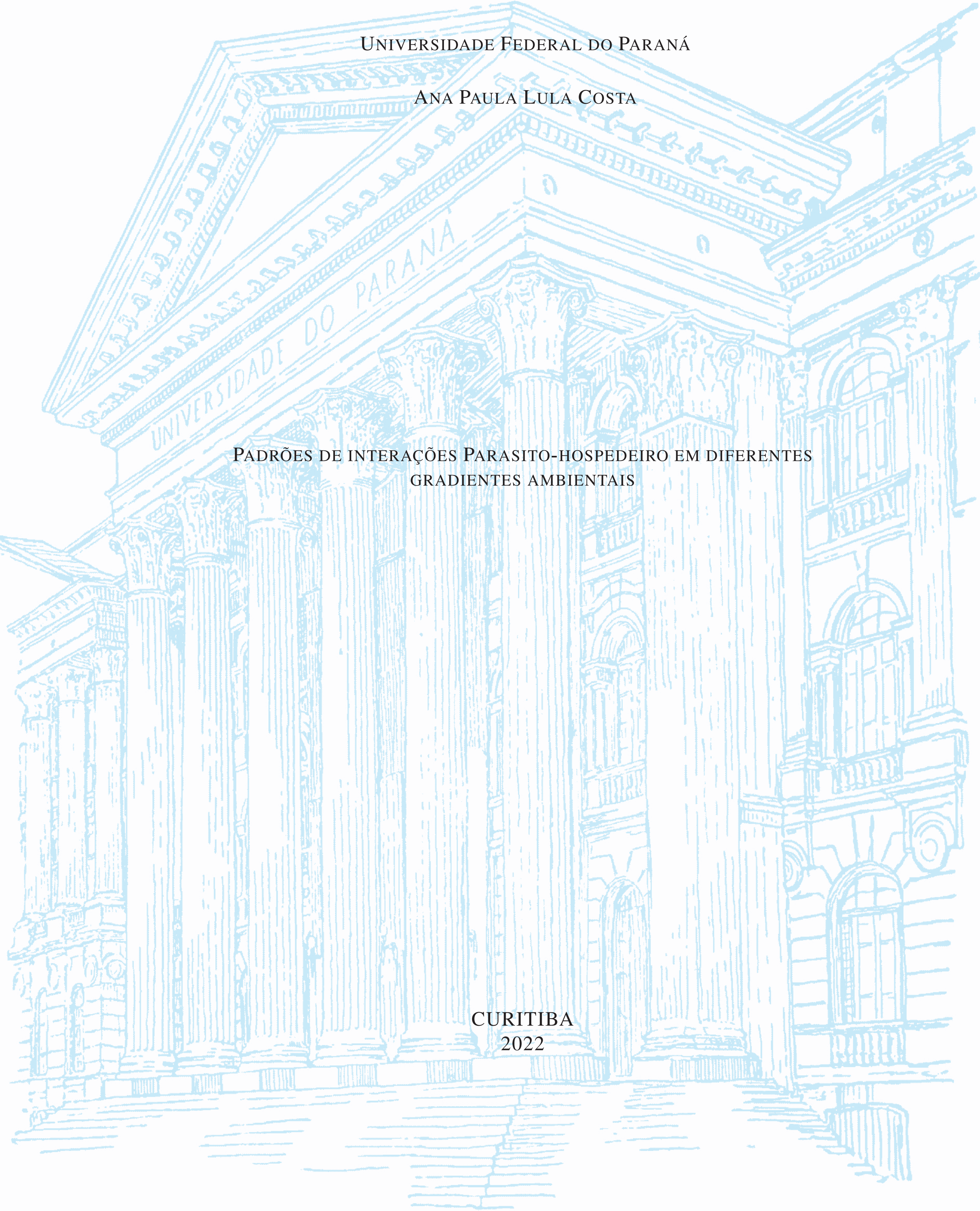

Universidade Federal do Paraná

Ana Paula Lula Costa

Padrões de interações Parasito-hospedeiro em diferentes gradientes ambientais

CURITIBA
2022

ANA PAULA LULA COSTA

PADRÕES DE INTERAÇÕES PARASITO-HOSPEDEIRO EM DIFERENTES GRADIENTES AMBIENTAIS

Tese apresentada no curso de Pós-graduação em Ecologia e Conservação do Setor de Ciências Biológicas da Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutora em Ecologia e Conservação.

Orientador: Prof. Dr. Andre Andrian Padial

CURITIBA
2022

DADOS INTERNACIONAIS DE CATALOGAÇÃO NA PUBLICAÇÃO (CIP)
UNIVERSIDADE FEDERAL DO PARANÁ
SISTEMA DE BIBLIOTECAS – BIBLIOTECA DE CIÊNCIAS BIOLÓGICAS

Costa, Ana Paula Lula.
Padrões de interações Parasito-hospedeiro em diferentes gradientes ambientais. / Ana Paula Lula Costa. – Curitiba, 2022.
1 recurso on-line : PDF.

Orientador: Andre Andrian Padial.

Tese (Doutorado) – Universidade Federal do Paraná, Setor de Ciências Biológicas. Programa de Pós-Graduação em Ecologia e Conservação.

1. Peixes – Ecologia. 2. Peixes de água doce – Parasitos. I. Título. II. Padial, Andre Andrian. III. Universidade Federal do Paraná. Setor de Ciências Biológicas. Programa de Pós-Graduação em Ecologia e Conservação.

Bibliotecária: Rosilei Vilas Boas CRB-9/939

MINISTÉRIO DA EDUCAÇÃO
SETOR DE CIÊNCIAS BIOLÓGICAS
UNIVERSIDADE FEDERAL DO PARANÁ
PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO
PROGRAMA DE PÓS-GRADUAÇÃO ECOLOGIA E
CONSERVAÇÃO - 40001016048P6

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CURITIBA, 17 de Agosto de 2022.

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19/08/2022 15:36:28.0
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Dedico este trabalho a todas as mulheres que buscam espaço e visibilidade na carreira científica

What you do makes a difference, and you have to decide what kind of difference you want to make.

— Jane Goodall

AGRADECIMENTOS

Foram quatro anos de muitas mudanças, dentro de um cenário mundialmente caótico. Eu comecei o doutoramento buscando aprimorar minha base teórica e metodológica na prática de conservação ecológica. Estou terminando-o com urgência em fazer e ensinar ciência de qualidade, e em trazer conhecimento e visibilidade para pesquisa e para a universidade. No fim, a base teórica foi uma singela parte do crescimento que tive como pessoa e profissional. E assim, começo agradecendo a todos e todas que me ajudaram neste processo.

As árvores maiores e mais resistentes são as que nutrem e mantem suas raízes fortes. Devo todo meu crescimento a minha base, meus pais, Wanderlei e Rubênia. Resisti e resisto até hoje a todas as dificuldades que se apresentam a mim porque tenho vocês como referência de força e motivação. Vocês são as luzes que me guiam e as raízes que me sustentam. Sou extremamente privilegiada porque em algum momento da vida vocês decidiram investir em meus sonhos e me deram a oportunidade de realiza-los. Meu amor e gratidão por vocês é eterno.

Minhas raízes criaram dois ramos irmãos. O historiador e a bióloga. Ele é 4 anos mais velho, mas é meu maior exemplo de ser humano, Daniel. Sua ética, empatia e modo de ver o mundo me guiam desde que nasci. E se sou tudo que sou hoje, é porque quis seguir minimamente os seus passos. Obrigada por ser meu apoio, meu amigo e conselheiro, enfim, obrigada por ser meu irmão. Não poderia deixar de agradece-lo também por ter trazido para nossa árvore da vida uma querida integrante, minha cunhada Bruna. Sua visão clara e objetiva sobre tantas coisas e sua preocupação e cuidado com todos e todas que estão a seu redor me fazem grata pela oportunidade de ter você também como minha família.

Agradeço imensamente meu orientador, professor Dr. André Padial. Obrigada por acreditar no meu conhecimento em ecologia parasitária e me permitir construir esta tese. Obrigada pelo apoio em campo e pelo pronto atendimento em todos os momentos que precisei. Aprendi muito sobre o seu olhar e te devo muito do meu crecimento profissional.

Desde a construção dos objetivos e hipóteses, até o campo, triagem e identificação das espécies de parasitos contei com a ajuda e cuidado de muitos professores. Gostaria de destacar primeiramente o pesquisador que tem me guiado desde o início da minha graduação: Dr. Ricardo Massato Takemoto. Agradeço pelas ideias compartilhadas junto a Dra. Sybelle Bellay, que trouxeram a construção do primeiro capítulo desta tese e pela parceria e auxílio na identificação dos parasitos. De fato, a identificação de todo material triado para esta tese não teria acontecido sem o auxílio do Ricardo e do Prof. Dr. Walter Boeger. Agradeço ao Walter e todo laboratório de Interações Biológicas por terem me adotado no doutorado, dando toda estrutura e base científica necessária para minha pesquisa. Aqui cabe também o agradecimento a uma pessoa essencial em todo processo, meu pupilo Luddy Searom. Sem ele não teria nem metade dos dados que apresento hoje nesta tese. Obrigada por confiar em mim para entrar na área da ecologia parasitária e por todo empenho na triagem e identificação dos dados.

Outros professores também foram essenciais nesta jornada. A começar pelo auxílio em campo do professor Dr. Jean Vitule, que me ensinou a arte de montar redes, retirar e identificar peixes, e até um pouquinho de pilotagem de barcos. As professoras doutoras Isabela Varassin, Karla Campião e Sabrina Araújo, pelas ricas discussões em reuniões e pelo exemplo como grandes mulheres pesquisadoras.

É com imenso orgulho que agradeço as instituições que me apoiaram financeiramente e estruturalmente na execução desta tese. Primeiramente agradeço a Universidade Federal do Paraná, por possibilitar toda a estrutura física para meu crescimento profissional. Em segundo, agradeço ao Programa de Pós-graduação em Ecologia e Conservação pelo apoio e estrutura intelectual. E, por fim, agradeço imensamente a instituição financiadora da minha bolsa, à CAPES, que possibilitou não só meu comprometimento integral a pesquisa como também a incrível chance de estender meu projeto para além mar, na Universidade de Zurique, na Suíça. Dentre todos os percalços passados nestes anos extremamente ameaçadores à ciência e educação, me sinto muitíssimo privilegiada por ter tido tamanha oportunidade.

Família é uma palavra com forte significado e que pode conceituar tão diferentes contextos. Em um primeiro momento, sou grata por ter uma família coesa e generosa, todos frutos das pessoas mais fortes e batalhadoras que conheci, minhas avós Maria e Virginia e meu avô Oldimar. A força de vocês permeará a eternidade e farei questão de levar todos ensinamentos comigo. Em um outro contexto, há pessoas que ganhamos durante a caminhada e que fazem dela muito mais bela e segura. Com isso sou grata a todo apoio que a Claúdia, Neto, Henrique e Gabriel me deram em toda minha construção de vida. E não é só de pessoas que uma família é constituída, portanto fica aqui meu amor ao meu irmãozinho de pelos, Spock, seu carinho e amor canino me deram forças para enfrentar todos esses anos.

Aqui ainda cabe a família que fiz durante o período de doutorado. A pessoa que compartilhei alegrias, frustações, viagens, problemas, novidades, uma casa, um gato e vários sonhos, a amiga de uma vida toda, Laryssa. Obrigada por estar comigo em tantos momentos, fomos força e apoio uma da outra e espero que seja assim por toda a vida. Não poderia deixar de agradecê-la também por trazer para minha vida o gato que acabou com todos meus preconceitos felinos e que foi meu querido estagiário em tantos dias de home office durante a quarentena, Francisco Caetano! Ao longo de nosso convívio muitas foram as pessoas queridas que passaram por nós, dentre elas, Josiane, Maira, Karen e Juliana são as que levarei comigo para onde eu for. Conviver e compartilhar a vida com vocês foi um grande aprendizado e só fez crescer minha admiração por todas. Vocês têm uma amiga em mim.

Durante um dos períodos mais difíceis do meu doutoramento eu me aproximei de um amigo muito querido e hoje ele é uma das partes mais importantes da minha vida. Fernando, obrigada por ser, e me permitir ser, apoio. Seu amor e confiança em mim me deram forças para que eu conseguisse realizar sonhos que nunca pensei que conseguiria. E acredite, nem nos meus maiores sonhos cogitei ter um companheiro como você. Por isso, obrigada por ser você.

Antes de entrar no doutorado me aventurei no ramo da consultoria com três grandes amigos. Grandes amigos que me ensinaram muito sobre trabalho em equipe, sobre sociedade e liderança. Eles também entenderam que ali ainda não era o meu lugar e que eu precisava dar outra chance à academia. Estes amigos me apoiaram durante o processo seletivo e comemoraram comigo a entrada na pós-graduação.

Obrigada pelo apoio, Douglas, Emanuel e Isadora.

Ah, à Isadora eu devo mais que um obrigada, já que ela tem meu amor todinho. Minha amiga improvável e eterna. Estaremos sempre juntas, sendo apoio e amizade uma da outra. Devo registrar aqui também meu amor e agradecimento a tantas outras amigas que me acompanharam nesta caminhada. Andressa, Carol, Eloá, Fernanda e Thaís. Amigas de uma vida toda. Amo ver o crescimento de vocês e torço sempre pela felicidade de todas.

Levo comigo também as amizades que fiz na pós-graduação e aos meus colegas de laboratório: Alejandro, Bryan, Elena, Elvira, Fabielle, Gabriela, Israel, Katlyn, Leticia, Luan, Pedro Calixto e Ribeiro, Rafael Fratoni e Oliveira, Rayane, Stephanie, Vanessa, Thais Zanata e Tiago. Obrigada pelas discussões, risadas, almoços, trilhas, Seu Nilson, e queridas festas da pós. Vocês foram refúgio e acalanto nestes quatro anos. Saibam que tem um pedacinho de vocês neste trabalho também. E um agradecimento especial à amiga que virou minha irmã, Lorraine. Obrigada por me ensinar a simplicidade e autenticidade da vida. Por me fazer querer me posicionar e lutar por um mundo melhor. Por ser uma conselheira sincera e real, e pelo apoio nestes quatro anos. Meu amor por você transpassa a distância Curitiba-Teresina.

Agora peço permissão para escrever em inglês os agradecimentos a todos e todas que me ajudaram durante o período que estive na Universidade de Zurique, durante meu doutorado sanduíche.

First, I am so grateful for the opportunity of working with an amazing scientist and wonderful person, Dr. Jordi Bascompte. I wanted to thank you, Jordi, for agreeing to have me on your team and for your patience during the one-year delay in my arrival in Switzerland. After that, I am thankful for all the learning experiences that I had during my time in the Bascompte lab. With you, I learned what really is to do science, and how to be truly amazed and curious by it.

During my time at the University of Zurich, I was lucky to meet such amazing people, that help me during my time abroad and with all the work that I was doing during this period. First I wanted to thank Marilia and Matt Hutchinson for "adopting"me during my semester in Switzerland. You both made me feel at home, thank you so much. After, I would like to thank all my colleagues at Bascompte lab, Fernando, Klementyna, Matt Barbour, Daniel, Rodrigo Cámara, Alessandro, and Nangsa. Thank you for all the rich discussions, during lab meetings or lunch. It was a pleasure getting to know a bit of every one of you. For my colleagues in our "aquarium office", Simon and Anitta, thank you for all the time and support during these months. And for my Brazilian friends in Zurich, Vanessa, Priscila, Bethania, Sophia, and Douglas. Thank you for having me in your Swiss lives and for accompanying me in so many adventures.

Finally, my time in Switzerland also allowed me to meet other incredible scientists that helped me during my academic journey. For that I thank Paulo Guimarães, Carlos Mélian and Cecilia Andreazzi. Thank you for all the discussions and so much rich advice. It was a pleasure being able to know and work with you.

RESUMO

Variações nos atributos funcionais dos indivíduos, assim como mudanças no ambiente podem afetar as diversas interações ecológicas, mudando a estrutura e estabilidade da comunidade e funcionamento do ecossistema como um todo. Dentre as interações ecológicas, a associação entre espécies hospedeiras e parasitas é regida por influências diretas e indiretas, configurando sua extrema complexidade. Parasitos sofrem com pressões diretas de seus hospedeiros e com pressões diretas ou indiretas do ambiente. Enquanto características específicas dos hospedeiros levam a diferentes comunidades parasíticas em um indivíduo, população ecomunidade. O ambiente traz mudanças na assembleia dentro de metapopulações e metacomunidades, que podem gerar trocas parasitárias e novas interações, muitas vezes mais virulentas. Com base nisso, compreender os mecanismos que regem as interações parasito-hospedeiro em diferentes escalas e como a estrutura das interações é organizada ao longo de gradientes ambientais pode trazer informações sobre os processos de transmissão parasitária e sobre a dinâmica da interação parasito-hospedeiro dentro de diferentes cenários. De fato, muitas questões ainda estão abertas sobre sua dinâmica em nível local e regional: Quais são os principais propulsores de composição parasitária em metapopulações? Quais fatores influenciam a estrutura das interações intra e interespecíficas em uma metacomunidade de hospedeiros? Como a rede parasito-hospedeiro se estrutura diante de diferentes pressões ambientais? Esta tese procurou investigar tais questões dentro de diferentes gradientes ambientais em comunidades de parasitos de peixe de água doce. Primeiramente foi investigada a estrutura da metacomunidade parasitária em uma metapopulação de peixes de uma planície de inundação. Neste estudo, vimos a mudança na estrutura da metacomunidade parasitária em períodos de seca e cheia do rio e a maior resposta dos ectoparasitos ao ambiente, em relação aos endoparasitos, mais influenciados por atributos funcionais do hospedeiro. Em um segundo momento, analisamos a estrutura da rede parasito-hospedeiro do Rio Guaraguaçu (costeiro com claro gradiente ambiental), levando em conta tanto aspectos intraespecíficos dos hospedeiros quanto as diferentes formas de parasitismo. Aqui mais uma vez foi possível observar a clara influência do ambiente em ectoparasitos, que apresentaram relação positiva entre a estrutura modular de sua rede de interação e o nível de perturbação antrópica do rio. Além disso, averiguamos a importância do fitness individual e a taxa de intensidade de infecção dos hospedeiros na compartimentalização das redes dentro do rio. Por fim, estudamos o padrão de estruturação das interações parasito-hospedeiro dentro da metarede do rio Guaraguaçu. Com isso foi possível analisar o papel e centralidade das espécies hospedeiras e parasitas na conectividade da rede de interação. Neste estudo encontramos um padrão claro de turnover de espécies e interações ao longo do rio, aliado ao conservatismo no papel das espécies. Ou seja, apesar do turnover, as espécies mais centrais de hospedeiros e parasitos foram as mesmas ao longo do rio. Nestes três momentos, separados em capítulos, apresentamos evidências sobre como diferentes mecanismos influenciam diferentes formas parasitárias: endo e ectoparasitismo. Além disso, destacamos a necessidade de considerar as variações intraespecíficas nos estudos das interações parasitárias, e como o ambiente muda a estrutura e estabilidade das interações, filtrando espécies que se tornam mais prevalentes e abundantes. Os resultados desta tese são importantes na compreensão dos mecanismos propulsores da transmissão e infecção parasitária em ambientes em constante mudança ambiental. Com isso, esperamos que os resultados encontrados aqui levem a medidas de monitoramento e gerenciamento de ações de recuperação e conservação dos ecossistemas costeiros e da manutenção da dinâmica das planícies de inundação. Ambos de imensurável importância na manutenção da diversidade global.

