



Universidade Federal do Rio Grande - FURG
Instituto de Ciências Biológicas
Pós-graduação em Biologia de Ambientes
Aquáticos Continentais



Metacomunidades de macrófitas em áreas úmidas da planície costeira do Rio Grande do Sul

Claudio Rossano Trindade Trindade

Orientadora: Fabiana Schneck

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Aluno: Claudio Rossano Trindade Trindade

Orientadora: Fabiana Schneck

Tese apresentada ao Programa de Pós-Graduação em Biologia de Ambientes Aquáticos Continentais como requisito parcial para a obtenção do título de Doutor em Biologia de Ambientes Aquáticos Continentais.

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ATA DE DEFESA DE TESE DE DOUTORADO EM BIOLOGIA DE AMBIENTES AQUÁTICOS CONTINENTAIS – Nº 004/2025

Às 14h (quatorze horas) do dia 05 (cinco) do mês de setembro de 2025 (dois mil e vinte e cinco), via Webconferência no endereço eletrônico: (<https://meet.google.com/xtz-zpsd-yyi>) reuniram-se docentes, discentes e comunidade em geral, para a Defesa Pública da Tese de Doutorado do acadêmico **Claudio Rossano Trindade Trindade**. A Tese intitulada “**Metacomunidades de macrófitas em áreas úmidas da planície costeira do Rio Grande do Sul**” foi avaliada pela Banca Examinadora composta pela Profª. Dra. Fabiana Schneck (Orientadora); Profº Dr. Leonardo Maltchik Garcia (FURG); Profª Dra. Priscilla de Carvalho (UFG) e Profº Dr. Andre Andrian Padial (UFPR). Após a defesa e arguição pública, a Banca Examinadora reuniu-se, para deliberação final, e considerou o acadêmico **APROVADO**. Desta forma, o acadêmico concluiu mais uma das etapas necessárias para a obtenção do grau de **DOUTOR EM BIOLOGIA DE AMBIENTES AQUÁTICOS CONTINENTAIS**. Nada mais havendo a tratar, às 17h40 (dezessete horas e trinta minutos) foi lavrada a presente ata, que lida e aprovada, foi assinada pelos membros da Banca Examinadora, pelo Acadêmico e pelo Coordenador adjunto do Curso.

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Poema NO FUNERAL DO BANHADO* de Joseti Gomes

Os olhos grandes da lua
vêm deitar sobre o silêncio
dos passos largos da noite...

O banhado sempre em festa,
hoje vestiu-se de luto
e calou-se por respeito
no leito do capinzal.
Irmanados no escuro
com o permissão das águas,
das corticeiras e juncos,
os sorros, lontras, capinchos
sofrem, sem um cochicho,
na noite do funeral.

Alguns partiram pra sempre
levando mais que seus gritos.
Eram lamentos, pedidos,
nos discursos pra ninguém...
Das margens vinham
anúncios
devastando a paz local.
Arrozais se agigantando,
invadindo sem piedade
a varanda onde dormiam
lagartos e tartarugas
que vinham beber do sol.

Não muito longe, o barulho
da força de alguns motores
vinha com tanta gula
drenando o sabor das águas,
abrindo canais profundos
e deixando cicatriz,
modificando o cenário
de folhas, flores e galhos
despidos do verde viço
agora, lama e raiz.

De um moirão, adoentado,
o chimango insistente
revezava com a coruja
o posto de sentinela,
enquanto em voos rasantes
o quero-quero, cantando,
anunciava a chegada
da fria devastação.
E num ensaio sentido
revoavam outras penas
assinalando cautela.
Ninguém conseguia
entender...

Todos prevendo a tristeza
foram perdendo a beleza
das manhãs alvorotadas.
Que triste era o olhar
do cardeal do banhado!
Um príncipe encurralado
que agora fica bombeando
um vão motivo qualquer
que justifique a matança
dos bichos desse lugar.

Estáticas, não distraídas,
garças de pernas compridas
são mastros para as
bandeiras
de uma paz tão desejada.
Colcha branca, encabulada,
na superfície que esconde
muitos seres submersos,
clamando por mais um dia
na luta da própria vida.
Nesta noite tão silente
não haverá pastoreio.

A caça foi abolida.
Ninguém dorme nesta hora.
Se alguns foram embora
há que se ter o respeito!
O homem é o predador
mais temido e mais feroz,
por isso calou-se a voz
num protesto por direitos.

A lua deixa seu brilho
escorrer nos pingos tristes
da chuva de terno negro.
Chega molhando o silêncio
desses que sofrem calados.
Os sapos, desesperados,
não resistindo essa dor
ecoam em melodias
os seus gritos de agonia
no funeral do banhado.

Pra onde irão esses juncos,
os aguapés, as boiadeiras?
Pra onde irão tantas penas,
tantas cores, tantos pios?
Por certo, ninhos vazios
irão servir de morada
pras lembranças
descascadas

dos senhores arrozeiros.
Se vivem só pro dinheiro,
reféns do dito consumo,
há muito perderam o rumo
e já não bebem da alma.

Que o céu abra as cancelas,
para cair mil estrelas que
a muito também morreram.
Que o homem, ao acordar,
se aperceba, envergonhado,
dos desvarios de seus atos.
E que Deus, benevolente,
conceda mais que o indulto
pros que negaram o luto
dessa paisagem antiga
que agoniza nas cantigas
dos sapos, desesperados!

* Poema escrito a partir dos
relatos e registros
fotográficos dos trabalhos de
campo que deram origem a
esta tese. Participou e foi
publicado no festival "Seival
da Música Instrumental e
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RESUMO

A Teoria de Metacomunidades tornou-se um dos grandes temas da Ecologia, possibilitando o entendimento de fatores que influenciam a dinâmica e a estrutura de comunidades biológicas em diferentes escalas, no espaço e no tempo. Minha tese avaliou questões relacionadas a metacomunidades de macrófitas aquáticas em áreas úmidas da planície costeira do estado do Rio Grande do Sul (PCRS), no sul do Brasil. Especificamente, estruturei a escrita em dois capítulos com os seguintes objetivos: i) analisar os Elementos da Estrutura de Metacomunidades (EMS) de macrófitas de áreas úmidas da PCRS, para a identificação de qual tipo de metacomunidade prevalece na planície costeira e suas relações ambientais e climáticas; ii) avaliar a contribuição local (LCBD; i.e. singularidade composicional) e a contribuição das espécies (SCBD) para a diversidade beta regional das metacomunidades de macrófitas aquáticas de áreas úmidas da PCRS e suas correlações ambientais e climáticas. Para isso realizei as coletas de dados entre janeiro e fevereiro de 2016 em 29 áreas úmidas ao longo dos 640 km de extensão da PCRS, onde, *in situ*, fiz o levantamento das espécies de macrófitas e coletei os dados ambientais (físicos e químicos) e, posteriormente, obtive os dados climáticos de toda a extensão da planície costeira. No primeiro capítulo, observei que a metacomunidade, influenciada pela temperatura média anual e pelo fósforo total, apresentou um padrão de distribuição Clementsiano, caracterizado pela distribuição em blocos discretos de espécies. Com relação aos grupos funcionais, verifiquei que as espécies emergentes apresentaram um padrão Clementsiano, também influenciadas pela temperatura média anual. Já as espécies flutuantes, influenciadas pelo fósforo total e pela altitude, apresentaram uma estrutura aninhada quase estocástica, enquanto as espécies submersas, determinadas pela temperatura média anual, exibiram um padrão Gleasoniano com distribuições contínuas ao longo da planície costeira. No segundo capítulo, encontrei que a singularidade composicional das comunidades de macrófitas não apresentou uma estrutura espacial clara, sendo positivamente relacionada à singularidade química da água e negativamente à temperatura média do trimestre mais seco. A contribuição das espécies para a diversidade beta foi maior para espécies flutuantes do que para emergentes e submersas. Além disso, o SCBD apresentou correlação com variáveis climáticas e relação positiva com a ocorrência de espécies, sugerindo que espécies com maior frequência de ocorrência contribuem mais para a diversidade beta regional. Com base nos achados nos dois capítulos foi possível identificar e compreender melhor os padrões que determinam a organização espacial das comunidades de macrófitas nas

áreas úmidas da PCRS, evidenciando a importância de preditores ambientais e climáticos na estruturação das comunidades, demonstrando que diferentes grupos funcionais respondem de maneira distinta a gradientes ambientais. Além disso, foi possível identificar os locais e as espécies mais importantes para a diversidade beta regional, contribuindo assim para o avanço do conhecimento. Por fim, esses achados ampliam nossa percepção sobre a ecologia de metacomunidades e, além disso, poderão ser úteis para a proteção e/ou conservação das áreas úmidas.

Palavras-chave: vegetação de áreas úmidas, distribuição espacial, diversidade beta, LCBD; SCBD; EMS, bioma Pampa.

ABSTRACT

The Metacommunity Theory has become one of the major themes in Ecology, enabling the understanding of factors that influence the dynamics and structure of biological communities across different spatial and temporal scales. My thesis addressed questions related to macrophyte metacommunities in wetlands of the coastal plain of the state of Rio Grande do Sul (PCRS), in southern Brazil. Specifically, I structured the writing into two chapters with the following objectives: i) to analyze the Elements of Metacommunity Structure (EMS) of macrophytes in wetlands of the PCRS, in order to identify which type of metacommunity prevails in the coastal plain and its environmental and climatic relationships; ii) to assess the local contribution (LCBD; i.e., compositional uniqueness) and the species contribution (SCBD) to the regional beta diversity of aquatic macrophyte metacommunities in wetlands of the PCRS and their environmental and climatic correlations. To this end, I conducted data collection between January and February 2016 in 29 wetlands along the 640 km extension of the PCRS, where, *in situ*, I surveyed aquatic macrophyte species and collected environmental data (physical and chemical) and later obtained climatic data for the entire extent of the coastal plain. In the first chapter, I observed that the metacommunity, influenced by mean annual temperature and total phosphorus, exhibited a Clementsian distribution pattern, characterized by discrete blocks of species distribution. Regarding the functional groups, I found that emergent species exhibited a Clementsian pattern, also influenced by mean annual temperature. Floating species, influenced by total phosphorus and altitude, showed a nearly stochastic nested structure, while submerged species, determined by mean annual temperature, displayed a Gleasonian pattern with continuous distributions along the coastal plain. In the second chapter, I found that the compositional uniqueness of macrophyte communities did not show a clear spatial structure, being positively related to water chemistry uniqueness and negatively related to the mean temperature of the driest quarter. Species contributions to beta diversity were higher for floating species than for emergent and submerged species. Furthermore, SCBD was correlated with climatic variables and showed a positive relationship with species occurrence, suggesting that species with higher frequency occurrence contribute more to overall beta diversity. Based on the findings from both chapters, it was possible to identify and understand the patterns that determine the spatial organization of macrophyte communities in the wetlands of the PCRS, highlighting the importance of environmental and climatic predictors in community structuring and demonstrating that different functional groups respond differently to

environmental gradients, thus contributing to the advancement of knowledge. Furthermore, it was possible to identify the most important sites and species for regional beta diversity. Finally, these findings broaden our understanding of metacommunity ecology and may also be useful for the protection and/or conservation of wetlands.

Key-words: wetland vegetation, spatial distribution, beta diversity, LCBD, SCBD, EMS, Pampa biome.

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Figure 2. Study area showing the 29 coastal wetlands sampled in the coastal plain of Rio Grande do Sul, Southern Brazil.

Figure 3. Patterns of Elements of Metacommunity Structure (EMS) for the total macrophytes metacommunity (all species), and emergent, floating (including both free-floating and rooted floating-leaved species), and submerged (including both fixed submerged and free-floating submerged species) metacommunities from the coastal plain of Rio Grande do Sul, Southern Brazil. Multiple Regression Tree (MRT) illustrating the hierarchical partitioning of sampling sites based on environmental variables. In the MRT, AMT represents annual mean temperature, and TP represents total phosphorus. Each terminal node (leaf) in the MRT displays the mean group score (top number) along the first axis of the Correspondence Analysis (CA) and the number of sampling units within that group (bottom number). The map shows the corresponding geographical distribution of these MRT-defined groups, with different colors indicating distinct groups associated with specific combinations of annual mean temperature, total phosphorus levels, and altitude.

Capítulo 2

Figure 1. Study area showing the 29 wetlands sampled (green circles) in the coastal plain of Rio Grande do Sul State, Southern Brazil. The inset shows South America, with Brazil shown in green.

Figure 2. Spatial variation in compositional uniqueness (LCBD) of macrophyte communities in the 29 sampled wetlands (a) and spatial autocorrelation analysis of LCBD (b). The size of the circles in plot a is proportional to the LCBD values.

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LISTA DE TABELAS

Capítulo 1

Table 1. Summary of the Elements of Metacommunity Structure (EMS) for the aquatic macrophyte metacommunity from the coastal plain of Rio Grande do Sul, Southern Brazil. Bold values are statistically significant

Capítulo 2

Table 1. Beta regression results on environmental uniqueness and climatic variables as predictors of the variation in compositional uniqueness (LCBD) of macrophytes in wetlands. LCEHPhy and LCEHWC, local contribution to environmental heterogeneity resulting from wetland physical characteristics and from water chemistry, respectively; MTWeQ, mean temperature of the wettest quarter; MTDrQ, mean temperature of the driest quarter; PS, precipitation seasonality; PCQ, precipitation of the coldest quarter. P values ≤ 0.05 are in bold.

Table 2. Fourth-corner results on the relationship (Pearson correlation, r) between species contribution to beta diversity (SCBD) and environmental predictors for the total macrophyte communities and separately for each life form. Significant P values (≤ 0.05) are in bold.

INTRODUÇÃO GERAL

Ecologia de Metacomunidades

Compreender como as espécies se distribuem no espaço e no tempo é uma questão central na Ecologia de Comunidades (Legendre e Gauthier, 2014; Barbier et al., 2025). Essa busca remonta aos estudos pioneiros de Alexander von Humboldt, no início do século XIX, e foi marcada por importantes avanços conceituais, incluindo os debates sobre a natureza das comunidades biológicas, como o clássico embate entre Clements e Gleason, no século passado. Ao longo do tempo, diferentes contribuições teóricas ampliaram a compreensão sobre os padrões de biodiversidade e os processos que estruturam as comunidades, incluindo conceitos sobre nicho, gradientes ambientais, diversidade e dinâmica de colonização (Hutchinson, 1957; Whittaker, 1960; MacArthur e Wilson, 1967; Connell, 1978; Tilman, 1982; Hubbell, 2001).

O debate entre Clements (1936) e Gleason (1926) ilustra visões contrastantes sobre a organização das comunidades ecológicas. Clements via as comunidades como unidades discretas e coesas, com fronteiras bem definidas, onde as espécies interagem de forma coordenada. Gleason, por sua vez, defendia uma abordagem individualista, na qual cada espécie responde de forma independente aos gradientes ambientais, e a composição das comunidades resulta da sobreposição das distribuições individuais, sem associações rígidas. Essa discussão histórica fundamentou desenvolvimentos posteriores na ecologia de comunidades, incluindo abordagens modernas, como a proposta de Vellend (2010), baseada nos mecanismos de seleção, dispersão, deriva e especiação; e a teoria de metacomunidades, que integra processos determinísticos e estocásticos para explicar padrões de distribuição de espécies (Leibold et al., 2004).

Histórico e definição da teoria de metacomunidades

O termo “metacomunidade” surgiu a partir da literatura sobre metapopulações (Hanski e Gilpin, 1991) e foi definido como um conjunto de comunidades locais conectadas pela dispersão de múltiplas espécies potencialmente interativas (Wilson, 1992; Leibold et al., 2004). Embora inicialmente tenha recebido pouca atenção empírica (Wilson, 1992; Duelli, 1997; Harrison, 1999), o conceito ganhou relevância a partir dos anos 2000, especialmente com os trabalhos de Hubbell (2001), Leibold e

Mikkelsen (2002) e Leibold et al. (2004), ampliando a compreensão de como processos locais e regionais interagem para moldar a diversidade biológica em diferentes escalas, desde pequenos fragmentos de habitat até gradientes biogeográficos continentais (Heino et al., 2015a; García-Girón et al., 2020).

A teoria de metacomunidades é conceitual e estruturada em quatro paradigmas principais: dinâmica de manchas (patch dynamics; que enfatiza o equilíbrio entre colonização e extinção em habitats semelhantes), seleção de espécies (species sorting; que ressalta a importância da heterogeneidade ambiental e a adaptação a condições locais), efeitos de massa (mass effects; em que alta dispersão permite a persistência de espécies em ambientes subótimos) e teoria neutra (neutral theory; que assume equivalência ecológica entre espécies e destaca o papel de processos estocásticos) (Leibold et al., 2004). Cada um enfatiza mecanismos distintos, desde a importância da heterogeneidade ambiental até os efeitos da dispersão, da estocasticidade e do equilíbrio entre colonização e extinção, oferecendo diferentes perspectivas para interpretar padrões de diversidade.

O framework de metacomunidades

O framework de metacomunidades é operacional e analítico, traduzindo a teoria em ferramentas concretas que permitem medir e testar padrões empíricos, revelando como os processos ecológicos se manifestam na distribuição real das espécies ao longo de gradientes ambientais (Leibold e Mikkelsen, 2002). Um exemplo é o framework dos Elementos da Estrutura de Metacomunidade (EMS – Elements of Metacommunity Structure), que se fundamenta em três métricas essenciais: coerência (coherence), substituição (turnover) e fronteiras de distribuição (boundary clumping) (Leibold e Mikkelsen, 2002; Presley et al., 2010). A coerência avalia a consistência das respostas das espécies ao longo de um gradiente ambiental, indicando se elas respondem de forma ordenada e não aleatória às variações ambientais; a substituição mede, como o próprio termo indica, a substituição de espécies entre locais adjacentes, revelando o grau de mudança composicional; e as fronteiras de distribuição analisam a coincidência dos limites geográficos ou ambientais das espécies, indicando agrupamentos ou compartimentos dentro da metacomunidade (Leibold e Mikkelsen, 2002; Presley et al., 2010).

A combinação dessas métricas possibilita a identificação de distintos padrões estruturais, tais como metacomunidades aninhadas, nas quais espécies com

distribuição restrita ao longo de um gradiente ambiental geralmente estão inseridas nas faixas ocupadas por espécies com distribuição mais amplas (Leibold e Mikkelsen, 2002; Presley et al., 2010; Vieira et al., 2020), padrões tipo tabuleiro de xadrez, associados a distribuições uniformemente espaçadas (Leibold e Mikkelsen, 2002; Presley et al., 2010; Presley et al., 2019), gradientes Clementsianos, com padrões de distribuição em blocos de espécies, e padrões Gleasonianos, em que as distribuições das espécies variam individualmente ao longo do gradiente (Presley et al., 2010; Heino et al., 2015b; García-Girón et al., 2020). Esses padrões refletem diferentes processos ecológicos dominantes, como filtros ambientais que determinam a seleção (Gascón et al., 2016), limitações na dispersão (Presley et al., 2010) ou a influência de eventos estocásticos na composição das comunidades (Leibold e Chase, 2017; Leibold et al., 2022). Dessa forma, a análise dos EMS tem se mostrado uma ferramenta valiosa para inferir os mecanismos estruturantes das comunidades, oferecendo uma interpretação robusta dos arranjos espaciais da biodiversidade e contribuindo para o entendimento da dinâmica ecológica dentro do contexto de metacomunidades (Heino et al., 2015b).

