amico, 2016). The imminent massive conversion of small and temporary ponds, in addition to causing direct losses of biodiversity and of a myriad of essential and unique ecosystem services (Calhoun et al., 2017b; Cohen et al., 2016), will also dramatically reduce the connectivity between the few large (≥ 1 ha) and permanent ponds that may remain and, consequently, compromise the viability of metapopulations (Gibbs, 2000) and metacommunities (Dias et al., 2016). In the short to medium term, the inadequacies herein mentioned can mean the extirpation of almost the totality of natural ponds outside conservation units in Brazil, given that just a tiny fraction of the original number of these ecosystems currently remains. In the long term, however, all ponds can be lost, once the successional process tends to transform permanent ponds in temporary ones (Biggs et al., 1994), without legal protection.

The NVPL also undermines pond conservation through the requirement of extremely narrow PPAs. In urban and rural areas, the width of the PPAs that must be maintained is 30 m and 50 m, respectively. However, landowners that suppressed PPAs before July 22, 2008, must restore them up to the width of only 5 m, 8 m, 15 m and 30 m on properties with up to 1, >1-2, >2-4 and >4 fiscal modules, respectively (for details about fiscal modules, see Brancalion et al., 2016). Considering that the area of ponds and of their catchments are positively correlated, and that the PPAs width is not proportionally adjustable to pond size, it is expected that most of the uplands in depressional watersheds will remain economically exploited or humanly inhabited (especially those around large ponds on small properties in irregular situation), which has been shown to deteriorate pond environmental properties (Novikmec et al., 2016) and reduce their conservation value (Stuber et al., 2016; Thornhill et al., 2017). Additionally, insufficient buffer zones can accelerate pond clogging, increasing the likelihood of invasions by exotic species (Tsai et al., 2012), causing the loss of ecosystem services (e.g., water storage capacity) and, ultimately, the disappearance of these wetlands from the landscapes (Bowen and Johnson, 2017). It is also important to mention that probably all the PPAs proposed in the NVPL cannot be considered buffer zones per se, but only part of the full range of terrestrial habitats essential for various semiaquatic species to complete their life cycles (Semlitsch and Bodie, 2003).

How PPAs can be restored in family farms is also a cause of great concern. Among the strategies foreseen in the NVPL, landowners can use exotic woody species in the restoration of 50% of the PPAs, even in grassy biomes, where afforestation can devastate ecosystem functions (Veldman et al., 2015). Exotic woody species within depressional watersheds can alter a range of pond environmental features, reducing species richness and abundance, and modifying community composition (Stenert et al., 2012). The consequences of this inadequacy, however, can be much more severe. In the Argentine Pampas, e.g., an *Eucalyptus camaldulensis* stand reduced groundwater to levels (>50 cm) (Engel et al., 2005) higher than the mean depth of temporary ponds (e.g., 26 cm) and close to the mean depth of permanent ones (e.g., 65 cm) (Hill et al., 2017). Changes of this magnitude in the groundwater table can dry temporary ponds and transform permanent ponds in temporary ones (unprotected by NVPL), determining the loss or collapse of biodiversity and ecosystem services, once hydrology is the core control of aquatic ecosystem functions (McLaughlin and Cohen, 2013). PPAs with exotic woody species, therefore, assume a contradictory role to their finality of safeguarding biodiversity and ecosystems' services and structure.

Another inadequacy in environmental terms is the authorization of aquaculture in converted PPAs on rural properties with ≤ 15 fiscal modules. However, although the NVPL refers only to PPAs, it does not provide explicit impediments to aquaculture (and any other practice) within ponds that are not legally protected, substantially expanding the possible multiplicity of environmental (reviewed by Martinez-Porchas and Martinez-Cordova, 2012) and biological (reviewed by De Silva, 2012) impacts resulting from such activities. The use of natural ponds for aquaculture, like conventional and organic rice cultivation (which includes the application of pesticides and fertilizers and/or intensive mechanization and water management), was shown to reduce species abundance and biomass and alter the communities functional and taxonomic diversity and composition (Dalzochio et al., 2016a,b; Linke et al., 2014). Moreover, aquaculture can compromise the provision of several pond services, like the water quality improvement (Hansen et al., 2018), through the discharge of polluted effluents (Rosa et al., 2013), and the hydrologic regulation (Rains et al., 2016), through water management (Dalzochio et al., 2016a). Aquaculture within PPAs, in turn, in addition to intensifying land use within depressional watersheds and maintaining portions of PPAs without native vegetation, whose negative impacts were mentioned previously, may have similar impacts on pond functions, mainly because of the temporary or permanent release of effluents into the ponds, either by surface (e.g., by the frequent practice of draining cultivated wetlands; Linke et al., 2014) or ground-water flows.

Lastly, the NVPL also threatens pond functions for not protecting swales and ephemeral streams that temporarily or permanently connect ponds to downgradient waterbodies/wetlands through surface water flows (see Fig. 2a and b in Lane et al., 2018). Since ecosystem functions emerge from multiple connections, the predictable degradation or loss of swales and ephemeral streams are expected to severely impair biodiversity and ecosystem services supported by ponds (Lane et al., 2018; Schofield et al., 2018).

Solutions to the inadequacies of the NVPL

We identified the following potential solutions to the inadequacies of the NVPL: (1) to adopt a clear and comprehensive definition of ponds; (2) to provide protection to the entire continuum of wetland connectivity (Cohen et al., 2016); (3) to require PPAs with at least 50 m width around ponds to maximize the retention of contaminants and sediments (Haukos et al., 2016) until more studies introduce biological criteria for the design of buffer zones (e.g., Semlitsch and Bodie, 2003); (4) to consider only the use of native species for the active restoration of PPAs; and (5) to explicitly prohibit the use of ponds and PPAs for the practice of aquaculture.

Final remarks

The regulation of the NVPL at the state level, currently underway, offers probably the best opportunity to supplant its inadequacies, since states can adopt more rigorous, but never more permissive, conservation measures than the federal law. Our suggestions, however, should be interpreted only as emergency strategies in an attempt to avoid the imminent collapse of pond functions in Brazil. Effective conservation initiatives, which will need to address the projected impacts of climate change (Junk et al., 2013) and the alarming rate of pond loss and degradation, will trigger a demand for actions that will make the Brazilian environmental legislation mostly obsolete. Therefore, we emphatically reinforce the need to create a national policy specifically focusing on wetland conservation (Junk et al., 2014), which should include the protection, restoration, management, mapping, monitoring and, especially, the creation (e.g., https://freshwaterhabitats.org.uk/projects/million-ponds/) of ponds. Dialogue between scientists and policymakers will be essential in this process (Azevedo-Santos et al., 2017; Karam-Gemael et al., 2017).

Acknowledgments We thank two anonymous reviewers for their helpful suggestions and comments on an earlier draft of the manuscript. DG was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES); RPM, RLB and SMT received grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq); RLB was also supported by Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ).

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Manuscrito II

Brazilian wetlands on the brink[II]

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[II] *Biodiversity and Conservation* 28, 255–257, 2019. https://doi.org/10.1007/s10531-018-1666-z. Redigido nas normas do referido periódico.

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To the Editor,

Wetlands harbor a huge biodiversity, provide essential services, and are key regulators of climate change (notably peatlands) (MA 2005). Brazil not only hosts the world's richest freshwater aquatic biota (Padial et al. 2017) but also leads in wetland area and peatland volume in the tropics and subtropics (Gumbricht et al. 2017). In 2012, controversial revisions to Brazil's "Forest Code", now renamed the "Native Vegetation Protection Law" (hereafter NVPL; Federal Law no. 12,651/2012; http://www.planalto.gov.br/ccivil_03/_ato2011-2014/2012/lei/l12651.htm), imposed catastrophic risks to wetlands. The reform was catalyzed mainly by the agribusiness sector, which argued that the Forest Code was too restrictive in the face of an alleged need for agricultural expansion (Metzger et al. 2010). However, this argument has been strongly contested by multiple studies (e.g., Soares-Filho et al. 2014; Strassburg et al. 2014; Brancalion et al. 2016). The question now is how to minimize the setbacks.

Riparian wetlands can now be cleared because the NVPL changed the basis for delimiting "buffer zones" (legally considered "Permanent Preservation Areas"; hereafter PPAs) from the maximum water level to the regular bed of watercourses, thus removing protection from many riparian areas, especially from the vast floodplains with flood pulses of high amplitude in Amazonia (Souza et al. 2011). Ponds <1 ha and wetlands adjacent to intermittent springs and ephemeral streams lost their legal protection. These habitats are also on the verge of destruction (Brancalion et al. 2016; Grasel et al. 2018). The same goes for large tracts of salt marshes and hypersaline areas, which can now be used for shrimp farming and salt exploitation, also threatening associated mangroves (Rovai et al. 2012; SBPC and ABC 2012). Other setbacks include the dramatic reduction in requirements for restoration of PPAs cleared before 22 July 2008 (Brancalion et al. 2016), allowing 50% of any required restoration of PPAs to be done with exotic woody species, and authorization of aquaculture in most cleared PPAs.

Among other consequences, setbacks associated with the NVPL may substantially increase greenhouse gas emissions (Moomaw et al. 2018), cause a massive loss of native species (Metzger et al. 2010; Volcan and Lanés 2018), introduce alien taxa (Pelicice et al. 2017), and jeopardize vital ecosystem services (MA 2005). However, Brazil now has a valuable opportunity to rescue its wetlands and so sustain its international treaties and its leadership in conservation. Although in force since 2012, the NVPL's 'regulation' (setting of rules to implement a law) is still in progress at the state level, where its setbacks can be attenuated through adoption of more rigorous policies. We urge policymakers and scientists to engage in open dialogue on this critical 'regulation'.

Acknowledgements DG was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES); PMF, JRSV, RLB, RPM, RRR and AAA received grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq); PMF, RLB and RRR were also supported by Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) and Rede Clima, Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ), and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), respectively.

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Manuscrito III

Brazil's Native Vegetation Protection Law jeopardizes wetland conservation: a comment on Maltchik et al.[III]

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[III] *Environmental Conservation* 46, 121–123, 2019. https://doi.org/10.1017/S0376892918000474. Redigido nas normas do referido periódico.

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Abstract

The future of Brazil’s vast and highly biodiverse wetlands depends on interpretation of the country’s new Native Vegetation Protection Law (NVPL). Maltchik *et al.* recently reviewed wetland-related terminologies and concepts in Brazilian legislation and concluded that all the country’s wetlands are legally protected under the NVPL. Here we show that this is not the case. Finally, we point to a unique opportunity for scientists to help minimize damage to wetlands by contributing to the state-level ‘regulation’ of the NVPL, now underway, and we argue that the country needs a national policy focused specifically on the conservation of these ecosystems.

Keywords wetland policy; terms; definitions; unsustainable legislation; biodiversity; ecosystem services

Brazil's vast and highly biodiverse wetlands are under relentlessly increasing threat, and input from the scientific community is crucial to help minimize the impact of recent legislative setbacks. Terminologies and concepts in laws affecting wetlands are part of this, and Maltchik et al. (2018) have contributed a comprehensive review of such elements. However, their treatment needs reinterpretation.

Maltchik et al. (2018) evaluated wetland-related terms and definitions in Brazil's federal and state legislations to contribute to the assessment of the efficacy of wetland conservation policies. Most of the terminologies they found had only regional application and poor or nonexistent conceptualization. The generic term 'wetlands' ('*áreas úmidas*' in Portuguese), which is the most basic and important term in any wetland policy, was only used in one law: the Native Vegetation Protection Law (hereafter NVPL; Federal Law no. 12,651/2012; Brazil 2012). Based on this term being better defined than other designations, and given the precedence of the NVPL over state laws, Maltchik et al. (2018) concluded that: (1) the term 'wetlands' represents all wetland types; (2) the clear descriptors of the term's definition allow the identification of the totality of wetland ecosystems; and (3), due to (1) and (2), the NVPL ensures the protection of all wetlands.

Maltchik et al. (2018) have provided important input for a better understanding of the adequacy of Brazil's legislation on wetlands; however, the generalizations that these authors make regarding the NVPL's protection of all wetlands is unfounded. The term 'wetlands' appears only twice in the NVPL and is not used in any conservation policy. Its first appearance is before its definition (Chapter I, Article III, Subsection XXV), and the second (Chapter II, Section I, Article VI, Subsection IX) is in a clause that specifies that wetlands (especially those of international relevance) may become protected only if declared to be of 'social interest' by an act of the President of the Republic. The term 'wetlands' and its definition therefore do not guarantee the protection of any wetland in Brazil.

Regardless of the effective use of terminologies, the elements reviewed by Maltchik et al. (2018) lead to conclusions different from those that they drew. The term ‘wetlands’, although generic when considered in isolation, does not represent all wetland types in the context of the NVPL; because its definition is highly exclusionary, using this term cannot ensure the effectiveness of wetland-related conservation policies. Examples of wetlands that clearly do not fit the NVPL’s definition are those that are subject to unpredictable (i.e., non-periodic) flood pulses (e.g., riparian wetlands adjacent to streams and low-order rivers), all areas that are permanently flooded (e.g., permanent ponds, lakes and lagoons) and all or any parts of these areas that are not subject to flooding but are temporarily or permanently saturated (Junk et al. 2014, Mitsch & Gosselink 2015).

An inclusive definition of ‘wetlands’ would also not guarantee the efficacy of wetland conservation strategies. As shown by Maltchik et al. (2018), Brazilian legislation is remarkably insufficient with regards to the representation and detection of singular wetland types (which is especially worrying in view of the extreme diversity and complexity of the country’s wetlands; see Junk et al. 2014). These shortcomings cannot be masked or overcome only by adoption of the generic term ‘wetlands’ (and hence its definition), since each wetland type has unique characteristics and therefore specific conservation needs (e.g., buffer zone width) that can only be met through their being recognized as particular landscape features. A single conservation measure cannot serve for ecosystems ranging from the vast Amazonian floodplains to small temporary ponds in the semi-arid zone. One of the main functions of the term ‘wetlands’ (if not the main one) is not to replace terms for specific wetland types, but to constitute elements representing and/or describing them (e.g., ‘upland-embedded wetlands’ as a description of ponds and lakes; Calhoun et al. 2017a) in order to ensure that they cover the full range of wetland subtypes (e.g., from temporarily saturated to permanently flooded areas). However, this crucial auxiliary function is not fulfilled in any Brazilian law (Maltchik et al. 2018).

Potentially negative consequences of the lack of this kind of application of the term 'wetlands' is exemplified by the NVPL's term 'ponds' ('*lagoas*' in Portuguese), which lacks conceptualization. As comprehensively defined, ponds are upland-embedded wetlands of ≤2 ha (Hamerlík et al. 2014). However, some researchers alternatively use the term 'pools' ('*poças*' in Portuguese) in place of 'temporary ponds' (e.g., De Meester et al. 2005). It is therefore unclear whether temporary ponds are protected by the NVPL, which may lead to exclusionary conservation policies and, consequently, to the collapse of unique ecosystem services (Calhoun et al. 2017b) and communities (Hill et al. 2017, Volcan & Lanés 2018) – in fact, the NVPL does not ensure the protection of any pond (Grasel et al. 2018b). Given the paramount importance of appropriate terms and definitions of wetland types in environmental policies, it should be recognized that Brazil's legislation seriously jeopardizes wetland conservation.

Deficiencies related to the elements used to represent and identify wetland systems, however, are not the only problems that compromise the conservation of these ecosystems in Brazil. While a detailed analysis of the country's wetland-related policies is beyond the scope of this comment article, it is also important to highlight that the NVPL's enactment in 2012 (when it replaced the old 1965 'Forest Code') imposed catastrophic risks to Brazil's wetland heritage (Grasel et al. 2018a). Setbacks or inadequacies in the NVPL that diverge from Maltchik et al.'s conclusions include:

- Removal of the protection conferred to ponds of <1 ha and wetlands associated with intermittent springs and ephemeral streams.
- Dramatic reductions in the requirements for restoration of 'buffer zones' (legally considered 'Permanent Preservation Areas'; hereafter PPAs) cleared before 22 July 2008, especially for those around ponds and lakes (for which protection with PPAs is now only 5–30 m) and adjacent to streams and rivers (where protection is only 5–100 m). This

protected vegetation is now delimited according to the size of the property, regardless of the size or width of the wetlands or waterbodies.

- Alteration of the basis for delimiting PPAs adjacent to streams and rivers from the maximum water level to the ‘regular bed’ of watercourses, thus reducing or removing protection from many riparian areas, especially from the vast Amazonian floodplains, which can reach widths of tens of kilometres and be ‘protected’ by PPAs as narrow as 5 m (Souza Jr et al. 2011, Brancalion et al. 2016).
- Authorization of aquaculture (including raising alien species) in converted PPAs around ponds and lakes and adjacent to either intermittent or permanent watercourses on rural properties with ≤15 fiscal modules (for details about fiscal modules, see Brancalion et al. 2016).
- Non-protection of mangroves, salt marshes and hypersaline areas (sensu Junk et al. 2014) through non-wetland PPAs (mangroves are themselves considered PPAs, but salt marshes and hypersaline areas are not).
- Permission to use salt marshes and hypersaline areas for shrimp farming (including exotic species) and salt production (10% of the area of these ecosystems can be used in the Amazon biome and 35% in other Brazilian biomes) (see also Rovai et al. 2012, Oliveira-Filho et al. 2016).
- Allowing 50% of any required restoration of PPAs around ponds, lakes and perennial springs and adjacent to intermittent/permanent watercourses and *veredas* (wetlands in the *Cerrado* biome) to be done using exotic woody species (even in grassy biomes).
- Establishment of the Rural Environmental Registry (known as the ‘CAR’) with poor provision for monitoring compliance with the rules for protection of waterbodies and wetlands, especially in the case of narrow or small aquatic ecosystems (e.g., Taniwaki et al. 2018).

Recognizing the limitations and problems of the NVPL is a pressing need in the current Brazilian political scenario. Although in force since 2012, the NVPL's 'regulation' (setting of rules to implement a law) at the state level is still underway, offering a unique opportunity to supplant its inadequacies. Therefore, scientists and policy-makers must engage in dialogue to regulate environmental legislation with evidence-based criteria (Azevedo Santos et al. 2017).

However, the legal mechanisms provided by the NVPL, even if improved at the state level, are clearly insufficient to promote wetland conservation in Brazil. Overcoming environmental challenges imposed, for example, by climate change (Junk et al. 2013), high rates of wetland loss (Creed et al. 2017) and the spread of exotic species (e.g., Stenert et al. 2016) will require the adoption of effective integrated strategies for the protection, restoration, management, creation, mapping and monitoring of wetlands (e.g., Grasel et al. 2018b). We emphatically recommend the creation of a national policy specifically focusing on wetland conservation.

Financial Support. DG was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) (grant number 1601741); grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) were received by PMF (573810/2008-7; 311103/2015-4), JRSV (310850/2012-6; 303776/2015-3), RRR (561897/2010-7) and RPM (300860/2016-1); and PMF and RRR were also supported by Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) (708565) and Rede Clima (01.13.0353-00), and by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (2013/50718-5; 1999/09635-0), respectively.

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Manuscrito IV

Comparative plant biodiversity among wetlands with contrasting legal protection status on Brazilian private lands: a case study and implications[IV]

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[IV] Manuscrito redigido nas normas do periódico *Perspectives in Ecology and Conservation*.

Highlights

- Brazilian legislation on private lands puts a series of wetlands at risk.
- Ponds are virtually unprotected and riparian areas' conservation is context-dependent.
- All wetland types show unique patterns of floristic diversity and composition.
- Wetland conservation depends on the protection of all wetland types.
- Urgent actions are needed to safeguard Brazil's wetland heritage and human well-being.

Graphical abstract

Abstract

Relatively recent changes in Brazil’s private land legislation have placed a number of wetlands at risk. Understanding the potential effects of these environmental setbacks is critical toward sustainability-oriented decision making. In the upper Uruguay River basin, southern Brazil, we investigated the diversity (alpha, beta and gamma) and composition of plant communities (herbaceous and woody) in wetlands with contrasting legal protection status at the national level: ponds (virtually unprotected), streamside wetlands and riverside wetlands (context-dependent protection). Among the study sites, all ponds and riparian areas are legally unprotected and protected, respectively. Each wetland type exhibited singular biodiversity patterns and contributions to conservation. Unprotected wetlands, in particular, showed the most peculiar floristic composition, a much higher number of unique herbaceous species and even higher diversity indices than protected wetlands, demonstrating that the removal of the protection conferred to ponds is inadequate. If the objective is to conserve wetlands’ biodiversity and maintain the services they provide, Brazil will need to take urgent measures to improve its environmental legislation.

Keywords Ponds; Streamside wetlands; Riverside wetlands; Plant diversity; Floristic composition; Environmental legislation.

Introduction

Wetlands are key reservoirs of plant biodiversity, harboring unique, rare and endangered species and very singular communities (Davies et al., 2008; Junk et al., 2014; Pitman et al., 2014). Specific wetland types share a particular range of environmental features (e.g., hydrological, physicochemical and spatial) and thus tend to show distinct diversity and composition patterns (Williams et al., 2004; Keddy, 2010; Draper et al., 2018). Appropriate protection of all wetland types is therefore essential to ensure the ecological integrity of watersheds (Flinn et al., 2008).

Despite their unique contributions to biodiversity conservation, wetlands on Brazilian private lands have become vulnerable after recent setbacks resulting from revisions to the country's "Forest Code" (Federal Law nº 4,771/1965), now renamed the "Native Vegetation Protection Law" (NVPL; Federal Law nº 12,651/2012) – see several examples in Grasel et al. (2018, 2019a,b). The NVPL's unsustainable policies, however, had very complex and heterogeneous impacts on wetlands: while many had their protection removed (e.g., almost all ponds; see Grasel et al., 2018), others are now subjected to a widely varying and context-dependent legal status (e.g., riparian areas; see Brancalion et al., 2016). In this scenario, evaluating the biodiversity patterns of different wetland types at the landscape scale is crucial to help understand the potential impacts of the mentioned legislative setbacks and support decision making. This is especially true because of the scarcity of related studies that have collectively addressed distinct species groups and adopted standardized sampling protocols, which makes it difficult to evaluate and base public policies.