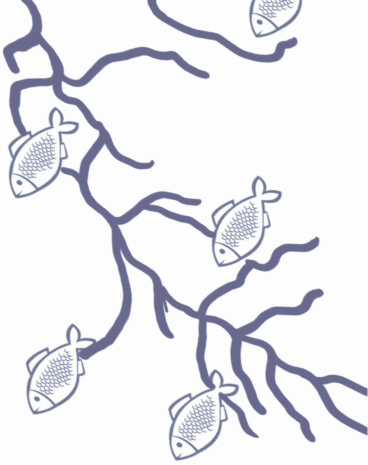
Palavras-chaves: Redes ecológicas; metacomunidade; ictioparasitologia; variação intraespecífica.

ABSTRACT

Individual variation, as well as changes in the environment, can affect the various ecological interactions, changing the structure and stability of the community and the functioning of the ecosystem as a whole. Among the ecological interactions, the host-parasite association is governed by direct and indirect influences, configuring its extreme complexity. Parasites suffer from direct pressures from their hosts and direct or indirect pressures from the environment. While specific host characteristics lead to different parasite communities within an individual, population, or community. The environment brings changes in the assembly within metapopulations and metacommunities, which can generate parasite exchanges and new, often more virulent, interactions. Based on this, understanding the mechanisms governing parasite-host interactions in different environmental gradients can bring information about parasite transmission processes and about host-parasite interaction dynamic in different scenarios.Indeed, many questions are still open about the dynamics of parasite-host interactions at local and regional levels: What are the main drivers of parasite composition in metapopulations? What factors influence the structure of intra- and interspecific interactions in a host metacommunity? How is the host-parasite network structure in the face of different environmental pressures? This thesis sought to investigate such questions within different environmental gradients in freshwater fish parasite communities. First, the structure of the parasite metacommunity in a floodplain fish metapopulation was investigated. In this study, we looked at the change in parasite metacommunity structure in periods of river drought and flood and the greater response of ectoparasites to the environment, relative to endoparasites, which are more influenced by functional host traits. In a second step, we analyzed the structure of the parasite-host network of the Guaraguaçu River (coastal with a clear environmental gradient), taking into account both intraspecific aspects of the hosts and the different forms of parasitism. Here, it was possible to observe the clear influence of the environment on ectoparasites, which showed a positive relationship between the modular structure of their interaction network and the level of anthropogenic disturbance of the river. Furthermore, we ascertained the importance of individual fitness and the rate of infection intensity of hosts in the modularity of networks within the river. Finally, we studied the structuring pattern of parasite-host interactions within the Guaraguaçu River metanetwork. With this, it was possible to analyze the role and centrality of host and parasite species in the connectivity of the metanetwork. In this study, we found a clear pattern of species turnover and interactions along the river, coupled with conservatism in the role of species. That is, despite the turnover, the most central host and parasite species were the same along the river. In these three moments, separated into chapters, we present evidence on how different mechanisms influence different parasitic forms: endo- and ectoparasitism. In addition, we highlight the need to consider intraspecific variation in studies of parasite interactions, and how the environment changes the structure and stability of interactions, filtering out species that become more prevalent and abundant. The results of this thesis are important for the understanding of mechanisms driving parasite transmission and infection in environments undergoing constant environmental change. Finally, we hope the results presented here lead to monitoring and management measures for recovery and conservation actions of coastal ecosystems and the maintenance of floodplain dynamics. Being both systems of immeasurable importance in maintaining global diversity.

Keywords: Ecological networks; metacommunity; ichthyoparasitology; intraspecific variation.

Sumário



Prefácio

O que faz andar a estrada? É o sonho. Enquanto a gente sonhar a estrada permanecerá viva. É para isso que servem os caminhos, para nos fazerem parentes do futuro.

— Mia Couto

Esta tese foi elaborada entre os anos 2018-2022, anos que ficaram marcados pela pandemia e negacionismo científico. Fazer pesquisa científica em meio a pandemia de Covid-19 no Brasil foi um imenso desafio em todas as áreas da ciência. Testemunhamos em 2018 o início de uma crise política e econômica que culminaria em um imenso desmanche educacional e científico nacional, intensificados em 2020, pela convergência das crises globais e nacionais. Por outro lado, a pandemia se mostrou um evento oportuno para nós, cientistas, mostrarmos a operação da ciência para a sociedade de um ponto de vista que até então não era importante: o do rigor da construção do conhecimento científico. A busca por respostas sobre o novo coronavírus ressaltou a curiosidade popular, e em pouco tempo, percebeu-se o quanto a população desconhecia a importância da operação e da aplicação científica. Um bom exemplo disso foi a falácia da eficácia de medicamentos contra o novo vírus (ex. cloroquina e nitazoxanida) sem os devidos experimentos controlados em ampla escala. Foi difícil trazer a compreensão do porquê de um dia para outro o remédio que parecia ser milagroso já não era mais aconselhado para o tratamento do Covid-19. E a explicação vem da base da metodologia científica. A rede de farsa científica envolveu médicos com carreira renomada e até mesmo portais de compilação de dados que foram compilados erroneamente em técnicas modernas de meta-análise [1].

Com base nesse contexto de circulação de informações, é importante delimitar que a maneira como pesquisadores e jornalistas comunicam resultados científicos afeta a interpretação sobre como fazer ciência. Esta falha leva a ilusão sobre a existência da verdade científica, e converge com a acurácia e construção de evidências, muitas vezes desqualificando ambas. O ensino hierárquico da condição de que a ciência constrói uma verdade irredutível por meio de teorias robustas e de difícil entendimento popular, pode também ter levado a uma perda da credibilidade científica por meio de alguns grupos sociais. Esta problemática, destacada na pandemia, mostra que a falha começa em nossa base educacional e é só refletida na divulgação. O doutoramento trouxe a oportunidade de reflexão sobre nosso papel como pesquisadores e até onde vai nossa responsabilidade social. Nós como cientistas devemos sempre procurar comunicar o conhecimento produzido em nossas pesquisas de modo que possa ser compreendido pela população. Mas com um diálogo trans e multidisciplinar, como evidenciado por Morin (2000):

> "para a educação do futuro, é necessário promover grande remembramento dos conhecimentos oriundos das ciências naturais, a fim de si-

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[1] (veja o site `https://hcqmeta.com/` e uma análise da falácia desses resultados em `https://www.youtube.com/watch?v=22QpMyu8SZs`)

> tuar a condição humana no mundo, dos conhecimentos derivados das ciências humanas para colocar em evidência a multidimensionalidade e a complexidade humanas, bem como integrar (na educação do futuro) a contribuição inestimável das humanidades, não somente a filosofia e a história, mas também a literatura, a poesia, as artes...A educação do futuro deverá ser o ensino primeiro e universal, centrado na condição humana. Estamos na era planetária; uma aventura comum conduz os seres humanos, onde quer que se encontrem. Estes devem reconhecer-se em sua humanidade comum e ao mesmo tempo reconhecer a diversidade cultural inerente a tudo que é humano. (Morin, 2000, p.47)

Dentro deste contexto, a pandemia também trouxe questões que remetem a dois problemas centrais da minha pesquisa: quais fatores são importantes na transmissão e infecção parasitárias em novos hospedeiros; e em um cenário de mudanças ambientais e emergência climática, o que esperar da relação parasito-hospedeiro e o surgimento de novas epidemias? Isto é válido tanto para saúde humana quanto para o funcionamento do ecossistema como um todo. Hoje é sabido que a troca de hospedeiros é algo bastante corriqueiro, sendo que parasitos não são vistos como espécies tão específicas quanto se pensava. De fato, cerca de 70% das doenças humanas são zoonoses, ou seja, de origem animal.

Dessa forma, a relação entre minha pesquisa e a reflexão acima deu origem a um artigo de divulgação publicado na revista Bioika em 2020. Neste artigo eu discuto sobre a relação entre a perda da diversidade presente nas florestas tropicais e a emergência de doenças. Nesse mesmo ano também ajudei a criar e gerenciar as redes sociais da pós-graduação de ecologia e conservação da UFPR. Experiências essas que foram muito importantes para minha formação como pesquisadora. Esta última afirmativa está ligada à convicção de que a geração de pesquisadores que vai se formar pós-pandemia trará uma nova ciência, mais democrática e holística, e que a nova forma de pensar ciência trará conhecimento necessário para que a sociedade consiga rever o modo como lidamos com o meio ambiente e o mundo a nossa volta.

Durante os quatro anos de desenvolvimento desta pesquisa de doutoramento, tive a oportunidade de traçar novas parcerias e executar muitos outros trabalhos que agregaram imensamente no meu crescimento profissional. Entre eles, destaco que participei da orientação de estudantes de graduação e da escrita de um importante capítulo de livro sobre Ecossistemas Aquáticos da Mata Atlântica. Contudo, gostaria de destacar também a minha participação no projeto de monitoramento que culminou nos dados utilizados em dois capítulos desta tese, o monitoramento do Rio Guaraguaçu, Paraná, Brasil [2]. Este projeto nasceu do sonho de dois professores, Andre Padial e Jean Vitule, e tem se mantido desde 2016, muitas vezes custeado por recursos dos próprios pesquisadores. O trabalho de coleta de dados robustos e de longa data é extremamente importante para a construção de teorias complexas e pesquisas de qualidade. Espero muito que a base de dados cunhada por este projeto seja útil para muitas outras perguntas e pesquisas sobre o tema. Desejo, também, que o projeto Guaraguaçu continue a crescer e trazer mais informações sobre os ecossistemas de rios costeiros, que são ambientes tão ricos e singulares.

Por fim, pretendo manter meu papel social na divulgação da ciência e trazer também os produtos desta tese tanto aos meus pares, para que sejam base para novos estudos sobre o tema, quanto em mídias sociais, e entre a comunidade do rio Garaguaçu, para que estes resultados ajudem na conservação e manutenção deste ecossistema.

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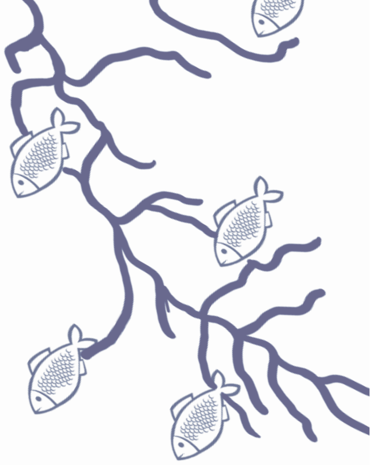
[2] veja em `https://lasbufprbio.wixsite.com/home`



Introdução geral

Words are, in my not-so-humble opinion, our most inexhaustible source of magic.

— *Harry Potter and the Deathly Hallows-Part 2*, 2011

Um dos principais objetivos dentro de ecologia de comunidades é entender processos e padrões que moldam a abundância e composição de espécie em diferentes escalas espaciais. O reconhecimento do papel dá dispersão de indivíduos entre populações e comunidades mudou o paradigma regente até a década de 1960, que via comunidade locais como unidades distintas (Ricklefs, 2008). Com isso, ficou claro que o fluxo entre processos locais e regionais regem a assembleia da comunidade. Processos de deriva, seleção e especiação são moldados pela dispersão de indivíduos e pelo fluxo entre populações e comunidades (Vellend, 2010). Já uma comunidade, é influenciada por eventos determinísticos, que consistem em fatores ambientais e ecológicos, e eventos estocásticos, não previstos por padrões ecológicos clássicos (Johnson et al., 2015). Apesar de teoricamente bem delimitados, ainda é necessário esmiuçar o papel das variações intra e interespecíficas dentro de diferentes tipos de interações nos padrões que levam a distribuição de espécies, assim como a importância de diferentes gradientes ambientais na manutenção das espécies e de suas relações ecológicas.

Diante desta problemática inicial, deve-se delimitar que as interações ecológicas dentro de uma comunidade são inúmeras e muitas vezes determinam a performance dos indivíduos e das populações (Runghen et al., 2021). Além disso, as associações entre espécies mudam conforme o ambiente e a escala espacial, e a manutenção dessas interações depende do nicho das espécies e de como elas se relacionam dentro das flutuações ambientais e populacionais, local e regionalmente (Johnson et al., 2015). Neste caso, as associações entre hospedeiros e parasitos afetam mutuamente ambos os níveis tróficos: a área dispersiva do hospedeiro limita a distribuição de seus parasitos, assim como um parasito regula o crescimento populacional de seu hospedeiro (Mihaljevic, 2012; Bolnick et al., 2020). De fato, o parasitismo se constitui como uma relação íntima e complexa, sendo estruturado por vários fatores eco-evolutivos e ambientais (Lima-Junior et al., 2021), podendo ser analisado em múltiplas escalas ecológicas. Por exemplo, podemos estudar a ecologia de uma comunidade parasitária em um indivíduo, em uma população ou em uma comunidade hospedeira. Esta complexidade torna o sistema parasito-hospedeiro extremamente interessante para analisar os contrates entre processos que moldam suas interações entre diferentes escalas ecológicas (Wendt et al., 2018; Warburton and Vonhof, 2018; Stephens et al., 2019; Bellay et al., 2020).

Pela visão da ecologia parasitária, um individuo hospedeiro é um habitat a ser ocupado e pode conter em si uma comunidade local de parasitos, chamada de infracomunidade. A população hospedeira pode por si conter seu pool de espécies de parasitos, sua comunidade componente (Bush et al., 1997). A transmissão e consequente persistência das espécies parasitas depende, portanto, da dinâmica populacional e do fluxo de indivíduos entre diferentes populações (Bolnick et al., 2020). Uma abordagem que melhor se encaixa no estudo dessa dinâmica é a de metacomunidades (Mihaljevic, 2012). Esta teoria consiste na análise de múltiplas comunidades locais interagindo entre si por meio da dispersão (Leibold et al., 2004). O que traz a possibilidade de investigar quais fatores estão influenciando na distribuição de parasitos entre hospedeiros em múltiplas escalas espaciais (Mihaljevic, 2012).

O estudo de metacomunidades é uma abordagem ideal na análise de como processos locais afetam a coexistência e dispersão de parasitos, sendo em um indivíduo, população ou comunidade hospedeira (Mihaljevic, 2012; Cardoso et al., 2020; Bolnick et al., 2020; Brian and Aldridge, 2021). Além dessa abordagem, há ainda a oportunidade de entender os mecanismos responsáveis pelo turnover de espécies ao longo de gradientes ambientais (Dallas and Poisot, 2018; Dallas and Jordano, 2022). Essas informações são importantes na análise de padrões ecológicos e epidemiológicos em diversos níveis de organização (Johnson et al., 2015). Ademais, informações dos atributos funcionais intra e interespecíficos precisam ser considerados em um contexto mais amplo. Neste sentido, é necessário aliar análises de redes ecológicas com a abordagem de metacomunidades, trabalhando tanto na estrutura das interações de espécies quanto nas interações das comunidades dentro de escalas espaciais ou temporais (Montoya, 2006; Hagen et al., 2012; Gilarranz et al., 2016; Tylianakis and Morris, 2017; Emer et al., 2018; Hackett et al., 2019).

Diante disso, verifica-se que as redes ecológicas são construídas por diferentes grupos de organismos (representados graficamente por nós ou vértices) conectados por suas interações (linhas ou arestas), no qual há uma direção a ser seguida pelas interações. Por exemplo, em interações tróficas, há uma linha entre recurso e consumidor (Dale and Fortin, 2010; Bascompte and Jordano, 2013). No caso das associações parasito-hospedeiro, as ligações podem ser representadas por redes antagonistas bipartidas (Delmas et al., 2018; Ings et al., 2009). O uso das redes ecológicas dentro de um gradiente ambiental traz a oportunidade de acharmos interações chave entre locais com diferentes níveis de perturbações e de estabelecer quais locais são importantes para a manutenção da dinâmica e estabilidade do ecossistema (Tylianakis and Morris, 2017; Emer et al., 2018). Além disso, os estudos sobre os diversos tipos de interação são necessários para estabelecer os diferentes padrões e estrutura da rede dentro de um contexto espacial. Alguns estudos já destacaram as diferenças entre interações mutualísticas e antagonistas em relação a conectância, aninhamento e modularidade dentro de um gradiente espacial (Hagen et al., 2012; Tylianakis and

Morris, 2017). Cabe agora novos estudos que entendam as consequências destas diferenças dentro de um gradiente espaço-temporal, principalmente em ambientes impactados antropicamente.

Doravante, quando pensamos em colonização de um novo local em termos parasitários, nos referimos a infecção de uma espécie parasita em um novo hospedeiro, seja um novo indivíduo ou uma nova espécie (a depender da escala de estudo). E quando falamos de dispersão de parasitos, nos referimos as rotas de transmissão deste dentro de um ambiente (Mihaljevic, 2012; Brooks et al., 2019). A infecção e a transmissão parasitária são regidas por influências diretas e indiretas. Parasitos sofrem com pressões diretas de seus hospedeiros e com pressões diretas ou indiretas do ambiente. Variações morfológicas e comportamentais em nível individual levam a diferentes comunidades parasíticas em indivíduos, populações e comunidades. Já o ambiente causa mudanças na assembleia dentro de metapopulações e metacomunidades. Dentro de um gradiente ambiental a prevalência e a taxa de infecção parasitária pode mudar, devido principalmente a abundância de hospedeiros adequados ou de condições favoráveis a transmissão (Bolnick et al., 2019). Compreender os mecanismos que regem as interações parasito-hospedeiro em diferentes gradientes ambientais podem revelar os processos que levam a troca parasitárias entre hospedeiros e novas infecções (Brooks et al., 2019).

Alguns estudos analisaram os fatores que moldam a estrutura das redes ao longo de gradientes ambientais (Guilhaumon et al., 2012; Bordes et al., 2015; Bellekom et al., 2021). A despeito disso, poucos estudos analisaram as interações sobre a perspectiva de infracomunidades parasitárias e a influência de fatores intraespecíficos na estruturação da rede (Pilosof et al., 2015; Campião and Dáttilo, 2020). Com isso, muitas questões ainda estão abertas sobre a dinâmica da interação parasito-hospedeiro em ambientes com um grande gradiente ambiental, tanto em relação a escala individual, quanto em escala de metapopulações e metacomunidades: quais são os principais propulsores de composição parasitária em metapopulações? Quais fatores influenciam a estrutura das interações intra e interespecíficas em uma metacomunidade de hospedeiros? Como a rede parasito-hospedeiro se estrutura diante de diferentes pressões ambientais? Esta tese procurou investigar tais questões dentro de diferentes gradientes ambientais em comunidades de parasitos de peixe de água doce.

Objetivos

Interações parasito-hospedeiro apresentam-se fundamentais e ao mesmo tempo negligenciadas em relação a estudos de diversidade e funcionamento ecossistêmico (Timi and Poulin, 2020). Processos de competição aparente, controle demográfico, facilitação de predação e indução de interações indiretas são alguns dos processos intermediados pelas associações parasito-hospedeiro (Sures et al., 2017; Buck, 2019). Ao mesmo tempo, essa associação é extremamente sensível às mudanças ambientais e sua resposta a diferentes gradientes pode trazer consequências na persistência das comunidades em escalas locais e regionais (de Abreu et al., 2022; Bordes et al., 2015). Estudos recentes vêm demonstrando como mudanças ambientais e na paisagem podem alterar a estrutura das interações parasito-hospedeiro, muitas vezes aumentando a prevalência e probabilidade de infecção de novos hospedeiros de certas espécies de parasitas (Bordes et al., 2015; Jaramillo and Rivera-Parra, 2018; Zohdy et al., 2019; de Abreu et al., 2022). Com isso, o estudo da mudança na diversidade e interação parasito-hospedeiro, atrelada aos principais fatores que influenciam não só na abundância e prevalência de parasitos, mas também no turnover e rearranjo das interações ao longo de diversos gradientes ambientais é de extrema importância. Portanto, o objetivo geral desta tese de doutorado foi analisar a estrutura das interações parasito-hospedeiro em várias escalas de metacomunidade e em diferentes gradientes ambientais.