Compreender as diferenças na composição de espécies entre comunidades é essencial para revelar os processos que estruturam a biodiversidade. Nesse contexto, a diversidade beta ocupa papel central na ecologia de metacomunidades, por expressar a variação espacial na composição e refletir dois componentes principais: a substituição de espécies entre locais (turnover), e diferenças de riqueza associadas ao ganho ou perda de espécies (nestedness ou richness difference) (Baselga, 2010; Anderson et al., 2011). O conceito foi inicialmente proposto por Whittaker (1960), que distinguiu a diversidade beta da diversidade alfa (local) e da diversidade gama (regional), destacando seu valor como medida de diferenciação entre comunidades. Desde então, a diversidade beta tornou-se uma das ferramentas centrais para investigar padrões de composição de espécies entre comunidades em diferentes escalas (Baselga, 2010; Anderson et al., 2011).

Nesse sentido, Legendre e De Cáceres (2013) propuseram um avanço importante ao relacionar a diversidade beta à variância total da matriz de dados de comunidade, permitindo seu particionamento em Contribuições Locais para a Diversidade Beta (LCBD) e Contribuições de Espécies para a Diversidade Beta (SCBD). Essa abordagem quantifica, respectivamente, a singularidade ecológica de cada local e a importância relativa de cada espécie para a diferenciação regional,

ampliando o poder interpretativo das análises ecológicas e fornecendo subsídios relevantes para estratégias de conservação (Heino et al., 2017). Estudos recentes vêm adotando essas métricas para avaliar como variáveis ambientais, espaciais e funcionais moldam os padrões de diversidade em diferentes ecossistemas (Li et al., 2020; Leão et al., 2020; Schneck et al., 2022).

A abordagem de particionamento da diversidade beta em LCBD e SCBD permite expressar, respectivamente, a singularidade ecológica dos locais e o grau de variação das espécies em toda a área de estudo. Altos valores de LCBD indicam locais com composições de espécies singulares, o que pode representar áreas prioritárias para conservação, ambientes degradados ou condições ecológicas especiais, incluindo a presença de espécies invasoras (Tonkin et al., 2016; Silva et al., 2024). Por sua vez, valores elevados de SCBD destacam espécies com maior contribuição para a heterogeneidade espacial, geralmente associadas à baixa ocupação, abundância intermediária e nicho ecológico restrito (Vilmi et al., 2017). Essas métricas podem ser relacionadas a características ambientais, espaciais ou funcionais: LCBD reflete variações em riqueza ou abundância ligadas a gradientes ambientais (Castro et al., 2019), enquanto SCBD tende a se correlacionar com traços como posição e amplitude de nicho, modo de alimentação, tamanho corporal e capacidade de dispersão das espécies (Ferreira et al., 2017). Assim, a análise conjunta de LCBD e SCBD oferece uma ferramenta robusta para compreender padrões espaciais de diversidade e os processos ecológicos que os estruturam.

Esse arcabouço conceitual e analítico foi fundamental para o desenvolvimento da teoria de metacomunidades (Leibold et al., 2004; Leibold e Chase, 2017), permitindo compreender o papel dos filtros ambientais, das limitações de dispersão, das interações bióticas e da estocasticidade na organização das comunidades (Heino, 2013; Thompson et al., 2020). Ele também foi essencial para explicar padrões de distribuição de espécies, variação na composição das comunidades e os processos ecológicos que moldam a biodiversidade em diferentes escalas, como evidenciado em estudos sobre a estruturação de comunidades aquáticas em diferentes paisagens (Heino et al., 2015a), a influência da conectividade regional sobre a biodiversidade funcional (De Bie et al., 2012; Padial et al., 2014) e as respostas da composição da comunidade à variação ambiental e espacial em distintos grupos biológicos (Alahuhta e Heino, 2013). Recentemente, têm-se integrado abordagens espaciais, funcionais e filogenéticas, permitindo compreender

melhor a organização das metacomunidades em diferentes contextos ambientais e taxonômicos (Stela et al., 2024; Barbier et al., 2025). Dessa forma, a ecologia de metacomunidades representa um marco teórico e analítico, permitindo investigar como fatores determinísticos e estocásticos atuam conjuntamente na geração e manutenção da biodiversidade (Ning et al., 2019).

Metacomunidades de macrófitas em wetlands

Áreas Úmidas (Wetlands)

As áreas úmidas (wetlands) são ecossistemas caracterizados pela presença de água, de forma temporária ou permanente, nos quais a interação entre água, solo e organismos é fundamental para a realização de múltiplas funções ecológicas e provisão de serviços ambientais, como a purificação da água, a mitigação de enchentes e a conservação da biodiversidade (Mitsch et al., 2023). Esses ambientes são ecossistemas extremamente dinâmicos, nos quais as variações no nível da água regulam as condições físicas, químicas e biológicas (Junk et al., 2014).

As áreas úmidas sustentam uma rica diversidade biológica ao oferecerem habitat e recursos adequados para inúmeras espécies (Mitsch et al., 2023), desde microorganismos até vertebrados de diferentes grupos, funcionando como áreas de reprodução, alimentação e refúgio para inúmeras espécies (Amezaga et al., 2002). Entre os componentes essenciais dessas áreas estão as plantas aquáticas, como as macrófitas (Santamaría, 2002), que desempenham funções ecológicas fundamentais, incluindo a estabilização do sedimento, a filtragem de nutrientes e poluentes, além de servirem como habitat e fonte de alimento para diversos organismos aquáticos (De Magalhaes et al., 2016).

Embora as áreas úmidas sejam fundamentais para a manutenção de uma parcela expressiva da biodiversidade global (Junk et al., 2014), eles figuram entre os ecossistemas mais vulneráveis (Amezaga et al., 2002; Kingsford et al., 2021; Mitsch et al., 2023). Esses ambientes enfrentam ameaças cada vez mais intensas, impulsionadas por fatores como as mudanças climáticas, que alteram seus regimes hidrológicos, a urbanização acelerada, que reduz e fragmenta suas áreas, a poluição, que compromete a qualidade da água e a saúde dos organismos, e a presença de espécies invasoras, que podem modificar suas dinâmicas ecológicas e reduzir a diversidade de espécies nativas (Erwin, 2009). Especificamente, as mudanças climáticas tendem a intensificar esses desafios ao alterar os padrões hidrológicos e

comprometer a estabilidade desses ecossistemas (Erwin, 2009). Essas pressões não apenas perturbam o equilíbrio ecológico das áreas úmidas, mas também aceleram a perda de biodiversidade e aumentam os riscos de desastres climáticos, tornando urgentes os esforços de conservação e proteção (Kingsford et al., 2021; Xi et al., 2021; Moreira et al., 2025).

No Brasil, além da degradação antrópica, as áreas úmidas apresentam flutuações sazonais nos níveis de água, causadas por secas e/ou inundações, o que molda suas condições físicas, químicas e biológicas, influenciando diretamente a composição e a distribuição das comunidades que habitam esses ecossistemas (Junk et al., 2014). No sul do Brasil, as áreas úmidas palustres, conhecidos internacionalmente como *marshes*, são ecossistemas dominados por vegetação herbácea, com pouca ou nenhuma presença de árvores, solos saturados e sujeitos a inundações sazonais ou permanentes (Mitsch et al., 2023). No Rio Grande do Sul, esses ecossistemas são popularmente chamados de banhados, correspondendo a cerca de 90% das áreas úmidas da região e exibindo grande heterogeneidade espacial e temporal, que varia desde áreas permanentemente alagadas até locais que permanecem saturados por longos períodos ao longo do ano (Maltchik et al., 2004). A predominância de vegetação herbácea, adaptada a solos saturados, cria diferentes microhabitats, moldando a composição e a distribuição das comunidades de plantas aquáticas e outros organismos associados (Maltchik et al., 2007).

Na Planície Costeira do Rio Grande do Sul (PCRS), os banhados, desempenham um papel crucial na manutenção da biodiversidade, sustentando comunidades diversificadas de organismos aquáticos que interagem de maneira complexa e contribuem para a estabilidade ecológica regional, como demonstrado em alguns estudos (Freygang et al., 2004; Quintela et al., 2006; Santos et al., 2012; Bastos et al., 2013; Lanés et al., 2016; Dias et al., 2017; Tozetti et al., 2023). Entretanto, esses ecossistemas enfrentam pressões crescentes devido a alterações hidrológicas e impactos antrópicos, como o plantio de espécies exóticas (Stenert et al., 2012), a expansão urbana e o turismo sazonal (Moura et al., 2015) e a intensificação da agricultura (Belloli et al., 2024). A degradação dessas áreas compromete não apenas os serviços ecossistêmicos essenciais, como a regulação do ciclo hidrológico e a filtragem de nutrientes, mas também afeta diretamente espécies adaptadas a essas condições únicas (Mitsch et al., 2023). Diante desse cenário, a implementação de estratégias eficazes de proteção e conservação (Hu et

al., 2017; Xu et al., 2020) tornam-se indispensáveis para garantir a preservação da biodiversidade e dos benefícios ecológicos proporcionados pelas áreas úmidas.

Macrófitas Aquáticas

As macrófitas aquáticas são plantas macroscópicas que habitam ecossistemas aquáticos e pertencem a diferentes grupos taxonômicos, como angiospermas, pteridófitas e macroalgas (Chambers et al., 2008; Murphy et al., 2019). Elas contribuem para a complexidade do habitat, oferecendo abrigo e substrato, além de desempenharem papéis fundamentais na produção primária, ciclagem de nutrientes, provisão de habitat, participação no ciclo da água e produção de gases, promovendo diversos serviços ecossistêmicos (Thomaz, 2023). Além da diversidade taxonômica, as macrófitas podem ser classificadas em grupos funcionais (emergentes, flutuantes e submersas) de acordo com suas características ecológicas e adaptações (Schneider et al., 2018). Essa classificação é relevante, pois cada grupo responde de forma distinta às mudanças ambientais e utiliza recursos como luz e nutrientes de maneira específica (Alahuhta et al., 2013; Schneider et al., 2018). Por exemplo, espécies emergentes dependem principalmente da luz e dos nutrientes do sedimento, enquanto as submersas são sensíveis às condições de luz subaquática, e as flutuantes respondem sobretudo à disponibilidade de nutrientes na água (Santamaría, 2002). Essas respostas diferenciadas tornam as macrófitas excelentes indicadoras de alterações ambientais. Sua diversidade funcional, ampla distribuição e sensibilidade a gradientes reforçam sua importância nos ecossistemas aquáticos continentais, justificando a relevância de estudos sobre metacomunidades de macrófitas (Alahuhta et al., 2021; Heino et al., 2022).

No contexto das metacomunidades, as macrófitas aquáticas são influenciadas por fatores ambientais e espaciais que atuam em diferentes escalas (Alahuhta et al., 2013; Gillard et al., 2020). O modo como esses fatores atuam na composição das comunidades é dependente da forma de vida (Alahuhta e Heino, 2013; Schneider et al., 2018; Trindade et al., 2018). Além disso, a variação na composição de espécies entre as comunidades também depende da região geográfica e da escala espacial analisadas (Grimaldo et al., 2016; García-Girón et al., 2020). Por exemplo, em riachos temperados, a riqueza e a estrutura das assembleias de macrófitas refletem uma combinação de fatores ambientais e espaciais, enquanto em riachos tropicais, a variação na riqueza está associada predominantemente a fatores espaciais,

possivelmente relacionados a condições climáticas de larga escala (Grimaldo et al., 2016). Em lagos, estudos globais que analisaram dados de seis continentes mostram que as metacomunidades de macrófitas exibem padrões de substituição agrupada de espécies, com múltiplos grupos respondendo de forma semelhante às variáveis ambientais regionais, embora essas relações sejam altamente dependentes do contexto local (García-Girón et al., 2020).

Embora estudos sobre metacomunidades tenham avançado em ecossistemas como lagos e riachos, ainda há lacunas significativas no conhecimento sobre a dinâmica das metacomunidades de macrófitas em áreas úmidas. Dessa forma, investigar as metacomunidades de macrófitas em áreas úmidas constitui uma abordagem promissora para compreender a biodiversidade aquática em diferentes escalas, integrando processos locais e regionais. Esse conhecimento é essencial para compreender como as flutuações hidrológicas e as mudanças ambientais, naturais ou antrópicas, moldam a biodiversidade nesses ecossistemas. Com isso, na planície costeira do Rio Grande do Sul, a investigação das metacomunidades de macrófitas pode fornecer subsídios importantes para estratégias de preservação e conservação das áreas úmidas dessa região. Além disso, considerando que as macrófitas são indicadoras ambientais, esses estudos podem ajudar a prever os impactos de alterações ambientais e proteger a biodiversidade em um cenário de mudanças globais.

Diante do contexto aqui apresentado, no Capítulo 1, explorei os Elementos da Estrutura de Metacomunidades (EMS; coerência, substituição e fronteiras de distribuição) como forma de identificar os padrões de estruturação das metacomunidades. Apliquei esse framework à comunidade total e a três grupos funcionais (emergentes, flutuantes e submersos), avaliando a influência de gradientes ambientais por meio de árvores de regressão. Hipotetizei que a metacomunidade total e as espécies emergentes apresentariam um padrão Clementsiano, associado à heterogeneidade ambiental e ao clima, enquanto os grupos flutuantes e submersos seguiriam um padrão Gleasoniano, determinado principalmente por variáveis limnológicas. No Capítulo 2, investiguei a diversidade beta de macrófitas aquáticas em 29 áreas úmidas costeiras no sul do Brasil, utilizando as métricas LCBD e SCBD para avaliar a contribuição de cada local e de cada espécie para a diversidade beta regional. Analisei as relações dessas métricas com variáveis ambientais (físicas e químicas e climáticas) e espaciais, com a expectativa de que áreas ambientalmente

únicas abrigassem comunidades com composição de espécies também únicas, e que espécies emergentes contribuísem menos para a diversidade beta regional em comparação às espécies flutuantes e submersas. Em conjunto, essas abordagens forneceram uma compreensão abrangente dos processos que estruturam as metacomunidades de macrófitas na planície costeira do Rio Grande do Sul.

Esses estudos contribuem para a ampliação do conhecimento sobre a teoria das metacomunidades e sobre a ecologia das macrófitas, revelando processos que contribuem para a estruturação da biodiversidade nas áreas úmidas costeiras. Além disso, os estudos resultantes desta tese podem fornecer subsídios essenciais para estratégias de preservação e conservação, fundamentais para a manutenção da integridade ecológica das áreas úmidas, que estão entre os ambientes mais ameaçados do planeta.

OBJETIVO GERAL

Minha tese objetiva avaliar questões relacionadas à distribuição e à organização espacial de metacomunidades de macrófitas em banhados da planície costeira do Rio Grande do Sul, no sul do Brasil. Para isso, desenvolvi um estudo na forma de subprojetos que constituíram os capítulos, como segue:

- 1) No primeiro capítulo avaliei os elementos da estrutura das metacomunidades de macrófitas em banhados costeiros e suas relações com variáveis limnológicas e climáticas.
- 2) No segundo capítulo determinei a singularidade composicional e contribuição de espécies para a diversidade beta de metacomunidades de macrófitas aquáticas em banhados costeiros.

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<https://doi.org/10.1016/j.gecco.2020.e01027>

CAPÍTULO 1

Elements of the structure of macrophyte metacommunities in coastal wetlands: relationships with limnological and climatic variables¹

Abstract

The Elements of Metacommunity Structure (EMS; coherence, turnover, and boundary clumping) framework allows the evaluation of species distribution patterns, including Clementsian patterns (discrete communities) and Gleasonian patterns (individualistic responses to gradients). Quasi-structures can also occur, representing intermediate patterns when results do not fully fit a specific model, such as stochastic species loss (quasi-nested) or quasi-Clementsian and quasi-Gleasonian patterns. We applied the EMS to the total macrophyte metacommunity and three functional groups (emergent, floating, and submerged) across 29 coastal wetlands in southern Brazil. We first hypothesized that the total metacommunity would show a Clementsian pattern, driven by environmental heterogeneity and climate, with high turnover and well-defined community boundaries. Our second hypothesis was that emergent species would form Clementsian communities, whereas floating and submerged groups would follow Gleasonian patterns, driven by limnological gradients. After applying the EMS, we used regression trees to assess the environmental influences on the observed patterns. The total metacommunity exhibited a Clementsian pattern, with clustered turnover and discrete boundaries, influenced by mean annual temperature and total phosphorus. Emergent species also showed a Clementsian pattern, shaped by temperature. Floating species, influenced by total phosphorus and altitude, exhibited a quasi-nested stochastic species loss structure, indicating a tendency toward nestedness without complete ordering. The submerged group, determined by temperature, exhibited a Gleasonian pattern, with turnover and random distribution of species ranges. Our findings highlight the influence of environmental and climatic variables on macrophyte structure in wetlands, revealing distinct functional group responses and enhancing understanding of species distribution in continental aquatic environments.

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Keywords: metacommunity, wetland vegetation, functional groups, subtropical, spatial distribution.

Introduction

Metacommunities are shaped by the complex interaction between environmental factors, dispersal, and biotic interactions, resulting in distinct patterns of spatial organization (Leibold et al., 2022). In metacommunity studies, these principles have guided the development of two main approaches: one based on patterns, focused on species co-occurrence (Leibold & Mikkelsen, 2002), and another mechanistic, centered on the processes that determine species distribution (Leibold et al., 2004). Consequently, these perspectives have collectively refined a theoretical framework essential for ecological studies on metacommunities (Logue et al., 2011; Leibold et al., 2022; Barbier et al., 2025), aiding in the identification and understanding of species distribution patterns in space and time (Alahuhta et al., 2021).

The debate about species distribution patterns was widely explored in the last century, for example, in the classic discussion involving the ideas of Clements (who viewed communities as discrete units with well-defined boundaries) and Gleason (who adopted a more continuous and individualistic view of species' responses to environmental gradients). This led ecologists to propose various idealizations based on the structure of incidence matrices to explain how species are distributed along environmental gradients. These idealizations facilitate the description of distinct distribution patterns, including checkerboard (Diamond, 1975), nested (Wright & Reeves, 1992), evenly spaced (Tilman, 1982), Gleasonian (Gleason, 1926), Clementsian (Clements 1936), and random (Leibold & Mikkelsen, 2002). With the advancement of the metacommunity theory, Leibold & Mikkelsen (2002) proposed an approach that allows for the simultaneous comparison of these patterns, assessing which best fits the metacommunity structure while considering alternatives that are not addressed by traditional idealizations. This approach is based on the analysis of the Elements of Metacommunity Structure (EMS), which consist of three main components: coherence, turnover, and boundary clumping (Leibold & Mikkelsen, 2002).