Here, our main goal was to compare the diversity and composition of plant communities among freshwater wetlands in the upper Uruguay River basin, Southern Brazil. To cover diversity across scales, we assessed both alpha (local), beta (among-site) and gamma (regional) diversity. We encompassed the three most common natural wetland types in the region: ponds, streamside wetlands and riverside wetlands. We hypothesized that each wetland type shows singular plant biodiversity patterns and contributions to conservation. In the studied wetland network, all ponds were totally unprotected, while all riparian areas, in contrast, were protected by the NVPL. Although this is a case study, we believe it transfers to the reality of a considerable part of the Brazilian territory, besides being an important contribution for other countries with similar wetland policies.

Material and methods

Study areas

The study was carried out in an ecotonal region between the semi-deciduous seasonal forest and the evergreen seasonal *Araucaria* forest in the upper Uruguay River basin, Santa Catarina State, Southern Brazil (Oliveira-Filho et al., 2015; Fig. 1). The climate in the region is subtropical humid without a noticeable dry season (Alvares et al., 2014). The annual means of temperature and rainfall are 18-20 °C and 1,900-2,000 mm, respectively (Wrege et al., 2012). Soils originate from basaltic rocks and are mostly eutrophic (IBGE, 1990), but substrates/soils such as those within and nearby ponds tend to be dystrophic (Grasel et al., 2020).

Across the landscape, we first identified three predominant natural wetland types: (1) ponds; (2) streamside wetlands; and (3) riverside wetlands – see their definitions in Table 1. We then selected eight study areas per wetland type (see Fig. 1 and Table S1) adopting the following criteria: (1) no evidence of anthropogenic habitat alteration; (2) no sign of recent natural resource exploitation; (3) relatively small percentage of area occupied by intensive land use activities within a 100 m radius; and (4) minimum distance of 1,500 m between study areas – information on the selected wetlands are provided in Table 1 and Table S1.

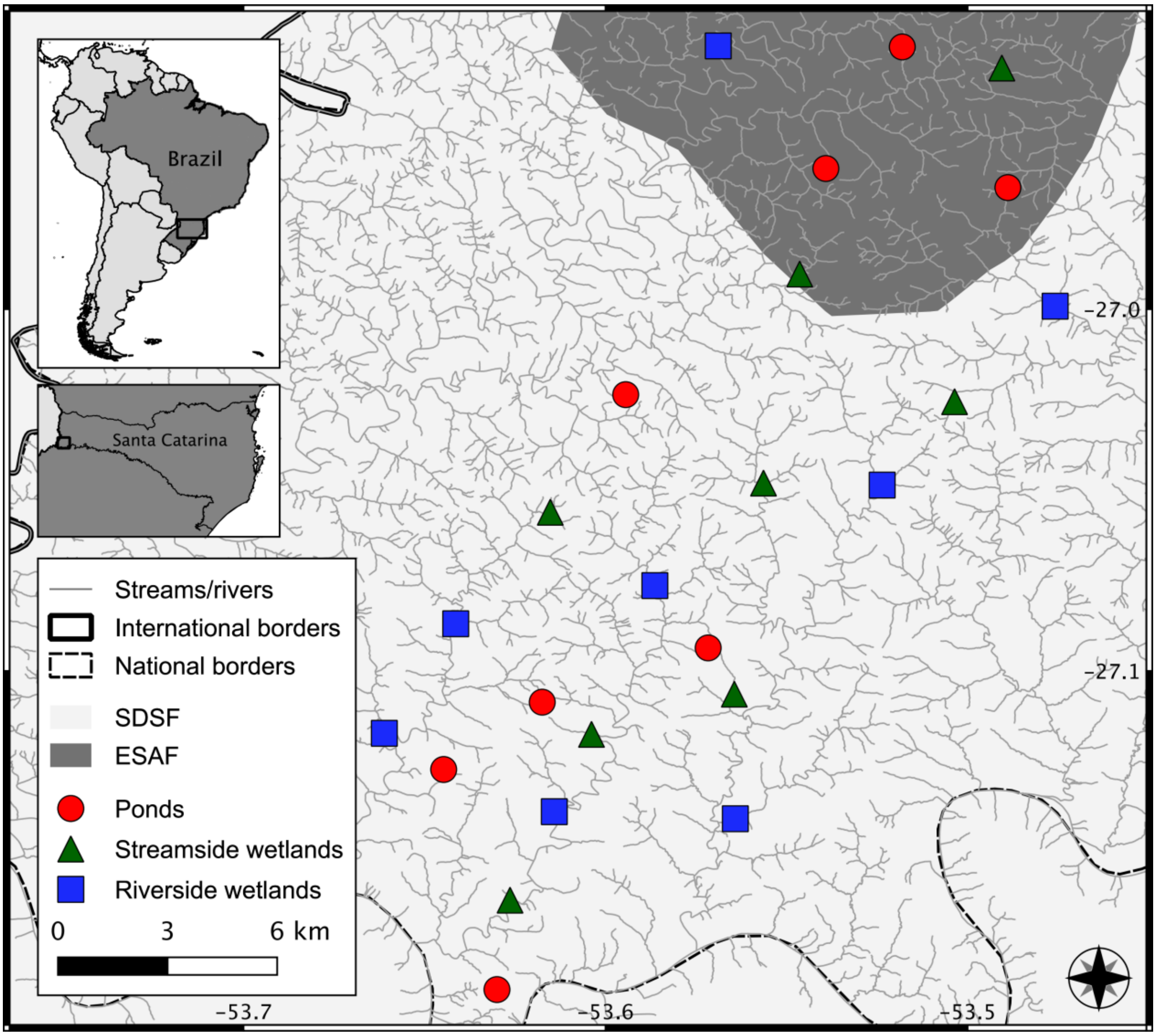

Fig. 1 Location of the study areas in the upper Uruguay River basin, Southern Brazil. SDSF, semi-deciduous seasonal forest; ESAF, evergreen seasonal *Araucaria* forest.

Wetlands' legal protection status

The main way in which ponds and riparian areas may be protected by the NVPL is through the requirement to maintain/restore vegetation strips called "Permanent Preservation Areas" (PPAs). In the case of ponds, PPAs must occur around them and, therefore, are formed by uplands. In the case of lotic ecosystems, however, PPAs must occur adjacent to

Table 1 Definitions and main characteristics of the selected wetlands in the upper Uruguay River basin, Southern Brazil.

Wetland type	Definition and main characteristics
Ponds	Permanent or temporary upland-embedded wetlands with ≤2 ha (Biggs et al., 2005). With the exception of one pond, which is permanently flooded, all are subjected to polymodal and unpredictable flood pulses of short duration (Junk et al., 2014) – i.e., are temporarily flooded –, but substrates are waterlogged all year around. Within-site and/or among-site vegetation physiognomies are highly variable, varying from predominantly herbaceous to arboreal communities (see Figs. S1 and S2). Hummocks of varying shapes, sizes (e.g., 0.5-5 m²) and heights (e.g., 10-30 cm) are common features in these ecosystems, especially in forested/swampy areas (see Fig. S1). Ponds range from 0.01–0.98 ha (mean = 0.30 ha).
Streamside wetlands	Riparian wetlands (sensu Junk et al., 2014) adjacent to watercourses ≤7 m wide (Bubíková and Hrivnák, 2018). Streamside wetlands are also subjected to polymodal and unpredictable flood pulses of short duration (Junk et al., 2014). However, as they occur in steep areas, soils are flooded only during heavy rainfall events and thus remain well-drained for most of the year. Preliminary field observations (e.g., litter removal or deposition after high water levels) and landowner interviews revealed that the chosen streamside wetlands are at least 1 m wide. All riparian areas are forested and their plant communities are physiognomically much less variable than those in ponds (see Figs. S1 and S2). Streams adjacent to the studied riparian areas are intermittent or permanent (none is ephemeral) and have 1.8–5 m wide (mean = 3.3 m).
Riverside wetlands	Riparian wetlands (sensu Junk et al., 2014) adjacent to watercourses >7 m wide (Bubíková and Hrivnák, 2018). The same topographic, hydrologic and

	physiognomic characteristics described for streamside wetlands applies here, except that riverside wetlands have been found to be at least 4 m wide (see Fig. S1). Rivers adjacent to the studied riparian areas are permanent and have 7.6–14.1 m wide (mean = 10.3 m).

All selected wetlands have natural origin. For a comprehensive definition of wetlands, see Junk et al. (2014).

watercourses, and may therefore be formed only by wetlands or by varying proportions of wetlands and uplands, depending on the width of the riparian areas and the required PPAs. For this article, we consider that a given wetland is legally "protected" under the NVPL if its entire local extent needs to be conserved and embraced by upland vegetation strips, regardless of the dimensions of the latter. Even though in many cases the size of these non-wetland areas may be clearly insufficient to serve effectively as buffer zones, wetlands with any level of protection by them can be considered to have a privileged legal status after the NVPL's enactment.

All ponds considered here are now unprotected because the NPVL has removed the need to protect <1 ha ponds through PPAs – all are smaller (see Table 1). However, these ponds are also dramatically threatened with degradation/conversion by a portfolio of other unsustainable policies or inadequacies, as are virtually all (if not all) ponds on Brazilian private lands – see Grasel et al. (2018) for details.

All chosen riparian areas, on the other hand, are legally protected. Since they occur adjacent to 1.8-14.1 m wide intermittent or permanent watercourses (see Table 1) and in areas that were in compliance with the old Forest Code, the NVPL requires the maintenance of PPAs with 30 m and 50 m wide next to streams/rivers with <10 m and 10-50 m wide, respectively. The selected riparian areas, for having a maximum of ca. 4 m wide (see Table 1), are therefore protected by uplands with several times the wetland areas' width (e.g., 30 and 12.5 times for streamside and riverside wetlands, respectively). The favorable legal status of these wetlands, however, is partly due to our criteria for selecting study sites, especially the third (see above). This is not the situation of all the riparian areas in the region, especially those inserted in landholdings that were not in conformity with the old Forest Code – see examples of threats to these ecosystems in Brancalion et al. (2016) and Grasel et al. (2019a,b). Nevertheless, in general, riparian areas are in a much less unfavorable legal protection situation than ponds (see Grasel et al., 2018 and the references right above).

Vegetation sampling

We sampled all herbaceous species and ≥0.3–≤1 m high plants of woody species (except bryophyte, climber and epiphyte species) – i.e., plants that roughly constitute the herb layer (Santos-Junior et al., 2018) – using the line intercept method (Canfield, 1941). In each study area, we surveyed the species' coverage in 40 linear meters by establishing transects arranged parallel and equidistantly in 30 m long stretches. For each wetland type, we defined a specific sampling design based on their abiotic and biotic particularities (see Table 1). In streamside and riverside wetlands, 40 and 10 transects of 1 and 4 m were established perpendicular to the watercourses, respectively (to their left or right) – streams and rivers were not sampled because of the absence of plants meeting the inclusion criteria. In ponds, we applied the same transect organization adopted for riverside wetlands, but the sampling effort was equally divided into two areas that best represented the vegetation's physiognomic diversity (e.g., treeless and forested patches). All surveys were conducted during the summer of 2016-2017. Species were identified through specialized bibliography, comparisons with herbaria exsiccates, and expert consultations.

Environmental variables

To help indirectly find potential main drivers of the investigated biodiversity patterns, we used an environmental dataset under construction formed by variables on topographic features, soil/substrate cover by rocks, soil/substrate physico-chemical properties, canopy openness, extent of land under intensive use within a 100 m radius and altitude for each inventoried wetland. Details on their acquisition are provided in Appendix A.

Data analysis

First, we used spline correlograms to test for spatial correlation of all the study areas' abiotic and biotic data employed in the analyses described below – see procedures and results in Appendix A. Since these tests pointed out no significant spatial correlation, spatial data were kept out from further analyses. We then investigated whether ponds and streamside and riverside wetlands differed in their environmental features and biodiversity parameters. To better comprehend the contributions of each wetland type to plant conservation, we compared their diversity and composition patterns considering native herbaceous and woody species separately and together.

Alpha diversity was evaluated through four parameters that successively increase the most common species weights and fit the Hill series (Hill, 1973): richness, exponential of Shannon's index, Simpson's inverse index and Berger-Parker's inverse index. Considering that species coverage is a measure of abundance and, in our case, a continuous variable, we used species coverage to compute the above-mentioned three last indices (in line with the approach adopted to assess gamma diversity; see below). To compare species diversity among wetland types, we used one-way analyses of variance (ANOVAs) and pairwise comparisons. The assumptions of normality of residuals and homogeneity of variances were assessed through Shapiro-Wilk's and Levene's tests, respectively. Data that showed normal and homoscedastic distribution were compared though parametric tests – type-II ANOVAs and Tukey's HSD pairwise tests –, while non-parametric tests – Kruskal-Wallis ANOVAs and Dunn's pairwise comparisons with *P*-values adjusted by the Bonferroni method – were used for variables that did not meet at least one of the above-mentioned premises. Following the same rationale of diversity profiles (Chao and Jost, 2015), a given wetland type was considered more diverse than its counterparts regarding any species group only when showing higher values for the entire series of diversity estimates.

Beta diversity was compared using permutational analyses of multivariate dispersions (PERMDISPs) with pairwise comparisons, where we used 9,999 permutations to assess significance and the Bonferroni method to adjust *P*-values (Anderson, 2006; Anderson et al., 2006). Such analyses were based on presence-absence data and Jaccard dissimilarity matrices, in consonance with most related studies. Additionally, we partitioned the wetland types' total beta diversity (Jaccard dissimilarity) into nestedness and turnover components. The same routine used to compare beta diversity (PERMDISP and post-hoc tests) was used to address among-site environmental heterogeneity. For this, we used a Euclidean distance matrix based on environmental data previously standardized to zero mean and unit standard deviation.

Gamma diversity was compared through diversity profiles (expressed as Hill numbers) with increasing values of q, thereby successively increasing the most common species weights. These profiles were built with 95% confidence intervals and corrected for under-sampling bias according to Chao and Jost (2015). In these analyses, we opted to use species coverage data because incidence-frequency data resulted in exceptionally large confidence intervals following our modest number of replicates.

Environmental conditions and species composition were compared through permutational multivariate analyses of variance (PERMANOVAs; Anderson, 2001) with pairwise contrasts using 9,999 permutations to assess significance and the same correspondent distance/dissimilarity matrices employed in PERMDISPs; *P*-values resulted from post-hoc tests were adjusted by the Bonferroni method. Since PERMANOVAs and pairwise comparisons may be significant due to the sample groups' location and/or dispersion, we used the results of PERMDISPs and post-hoc tests – and ordination plots; see below – to interpret the resulting patterns (Anderson et al., 2008). Complementarily, we tested if environmental variables differed separately among wetland types using ANOVAs and pairwise tests following the same routine used to compare alpha diversity.

Lastly, we build ordination plots to visualize patterns tested with PERMDISPs, PERMANOVAs and pairwise tests. A principal component analysis (PCA) was calculated based on the above-mentioned matrix of standardized environmental data, while non-metric multidimensional scaling (NMDS) ordinations (optimized for two dimensions) were computed based on matrices with species presence-absence data and the Jaccard dissimilarity index.

All analyses were performed in R (R Core Team, 2020) using packages 'SpadeR' (Chao et al. 2016), 'lawstat' (Gastwirth et al., 2019), 'betapart' (Baselga et al., 2018), 'FSA' (Ogle et al., 2019) and 'vegan' (Oksanen et al., 2019).

Results

Environmental characteristics

Most environmental variables differed only between lentic and lotic habitats (Table S2). For example, ponds showed the lowest values of average elevation, slope, rock cover, pH and base saturation (i.e., most presented dystrophic substrates, while all riparian areas exhibited eutrophic soils), and the highest of aluminum saturation, canopy openness and canopy openness amplitude. The main differences between the two riparian ecosystems related to average elevation and slope, greater in riverside wetlands, and rock cover, higher in streamside wetlands. Proportion of area under intensive use around study sites was similar among all wetland types and thus anthropic activities probably had little or no effect on the observed abiotic and biotic patterns. For more details, see Table S2.

Among-site environmental heterogeneity was greater in ponds than in streamside and riverside wetlands, while in the last two it was similar (Table S3; Figs. S3 and S4). Environmental conditions differed among all wetland types – especially between lentic and lotic habitats –, independently of the sample groups' multivariate dispersions (Table S3; Fig. S4).

Alpha diversity

Streamside and riverside wetlands were alike in all alpha diversity metrics for all plant groups, while ponds showed the lowest indices in general (Fig. 2a-c; Table S4). However, as higher weights were given to more abundant species, ponds remained less diverse than lotic environments only in relation to woody species (Fig. 2a-c; Table S4).

Beta diversity

Beta diversity of herbaceous species differed among all wetland types and showed the following pattern: ponds > riverside wetlands > streamside wetlands (Fig. 2d; Table S3; see

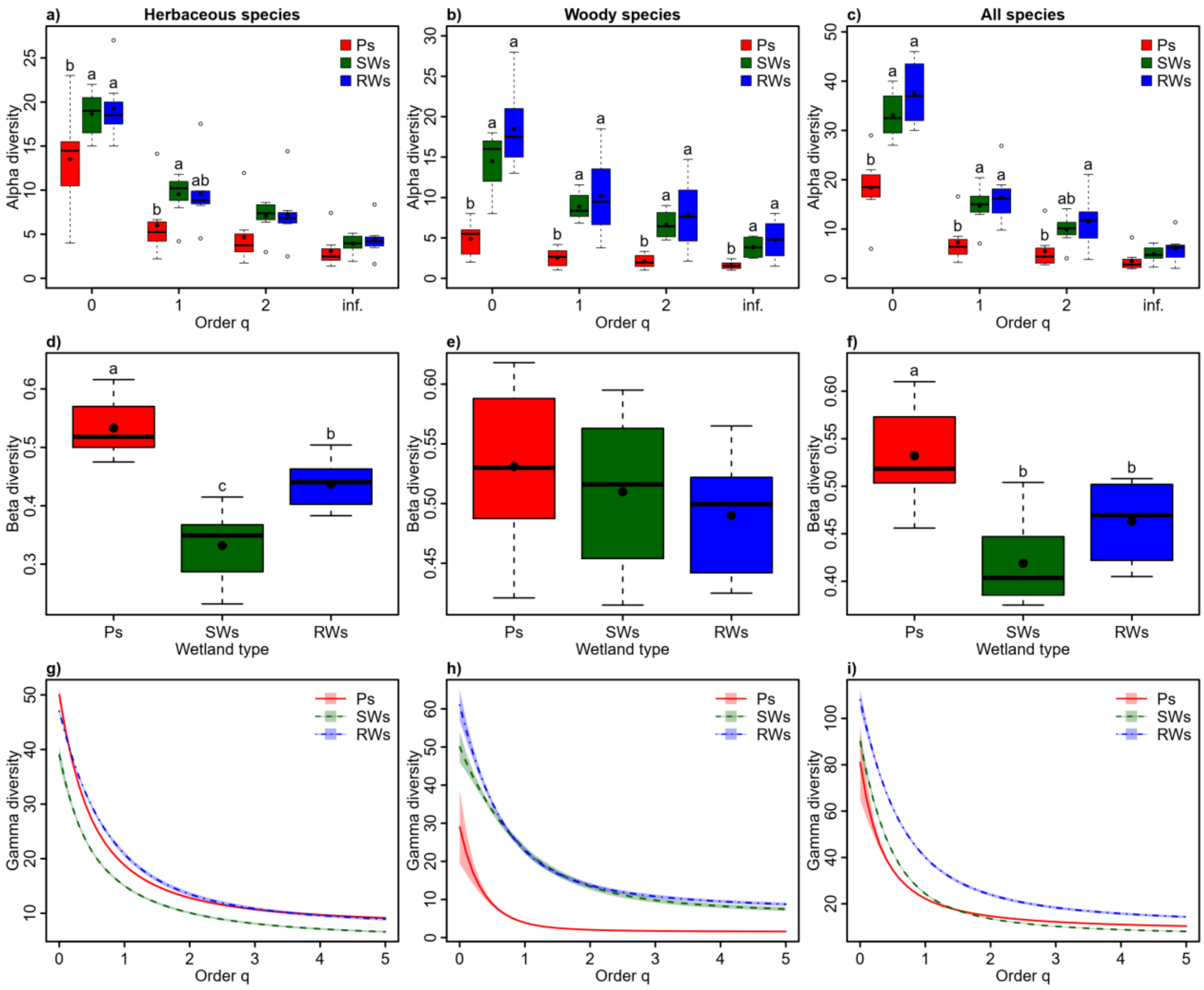

Fig. 2 Diversity patterns in ponds (Ps), streamside wetlands (SWs) and riverside wetlands (RWs) in the upper Uruguay River basin, Southern Brazil. a-c) Boxplots for alpha diversity parameters. Boxes show the 25th and 75th percentiles, medians (thick lines) and means (black dots), while staples indicate the smallest and highest values (excluding outliers). Outliers are shown as hollow circles. Different letters above the top staples within each species group and diversity parameter indicate significant differences ($P < 0.05$) according to Tukey's HSD or Dunn's pairwise comparisons (see Table S4). $Q = 0$, 1, 2 and inf. (infinity) correspond to richness, the exponential of Shannon's index, the Simpson's inverse index and the Berger-Parker's inverse index, respectively. d-f) Boxplots for beta diversity showing distances to median resulted from permutational analyses of multivariate dispersions (PERMDISPs). Boxes and staples show the same type of information presented in a-c. Different letters above the top staples indicate significant differences ($P < 0.05$) according to PERMDISP post-hoc tests (see Table S3). g-i) Diversity profiles for gamma diversity. Shaded areas indicate the 95% confidence intervals. $Q = 0$, 1 and 2 correspond to the same parameters described for alpha diversity.