O PRIMEIRO CAPÍTULO[3] teve como principal objetivo investigar como uma metacomunidade parasita é estruturada em uma metapopulação de hospedeiros. Isto em um rio de planície de inundação marcado por constantes mudanças hidrológicas, entre regimes de seca e cheia. Este capítulo foi trabalhado com base em um peixe hospedeiro de hábito migratório e bem distribuído ao longo do rio. As análises foram feitas levando em conta as diferentes formas parasitárias encontradas, especificamente, ecto e endoparasitos, a fim de verificar se há diferença no padrão de distribuição dessas duas formas. Para detalhar a metacomunidade dos ecto e endoparasitos, nós usamos 3 abordagens dentro do escopo de metacomunidade. Primeiramente analisamos os elementos da estrutura de metacomunidade, que nos mostra seu padrão de disposição dentro do gradiente ambiental. Após isso, foi feita uma análise de variância, que indica quais fatores, ambientais, espaciais ou biológicos, mais influenciam a estrutura vista anteriormente. Por fim, foi analisada a dissimilaridade da composição parasitária ao longo do rio, visualizada em mapas de cores

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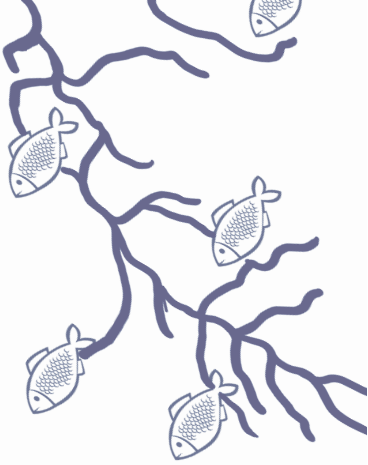
[3] Publicado na revista Hydrobiology (`https://link.springer.com/article/10.1007/s10750-021-04695-7`).

RGB.Este capítulo trouxe as diferentes respostas das diferentes formas parasitárias e a importância do pulso de inundação também para interação parasito-hospedeiro.

No SEGUNDO capítulo foi investigada a estrutura das interações parasíticas em uma metacomunidade de hospedeiros presente no rio Guaraguaçu, costeiro e de elevado impacto antrópico. Especificamente, focamos nos fatores que influenciam mudanças nas infracomunidades parasíticas, a fim de responder duas perguntas principais: o gradiente de perturbações antrópicas pode influenciar a estrutura da rede de interações, baseada em indivíduos hospedeiros? E, a compartimentalização desta rede, medida pela modularidade, é determinada por fatores intraespecíficos dos hospedeiros? Para responder tais questões foi feito o que chamamos de rede mista, formada por indivíduos de hospedeiros se relacionando com espécies de parasitos. Estas foram classificadas em relação a forma de vida dos parasitos, ecto e endoparasitos. Neste capítulo nós trabalhamos com a métrica de modularidade das redes, uma vez que ela tende a aumentar em relação a perturbações antrópicas. O valor de modularidade das redes de diferentes partes do rio foi relacionado aos fatores antrópicos coletados ao longo do rio. Por fim, para responder a segunda pergunta, classificamos as espécies de parasitos e os indivíduos hospedeiros pela identidade do módulo em que ficaram enquadrados. Os atributos intraespecíficos dos hospedeiros foram então relacionados a classificação baseada na modularidade. Este capítulo mostrou que sim, há uma relação entre a estrutura da rede e o aumento das perturbações antrópicas, e que fatores intraespecíficos relacionados ao fitness dos hospedeiros são importantes para manutenção da estrutura da rede de interação.

O TERCEIRO CAPÍTULO teve como objetivo principal verificar a conectividade das interações parasito-hospedeiro dentro do rio Guaraguaçu. Procuramos também responder duas principais perguntas: existe um turnover de interações ao longo do rio Guaraguaçu? E, quais fatores biológicos são propulsores da centralidade e do papel das espécies na conexão das interações ao longo do rio? Para responder ambas as questões nos baseamos na construção de uma metarede, que permite analisar quais aspectos ecológicos e funcionais dos parasitos e biológicos ou espaciais dos hospedeiros estão relacionados ao papel e centralidade das espécies dentro do rio. Aqui, foram trabalhadas 4 métricas de centralidade, calculadas tanto para cada setor amostrado no rio, quanto para o rio como um todo. Construímos também a métrica do papel das interações, neste caso baseado no agrupamento das espécies pelo seu local de coleta. As informações resultantes das métricas foram contrastadas com a identidade taxonômica das espécies e com seus atributos funcionais e ecológicos. Neste capítulo evidenciamos o turnover de espécies e interações ao longo do Rio

Guaraguaçu, além de relacionar a importância das espécies na conectividade do rio com fatores ecológicos e espaciais.



Capítulo 1

> *Nothing is absolute. Everything changes, everything moves,*
> *everything resolves.*
>
> — Frida Kahlo

Metacommunity of a host metapopulation: explaining patterns and structures of a fish parasite metacommunity in a Neotropical floodplain basin

Ana Paula Lula Costa[1,2], Ricardo Massato Takemoto[3], Maria de los Angeles Peres Lizama[4], André Andrian Padial[1]

1. Programa de Pós-graduação em Ecologia e Conservação
   Universidade Federal do Paraná
   Curitiba, PR, Brazil

2. Corresponding author: anapaulalula@gmail.com

3. Núcleo de Pesquisa em Ecologia, Limnologia e Aquicultura - Nupélia
   Universidade Estadual de Maringá
   Maringá, PR, Brazil

4. Programa Pós-Graduação em Tecnologias Limpas/ICETI/UNICESUMAR
   Maringá, PR, Brazil

Abstract

Host-parasite metacommunities are influenced by a myriad of factors at local and large scales, though little is known about which process affects this relation in different scales. Here we tested how local habitat characteristics and host traits explained the parasite metacommunity of a migratory fish in a large Brazilian river floodplain. The parasite metacommunity structure showed a Clementsian pattern, which indicates a more deterministic assembly pattern, that was in accordance with partial Redundancy Analysis results. Such result indicated that species filtering is the predominant mechanism driving community assembly. Patterns were clearer in the dry season of the floodplain. Environmental determinism seems to explain ectoparasite metacommunity in the dry season, in contrast with endoparasites that were more related to host traits. Overall, our results indicated that ectoparasitism is an interaction marked by opportunity, whereas endoparasitism is likely related to host features. Thus, we argue that metacommunity structuring of parasites depends on the infection strategy. Our results show that floodplain dynamics are central not only for free-living animal organizations but also for symbiotic interactions. Here, we highlight the importance to understand the factors influencing the distribution of parasites to predict their transmission, as well as the importance of floodplain dynamics and its hydrological regime on the maintenance of ecological interactions.

Keywords: Parasite distribution, *Prochilodus lineatus*, Beta diversity, Variation partitioning, Elements of metacommunity structuring.

Capítulo 1

Introduction

Determining the relationships of species assemblages with spatial and/or temporal gradients is a major goal in community ecology and central in the metacommunity framework (Leibold et al., 2004). The processes underlining the differences between local and regional community go beyond deterministic factors and can result in a combination of structures influenced by the environment, biological and historical features (**?**). Even so, general mechanisms driving community assembly can change across different scales and environmental gradients, for free-living and symbiotic species (Vellend, 2010). This paper aimed to analyze the factors that influence the pattern and structure of a parasite metacommunity. We expect different drivers influence different groups of parasites, as well as we hope to find a clear influence of the floodplain dynamics on the parasite distribution.

By definition, a metacommunity is composed of a set of local communities, all linked by dispersal of species and individuals within the regional species pool (Leibold et al., 2004; Winegardner et al., 2012). The presence or absence of a species in a local community depends on its individual response to environmental heterogeneity, biological interactions, dispersal, and/or stochastic events. The combination of such mechanisms leads to different patterns of distribution of the set of species that vary among local communities. Variation in species composition can be described by the turnover (i.e., replacement of species) or the nestedness (i.e., differences in species richness; Baselga (2010)). The distribution patterns can also be used to elucidate how the metacommunity is structured along a spatial or environmental gradient (e.g Leibold and Mikkelson, 2002). A common approach is to evaluate patterns of coherence, turnover, and boundary clumping in community distribution. The combination of patterns of each of these elements and their significance compared to null models result in six possible structures of distribution: Checkboard, Neutral, Clementsian, Gleasonian, Evenly Spaced and Nested (Leibold and Mikkelson, 2002; Presley et al., 2010).

Metacommunity structuring is described mostly for free-living organisms, while less often investigated are the determinants of symbiotic species metacommunities. Even so, there is a growing use of metacommunity framework in different approaches to embody patterns in symbiotic species (Richgels et al., 2013; Dallas and Presley, 2014; Mihaljevic et al., 2018), which may inform how metacommunity organization may depend on biotic interactions (Bolnick et al., 2020, e.g)[and references therein]. We here used the host metapopulation as a proxy of the parasite metacommunity (see also Mihaljevic, 2012). The main difference between free-living and symbiotic metacommunities is that the geographical location of symbiotic local communities may not be constant if the symbiotic host is a moving organism. Therefore, symbiotic species can interact between hosts of the same location, and between hosts from different locations when the host moves. Parasite metacommunity can easily be influenced by biotic and abiotic factors on a local scale but this deterministic relationship can change on a regional scale and across, different ecosystems (Bolnick et al., 2020; Richgels et al., 2013). It is well known that a myriad of biological factors associated with the host may influence the probability of parasite infection on a local scale, such as host age, condition factor, sex, and population density (Bolnick et al., 2020; Richgels et al., 2013; Poulin, 2007). The environmental conditions where the host inhabits may also influence parasite infection, either directly considering that ectoparasites are filtered by the environment, or indirectly given that most endoparasites life cycles depend on host availability (Dallas, 2014; Poulin, 2011). In addition, host movements are the main dispersal routes for parasite dispersion at larger scales (Vitone et al., 2004; Poulin, 2011).

Floodplain systems are composed of rivers and lakes connected permanently or temporarily by flood pulses, which promote high ecological heterogeneity. As a generalization, habitats are homogenized during flood events, making mass effects mechanisms important determinants of communities (Thomaz et al., 2007). During dry seasons, the high isolation of the rivers and lakes may lead to a higher relative influence of local factors and dispersal limitation on communities. For instance, the flood allows fish species to disperse (Agostinho et al., 2009); as in the case with migratory fish which have their reproductive life cycle driven by the flood regime, such as the streaked prochilod *Prochilodus lineatus* Valenciennes, 1836. This species uses lakes as a nurseries for its juveniles and returns to the main river between their first or second year, thus exhibiting a metapopulation dynamics (Gubiani et al., 2007). Although the parasite community of streaked prochilod has been shown to fluctuate temporally with the flooding regime in the Parana river floodplain (Lizama et al., 2006a,b), the metacommunity patterns and structure of the parasite fauna has not been fully investigated.

Here, we followed a metacommunity perspective to investigate how the species composition of endo- and ectoparasites in *P. lineatus* migratory fish is determined by biotic and abiotic factors, especially by host traits and the seasonal dry and flood periods in the Upper Parana´ River floodplain. As host-parasite interactions depend on eco-evolutionary history and interdependency relations, we expect that the structure of the metacommunity should be based on the formation of different groups responding deterministically to a gradient of host and environmental features, which generate a Clementsian pattern of metacommunity sensu (Leibold and Mikkelson, 2002). In the case of ectoparasites, we expect that the metacommunity will be influenced more by the local habitat characteristics than by the functional traits of fish hosts. For endoparasites, we expect that the host traits may be more important for the parasite metacommunity composition, because host traits have a fundamental role in the infection probability of parasites with complex life cycles (Berkhout et al., 2020).We also hypothesized that the compositional variation of parasites will differ between the flood and dry periods: during the flood period, variation in the composition of both parasites will be lower among the different local component communities, due to the mass effects of floods. We expect that such a 'biotic homogenization' pattern will be particularly observed for ectoparasites. We also explored nestedness and turnover components of beta diversity to describe their relative contribution and possible patterns in the dry and flood periods.

Methods

Study Area

The Upper Parana River floodplain is one of the most important ecosystems for conservation in the whole Parana River basin, the second largest hydrographic basin in Brazil (Agostinho et al., 2004). It is the only free-flowing fluvial complex without dams of the Upper Parana River and has a linear extent of 230 km between two major dam constructions - the Porto-Primavera and Itaipu Reservoirs. It is characterized by the Parana River itself and two main tributaries, Baia and Ivinheima Rivers, besides secondary channels and hundreds of associated lakes. This area presents high heterogeneity of habitats and aquatic biodiversity, although natural dynamics of flood pulses are now regulated by upstream and downstream reservoirs (Agostinho et al., 2004).

Data sampling

In our study, we used existing ecological datafrom a Long Term Ecological Research (LTER) program to analyze parasite metacommunity patterns from a new perspective. We used data sampled in 2000 and 2001 from the LTER that occurs in the Upper Parana River floodplain since 1999, carried out by the Nupelia research group in Universidade Estadual de Maringá, Paraná State, South Brazil (see details in `https://www.nupelia.uem.br/`). We also used an extra sampling effort made in parallel to the LTER project, in the same period between February-2000 to February-2001 (see description of the data in (Lizama et al., 2006a,b). Fish hosts were collected in habitats including the main channel of Parana River and its main two tributaries, as well as in 16 lakes with and without a permanent connection to the river channel, using standardized gillnets following the protocol of the long-term ecological monitoring project of NUPELIA research group (see `http://www.peld.uem.br/`) (Lizama et al., 2006a,b). This included information on fish traits, environmental and spatial data (see `http://www.peld.uem.br/`).

The collections of parasites were conducted with exhaustive inspection of organs and the visceral cavity of hosts. Collected parasites were individualized and identified under a stereoscopic microscope. Helminths were fixed in 4 % formalin, observed and measured as permanent mounts stained with Carmalumem Mayer, and mounted in Canada balsam. Ectoparasites were mounted in Hoyer's medium on microscopic slides for examination (Lizama et al., 2006a,b) The methodology followed the procedures of Eiras et al. (2003) and Lizama et al. (2006a,b). The parasites were identified based on Thatcher (1978, 1979, 1993); Thatcher and Varella (1981); Thatcher and Boeger (1984b); Moravec et al. (1998). The dataset contains the abundance of 39 parasite species in 148 hosts, sampled in the 18 sites described in Figure 2. We split parasite fauna into four matrices: ectoparasites and endoparasites abundances sampled in the dry and flood periods.

The following hosts' functional traits were measured: total weight (g), length (cm), age, sex, stages of gonadal maturity level, and condition factor (Lizama et al., 2006a,b, see details in). The environmental variables used to describe local habitat conditions were: depth (m), water temperature (°C), dissolved oxygen (mg/L), pH, conductivity (μ S/cm), Secchi depth (cm), turbidity (NTU), alkalinity (meq/L), chlorophyll (mg/L), total nitrogen (mg/L), nitrate (mg/L), ammonium (mg/L) and total phosphorus (mg/L) (Roberto et al., 2009, see for details). In addition, a measure of population density by sample site was used based on the average of fish specimens sampled by the site in each period. The metadata describing all data used here, for science reproducibility, is available in the Supplementary Material, as well as correlations charts showing variables distribution and cross-correlations of host's traits and environmental variables (Figures 6 and 7).

Data analyses

We did not focus on making a description of the parasite community and species relationships between parasites and host traits or flooding phases (already done by (Lizama et al., 2006a,b). Here, we used the already described data to apply the metacommunity framework and investigate metacommunity patterns and their likely correlates. For that, we define as infracommunity the local parasite community of one host, sensu Bush et al. (1997). We also define local component community as the sum of parasite infracommunities of a host local population – the population of hosts in the same location, where parasites may have a higher infection exchange. Each local component community has a probability of transmission between hosts. In this case, the infracommunities are also connected by the host movements between the local populations, so that the presence of a parasite species in an infracommunity is given by the host movement versus the probability of parasite infection in this host. Finally, the set of local component communities of the host population is defined as the parasite metacommunity. The conceptual model proposed here is described in Figure 1.

Analyses were made with four response infracommunity matrices: with host individuals (rows of the matrix) sampled in the dry or flood periods; considering ectoparasite and endoparasite species abundances (columns of the matrix). To explain response matrices, three predictor matrices were used: host individuals (rows) by its functional traits (columns); host individuals (rows) by environmental variables (columns); host individuals (rows) by latitude and longitude of host sampling site (columns). Hosts' functional traits were transformed in a Gower distance matrix and ordered with a Principal Coordinate Analysis PCoA. The environmental variables were associated with hosts according to the location/period in which the host was sampled. If more than one host was sampled simultaneously, values of environmental variables were repeated. The environmental matrix was standardized and ordered with a PCoA. All PCoA axes with positive eigenvalues were used to compose host traits and environmental variables summary matrices. A spatial matrix was made by applying PCNM (principal coordinates of neighbor matrices) (Borcard et al., 1992) in geographical coordinates of lakes and rivers in which host individuals were sampled. Therefore, spatial variables represent hypotheses of individual dispersion. Likewise for the environmental matrix, if two or more individuals were sampled at the same location, PCNM values were repeated.

We then used a variation partitioning procedure based on a partial Redundancy Analyses pRDA (Borcard et al., 1992) separately for the ectoparasite and endoparasite fauna of *P. lineatus* in each flood season using the three above mentioned predictor matrices. We filtered only the most important predictor variables of each predictor matrix using forward model selections. The significance of the pRDA components was accessed after 999 permutations. In pRDA, high shared fractions between PCNM and environmental matrix can indicate spatial autocorrelation of environmental predictors. To clarify this phenomenon, we tested for spatial autocorrelation in environmental variables using Moranâns I coefficient. Few variables had spatial autocorrelation (Table 1), which anticipate low shared fraction of PCNMs and environmental predictors in explaining parasite metacommunities.

We also described the spatial distribution of beta diversity. For that, the community matrix was transformed in a presence/absence matrix to estimate beta diversity indexes proposed by (Baselga, 2010), partitioning the Sorensen beta diversity (β sor) hereafter into Simpson i.e. real turnover (β sim) and Nestedeness (β nes) dissimilarities that indicate variation due only to differences in species richness. To visualize the parasite dissimilarity across space, the four infracommunities matrices were transformed to a β sor, β sim, β nes dissimilarity data and used in a nonmetric multidimensional scaling (NMDS). Then, we used its components to make a recluster analysis that results in RGB color maps. This analysis uses a red-green-blue space to scale the dissimilarity, relating hosts with low dissimilarities with similar colors. The dots given by the RGB space were plotted in the sampling coordinates where hosts were sampled, and then on the map of the study area.