Coherence evaluates interruptions in species distributions (incorporated absences) (Leibold & Mikkelsen, 2002). Negative coherence indicates rare

checkerboard patterns, usually resulting from detection errors (Presley et al., 2019), while positive coherence reflects fewer absences than expected, allowing different types of structure to be distinguished via turnover and boundary clumping; if there is no significant difference from random, the structure is considered random (Presley et al., 2010). Turnover measures how often one species replaces another between sites (Leibold & Mikkelsen, 2002), being negative in nested distributions and positive in Gleasonian, Clementsian, or evenly spaced structures, which are distinguished by boundary clumping (Leibold & Mikkelsen, 2002; Presley et al., 2010). Boundary clumping is assessed using Morisita's dispersion index and tested by chi-square (Leibold & Mikkelsen, 2002), allowing the identification of structural patterns: Clementsian (clustered boundaries), evenly spaced (hyperdispersed boundaries), and Gleasonian (randomly distributed boundaries) (Presley et al., 2010). In addition to the main patterns, there are quasi-structural subtypes: non-significant negative turnover indicates quasi-nestedness, while non-significant positive turnover indicates quasi-evenly spaced, quasi-Gleasonian, or quasi-Clementsian patterns (Presley et al., 2010, see Figure 1, for a schematic representation of the EMS patterns).

The EMS framework focuses on the analysis of metacommunity structure to identify species distribution patterns without necessarily implying the processes that led to these patterns (Leibold & Mikkelsen, 2002). In this sense, studies have evolved toward a broader understanding of the patterns that may emerge in response to different ecological factors, as demonstrated by research conducted on various biological groups in different environments, such as bacteria, algae, macrophytes, invertebrates, and fish in Finnish lotic and lentic systems (Heino et al., 2015); macrophytes in lakes across six continents (García-Girón et al., 2020); fish in Neotropical streams in Brazil (Vieira et al., 2020); and zooplankton in wetlands in the northeastern Iberian Peninsula, Spain (Gilbert et al., 2023). These studies demonstrate that, although mechanisms vary among biological groups, EMS analysis has proven to be a robust tool for understanding the patterns and processes that structure biological diversity in aquatic ecosystems, with the patterns found for these groups being related to environmental variables (Gascón et al., 2016). For example, Heino et al. (2015) identified six types of metacommunities (Clementsian, quasi-nested, random, quasi-Clementsian, Gleasonian, and quasi-Gleasonian), relating them to a positive relationship between turnover and beta diversity, highlighting the influence of ecological gradients on metacommunity organization. Similarly, García-

Girón et al. (2020) showed that, at global scales, lake macrophyte metacommunities followed Clementsian and quasi-Clementsian structures related to climatic and geographical gradients. Vieira et al. (2020) found nested (hyperdispersed species loss) and Clementsian patterns, suggesting that a core subset of fish species may be potentially isolated by water physicochemical conditions or stream channel morphology. Recently, in Mediterranean wetlands, Gilbert et al. (2023) found that nestedness was the predominant pattern for zooplankton metacommunities, with land use and limnological characteristics being key influences.

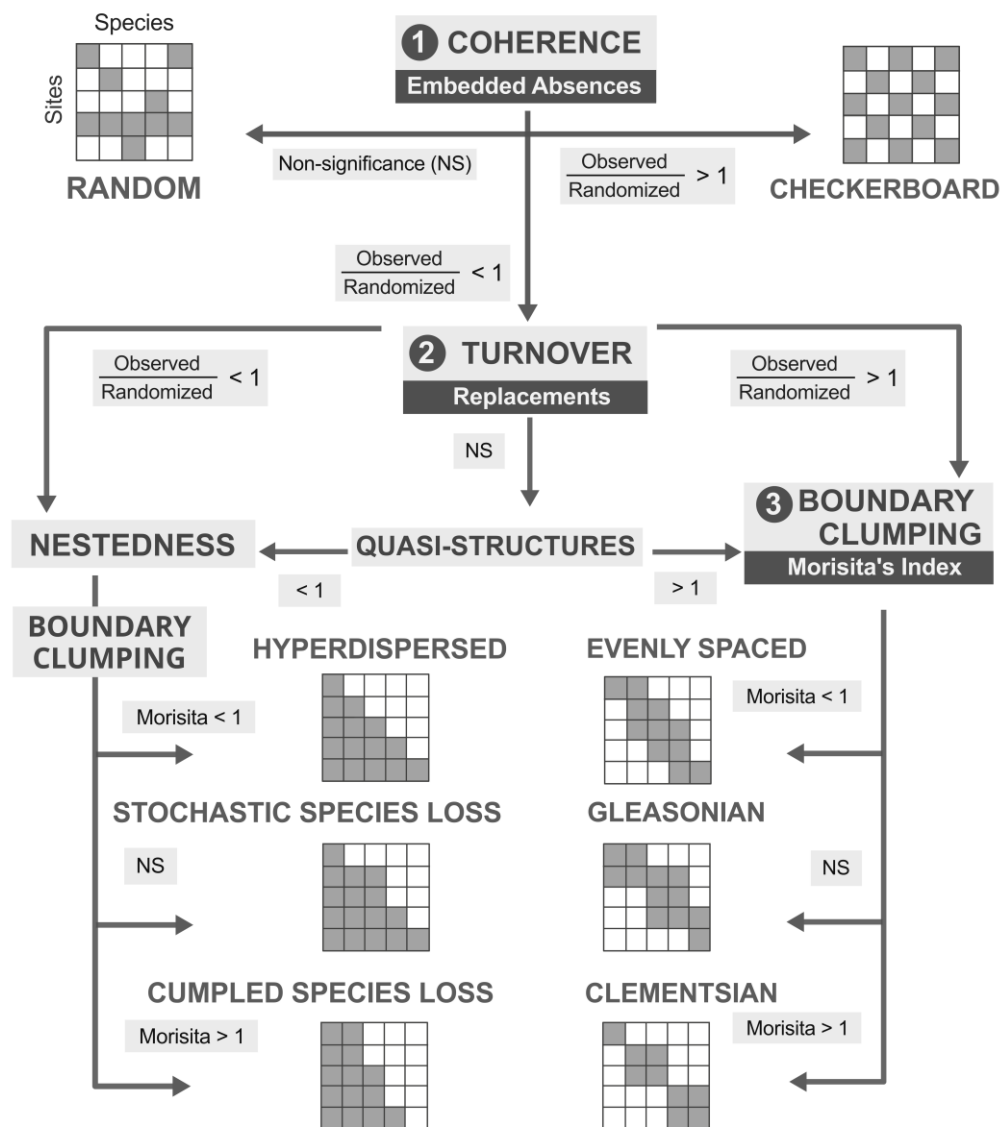


Figure 1. Diagram of metacommunity types. Adapted from Leibold and Mikkelsen (2002), Presley et al. (2010), and Gascón et al. (2016).

Wetlands are ecosystems characterized by water saturation, either temporarily or permanently, where the interaction between water, soil, and organisms results in a variety of ecological functions and environmental services, such as water purification, flood control, and biodiversity preservation (Mitsch & Gosselink, 2000). Although wetlands play a crucial role in maintaining a significant part of global biodiversity (Junk et al., 2014) and environmental services (Xu et al., 2020), they are among the most vulnerable ecosystems (Kingsford et al., 2021) and face increasing threats from climate change, urbanization, pollution, and the presence of invasive species (Erwin, 2009). It is estimated that 3.4 million km² of inland wetlands have been lost since 1700, primarily due to conversion into agricultural land (Fluet-Chouinard et al., 2023). Another concern relates to climate change, which may intensify problems by altering hydrological patterns and compromising the stability of these ecosystems (Xi et al., 2021). These pressures not only disrupt the ecological balance of wetlands but also accelerate biodiversity loss and increase the risks of climate-related disasters, making conservation and protection efforts more urgent than ever (Kingsford et al., 2021).

Aquatic macrophytes play a fundamental role in wetland ecosystems (De Magalhaes et al., 2016), exhibiting diverse adaptive strategies that enable them to thrive across a variety of habitats (Santamaría, 2002; Lacoul & Freedman, 2006; Lind et al., 2022). These organisms have different life forms, such as emergent species that grow above the water surface and floating and submerged species that occupy distinct niches within the water column (Chambers et al., 2008; Schneider et al., 2018; Murphy et al., 2019). Due to their distinct ecological requirements, local and regional environmental factors, as well as spatial processes, influence the distribution of different life forms in distinct ways (Gillard et al., 2020; García-Girón et al., 2021; Jewell et al., 2023).

In previous studies, we have shown that environmental and spatial factors influence macrophyte communities in wetlands, where floating and submerged species were primarily influenced by water quality and spatial factors, respectively, while emergent species, with broader distribution, were more affected by climatic conditions (Trindade et al., 2018). Recently, we demonstrated that environmental filters were essential for determining the compositional uniqueness of wetland metacommunities, especially for submerged and floating macrophyte groups

(Trindade & Schneck, 2024). These studies show that separating the community (total data matrix) into functional groups (emergent, floating, and submerged) can reveal hidden patterns in the total data set, helping to improve our understanding of the spatial organization of metacommunities. Understanding theoretical metacommunity models is essential for interpreting the distribution patterns in empirical data across environmental gradients (Presley et al., 2010). This knowledge is crucial for supporting conservation and preservation strategies for biodiversity, especially in ecosystems impacted by human activities (García-Girón et al., 2020) that, combined with climate change, threaten the stability and functionality of wetland ecosystems.

Here, we analyzed the Elements of Metacommunity Structure (EMS) of aquatic macrophytes in 29 freshwater wetlands along 640 km of the coastal plain of Rio Grande do Sul, in Southern Brazil, to identify which metacommunity patterns prevail in these wetlands and their relationship with limnological variables (chemical and physical variables; operating at local scales) and climatic variables (operating at regional scales). Considering the variety of strategies exhibited by different macrophyte life forms in response to environmental conditions, we partitioned the total data matrix (all species) into functional groups (emergent, floating, and submerged) and applied EMS separately for each group, also evaluating their relationships with limnological (local) and climatic (regional) variables. We expect that the Clementsian pattern will prevail, in response to environmental heterogeneity and regional climate structuring, resulting in greater species turnover, forming communities with more discrete distribution boundaries. This expectation is based on the assumption that strong environmental and climatic gradients act as ecological filters, promoting the clustering of species with similar tolerances into distinct communities. In Clementsian metacommunities, species distributions tend to be more cohesive along environmental gradients, reflecting shared responses to abiotic factors, which leads to high turnover and well-defined boundaries (Clements 1916; Leibold & Mikkelsen, 2002). We also expect that metacommunity patterns will differ for functional groups, determined by distinct gradients (e.g., local and regional). Emergent species are expected to present Clementsian patterns shaped by limnological and climatic variables, while submerged and floating groups will show Gleasonian distribution patterns, driven by limnological factors. Specifically, emergent species are expected to exhibit Clementsian patterns because they are

rooted in sediment and directly exposed to atmospheric variability, which promotes a more cohesive and synchronized response to broad-scale environmental and climatic gradients (Clements, 1916; García-Girón et al., 2020). In contrast, submerged and floating species tend to display Gleasonian patterns, characterized by more individualistic distributions influenced primarily by local limnological factors such as light availability, nutrient concentration, and water depth, which vary at finer spatial scales (Gleason, 1926; Trindade et al., 2018).

Material and Methods

Study area

We sampled the macrophyte metacommunities in 29 wetlands located within the coastal plain of Rio Grande do Sul in Southern Brazil (Figure 2). The coastal plain spans approximately 640 km, encompassing 22,740 km² of emerged land and 14,260 km² of water surfaces, totaling 37,000 km² (Schwarzbald & Schäfer, 1984). This landscape is the result of a long geological process that began in the Cenozoic Era. During this Era, especially in the Quaternary period, the coastal plain expanded significantly due to the deposition of alluvial fans and the formation of barrier-lagoon systems. As a result of this process, large bodies of water emerged, such as the Patos Lagoon and the Mirim and Mangueira Lakes (Barboza et al., 2009). Currently, the coastal plain presents a rich diversity of natural environments, including estuaries, deltas, beaches, rivers, and streams. In addition, there are savannas, palm groves, flooded fields, and forests that can be seasonal, temporary, or permanent, as well as lakes and lagoons. Some wetlands may be permanently or temporarily flooded (Becker et al., 2007). The climate of the region is humid subtropical (Cfa) according to the Köppen Classification System. The annual precipitation ranges from 1,000 to 1,500 mm, while the average annual temperature is between 16 and 20 °C (Alvares et al., 2014). During the hottest period of the year, from December to March, the average temperatures range from 22 to 26 °C. In contrast, during the coldest period, from July to September, the average is between 10 and 15 °C (Nimer, 1977).

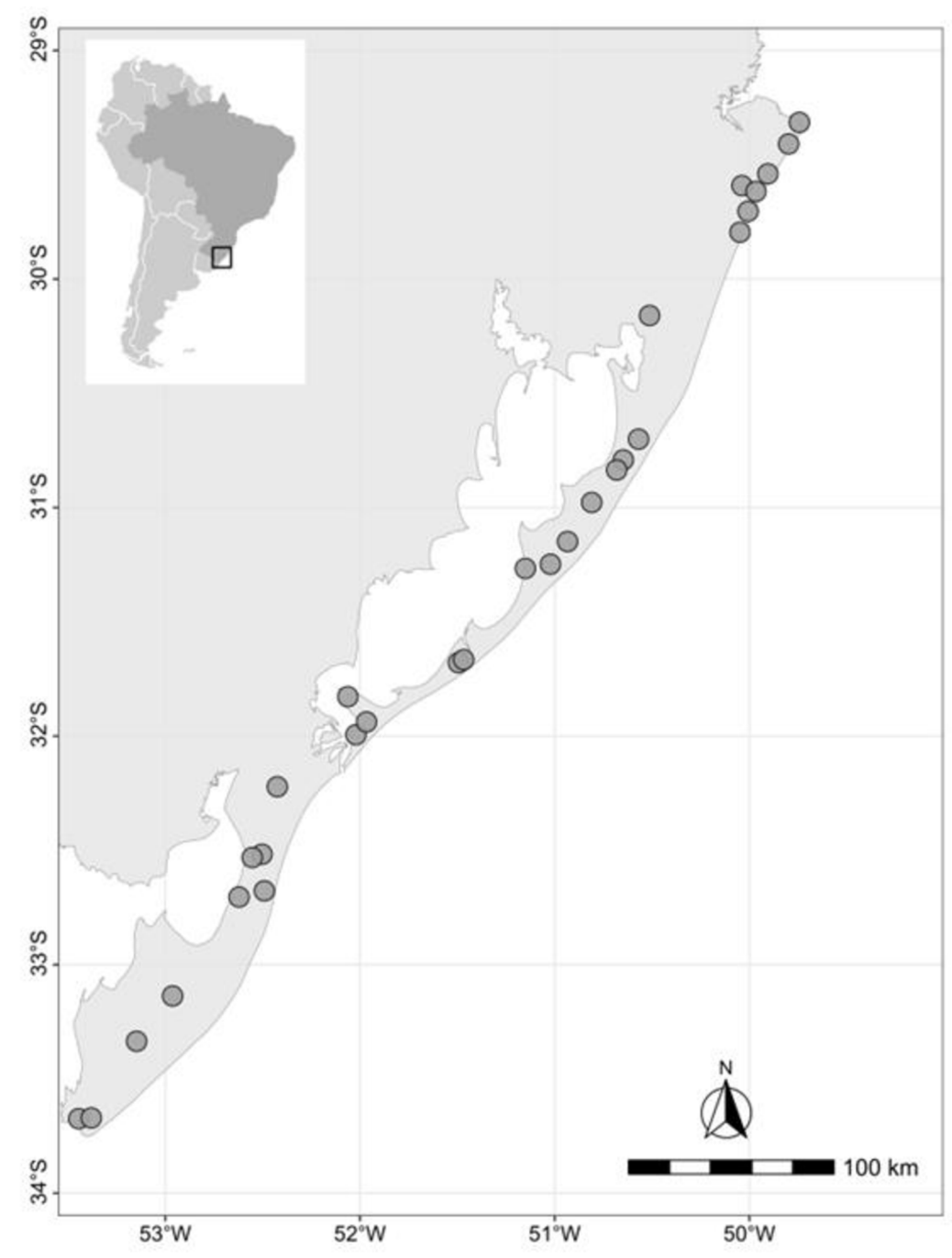


Figure 2. Study area showing the 29 coastal wetlands sampled in the coastal plain of Rio Grande do Sul, Southern Brazil.

We conducted the study during the austral summer of 2016 (January to February), a period characterized by low rainfall. We selected the wetlands based on the definition by Mitsch & Gosselink (2000), focusing on areas with saturated soils or shallow waters, where vegetation is adapted to moist and flooded conditions. Using

this criterion, we selected freshwater wetlands that could be traversed in their entirety for data collection. To ensure that the areas met the objectives of our investigation, we visually inspected each one, avoiding large wetlands or those with undefined boundaries. We also excluded wetlands connected to other aquatic environments, as well as those surrounded by monocultures, such as soybean, rice, pine, and eucalyptus plantations. Additionally, we selected wetlands without connection to the ocean and, therefore, classified them as freshwater (in situ salinity measured = 0 in all 29 sampled wetlands). The areas of the wetlands ranged from 0.19 to 5 hectares, with an average depth of 30 ± 10 cm. We previously used this same dataset to evaluate the relative importance of environmental and spatial factors in macrophyte species richness and community composition (Trindade et al., 2018) and to determine the compositional uniqueness and the importance of species for regional beta diversity (Trindade & Schneck, 2024).

Macrophyte sampling

We sampled the macrophyte communities in each wetland through a comprehensive visual survey of the vegetation across the area, with the same researcher responsible for recording the species at all sites. We conducted a single sampling event in each wetland, with a total time of extensive visual survey varying among the wetlands (60–90 minutes). Sampling was always interrupted after 20 minutes of walking through the wetland without registering a new species. We identified the macrophytes based on specialized literature (Cordazzo & Seeliger, 1995; Irgang & Gastal, 1996) and consultation with botanical experts. We classified the macrophyte species into three functional groups following Irgang & Gastal (1996): emergent, floating (including both free-floating and rooted floating-leaved species), and submerged (encompassing both fixed submerged and free-floating submerged species). We recorded 114 macrophyte species across 29 wetlands, with 90 species in the emergent group, 14 in the floating group, and 10 in the submerged group. For further details about the macrophyte species composition and richness, see Trindade et al. (2018).

Environmental and climatic variables

In each wetland, we determined the environmental variables using a Horiba U50 multiparameter probe. We randomly selected five points in each wetland to

measure dissolved oxygen (DO; mg L⁻¹), pH, electrical conductivity (COND; μ S cm⁻¹), and total dissolved solids (TDS; g L⁻¹). Additionally, we determined the depth (cm) using a graduated ruler and collected water samples for total nitrogen (TN; mg L⁻¹; Allen et al., 1974) and total phosphorus (TP; mg L⁻¹; Valderrama, 1981; Baumgarten & Rocha 1996) analysis (Table S1). Using a GPS (Garmin eTrex), we recorded the altitude (ALT; m.a.s.l.) and geographic coordinates of each wetland, which we later used to calculate the surface area using Google Earth Pro and Quantum GIS (QGIS 3.22 Essen).