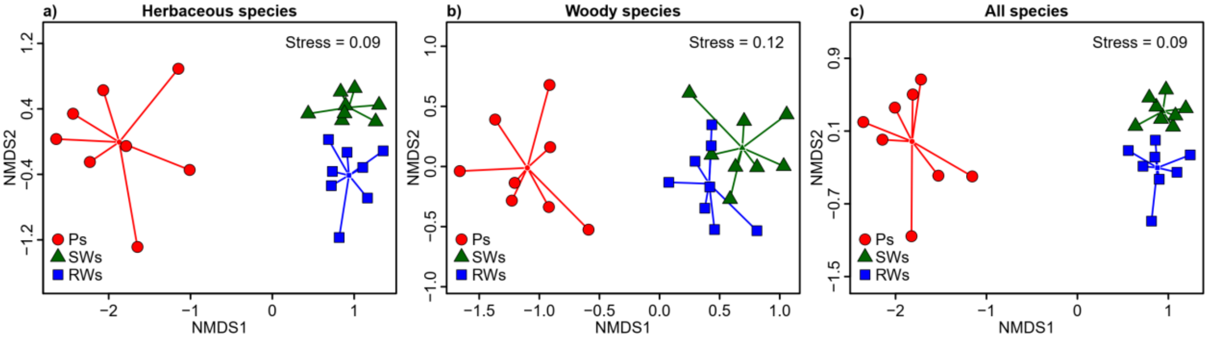

Fig. 3 Composition patterns in ponds (Ps), streamside wetlands (SWs) and riverside wetlands (RWs) in the upper Uruguay River basin, Southern Brazil, showed through non-metric multidimensional scaling (NMDS) ordinations. Segments connect samples to their group centroids.

also Figs. 3a and S5a). For woody species, no difference was observed (Fig. 2e; Table S3; see also Figs. 3b and S5b). When assessing the global set of species, ponds again had the highest beta diversity, but streamside and riverside wetlands were similar (Fig. 2f; Table S3; see also Figs. 3c and S5c). Total beta diversity in all cases was almost entirely explained by species turnover instead of nestedness (Fig. S5d-f).

Gamma diversity

Gamma diversity of herbaceous species was higher in ponds and riverside wetlands than in streamside wetlands, whereas the first two showed similar diversity (Fig. 2g). Woody species were less diverse in ponds than in streamside and riverside wetlands, which in turn showed overlapping diversity profiles (Fig. 2h). When all species were considered, gamma diversity was greater in riverside wetlands than in ponds and streamside wetlands, while the last two had similar diversity (Fig. 2i).

The list of species is shown in Table S5, and the richness per species group and wetland type, as well as in the global inventory, are presented in Fig. S6. Ponds exhibited the vast majority of exclusive herbaceous species and also the largest number of unique species of the global set of species, while riverside wetlands showed the greatest number of exclusive woody species – see details in Fig. S7.

Species composition

The composition of herbaceous and woody species differed among all wetland types when considered separately and together, regardless of the sample groups' multivariate dispersions (Fig. 3a-c; Table S3). Overall, the most striking compositional differences were observed between ponds and riparian areas (Fig. 3a-c).

Discussion

Results showed that, in general, each wetland type presented very singular diversity and composition patterns and contributions to conservation, corroborating our hypothesis. However, when the characteristics of the different wetland types are assessed in more detail, their uniqueness depends on the specific parameters investigated. Below, we briefly discuss each of them. Unfortunately, the scarcity of studies that have collectively addressed distinct wetland types and plant groups in a standardized manner and the variety of methods used to evaluate biodiversity make it difficult to assess how recurrent our findings are.

Alpha diversity

Riparian areas tended to show the highest values of all alpha diversity indices, which is most likely linked to their habitat complexity. For example, streamside and riverside wetlands presented the highest elevation ranges, implying in spatially variable inundation regimes in terms of amplitude, duration and frequency (Wittmann, 2012; Junk et al., 2014). These ecosystems thus show well-known characteristics for generating alpha diversity, such as environmental heterogeneity and gradients of disturbance (Pollock et al. 1998). Although similarly diverse to riverside wetlands, streamside wetlands tended to show slightly lower alpha diversity values as a whole, which is possibly related to two main reasons: (1) lower elevation amplitudes and hence lower habitat complexity; and (2) relatively great coverage by rocks, which may have reduced the availability of suitable niches for the establishment of some species.

Ponds, in turn, had overall the lowest alpha diversity indices, although their diversity patterns of herbaceous and woody species differed sharply from those of riparian areas. The herbaceous component in ponds was similarly diverse to that of streamside and riverside wetlands, which might be primarily attributed to the large mean canopy openness recorded in most sites and the permanently wet conditions (Hassall et al., 2011; Bando et al., 2015). In addition, ponds showed relatively high within-site heterogeneity related to light incidence and, to a lesser extent, to hydrological conditions, which may have favored niche partitioning (Holtmann et al., 2019). The diversity of woody species in ponds, however, was much lower than that in riparian areas, which is explained by the strong selective pressure that swampy conditions exert on this plant group (Keddy, 2010; Pitman et al., 2014) – furthermore, the high levels of aluminum saturation may have been an additional stressor (Delhaize and Ryan, 1995; Grasel et al., 2020). When the global set of species was analyzed, ponds were again as diverse as riparian areas, mainly because of their high diversity in herbaceous species.

Beta diversity

Beta diversity of herbaceous species was higher in ponds than in riparian areas, which can essentially be the result of their greater among-site environmental heterogeneity reflecting specific conditions of their micro-catchments (Davies et al., 2008). Complementary explanations also include the ponds' high susceptibility to stochastic events due to their small sizes (Scheffer et al., 2006), and their different levels of connectivity with other wetlands, making the occupation of ponds by species with distinct dispersion capacities irregular (Flinn et al., 2010). Lotic systems, in contrast, are highly connected and, as showed here, present much less variable physico-chemical conditions than ponds, thus favoring more uniform plant communities at the regional level (Williams et al., 2004). Even so, riverside wetlands showed greater beta diversity than streamside wetlands. A potential explanation is that the latter exhibited greater within-site environmental heterogeneity, which may have promoted more complex species combinations at the site level and, consequently, a higher dissimilarity in species composition at the landscape scale.

Beta diversity of woody species, on the other hand, was similar among all wetland types. The most likely reason why ponds did not show the greatest beta diversity again – despite this trend has been observed (see Figs. 2e, 3b and S5b) – was their previously mentioned environmental harshness, which may have prevented their high among-site environmental heterogeneity from being translated into beta diversity by decisively limiting the establishment of woody species (Keddy, 2010) – indeed, many sampling sites were shrubless and/or treeless. Likewise, riverside wetlands did not repeat a greater beta diversity compared to streamside wetlands. As suggested above, a greater local environmental heterogeneity in riverside than in streamside wetlands may have favored higher beta diversity of herbaceous species in the former. However, woody species are less sensitive to environmental changes (Lite et al., 2005), indicating that riverside wetlands' intra-site environmental diversity may have been too modest for similar effects to be observed for this plant group.

With respect to the global set of species, results clearly reflect the overall trend: beta diversity higher in ponds than in riparian areas and similar between streamside and riverside wetlands.

Gamma diversity

The highest gamma diversity of herbaceous species was found in ponds and riverside wetlands, which is mainly related to their greater beta diversity (species turnover) in relation to streamside wetlands, since alpha diversity was similar among all wetland types.

In terms of woody species, gamma diversity was much higher in riparian areas than in ponds, clearly reflecting the great challenges that swampy conditions impose to the establishment and development of woody species (Pitman et al., 2014).

Regarding the global set of species, riverside wetlands presented the greatest gamma diversity, which is explained by their high diversity in all plant groups. In turn, streamside wetlands and ponds were between the richest and poorest ecosystems, depending on the plant group, which clarifies why they appear together in second place.

Species composition

Floristic composition of all plant groups differed among all wetland types – notably between lentic and lotic systems –, which is likely to be more closely related to the specific environmental conditions in each of these ecosystems (Keddy, 2010; Draper et al., 2018).

Indeed, the spatial organization of the sample groups in PCA and NMDSs is similar, evidencing a correspondence between specific environmental characteristics and plant communities.

Final remarks and implications

As indicated by our results, each wetland type offer important contributions to plant conservation and is therefore crucial to maintaining ecosystems' functioning and services. Ponds, in particular, presented the most peculiar floristic composition, a much larger number of unique herbaceous species and, depending on the parameter and species group, even higher levels of plant diversity compared to riparian areas, revealing that the removal of the protection conferred to ponds is unsustainable (Grasel et al., 2018). Similarly, many riparian areas have also become seriously threatened after the NVPL's enactment, although their legal status is much less critical than that of ponds (see Brancalion et al., 2016; Grasel et al., 2018, 2019a,b).

The potential consequences of the NVPL's unsustainable policies include habitat degradation and conversion, alteration of communities' composition, species extinction and loss of valuable ecosystem services (Brancalion et al., 2016; Cohen et al., 2016; Grasel et al., 2018, 2019a,b; Guidotti et al., 2020). Brazil urgently needs to reverse a series of recent legislative setbacks under penalty of promoting irreparable damage to its natural heritage and human well-being.

Acknowledgments We thank Ricardo Ribeiro Rodrigues for helpful suggestions and comments on an earlier draft of the manuscript, Manueli Blatt Spezia for fieldwork assistance, Luíz Fernando Esser for producing Fig. 1, Vander Kaufmann for providing watercourses shapefiles from the Santa Catarina State used in Fig. 1, and the following researchers for help in identifying species and/or resolving nomenclatural issues: André Luís de Gasper, Ilsi Iob

Boldrini, Marco Octávio de Oliveira Pellegrini, Maria Salete Marchioretto, Sérgio Augusto de Loreto Bordignon, Monica Gomes Buchoski, Silviane Cocco Pesamosca, Danilo Soares Gissi, João Marcelo Alvarenga Braga, Martin Molz, Carlos Alberto Ferreira Júnior, Emerson Ricardo Pansarin, Jefferson Prado, Luis Adriano Funez, Maria de Fátima Freitas, Regina Celis Lopes Affonso and Marília Cristina Duarte. DG was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Finance Code 001.

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Appendix A

Acquisition of environmental variables

Topographic variables

We obtained two topography-related proxies for environmental conditions and heterogeneity – here also used as surrogates for hydrological characteristics: (1) average elevation and (2) slope (e.g., Budke et al., 2007; Grasel et al., 2020). Because ponds and riparian areas differed markedly in their hydrological features (see Table 1), we adopted distinct starting points to measure the elevation of transects in these ecosystems in order to better capture differences in water availability: the edges of ponds and the lower boundary of the riparian areas. Thus, the measurements resulted in generally negative values for ponds and positive values for streamside/riverside wetlands. Elevations were measured at 1 m intervals and obtained using two tape measures graduated in millimeters and a 20 m long water-filled levelling hose. Each transect in the center of five contiguous transects was selected for the topographic survey. Average elevation was the mean of all measured elevations, and slope was the average of the transects maximum elevation.

Soil/substrate cover by rocks

Soil/substrate cover by ≥5 mm rocks (variable rock cover) was measured using the line intercept method (Canfield, 1941). These measurements were performed on the same transects used for the topographic surveys (see above).

Soil/substrate chemical and textural features

We acquired soil/substrate physico-chemical properties from the analysis of composite samples. Each composite sample consisted of two simple 20 cm depth samples, which were collected in the center of the two 15 m stretches inventoried in each wetland. The analyses were performed by the Universidade Federal do Rio Grande do Sul's soil laboratory, based on Embrapa's (1997) protocols. The following variables were obtained: clay, silt, sand, organic matter (O.M.), phosphorus (P), potassium (K), aluminum (Al), calcium (Ca), magnesium (Mg), sulfur (S), zinc (Zn), copper (Cu), boron (B), manganese (Mn), pH in water suspension (pH), potential acidity (Al+H), cation exchange capacity (CEC), sum of bases (SB), base saturation (V), and aluminum saturation (m).

Canopy openness

Canopy openness was estimated by obtaining two hemispherical images per study area at the same soil collection sites (see above). These were taken at ca. 1.3 m above soil/substrate using a Canon Digital EOS Rebel XT camera equipped with a Raynox DCR-CF185PRO fisheye lens and attached to a tripod. Images were obtained on cloudy days, early mornings or late afternoons. The percentage of canopy openness was estimated using the software Gap Light Analyzer (Frazer et al., 1999). With this information, we created two variables: (1) canopy openness, which was the mean percentage of canopy openness – a proxy for light availability; and (2) canopy openness amplitude, which was the difference in canopy openness between the two analyzed images – a surrogate for environmental heterogeneity.

Intensive land use area

We estimated the percentage of intensive land use area within a 100 m radius from the center of the study sites using Google Earth Pro. The procedure consisted basically in calculating the proportion of areas under agricultural use (almost the totality of areas under intensive use) or occupied by roads and edifications – based on images from October 28, 2018. Such areas were generally easily differentiated from natural and conserved environments, but historical images and field observations were used to make decisions in exceptional cases.

Procedures and results of spatial correlation analyses

Procedures

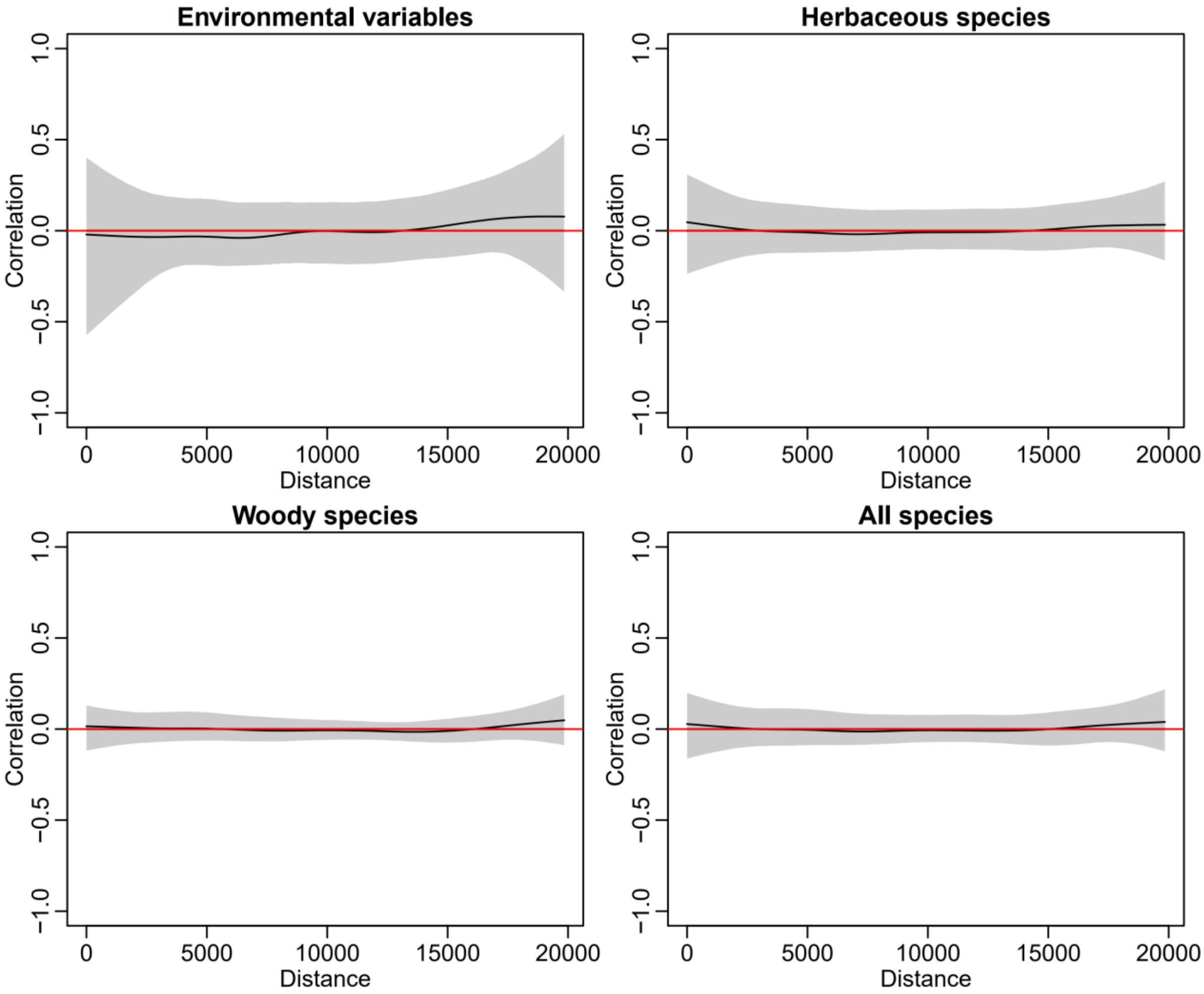
Before performing spatial correlation analyses through spline correlograms, we tested the assumption of second-order stationarity of the abiotic and biotic data described in the main text using trend surface analysis (Borcard et al., 2018). For multivariate data, i.e., the matrix of standardized environmental variables and the matrices of species presence-absence per species group, we employed redundancy analyses, and for univariate data, i.e., alpha diversity parameters, we used multiple linear regression analyses. In all cases, the study areas' abiotic and biotic data were used as response variables and the correspondent geographic coordinates as predictor variables. Trend surface analyses showed that no dataset presented significant trend surface (P <0.05), which means that they did not need to be detrended before being used in correlograms (Borcard et al., 2018).

We then used spline correlograms to test for spatial correlation of the aforementioned abiotic and biotic data using 9,999 bootstrap resamples to calculate 95% confidence envelopes (for more details, see Bjørnstad and Falk, 2001).

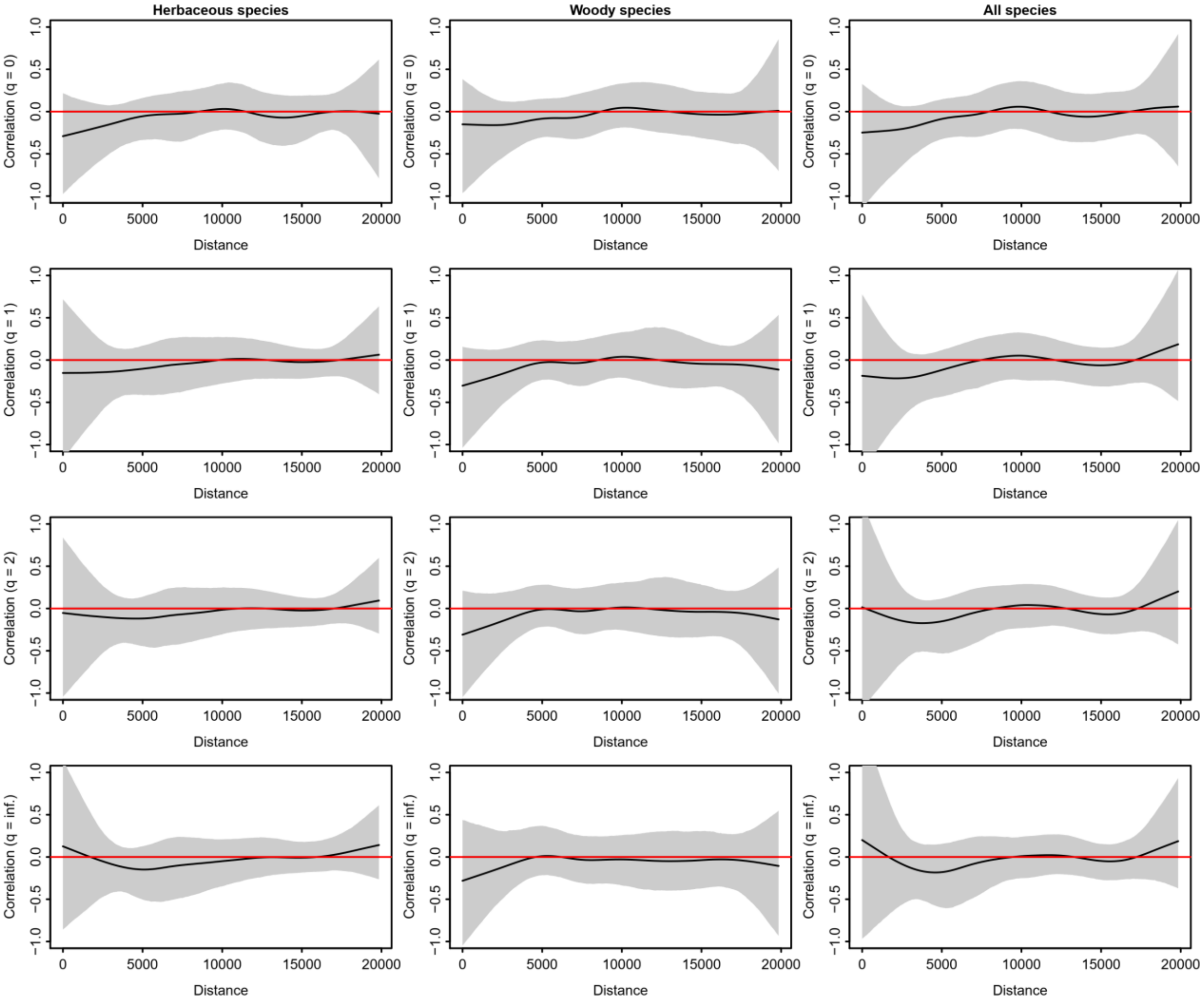
All analyses were performed in R (R Core Team, 2020) using packages 'vegan' (Oksanen et al., 2019) and 'ncf' (Bjørnstad and Cai, 2020).