Table 1: Moran's I autocorrelation coefficients between environmental variables and sample points coordinates for each group of parasites. Endo: endoparasites, Ecto: ectoparasites, M: Moran's I value, P: P.value. Variables: ADS: host densification; ABS: parasite total abundance; Riq: parasite total richness; Prof: depth; Temp.: temperature; OD: dissolved oxygen; pH: pH; Cond.: Conductivity; Secchi: Secchi transparency; Turb.: Turbidity; Nt: total nitrogen; Nh4: ammonium; PT: total phosphorus.

		ADS	ABS	Riq	Prof	Temp	OD	pH	Cond	Secchi	Turb	Nt	Nh4	PT
Endo	M	-0.01	-0.03	-0.02	-0.01	0.01	-0.01	-0.01	0.01	0.00	0.01	-0.03	0.00	0.01
	P	0.99	0.25	0.71	0.91	0.15	0.81	0.87	0.16	0.40	0.31	0.25	0.68	0.35
Ecto	M	0.01	-0.01	0.01	-0.07	-0.06	-0.07	-0.03	-0.01	-0.02	0.01	-0.04	-0.03	0.00
	P	0.23	0.93	0.15	0.00*	0.00*	0.00*	0.24	0.97	0.33	0.26	0.02*	0.10	0.54

Finally, we analyzed the Elements of Metacommunity Structure (EMS) to determine the underlying pattern of parasite metacommunity distribution (Leibold and Mikkelson, 2002). It is based on three features of compositional variation across local communities (Presley et al., 2010): coherence, species turnover, and range boundary clumping, based on ordination reciprocal averaging. Coherence assumes that there is a contiguous species distribution across an ecological gradient, resulting in few interruptions absences (zeros in the presence/absence matrix) in the species composition matrix, i.e. a continuous distribution meaning few absences within the ordinated species composition matrix. Turnover means the replacement of species across gradients (in this case, parasite species replacement across hosts), while nestedness represents a gradient where the community composition from hosts with the lowest species richness is a subgroup of the community from hosts with the highest species richness. Boundary clumping is based on the assumption that some species features lead to clusters along a spatial gradient, in line with a scenario dominated by competition for resources (Leibold and Mikkelson, 2002; Presley et al., 2010). The range and value of these characteristics are lead to six metacommunity patterns: random, checkboards, nested, evenly spaced, Gleasonian, and Clementsian (Leibold and Mikkelson, 2002).

All analyses were conducted in the software R (Leibold and Mikkelson, 2002)(Team et al., 2020) with packages vegan (Oksanen et al., 2015), metacom (Dallas, 2014), betapart (Baselga and Orme, 2012), and recluster (Dapporto et al., 2013). A scheme of the analyses and study design can be seen in Figure 8, as well as the summary R script used.

Results

Overview of parasite component community variation

In the dry season, 40 hosts were parasitized by 13 ectoparasite species and 37 hosts were parasitized by 17 endoparasite species. In the flood season, there were 72 hosts parasitized by 17 ectoparasites and 59 hosts parasitized by 19 endoparasites. The only predictors that explained parasite community structuring were PCoA axes from host traits and environmental variables (Figure 3). PCNMs representing spatial variables were not significant, and most variation in community structuring was unexplained (Figure 4 and 5). PCoA axes of environmental variables were relatively more important explaining infracommunity variation of ectoparasites (16% of variation), followed by PCoA axes of host traits (6% of variation) in the dry season. The joint explanations of environmental variables with traits (6% of variation) and spatial variables (5% of variation) were also relevant, although not possible to test for significance in pRDA analytical framework (see Borcard et al., 1992). In the flood season, ectoparasite community structuring was poorly explained by predictor matrices. For endoparasites, host traits were the only significant predictor matrix in all seasons, explaining 7 % during the flood and 22% during the dry season (Figure 3). The most important environmental variables for ectoparasites, identified by Pearson's correlation coefficients between original variables and PCoA axes selected in pRDA, were temperature (°C), Secchi disk transparency (cm), ammonium (mg/L), and host density (Table 2). The most important host traits (identified by a similar procedure abovementioned) were total length (cm) for ectoparasites and endoparasites, and total weight (g) for ectoparasites (Table 2). It is important to note that coefficients between environmental variables and host traits with PCOA axes were very low (Tables 2 and 3), but they were used not to interpret the direct effect of the variables in parasite metacommunity. Instead, they only indicated the relative importance of the variables for PCoA axes generation, which in turn were used as correlates of parasite community structuring.

Table 2: Correlation coefficients between environment variables and PCoA scores from the axes chosen in the forward selection used in pRDA for ectoparasites during the drought period - environmental variables were significant predictors in pRDA only for ectoparasites during drought period, see Figure 3. Environmental variables: Depth = site depth (m), Temp = water temperature (°C), DO = dissolved oxygen (mg/L), pH, Cond = conductivity (μS/cm), Secc = secchi disk transparency (cm), Turb = turbidity (NTU), TN = total nitrogen (mg/L), NH4 = ammonium (mg/L), TP = total phosphorus (mg/L), ADS = P. lineatus densification per site.

	Environmental variables										
Axis	Depth	Temp	DO	pH	Cond	Secc	Turb	TN	NH4	TP	ADS
10	-0.03	-0.02	0.08	-0.07	-0.08	-0.04	-0.07	0.05	-0.05	-0.14	-0.05
7	0.04	-0.01	-0.05	0.18	-0.16	-0.27	-0.23	-0.10	-0.24	-0.07	-0.05
6	-0.12	0.21	0.06	0.02	-0.16	0.26	-0.15	-0.09	-0.44	0.19	0.35

Beta diversity components

The mean infracommmunity βsor values were 0.94 in the dry period and 0.97 in the flood period for ectoparasites, and 0.93 in the dry period and 0.96 in the flood period for endoparasites. Most variation in the composition of parasites was a result of the turnover of species, with βsim mean values of 0.89 in the dry period and 0.94 in the flood period for ectoparasites, and of 0.90 in the dry period and 0.93 in the flood period for endoparasites.

Table 3: Correlation coefficients between traits and PCoA scores from the axes chosen 697 in the forward selection used in pRDA for each parasite group in each period in which 698 traits were significant predictors (see pRDA results in Figure 3). Traits: LE = length 699 (cm), WT = total weight (g), F = dummy indicator of females, MAT = stages of gonadal 700 maturity level, Kn = condition factor.

Parasite group	Period	Traits					
		Axis	LE	WT	F	MAT	Kn
Endoparasites	Drought	16	0.02	0.03	-0.01	0.01	-0.01
		13	0.03	0.05	-0.01	0.01	-0.02
	Flood	9	0.01	0.11	-0.02	-0.01	-0.01
Ectoparasites	Drought	8	-0.03	0.01	-0.02	0.02	-0.02

Elements of metacommunity structure

The elements of the metacommunity showed a positive and significant value for coherence, turnover, and boundary clumping for ectoparasites during the dry period, and also during all periods for endoparasites, which indicates a 'Clementsian' underlying structure of species distribution. A Clemensitian gradient indicates that this parasite metacommunity seems to have a deterministic pattern of distribution, which is supported by the fact that significant fractions were observed in pRDA variation partitioning, Figure 3. For ectoparasites composition during the flood period, the community showed a evenly structure pattern, that is more homogenous distribution than expected by chance, once boundary clumping was not significant (Table4).

Table 4: Result of the Element of Metacommunity Structure analyses for ecto and 704 endoparasite metacommunities of Prochilodus lineatus (Valenciennes, 1836) 705 (Characiforme; Prochilodontidae) in the Upper Paraná River floodplain. The values for 706 the elements coherence, turnover and boundary clumping are shown, following 707 Leibold Mikkelson (2002). * indicate elements with values lower than expected by 708 the null model ($P < 0.05$).

Element	Ectoparasites		Endoparasites	
	Dry season	Flood season	Dry season	Flood season
Coherence	9.7e+01*	3.53e+02*	1.67e+02*	2.99e+02*
Turnover	1.45e+03*	1.36e+04*	2.11e+02*	9.974e+03*
Boundary Clumping	2.89*	0.86	1.89*	1.9*

Discussion

We described the likely determinants of the parasite metacommunity from a fish with metapopulation dynamics. We considered that the local parasite community, defined as infracommunity, varies among hosts metapopulation and there was no evidence that variation was dependent on only the spatial distance among them.

As in many metacommunity studies, the variation explained by matrices of correlates was low compared to the unexplained fraction (e.g Algarte et al., n.d.; Mozzaquattro et al., 2020); in our study most variation also remained in the unexplained portion, see Figure 3). The likely reason for this relies on the complexity of ecological communities and the numerous interacting mechanisms explaining ecological patterns (Low-Décarie et al., 2014). Also, a more extensive sampling over a greater ecological gradient may improve explanation powers (see Heino et al., 2015), but our sampling effort was limited by the design of the standardized monitoring effort (see Methods). Even so, the comparative nature of our analyses allowed us to identify the (relatively) most important predictor of ectoparasites and endoparasites, and interesting patterns were detected. As expected, host traits explained more about the infracommunity structuring than environmental or spatial variables, especially for endoparasites. Host traits were already demonstrated as very important to explain parasite species richness of fishes (Bolnick et al., 2020). Here, we add to this knowledge by demonstrating that host traits also explain fish parasite community variation depending on the infection strategy and flood regime in floodplains. Metacommunity determinism was relatively lower during the flood period, likely due to mass effects and the homogenization during floods (Thomaz et al., 2007) that extends to metacommunity organization (Petsch et al., 2017). Thus, we argue that hydrological regimes are central not only for the community organization of free-living animals but also for symbiotic organisms, such as parasites (already sugested by Lizama et al., 2006a,b; Lima Jr et al., 2012). Although we did expect some role of host traits in ectoparasite metacommunity, we could not find consistent relationships of host traits in ectoparasite community structuring. Their distribution showed a clear pattern: habitat environmental determinism seems to explain ectoparasite metacommunity particularly in the dry period. The fact that ectoparasite community structuring is poorly explained during floods is in line with the hypothesis that ectoparasitism is an interaction marked by opportunism in infection (Brooks et al., 2019).

Given the percentage of explained and unexplained variation in pRDA, we argue that the signs of determinism in parasites metacommunity of *P. lineatus* were better identified in the dry period, likely due to the fact that the mass effects and flood homogenization is prevalent during floods (Thomaz et al., 2007; Fernandes et al., 2014; Chaparro et al., 2018). It is well established that the hydrologic regime is the most important factor controlling the environmental heterogeneity and consequent community organization in floodplain systems (Petsch et al., 2017; Chaparro et al., 2018). Extending the rationale for parasite community organization, our results are in line with the well-known correlation of migration behavior and parasite diversity and distribution (Caro et al., 1997; Figuerola and Green, 2000; Koprivnikar and Leung, 2015; Shaw et al., 2018). *P. lineatus* is a model species for such inference, since it has increased movements during flood periods, which can increase the probability of common infections and interchange of parasites between the host local populations (see also Gubiani et al., 2007; Poulin, 2011).

In addition, abiotic features had a significant influence on ectoparasite diversity in the dry period. This result can be explained by the fact that ectoparasites are more exposed to the local environmental conditions, mostly for their probability of infection, because most ectoparasites have monoxenic life cycles (Poulin, 2011; Krasnov et al., 2015; Lacerda et al., 2018). Other studies analyzing the contribution of environment and host traits also found a relationship between parasites and environmental features, mainly for monogeneans (Berkhout et al., 2020). It is important to note that the environment may have a direct and indirect effect on parasites, as suggested by Berkhout et al. (2020). Indeed, it has been suggested that non-favorable environmental conditions affect the abundance of ectoparasites like monogeneans and copepods, suggesting they could be good environmental bioindicators (Madi and Ueta, 2009). This is in line with our results, given the negative relationships between ectoparasite abundances and environmental variables related to an increase in nutrients such as phosphorus and nitrogen (Falkenberg et al., 2019).

Here, we focused on comparing strategies of infection, but future studies could dig even further and consider other biological features of parasite groups to help explaining parasite metacommunity structure. Also, it is interesting that one of the most important environmental variables explaining ectoparasites was the density of hosts, in line with previous studies suggesting that ectoparasite infection is mainly determined by host density (Arneberg et al., n.d.; Arneberg, 2002; Blasco-Costa et al., 2015) highlighting the opportunism of ectoparasites. It is expected that host density increases in channels and lagoons in the dry periods, favoring the infection by ectoparasites citeplizama2006influence. Our results tend to support that ectoparasitism distribution in a metapopulation is marked by its capacity of infection when densification of hosts increase, meaning that opportunity prevails over host health conditions (Richgels et al., 2013; Brooks et al., 2019).

Compared to ectoparasites, endoparasite community structuring was better explained by host features. Among the correlated traits, host length (cm) and weight (g) were selected as they are commonly related to parasite diversity (Vidal-Martínez and Poulin, 2003; Poulin and Leung, 2011a). The size of the host promotes more space and resources, resulting in a more diverse parasite fauna. Also, length is related to the age and feeding rate, which is the main infection source of endoparasites (González and Poulin, 2005; Combes, 2005). Accordingly, the abundance of parasites was well related to host length (Lizama et al., 2006b), which is mostly observed for endoparasites (Poulin and Leung, 2011a). Our results also corroborate the hypothesis that endoparasites are indicators particularly of ‘ecosystem functioning’ and not ‘environmental filtering’. This is because endoparasites partially explain the functioning of hosts, such as their diet and predators. Although many endoparasites may suffer indirect effects of the environment, the feature at microhabitat level - *i.e.* host traits - seems to have a higher relative power of explanation for parasite community structuring (Combes, 2005)(see also Bolnick et al., 2020).

It is interesting to note that the patterns above discussed were reinforced by our analytical approach. The metacommunity structure of P. lineatus parasites showed a Clementsian pattern of distribution when pRDA results showed significant correlates. Clementsian pattern represents a distribution based on an ecological gradient (Leibold and Mikkelson, 2002; Presley et al., 2010). Even though we did not find high percentages of explanations – avoiding a definite conclusion – we can infer that whereas the ecological gradient for endoparasites has its structure relatively more explained by host traits, the ecological gradient of ectoparasites was more related to environmental features. During the flood period, the distribution pattern of ectoparasites had an ‘evenly spaced structure’, in line with the mass effects and flood homogenization hypothesis (Thomaz et al., 2007; Bozelli et al., 2015). Particularly for ectoparasites, the migration and densification behavior of *P. lineatus* may increase the opportunity of infection and favor species that has better capacity of exploitation, resulting in an evenly space structure (Lizama et al., 2006b; Brooks et al., 2019).

Relatedly, the detritivorous habit of *P. lineatus* makes them more exposed to intermediated hosts and other parasite life forms (Lizama et al., 2006b). Indeed, host diet is a central feature explaining parasite communities (Bolnick et al., 2020). Dry periods with a low flow pattern may increase the diversity of benthic species, most common intermediated hosts and eggs, and larval forms of ectoparasites, which may increase the probability of parasite infection (Lizama et al., 2006b). On the other hand, parasite dispersal and distribution is likely enhanced during flood, explaining the no importance of spatial variables that would indicate dispersal limitation (Heino et al., 2015). Many studies demonstrated that the ecological variables representing deterministic mechanisms are more important for the distribution of parasites than mechanisms related to stochasticity (Maestri et al., 2017; Blasco-Costa et al., 2015). Our results also indicated that spatial variables unrelated to environment and host traits (i.e., the pure fraction in pRDA, see Borcard et al., 1992) were not important for ectoparasites and endoparasites. The fact that spatial variables were not important may be due to the movement behavior of *P. lineatus*, in which specimens can easily reach any location of our sampling extent during short-time movements if lakes have a watercourse connection - which is temporally variable, but common in the Upper Paraná River floodplain, see (Agostinho et al., 2009). In addition, at the spatial scale studied here, environmental variables exhibit low spatial autocorrelation (see Table 1). Spatial variables are usually identified as important metacommunity determinants in communities with dispersal limitations (Heino et al., 2015). The sampling sites with more dissimilar diversity are indeed located in more isolated areas in the RGB maps, indicating some spatial signal in beta diversity, but clearly not enough to generate patterns only explained by spatial dynamics. Apart from the possible scale limitation, it seems that such sign of spatial variables was related at least partially to the explanation of environmental variables, given the joint fractions in pRDA at least for ectoparasites during dry periods (see Figure 3).

We further investigate patterns in beta diversity components of fish parasite metacommunities. Turnover was prevalent in parasite distribution in relation to nestedness. Whereas studies in parasite metacommunities have described different metacommunity patterns, our results contrast with most studies showing that parasites have mostly a nested metacommunity pattern (Timi et al., 2010; Mihaljevic et al., 2018; Bolnick et al., 2020). However, we must highlight that most studies investigating nestedness use NODF metric to measure the nested pattern of the host-parasite network (Bellay et al., 2011; Lima Jr et al., 2012), and not beta-diversity indexes of metacommunity (but see Mihaljevic et al., 2018). Moreover, previous studies about host-parasite beta diversity addressing the infracommunity structuring of a single host species across show that parasite species richness tends to vary along an environmental gradient (Richgels et al., 2013; Berkhout et al., 2020; Bolnick et al., 2020). Yet, the determinist structure found in both ectoparasite and endoparasite community structuring, explained either by environmental filtering or hosts health conditions, may explain the parasite turnover across the studied gradient (see also Richgels et al., 2013).

Although we always had a lower explanation power (i.e., under 20%), we could identify interesting patterns of a compositional dissimilarity on *P. lineatus* parasite metacommunity. We highlight the need for more robust and accessible data that can be used in the analyses of local and regional variance, as well as long period research data that is fundamental to analyses temporal beta-diversity patterns. However, this was the first attempt to understand the features that shape host-parasite interactions on floodplain ecosystems. We showed evidence that host traits are relatively more important for endoparasites, and environmental features are relatively more important for ectoparasite species composition. Even so, we could not rule out that environment may have an indirect effect on endoparasites given environmental features likely determine the host distribution (Berkhout et al., 2020; Krasnov and Poulin, 2010; Maestri et al., 2017; Clark et al., 2018). Here, we also emphasized the need to study parasite beta diversity across ecological gradients. We demonstrated that parasite abundance and composition at least partially depend on the local environment and host conditions, in line with other studies with parasite metacommunity (Richgels et al., 2013; Dallas, 2014; Bolnick et al., 2020). Whereas an opportunist pattern is a likely mechanism driving ectoparasite assemblages, a more 'niche–based' pattern and species specificity according to host traits is the most likely for endoparasites metacommunity. Our study highlights the need for implementing a metacommunity framework to understand the features that shape host-parasite interactions on freshwater parasite communities, following a growing literature (e.g. Richgels et al., 2013; Mihaljevic et al., 2018). Besides, floodplain ecosystems have been hugely threatened by the construction of dams and reservoirs (Nislow et al., 2002; Latrubesse et al., 2017; Nielsen et al., 2020), which makes studies about the influence of its dynamics on the maintenance of ecological interactions even more important.