We used 12 bioclimatic variables at a spatial resolution of 1 km², derived from the combination of temperature and precipitation data from the global dataset WorldClim2 (Fick & Hijmans, 2017). The climatic variables we used are: annual mean temperature (AMT; °C), temperature seasonality (TS; standard deviation $\times 100$), maximum temperature of the warmest month (MAXTW; °C), minimum temperature of the coldest month (MINTC; °C), mean temperature of the wettest quarter (MTWeQ; °C), mean temperature of the driest quarter (MTDrQ; °C), annual precipitation (AP; mm), precipitation seasonality (PS; coefficient of variation), precipitation of the wettest quarter (PWeQ; mm), precipitation of the driest quarter (PDQ; mm), precipitation of the warmest quarter (PWQ; mm), precipitation of the coldest quarter (PCQ; mm) (Table S1). These variables were also selected by Trindade & Schneck (2024) due to their significant role in the dynamics of macrophyte metacommunities.

Data analyses

To determine the prevailing macrophyte metacommunity patterns in the wetlands of the coastal plain of Rio Grande do Sul, we used the Elements of Metacommunity Structure (EMS) approach originally proposed by Leibold & Mikkelsen (2002) and expanded by Presley et al. (2010). Initially, we evaluated the EMS in the total metacommunity (all species; complete data matrix) and then decomposed the data matrix into three functional groups (emergent, floating, and submerged) and applied the same method to each of the functional groups separately. The method is based on ordination of the incidence matrix, performing reciprocal averaging (Correspondence Analysis – CA), which allows the construction of a gradient where sites are ordered according to species composition and species are ordered according to site occurrences (Leibold & Mikkelsen, 2002). After this

procedure, it is possible to analyze the different metacommunity elements hierarchically: 1) coherence, 2) turnover, and 3) clustering boundary.

Coherence is assessed by the number of interruptions in species distributions or site compositions (embedded absences), which correspond to gaps in species distribution ranges (García-Girón et al., 2020) in the ordinated empirical incidence matrix. This value is then compared to a null distribution of embedded absences generated from 1000 simulated matrices. When the observed number of embedded absences is lower than expected by chance, the metacommunity is considered coherent. When coherence is significantly positive, species distributions respond similarly to a common environmental gradient represented by the ordinated site-by-species presence-absence matrix, indicating that communities are structured by turnover or clustering boundaries. On the other hand, non-significant coherence indicates that species are randomly distributed, suggesting they do not respond to a common environmental gradient (Leibold & Mikkelsen, 2002). Finally, if coherence is negative, it indicates checkerboard distributions (Presley et al., 2019).

In cases where metacommunities exhibit positive and significant coherence, the next step is to analyze turnover. Turnover is measured as the number of times one species replaces another between two sites for each possible pair of species and for each possible pair of sites. The number of observed replacements is then compared to a null distribution that randomly shifts the entire range of species distributions (Leibold & Mikkelsen, 2002). The turnover assessment allows for identifying the following structures: significantly positive turnover (i.e., the number of observed replacements is higher than expected by chance) indicates Gleasonian, Clementsian, or uniformly spaced distributions, requiring additional analysis of clustering boundaries to identify them; significantly negative turnover (i.e., the observed replacement is lower than expected by chance) indicates a nested structure (i.e., hyperdispersed species loss, random species loss, and clumped species loss) (Presley et al., 2010). Cases of significant positive coherence and non-significant turnover can be interpreted as quasi-structures (Presley et al., 2010).

The boundary clump is assessed using the Morisita Dispersion Index (IM), followed by a goodness-of-fit test χ^2 , which allows the identification of Clementsian structures ($IM > 1$; clustered boundaries), uniformly spaced distributions ($IM < 1$; hyperdispersed boundaries), and Gleasonian structures (IM not significant; randomly distributed boundaries) (Presley et al., 2010). In addition, it is possible to identify six

subtypes, as proposed by Presley et al. (2010). For example, non-significant negative turnover refers to quasi-nestedness (clumped species loss, stochastic species loss, and hyperdispersed species loss), and non-significant positive turnover refers to quasi-evenly spaced, quasi-Gleasonian, or quasi-Clementsian patterns. For the coherence, turnover, and clustering boundary analyses, we used the metacom package (Dallas, 2022). To test the significance of the coherence and turnover index values, we used null models, utilizing the "r1" and "quasi-swap" functions from the vegan package (Oksanen et al., 2025). We used 1000 simulations to generate random matrices for testing coherence and turnover.

To identify the environmental gradients responsible for the metacommunity patterns found in the wetlands, we constructed multiple regression trees (MRT) for each dataset: all species, emergent, floating, and submerged species. We used the first axis of the correspondence analysis (CA) as the response variable, with the local environmental and climatic variables as predictors. For the selection of predictor variables, we performed a multicollinearity analysis using the Variance Inflation Factor (VIF) and excluded variables with $VIF > 3$ (Table S2) (Fox & Weisberg, 2011). After variable selection, we used the following predictors for the MRT: local environmental variables (ALT, AREA, DEPH, DO, pH, TDS, TN and TP) and climatic variables (AMT, MTD_rQ and PS) (Table S2). We used the rpart package (Therneau & Atkinson, 2025) for MRT. All analyses were performed in the R environment (R Core Team, 2025).

Results

Elements of the metacommunity structure of aquatic macrophytes in wetlands

The total metacommunity (all species) exhibited positive and significant coherence (Observed/Randomized < 1), indicating few interruptions in species distributions between sites. Moreover, significant positive turnover (Observed/Randomized > 1) suggested substantial species replacement across the sampled sites and the Morisita dispersion index showed a value greater than 1, reflecting high species overlap in the studied wetlands. Together, these results indicate that the observed metacommunity type was Clementsian (Table 1 and Figure S1a), characterized by species replacement in blocks, suggesting community organization in groups with a substitution of dominant species along environmental gradients.

Similarly, emergent species exhibited a Clementsian pattern, characterized by a significant positive coherence (Observed/Randomized < 1), significant positive turnover (Observed/Randomized > 1), and an Morisita dispersion index greater than 1 (Table 1 and Figure S1b). Floating species exhibited positive and significant coherence (Observed/Random < 1), but non-significant turnover (Observed/Random < 1) and non-significant Morisita dispersion index > 1, a metacommunity structure classified as quasi-nested stochastic species loss (Table 1; Figure S1c). This pattern indicates that, although there is a tendency toward nestedness, in which communities with fewer species share part of the species found in richer communities, the structure is not fully ordered. Finally, submerged species also exhibited positive and significant coherence (Observed/Random < 1) and turnover (Observed/Random > 1), highlighting the importance of species replacement along environmental gradients. The Morisita dispersion index was greater than 1 but not significant, suggesting moderate species overlap across sampling sites, classifying this metacommunity as Gleasonian (Table 1 and Figure S1d), which is characterized by individualistic species distributions and no clear boundary pattern.

Table 1. Summary of the Elements of Metacommunity Structure (EMS) for the aquatic macrophyte metacommunity from the coastal plain of Rio Grande do Sul, Southern Brazil. Bold values are statistically significant

Element	Total community	Emergent	Floating	Submerged
Number of communities	29	29	27	22
Coherence				
Observed	1,679	1,282	93.000	27.000
Randomized	2,345	1,829	160.384	102.403
Observed/Randomized	0.715	0.700	0.579	0.263
<i>P-value</i>	< 0.001	< 0.001	< 0.001	< 0.001
Turnover				
Observed	85,940	49,979	1,395	662.000
Randomized	52,805	28,451	2,070	408.708
Observed/Randomized	1.627	1.756	0.673	1.619
<i>P-value</i>	< 0.001	< 0.001	0.246	0.018
Boundary clumping				
Morisita's index	1.610	1.799	1.071	1.318
<i>P-value</i>	< 0.001	< 0.001	0.328	0.231
<i>Degrees of freedom</i>	26	24	24	19
EMS type	Clementsian	Clementsian	Quasi-nested stochastic	Gleasonian

Element	Total community	Emergent	Floating	Submerged
Number of communities	29	29	27	22
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Turnover				
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Observed/Randomized	1.627	1.756	0.673	1.619
<i>P-value</i>	< 0.001	< 0.001	0.246	0.018
			species loss	

Environmental and climatic factors determining the metacommunity types of macrophytes in wetlands

Regarding the dataset of the total metacommunity (all species), the main environmental variables related to species distributions were annual mean temperature (AMT) and total phosphorus (TP). The AMT was the variable responsible for the first split, forming two major branches: the first included communities in wetlands with AMT < 18 °C (CA Axis 1 = -0.907; n = 7), located in the southern portion of the coastal plain (Figure 3, Table S3 and Figure S2a). The second branch included communities in wetlands with AMT > 18 °C, with an internal node based on total phosphorus concentration that separated the communities into two subgroups: the first with TP < 0.3 mg L⁻¹ (CA Axis 1: 0.010; n = 15) and the second with TP > 0.3 mg L⁻¹ (CA Axis 1: 0.773; n = 7), located in the central and north portions of the coastal plain.

Regarding the functional groups, distinct environmental variables explained species distributions. For emergent species, we identified that annual mean temperature (AMT) was the variable responsible for the root node, separating communities into two major branches (Figure 3, Table S3 and Figure S2b). The first branch, corresponding to AMT < 19 °C (CA Axis 1: -0.368; n = 19), formed two groups of communities, whose distributions were determined by temperatures below 19 °C, located in the northern and southern regions of the studied coastal plain (Figure 3). The second branch, with AMT > 19 °C (CA Axis 1: 0.657; n = 10), resulted in another group of communities distributed in warmer areas (Figure 3) in the central part of the coastal plain.

For floating species, we observed that total phosphorus (TP) was the variable responsible for the first split, generating two main nodes (Figure 3, Table S3 and Figure S2c). The first node grouped communities with $TP < 0.045 \text{ mg L}^{-1}$, while the second node included communities with $TP > 0.045 \text{ mg L}^{-1}$. Within the group with $TP > 0.045 \text{ mg L}^{-1}$, a second split based on altitude created two internal nodes: one grouping communities distributed in areas with altitudes $< 9 \text{ m.a.s.l.}$ (CA Axis 1: 0.295; $n = 9$ communities), and the other grouping communities in areas with altitudes $> 9 \text{ m.a.s.l.}$ (CA Axis 1: 1.890; $n = 11$ communities). Communities with $TP < 0.045 \text{ mg L}^{-1}$ underwent no further splits (CA Axis 1: 0.537; $n = 7$ communities). Communities within the three branches from the regression tree were distributed throughout the sampling area.

Finally, the distribution of submerged species was mainly related to annual mean temperature (AMT), which was the variable responsible for splitting the data into two major branches (Figure 3, Table S3 and Figure S2d): the first, with $AMT < 18 \text{ }^{\circ}\text{C}$ (CA Axis 1: -0.990; $n = 7$ communities), and the second with $AMT > 18 \text{ }^{\circ}\text{C}$ (CA Axis 1: 0.453; $n = 15$ communities). The first branch, included communities in the southern colder portion of the sampling area, whereas the second branch included communities distributed in the central and northern portions of the sampling area.

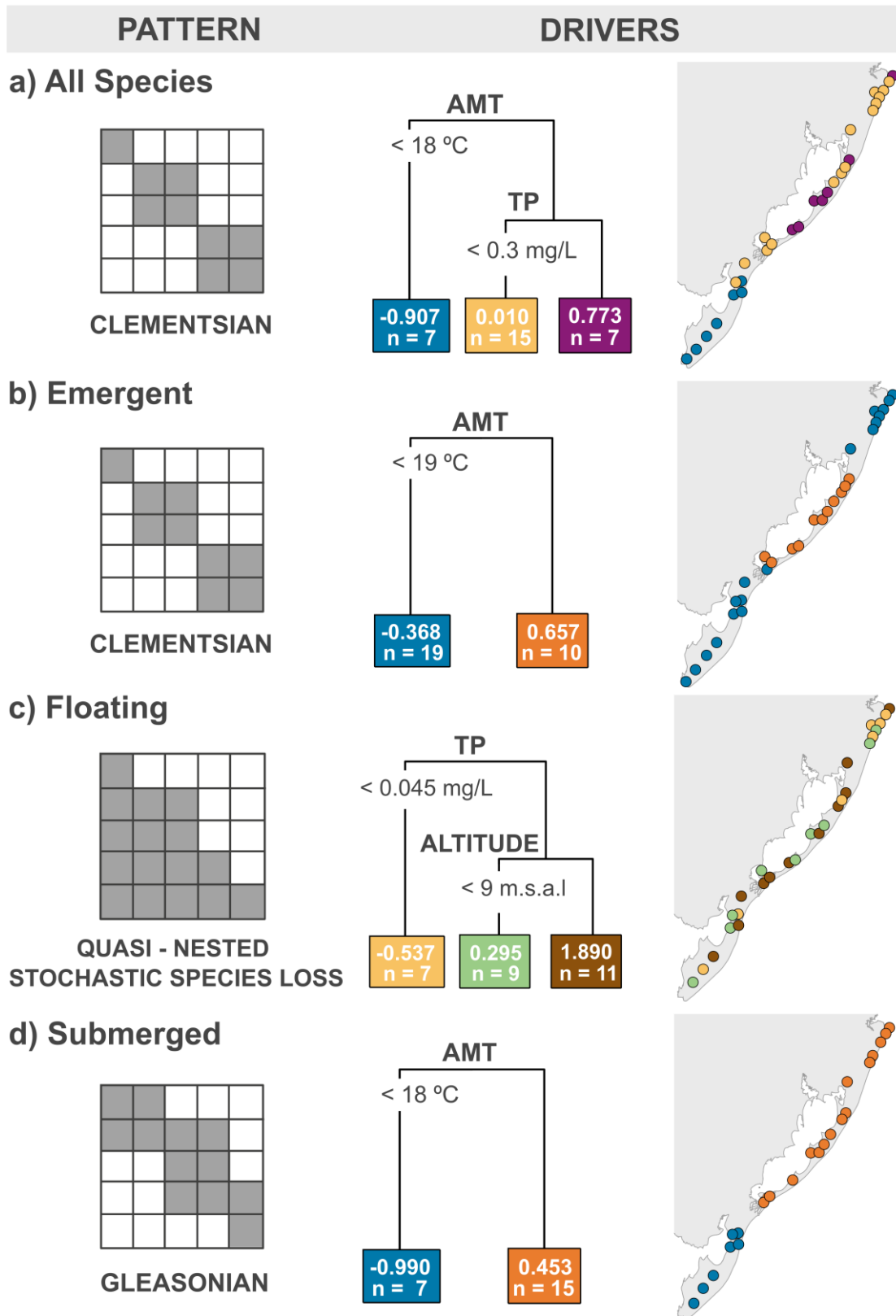


Figure 3. Patterns of Elements of Metacommunity Structure (EMS) for the total macrophytes metacommunity (all species), and emergent, floating (including both free-floating and rooted floating-leaved species), and submerged (including both

fixed submerged and free-floating submerged species) metacommunities from the coastal plain of Rio Grande do Sul, Southern Brazil. Multiple Regression Tree (MRT) illustrating the hierarchical partitioning of sampling sites based on environmental variables. In the MRT, AMT represents annual mean temperature, and TP represents total phosphorus. Each terminal node (leaf) in the MRT displays the mean group score (top number) along the first axis of the Correspondence Analysis (CA) and the number of sampling units within that group (bottom number). The map shows the corresponding geographical distribution of these MRT-defined groups, with different colors indicating distinct groups associated with specific combinations of annual mean temperature, total phosphorus levels, and altitude.

Discussion

Understanding the factors that determine the distribution of species, whether in space or time, is a challenging topic in community ecology (García-Girón et al., 2021; Leibold et al., 2022; Guzman et al., 2022; Barbier et al., 2025). In recent years, we began expanding knowledge on the distribution of macrophytes in wetlands by applying the main approaches of metacommunity ecology to aquatic macrophyte assemblages along the 640 km of the coastal plain in southernmost Brazil. Initially, using this same dataset, we found that species composition and richness of macrophytes are influenced by environmental and spatial variables, with the relative influence of these variables depending on the functional group (Trindade et al., 2018). Recently, we observed that the compositional uniqueness of assemblages is determined by environmental filters, particularly water chemistry and climatic variables (Trindade & Schneck, 2024). Based on these studies, we formulated the hypotheses that guided the present study, aiming to understand which distribution patterns of the macrophyte metacommunity prevail in the coastal plain of Rio Grande do Sul. To this end, we analyzed the Elements of Metacommunity Structure (EMS) to identify the best fit of our empirical data (total dataset and functional groups: emergent, floating, and submerged) to the idealized metacommunity types proposed by Leibold & Mikkelsen (2002) and complemented by Presley et al. (2010). Additionally, we used regression trees to identify the environmental variables responsible for the observed species distribution patterns. Our results indicate that the total dataset of the macrophyte metacommunity in the wetlands of the coastal plain of Rio Grande do Sul exhibited a Clementsian distribution pattern, driven by

annual mean temperature and total phosphorus. In line with our hypothesis, we also detected distinct metacommunity patterns for each functional group, determined by a few environmental and climatic factors.

The Clementsian structure observed for the total metacommunity is characterized by species replacement in clusters. Clementsian structures generally exhibit coherent species distributions, with species associations responding similarly to environmental gradients (Leibold & Mikkelsen, 2002; Presley et al., 2010), and differing from other species groups (Clements, 1916). Clementsian patterns have been documented in metacommunity studies for various biological communities and aquatic systems (Heino et al. 2015), including microcrustaceans in wetlands (Gascón et al. 2016), benthic invertebrates in streams (Tonkin et al. 2016) and macrophytes in lakes (García-Girón et al. 2020). The macrophyte metacommunities analyzed by García-Girón et al. (2020) were predominantly structured by Clementsian and almost Clementsian patterns along a 10,000 km latitudinal gradient, suggesting the presence of groups of species with similar responses to environmental factors.

Here, we analyzed macrophytes from wetlands, which exhibit distinct dynamics compared to lakes due to their higher hydrological heterogeneity. In our study, annual mean temperature and total phosphorus were identified as key factors structuring communities in the coastal plain. Temperatures below 18 °C were an important driver of community structure in the southern portion of the coastal plain, consistent with studies highlighting temperature as a key environmental filter influencing species distribution and abundance in subtropical regions (Pereira et al., 2012). Meanwhile, higher temperatures, together with variations in phosphorus concentration, were the primary drivers of community distribution in the central and northern portions of the coastal plain, reflecting the role of phosphorus as an environmental filter, selecting different communities, and influencing species richness and composition (Jewells et al., 2023). Phosphorus availability is fundamental for controlling primary productivity and nutrient dynamics, which directly impact species distribution (Alahuhta et al., 2021). These results highlight the complex interaction between temperature and phosphorus in structuring metacommunities, with temperature acting as a thermal filter and phosphorus as a nutritional filter favoring species with specific requirements (Jewell et al., 2023).

Our results also showed a Clementsian distribution pattern for emergent species, the sole functional group present in all the studied wetlands and the one that

dominated the communities, highlighting their relevance in the studied coastal plain. Some plants, such as *Schoenoplectus californicus* (C. A. Mey) Soják (occurrence = 18 wetlands), exhibited broad environmental adaptability, explaining their consistent presence, while others had more restricted distributions, such as *Senecio bonariensis* Hok & Ard. (occurrence = 1 wetland). Emergent species are exposed to daily and seasonal temperature fluctuations, which can influence their growth and reproduction, affecting processes such as germination, biomass production, and competitiveness, as well as modifying vegetation dynamics and ecological interactions (Santamaría, 2002).