Results

As showed below, no evaluated dataset presented significant spatial correlation for any spatial distance:



Multivariate spatial correlograms based on environmental variables and plant species composition in ponds, streamside wetlands and riverside wetlands in the upper Uruguay River basin, Southern Brazil. Shaded areas are de 95% bootstrap confidence envelopes. Distance is given in meters.



Univariate spatial correlograms based on alpha diversity parameters of plant species sampled in ponds, streamside wetlands and riverside wetlands in the upper Uruguay River basin, Southern Brazil. Shaded areas are de 95% bootstrap confidence envelopes. Distance is given in meters. *q* = 0, richness; *q* = 1, exponential of Shannon's index; *q* = 2, Simpson's inverse index; *q* = inf. (infinity), Berger-Parker's inverse index.

Table S1 Complementary information on the 24 wetlands studied in the upper Uruguay River basin, Southern Brazil.

Wetland	Water regime	Latitude	Longitude	Altitude (m)	Municipality
P 1	PS	26°55'39"	53°31'05"	575	Descanso
P 2	PS	26°57'40"	53°32'21"	573	Iporã do Oeste
P 3	PS	26°57'59"	53°29'20"	537	Iporã do Oeste
P 4	PS	27°01'25"	53°35'40"	514	São João do Oeste
P 5	PS	27°05'37"	53°34'18"	498	São João do Oeste
P 6	PS	27°06'31"	53°37'03"	483	São João do Oeste
P 7	PS	27°07'38"	53°38'41"	384	Itapiranga
P 8	PF	27°11'17"	53°37'48"	370	Itapiranga
SW 1	PW	26°56'00"	53°29'26"	452	Descanso
SW 2	PW	26°59'25"	53°32'47"	491	Iporã do Oeste
SW 3	PW	27°01'32"	53°30'13"	448	Iporã do Oeste
SW 4	PW	27°02'53"	53°33'23"	367	São João do Oeste
SW 5	PW	27°03'22"	53°36'55"	397	São João do Oeste
SW 6	PW	27°06'23"	53°33'52"	272	São João do Oeste
SW 7	PW	27°07'03"	53°36'14"	296	São João do Oeste
SW 8	PW	27°09'48"	53°37'35"	216	Itapiranga
RW 1	PW	26°55'38"	53°34'08"	381	Santa Helena
RW 2	PW	26°59'57"	53°28'33"	313	Iporã do Oeste
RW 3	PW	27°02'55"	53°31'25"	361	Iporã do Oeste
RW 4	PW	27°04'35"	53°35'11"	334	São João do Oeste
RW 5	PW	27°05'13"	53°38'29"	276	São João do Oeste
RW 6	PW	27°07'02"	53°39'40"	231	Itapiranga
RW 7	PW	27°08'20"	53°36'51"	245	São João do Oeste
RW 8	PW	27°08'27"	53°33'51"	218	São João do Oeste

P, pond; SW, streamside wetland; RW, riverside wetland; PS, permanently saturated (at least in some patches; frequently flooded); PF, permanently flooded (at least in some patches; otherwise permanently saturated); PW, predominantly well-drained (frequently flooded, at least partially).

Table S2 Environmental variables (EVs) in ponds (Ps), streamside wetlands (SWs) and riverside wetlands (RWs) in the upper Uruguay River basin, Southern Brazil, compared though parametric or non-parametric analysis of variance (one-way type-II ANOVAs or Kruskal-Wallis tests, respectively) and pairwise tests (Tukey's HSD or Dunn's tests, respectively). Columns from Ps to RWs show means or medians of data analyzed by parametric or non-parametric tests, respectively, followed by minimum and maximum values between parenthesis. Different superscript letters indicate significant differences (P <0.05).

EV	Ps (n = 8)	SWs (n = 8)	RWs (n = 8)	F	H	df	*P*	Tests used
AE (cm)	-23.1 (-54.1–-8.8)^{c}	53.3 (30.3–73.9)^{b}	105.5 (82.7–125.0)^{a}	158.60		2	**<0.001**	Parametric
Slope (cm)	15.2 (2.0–38.9)^{c}	53.3 (30.3–73.9)^{b}	138.0 (97.9–172.4)^{a}	110.00		2	**<0.001**	Parametric
CO (%)	41.2 (7.6–69.9)^{a}	7.4 (5.1–9.8)^{b}	10.4 (7.4–14.4)^{ab}		11.83	2	**0.003**	Non-parametric
COA (%)[*]	17.4 (2.6–36.6)^{a}	2.4 (0.8–7.0)^{b}	1.5 (0.4–4.2)^{b}	18.27		2	**<0.001**	Parametric
RC (cm)	0.0 (0.0–0.0)^{b}	244.0 (22.0–353.0)^{a}	6.5 (0.0–169.0)^{b}		17.60	2	**<0.001**	Non-parametric
ILUA (%)	11.7 (0.3–64.3)	16.2 (0.0–52.9)	29.4 (26.0–42.7)		1.90	2	0.388	Non-parametric
Altitude (m)	491.8 (370.0–575.0)^{a}	367.4 (216.0–491.0)^{b}	294.9 (218.0–381.0)^{b}	12.24		2	**<0.001**	Parametric
Clay (%)[*]	46.6 (41.0–50.0)^{a}	31.1 (23.0–47.0)^{b}	27.0 (22.0–34.0)^{b}	24.37		2	**<0.001**	Parametric
Silt (%)	49.0 (43.0–54.0)^{a}	31.5 (25.0–33.0)^{b}	29.0 (22.0–32.0)^{b}		16.66	2	**<0.001**	Non-parametric
Sand (%)	4.3 (2.0–9.0)^{b}	38.4 (28.0–45.0)^{a}	44.5 (37.0–52.0)^{a}	156.40		2	**<0.001**	Parametric
pH	4.5 (4.3–4.8)^{b}	5.8 (5.4–6.0)^{a}	5.9 (5.6–6.2)^{a}	82.34		2	**<0.001**	Parametric

P (mg/dm^3)	11.5 (3.6–37.0)	10.5 (7.6–20.0)	6.5 (4.0–12.0)		3.77	2	0.152	Non-parametric
K (mg/dm^3)*	50.3 (22.0–71.0)^b	232.8 (164.0–306.0)^a	154.4 (55.0–298.0)^a	27.45		2	**<0.001**	Parametric
O.M. (%)*	5.6 (3.3–10.0)^a	3.8 (2.7–5.8)^b	3.3 (2.5–4.5)^b	7.46		2	**0.004**	Parametric
Al (cmol$_c$/dm^3)	2.9 (0.7–6.7)^a	0.0 (0.0–0.1)^b	0.0 (0.0–0.0)^b		19.56	2	**<0.001**	Non-parametric
Ca (cmol$_c$/dm^3)	5.9 (2.7–10.3)^b	14.8 (10.7–18.4)^a	15.1 (11.7–20.2)^a	30.1		2	**<0.001**	Parametric
Mg (cmol$_c$/dm^3)	1.3 (0.6–2.8)^c	5.1 (4.2–5.8)^b	6.4 (4.8–8.5)^a	71.44		2	**<0.001**	Parametric
Al+H (cmol$_c$/dm^3)	17.1 (6.9–24.4)^a	3.1 (2.5–4.9)^b	3.3 (2.5–4.4)^b		15.59	2	**<0.001**	Non-parametric
CEC (cmol$_c$/dm^3)	23.8 (17.2–32.3)	24.0 (18.2–29.2)	25.3 (20.6–32.0)	0.28		2	0.759	Parametric
SB (cmol$_c$/dm^3)	7.4 (4.1–13.3)^b	20.5 (15.7–24.8)^a	21.9 (17.1–29.5)^a	43.33		2	**<0.001**	Parametric
V (%)	27.5 (16.0–61.0)^b	86.5 (79.0–89.0)^a	85.5 (80.0–92.0)^a		15.49	2	**<0.001**	Non-parametric
m (%)	31.6 (6.1–59.5)^a	0.0 (0.0–0.5)^b	0.0 (0.0–0.0)^b		19.56	2	**<0.001**	Non-parametric
S (mg/dm^3)*	18.5 (12.0–24.0)^a	12.8 (6.5–23.0)^b	10.3 (7.3–15.0)^b	7.95		2	**0.003**	Parametric
Zn (mg/dm^3)	5.7 (2.4–9.2)^b	12.2 (9.3–15.0)^a	10.0(8.1–14.0)^a	19.25		2	**<0.001**	Parametric
Cu (mg/dm^3)	4.7 (3.0–7.1)	4.9 (3.1–7.9)	5.8 (3.3–8.4)	1.13		2	0.342	Parametric
B (mg/dm^3)*	0.5 (0.3–0.8)	0.4(0.3–0.5)	0.4 (0.2–0.6)	2.92		2	0.076	Parametric
Mn (mg/dm^3)*	12.0 (4.0–28.0)^b	36.3 (21.0–64.0)^a	43.9 (29.0–61.0)^a	20.76		2	**<0.001**	Parametric

AE, average elevation; CO, canopy openness; COA, canopy openness amplitude; RC, rock cover; ILUA, intensive land use area; pH, pH in water suspension; P, phosphorus; K, potassium; O.M., organic matter; Al, aluminum; Ca, calcium; Mg, magnesium; Al+H, potential acidity; CEC, cation exchange capacity; SB, sum of bases; V, base saturation; m, aluminum saturation; S, sulfur; Zn, zinc; Cu, copper; B, boron; Mn, manganese; *, data log-transformed to meet the assumptions of normality and/or homoscedasticity. Significant *P*-values are shown in bolt type.

Table S3 Results of permutational analyses of multivariate dispersions (PERMDISPs), permutational multivariate analyses of variance (PERMANOVAs) and pairwise tests comparing patterns of environmental characteristics and species composition among ponds (Ps), streamside wetlands (SWs) and riverside wetlands (RWs) in the upper Uruguay River basin, Southern Brazil.

	PERMDISP				PERMANOVA			
	df	SS	Pseudo-F	*P* (perm)	df	SS	Pseudo-F	*P* (perm)
Environmental characteristics	2	12.202	10.604	**<0.001**	2	369.680	15.445	**<0.001**
Residuals	21	12.082			21	251.320		
Ps × SWs				**0.008**	1	227.765	15.853	**<0.001**
Ps × RWs				**0.005**	1	288.869	21.894	**<0.001**
SWs × RWs				0.804	1	37.883	4.541	**0.001**
Herbaceous species	2	0.163	30.410	**<0.001**	2	3.246	7.278	**<0.001**
Residuals	21	0.056			21	4.683		
Ps × SWs				**<0.001**	1	2.124	9.412	**<0.001**
Ps × RWs				**0.003**	1	1.819	6.708	**<0.001**
SWs × RWs				**0.004**	1	0.926	5.377	**0.001**
Woody species	2	0.007	0.911	0.412	2	2.468	4.102	**<0.001**
Residuals	21	0.080			21	6.316		

Ps × SWs					1	1.639	5.236	**<0.001**
Ps × RWs					1	1.566	5.200	**<0.001**
SWs × RWs					1	0.496	1.722	**0.011**
All species	2	0.052	11.909	**<0.001**	2	2.897	5.617	**<0.001**
Residuals	21	0.046			21	5.416		
Ps × SWs				**0.004**	1	1.907	7.227	**<0.001**
Ps × RWs				**0.032**	1	1.705	5.970	**<0.001**
SWs × RWs				0.240	1	0.734	3.272	**0.002**

Significant *P*-values (<0.05) are shown in bolt type.

Table S4 Alpha diversity parameters of ponds (Ps), streamside wetlands (SWs) and riverside wetlands (RWs) in the upper Uruguay River basin, Southern Brazil, compared though parametric or non-parametric analysis of variance (one-way type-II ANOVAs or Kruskal-Wallis tests, respectively) and pairwise tests (Tukey's HSD or Dunn's tests, respectively). Columns from Ps to RWs show means or medians of data analyzed by parametric or non-parametric tests, respectively, followed by minimum and maximum values between parenthesis. Different superscript letters indicate significant differences (*P* <0.05).

Species group	Parameter	Ps (n = 8)	SWs (n = 8)	RWs (n = 8)	F	H	df	*P*	Tests used
Herbaceous species	*q* = 0	13.50 (4.00–23.00)^{b}	18.63 (15.00–22.00)^{a}	19.25 (15.00–27.00)^{a}	4.84		2	**0.019**	Parametric
	q =1	5.20 (2.21–14.13)^{b}	10.21 (4.21–11.80)^{a}	8.81 (4.52–17.52)^{ab}		6.32	2	**0.042**	Non-parametric
	q = 2	3.74 (1.75–11.95)	7.38 (2.97–8.60)	6.83 (2.49–14.41)		5.74	2	0.057	Non-parametric
	q = inf.*	3.07 (1.37–7.42)	3.92 (1.91–5.12)	4.39 (1.62–8.37)	1.96		2	0.166	Parametric
Woody species	*q* = 0	4.88 (2.00–8.00)^{b}	14.50 (8.00–18.00)^{a}	18.50 (13.00–28.00)^{a}	28.72		2	**<0.001**	Parametric
	q =1*	2.56 (1.02–4.18)^{b}	8.87 (6.81–11.57)^{a}	10.20 (3.79–18.49)^{a}	26.00		2	**<0.001**	Parametric
	q = 2*	2.10 (1.01–3.33)^{b}	6.65 (4.75–9.01)^{a}	7.89 (2.12–14.71)^{a}	17.63		2	**<0.001**	Parametric
	q = inf.*	1.59 (1.00–2.42)^{b}	3.84 (2.49–5.22)^{a}	4.78 (1.49–8.02)^{a}	12.39		2	**<0.001**	Parametric
All species	*q* = 0	18.38 (6.00–29.00)^{b}	33.13 (27.00–40.00)^{a}	37.63 (30.00–46.00)^{a}	23.57		2	**<0.001**	Parametric
	q =1	7.27 (3.22–16.60)^{b}	14.71 (7.07–20.41)^{a}	16.47 (9.78–26.88)^{a}	9.84		2	**<0.001**	Parametric
	q = 2	5.47 (2.75–13.72)^{b}	9.85 (4.06–14.09)^{ab}	11.47 (3.82–21.07)^{a}	4.84		2	**0.019**	Parametric

	q = inf.	3.49 (1.92–8.29)	4.93 (2.26–7.15)	5.99 (2.02–11.38)	2.63	2	0.096	Parametric

q = 0, richness; q = 1, exponential of Shannon's index; q = 2, Simpson's inverse index, q = inf. (infinity), Berger-Parker's inverse index. *, data log-transformed to meet the assumptions of normality and/or homoscedasticity. Significant *P*-values are shown in bolt type.

Table S5 Species sampled in ponds (Ps), streamside wetlands (SWs) and riverside wetlands (RWs) in the upper Uruguay River basin, Southern Brazil.

Family/Species	Growth form	Ps	SWs	RWs
Acanthaceae				
Dicliptera squarrosa Nees	Woody	X		
Hygrophila costata Nees	Woody	X		X
Justicia brasiliana Roth	Woody		X	X
Justicia carnea Lindl.	Woody		X	X
Justicia floribunda (C.Koch) Wassh.	Woody		X	X
Justicia yhuensis Lindau	Herbaceous		X	
Ruellia angustiflora (Nees) Lindau ex Rambo	Woody	X	X	X
Stenandrium mandioccanum Nees	Herbaceous			X
Amaranthaceae				
Alternanthera micrantha R.E.Fr.	Herbaceous		X	X
Alternanthera reineckii Briq.	Herbaceous	X		
Chamissoa acuminata Mart.	Woody		X	
Anemiaceae				
Anemia phyllitidis (L.) Sw.	Herbaceous	X	X	X

Annonaceae				
Annona rugulosa (Schltdl.) H.Rainer	Woody			X
Apocynaceae				
Tabernaemontana catharinensis A.DC.	Woody			X
Araceae				
Lemna valdiviana Phil.	Herbaceous	X		
Araliaceae				
Hydrocotyle callicephala Cham & Schltdl.	Herbaceous		X	X
Hydrocotyle leucocephala Cham. & Schltdl.	Herbaceous		X	X
Arecaceae				
Syagrus romanzoffiana (Cham.) Glassman	Herbaceous	X	X	X
Aspleniaceae				
Asplenium claussenii Hieron.	Herbaceous		X	
Asplenium inaequilaterale Willd.	Herbaceous		X	X
Asteraceae				
Elephantopus mollis Kunth	Herbaceous			X
Exostigma rivulare (Gardner) G.Sancho	Herbaceous			X

Vernonanthura cf. *divaricata* (Spreng.) H.Rob.	Woody		X	
Athyriaceae				
Diplazium cristatum (Desr.) Alston	Herbaceous		X	X
Diplazium herbaceum Fée	Herbaceous		X	X
Blechnaceae				
Blechnum gracile Kaulf.	Herbaceous			X
Blechnum occidentale L.	Herbaceous			X
Lomariocycas schomburgkii (Klotzsch) Gasper & A.R. Sm.	Herbaceous	X		
Boraginaceae				
Cordia americana (L.) Gottschling & J.S.Mill.	Woody			X
Cordia ecalyculata Vell.	Woody			X
Bromeliaceae				
Bromelia balansae Mez	Herbaceous	X		
Cannaceae				
Canna indica L.	Herbaceous		X	
Cardiopteridaceae				
Citronella paniculata (Mart.) R.A.Howard	Woody			X

Commelinaceae				
Commelina diffusa Burm.f.	Herbaceous	X	X	
Commelina obliqua Vahl	Herbaceous	X	X	X
Tradescantia cymbispatha C.B.Clarke	Herbaceous		X	
Tradescantia fluminensis Vell.	Herbaceous	X	X	X
Tradescantia umbraculifera Hand.-Mazz.	Herbaceous			X
Cyperaceae				
Carex longii Mackenz.	Herbaceous	X		
Carex polysticha Boeckeler	Herbaceous	X		
Carex sellowiana Schltdl.	Herbaceous			X
Cyperus haspan L.	Herbaceous	X		
Cyperus incomtus Kunth	Herbaceous			X
Cyperus luzulae (L.) Retz.	Herbaceous	X		
Cyperus prolixus Kunth	Herbaceous	X		
Eleocharis acutangula (Roxb.) Schult.	Herbaceous	X		
Eleocharis contracta Maury	Herbaceous	X		
Eleocharis montana (Kunth) Roem. & Schult.	Herbaceous	X		

Rhynchospora asperula (Nees) Steud.	Herbaceous	X		
Rhynchospora cf. *conferta* (Nees) Boeckeler	Herbaceous	X		
Rhynchospora cf. *corymbosa* (L.) Britton	Herbaceous	X		
Rhynchospora mariscululus Lindl. & Nees	Herbaceous	X		
Scleria latifolia Sw.	Herbaceous	X		
Dennstaedtiaceae				
Dennstaedtia dissecta T.Moore	Herbaceous		X	
Dennstaedtia globulifera (Poir.) Hieron.	Herbaceous		X	X
Dryopteridaceae				
Ctenitis submarginalis (Langsd. & Fisch.) Ching	Herbaceous		X	X
Didymochlaena truncatula (Sw.) J.Sm.	Herbaceous		X	X
Lastreopsis effusa (Sw.) Tindale	Herbaceous		X	X
Megalastrum connexum (Kaulf.) A.R.Sm. & R.C.Moran	Herbaceous		X	X
Erythroxylaceae				
Erythroxylum deciduum A.St.-Hil.	Woody		X	
Euphorbiaceae				
Acalypha gracilis Spreng.	Woody		X	X

Actinostemon concolor (Spreng.) Müll.Arg.	Woody	X	X	X
Bernardia pulchella (Baill.) Müll.Arg.	Woody			X
Gymnanthes klotzschiana Müll.Arg.	Woody	X	X	X
Sebastiania brasiliensis Spreng.	Woody	X	X	X
Fabaceae				
Calliandra foliolosa Benth.	Woody		X	X
Desmodium affine Schltdl.	Woody		X	
Holocalyx balansae Micheli	Woody	X		
Inga marginata Willd.	Woody		X	X
Lonchocarpus nitidus (Vogel) Benth.	Woody			X
Machaerium stipitatum Vogel	Woody		X	
Muellera campestris (Mart. ex Benth.) M.J. Silva & A.M.G. Azevedo	Woody		X	X
Parapiptadenia rigida (Benth.) Brenan	Woody			X
Hydroleaceae				
Hydrolea elatior Schott	Woody	X		
Juncaceae				
Juncus densiflorus Kunth	Herbaceous	X		

Lamiaceae				
Hyptis cf. *balansae* Briq.	Woody	X		
Hyptis lorentziana O.Hoffm.	Woody	X		
Ocimum carnosum (Spreng.) Link & Otto ex Benth.	Woody			X
Scutellaria racemosa Pers.	Herbaceous	X		
Scutellaria uliginosa A.St.-Hil. ex Benth.	Herbaceous			X
Lauraceae				
Nectandra lanceolata Nees	Woody	X	X	X
Nectandra megapotamica (Spreng.) Mez	Woody		X	X
Ocotea diospyrifolia (Meisn.) Mez	Woody		X	X
Linderniaceae				
Micranthemum umbrosum (Walter ex J.F.Gmel.) S.F.Blake	Herbaceous	X		
Loganiaceae				
Spigelia scabra Cham. & Schltdl.	Herbaceous		X	X
Strychnos brasiliensis Mart.	Woody		X	X
Malvaceae				
Hibiscus striatus Cav.	Woody	X		