Figures

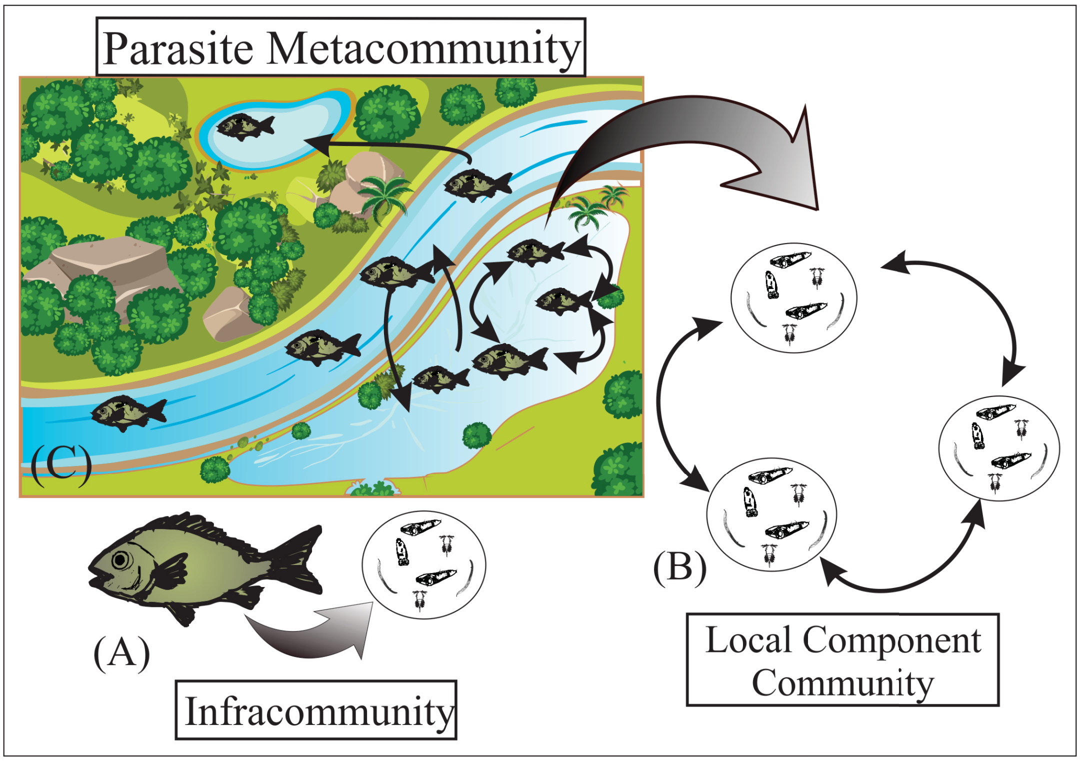


Figure 1: Conceptual model of the fish parasite metacommunity. A) Infracommunity: a 713 single host containing a parasite community. B) Local component community: a set of 714 infracommunities of a host local population. Here each infracommunity has a 715 probability of transmission between hosts. C) Metacommunity: set of the local 716 component community of a host metapopulation. The probability of parasite infection is 717 supposed to be linked with the host migration between local populations.

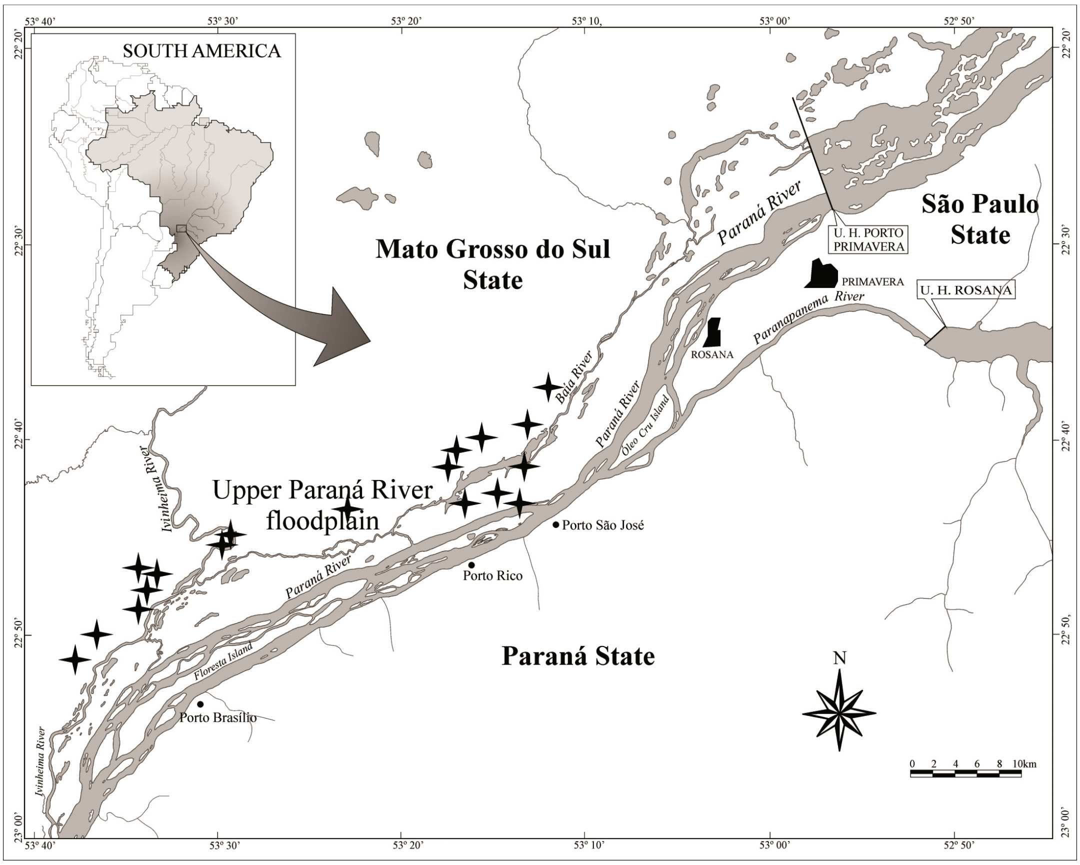


Figure 2: Location of the sampled sites of *Prochilodus lineatus* in the Upper Paraná 720 River Floodplain, Paraná, Brazil. Map adapted from: `http://www.peld.uem.br/peld-721Estado_Conservacao.htm.`

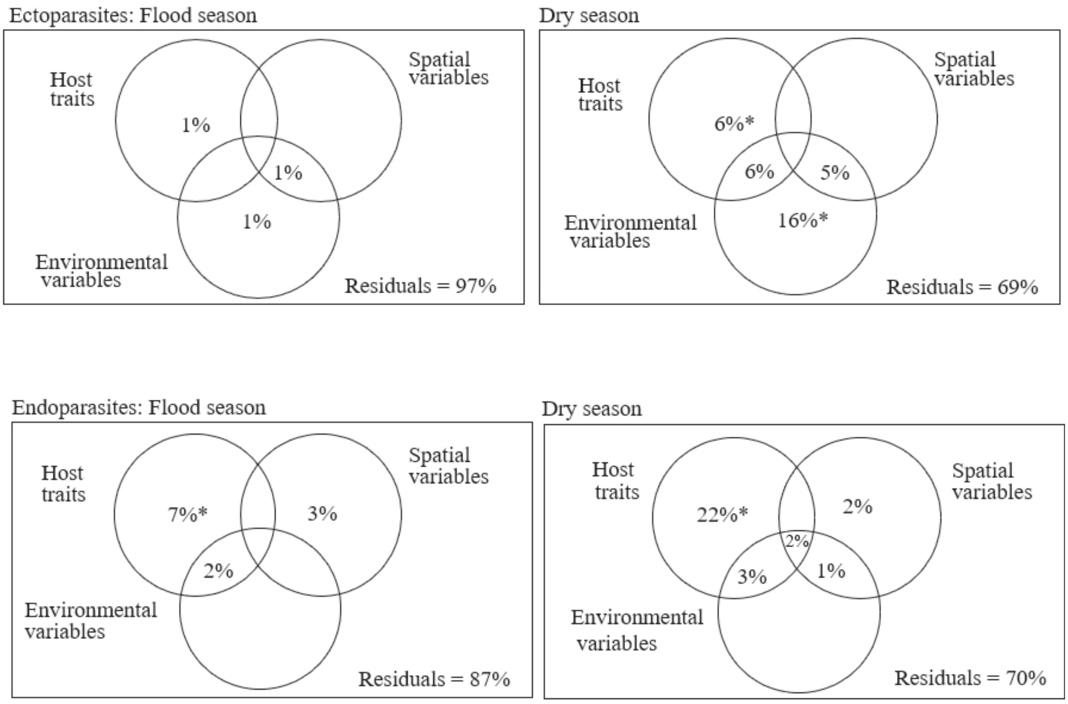


Figure 3: Result of the variation partitioning analyses based on pRDA to explain the variation in the ecto and endoparasites infracommunities of *Prochilodus lineatus* in the Upper Paraná River floodplain, during the dry and flood season.

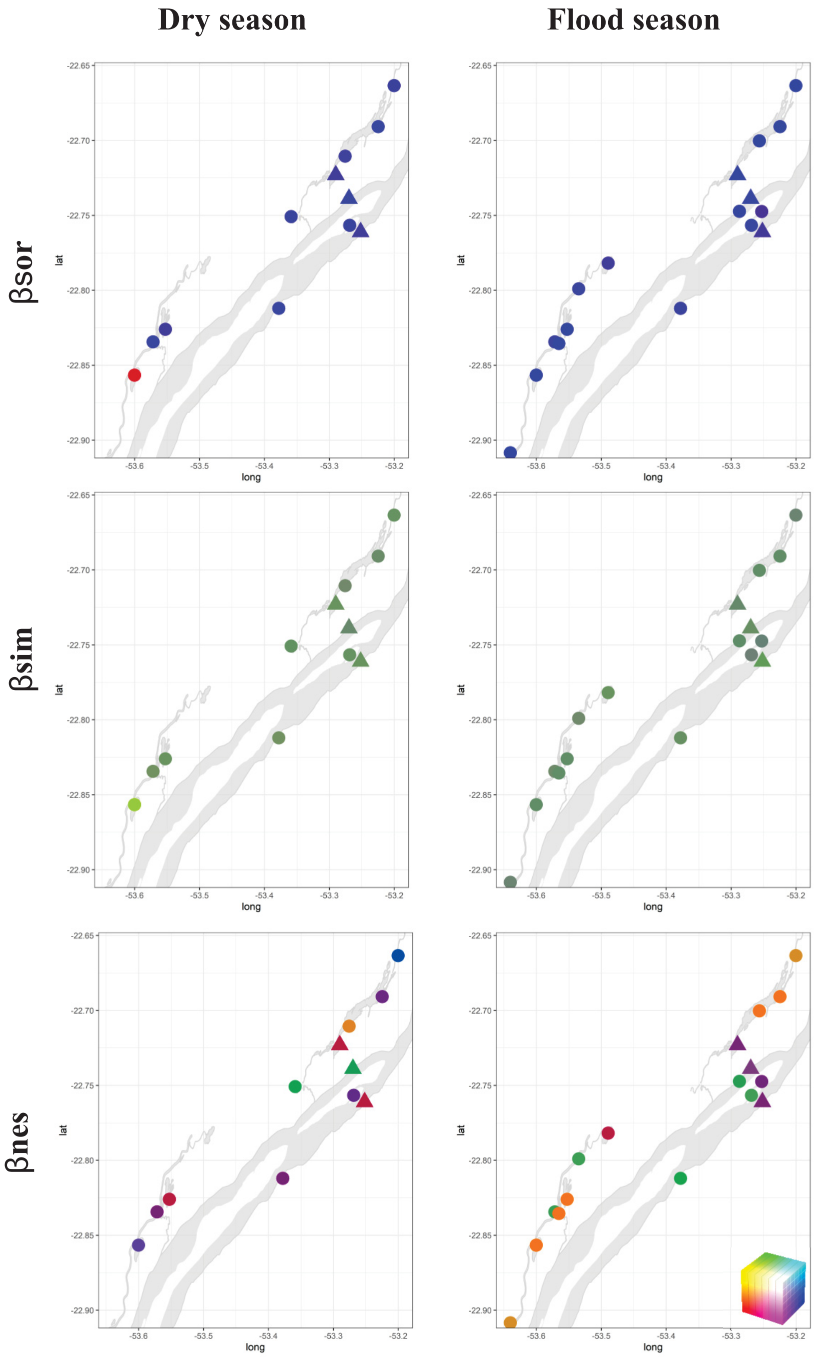


Figure 4: RGB color maps based on non-metric multidimensional scaling for Beta Sor (Sorensen dissimilarity), Beta Sim (turnover) and Beta Nes (nestedness) of ectoparasites along Upper Paraná River Floodplain in the dry season (left column) and flood season (right column). Similar colors indicate sites with similar parasite compositions for each beta diversity dissimilarity index. Triangles are river channel sites, and circles are lake sites.

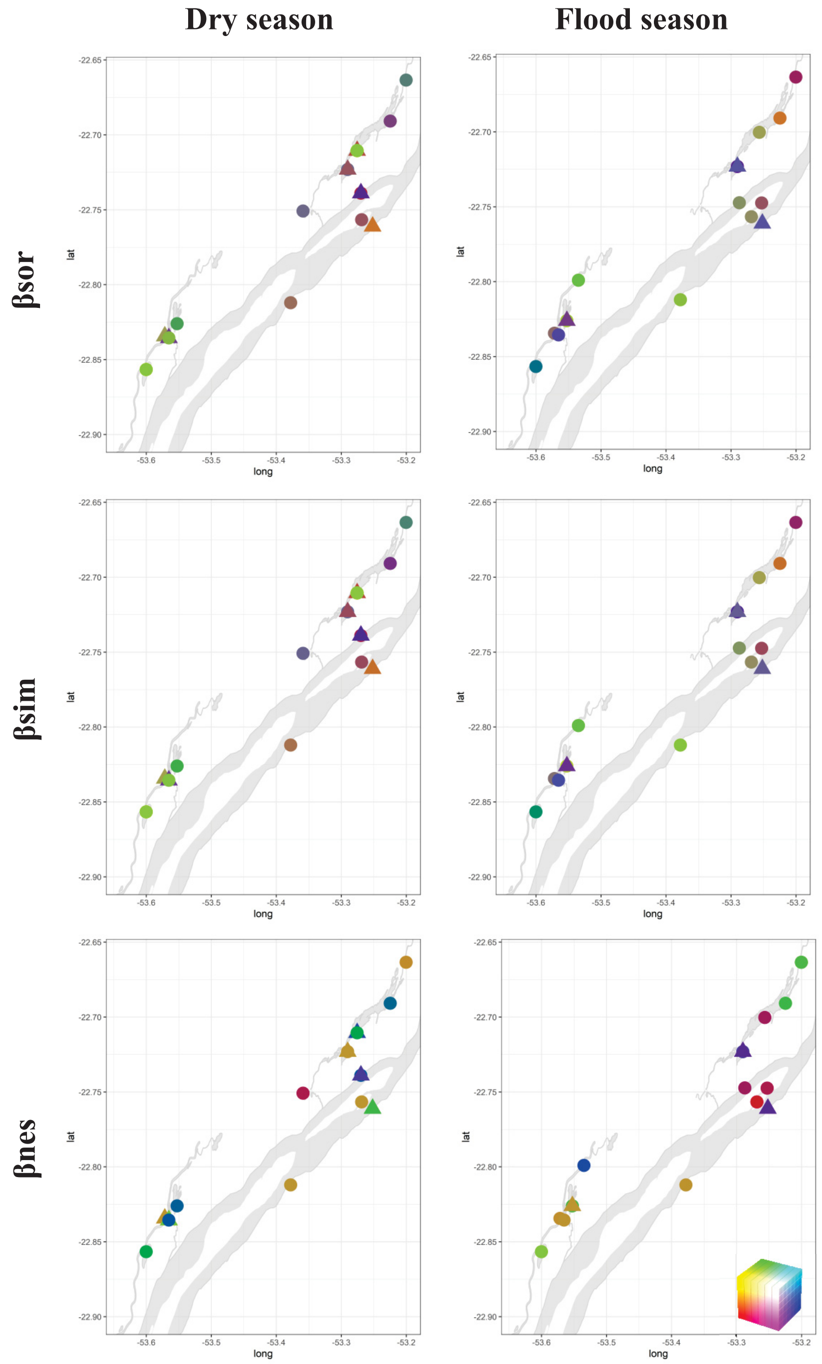


Figure 5: RGB color maps based on non-metric multidimensional scaling for Beta Sor (Sorensen dissimilarity), Beta Sim (turnover) and Beta Nes (nestedness) of endoparasites along Upper Paraná River Floodplain in the dry season (left column) and flood season (right column). Similar colors indicate sites with similar parasite compositions for each beta diversity dissimilarity index. Triangles are river channel sites, and circles are lake sites.

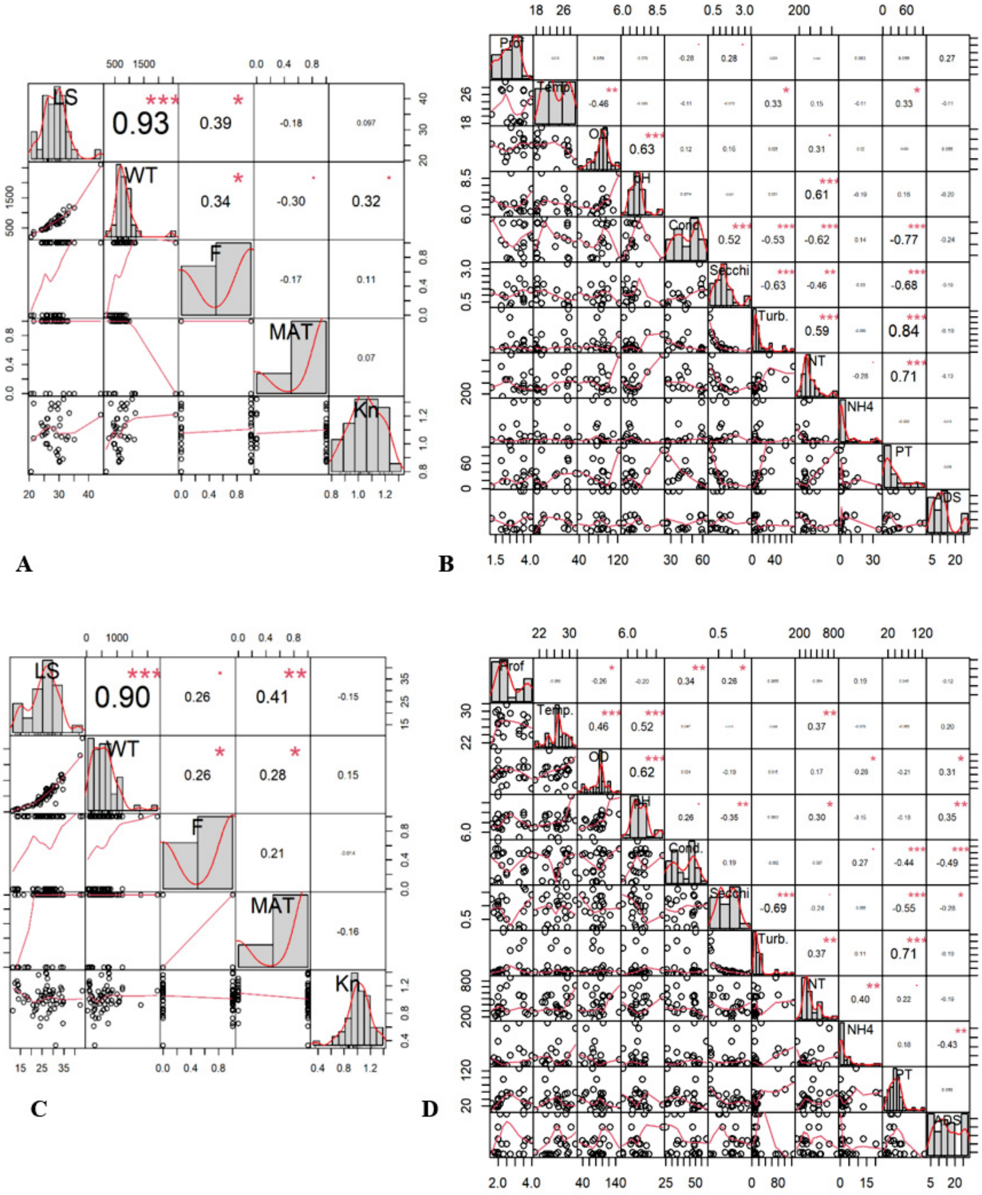


Figure 6: Chart correlation and variables distribution for all predictor variables used in RDAp analyses to explain the endoparasite community. A. traits in drought season; B. environmental variables in drought season; C. traits in flood season; D. environmental in flood season.