Regarding floating species, we initially hypothesized that this group would exhibit a Gleasonian pattern, characterized by individualistic species responses to environmental gradients and high species turnover. However, our analysis revealed a quasi-nested structure with stochastic species loss, indicating a high degree of species overlap and a gradual and somewhat unpredictable loss of species richness. This suggests that floating species may have broader ecological tolerances than expected in strictly nested communities, allowing them to persist across a wider range of environmental conditions. In classic nested metacommunities, species loss follows predictable patterns, with three distinct forms of species loss identified by Presley et al. (2010). In our case, although there is evidence of nestedness, the pattern is not strong enough to be considered fully predictable or entirely random.

Among the deterministic factors, total phosphorus availability emerged as a key driver in structuring the floating species community. Phosphorus had a strong influence on species occurrence, such that variations in phosphorus levels affected which species could persist in the studied wetland. These patterns are consistent with previous studies showing that variations in phosphorus levels drive changes in species communities (Jewells et al., 2023; Crocker et al., 2023). Additionally, altitude played a significant role, possibly exerting its influence through the modulation of hydrological conditions. For example, it could be expected that during periods of drought, lower-lying areas would exhibit prolonged retention of water, while higher areas would experience more rapid desiccation, influencing habitat suitability. This is consistent with the findings of Rolon et al. (2010), who reported that altitude affected macrophyte species richness in the same coastal plain studied here. However, the distribution of floating species does not strictly conform to hierarchical environmental constraints or, in other words, it does not exhibit a clearly defined distribution pattern.

Instead, it suggests an interaction between stochastic processes (e.g., dispersal limitation, demographic stochasticity) and local environmental filtering, particularly by total phosphorus and altitude.

The Gleasonian pattern we found for the submerged functional group indicates that species replacement occurs gradually and diffusely (Leibold & Mikkelsen, 2002), with no abrupt boundaries in species composition. This pattern suggests the influence of weaker environmental gradients in the aquatic environment, particularly those associated with annual mean temperature. In a Gleasonian structure, as originally described by Gleason (1926), species respond individualistically to environmental conditions, and community composition arises from the overlap of these individual responses rather than from cohesive species groups. As a result, turnover is positive and significant, but the distribution of species' ranges along environmental gradients tends to be random, not differing significantly from what would be expected by chance (Leibold & Mikkelsen, 2002). Our results indicate that annual mean temperature played a key role in shaping this pattern of gradual and diffuse species replacement, reflecting the interaction between environmental conditions and species-specific tolerances. Temperature is known to influence key physiological processes such as photosynthesis and nutrient uptake, which affect the growth, survival, and distribution of submerged macrophytes (Santamaría, 2002). For example, two species recorded only in the southernmost wetlands *Stuckenia pectinata* (L.) Börner and *Cabomba caroliniana* A. Gray are adapted to cooler conditions and show physiological stress at temperatures above 30 °C (Xian et al., 2024). In general, submerged plants exhibit optimal photosynthetic and respiratory performance within a relatively narrow thermal window (20–35 °C), with limited acclimation capacity (Santamaría, 2002), which may explain their diffuse and gradient-dependent distributions.

The application of EMS has limitations, such as sampling methods, site and species selection, and the spatial and temporal scales adopted (Leibold & Mikkelsen, 2002). Previous studies have highlighted similar or divergent patterns, indicating multiple factors that structure communities, including unmeasured variables, scale influence, and biotic interactions (García-Girón et al., 2020; Leibold et al., 2022). Despite these caveats, combining EMS with other approaches can enhance the understanding of species distribution patterns and their determinants. While there is an overall structure, each functional group responded specifically to environmental

variables, confirming that analyzing the total metacommunity can obscure specific patterns. By distinguishing macrophyte species into functional groups, we revealed dynamics that would be hidden in a general approach, contributing to a more detailed understanding of metacommunity dynamics. For instance, on one hand, Clementsian patterns with high turnover indicate the importance of protecting wetlands along the entire studied coastal plain. On the other hand, the almost stochastic loss of floating species suggests that targeted strategies, such as the protection and restoration of specific areas, may be necessary.

In summary, the total macrophyte metacommunity, representing the complete set of sampled species, exhibited a metacommunity structure consistent with the Clementsian pattern, characterized by significant coherence, turnover, and clumped distributional boundaries. This means that species within the metacommunity are distributed coherently, with block replacement and aggregated boundaries among them, indicating that species tend to respond similarly to environmental gradients, with block species replacement along those gradients. However, when partitioning the total matrix into functional groups, we observed distinct patterns, revealing that different life forms may respond in varied ways to the same environmental gradients, depending on the perspective of analysis. The separate analysis of functional groups, combined with the application of the Elements of Metacommunity Structure (EMS), refined the interpretation of macrophyte distribution patterns in wetlands. Furthermore, the use of regression trees helped identify the main environmental and climatic factors associated with the observed metacommunity types, contributing to a broader understanding of the structure and processes shaping these metacommunities.

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Author contribution statement

All authors contributed to the study conception and design. Material preparation, data collection were performed by CRTT. Analyses were performed by CRTT, and MGJ. Funding acquisition and Supervision FS. The first version of the manuscript was written by CRTT, and all authors commented on previous versions of the manuscript and read and approved the final manuscript.

Data Availability Statement

The data will be made available upon request to the corresponding author.

Conflict of Interest Statement

The authors declare that they have no conflict of interest.

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Supplementary Material

Ecological Research

Elements of the structure of macrophyte metacommunities in coastal wetlands: relationships with limnological and climatic variables

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Tables

Table S1. Environmental variables in the wetlands of the coastal plain of Rio Grande do Sul, Southern Brazil.

Environmental variables	Min	Max	Mean $\pm$ sd
Depth (cm)	12	50	30 $\pm$ 10
Dissolved Oxygen (mg L ⁻¹)	3.0	9.7	5.9 $\pm$ 1.4
pH	4.4	7.8	6.1 $\pm$ 0.7
Electrical Conductivity (μ S cm ⁻¹)	25.0	587.8	109.1 $\pm$ 105.7
Total Dissolved Solids (g L ⁻¹)	0.02	0.4	0.1 $\pm$ 0.1
Total Nitrogen (mg L ⁻¹)	0.6	12.3	3.6 $\pm$ 3.0
Total Phosphorus (mg L ⁻¹)	0.004	1.2	0.2 $\pm$ 0.3
Wetland Area (ha)	0.2	5	4.5 $\pm$ 4.0
Annual Precipitation (mm)	1172	1491	1335.1 $\pm$ 111.4
Precipitation Seasonality (coef. of variation)	7	18	12.3 $\pm$ 3.2

Precipitation of Wettest Quarter (mm)	312	404	372.2 ± 29.0
Precipitation of Driest Quarter (mm)	230	247	385.0 ± 35.6
Precipitation of Warmest Quarter (mm)	295	383	336.8 ± 30.0
Precipitation of Coldest Quarter (mm)	300	404	359.6 ± 31.1
Annual Mean Temperature (°C)	16.8	18.9	18.2 ± 0.7
Temperature Seasonality (SD*100)	279	383	339 ± 31
Max Temperature of Warmest Month (°C)	26.4	28.4	27.6 ± 0.7
Min Temperature of Coldest Month (°C)	8.1	11.4	9.6 ± 1.1
Mean Temperature of Wettest Quarter (°C)	12.7	19.5	15.1 ± 1.8
Mean Temperature of Driest Quarter (°C)	15.4	21.9	20.0 ± 2.3
Altitude (m)	2	22	10.1 ± 5.1

SD: standard deviation

Table S2. Variation inflation factors (VIFs) estimated to control for multicollinearity. Bold values indicate the explanatory variables selected for the final models (VIF < 3). DO = Dissolved Oxygen; TDS = Total Dissolved Solids; TN = Total Nitrogen; TP = Total Phosphorus; AMT = Annual Mean Temperature; AP = Annual Precipitation; PS = Precipitation Seasonality; PWeQ = Precipitation of Wettest Quarter; PDQ = Precipitation of Driest Quarter; PWQ = Precipitation of Warmest Quarter; PCQ = Precipitation of Coldest Quarter; TS = Temperature Seasonality; MAXTW = Max Temperature of Warmest Month; MINTC = Min Temperature of Coldest Month; MTWeQ = Mean Temperature of Wettest Quarter; MTDQ = Mean Temperature of Driest Quarter; ALT = Altitude (m).

Variables	VIF 1	VIF 2	VIF 3	VIF 4	VIF 5	VIF 6	VIF 7	VIF 8	VIF 9	VIF 10
Depth	2.70	2.63	2.29	2.25	1.70	1.68	1.67	1.47	1.44	1.42
DO	3.71	3.64	3.53	2.52	2.26	2.11	2.11	1.93	1.93	1.88
pH	5.43	4.78	4.31	2.77	2.76	2.75	2.64	2.59	2.42	2.41
TDS	4.56	4.14	4.13	3.44	2.91	2.91	2.91	2.70	2.63	2.57
TN	4.39	3.89	3.42	3.28	2.50	2.18	2.14	2.07	1.88	1.75
TP	3.37	3.26	3.13	2.58	2.57	2.52	2.50	2.50	2.38	2.16
Area	3.97	3.86	3.85	3.08	3.07	2.97	2.69	2.58	2.53	2.05
AMT	708.96	573.66	545.41	423.55	79.11	26.73	25.23	4.03	2.50	2.45
AP	5941.78	-	-	-	-	-	-	-	-	-
PS	102.64	68.63	61.59	10.50	8.93	8.88	8.74	5.03	2.78	2.24
PWeQ	733.10	731.19	572.39	-	-	-	-	-	-	-

PDQ	2077.79	756.31	-	-	-	-	-	-	-	-
PWQ	44.52	29.58	26.35	25.54	24.55	24.43	33.20	-	-	-
PCQ	541.08	155.30	96.55	19.89	18.53	15.57	8.09	7.34	-	-
TS	598.66	557.43	291.23	284.92	218.19	-	-	-	-	-
MAXTW	35.29	32.77	32.59	26.22	23.32	8.43	8.17	4.45	3.23	-
MINTC	514.92	465.09	445.90	439.62	-	-	-	-	-	-
MTWeQ	1560.84	658.33	405.85	141.39	89.52	51.06	-	-	-	-
MTDrQ	18.14	13.26	10.93	9.62	7.24	6.70	5.04	4.29	2.88	1.99
ALT	9.61	6.36	5.90	3.45	3.45	3.45	3.45	2.77	2.70	2.52

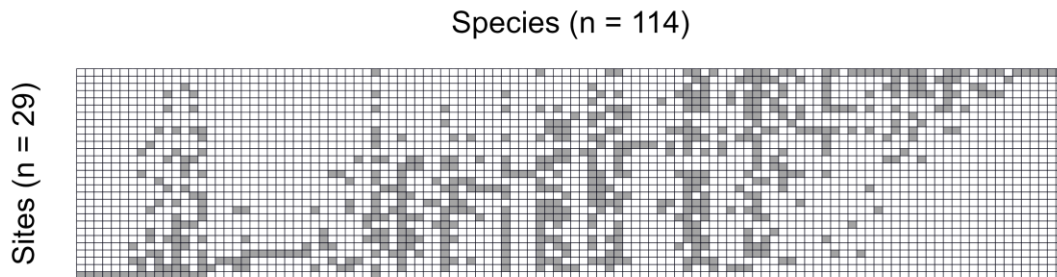
Table S3. Summary of the multiple regression tree (MRT) for the a) total community b) emergent, c) floating (including both free-floating and rooted floating-leaved species), and d) submerged (including both fixed submerged and free-floating submerged species) metacommunities from the coastal plain of Rio Grande do Sul, Southern Brazil.

	Error	Cross-validation	Std. Error	Complexity parameter
a) Total community				
Total tree	1.000	1.070	0.796	0.210
Split 1	0.789	1.289	0.794	0.081
Split 2	0.707	1.210	0.730	0.010
b) Emergent				
Total tree	1.000	1.068	0.653	0.281
Split 1	0.718	0.982	0.553	0.010
c) Floating				
Total tree	1.000	1.054	0.196	0.251
Split 1	0.748	1.544	0.299	0.209

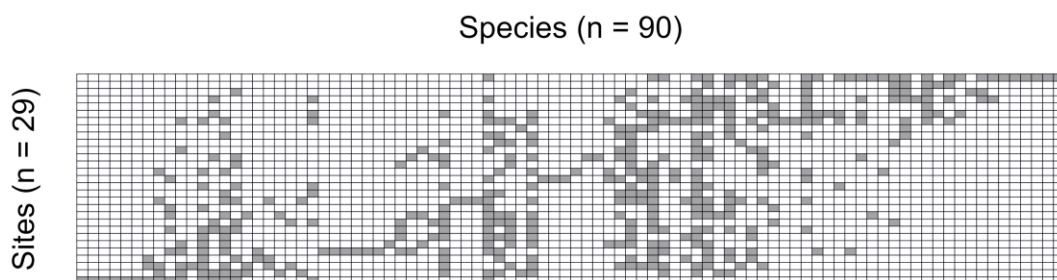
Split 2	0.539	1.544	0.299	0.010
d) Submerged				
Total tree	1.000	1.137	0.411	0.481
Split 1	0.518	1.339	0.592	0.010

Figures

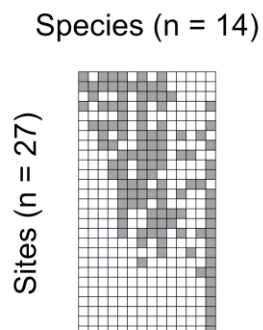
a) All Species



b) Emergent



c) Floating



d) Submerged

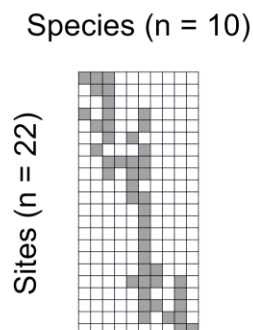


Figure S1. Types of aquatic macrophyte metacommunities in the 29 wetlands of the coastal plain of Rio Grande do Sul, Southern Brazil, identified after applying EMS: Total community – Clementsian pattern; Emergent group – Clementsian pattern; Floating group (including both free-floating and rooted floating-leaved species) – Quasi-nested stochastic structure pattern; Submerged group (including both fixed submerged and free-floating submerged species) – Gleasonian pattern. Outputs from the ESM analysis in the “metacom” package.

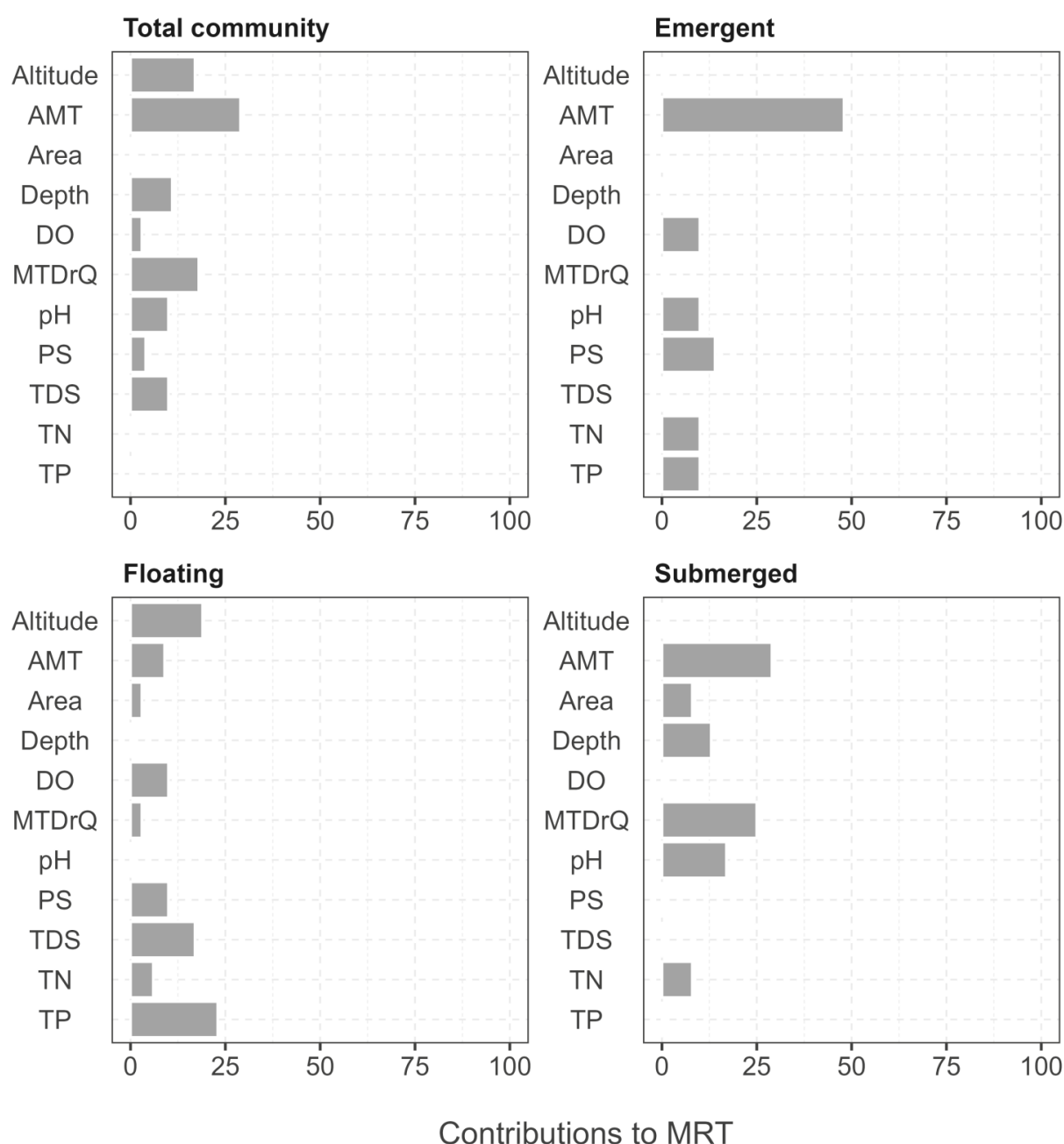


Figure S2. Environmental and climate variables importance for each multiple regression tree (MRT). The floating group includes both free-floating and rooted floating-leaved species and the submerged group includes both fixed submerged and free-floating submerged species. Variables included: AMT, Annual Mean Temperature; DO, Dissolved Oxygen; MTDrQ, Mean Temperature of Driest Quarter; PS, Precipitation Seasonality; TDS, Total Dissolved Solids; TP, Total Phosphorus, and TN Total Nitrogen.