Pavonia sepium A.St.-Hil.	Woody		X	X
Marantaceae				
Ctenanthe muelleri Petersen	Herbaceous		X	X
Goeppertia longibracteata (Lindl.) Borchs. & Suárez	Herbaceous		X	X
Melastomataceae				
Leandra australis (Cham.) Cogn.	Woody	X		
Miconia pusilliflora (DC.) Naudin	Woody	X	X	
Meliaceae				
Cabralea canjerana (Vell.) Mart.	Woody		X	
Guarea macrophylla Vahl	Woody		X	X
Trichilia catigua A.Juss.	Woody	X	X	X
Trichilia clausseni C.DC.	Woody		X	X
Trichilia elegans A.Juss.	Woody		X	X
Monimiaceae				
Hennecartia omphalandra J.Poiss.	Woody		X	
Moraceae				
Dorstenia tenuis Bonpl. ex Bureau	Herbaceous		X	

Sorocea bonplandii (Baill.) W.C.Burger et al.	Woody	X	X	X
Myrtaceae				
Calyptranthes concinna DC.	Woody			X
Campomanesia xanthocarpa (Mart.) O.Berg	Woody		X	X
Eugenia burkartiana (D.Legrand) D.Legrand	Woody		X	X
Eugenia hiemalis Cambess.	Woody			X
Eugenia involucrata DC.	Woody			X
Eugenia pyriformis Cambess.	Woody			X
Eugenia uniflora L.	Woody			X
Myrcia cf. *selloi* (Spreng.) N.Silveira	Woody			X
Nyctaginaceae				
Pisonia ambigua Heimerl	Woody			X
Onagraceae				
Ludwigia cf. *grandiflora* (Michx.) Greuter & Burdet	Herbaceous	X		
Ludwigia peruviana (L.) H.Hara	Woody	X		
Ludwigia sericea (Cambess.) H.Hara	Woody	X		
Orchidaceae				

Aspidogyne kuczynskii (Porsch) Garay	Herbaceous		X	
Corymborkis flava (Sw.) Kuntze	Herbaceous		X	
Osmundaceae				
Osmunda spectabilis Willd.	Herbaceous	X		
Piperaceae				
Peperomia balansana C.DC.	Herbaceous			X
Piper amalago L.	Woody		X	
Piper gaudichaudianum Kunth	Woody		X	X
Piper mikanianum (Kunth) Steud.	Woody		X	X
Poaceae				
Dichanthelium superatum (Hack.) Zuloaga	Herbaceous	X		
Hildaea pallens (Sw.) C.Silva & R.P.Oliveira	Herbaceous	X	X	X
Luziola peruviana Juss. ex J.F.Gmel.	Herbaceous	X		
Ocellochloa stolonifera (Poir.) Zuloaga & Morrone	Herbaceous	X		X
Olyra humilis Nees	Herbaceous	X		X
Oplismenus hirtellus (L.) P.Beauv.	Herbaceous	X	X	X
Parodiophyllochloa pantricha (Hack.) Zuloaga & Morrone	Herbaceous	X	X	

Paspalum mandiocanum Trin.	Herbaceous	X		
Pharus lappulaceus Aubl.	Herbaceous	X	X	X
Pseudechinolaena polystachya (Kunth) Stapf	Herbaceous		X	X
Rugoloa pilosa (Sw.) Zuloaga	Herbaceous			X
Rugoloa polygonata (Schrad.) Zuloaga	Herbaceous	X		
Setaria sulcata Raddi	Herbaceous	X		
Steinchisma hians (Elliott) Nash	Herbaceous			X
Steinchisma laxum (Sw.) Zuloaga	Herbaceous	X		X
Trichanthecium schwackeanum (Mez) Zuloaga & Morrone	Herbaceous	X		
Polygonaceae				
Polygonum hydropiperoides Michx.	Herbaceous	X		
Polygonum meisnerianum Cham.	Herbaceous	X		
Polygonum punctatum Elliott	Herbaceous	X		
Ruprechtia laxiflora Meisn.	Woody		X	
Pontederiaceae				
Heteranthera zosterifolia Mart.	Herbaceous	X		
Primulaceae				

Myrsine balansae (Mez) Otegui	Woody		X	X
Pteridaceae				
Adiantopsis radiata (L.) Fée	Herbaceous	X		
Doryopteris concolor (Langsd. & Fisch.) Kuhn	Herbaceous	X		X
Doryopteris patula Fée	Herbaceous	X	X	
Pteris deflexa Link	Herbaceous		X	X
Tryonia myriophylla (Sw.) Schuettp., J.Prado & A.T.Cochran	Herbaceous	X		
Rosaceae				
Prunus myrtifolia (L.) Urb.	Woody			X
Rubiaceae				
Galianthe brasiliensis (Spreng.) E.L.Cabral & Bacigalupo	Woody			X
Galianthe hispidula (A.Rich. ex DC.) E.L.Cabral & Bacigalupo	Herbaceous		X	X
Palicourea mamillaris (Müll.Arg.) C.M.Taylor	Woody	X	X	X
Psychotria carthagenensis Jacq.	Woody	X		X
Psychotria leiocarpa Cham. & Schltdl.	Woody		X	X
Rutaceae				
Balfourodendron riedelianum (Engl.) Engl.	Woody		X	X

Pilocarpus pennatifolius Lem.	Woody		X	X
Salicaceae				
Casearia sylvestris Sw.	Woody	X		
Sapindaceae				
Allophylus edulis (A.St.-Hil. et al.) Hieron. ex Niederl.	Woody		X	X
Allophylus guaraniticus (A. St.-Hil.) Radlk.	Woody		X	X
Cupania vernalis Cambess.	Woody		X	X
Matayba elaeagnoides Radlk.	Woody	X		X
Sapotaceae				
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	Woody		X	X
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	Woody		X	X
Selaginellaceae				
Selaginella muscosa Spring	Herbaceous			X
Selaginella sulcata (Desv. ex Poir.) Spring	Herbaceous			X
Solanaceae				
Brunfelsia pilosa Plowman	Woody		X	
Cestrum strigilatum Ruiz & Pav.	Woody		X	X

Styracaceae				
Styrax leprosus Hook. & Arn.	Woody		X	
Thelypteridaceae				
Amauropelta opposita (Vahl) Pic. Serm.	Herbaceous	X		
Amauropelta regnelliana (C.Chr.) Salino & T.E.Almeida	Herbaceous			X
Christella dentata (Forssk.) Brownsey & Jermy	Herbaceous		X	X
Cyclosorus interruptus (Willd.) H. Ito	Herbaceous	X		
Goniopteris riograndensis (Lindm.) Ching	Herbaceous		X	X
Goniopteris scabra (C.Presl) Brade	Herbaceous		X	X
Urticaceae				
Boehmeria caudata Sw.	Woody		X	X
Boehmeria cylindrica (L.) Sw.	Woody	X		
Pilea pubescens Liebm.	Herbaceous		X	X
Verbenaceae				
Bouchea fluminensis (Vell.) Moldenke	Woody			X
Violaceae				
Pombalia bigibbosa (A.St.Hil.) Paula-Souza	Woody		X	X

The species' occurrence in the different wetland types is indicated by "X". Family names are in accordance with APG IV (2016) and PPG I (2016), while species nomenclature is based on Flora do Brasil (2020) – except for *Hibiscus striatus* Cav., only recently registered in the country (Rigueiral et al., 2019).

Fig. S1 Legally unprotected (lentic) and protected (lotic) wetlands in private lands located in the upper Uruguay River basin, Southern Brazil. In most pond images, water table is omitted by emergent or free-floating macrophytes. Author of the images: Daniel Grasel.

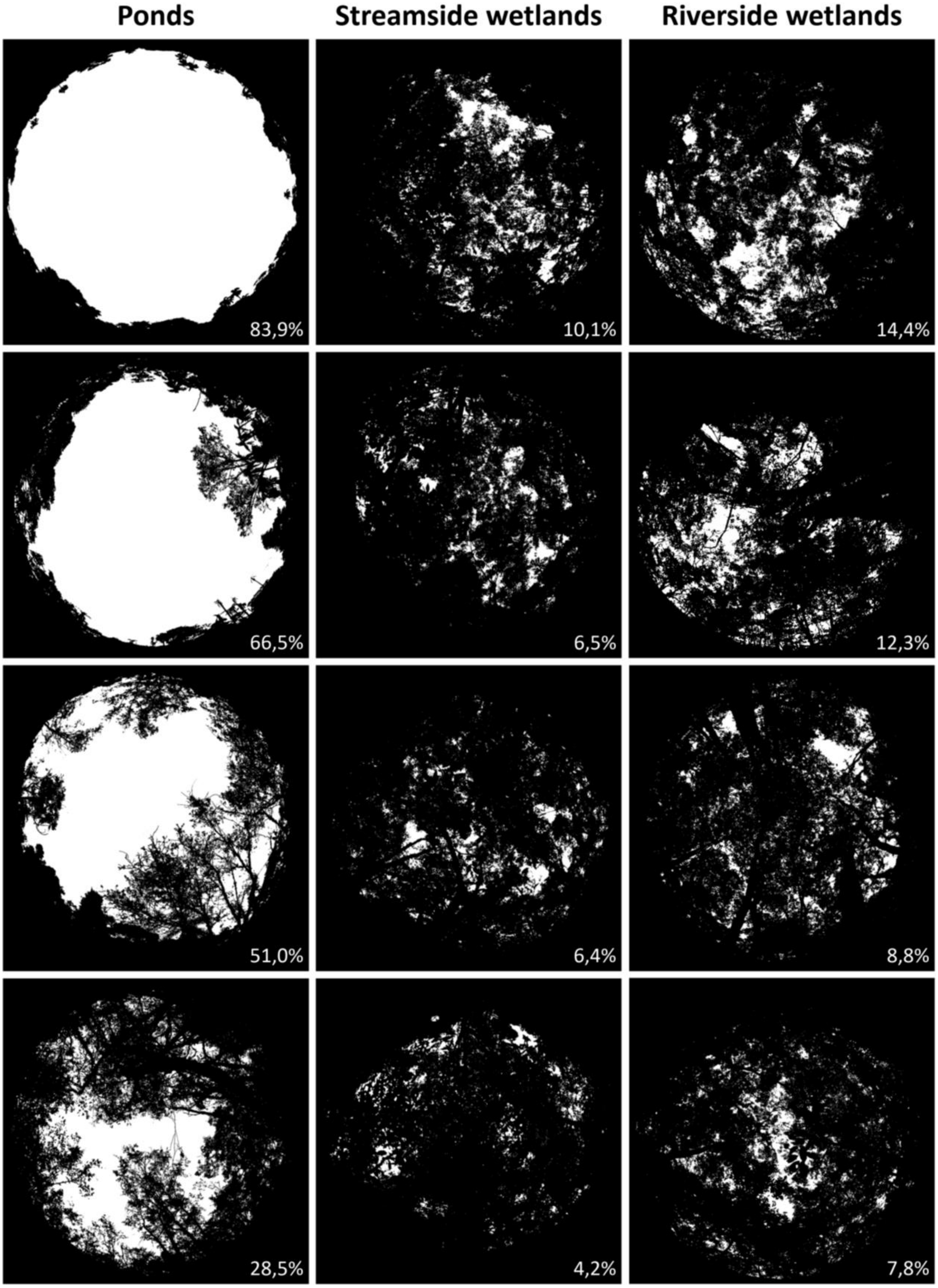


Fig. S2 Hemispherical images of sites with different levels of canopy openness (see percentages in each image) in three wetland types in the upper Uruguay River basin, Southern Brazil. Author of the images: Daniel Grasel.

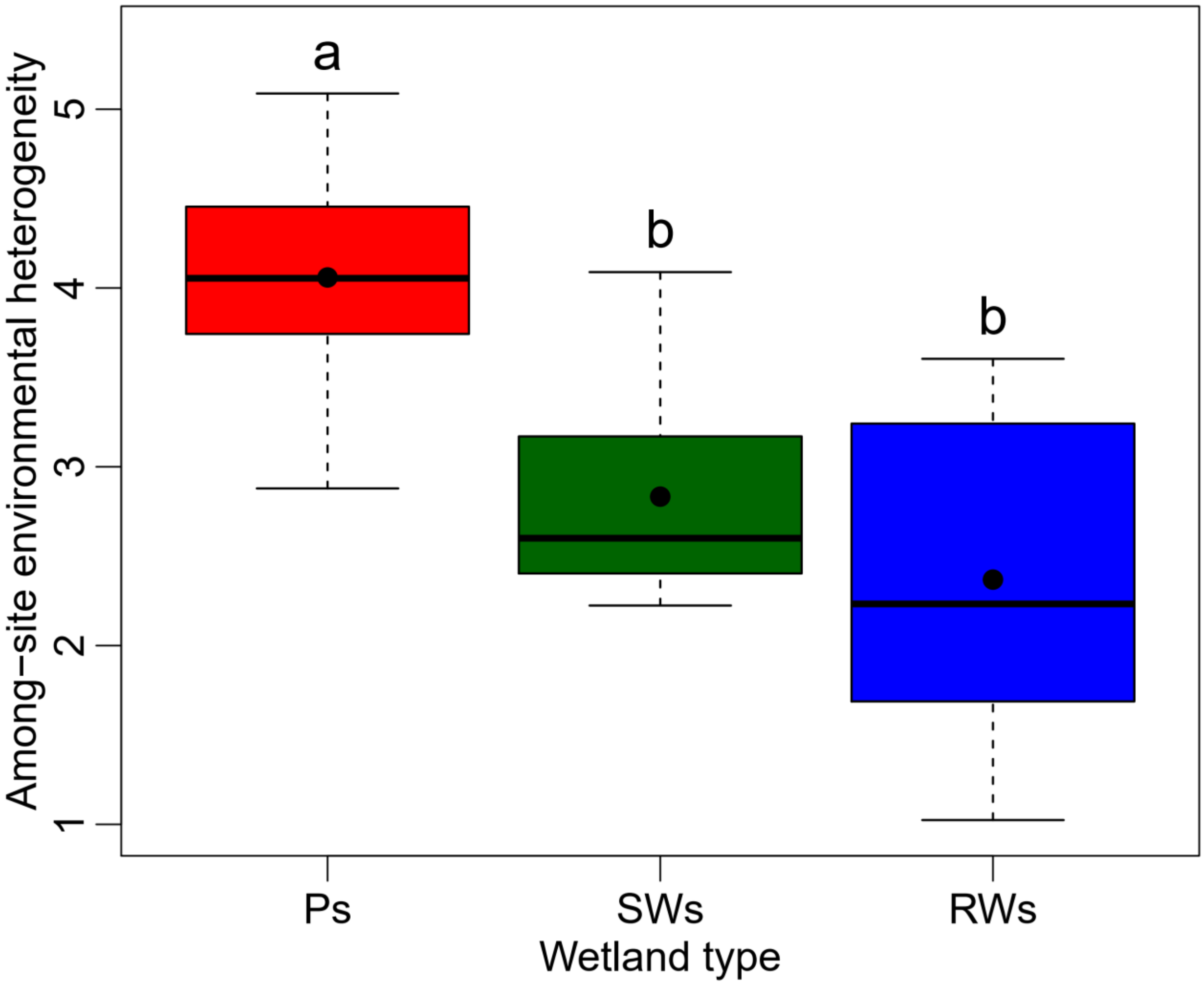


Fig. S3 Boxplots for among-site environmental heterogeneity showing distances to median resulted from permutational analyses of multivariate dispersions (PERMDISPs) comparing ponds (Ps), streamside wetlands (SWs) and riverside wetlands (RWs) in the upper Uruguay River basin, Southern Brazil. Boxes show the 25^{th} and 75^{th} percentiles, medians (thick lines) and means (black dots), while staples indicate the smallest and highest values. Different letters above the top staples indicate significant differences (P <0.05) according to PERMDISP post-hoc tests (see Table S3).

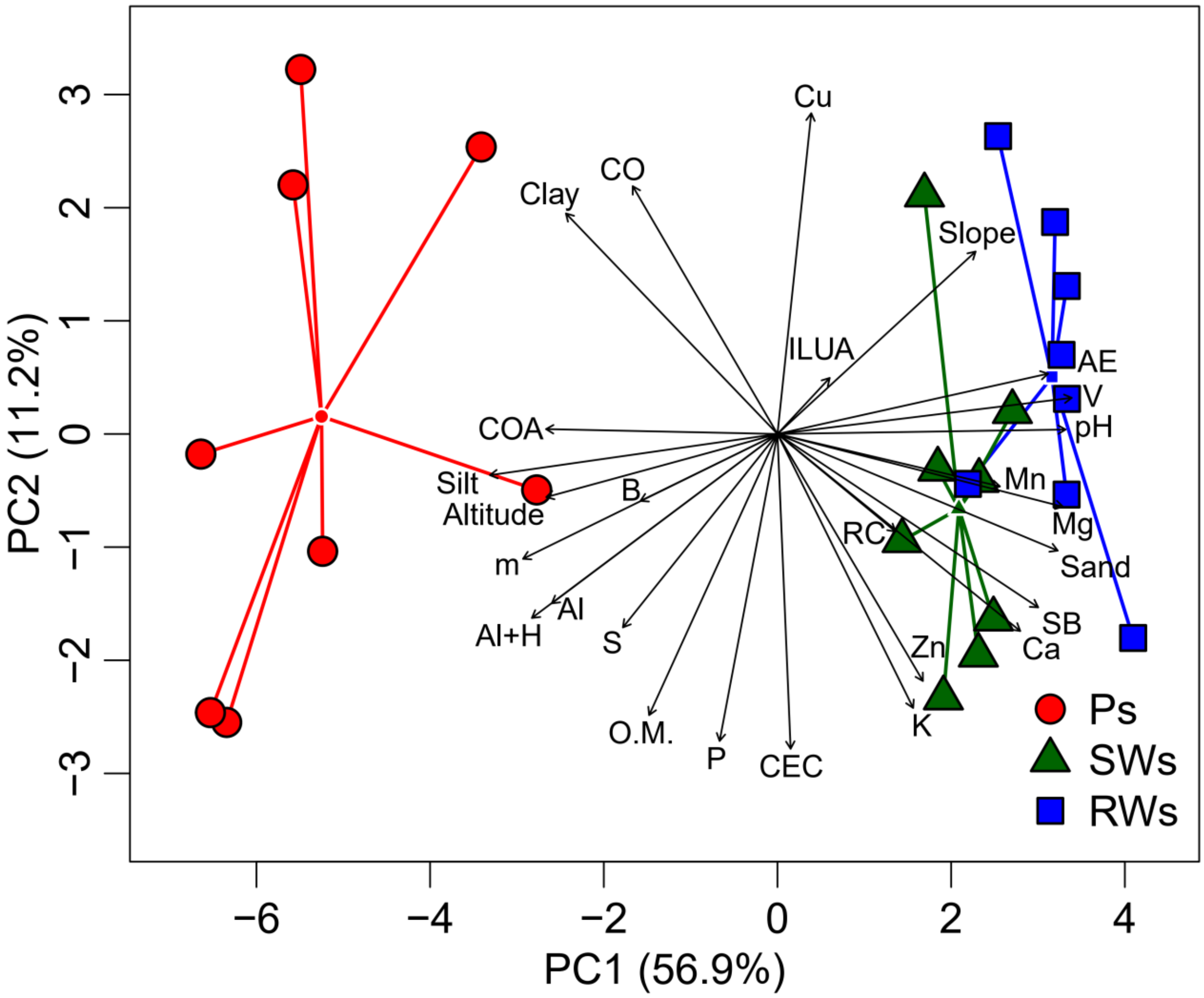


Fig. S4 Principal component analysis (PCA) biplot for environmental variables in ponds (Ps), streamside wetlands (SWs) and riverside wetlands (RWs) in the upper Uruguay River basin, Southern Brazil. The first two axes explain 68.1% of variance. Red green and blue segments connect samples to their group centroids. AE, average elevation; CO, canopy openness; COA, canopy openness amplitude; RC, rock cover; ILUA, intensive land use area; pH, pH in water suspension; P, phosphorus; K, potassium; O.M., organic matter; Al, aluminum; Ca, calcium; Mg, magnesium; Al+H, potential acidity; CEC, cation exchange capacity; SB, sum of bases; V, base saturation; m, aluminum saturation; S, sulfur; Zn, zinc; Cu, copper; B, boron; Mn, manganese.