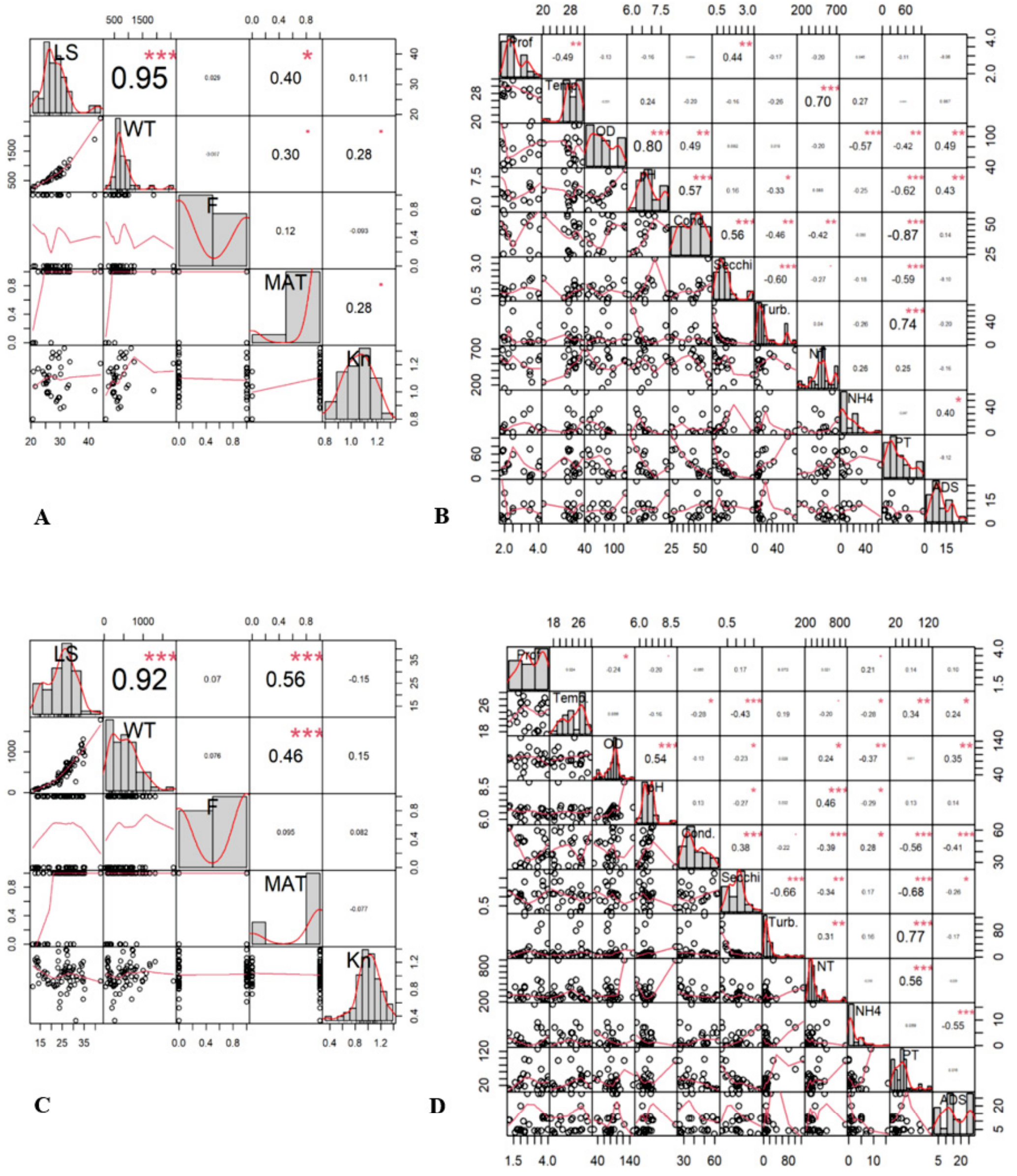


Figure 7: Chart correlation and variables distribution for all predictor variables used in RDAp analyses to explain the ectoparasite community. A. traits in drought season; B. environmental variables in drought season; C. traits in flood season; D. environmental in flood season.

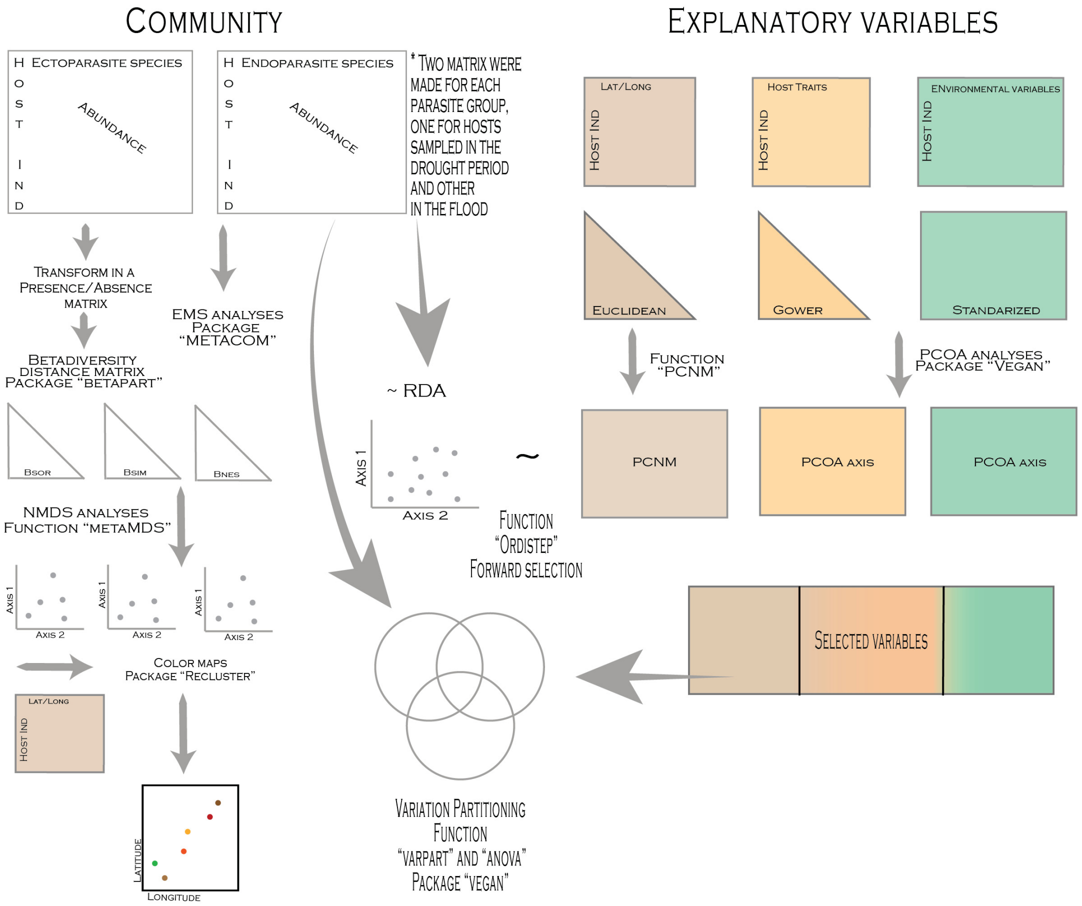
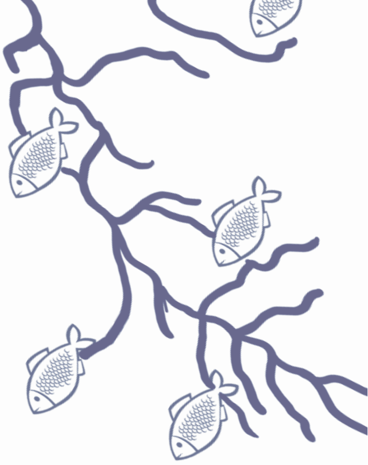


Figure 8: Schematic framework of the beta-diversity analyses.



Capítulo 2

Life is caught up in the task of writing an endless story

— Ramon Margalef

Human perturbation shifts host-parasite modularity in a neotropical river: the role of host intraspecific traits and parasitism form on network structure

Ana Paula Lula Costa[1,3], Andre Andrian Padial[1] & Jordi Bascompte[2]

1. Programa de Pós-graduação em Ecologia e Conservação
   Universidade Federal do Paraná
   Curitiba, PR, Brazil
2. Department of Evolutionary Biology and Environmental Studies
   University of Zurich
   Zurich, Switzerland
   8057

3. Corresponding author: anapaulalula@gmail.com

Abstract

Parasitism is an association based on species population dynamics and environmental factors. As a result, important information is lost when studying species-by-species network structures. Here we analyze changes in modularity, considering the host individual variation and the different forms of parasitism: ecto and endoparasitism. For this, we used a network approach based on mixed networks, simply defined by a bipartite configuration, where host individuals nodes are linked with parasite species by their interactions. We used a fish-parasite mixed networks of a coastal river with a high perturbation level, in order to understand how anthropogenic perturbation gradient influences the structure of host-parasite networks. As well as how the modules of host-parasite mixed networks is influenced by intraspecific traits. Our results showed that different forms of parasitism respond differently to the environment, once just ectoparasites' modularity increased with human perturbation. In addition, mixed-network's modules were intrinsically related to individual variation, with host fitness being the most important trait, regardless of the parasite's life forms. Besides, parasite intensity of infection was also related to modularity, mostly for endoparasites. Our results showed a host-parasite network with changes in community equilibrium and increasing of species with opportunistic behavior. Accordingly, we highlight host-parasite networks' sensitivity to ecological gradients marked by human perturbation and the importance of individual fitness variation for community stability and persistence. Indeed, our results demonstrated that a mixed network approach can elucidate the role of the river gradient on host population and parasite distribution. Besides the direct link between the environment and the parasite's life history. An important outcome once a major part of studies tend to work with host-parasite networks, regardless of the parasite's life forms.

Keywords: mixed network, individual variation, environmental gradient, fish-parasite interaction.

Introduction

A long-lasting issue in parasite ecology is to understand what determines the distribution of parasites inside a host community (González and Poulin, 2005; Dallas, 2014; Krasnov et al., 2015). Parasitism is a complex relation driven by co-evolutionary processes. Both the dynamic of host populations and the ecosystem play a major role in this type of interaction (Krasnov et al., 2015). Analyzing the structure of interaction may help us distinguish which drivers, environmental or biological, are determining host-parasite relations (Runghen et al., 2021). Studies concerning parasite interactions found interesting patterns related to network structure and environmental gradients in a species-by-species resolution (*e.g.* Lima Jr et al., 2012; Bellay et al., 2013; Bordes et al., 2015). Few studies that take into consideration host individual variation reveals a huge gap in our current knowledge (Guimarães, 2020). It is known that host intraspecific traits may shape parasite abundance and composition inside a metapopulation (Costa et al., 2021). Whereas how it determines parasite distribution and network structure in a community of hosts is still an open question. A better understanding of this question may elucidate how parasite interactions will be shaped in an ecosystem in changes resulting from human impact and climate emergencies (Runghen et al., 2021).

The diversity of parasites varies within a host population based on the host's sex, behavior, or body size (Poulin and Leung, 2011b; Bellay et al., 2018), as individual variation may cause changes in the susceptibility of hosts to parasitic infection. (Rigaud et al., 2010; Pilosof et al., 2015). More than host features, the environment can influence parasite transmission dynamics between hosts (Sures et al., 2017; Lima-Junior et al., 2021). Parasitism transmission mode (by contact or trophically transmitted) is a key feature concerning their distribution (Bellay et al., 2015). For instance, ectoparasites, transmitted by contact, are known to have a more modular structure. In turn, endoparasites are trophically transmitted, and have a nested structure (Bellay et al., 2015). However, due to specialized interactions, these patterns may change concerning host individual variation. Based on the highly level of specialisation of most parasites, one can expect a modular structure for both types of parasitism. Although it is not clear if values of modularity may vary between different modes of transmission across a gradient (Campião and Dáttilo, 2020; Pilosof et al., 2015). To address this issue, we will use a network approach based on mixed networks, simply defined by a bipartite configuration, where host individual nodes are linked with parasite species by their interactions.

Regarding the concept of mixed networks, few studies bring some enlightenment about its structure and interaction dynamics (Pilosof et al., 2015; Dallas, Laine and Ovaskainen, 2019; Campião and Dáttilo, 2020), more specifically, its modularity structure- a metric described by the tendency of clustering formation in a network (Bascompte and Jordano, 2013). Regarding species-by-species networks, modularity has been connected to parasite specialization and their phylogeny, in the case of hosts (Krasnov et al., 2012; Bellay et al., 2013; Runghen et al., 2021). In addition to the host-parasite interaction, modularity has also been associated with network resilience, as shown in studies relating, for the first time, environmental perturbation and modularity (May, 1972; Stouffer and Bascompte, 2011). Later, spatial modularity has brought insights into network connectance and stability, with the idea that modularity buffers the spread of impacts across a gradient (Bordes et al., 2015; Gilarranz et al., 2017). Thus, one may expect interaction networks to become more modular and less connected on a human perturbation gradient while maintaining species richness across the ecosystem (Bordes et al., 2015; Gilarranz et al., 2016; Runghen et al., 2021).

Further, human perturbation can, directly and indirectly, influence host-parasite interactions (Pilosof et al., 2012). Different parasitism forms have different behaviors concerning perturbation. The major metric of changes due to environmental impacts is parasite abundance and intensity of infection. It is known that ectoparasites are more directly influenced by environmental changes, while endoparasites are more affected by changes in the density and susceptibility of their hosts (Buck, 2019). Although these different patterns are well documented in the literature, most interaction network studies do not separate ecto and endoparasites (Bellay et al., 2015; Dallas and Becker, 2021). Subsetting parasite networks can result in more accurate associations, once host traits and individual behavior change infection probabilities in different ways, depending on parasitism form (Bellay et al., 2015; Costa et al., 2021). Thus, looking specifically at each group of parasites may help us better understand the different roles of biological and environmental attributes in their interaction organization (Dallas and Becker, 2021).

While parasites have complex responses to environmental perturbation, hosts may modify their individual trophic and social behavior, as well as their reproduction and growth rates (Sures et al., 2017; Des Roches et al., 2018). Such variations affect population stability and persistence, by, for example, excluding higher fitness by disruptive selection (Bolnick et al., 2003). Which can quickly modify community equilibrium and ecosystem functioning (Bolnick et al., 2011). Here, we used fish-parasite mixed networks of a coastal river with a high perturbation level, to analyze changes in modularity and its consecutive modules, taking into account the different forms of parasitism: ecto and endoparasitism. We aimed to answer two major questions. (1) Can the anthropogenic perturbation gradient influence the structure of host-parasite networks? In this case, we expect higher modularity in sites with higher anthropogenic perturbation, which may be a consequence of a higher mean intensity of infection. We also expect that such a pattern is better observed for ectoparasites, once they tend to respond better to environmental changes. Our second question tries to unveil the influence of individual variation in levels of perturbation. (2) Are host-parasite mixed- networks' modules influenced by intraspecific traits? If so, do the same traits affect modules configuration over the gradient? We expect different traits to be related to modules configuration in different river stretches.

Methods

Study area and data sample

The Guaraguaçu River is one of the main rivers in the Coastal Basin of the State of Paraná. Its source is located in the pristine mountain freshwaters of Atlantic Forest, and its mouth is located in a dense mangrove of Paranaguá Bay (Galvanese et al., 2022). The river has a total length of 60 km, with a normal upstream-downstream flow during ebb tide and counterflow during high tide. This pattern brings an inverted flow dynamic to the river twice a day, depending on the tide table (Silva, 2008; Galvanese et al., 2022). Due to the river's environmental characteristics and human pressures, we were able to categorize it in four clear distinct sectors, following the continuous distance of the river. These sampling sectors were distant from each other by an average of 4 km, with the maximum linear distance between the first and last sector being of 13 km.

The 1st sector, located in the upstream part, has a very conserved and pristine environment. Its margins are characterized by the dominance of the tree species *Tabebuia cassinoides* (Lam.) DC., and an average width of 10-15 m (Galvanese et al., 2022). The following sectors have a higher influence on the counterflow. The 2nd sector is strongly influenced by anthropogenic impacts. Two rectified channels, one for water supply capturing and the other for sewage effluent deposit of a sanitary landfill were opened in this sector (Galvanese et al., 2022). The 3rd sector is located inside the Guaraguaçu River Ecological Station, a restored environment that was planned to buffer upstream impacts. Sector 4th is near the mouth of the river, within a dense mangrove ecosystem with high tidal influence, and greater salinity (Silva, 2008; Galvanese et al., 2022) (Figure 1). To better describe the environmental gradient along the river, the following abiotic variables were collected: Secchi disk depth (transparency), salinity, conductivity, pH, and a metric of Human influence level, measured by the landscape percentage with human occupation (houses, roads, agriculture systems) in 1 km radius circle from each sampled point (Appendix A).

The fish sampling was performed following the protocol of the Guaraguacu River Monitoring project, Parana, Brazil. Ichthyofauna sampling survey was made with the use of 10 gillnets of 20 meters (2, 4, 6, and 8 mm) and 10 traps (drum nets) in each sector, to capture individuals of all sizes. The method was the same between the four sectors of the river, according to the heterogeneity of the spatial gradient and covering practically all its extension. Nets were arranged in a paired fashion, used to sample associated fauna from native and non-native macrophyte banks. For the sectors where non-native banks did not occur (i.e. sectors 1 and 4) traps and gillnets were paired in native macrophytes banks and the closer structured microhabitat. Each fish individual were identified, measured (total length and standard length, cm), weighed (g), and their sex and gonadal maturation were identified. The gills and viscera were removed and subsequently searched for metazoan parasites (ectoparasites and endoparasites). The organs were examined under a stereoscopic microscope to collect parasites. The methodology for fixing the parasites followed the protocol established by Eiras et al. (2006). Parasites were identified using the following works: Kohn et al. (2006, 2007), Thatcher and Boeger (1984b,a), Thatcher and Varella (1981), Thatcher (2006), Moravec et al. (1998). A total of 159 individuals, summarized in 12 fish species, and 68 different species of parasites (36 species of ectoparasites and 32 species of endoparasites) were sampled in the Guaraguaçu river. Of those, 32 fishes were sampled in sector 1, 42 in sector 2, 38 in sector 3, and 47 in sector 4 (Appendix A).