CAPÍTULO 2

Compositional uniqueness and species contribution to beta diversity of aquatic macrophyte metacommunities from coastal wetlands²

Abstract

The partitioning of overall beta diversity into local contributions (LCBD; compositional uniqueness) and species contributions (SCBD) has enhanced the understanding of the organization of metacommunities. Here, we evaluated LCBD and SCBD of aquatic macrophyte metacomunnties from 29 subtropical coastal wetlands, covering an extension of 640 km, in Southern Brazil. Furthermore, we assessed the environmental uniqueness, considering both the physical and chemical variables of water in wetlands, as well as climatic variables. We assessed the environmental and spatial correlates of LCBD and the environmental correlates of SCBD. We expected that (i) communities with greater compositional uniqueness would be found in environmentally more unique wetlands; (ii) the compositional uniqueness would also be related to climatic variables that determine the hydrological changes in wetlands; (iii) the contribution of emergent species to beta diversity would be lower than of floating and submerged species. The compositional uniqueness did not present a clear spatial structure, being positively related to uniqueness in water chemistry and negatively to the mean air temperature during the driest quarter. The species contribution to beta diversity was higher for floating species than for emergent ones. Moreover, SCBD correlated to climatic variables and presented a positive relationship with site occupation, suggesting that more frequent species in terms of site occurrence contribute most to beta diversity. Our results show the importance of local environmental and broader climatic predictors in determining the compositional uniqueness of macrophyte communities and the species contributions to overall beta diversity in the coastal wetlands of Southern Brazil.

Keywords: LCBD, SCBD, beta diversity, wetland vegetation, hydrophytes

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Introduction

Untangling the variation in species composition among sites in a geographic area (beta diversity; Whittaker 1960; Anderson et al. 2011) into its components is fundamental to understand how biodiversity varies in space (Li et al. 2020; Panja et al. 2022; García-Girón et al. 2023) and time (Legendre and Gauthier 2014; Winegardner et al. 2017; Legendre and Condit 2019). In this context, partitioning overall beta diversity into the contribution of each local community (local contribution to beta diversity, LCBD) and of each species (species contribution to beta diversity, SCBD) (*sensu* Legendre and De Cáceres 2013) may shed light on the distinct factors affecting the organization of metacommunities (Tonkin et al. 2016; Schneck et al. 2022).

The contribution of each local community to beta diversity (LCBD) depends on its compositional uniqueness, that is, the degree of differentiation in species composition in relation to the regional typical community composition (Legendre and De Cáceres 2013). More unique species compositions can be related either to unique environmental characteristics or to dispersal limitation due to geographic distance among sites (Heino et al. 2017; Landeiro et al. 2018). In freshwater ecosystems, compositional uniqueness was shown to be positively related to environmental uniqueness generated by stream physical characteristics for diatoms (Castro et al. 2019), insects (Schneck et al. 2022) and macrophytes (Bomfim et al. 2023). However, this relationship between compositional and environmental uniqueness is not explicitly considered in most studies (e.g., Tonkin et al. 2016; Bomfim et al. 2023; but see Heino et al. 2022). Moreover, most previous studies on freshwaters have focused on evaluating local environmental correlates of compositional uniqueness (e.g., Heino and Grönroos 2017; Leão et al. 2020), so that the knowledge about the importance of regional-scale environmental gradients, such as climate, is scarce (Benito et al. 2020; Panja et al. 2022; Martínez-Román et al. 2023).

Species that contribute the most to beta diversity (SCBD) within a region of interest are those that vary more or less than average among sites (Legendre and De Cáceres 2013). For freshwater communities it has been shown that species with high SCBD have either intermediate (Szabó et al. 2019; Pozzobom et al. 2020) or high occupancy (Vilmi et al. 2017a) and are regionally abundant (Vilmi et al. 2017a; Szabó et al. 2019). However, an alternative approach to better understand why certain

species or groups of species may contribute more than others to beta diversity would be to relate SCBD to species traits (Li et al. 2020; Schneck et al. 2022) or functional groups (Heino and Grönroos 2017; Pozzobom et al. 2020) and environmental variables (Schneck et al. 2022). For example, in a study conducted in Brazilian floodplain lakes, functional groups of aquatic macrophytes partially explained SCBD (Pozzobom et al. 2020).

Wetlands are functionally complex ecosystems characterized by fluctuations in water level, which determine their physical, chemical, and biological conditions (Junk et al. 2014). Despite harboring a significant portion of biodiversity, these ecosystems are among the most vulnerable in the world (Junk et al. 2014), especially due to the influence of factors such as climate change, urban development, pollution, and invasive species, highlighting the urgency of protection and conservation actions (Maltchik et al. 2004). In Southern Brazil, palustrine wetlands represent a large proportion of wetlands, approximately 90%, and they can vary from permanently flooded to never flooded, but remain saturated for long periods during the annual cycle (Maltchik et al. 2004). They include a variety of formations such as marshes, shallow lakes, meanders, and floodplains influenced by factors such as precipitation, surface runoff, and groundwater discharge (Maltchik et al. 2004).

Aquatic macrophytes are a key component in wetlands (De Magalhaes et al. 2016) and are characterized by a wide range of strategies that enables them to establish in distinct habitats (Santamaría 2002; Lacoul and Freedman 2006). Some species can grow through the water surface, while others live floating or submerged in the water column (Chambers et al. 2008; Murphy et al. 2019). Due to such distinct architecture, the importance of local and regional environmental factors and spatial processes in determining the distribution of species (Alahuhta and Heino 2013; Gillard et al. 2020) differs among life forms (Schneider et al. 2018; Trindade et al. 2018; Garcia-Girón et al. 2023). For example, in subtropical coastal wetlands, it has been shown that the distribution of floating and submerged species was mainly influenced by water quality and spatial variables, respectively, while emergent species, characterized by a broader distribution, were influenced by climatic variables (Trindade et al. 2018). Moreover, it has been suggested that relating SCBD values to macrophyte life forms can improve our ability to detect species that contribute more to beta diversity (Pozzobom et al. 2020; Bomfim et al. 2023). Finally, identifying communities and species contributing the most to beta diversity would help

understand key aspects of the organization of macrophyte metacommunities in wetlands.

We investigated the contribution of local communities and species to beta diversity of aquatic macrophytes in coastal wetlands, over c. 640 km in subtropical Brazil. We assessed the environmental and spatial correlates of LCBD and the environmental and biological correlates of SCBD. We expected that: (i) communities with greater compositional uniqueness would be found in environmentally more unique wetlands; (ii) given the large spatial scale of our study, compositional uniqueness would also be related to climatic variables that determine the hydrological changes in wetlands; (iii) the contribution of emergent species to beta diversity would be lower than of floating and submerged species because the first ones are less dependent on water quality and are more widely distributed.

Material and Methods

Study area

We conducted the study in 29 wetlands at the coastal plain of Rio Grande do Sul State, between coordinates (29°16'14.96" S and 49°37'15.08" W) and (33°37'25.15" S and 53°13'46.56" W), South Brazil (Fig. 1). The coastal plain extends approximately 640 km, covering 22.740 km² of emerged lands and 14.260 km² of water surfaces, totaling 37.000 km² (Schwarzbold and Schäfer 1984). Originating from the Cenozoic, the coastal plain expanded primarily during the Quaternary period through alluvial fans and barrier-lagoon depositional systems, forming large bodies of water such as the Patos lagoon and lakes Mirim and Mangueira (Barboza et al. 2009). Currently, the landscape of the coastal plain consists of estuaries and deltas, marine beaches, rivers and streams, savannas, palm groves, flooded fields and forests (seasonal, temporary, or permanent), lakes and lagoons, and permanently or temporarily wetlands (known in southern Brazil as *banhados*) (Becker et al. 2007). The climate of the region is humid subtropical (Maluf 2000). Annual precipitation varies between 1000 and 1500 mm, and the average annual temperature ranges between 16 and 20 °C, with average temperatures between 22 and 26 °C in the hottest months and between 10 and 15 °C in the coldest months (Nimer 1977).

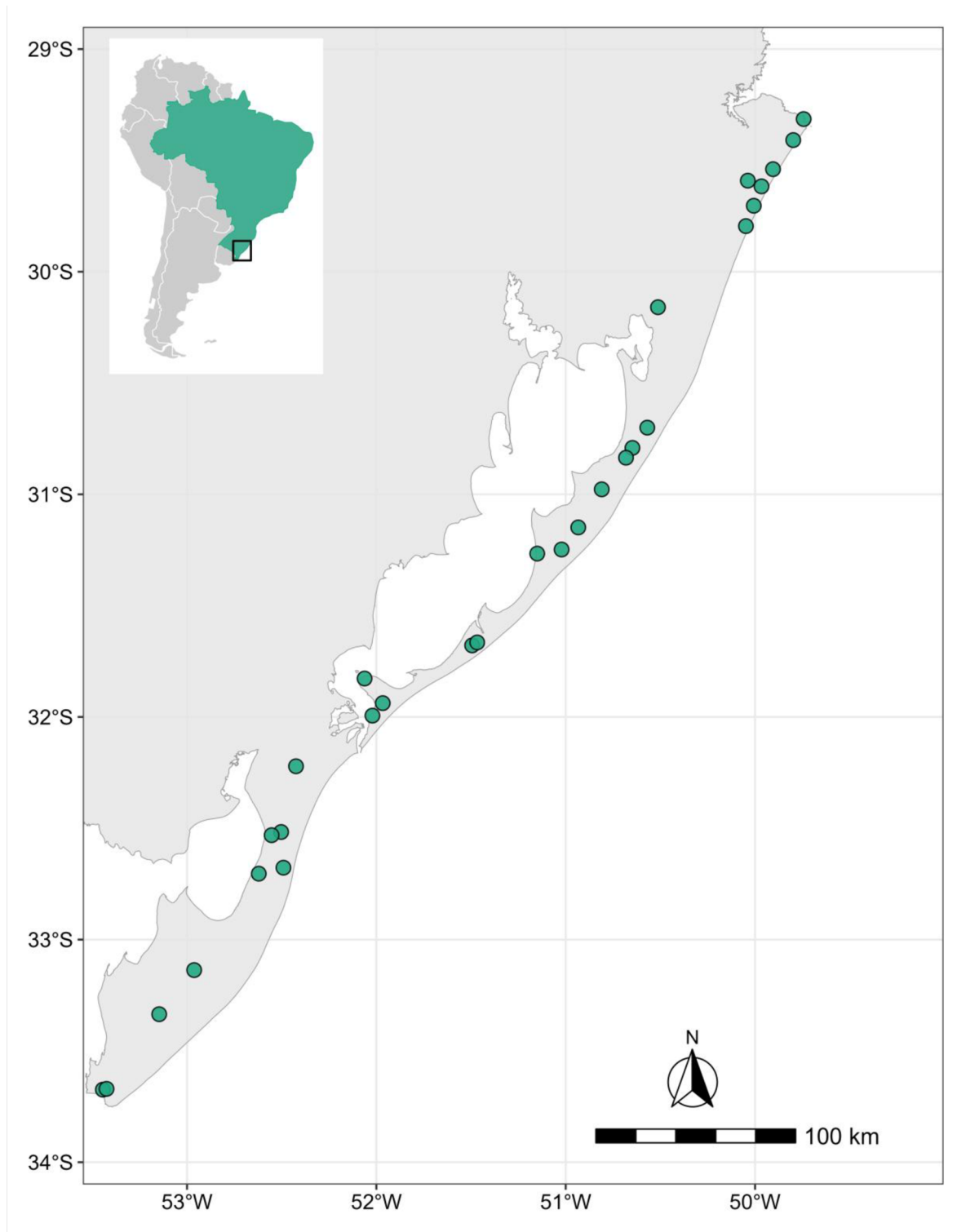


Figure 1. Study area showing the 29 wetlands sampled (green circles) in the coastal plain of Rio Grande do Sul State, Southern Brazil. The inset shows South America, with Brazil shown in green.

To select the sampling sites, we chose areas with saturated soils or shallow waters, where vegetation is adapted to moist conditions and flooding, following the definition of wetlands by Mitsch and Gosselink (2000). Based on this criterion, we selected freshwater wetlands that allowed us to walk through their entire extent for sampling data. We checked all areas where it was possible to observe the surroundings to ensure they met the objectives of our study.

We avoided large wetlands and those that had not clearly defined areas borders, which would be difficult to visually inspect; we also discarded wetlands clearly connected to other aquatic environments, as well as those near monocultures or other human activities. Despite being in a coastal plain, the sampled wetlands did not have any connection with the ocean and are characterized as freshwaters (*in situ* measured salinity = zero in all 29 sampled wetlands). Additionally, we used geographic coordinates to ensure that the chosen areas represented the coastal plain extensively. The wetlands' area ranged from 0.19 to 5 hectares, with an average depth of 30 ± 10 cm. Each wetland was sampled once during the austral summer of 2016, a period characterized by low volume of rainfall. We used this dataset previously to evaluate the relative role of environmental and spatial factors on macrophyte species richness and assemblage composition (Trindade et al. 2018).

Aquatic macrophytes

To determine the richness and composition of aquatic macrophyte assemblages, we conducted a thorough visual survey of the vegetation. This study took place during a period of low precipitation, which may influence the size of wetland areas, thus facilitating our walk throughout each visited wetland area. The same researcher recorded the species in all sampled wetlands. The time spent searching for species varied among wetlands (from 60 to 90 minutes), being always interrupted after 20 minutes of walking without registering a new species. We identified the species based on specialized literature (Cordazzo and Seeliger 1995; Irgang and Gastal 1996), as well as collaboration with specialists. We registered 114 aquatic macrophytes species: 90 emergent, 14 floating (including free-floating and rooted floating-leaved species), and 10 submerged (including fixed submerged and free-floating submerged species); detailed information is available in Trindade et al. (2018).

Local environmental variables

In each wetland, we used a multi-parameter water quality meter (Horiba-U50) to measure the following environmental variables at five random points: dissolved oxygen (DO; mg L⁻¹), pH and electrical conductivity (COND; $\mu\text{S cm}^{-1}$) (Supplementary Material, Table 1). We also collected three water samples for analyses of total phosphorus (TP; mg L⁻¹; Valderrama 1981; Baumgarten and Rocha 1996) and total nitrogen (TN; mg L⁻¹; Allen et al. 1974). We determined mean depth of the wet area (cm), using a graduated ruler at the same five points we measured the environmental variables. We recorded the altitude (m) and geographic coordinates at the central point of each wetland and used Google Earth Pro and Quantum Gis (QGis 3.22 Essen) to obtain wetland area (ha).

Climatic variables

We used 12 bioclimatic variables at a spatial resolution of a 1 km² grid originated from the combination of temperature and precipitation from the global dataset of Worldclim2 (Fick and Hijmans 2017). For our purpose, we obtained the following data: annual mean temperature (AMT; mm), temperature seasonality (TS; standard deviation $\times 100$), maximum temperature of warmest month (MAXTW; °C), minimum temperature of coldest month (MINTC; °C), mean temperature of wettest quarter (MTWeQ; °C), mean temperature of driest quarter (MTDrQ; °C), annual precipitation (AP; mm), precipitation seasonality (PS; coefficient of variation), precipitation of wettest quarter (PWeQ; mm), precipitation of driest quarter (PDQ; mm), precipitation of warmest quarter (PWQ; mm) and precipitation of coldest quarter (PCQ; mm). These are the same bioclimatic variables selected by Trindade et al. (2018) because of their importance for the organization of macrophyte communities. However, here we opted not to include annual evapotranspiration because the available database is based on the previous version of Worldclim (Hijmans et al. 2005).

Data analyses

We calculated the total beta diversity (BD_{Total}) and partitioned it into the compositional uniqueness or local contribution (LCBD) and the species contribution to beta diversity (SCBD) following Legendre and De Cáceres (2013). For these analyses, we used presence-absence data and the Hellinger distance. LCBD and

SCBD vary between 0 and 1, so that values closer to 1 indicate local communities and species that contribute more to beta diversity (Legendre and De Cáceres 2013).

We used the same approach to calculate local environmental uniqueness (LCEH or local contribution to environmental heterogeneity, as defined by Castro et al. 2019 and Schneck et al. 2022). We used Euclidean distance on two subsets of standardized environmental variables to obtain metrics on the wetlands physical (LCEH_{Phy}; area, depth, and altitude) and water chemical uniqueness (LCEH_{WC}; dissolved oxygen, pH, electric conductivity, total nitrogen, and total phosphorus). To verify which variables contributed more to environmental uniqueness, we correlated the LCEH values with environmental variables using Pearson's correlation.

First, we used Pearson's correlation to evaluate how LCBD relates to species richness. Next, we used beta regression (Cribari-Neto and Zeileis 2010) to model the relationship between LCBD and six predictors (LCEH_{Phy}, LCEH_{WC} and the climatic variables MTWeQ, MTDrQ, PS and PCQ). This final model was defined after excluding the other eight climatic variables due to multicollinearity (AMT, TS, MAXTW, MINTC, AP, PWeQ, PDQ and PWQ) using a variance inflation factor (VIF) criterion lower than 3. Then, we analyzed the spatial autocorrelation in the model residuals using Moran's I correlograms. Residuals were spatially independent ($P > 0.05$, after Bonferroni's correction for multiple tests; Oden 1984) and thus we did not include spatial variables in the LCBD regression model. Finally, we used Moran's I correlograms to evaluate whether geographically closer wetlands showed more similar values of compositional uniqueness. The use of Moran's I based correlograms to test for spatial autocorrelation in the residuals of the regression model and in the response variable (LCBD) followed Zuur et al. (2010) and Heino et al. (2017).

For SCBD we used Pearson's correlation to explore how it relates to the occurrence of each species (the number of wetlands in which each species occurs). Following, we tested whether macrophyte life forms differ in their SCBD values and we used a beta regression with SCBD as the response variable and life form with three levels as the predictor. After that, we evaluated the pairwise comparisons through simultaneous tests and adjusted P values using the Holm correction. Finally, to advance our understanding on the species-environment relationship for those species that contribute the most to beta diversity, we used the fourth-corner analysis (Dray and Legendre 2008; see Schneck et al. 2022 for a similar approach). We used a matrix of sites and the six predictors, a second matrix of sites and species

presence-absence, and a vector of SCBD values. Significance of correlations were assessed through 5999 permutations using model 6 from Dray et al. (2014) and corrected for multiple tests using the Holm correction. This analysis was repeated for the complete set of macrophyte species and separately for each life form.

We performed all analyses in R environment (R Core Team 2023). We used package 'adespatial' (Dray et al. 2020) to calculate LCB, SCBD and LCEH, 'pgirmess' (Giraudoux 2018) for correlograms, 'betareg' (Cribari-Neto and Zeileis 2010) for beta regressions, 'multcomp' for pairwise comparisons (Hothorn et al. 2008) and 'ade4' (Dray and Dufour 2007) for the fourth corner analysis.

Results

Total beta diversity of the macrophyte wetland communities was 0.65. Compositional uniqueness (LCB) ranged from 0.023 to 0.056 (Fig. 2a) and no spatial structure was observed in LCB values (Fig. 2b; none distance class was significant; $P > 0.05$). We found a negative correlation between LCB and species richness ($r = -0.394$; $P = 0.034$; Fig. 3). The regression model showed that compositional uniqueness was positively related to water chemistry uniqueness (LCEH_{WC}) and negatively related to the mean temperature of the driest quarter (MTDrQ) (model *pseudo* $R^2 = 0.435$; Table 1). Finally, LCEH_{WC} was positively correlated to total phosphorus and electrical conductivity ($r = 0.73$; $r = 0.82$, respectively; $P < 0.0001$).