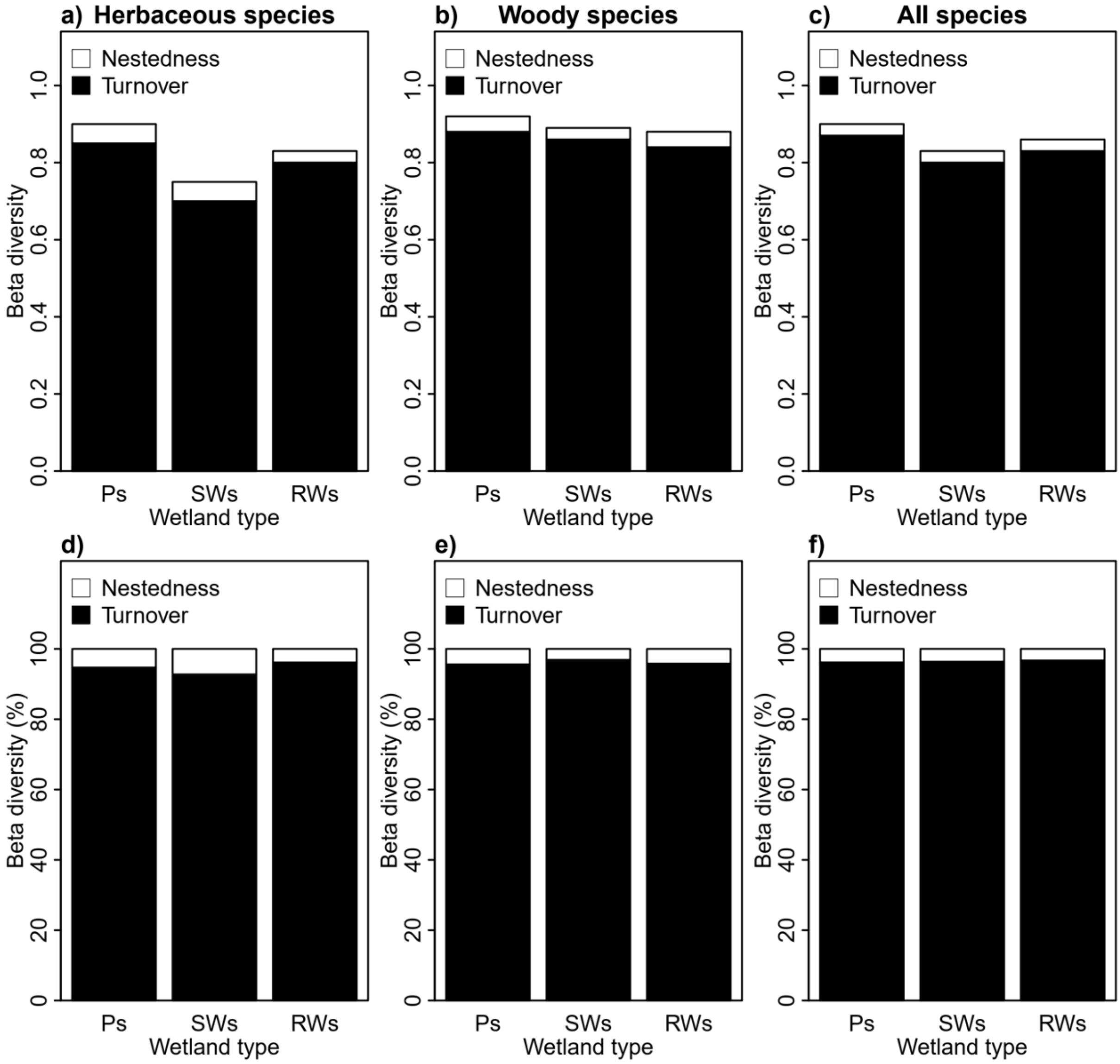


Fig. S5 Contribution of species turnover and nestedness to total beta diversity in ponds (Ps), streamside wetlands (SWs) and riverside wetlands (RWs) in the upper Uruguay River basin, Southern Brazil.

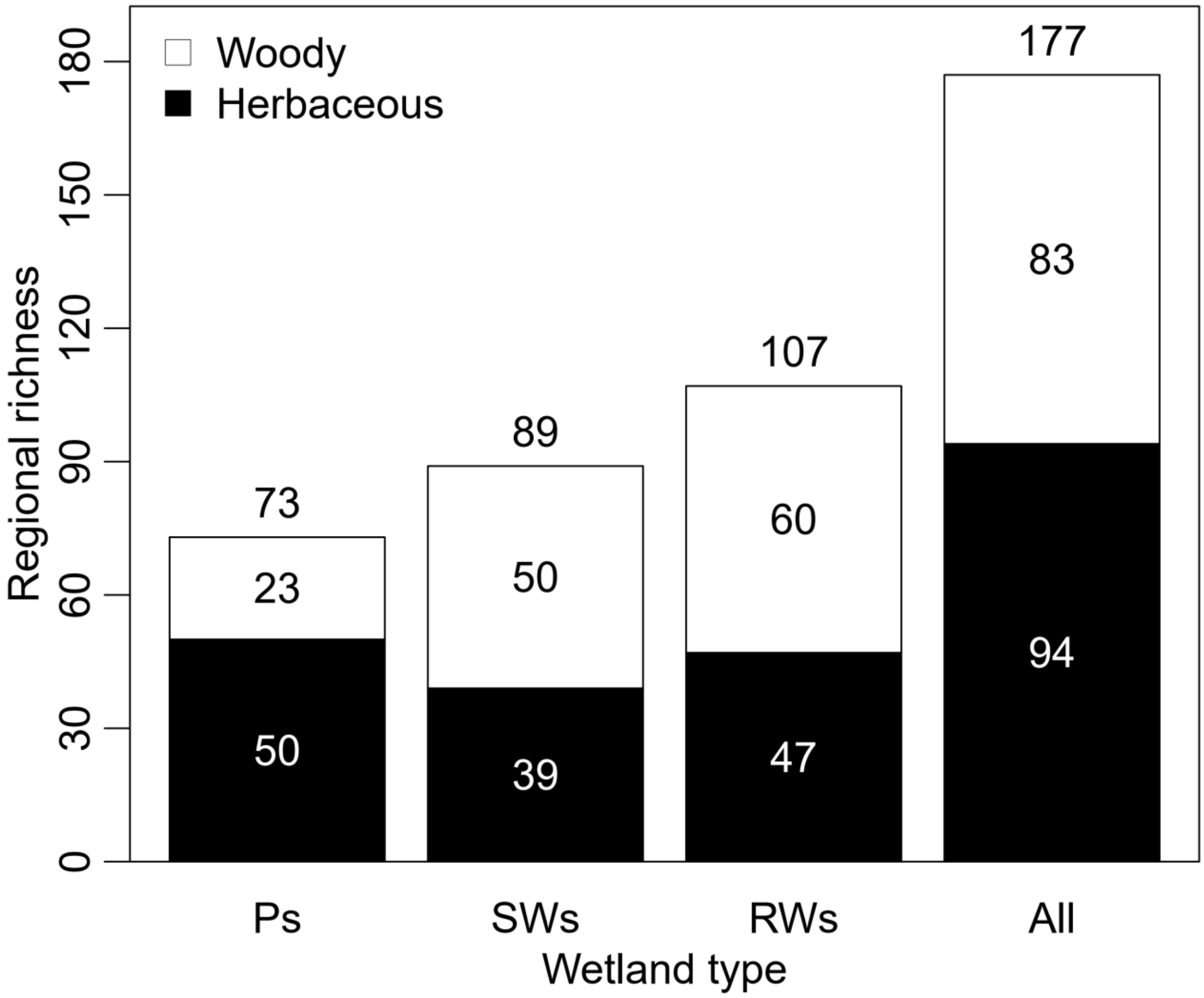


Fig. S6 Observed regional richness in ponds (Ps), streamside wetlands (SWs), riverside wetlands (RWs) and in the global set of wetlands (All) in the upper Uruguay River basin, Southern Brazil.

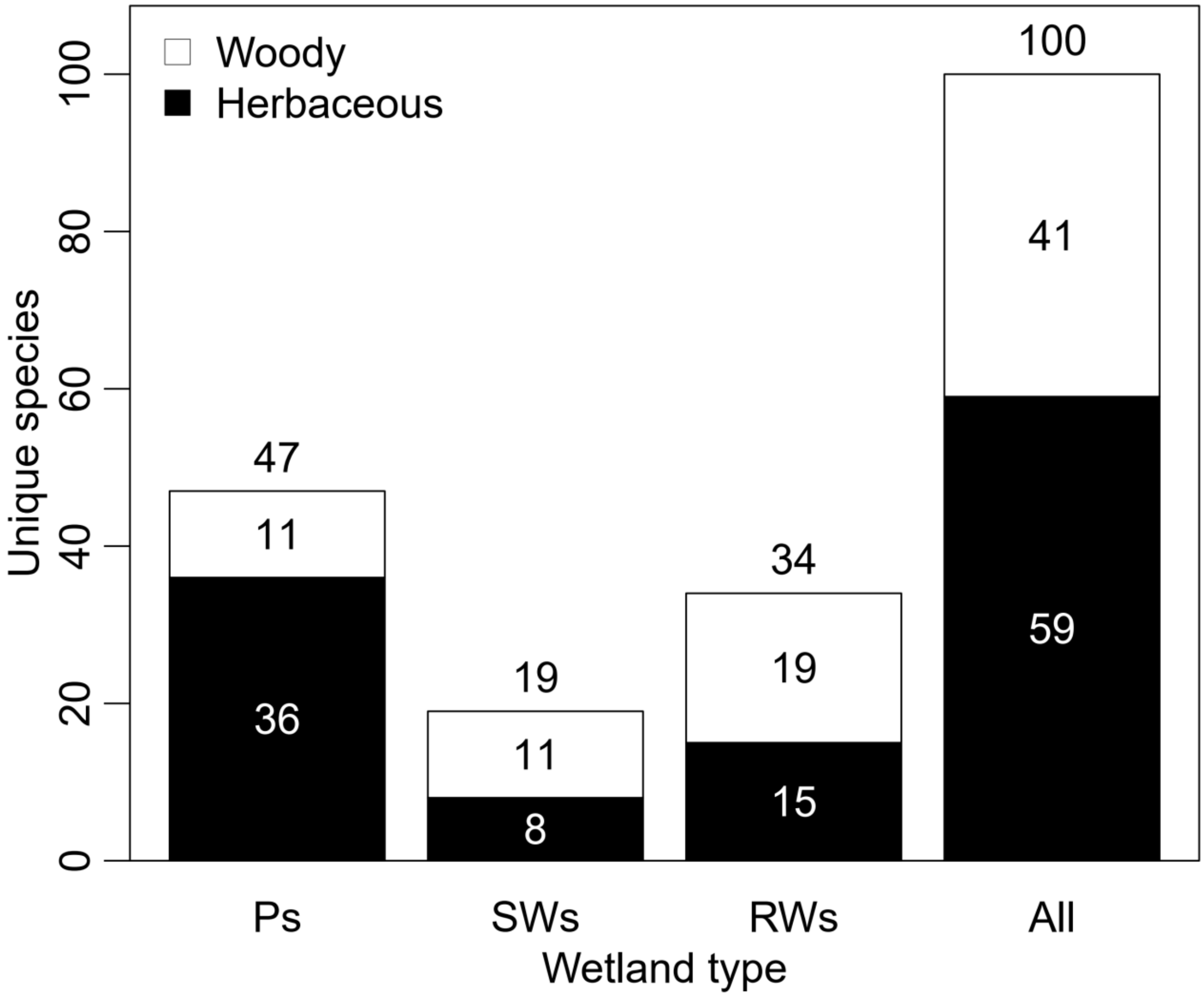


Fig. S7 Number of unique species sampled in ponds (Ps), streamside wetlands (SWs) and riverside wetlands (RWs) and the total number of species exclusive to a specific wetland type (All) in the upper Uruguay River basin, Southern Brazil.

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Manuscrito V

Ponds make pivotal contributions to wetlands' beta and gamma plant diversity but are virtually unprotected by Brazil's private land legislation[V]

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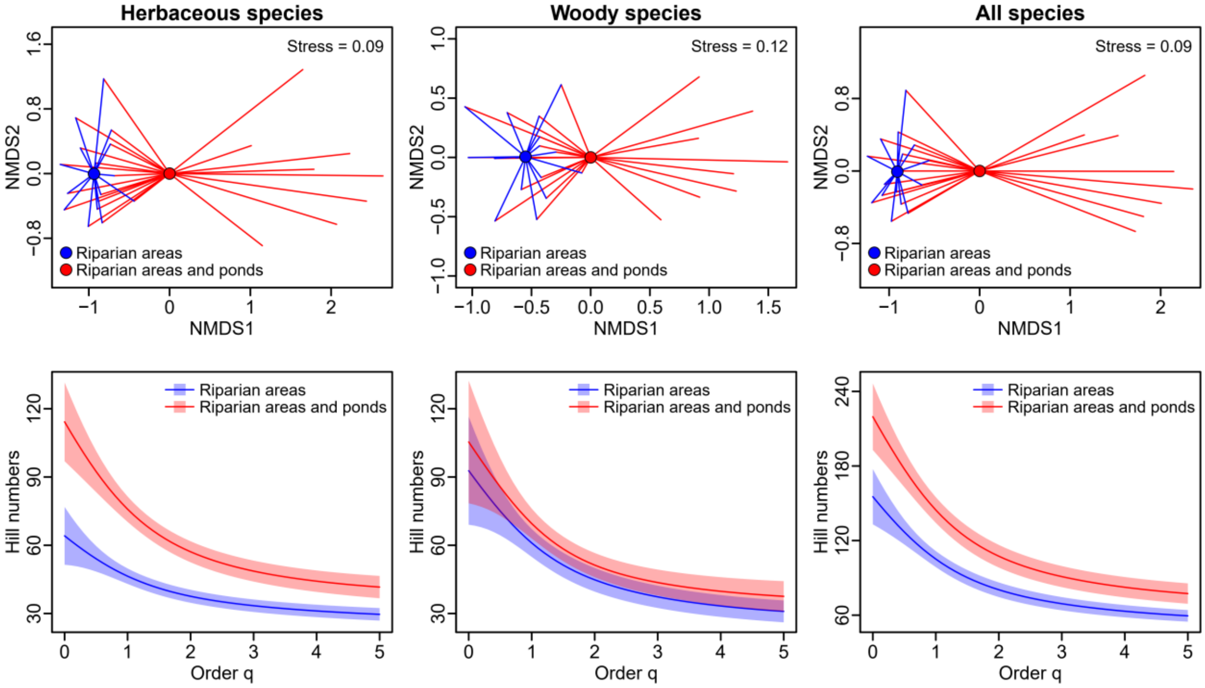
[V] Manuscrito redigido nas normas do periódico *Perspectives in Ecology and Conservation*.

Highlights

- Recently, Brazilian ponds on private lands practically lost their legal protection.
- Do ponds significantly contribute to wetlands' beta and gamma plant diversity?
- Ponds make essential contributions to wetland' beta and gamma plant diversity.
- Brazil's urgently needs to move towards sustainable pond management.

Graphical abstract



Abstract

In 2012, almost all Brazilian ponds on private properties lost their legal protection. Here, we investigated whether ponds contribute significantly to wetlands' beta and gamma plant diversity. In the upper Uruguay River basin, southern Brazil, we sampled herbaceous and woody species in three wetland types largely prevalent in the region: ponds, streamside wetlands and riverside wetlands. The plant communities of riparian areas (SR) were then compared with those of the global set of wetlands (SRP) to enable the assessment of the differential in the diversity estimates promoted by the addition of ponds. To increase our understanding of the plant diversity patterns, we considered herbaceous and woody species separately and together. Results showed that both beta and gamma diversity, except, in the second case, that of woody species, were substantially higher in SRP than in SR, clearly demonstrating the essential contribution of ponds to wetlands' plant diversity. Our findings point to the need for profound changes in Brazil's environmental legislation in order to promote the sustainable management of wetlands.

Keywords Upland-embedded wetlands; Streamside wetlands; Riverside wetlands; Plant biodiversity; Wetland conservation; Environmental legislation.

Introduction

In 2012, Brazilian ponds on private lands suffered hard blows. After revisions to the country's "Forest Code" (Federal Law nº 4,771/1965), which culminated in the Native Vegetation Protection Law (NVPL; Federal Law nº 12,651/2012), almost all of these ecosystems were pushed to the brink. Examples of legislative changes that have put ponds at risk include: (1) removal of the protection of <1 ha ponds; (2) great reduction in requirements for restoration of most converted buffer zones (legally termed "Permanent Preservation Areas" – PPAs); (3) permission to utilize most cleared PPAs for aquaculture; and (4) authorization for the use of alien woody species to restore 50% of PPAs – see details and potential effects of these inadequacies in Brancalion et al. (2016) and Grasel et al. (2018, 2019a,b). Such setbacks were added to problems already existing in the former Forest Code and, to a large extent, retained by the NVPL, as the use of poor wetland-related terms and definitions, which generate great uncertainties about the NVPL's scope (Maltchik et al., 2018; Grasel et al., 2019a), and the provision of insufficient mechanisms for monitoring landholdings' environmental compliance (e.g., Taniwaki et al., 2018).

The aforementioned inadequacies are in dissonance with the growing body of evidence that points to the vital importance of ponds for the conservation of wetland plants at the regional level (Williams et al., 2004; Biggs et al., 2005; Davies et al., 2008; Flinn et al., 2008; Grasel et al., 2020b). Particularly relevant contributions concern the herbaceous component. For example, compared to riparian areas alongside streams and rivers, ponds were shown to present: (1) distinct floristic composition, attributed mainly to their great habitat unicity; (2) higher beta diversity, explained primarily by their high among-site environmental heterogeneity; and (3) comparable or even higher gamma diversity, determined essentially by their high beta diversity (Grasel et al., 2020b; see similar results in: Williams et al., 2004; Davies et al., 2008). Regarding the woody component, ponds were also shown to exhibit (1) the greatest floristic singularity compared to lotic wetlands, but only (2) comparable beta diversity and (3) much lower gamma diversity, limited by the strong selective pressure that swampy conditions impose to these plant group (Grasel et al., 2020b; see similar findings in: Pitman et al., 2014; Draper et al., 2018). Still, despite the modest contributions related to woody communities, the high conservation value of ponds is unquestionable. However, the extent to which ponds support wetlands' plant diversity in a landscape perspective remains largely unknown. Such information is of utmost relevance to subsidize watersheds' sustainable management, especially in view of the negligible protection offered to ponds and the increasing anthropogenic pressure to which these ecosystems have been subjected in Brazil and in other regions of the world (e.g., Calhoun et al., 2017; Grasel et al., 2018; Hill et al., 2018).

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 contemplated three wetland types widely prevalent in the region: ponds, streamside wetlands and riverside wetlands. We then compared the diversity of riparian areas (SR) with that of the global set of wetlands (SRP) so that increases from SR to SRP estimates could only be attributed to ponds. Such analyzes were made considering herbaceous and woody species separately and together. We hypothesized that: (1) beta diversity is greater in SRP than in SR, regardless of the plant group; (2) SRP holds higher gamma diversity than SR, except for woody species.

Material and methods

Study areas

The study was conducted in a transition zone between the semi-deciduous seasonal forest and the evergreen seasonal *Araucaria* forest in the upper Uruguay River basin, Santa Catarina State, Southern Brazil (Oliveira-Filho et al., 2015; Fig. 1). The regional climate is subtropical humid without a pronounced dry season (Alvares et al., 2014); the annual averages of temperature and precipitation are 18-20 °C and 1,900-2,000 mm, respectively (Wrege et al., 2012). The bedrock is basalt and most upland and wetland soils/substrates are eutrophic, but areas such as ponds and adjacent sites show predominantly dystrophic ones (IBGE, 1990; Grasel et al., 2020a,b).

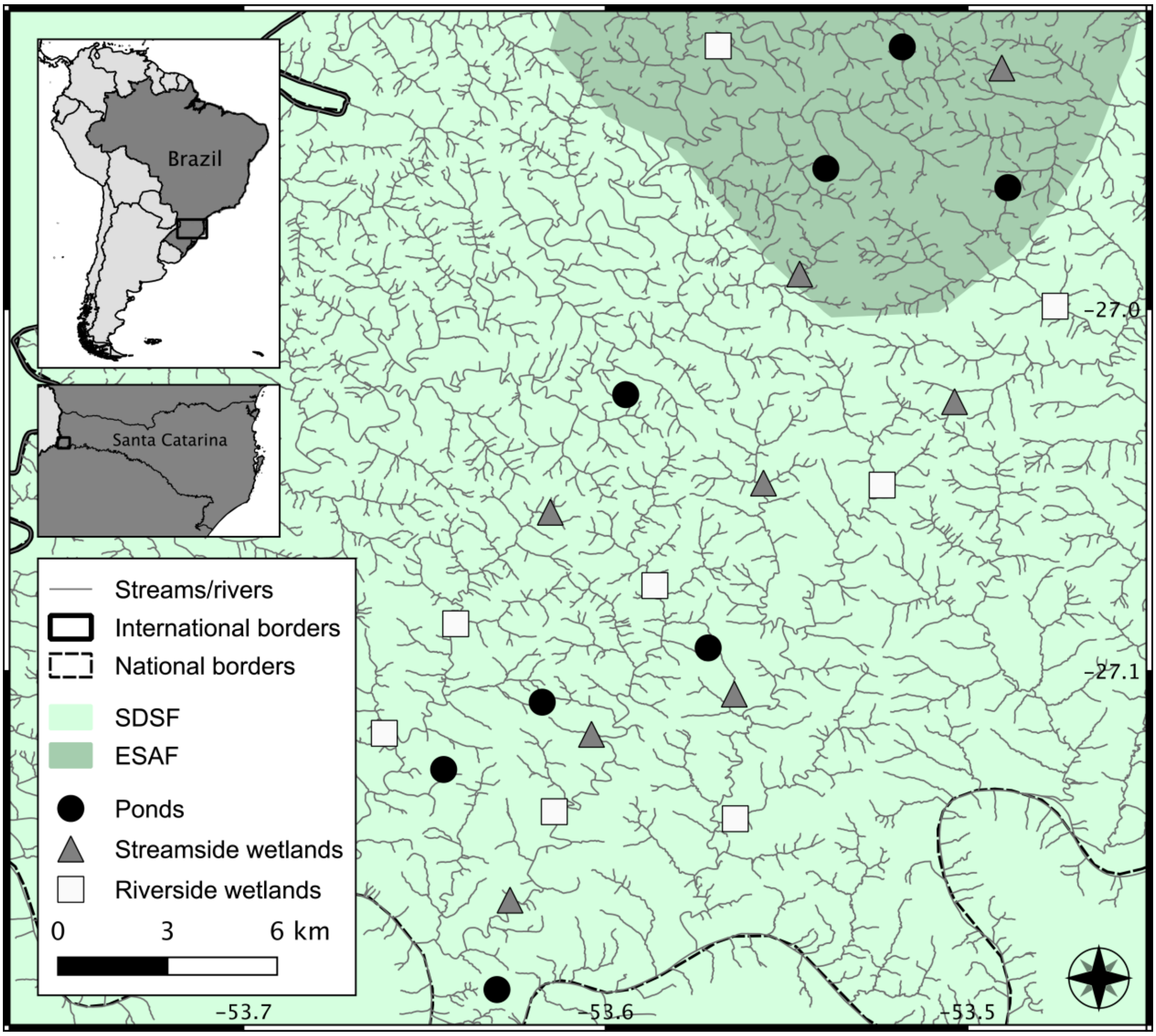


Fig. 1 Location of the study sites in the upper Uruguay River basin, Southern Brazil. SDSF, semi-deciduous seasonal forest; ESAF, evergreen seasonal *Araucaria* forest.