Functional Traits

We used the intraspecific characteristics of fishes collected in the field: length, weight, sex, and gonadal maturity level. Fish growth condition- an index often related to parasitism effects- was also calculated as a proxy of individual health or fitness (Timi and Poulin, 2020). The index is described as the relative conditional factor

(Kn) (Le Cren, 1951), and can be calculated by:

$$Kn = \frac{W}{\hat{W}}.$$

Where *W* is the individual weight, the expected weight calculated by the smoothed mean weights. Individuals with Kn lower than 1 are related to a below-average growth condition (Ogle, 2018). Alternatively to other conditional factor' indexes, this measure allow us to distinguish its relation to length and other traits across multiple fish species individuals (Le Cren, 1951). Parasite richness in each individual was also an intraspecific trait of the host, as well as a rate of individual infection, calculated by the sum of the abundance of all parasites species presented in a fish individual.

We separated parasite species by their parasitism form: ecto or endoparasitism. Ectoparasites are transmitted by contact and have a single-host cycle, whereas endoparasites are trophically transmitted with multi-host cycles (Bush et al., 2001). Parasites' abundance, as well as the organ in which they were found inside the host, were also recorded as traits related to the parasitism interaction (Dallas, Laine and Ovaskainen, 2019). We also calculate a mean intensity of infection per sector for both ecto and endoparasites, which was the sum of the parasite's abundance divided by the number of hosts sampled in each site.

Network structure and statistical analyses

We used a mixed network structure to describe host-parasite interactions, characterized by a bipartite network with host individuals as nodes on one side linked with parasite species on the other side. The abundance of parasite species in each individual was used to compute a weighted mixed network. We chose to divide parasite species by their parasitism form, resulting in 2 mixed networks by sector, and 8 mixed networks over the river gradient. We used the metric of Dorman and Strauss's weight version of bipartide modularity, maximized by Beckett (Beckett, 2016) to analyze how interactions were grouped concerning each parasitism form (Dormann and Strauss, 2014). After, we analyzed if the values calculated were higher than expected by a null model that keeps connectance (number of links in the matrix) constant (Patefield, 1981). To relate the modularity of the different mixed networks, we normalized their values by calculating the z-scores, as follows:

$$Zs = \frac{Qe - Qn}{Qsd}.$$

Where Qn is the raw estimate of modularity for an empirical network, Qe and Qsd are the mean and standard error value of modularity for a population of randomized networks (n = 100).

We made a principal components analysis to select the environmental variables that most distinguish river sectors. Conductivity, human influence level, and transparency were variables mostly related to sector characterization (Appendix A). We chose to calculate independent linear models for each variable to understand the relationship between environmental variables to network modularity. We also predict that the environmental gradient through the river would change parasite richness and intensity of infection rates. Thus, we contrasted this metrics with environmental variables to analyze if these patterns would indeed change. And then, environmental variables were related to modularity values.

Aiming to analyze which functional traits were mostly related to the modularity of the mixed-networks, we classified each host individuals and parasite species for their module configuration. The classification was made for each mixed network, in order to verify if the same traits were selected in all sites and for different parasitism forms. Before conducting relationship analyses, we replicated the module structure of the network 50 times and compared their group division, to check their similarity. After verifying module configuration invariability, we used general mixed models with species identity as a random factor to analyse the relation of host intrinsic traits to module configuration. For parasite species, we looked for a relationship between their abundance and module configuration. All analyses were calculated by the packages “vegan” (Oksanen et al., 2015), “Lmperm” (Wheeler et al., 2016), “igraph” (Csardi and Csardi, 2007) “MASS” (Ripley et al., 2013) and “lme4” (Pinheiro et al., 2007) in the software R (Team et al., 2020).

Results

Networks were significantly and highly modular, with a minimum of 5 modules and a maximum of 12 (Figure 2 and 3). All observed values were higher than randomly expected, as we can see in Table 1. When replicating the module structure of the network, the number of modules in each network was the same. As for the identity of nodes inside the modules, we filtered each value to see which were the distinct modules in all replicates. All nodes end up in the same module.

Table 1: Modularity values of each mixed network. Modularity: Newman's modularity values, Null: Mean value of null models modularity. z-score: Standardized modularity values calculated by z-score. Modules: number of modules resulted for each mixed network.

Sectors	Modularity	Null	z.values	Modules
Ectoparasites				
1	0.690	0.316	1.182	5
2	0.321	0.079	3.073	9
3	0.591	0.196	2.006	7
4	0.776	0.493	0.574	11
Endoparasites				
1	0.395	0.144	1.736	5
2	0.537	0.250	1.145	8
3	0.544	0.234	1.329	6
4	0.733	0.450	0.627	12

Environmental effects had different influences on the structure of host-parasite interactions. Ectoparasite's mean intensity was positively related to human perturbation (r^2= 0.89, p-value= 0.03) and negatively related to transparency level (r^2= 0.96, p-value= 0.01), measured by the Secchi disk depth. Both ecto and endoparasite's modularity was positively related to mean intensity of infection (Figure 7). Ectoparasites modularity was also positively related to anthropogenic influence and negatively related to transparency level (Figure 5 A e B)(p-values slightly higher than 0.05, likely due to small sample size, n = 4), but not endoparasite's (r^2 0.01, p-value= 0.94;r^2 = 0.02, p-value= 0.85). Despite the small number of sites, the high coefficient value of determination indicates a pattern of positive relation of anthropogenic influence to ectoparasite infection rates and modularity.

Traits relation to module configuration was only significant for host' models (Table 2). For ectoparasites and endoparasites networks, host models with higher accuracy had growth condition index- fitness related- as the most important traits (Figure 6). Apart from for endoparasites' networks in sectors 2 and 3 (most disturbed), that had intensity of infection rates explaining better module configuration (Figure 7). We ran a Pos-hoc analysis presented in the Appendix, to better describe relationships.

Table 2: Generalized linear mixed models between hosts intraspecific features and modules configuration. Columns are referred to host's traits, being: Intensity: Intensity of infection in each individual; Weight: host individual weight; Length: host individual length; Kn: Host growth condition index. AIC: Akaike information criterion, Chisq: Value of the chi-square analyses, p: p-value, df: degrees of freedom.**values with non random effect.

	Ectoparasites				Endoparasites			
	Intensity	Weight	Length	Kn	Intensity	Weight	Length	Kn
Sector 1								
AIC	81.7	61.48	143.7	-6.19	71.41	223.090	106.35	-4.44
Chisq	5.663	50.31	101.5	73.314	5.77	1158	19.570	40.67
p	0.2258	0.001	0.001	0.001	0.2166	0.01	0.49	0.001
df	7	7	6	7	6	7	6	7
Sector 2								
AIC	90.09	46.3	25.08	17.46	46.13	301.41	139.3	36.1
Chisq	17.37	15.7	7.9	17.04	5.47	67.48	13.06	20.44
p	0.02	0.04	0.44	0.02**	0.001	0.690	0.01	0.466
df	11	11	11	11	10	10	10	10
Sector 3								
AIC	293.3	434.46	201.37	-21.14	104.48	38.1	92.97	16.71
Chisq	33.43	131.32	76.53	162.57	245.77	6.24	8.03	16.19
p	0.001	0.001	0.001	0.001**	0.001	0.28	0.15	0.001
df	9	9	9	8	7	8	8	8
Sector 4								
AIC	303.27	97.72	41.65	49.47	77.35	344.77	37.56	29.41
Chisq	43.18	55.43	55.65	86.4	8.9	108.04	46.91	89.38
p	0.001	0.001	0.001	0.001	0.63	0.001	0.001	0.001
df	13	13	13	13	14	14	14	14

Ectoparasites module configuration in sectors 2 and 3 was better explained by host fitness without species taxonomy as a random factor. What allows us to say that ectoparasites module configuration, in this case, was strongly related to host fitness, despite species identity (Figure 6). In the other models presented on Table 2, besides taxonomy influence, intraspecific traits predicted better module configuration.

Discussion

Parasitism is an association based on individual and environmental factors (Bolnick et al., 2019). For this reason, important information is lost when studying species-by-species network structures. Here we demonstrated that a mixed network approach can elucidate the role of population dynamics across parasite distribution and the direct link between the environment and the parasite's life history. One of the possible reasons is that parasitism forms had different responses to the environmental gradient. Besides, network module configuration was intrinsically related to individual variation, with drivers varying concerning life history and human perturbation. Here we acknowledge the importance of host phylogeny in network's structure, highlighting the species identity effect in the level of modularity found along the river. However, its was also clear that taking out species identity, the fitness similarity was the main factor concerning module configuration.

We first acknowledge that modularity increases in highly perturbed sites, mainly for ectoparasites. However, in both parasite forms modularity was related to the mean intensity of infection. We indeed expected that mixed networks would be modular due to the highly phylogenetic influence concerning parasitism relations (Pilosof et al., 2015). Even so, the threshold that goes beyond host species taxonomy brought important insights considering which features can be related to parasite distribution between hosts (Dallas, Han, Nunn, Park, Stephens and Drake, 2019). For instance, following the idea that contact transmitted infestation of some kind of parasites can change the schooling behavior of fish population (Minchella and Scott, 1991). One may suggest that fish populations can diminish infection intensity by avoiding highly infected individuals (Wellnitz et al., 2003; Poulin, 2018). What seems to be the case between modularity and intensity of infection observed in our study, although a definitive response could be better obtained using experimental studies. In fact, the aggregate distribution pattern of parasites can be another ecological factor determining modularity relation to infection (Poulin, 2013).

Previous studies suggest a positive relation between modularity and human perturbation (Stouffer and Bascompte, 2011; Gilarranz et al., 2017). We found the same relation mainly for ectoparasite's mixed networks. In addition to anthropic impacts, the river also showed signs of eutrophication, mainly by the decrease of transparency level concerning human perturbation (Budahn et al., 2002). Eutrophication often leads to an impact on species diversity, decreasing richness and increasing the abundance of a few dominant species (Budria, 2017). The decrease in interaction heterogeneity can be seen as a tipping point in network stability (Carpenter et al., 2015). Ectoparasites' increase in infection intensity can be a consequence of eutrophication, as well as their modular structure. Taking into account that ecological interaction configurations are shaped by individual responses to the environment (Miguel et al., 2018), one could relate higher modularity as an attempt of the host to cope with perturbation. A more modular structure can be an useful way to buffer infection of dominant species and maintain community stability (Minchella and Scott, 1991; Gilarranz et al., 2017).

Although endoparasites modularity was related to infection intensity, there was no sign of relation with any environmental variable. Helminth parasites with complex cycles depend on their host trophic relations to succeed (Adamson and Caira, 1994). This demands an ecological balance inside the community, which may not be favored in a highly perturbed site. In contrast, ectoparasites are more capable of increasing their distribution ranges, apart from their hosts, which may lead to a higher probability of infection (Carlson et al., 2017). Indeed, parasites with contact transmission are known for having opportunistic behavior, taking advantage of favorable environmental conditions, and increasing their abundance and prevalence (Costa et al., 2021; Korine et al., 2017). Although we did not measure the nutrient ratio of each site, we may expect an increase in primary production on eutrophic sites and a consequent decrease in transparency (Carpenter et al., 2015). Some hosts can increase their density, and opportunistic parasites may be favored by the number of resources, increasing their abundance and infection rates (Budria, 2017).

Our results corroborated with a previous study suggesting that module configuration determinants in mixed networks are linked to host body size (Pilosof et al., 2015). Relatedly, host fitness was the major determinant of module configuration in most sites, apart from the form of parasitism. In our case, fitness was described by host growth conditions. Parasitism can change the growth condition of fishes, once high or new infections demand physiological and behavioral changes, redirecting energy spend on growth and reproduction, decreasing fitness (Marcogliese, 2004). Although our results did not make a direct relationship between growth conditions and parasite infection, we can suggest that infection influenced the increased fitness similarity of hosts inside the modules. This pattern was even more evident for ectoparasite interactions in perturbed sites, once fitness relation to module configuration was higher when we removed the taxonomy influence. In summary, apart from species identity clear influence, our results support the hypothesis that ectoparasite distribution in perturbed sites was driven by individual fitness. Such a pattern can be related to a frequency-dependent transmission, in which contact-transmitted parasites are more related to the number of infected hosts, rather than to species-specific relations (Rudolf and Antonovics, 2005).

Endoparasites interaction's module configuration also showed a different pattern in perturbed sites, being infection rate the most determinant trait. Here, what is interesting to note is that although there was no relationship between modularity values and perturbation, sites with higher perturbation presented their module configuration based on infection rates and fitness similarity between host individuals. Such a result reinforces our hypothesis that modularity can be seen as a way of buffering infection levels inside a host community. It is clear that human perturbation in sites affected endoparasite interaction structure. Trophically-transmitted parasites rely on host predation interactions, and changes in water transparency, for instance, may limit the probability of encounters between intermediate and final hosts (Budria, 2017). This may be one of the reasons there was no relationship between endoparasite intensity of infection and human perturbation. This limitation can also be the reason for hosts with similar fitness having similar infection rates, once the probability of food acquisition and parasite infection is limited by the same drivers.

Our results also highlight the importance of individual fitness variation for community stability and persistence, as well as suggest that different forms of parasitism respond differently to the environment. This is an important outcome once a major part of studies tend to work with host-parasite networks, regardless of the parasite's life forms (Costa et al., 2021; Dallas and Becker, 2021). Here, we state that simple species-species network configurations lose a lot of information, mostly when looking into human perturbation effects in network structure. Understanding how individual traits vary with perturbation can elucidate the dynamics influencing interaction organization and may reveal which traits are more related to infection susceptibility (Bolnick et al., 2003). Notably, our results showed a host-parasite community with signs of stability loss, changes in community equilibrium, and increasing in dominant and opportunistic species. This scenario favors the emergence of new parasite interactions, that can turn into more virulent and intense infections (Zohdy et al., 2019). Therefore, we demonstrate the importance of monitoring and restoration of perturbed areas, trying to diminish the spread and probability of new potential environmental threats.

In essence, we could characterize the studied river system by a huge distinction between pristine and perturbed sites, in which we demonstrate that the host-parasite network structures are sensitive to ecological gradients marked by human perturbation. And that modularity is related to perturbation even for mixed networks, being this pattern related to host individual fitness and infection rate. Thus, one could say that host-parasite network stability seems to be held by not only a modular structure but also by the interaction with more stable environments. This assumption lead to equally interesting insights. For example, future studies should address the possibility that the maintenance of species flow between pristine and perturbed areas is central to the stability of freshwater systems. It would also be important to analyze if the river area chosen to be preserved can influence network stability. That is, if a more diverse site was the most perturbed, should it change interaction organization and community persistence? This is an important question to be addressed in a time when freshwater environments are facing high anthropogenic pressures, like deforestation of riparian forests, eutrophication, and dam constructions.

Figures

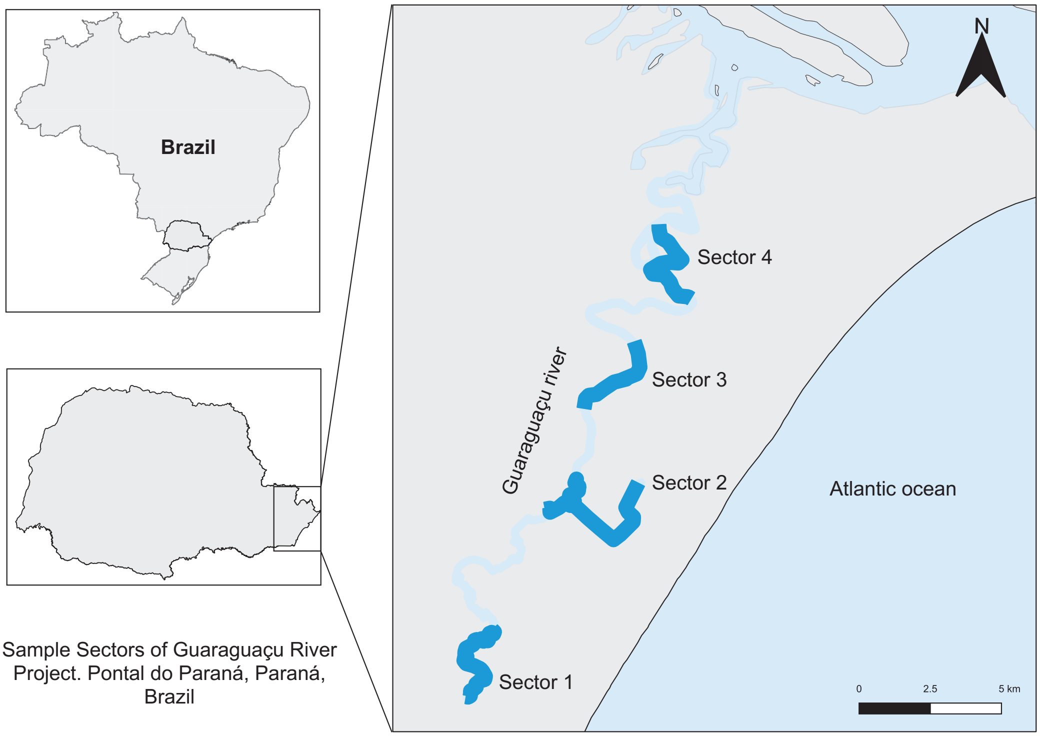


Figure 1: Map of the Guaraguaçu River, Parana, Brazil. Sectors where fishs were sampled correspond to the highlighted parts of the river

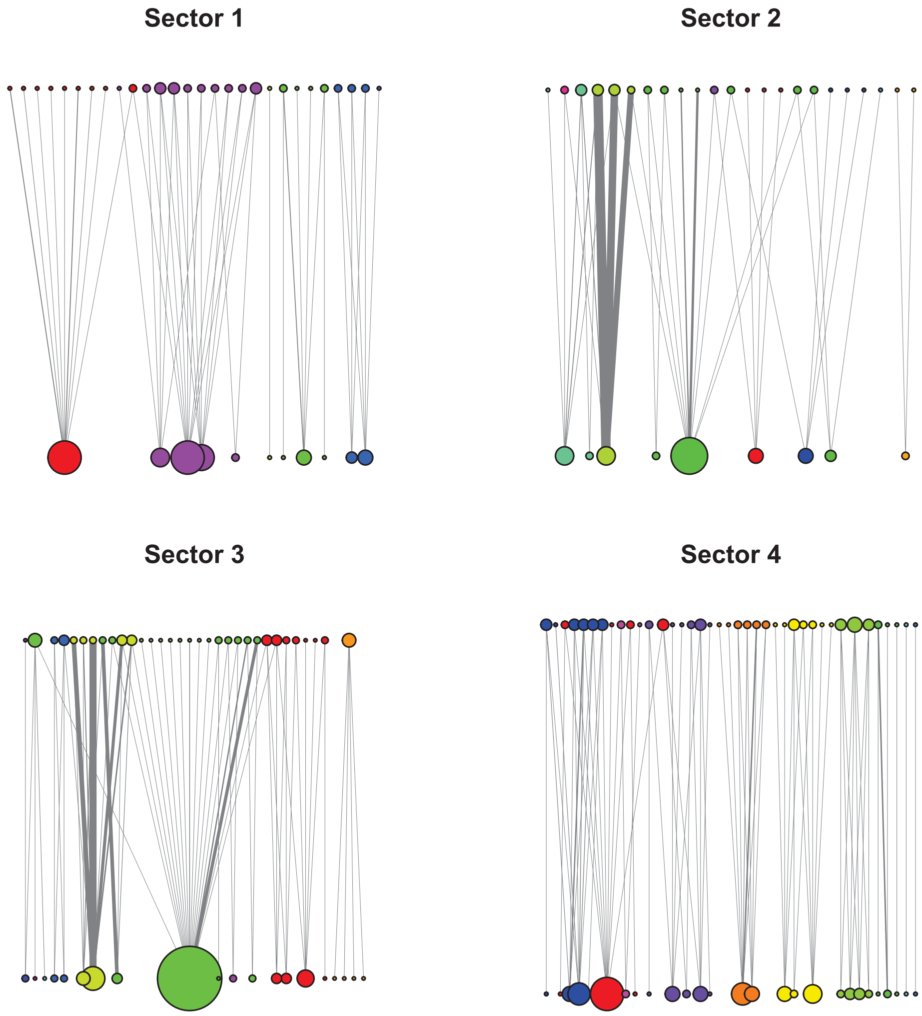


Figure 2: Host-parasite bipartite network for ectoparasites in each sector of the Guaraguaçu River. The color of each node represents its module's configuration and the size its degree. Line width represents their interaction weight