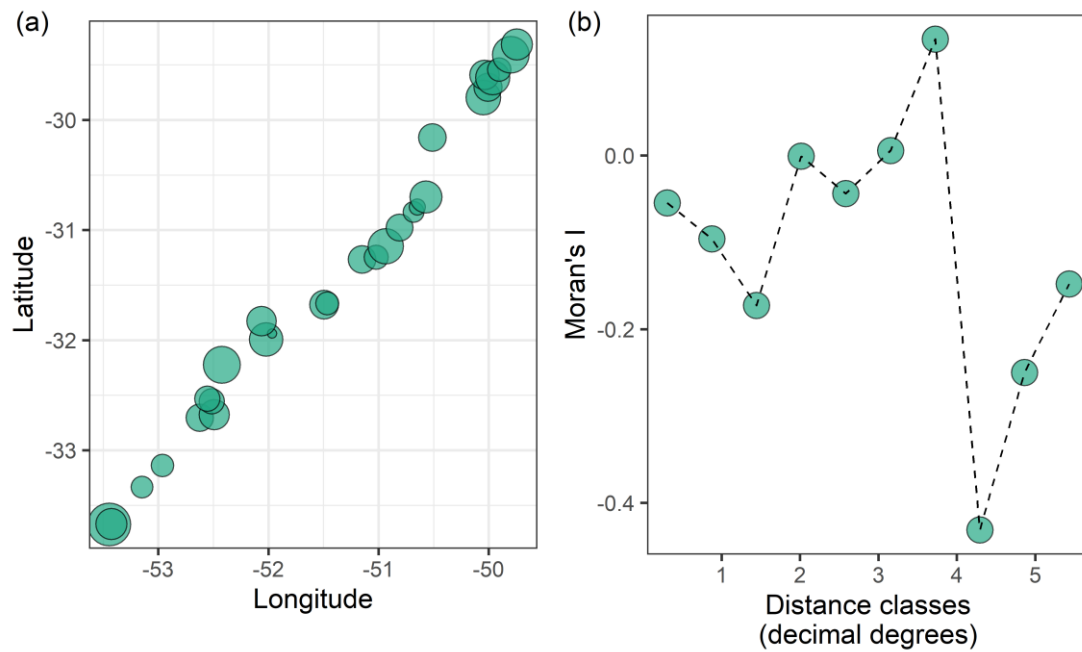


Figure 2. Spatial variation in compositional uniqueness (LCBD) of macrophyte communities in the 29 sampled wetlands (a) and spatial autocorrelation analysis of LCBD (b). The size of the circles in plot a is proportional to the LCBD values.

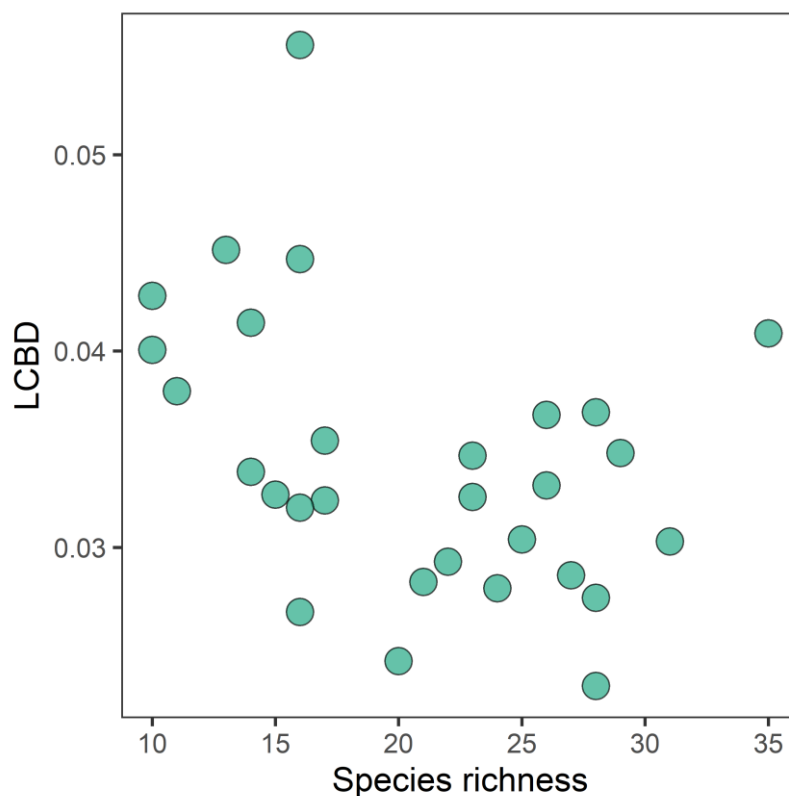


Figure 3. Correlation between compositional uniqueness (LCBD) and species richness of macrophytes in the 29 sampled wetlands.

Table 1. Beta regression results on environmental uniqueness and climatic variables as predictors of the variation in compositional uniqueness (LCBD) of macrophytes in wetlands. LCEH_{Phy} and LCEH_{WC}, local contribution to environmental heterogeneity resulting from wetland physical characteristics and from water chemistry, respectively; MTWeQ, mean temperature of the wettest quarter; MTD_rQ, mean temperature of the driest quarter; PS, precipitation seasonality; PCQ, precipitation of the coldest quarter. P values ≤ 0.05 are in bold.

	Estimate	Std. error	z	P	Model pseudo R ²
(Intercept)	-3.341	0.028	-118.424		
LCEH _{Phy}	0.009	0.034	0.255	0.798	
LCEH _{WC}	0.100	0.026	3.872	<0.001	
MTWeQ	0.039	0.034	1.135	0.256	
MTD _r Q	-0.110	0.045	-2.420	0.016	
PS	0.064	0.038	1.683	0.092	
PCQ	0.074	0.048	1.548	0.122	0.435

The SCBD values ranged from 0.002 to 0.023 (0.009 ± 0.01). Of the 114 registered species, 47 species (or 41% of the total) contributed more than the average to beta diversity (Fig. 4a). The three species that most contributed to beta diversity were *Schoenoplectus californicus* (C. A. Mey) Soják (SCBD = 0.023; occurrence = 18 sites), *Nymphoides humboldtiana* (Kunth) Kuntze (SCBD = 0.021; occurrence = 20) and *Cyperus esculentus* L. (SCBD = 0.020; occurrence = 16) (Supplementary Material, Table 2). We found a positive correlation between SCBD values and species occurrence ($r = 0.91$; $P < 0.0001$) (Fig. 4b). When comparing SCBD values among life forms, we found that floating species had higher SCBD than emergent species ($P = 0.002$); however, submerged species did not differ from floating or emergent ones ($P > 0.05$; Fig. 4c). According to the fourth corner analysis, SCBD was positively correlated with mean temperature of the driest quarter (MTD_rQ) and with precipitation of the coldest quarter (PCQ) (Table 2). However, when testing the SCBD-environment separately for each life form, it was clear that this pattern was driven by emergent species (Table 2).

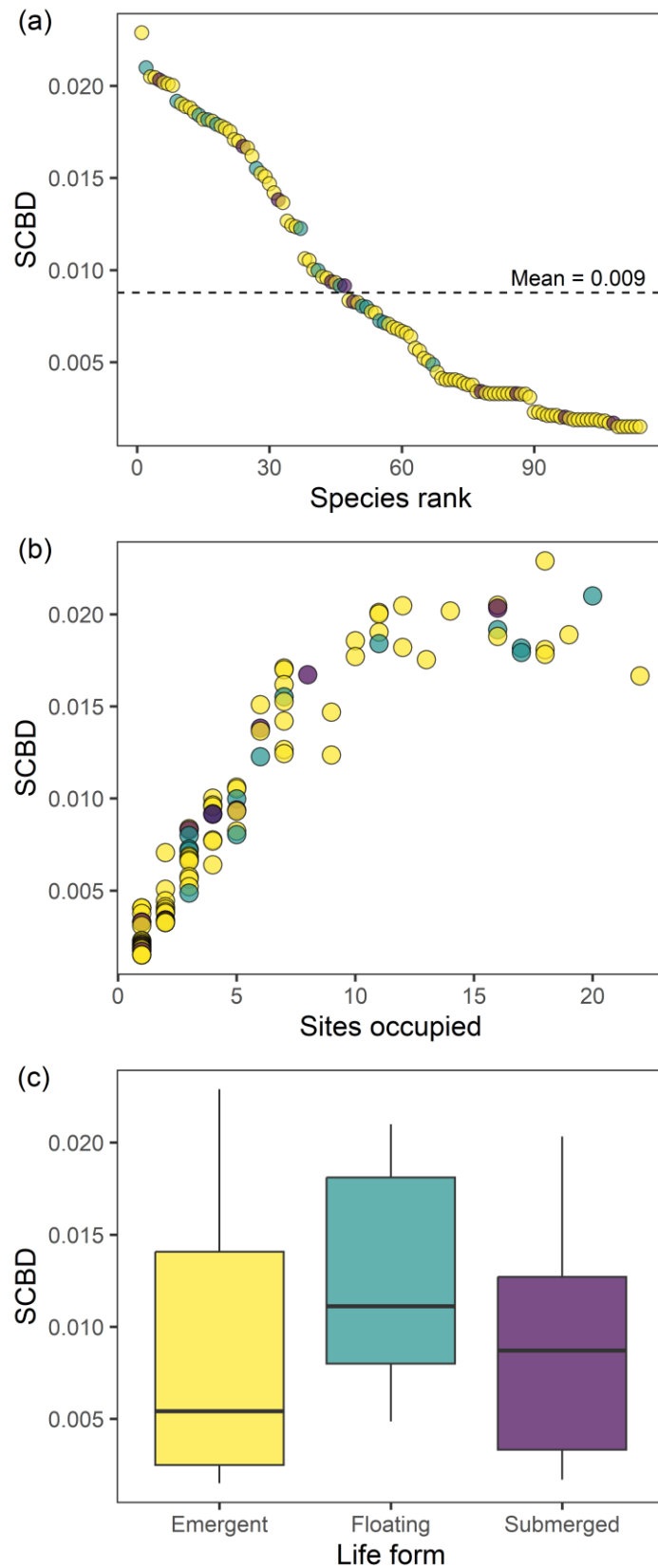


Figure 4. Species contribution to beta diversity (SCBD) of macrophytes and its rank distribution (a), correlation between SCBD and the species occurrence in the wetlands (b) and boxplots of SCBD for the three life forms (c). The colors in plots (a)

and (b) correspond to the life form in plot (c). In boxplots, the median is represented by a heavy horizontal line, while the first and third quartiles are depicted by the ends of the box. The whiskers indicate the minimum and maximum values.

Table 2. Fourth-corner results on the relationship (Pearson correlation, r) between species contribution to beta diversity (SCBD) and environmental predictors for the total macrophyte communities and separately for each life form. Significant P values (≤ 0.05) are in bold.

Variable	Dataset	r	P
LCEH _{Phy}	All species	0.070	0.733
	Emergent	0.065	0.918
	Floating	0.029	>0.999
	Submerged	0.094	>0.999
LCEH _{WC}	All species	-0.107	0.306
	Emergent	-0.122	0.280
	Floating	0.149	0.747
	Submerged	0.098	>0.999
MTWeQ	All species	-0.144	0.163
	Emergent	-0.180	0.081
	Floating	0.100	>0.999
	Submerged	0.011	>0.999
MTDrQ	All species	0.194	0.021
	Emergent	0.214	0.032
	Floating	0.039	>0.999
	Submerged	0.205	>0.999
PS	All species	0.024	0.752
	Emergent	0.026	0.918
	Floating	-0.076	>0.999
	Submerged	0.136	>0.999
PCQ	All species	0.193	0.027
	Emergent	0.219	0.028
	Floating	0.070	>0.999
	Submerged	0.138	>0.999

Discussion

Our findings indicate that the compositional uniqueness of macrophyte metacommunities from the studied coastal wetlands, which span approximately 640 km, is related not to wetland location but to local environmental uniqueness and climatic characteristics. Specifically, compositional uniqueness was positively related to local environmental uniqueness based on water chemistry of the wetlands, and negatively related to the mean temperature of the driest quarter. Regarding the species contribution to beta diversity, the floating life form showed the highest SCBD values. Moreover, the species that most contributed to beta diversity were positively correlated with two climatic variables (precipitation of the coldest quarter and mean temperature of the driest quarter) but did not relate to local environmental uniqueness. Despite being well known that water chemistry (Akasaka et al. 2010; Alahuhta et al. 2013) and climate (Alahuhta et al. 2021; García-Girón et al. 2023) influence the diversity of aquatic plants, we showed here that the degree of uniqueness of macrophyte communities and the species contribution to overall beta diversity are also correlated with those variables.

Our results on LCBD showed that the most unique macrophyte communities had a reduced set of species and were found in wetlands characterized by low mean air temperature during the driest period of the year and that differed the most from the average local environmental characteristics. This indicates that regional climate and unique environmental water chemistry conditions played a role in selecting communities with a more unique species composition. Despite understanding beta diversity patterns is not an easy task, as numerous factors can influence the distribution of species locally and regionally (Alahuhta et al. 2013; Vilmi et al. 2017b; Gillard et al. 2020) some previous studies have also found clear correlates of compositional uniqueness from freshwater communities (e.g., Leão et al. 2020; Pozzobom et al. 2020; Schneck et al. 2022). Most of these studies focused on gradients of environmental degradation and found that more unique communities occurred in freshwater environments with reduced forest cover and more degraded conditions (e.g., diatoms and insects: Schneck et al. 2022; aquatic macrophytes: Bomfim et al. 2023). Our results, even without a sampling design focused in a pre-defined environmental gradient, showed a positive correlation between environmental uniqueness based on water chemistry (LCEHwc) and total water phosphorus or electrical conductivity, variables that are generally associated with

increased degradation of aquatic environments (Wu et al. 2020; Liu et al. 2022). We thus suggest that the uniqueness in water chemistry conditions was driven by increased phosphorus concentrations and electrical conductivity, selecting a reduced set of species, and thus resulting in poorer and unique communities.

In addition to water chemistry, the increase in compositional uniqueness with the decrease in mean air temperature during the driest period of the year suggests the importance of wetland hydroperiod in selecting unique communities of aquatic plants. This is because hydroperiod is known to influence species richness and community structure (Neiff 1996; Mitsch and Gosselink 2000; Maltchik et al. 2007; Schneider et al. 2018). During the driest period, high temperatures can cause increased desiccation of wetlands, which can favor the emergent life-form (Trindade et al. 2018). This can lead to some species becoming more common in the overall coastal plain (see Fig. 4b) and, as a result, reduce LCBD.

The absence of a defined spatial structure in LCBD indicates that the spatial location of the wetlands in the landscape was not a key factor in determining the compositional uniqueness of the macrophyte communities. The lack of a spatial pattern may reflect the high dispersal potential of aquatic plants (Viana et al. 2016), which, despite being considered passive dispersers, can reach long distances transported by different vectors (Soons 2006; Soons et al. 2016) such as water, wind, animals and humans (Santamaría 2002; Lacoul and Freedman 2006; Chambers et al. 2008; Lobato-de Magalhães et al. 2023). Therefore, our results indicate that niche processes exert more influence than dispersal limitation on the compositional uniqueness of wetland macrophyte communities, at least at a regional scale as the one studied here (~640 km).

The result that species with high SCBD values had intermediate to broad distributions was already shown for freshwater organisms (e.g., Pozzobom et al. 2020; Schneck et al. 2022). It could be understood that species with higher SCBD values have less dispersal limitation and greater colonization capacity. Moreover, 41% of the total species had SCBD values above the global average SCBD, indicating that a large number of species contributed to the variation in community compositions along the coastal plain. This is consistent with the high value of global beta diversity we found, suggesting that compositional differences between communities are mediated to a greater extent by the replacement of species with high SCBD than by species with restricted occurrences and low SCBD.

Floating species stood out as having the highest SCBD, similarly as found by Pozzobom et al. (2020). This life-form is strongly dependent on the presence of water and on the limnological characteristics of the wetland (Lacoul and Freedman 2006), being good competitors for resources (Henry-Silva et al. 2008). Despite the potential dependence of floating species from the water column's nutrient concentrations, no correlation of SCBD with water chemistry uniqueness was observed either for floating or other life-forms. However, the positive correlation between SCBD and climate variables indicates that the species that most contributed to beta diversity occurred at wetlands characterized by high mean air temperature and precipitation at specific periods of the year. Temperature and precipitation can affect the species richness and composition of macrophyte communities (Lacoul and Freedman 2006; Maltchik et al. 2007). For example, temperature can strongly influence the distribution of emergent and floating species, as they remain exposed to the air, unlike submerged species that develop underwater in a more stable environment (Viana et al. 2016). High temperatures during the driest period can also affect the water balance of the wetlands, causing the desiccation of environments and, consequently, influencing both the richness and composition of the communities (Maltchik et al. 2007). Moreover, precipitation can be one of the main limiting factors for the diversity of aquatic plants due to fluctuations in water levels (Lacoul and Freedman 2006; Maltchik et al. 2007). Intermittent wetlands, that remain only with saturated soil during a period of the year, limit the presence of submerged species and most floating species, favoring the colonization of emergent species, which can lead to a high contribution to beta diversity, as we found here.

Conclusion

When partitioning the total beta diversity of macrophyte communities, it was shown that local environmental factors and climate were the main correlates of compositional uniqueness. More unique communities had lower species richness and occurred in environmentally more unique sites with reduced mean air temperature at the driest period of the year. Furthermore, SCBD was related to climatic variables, and floating species stood out in their relative importance to overall beta diversity. These results enhance our understanding of the organization of macrophyte metacommunities in wetlands. Studies as the one here are essential to shed light on why certain local communities and some species contribute more to beta diversity

than others, especially considering the increasing human impacts on wetlands around the world, mostly related to landscape modification for agriculture, livestock farming, and urbanization, in addition to ongoing climate change that may intensify the effects of these human activities.

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All authors contributed to the study conception and design. Material preparation and data collection were performed by [Claudio Rossano T. Trindade]. Analyses were performed by [Claudio Rossano T. Trindade] and [Fabiana Schneck]. Funding acquisition and supervision [Fabiana Schneck]. The first version of the manuscript was written by [Claudio Rossano T. Trindade] and both authors edited on previous versions of the manuscript, and read and approved the final manuscript.

Conflict of interest

The authors declare that they have no conflict of interest.

Data availability

The data will be made available upon request to the corresponding author.

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Supplementary Material

Aquatic Sciences

Compositional uniqueness and species contribution to beta diversity of aquatic macrophyte metacommunities from coastal wetlands

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Table 1. Environmental variables in wetlands of southern Brazil.