In this region, we first distinguished three widely prevalent natural wetland types: (1) ponds (lentic habitats); (2) streamside wetlands; and (3) riverside wetlands (lotic habitats) – see definitions in Table 1. Next, we chose eight study areas by wetland type based on four criteria: (1) no 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 1,500 m between study sites – the main features of the selected wetland types are shown in Table 1.

Table 1 Definitions and main features of the selected wetlands in the upper Uruguay River basin, Southern Brazil.

Wetland type	Definition and main features
Ponds	Upland-embedded wetlands with ≤2 ha (Biggs et al., 2005). Among the selected ponds, seven are subjected to polymodal and unpredictable flood pulses of short duration (Junk et al., 2014) – i.e., they are only temporarily flooded, but their substrates are waterlogged throughout all the year –, and one is permanently flooded. The vegetation physiognomies of these ecosystems are highly variable within and/or among sites, ranging from predominantly herbaceous to arboreal communities. All ponds are at least partially hummocked, especially in swampy areas. Ponds vary from 0.01 to 0.98 ha (average = 0.30 ha).
Streamside wetlands	Riparian wetlands alongside watercourses ≤7 m wide (Junk et al., 2014; Bubíková and Hrivnák, 2018). As most chosen ponds, streamside wetlands are also subjected to polymodal and unpredictable flood pulses of short duration (Junk et al., 2014). Nevertheless, these ecosystems show well-drained soils during most of the year because they occur in steep areas achieved by inundations only during heavy rainfall events. Streamside wetlands were found to be at least 1 m wide, which was verified through landowner interviews and field observations (e.g., flooding extent during high water levels). All these riparian areas are forested and vegetation is physiognomically little variable. Streams adjacent to the studied riparian areas are intermittent or permanent (none is ephemeral) and have 1.8 to 5 m wide (average = 3.3 m).
Riverside wetlands	Riparian wetlands alongside watercourses >7 m wide (Junk et al., 2014; Bubíková and Hrivnák, 2018). Riverside wetlands share the same features described for streamside wetlands, except that they are at least 4 m wide.

	These areas are adjacent to rivers with 7.6 to 14.1 m wide (average = 10.3 m).

Species survey

Using the line intercept method (Canfield, 1941), we inventoried plants that approximately constitute the herb layer: herbaceous species and ≥0.3–≤1 m high plants of woody species – except bryophyte, climber and epiphyte species (Santos-Junior et al., 2018). In each study site, we recorded the species occurrence in 40 linear meters using a specific sampling protocol for each wetland type due to their abiotic and biotic particularities (see Table 1). In streamside and riverside wetlands, we established 40 and 10 transects of 1 m and 4 m wide, respectively, oriented perpendicular to the watercourses (to their left or right) and distributed equidistantly in 30 m long stretches – as streams and rivers did not exhibit plants that met the inclusion criteria, inventories were not extended to these areas. In ponds, we adopted the same transect length and organization used in riverside wetlands, 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 the summer of 2016-2017 and their identification was made through consults to specialized bibliography, herbaria exsiccates and specialists.

Data analysis

First, we tested whether the species composition data of all plant groups used in the analyses described below were spatially structured using Mantel correlograms – see analyses and results in Appendix A. Given that these tests showed no significant correlation for any distance class, plant communities were considered to be spatially independent. We then explored whether SR and SRP differed in their contributions to beta and gamma plant diversity considering native herbaceous and woody species separately and pooled.

Beta diversity was compared through permutational analyses of multivariate dispersions (PERMDISPs) using 9,999 permutations to assess significance (Anderson, 2006; Anderson et al., 2006). These tests were based on presence-absence data and Jaccard dissimilarity matrices, in line with most similar studies. To visually assess beta diversity patterns, we built violin/box plots based on the wetland groups' distances to median resulted from PERMDISPs and non-metric multidimensional scaling (NMDS) ordinations (optimized for two dimensions) based on matrices with species presence-absence data and the Jaccard dissimilarity index. To explore the underlying processes driving beta diversity, we partitioned the wetland sets' total beta diversity (Jaccard dissimilarity) into nestedness and turnover components.

Gamma diversity was compared using diversity profiles (expressed as Hill numbers) under both the empirical and Chao and Jost's (2015) approach, the latter being a correction for under-sampling bias. These profiles were based on incidence-frequency data, constructed with 95% confidence intervals and generated for q = 0–5, where q = 0, 1 and 2 correspond to richness, the exponential of Shannon's index and the Simpson's inverse index, respectively. Complementarily, we built sample-based interpolation (rarefaction) and extrapolation (up to triple the samples) curves with 95% confidence intervals based on 999 bootstrap replicates. Such curves were also expressed as Hill numbers and generated for q = 0, 1 and 2.

All analyses were performed in R (R Core Team, 2020) using packages 'vegan' (Oksanen et al., 2019), 'betapart' (Baselga et al., 2018), 'SpadeR' (Chao et al. 2016) and 'iNEXT' (Hsieh et al., 2016).

Results

Beta diversity

Beta diversity was greater in SRP than in SR considering all plant groups (Fig. 2; Table S1). Mean distances to median resulted from PERMDISPs were 13.5–24.9% higher for SRP than for SR (see details in Table S2). In all cases, total beta diversity was almost entirely explained by species turnover rather than nestedness (Fig. S1).

Gamma diversity

Gamma diversity was higher in SRP than in SR with respect to all plant groups, except for woody species (Fig. 3). Diversity estimates were 13.6–78.1% higher in SRP than in SR (Table S3). For details on observed and estimated gamma diversity parameters, see Table S3. Species recorded in SR and SRP are shown in Table S4.

Discussion

Results showed that ponds make essential contributions to wetlands' regional plant diversity. Both beta and gamma diversity, except, in the latter case, that of woody species, were significantly higher in SRP than in SR, corroborating our hypotheses. Bellow, we briefly discuss the observed diversity patterns.

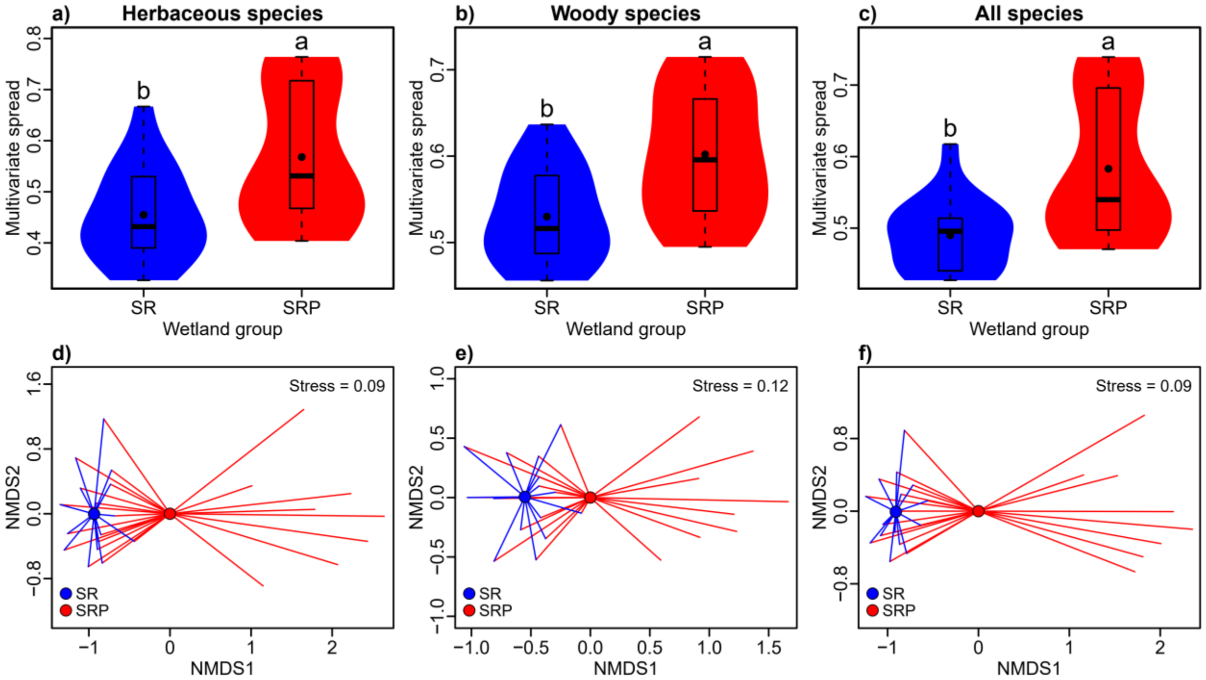


Fig. 2 Beta diversity patterns for riparian areas (streamside and riverside wetlands; SR) and the global set of wetlands (riparian areas and ponds; SRP) sampled in the upper Uruguay River basin, Southern Brazil. a-c) Violin and box plots displaying distances to median resulted from permutational analyses of multivariate dispersions (PERMDISPs). Boxes show the 25th and 75th percentiles, medians (thick lines) and means (black dots), while staples indicate the smallest and highest values. Different letters above the top staples indicate significant differences (*P* <0.05) according to PERMDISPs (see Table S1). d-f) Non-metric multidimensional scaling (NMDS) ordinations. Segments connect samples to their group centroids.

Beta diversity

The greater floristic heterogeneity in SRP than in SR in relation to all plant groups may be essentially attributed to the striking habitat differences between lotic and lentic wetlands. In comparison to riparian areas, ponds were shown to differ in a myriad of environmental features related, for example, to hydrology, soil/substrate physico-chemical

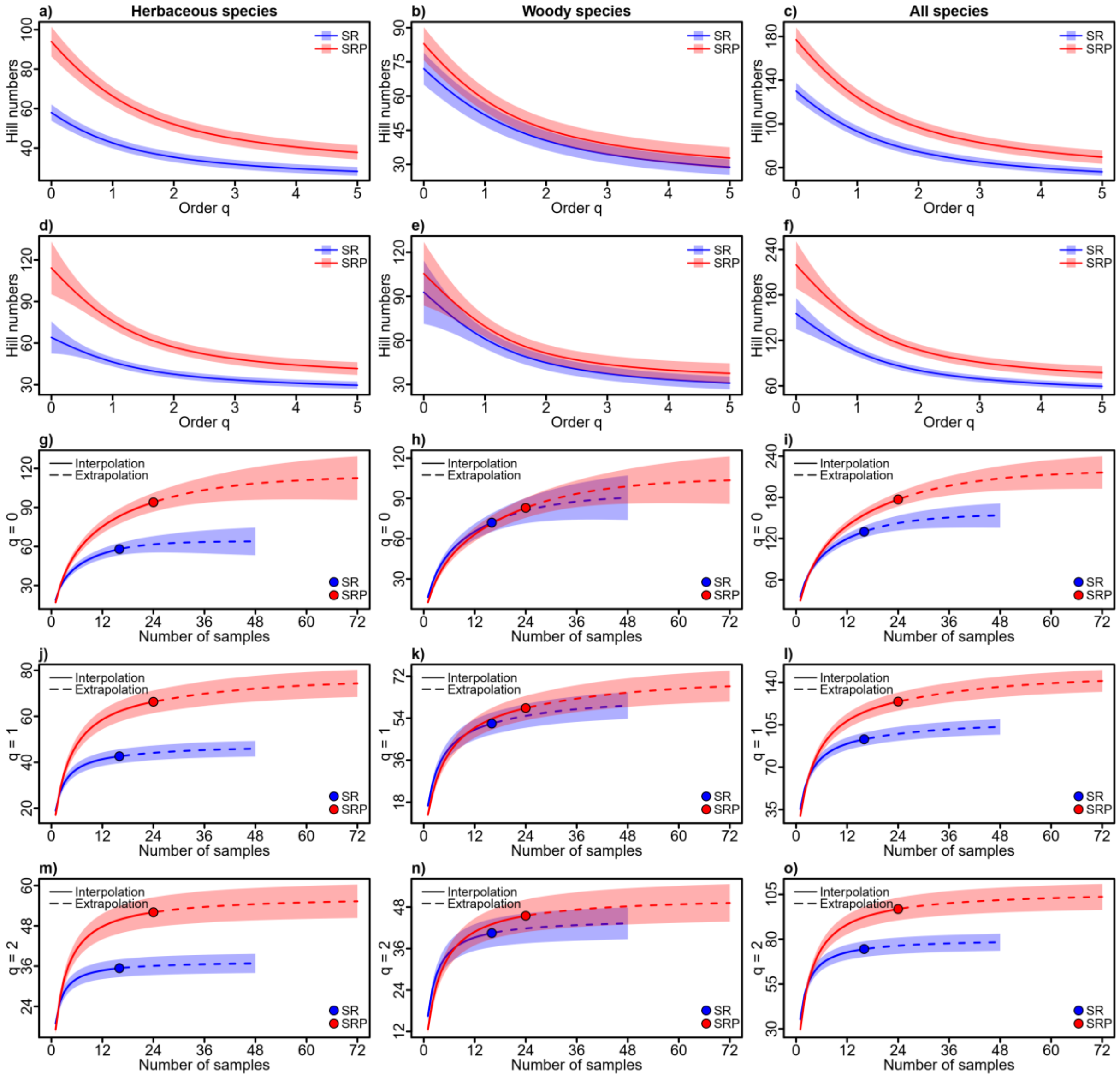


Fig. 3 Gamma diversity patterns for riparian areas (streamside and riverside wetlands; SR) and the global set of wetlands (riparian areas and ponds; SRP) sampled in the upper Uruguay River basin, Southern Brazil. Figures show diversity profiles (a-c) and sample-based interpolation (rarefaction) and extrapolation curves (d-l). Shaded areas indicate the 95% confidence intervals. *Q* = 0, 1 and 2 correspond to richness, the exponential of Shannon's index and the Simpson's inverse index, respectively.

properties and light availability (Giehl and Jarenkow, 2008; Mitsch and Gosselink, 2015; Grasel et al., 2020a,b). Such environments therefore constitute ecological niches very different from those formed by lotic wetlands, promoting the establishment of a particular suite of species from the regional pool and, consequently, making fundamental contributions to wetlands' beta diversity (Davies et al., 2008; Draper et al., 2018; Grasel et al., 2020b).

In addition to their great habitat uniqueness, ponds also present other characteristics that may help explain higher levels of beta diversity in SRP than in SR, including their exceptionally high among-site environmental heterogeneity, varying levels of connectivity with other wetland ecosystems, and high susceptibility to random episodes because of their small sizes (Williams et al., 2004; Scheffer et al., 2006).

Gamma diversity

The increase in herbaceous species' gamma diversity from SR to SRP may be primarily explained by two attributes exhibited by ponds: great floristic singularity and high species turnover. Such characteristics, added to the fact that these ecosystems tend to exhibit only slightly lower or similar alpha diversity indices in comparison to those of lotic systems, ensure that ponds contribute essentially to boost wetland networks' gamma diversity (Williams et al., 2004; Grasel et al., 2020b).

Regarding the woody component, however, the increase in gamma diversity from SR to SRP was not significant. This finding is mainly due to the environmental stressors formed under the water regimes presented by the inventoried ponds, such as substrate anoxia and phytotoxins, which exert strong selective pressure on most woody species of the regional pool (Pezeshki and DeLaune, 2012; Pitman et al., 2014). Therefore, the higher gamma diversity in SRP than in SR with regard to the global set of species is fundamentally explained by the contributions made by herbaceous species.

Final remarks

We showed that ponds make crucial contributions to wetland networks' beta and gamma plant diversity. The imminent degradation and/or conversion of ponds on Brazilian private lands therefore can be expected to generate negative effects on biodiversity, in addition to resulting in the loss of a portfolio of valuable ecosystem services (Cohen et al., 2016; Evenson et al., 2018; Grasel et al., 2020b). This scenario adds to the already high wetland conversion rates in South America (Creed et al., 2017) and the limited effectiveness of Brazil's protected areas in safeguarding wetland ecosystems, since they are biased towards the conservation of terrestrial habitats (Azevedo-Santos et al., 2019). We recommend that Brazil promote adjustments to its environmental legislation in order to provide not only the protection of the remaining ponds, but also strategies that guarantee their effective conservation in the future, such as the implementation of legal mechanisms aimed at their restoration, management, mapping, monitoring and creation. The establishment of an evidence-based national policy focused on wetland conservation is probably the best way to materialize such measures (Junk et al., 2014; Grasel et al., 2018).

Acknowledgments We thank Manueli Blatt Spezia for fieldwork assistance and Luíz Fernando Esser for producing Fig. 1. DG was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Finance Code 001.

Declarations of interest: none.

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Appendix A

Spatial correlation analyses

Analyses

Before performing Mantel correlograms, we tested the assumption of second-order stationarity of all plant groups (herbaceous and woody species treated separately and combined) composition data using trend surface analyses (Borcard et al., 2018). For that, we used redundancy analyzes, in which the binary plant composition data per study area and the respective geographic coordinates were used as response and predictor variables, respectively. These analyses showed that no dataset presented significant trend surface (P <0.05), indicating that data detrending was not necessary before performing correlograms (Borcard et al., 2018).

Then, we performed Mantel correlograms using Jaccard dissimilarity matrices based on species presence-absence data per plant group and a matrix of geographic coordinates. The number of distance classes was computed using Sturge's rule. Mantel statistics were calculated using Pearson's r coefficient and tested for significance using 9,999 permutations – resulting P-values were adjusted by the progressive Holm method.

Analyses were performed in R (R Core Team, 2020) using package 'vegan' (Oksanen et al., 2019).

Results

Results showed that no dataset presented significant spatial correlation (P <0.05) for any distance class:

Mantel correlograms based on plant species composition in ponds, streamside wetlands and riverside wetlands in the upper Uruguay River basin, Southern Brazil. Hollow circles indicate non-significant Mantel statistics.

Results of Mantel correlograms.

			Herbaceous species			Woody species			All species		
DC	CI	ND	MC	*P*	*P* (corrected)	MC	*P*	*P* (corrected)	MC	*P*	*P* (corrected)
1	3,1	64	-0,0653	0,140	0,140	-0,0535	0,188	0,188	-0,0592	0,157	0,157
2	6,1	106	0,0924	0,071	0,141	0,0736	0,120	0,241	0,0919	0,066	0,133
3	9,1	98	-0,0003	0,507	0,507	0,0392	0,252	0,376	0,0088	0,427	0,427
4	12,1	68	0,0138	0,428	0,856	-0,0361	0,273	0,564	0,0012	0,507	0,855
5	15,0	56	0,0534	0,170	0,559	0,0021	0,493	0,756	0,0346	0,271	0,813
6	18,0	54	-0,0346	0,255	0,764	0,0371	0,253	1,000	-0,0081	0,431	1,000
7	21,0	40	-0,0047	0,482	1,000	-0,0533	0,197	1,000	-0,0226	0,362	1,000
8	24,0	40	-0,0346	0,315	1,000	-0,0248	0,358	1,000	-0,0346	0,304	1,000
9	27,0	18	-0,0818	0,106	0,844	0,0096	0,430	1,000	-0,0556	0,201	1,000
10	30,0	8	-0,0089	0,507	1,000	-0,0673	0,160	1,000	-0,0360	0,329	1,000

DC, distance class; CI, class index (lag; in kilometers); ND, number of distances per class; MC, Mantel statistic.

Table S1 Results of permutational analyses of multivariate dispersions comparing riparian areas (streamside and riverside wetlands) with the global set of wetlands (riparian areas and ponds) sampled in the upper Uruguay river basin, Southern Brazil.

	df	SS	Pseudo-F	*P* (perm)
Herbaceous species	1	0.123	8.916	**0.005**
Residuals	38	0.523		
Woody species	1	0.049	11.324	**0.002**
Residuals	38	0.166		
All species	1	0.082	12.158	**0.001**
Residuals	38	0.258		

Significant *P*-values (<0.05) are shown in bolt type.

Table S2 Mean distances to median resulted from permutational analyses of multivariate dispersions comparing riparian areas (streamside and riverside wetlands; SR) with the global set of wetlands (riparian areas and ponds; SRP) sampled in the upper Uruguay river basin, Southern Brazil.

Species group	SR	SRP	Increase	
Herbaceous species	0.455	0.568	0.113	24.9%
Woody species	0.530	0.602	0.072	13.5%
All species	0.490	0.582	0.093	18.9%

“Increase” represents the increase in mean distance to median from SR to SRP, also given in relative values.

Table S3 Observed and estimated gamma diversity values for riparian areas (streamside and riverside wetlands; SR) and the global set of wetlands (riparian areas and ponds; SRP) sampled in the upper Uruguay river basin, Southern Brazil, assessed through diversity profiles (under the empirical and Chao and Jost's (2015) approach; EA and CJA, respectively) and interpolation (rarefaction) and extrapolation curves (IC and EC, respectively).