Environmental variables	Min	Max	Mean $\pm$ sd
Depth (cm)	12	50	30 $\pm$ 10
Dissolved Oxygen (mg L ⁻¹)	3.0	9.7	5.9 $\pm$ 1.4
pH	4.4	7.8	6.1 $\pm$ 0.7
Electrical Conductivity (μ S cm ⁻¹)	25.0	587.8	109.1 $\pm$ 105.7
Total Dissolved Solids (g L ⁻¹)	0.02	0.4	0.1 $\pm$ 0.1
Total Nitrogen (mg L ⁻¹)	0.6	12.3	3.6 $\pm$ 3.0
Total Phosphorus (mg L ⁻¹)	0.004	1.2	0.2 $\pm$ 0.3
Wetland Area (ha)	0.2	5	4.5 $\pm$ 4.0
Annual Precipitation (mm)	1172	1491	1335.1 $\pm$ 111.4
Precipitation Seasonality (coefficient of variation)	7	18	12.3 $\pm$ 3.2
Precipitation of Wettest Quarter (mm)	312	404	372.2 $\pm$ 29.0
Precipitation of Driest Quarter (mm)	230	247	385.0 $\pm$ 35.6
Precipitation of Warmest Quarter (mm)	295	383	336.8 $\pm$ 30.0
Precipitation of Coldest Quarter (mm)	300	404	359.6 $\pm$ 31.1
Annual Mean Temperature (°C)	16.8	18.9	18.2 $\pm$ 0.7
Temperature Seasonality (standard deviation*100)	279	383	339 $\pm$ 31
Max Temperature of Warmest Month (°C)	26.4	28.4	27.6 $\pm$ 0.7

Min Temperature of Coldest Month (°C)	8.1	11.4	9.6 ± 1.1
Mean Temperature of Wettest Quarter (°C)	12.7	19.5	15.1 ± 1.8
Mean Temperature of Driest Quarter (°C)	15.4	21.9	20.0 ± 2.3
Altitude (m)	2	22	10.1 ± 5.1

Table 2. Species found in the study, functional group (E; emergent; F; floating; S: submerged), number of occurrences, occurrence locations, and SCBD values

Aquatic Macrophytes	Functional group	Occurrence	Sites of occurrence	SCBD
<i>Acmella decumbens</i> (Sm.) R.K. Jansen	E	1	1	0.003
<i>Alternanthera philoxeroides</i> (Mart.) Griseb.	E	11	1,2,4,6,7,11,14,16,22,25,29	0.018
<i>Azolla filiculoides</i> Lam.	F	16	2,3,4,5,7,11,12,13,14,15,16,18,22,26,27,29	0.018
<i>Bacopa monnieri</i> (L.) Wettst.	E	19	3,4,6,7,8,9,11,13,15,16,17,18,19,22,24,25,26,27,29	0.019
<i>Bacopa</i> sp.	E	5	11,13,14,15,29	0.011
<i>Begonia cucullata</i> var. <i>cucullata</i> Willd.	E	4	25,26,27,29	0.006
<i>Briza minor</i> L.	E	1	6	0.003
<i>Cabomba caroliniana</i> A. Gray	S	1	2	0.002
<i>Canna</i> sp1.	E	1	23	0.004
<i>Canna</i> sp2.	E	1	1	0.003
<i>Centella asiatica</i> (L.) Urb.	E	12	6,8,9,18,20,21,23,24,25,26,27,28	0.020
<i>Cephalanthus glabratus</i> (Spreng.) K. Schum.	E	1	8	0.002
<i>Ceratophyllum demersum</i> L.	S	1	7	0.002
<i>Chrysanthemum myconis</i> L.	E	1	1	0.003
<i>Cladium jamaicense</i> Crantz	E	1	1	0.003
<i>Cyperus brevifolius</i> (Rottb.) Endl. ex Hassk	E	2	2,3	0.004
<i>Cyperus</i> sp1.	E	1	29	0.002
<i>Cyperus byssaceus</i> Pereira-Silva	E	1	1	0.003
<i>Cyperus esculentus</i> L.	E	16	2,3,8,11,16,17,19,20,21,22,24,25,26,27,28,29	0.020
<i>Cyperus giganteus</i> Vahl	E	1	24	0.002
<i>Cyperus haspan</i> L.	E	1	12	0.002

<i>Cyperus luzulae</i> (L.) Retz.	E	1	9	0.004
<i>Cyperus polystachyus</i> Jungh.	E	9	2,4,7,11,12,25,26,27,29	0.012
<i>Cyperus rigens</i> var. <i>rigens</i> J. Presl & C. Presl	E	2	2,8	0.004
<i>Cyperus surinamensis</i> Rottb.	E	2	3,26	0.003
<i>Daphnopsis racemosa</i> var. <i>leptostachys</i> Griseb.	E	1	8	0.002
<i>Dichanthelium sabulorum</i> (Lam.) Gould & C.A. Clark	E	1	26	0.002
<i>Diodia saponariifolia</i> (Cham. & Schltdl.) K. Schum.	E	1	25	0.002
<i>Drosera brevifolia</i> Pursh.	E	3	23,24,26	0.007
<i>Echinochloa polystachya</i> (Kunth) Hitchc.	E	3	1,7,16	0.007
<i>Echinodorus grandiflorus</i> (Cham. & Schltr.) Micheli.	E	3	7,8,16	0.006
<i>Echinodorus longipetalus</i> Micheli	E	1	2	0.007
<i>Eleocharis acutangula</i> (Roxb.) Schult.	E	1	7	0.002
<i>Eleocharis</i> sp1.	E	4	4,6,9,25	0.010
<i>Eleocharis</i> sp2.	E	7	17,20,23,24,25,26,28	0.016
<i>Eleocharis</i> sp3.	E	7	6,7,8,9,17,19,27	0.017
<i>Eleocharis minima</i> Kunth	S	4	15,20,23,26	0.009
<i>Eleocharis sellowiana</i> Kunth	E	3	6,9,25	0.008
<i>Enydra anagallis</i> Gardner	E	14	2,3,7,10,11,12,13,14,15,16,18,22,27,29	0.020
<i>Eriocaulon modestum</i> Kunth	E	7	21,23,24,25,26,27,28	0.015
<i>Eryngium horridum</i> Malme	E	1	26	0.002
<i>Eryngium pandanifolium</i> Cham. & Schltdl.	E	7	1,2,11,12,15,24,27	0.012
<i>Erythrina crista-galli</i> L.	E	1	29	0.002

<i>Fuirena robusta</i> Kunth	E	2	27,28	0.005
<i>Gymnocoronis spilanthoides</i> (D.Don) DC.	E	1	9	0.004
<i>Heteranthera reniformis</i> Ruiz & Pav.	E	9	5,11,14,16,24,25,26,28,29	0.015
<i>Hydrocleys nymphoides</i> (Willd.) Buchenau	E	3	3,4,5	0.007
<i>Hydrocotyle bonariensis</i> Lam.	E	10	1,2,8,11,12,13,15,16,18,23	0.019
<i>Hydrocotyle ranunculoides</i> L. f.	E	13	1,2,3,4,6,7,8,11,14,19,20,25,29	0.018
<i>Ischaemum minus</i> J. Presl	E	7	1,2,4,5,7,25,29	0.013
<i>Juncus bufonius</i> L.	E	1	12	0.002
<i>Juncus</i> cf. <i>pallescent</i> Lam.	E	1	26	0.002
<i>Juncus densiflorus</i> Kunth	E	2	6,26	0.004
<i>Leersia hexandra</i> Sw.	E	7	1,15,21,22,25,27,28	0.017
<i>Lemna valdiviana</i> Phil.	F	3	11,16,22	0.007
<i>Lilaeopsis</i> sp.	E	18	3,4,5,7,8,11,12,16,18,20,21,22,24,25,26,27,28,29	0.018
<i>Limnobiium laevigatum</i> (Humb. & Bonpl. ex Willd) Heine	F	5	3,5,7,12,20	0.010
<i>Lobelia hederacea</i> Cham.	E	3	12,14,15	0.007
<i>Ludwigia longifolia</i> (DC.) H. Hara	E	4	7,8,10,26	0.010
<i>Ludwigia peploides</i> (Kunth) P. H. Raven	E	11	3,4,5,7,8,9,12,17,19,20,24	0.020
<i>Ludwigia uruguayensis</i> (Cambess.) H. Hara	E	18	1,2,3,4,5,8,9,11,14,15,19,20,22,24,25,26,27,29	0.018
<i>Luziola peruviana</i> Juss. ex J.F.Gmel.	E	22	2,3,4,5,6,7,8,9,10,11,12,14,18,19,20,21,22,23,24,25,26,27	0.017
<i>Marsilea deflexa</i> A. Braun	E	1	4	0.002
<i>Mayaca fluviatilis</i> Aubl.	S	8	10,15,23,24,25,26,27,28	0.017
<i>Mimosa</i> sp.	E	1	25	0.002
<i>Myriophyllum aquaticum</i> (Vell.) Verdc.	E	16	2,3,4,6,7,8,10,11,12,14,15,16,18,20,25,27	0.019
<i>Nitella</i> sp.	S	3	3,4,21	0.008
<i>Nymphoides humboldtiana</i> (Kunth) Kuntze	F	20	3,4,5,6,9,10,13,14,15,16,17,19,20,21,23,24,26,27,28,29	0.021

<i>Oldenlandia salzmännii</i> (DC.) Benth. & Hook.f. ex B.D.Jacks.	E	1	9	0.004
<i>Paepalanthus planifolius</i> (Bong.) Körn.	E	2	26,27	0.003
<i>Panicum prionitis</i> Nees	E	4	2,3,24,21	0.010
<i>Paspalidium paludivagum</i> (Hitchc. & Chase) Parodi	E	1	1	0.003
<i>Paspalum acuminatum</i> Raddi	E	1	29	0.002
<i>Paspalum quadrifarium</i> Lam.	E	3	3,12,29	0.006
<i>Phyllanthus</i> sp.	E	2	16,29	0.004
<i>Pistia stratiotes</i> L.	F	6	11,12,14,15,16,22	0.012
<i>Polygonum ferrugineum</i> Wedd.	E	10	3,4,7,10,11,12,13,14,15,25	0.018
<i>Polygonum hydropiperoides</i> Michx.	E	5	1,2,6,7,8	0.011
<i>Polygonum</i> sp1.	E	1	26	0.002
<i>Polygonum punctatum</i> Elliot	E	11	2,3,6,10,14,15,16,19,20,25,29	0.019
<i>Polypogon elongatus</i> Kunth	E	1	26	0.002
<i>Pontederia cordata</i> L.	E	11	5,6,7,8,12,13,17,23,24,26,27	0.020
<i>Pontederia azurea</i> (Sw.) Kunth	F	4	2,12,20,28	0.009
<i>Pontederia crassipes</i> (Mart.) Solms	F	3	2,7,26	0.005
<i>Pontederia rotundifolia</i> L. f.	E	1	29	0.002
<i>Pontederia subovata</i> (Seub.) Lowden	E	3	2,3,7	0.005
<i>Rhynchospora corymbosa</i> (L.) Britton	E	1	29	0.002
<i>Rhynchospora</i> sp1.	E	2	29	0.003
<i>Rhynchospora</i> sp2.	E	1	27	0.002
<i>Ricciocarpos natans</i> (L.) Corda	F	16	2,3,4,5,7,8,11,12,13,14,16,18,19,20,22,29	0.019
<i>Sagittaria montevidensis</i> Cham. & Schltdl.	E	6	1,3,9,11,22,29	0.014
<i>Salvinia herzogii</i> de la Sota	F	17	2,3,7,8,11,12,13,14,15,16,18,19,20,22,24,27,29	0.018

<i>Salvinia minima</i> Bak	F	5	2,3,7,12,29	0.008
<i>Schoenoplectus californicus</i> (C.A.Mey) Soják	E	18	4,5,6,7,8,10,11,12,13,14,15,16,17,18,19,20,21,23	0.023
<i>Senecio bonariensis</i> Hook & Arn.	E	1	26	0.002
<i>Sesbania punicea</i> (Cav.) Benth.	E	1	8	0.002
<i>Sphagnum</i> sp.	E	6	10,15,23,24,26,28	0.015
<i>Spirodela intermedia</i> W. Koch	F	3	11,14,18	0.007
<i>Stuckenia pectinata</i> (L.) Börner	S	5	2,3,4,5,7	0.009
<i>Syngonanthus caulescens</i> (Poir.) Ruhland	E	4	18,25,26,27	0.008
<i>Thalia multiflora</i> Horkel ex Körn.	E	5	18,14,16,24,25	0.009
<i>Thelypteris interrupta</i> (Willd.) K. Iwats.	E	4	24,25,26,28	0.008
<i>Pleroma</i> sp1	E	1	29	0.002
<i>Pleroma</i> sp2	E	5	1	0.008
<i>Typha domingensis</i> Pers.	E	7	1,15,18,19,24,25,27	0.014
<i>Utricularia breviscapa</i> Wright ex Griseb.	S	1	28	0.003
<i>Utricularia foliosa</i> L.	S	16	3,4,5,6,7,8,11,14,16,19,20,21,23,24,27,28	0.020
<i>Utricularia gibba</i> L.	S	6	4,8,17,25,27,28	0.014
<i>Utricularia subulata</i> L.	S	2	24,26	0.003
<i>Wolffia brasiliensis</i> Wedd.	F	3	4,5,18	0.008
<i>Wolffia columbiana</i> Karsten.	F	7	11,13,14,15,16,19,22	0.016
<i>Wolffiella oblonga</i> (Phil.) Hegelm.	F	11	3,4,5,7,11,12,13,15,18,19,20	0.018
<i>Xyris jupicai</i> Rich.	E	2	24,26	0.003
<i>Zizaniopsis bonariensis</i> (Balansa & Poitr.) Speg.	E	2	7,15	0.004

CONSIDERAÇÕES FINAIS E PERSPECTIVAS

Compreender como as espécies se distribuem no espaço e no tempo tem sido uma questão desafiadora para ecólogos, tornando-se um dos temas centrais da Ecologia de Comunidades. Abordagens como a teoria de metacomunidades, que integram diferentes legados teóricos, ajudam nessa compreensão, ao considerar simultaneamente fatores locais e regionais na estruturação da biodiversidade em diferentes escalas. Nesse sentido, minha tese objetivou a aplicação de diferentes abordagens analíticas, como o *framework* dos Elementos da Estrutura de Metacomunidades (EMS) e a determinação da singularidade composicional e a importância relativas das espécies para a diversidade beta regional (LCBD e SCBD, respectivamente) de metacomunidades de macrófitas em banhados da planície costeira do Rio Grande do Sul, no sul do Brasil. A partir da aplicação dessas abordagens, busquei determinar em que medida fatores ambientais locais e variáveis climáticas regionais estão relacionados à composição e distribuição das espécies ao longo de um extenso gradiente espacial de aproximadamente 640 km da planície costeira.

Os banhados da planície costeira do Rio Grande do Sul são ecossistemas de alta relevância ecológica, mas fortemente ameaçados por pressões antrópicas e mudanças climáticas. Nesses ambientes, as macrófitas atuam como elementos chave, refletindo as condições locais e regionais com alta sensibilidade. Os resultados apresentados na tese demonstraram que a distinção funcional entre macrófitas emergentes, flutuantes e submersas revelou padrões de metacomunidades contrastantes, Clementsiano, quase aninhado e Gleasoniano, respectivamente. Isso evidenciou que diferentes grupos funcionais respondem a diferentes filtros ecológicos. Além disso também demonstramos que a singularidade composicional das metacomunidades de macrófitas (LCBD) nessas áreas está associada a condições ambientais singulares, especialmente relacionadas à química da água e a temperaturas mais baixas no período mais seco do ano, indicando que comunidades únicas tendem a ocorrer em ambientes com filtros ambientais mais fortes. Por outro lado, a contribuição das espécies para a diversidade beta (SCBD) esteve mais fortemente relacionada a variáveis climáticas do que ambientais, com destaque para as espécies flutuantes, que apresentaram os maiores valores, sugerindo que essas espécies contribuem amplamente para a substituição regional, mesmo sem estarem restritas a habitats específicos. Esses achados reforçam a importância de abordagens que integrem taxonomia e funcionalidade para compreender a estrutura das

comunidades. Além disso, ressaltam o papel das macrófitas como indicadores eficientes, fundamentais para orientar estratégias de conservação que considerem a heterogeneidade ambiental, frente às crescentes transformações globais, sejam elas naturais ou antrópicas.

Os resultados integrados desta tese reforçam que abordagens distintas e complementares permitem acessar diferentes dimensões dos processos que estruturam comunidades biológicas. A aplicação de diferentes abordagens analíticas garantiu uma base empírica sólida para interpretar a influência de filtros ambientais locais e climáticos regionais. Além disso, a distinção entre grupos funcionais foi importante para revelar padrões que seriam obscurecidos em análises generalizadas, destacando a importância de abordagens que considerem tanto a composição taxonômica quanto os atributos funcionais das espécies. Em suma, a utilização desse arcabouço teórico e suas ferramentas estatísticas ajudaram a compreender, um pouco melhor, como fatores locais e regionais estruturam a vegetação aquática nas áreas úmidas investigadas.

Por fim, avançar na compreensão das metacomunidades exige incorporar de forma mais explícita as interações bióticas, que podem modular ou até sobrepor os efeitos dos filtros ambientais e espaciais sobre a composição das comunidades (Leibold et al., 2022; Barbier et al., 2025). Em ambientes como *wetlands*, onde a heterogeneidade ambiental é marcante, agregar essas interações aos modelos de metacomunidade pode revelar mecanismos ocultos de coexistência e substituição de espécies, especialmente em grupos funcionais com nichos sobrepostos. Tais abordagens são promissoras para estudos futuros que busquem entender de forma mais completa a complexa dinâmica ecológica das áreas úmidas.

Finalmente, espero que os resultados apresentados aqui neste estudo possam contribuir para a melhor compreensão sobre metacomunidades em *wetlands* e que, de alguma forma, sejam úteis na elaboração de estratégias de preservação e/ou conservação, em prol da biodiversidade e da gestão sustentável dos *wetlands* costeiros, especialmente, da Planície Costeira do Rio Grande do Sul.

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ANEXOS

Participação em publicação de artigo do grupo de pesquisa coordenado pela Profa. Dra. Fabiana Schneck.

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Negative effects of cigarette butt leachate on freshwater phytoplankton communities

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Abstract

We experimentally tested the effects of different concentrations of cigarette butt leachate on freshwater phytoplankton chlorophyll-*a*, species richness, cell density, and community composition. For this, we sampled the phytoplankton from a eutrophic lake and acclimated it for 24 h in microcosms. We then conducted the experiment in microcosms maintained for 96 h. The experiment consisted of four treatments: control and leachate from 1 butt L⁻¹ (T1), 5 butts L⁻¹ (T5), and 10 butts L⁻¹ (T10), which were prepared by diluting a stock solution of leachate from 50 butts L⁻¹. We found that algal chlorophyll-*a* content was not affected by different leachate concentrations. In contrast, phytoplankton cell density decreased in a dose-dependent manner as concentrations of the leachate increased. Similarly, the number of species was highest in the control group relative to all other treatments, with T1 and T5 showing higher species richness than T10. Additionally, the exposition to different concentrations of the leachate impacted community composition across all treatments in comparison to the control group. Our results suggest that cigarette butt leachate alters the number of cells and species, as well as the distribution of abundance, without necessarily reducing chlorophyll-*a* concentrations. Our findings indicate that to gain a comprehensive understanding of the effects of cigarette butt leachate on freshwater ecosystems, it is essential to evaluate more realistic scenarios that incorporate aquatic communities, rather than isolated species.

Keywords Aquatic community · Water contamination, · Plankton diversity · Cigarette leaching, · Microalgae · Species composition