		Observed – EA and IC				Estimated - CJA				Estimated - EC			
Species group	Parameter	SR	SRP	Increase		SR	SRP	Increase		SR	SRP	Increase	
Herbaceous species	*q* = 0	58.0	94.0	36.0	62.1%	64.1	114.2	50.1	78.1%	64.0	112.6	48.6	76.0%
	q = 1	42.6	66.3	23.7	55.7%	46.4	75.9	29.4	63.5%	45.9	74.3	28.5	62.0%
	q = 2	35.4	52.0	16.7	47.1%	37.6	57.1	19.6	52.1%	36.8	55.3	18.5	50.3%
Woody species	*q* = 0	72.0	83.0	11.0	15.3%	92.8	105.4	12.6	13.6%	90.5	103.6	13.1	14.4%
	q = 1	51.7	58.3	6.6	12.9%	61.0	69.5	8.5	14.0%	59.4	67.7	8.3	14.0%
	q = 2	40.5	45.5	5.0	12.4%	44.8	51.3	6.5	14.4%	43.3	49.2	5.9	13.7%
All species	*q* = 0	130.0	177.0	47.0	36.2%	155.3	219.6	64.3	41.4%	153.7	216.2	62.5	40.7%
	q = 1	93.0	124.2	31.2	33.5%	105.1	144.6	39.5	37.6%	103.2	141.3	38.0	36.9%
	q = 2	74.5	96.9	22.4	30.0%	80.4	107.4	27.0	33.5%	78.4	103.6	25.3	32.3%

"Increase" represents the increase in diversity values from SR to SRP, also given in relative values. *q* = 0, richness; *q* = 1, exponential of Shannon's index; *q* = 2, Simpson's inverse index.

Table S4 Species recorded in riparian areas (streamside and riverside wetlands; SR) and in the global set of wetlands (riparian areas and ponds; SRP) studied in the upper Uruguay River basin, Southern Brazil.

Family/Species	GF	SR	SRP
Acanthaceae			
Dicliptera squarrosa Nees	Woody		X
Hygrophila costata Nees	Woody	X	X
Justicia brasiliana Roth	Woody	X	X
Justicia carnea Lindl.	Woody	X	X
Justicia floribunda (C.Koch) Wassh.	Woody	X	X
Justicia yhuensis Lindau	Herbaceous	X	X
Ruellia angustiflora (Nees) Lindau ex Rambo	Woody	X	X
Stenandrium mandioccanum Nees	Herbaceous	X	X
Amaranthaceae			
Alternanthera micrantha R.E.Fr.	Herbaceous	X	X
Alternanthera reineckii Briq.	Herbaceous		X
Chamissoa acuminata Mart.	Woody	X	X
Anemiaceae			
Anemia phyllitidis (L.) Sw.	Herbaceous	X	X
Annonaceae			
Annona rugulosa (Schltdl.) H.Rainer	Woody	X	X
Apocynaceae			
Tabernaemontana catharinensis A.DC.	Woody	X	X
Araceae			
Lemna valdiviana Phil.	Herbaceous		X
Araliaceae			
Hydrocotyle callicephala Cham & Schltdl.	Herbaceous	X	X

Hydrocotyle leucocephala Cham. & Schltdl.	Herbaceous	X	X
Arecaceae			
Syagrus romanzoffiana (Cham.) Glassman	Herbaceous	X	X
Aspleniaceae			
Asplenium claussenii Hieron.	Herbaceous	X	X
Asplenium inaequilaterale Willd.	Herbaceous	X	X
Asteraceae			
Elephantopus mollis Kunth	Herbaceous	X	X
Exostigma rivulare (Gardner) G.Sancho	Herbaceous	X	X
Vernonanthura cf. *divaricata* (Spreng.) H.Rob.	Woody	X	X
Athyriaceae			
Diplazium cristatum (Desr.) Alston	Herbaceous	X	X
Diplazium herbaceum Fée	Herbaceous	X	X
Blechnaceae			
Blechnum gracile Kaulf.	Herbaceous	X	X
Blechnum occidentale L.	Herbaceous	X	X
Lomariocycas schomburgkii (Klotzsch) Gasper & A.R. Sm.	Herbaceous		X
Boraginaceae			
Cordia americana (L.) Gottschling & J.S.Mill.	Woody	X	X
Cordia ecalyculata Vell.	Woody	X	X
Bromeliaceae			
Bromelia balansae Mez	Herbaceous		X
Cannaceae			
Canna indica L.	Herbaceous	X	X
Cardiopteridaceae			
Citronella paniculata (Mart.) R.A.Howard	Woody	X	X
Commelinaceae			

Commelina diffusa Burm.f.	Herbaceous	X	X
Commelina obliqua Vahl	Herbaceous	X	X
Tradescantia cymbispatha C.B.Clarke	Herbaceous	X	X
Tradescantia fluminensis Vell.	Herbaceous	X	X
Tradescantia umbraculifera Hand.-Mazz.	Herbaceous	X	X
Cyperaceae			
Carex longii Mackenz.	Herbaceous		X
Carex polysticha Boeckeler	Herbaceous		X
Carex sellowiana Schltdl.	Herbaceous	X	X
Cyperus haspan L.	Herbaceous		X
Cyperus incomtus Kunth	Herbaceous	X	X
Cyperus luzulae (L.) Retz.	Herbaceous		X
Cyperus prolixus Kunth	Herbaceous		X
Eleocharis acutangula (Roxb.) Schult.	Herbaceous		X
Eleocharis contracta Maury	Herbaceous		X
Eleocharis montana (Kunth) Roem. & Schult.	Herbaceous		X
Rhynchospora asperula (Nees) Steud.	Herbaceous		X
Rhynchospora cf. *conferta* (Nees) Boeckeler	Herbaceous		X
Rhynchospora cf. *corymbosa* (L.) Britton	Herbaceous		X
Rhynchospora marisculus Lindl. & Nees	Herbaceous		X
Scleria latifolia Sw.	Herbaceous		X
Dennstaedtiaceae			
Dennstaedtia dissecta T.Moore	Herbaceous	X	X
Dennstaedtia globulifera (Poir.) Hieron.	Herbaceous	X	X
Dryopteridaceae			
Ctenitis submarginalis (Langsd. & Fisch.) Ching	Herbaceous	X	X
Didymochlaena truncatula (Sw.) J.Sm.	Herbaceous	X	X

Lastreopsis effusa (Sw.) Tindale	Herbaceous	X	X
Megalastrum connexum (Kaulf.) A.R.Sm. & R.C.Moran	Herbaceous	X	X
Erythroxylaceae			
Erythroxylum deciduum A.St.-Hil.	Woody	X	X
Euphorbiaceae			
Acalypha gracilis Spreng.	Woody	X	X
Actinostemon concolor (Spreng.) Müll.Arg.	Woody	X	X
Bernardia pulchella (Baill.) Müll.Arg.	Woody	X	X
Gymnanthes klotzschiana Müll.Arg.	Woody	X	X
Sebastiania brasiliensis Spreng.	Woody	X	X
Fabaceae			
Calliandra foliolosa Benth.	Woody	X	X
Desmodium affine Schltdl.	Woody	X	X
Holocalyx balansae Micheli	Woody		X
Inga marginata Willd.	Woody	X	X
Lonchocarpus nitidus (Vogel) Benth.	Woody	X	X
Machaerium stipitatum Vogel	Woody	X	X
Muellera campestris (Mart. ex Benth.) M.J. Silva & A.M.G. Azevedo	Woody	X	X
Parapiptadenia rigida (Benth.) Brenan	Woody	X	X
Hydroleaceae			
Hydrolea elatior Schott	Woody		X
Juncaceae			
Juncus densiflorus Kunth	Herbaceous		X
Lamiaceae			
Hyptis cf. *balansae* Briq.	Woody		X
Hyptis lorentziana O.Hoffm.	Woody		X
Ocimum carnosum (Spreng.) Link & Otto ex Benth.	Woody	X	X

Scutellaria racemosa Pers.	Herbaceous		X
Scutellaria uliginosa A.St.-Hil. ex Benth.	Herbaceous	X	X
Lauraceae			
Nectandra lanceolata Nees	Woody	X	X
Nectandra megapotamica (Spreng.) Mez	Woody	X	X
Ocotea diospyrifolia (Meisn.) Mez	Woody	X	X
Linderniaceae			
Micranthemum umbrosum (Walter ex J.F.Gmel.) S.F.Blake	Herbaceous		X
Loganiaceae			
Spigelia scabra Cham. & Schltdl.	Herbaceous	X	X
Strychnos brasiliensis Mart.	Woody	X	X
Malvaceae			
Hibiscus striatus Cav.	Woody		X
Pavonia sepium A.St.-Hil.	Woody	X	X
Marantaceae			
Ctenanthe muelleri Petersen	Herbaceous	X	X
Goeppertia longibracteata (Lindl.) Borchs. & Suárez	Herbaceous	X	X
Melastomataceae			
Leandra australis (Cham.) Cogn.	Woody		X
Miconia pusilliflora (DC.) Naudin	Woody	X	X
Meliaceae			
Cabralea canjerana (Vell.) Mart.	Woody	X	X
Guarea macrophylla Vahl	Woody	X	X
Trichilia catigua A.Juss.	Woody	X	X
Trichilia clausseni C.DC.	Woody	X	X
Trichilia elegans A.Juss.	Woody	X	X
Monimiaceae			

Hennecartia omphalandra J.Poiss.	Woody	X	X
Moraceae			
Dorstenia tenuis Bonpl. ex Bureau	Herbaceous	X	X
Sorocea bonplandii (Baill.) W.C.Burger et al.	Woody	X	X
Myrtaceae			
Campomanesia xanthocarpa (Mart.) O.Berg	Woody	X	X
Eugenia burkartiana (D.Legrand) D.Legrand	Woody	X	X
Eugenia hiemalis Cambess.	Woody	X	X
Eugenia involucrata DC.	Woody	X	X
Eugenia pyriformis Cambess.	Woody	X	X
Eugenia uniflora L.	Woody	X	X
Myrcia cruciflora A.R.Lourenço & E.Lucas	Woody	X	X
Myrcia cf. *selloi* (Spreng.) N.Silveira	Woody	X	X
Nyctaginaceae			
Pisonia ambigua Heimerl	Woody	X	X
Onagraceae			
Ludwigia cf. *grandiflora* (Michx.) Greuter & Burdet	Herbaceous		X
Ludwigia peruviana (L.) H.Hara	Woody		X
Ludwigia sericea (Cambess.) H.Hara	Woody		X
Orchidaceae			
Aspidogyne kuczynskii (Porsch) Garay	Herbaceous	X	X
Corymborkis flava (Sw.) Kuntze	Herbaceous	X	X
Osmundaceae			
Osmunda spectabilis Willd.	Herbaceous		X
Piperaceae			
Peperomia balansana C.DC.	Herbaceous	X	X
Piper amalago L.	Woody	X	X

Piper gaudichaudianum Kunth	Woody	X	X
Piper mikanianum (Kunth) Steud.	Woody	X	X
Poaceae			
Dichanthelium superatum (Hack.) Zuloaga	Herbaceous		X
Hildaea pallens (Sw.) C.Silva & R.P.Oliveira	Herbaceous	X	X
Luziola peruviana Juss. ex J.F.Gmel.	Herbaceous		X
Ocellochloa stolonifera (Poir.) Zuloaga & Morrone	Herbaceous	X	X
Olyra humilis Nees	Herbaceous	X	X
Oplismenus hirtellus (L.) P.Beauv.	Herbaceous	X	X
Parodiophyllochloa pantricha (Hack.) Zuloaga & Morrone	Herbaceous	X	X
Paspalum mandiocanum Trin.	Herbaceous		X
Pharus lappulaceus Aubl.	Herbaceous	X	X
Pseudechinolaena polystachya (Kunth) Stapf	Herbaceous	X	X
Rugoloa pilosa (Sw.) Zuloaga	Herbaceous	X	X
Rugoloa polygonata (Schrad.) Zuloaga	Herbaceous		X
Setaria sulcata Raddi	Herbaceous		X
Steinchisma hians (Elliott) Nash	Herbaceous	X	X
Steinchisma laxum (Sw.) Zuloaga	Herbaceous	X	X
Trichanthecium schwackeanum (Mez) Zuloaga & Morrone	Herbaceous		X
Polygonaceae			
Polygonum hydropiperoides Michx.	Herbaceous		X
Polygonum meisnerianum Cham.	Herbaceous		X
Polygonum punctatum Elliott	Herbaceous		X
Ruprechtia laxiflora Meisn.	Woody	X	X
Pontederiaceae			
Heteranthera zosterifolia Mart.	Herbaceous		X
Primulaceae			

Myrsine balansae (Mez) Otegui	Woody	X	X
Pteridaceae			
Adiantopsis radiata (L.) Fée	Herbaceous		X
Doryopteris concolor (Langsd. & Fisch.) Kuhn	Herbaceous	X	X
Doryopteris patula Fée	Herbaceous	X	X
Pteris deflexa Link	Herbaceous	X	X
Tryonia myriophylla (Sw.) Schuettp., J.Prado & A.T.Cochran	Herbaceous		X
Rosaceae			
Prunus myrtifolia (L.) Urb.	Woody	X	X
Rubiaceae			
Galianthe brasiliensis (Spreng.) E.L.Cabral & Bacigalupo	Woody	X	X
Galianthe hispidula (A.Rich. ex DC.) E.L.Cabral & Bacigalupo	Herbaceous	X	X
Palicourea mamillaris (Müll.Arg.) C.M.Taylor	Woody	X	X
Psychotria carthagenensis Jacq.	Woody	X	X
Psychotria leiocarpa Cham. & Schltdl.	Woody	X	X
Rutaceae			
Balfourodendron riedelianum (Engl.) Engl.	Woody	X	X
Pilocarpus pennatifolius Lem.	Woody	X	X
Salicaceae			
Casearia sylvestris Sw.	Woody		X
Sapindaceae			
Allophylus edulis (A.St.-Hil. et al.) Hieron. ex Niederl.	Woody	X	X
Allophylus guaraniticus (A. St.-Hil.) Radlk.	Woody	X	X
Cupania vernalis Cambess.	Woody	X	X
Matayba elaeagnoides Radlk.	Woody	X	X
Sapotaceae			
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	Woody	X	X

Chrysophyllum marginatum (Hook. & Arn.) Radlk.	Woody	X	X
Selaginellaceae			
Selaginella muscosa Spring	Herbaceous	X	X
Selaginella sulcata (Desv. ex Poir.) Spring	Herbaceous	X	X
Solanaceae			
Brunfelsia pilosa Plowman	Woody	X	X
Cestrum strigilatum Ruiz & Pav.	Woody	X	X
Styracaceae			
Styrax leprosus Hook. & Arn.	Woody	X	X
Thelypteridaceae			
Amauropelta opposita (Vahl) Pic. Serm.	Herbaceous		X
Amauropelta regnelliana (C.Chr.) Salino & T.E.Almeida	Herbaceous	X	X
Christella dentata (Forssk.) Brownsey & Jermy	Herbaceous	X	X
Cyclosorus interruptus (Willd.) H. Ito	Herbaceous		X
Goniopteris riograndensis (Lindm.) Ching	Herbaceous	X	X
Goniopteris scabra (C.Presl) Brade	Herbaceous	X	X
Urticaceae			
Boehmeria caudata Sw.	Woody	X	X
Boehmeria cylindrica (L.) Sw.	Woody		X
Pilea pubescens Liebm.	Herbaceous	X	X
Verbenaceae			
Bouchea fluminensis (Vell.) Moldenke	Woody	X	X
Violaceae			
Pombalia bigibbosa (A.St.Hil.) Paula-Souza	Woody	X	X

Family names are in accordance with APG IV (2016) and PPG I (2016), while species nomenclature is based on Flora do Brasil (2020) – except for *Hibiscus striatus* Cav., not yet registered in this database (but see Rigueiral et al., 2019). GF, growth form; X, species occurrence.

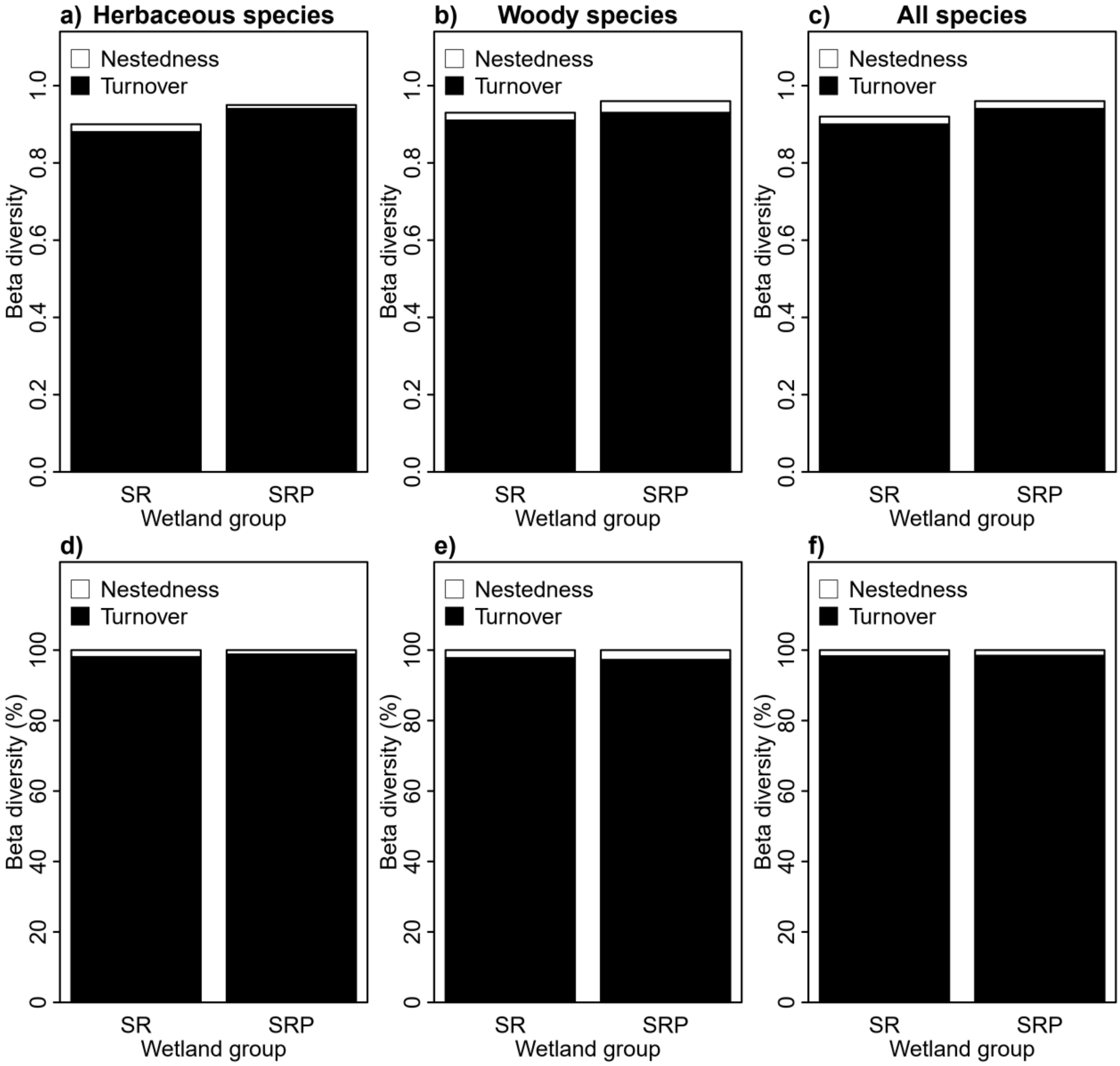

Fig. S1 Partitioning of total beta diversity into turnover and nestedness components for riparian areas (streamside and riverside wetlands; SR) and the global set of wetlands (riparian areas and ponds; SRP) sampled in the upper Uruguay river basin, Southern Brazil.

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Considerações finais

Com esta Tese, contribuí com a identificação e divulgação de políticas e medidas insustentáveis relacionadas à gestão de áreas úmidas no âmbito da LPVN, reforcei a necessidade da sua regulamentação sustentável nos estados, corrigi interpretações equivocadas sobre a suposta proteção que ela confere a todas as áreas úmidas, e realizei pesquisas sobre a biodiversidade vegetal em diferentes tipos de áreas úmidas na bacia do alto Rio Uruguai, a saber, lagoas e áreas ripárias adjacentes a córregos e rios, a fim de criar aporte teórico para a gestão sustentável desses ecossistemas. A maioria das contribuições foram focadas em lagoas, o que se justifica pela excepcional ameaça de degradação e conversão que elas enfrentam, bem como pela sua grande relevância para a conservação da biodiversidade.

As contribuições relacionadas com as pesquisas de campo são provavelmente as primeiras que abordaram coletivamente a biodiversidade vegetal de lagoas e áreas ripárias adjacentes a córregos e rios em escala de paisagem, que contemplaram tanto espécies herbáceas como lenhosas, e que foram realizadas através de protocolos de amostragem padronizados, gerando, portanto, dados inéditos. De modo geral, mostrei que cada tipo de área úmida estudado apresenta padrões únicos de diversidade e composição, contribuindo, assim, de forma singular para a conservação da biodiversidade vegetal, o que implica que a gestão sustentável de áreas úmidas passa necessariamente pela adequada conservação do contínuo de conectividade desses ecossistemas. Além disso, mostrei que lagoas apresentaram a maior singularidade florística, o maior número de espécies herbáceas exclusivas e níveis de diversidade até maiores do que áreas ripárias, evidenciando que a remoção de sua proteção legal é inadequada.

A LPVN representa um grande retrocesso na gestão do patrimônio de áreas úmidas no Brasil. Mesmo que o processo de regulamentação da lei nos estados possibilite que suas inadequações sejam parcialmente suplantadas, é improvável que esse processo por si só resulte em medidas que atendam de forma satisfatória as necessidades de conservação. O Brasil precisa urgentemente de uma política nacional focada na gestão de áreas úmidas e que seja fundamentada no conhecimento científico.

Por fim, vale ressaltar que os dados de campo coletados ainda resultarão em contribuições adicionais, incluindo artigos sobre a diferenciação florística e sobre os determinantes dos padrões de biodiversidade vegetal nas áreas úmidas estudadas.