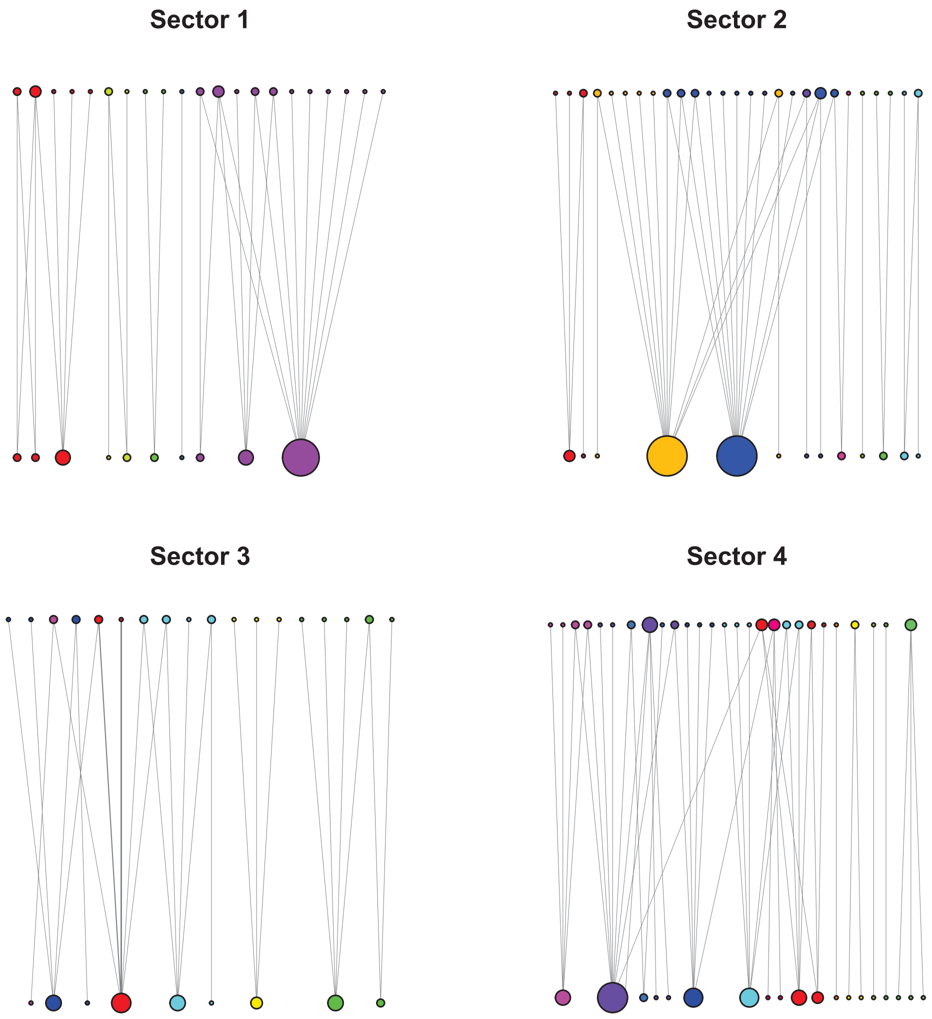


Figure 3: Host-parasite bipartite network for ectoparasites in each sector of the Guaraguaçu River. The color of each node represents its module's configuration and the size its degree. Line width represents their interaction weight

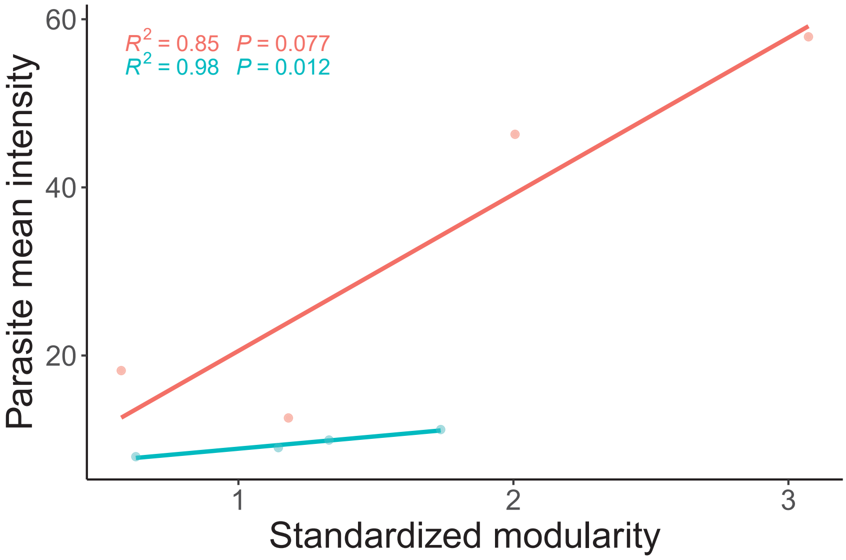


Figure 4: Relation between parasite mean intensity in each sector and modularity. Red lines correspond to ectoparasite networks and blue lines to endoparasite networks. R^2 and p-value refer to linear model results

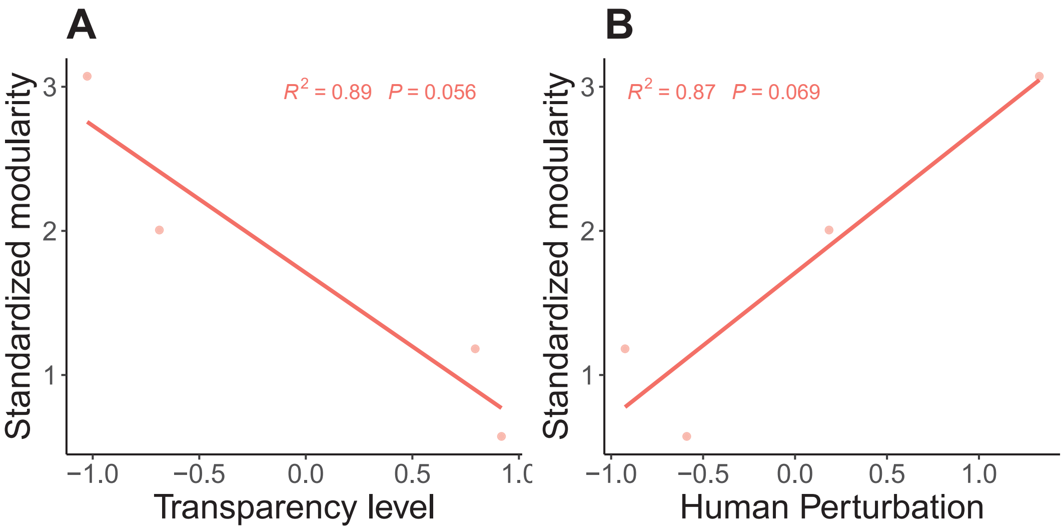


Figure 5: Relation of environment variables to ectoparasite's modularity. Red lines correspond to ectoparasite networks. A: Relation between modularity of each sector and transparency level, calculated with the standardized value of Secchi disk depth(cm). B: Relation between modularity and Human perturbation level, calculated with the standardized value of anthropogenic influence. R^2 and p-value refer to linear model results

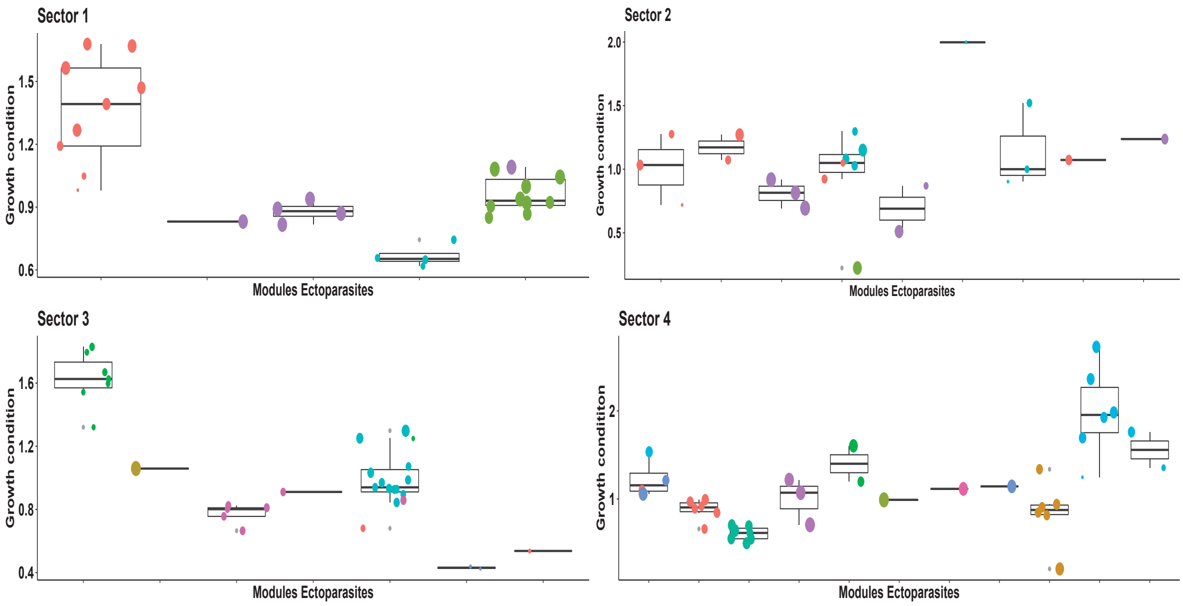


Figure 6: Boxplot between the main determinant traits of hosts and their modules configuration. Colors correspond to fish species and size to intensity of infection in each host

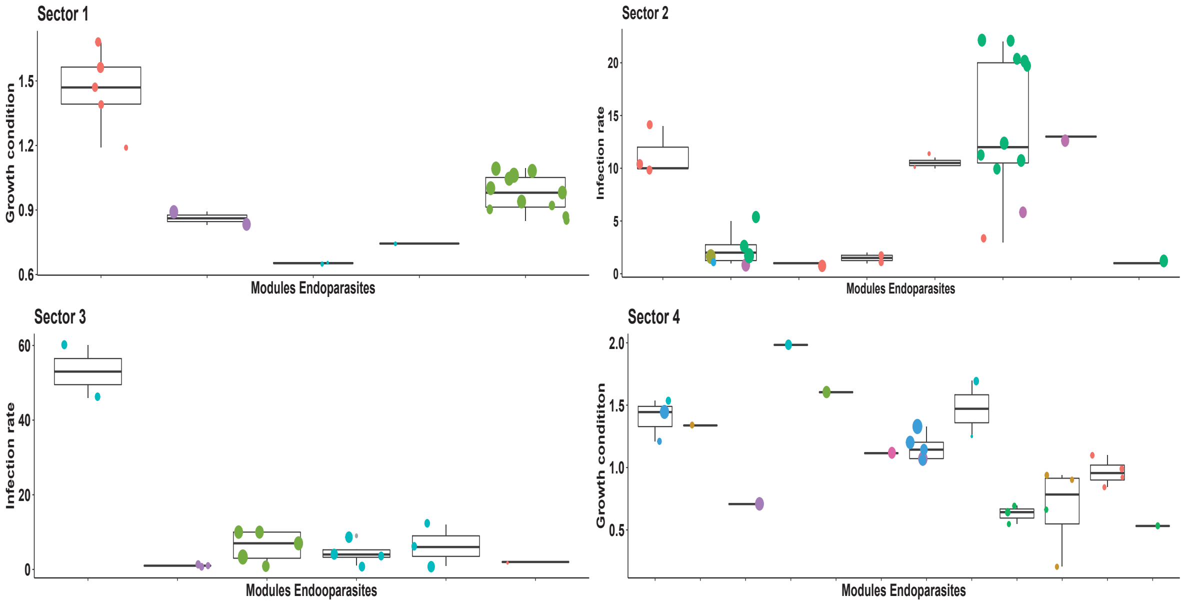
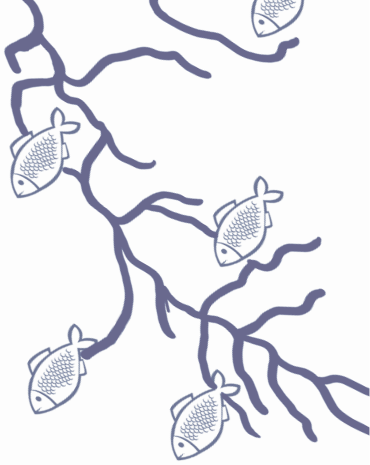


Figure 7: Boxplot between the main determinant features of hosts and their modules configuration. Colors correspond to fish species and size to intensity of infection in each host



Capítulo 3

> *Nobody ever figures out what life is all about, and it doesn’t matter. Explore the world. Nearly everything is really interesting if you go into it deeply enough*
>
> — Richard Feynmann

Parasite's turnover and centrality conservatism drives the structure of a neotropical river metanetwork

Ana Paula Lula Costa[1,2,3], Andre Andrian Padial[1] & Jordi Bascompte[2]

1. Programa de Pós-graduação em Ecologia e Conservação
   Universidade Federal do Paraná
   Curitiba, PR, Brazil

2. Department of Evolutionary Biology and Environmental Studies
   University of Zurich
   Zurich, Switzerland
   8057

3. Corresponding author: anapaulalula@gmail.com

Abstract

Host-parasite interaction variation across spatial gradients can be related to environmental and biological factors. Host species distribution patterns direct influence parasite diversity, and changes in species importance can lead to changes in network connectivity patterns. To know the role of host and parasite species in network connectivity can bring important information on parasite contribution to network structure and host contribution to transmission and infection dynamics. We used a metanetwork approach to describe how a fish-parasite metacommunity is structured along a neotropical tidal river gradient. We aimed to identify species' roles and centralities within and among stretches of the river, besides finding what ecological traits are related to such metrics in the metanetwork. Our results showed a clear turnover of species and interactions along the river, but with the same species of hosts and parasites being central across different river stretches. Fish and parasite centrality were related in the way that highly central parasites were found infecting central hosts. However, this was only for parasites with high abundance and prevalence. In addition to ecological traits, the development stage was also related to parasite centrality. Host traits showed contrasting relations to centrality based on river stretches, clearly showing the importance of the environment in the role of the host in parasite infection. Here we also saw natural and anthropic filtering in the river, which may be conducting both a natural turnover of species and a conservatism in species role in relation to network connectivity along the river.

Keywords: species role, host-parasite network, beta diversity, spatial gradient.

Introduction

Community ecology has a persistent issue concerning the rules that drives species distribution across scales. From a regional perspective, we have already known patterns, like the variation tendency of species composition across different sites. A pattern that mainly occurs due to known mechanisms, like environmental change, ecological drift, or random dispersal (Nekola and White, 1999; Soininen et al., 2007). There is extensive literature describing species turnover for different communities, whereas there is still a lack of studies accounting for a turnover in ecological interactions over environmental gradients, mainly host-parasite ones (Dallas and Poisot, 2018). Here we address this issue by focusing on a host-parasite interaction network of a fish metacommunity inside a neotropical river gradient.

Turnover of host-parasite communities was explored for a set of different host taxons and habitats (Poulin, 2003; Krasnov and Poulin, 2010; Espínola-Novelo et al., 2020). Most studies acknowledge the relation between parasite composition dissimilarity and geographical distance. Apart from this, mechanisms change across hosts and habitats (Krasnov et al., 2010), mostly due to species response to environmental gradient, along with their dispersal ability. Indeed, parasite species composition is usually related to host distribution, in a way that species infecting widely distributed hosts have a higher chance of maintaining their presence throughout the environment (Poulin, 2003). Though, environmental factors may lead to limitations in species presence, by changing the abundance of intermediate and suitable hosts, or by affecting the free stages of some groups of parasites (Bolnick et al., 2020). Consequently, parasite community composition can change depending on host populations (Bolnick et al., 2020; Costa et al., 2021), and it is not yet clear which drivers are under the persistence of some parasite species over others across an environmental gradient.

One of the main approaches to relating host-parasite distribution with species persistence is the metacommunity (Cardoso et al., 2020). That simply consists of the analyses of a set of communities linked by dispersal (Leibold et al., 2004). Most studies using the metacommunity approach measure the structure of species composition given a regional pool of species and their distribution inside different local communities (Mihaljevic, 2012). Here, we will focus on a local community of host species sampled in the same stretch of a subtropical tidal river that may or not interact with each other by parasite transmission. Additionally, we will gather the entire regional community of hosts connected throughout the river by parasite transmission. In this framework, we may have the same parasite species infecting different species of hosts within the same river location and/or across the river. While different sets of parasite communities of the same host species may be found in different locations. In the first case, parasite species would be the major connectors of different host species; and in the second case, host species would be the ones connecting different communities of parasites. Therefore, by analyzing the river connectivity by species interactions, we are able to investigate community structure and persistence (Tylianakis and Morris, 2017), and in the case of parasites, transmission dynamics (Bellekom et al., 2021). We thus combined the metacommunity framework with the analyses of ecological networks, by a metanetwork approach.

A metanetwork consists of a framework based on local networks connected by species movements and their interactions over a spatial gradient (Tylianakis and Morris, 2017; Emer et al., 2018). An important approach to help us understand how interactions persistence or rewiring may connect an ecosystem (Li et al., 2020). By seeing not only the pattern of hosts and parasite distribution but also interaction and species persistence across a gradient, we can explore which drivers are allowing or constraining interaction occurrences. The importance of a species in the connectivity within and between networks allows one to quantify parasite species contribution to network structure; and host species contribution to parasite diversity and transmission (Dallas, Han, Nunn, Park, Stephens and Drake, 2019). This can reveal the parasite's exploitation ability and environmental adaptability traits related to parasite probability of host switching, and consequently novel interaction occurrences (Brooks et al., 2019).

One of the measures used to analyze the importance of a species in a network is centrality. There are many centrality metrics, and each one can show one different aspect of a species' relative importance (Gómez et al., 2013). Beyond that, centrality brings complementary information for beta-diversity analyses, by showing shared interactions over different species and sites, thus complementing metacommunity understanding (Dallas, Han, Nunn, Park, Stephens and Drake, 2019). Analogous to centrality the species' roles among and within different modules or sites also can be estimated (Li et al., 2020; Dallas, Han, Nunn, Park, Stephens and Drake, 2019). We investigated the beta-diversity of interactions and species connectivity importance to describe how a fish-parasite metacommunity is structured along the river gradient. Specifically, we aimed to identify species' roles and centralities within and among stretches of the river, besides finding what ecological traits are related to such metrics in the metanetwork. We specifically aimed to answer two main questions: 1) Is there a turnover of species interactions along the river? And if so, does species centrality change along with species distribution? We expect a higher turnover of interactions along the river gradient, along with changes in which species of host and parasites will be central on each stretch of the river; 2) Which drivers determine parasites species' role and centralization in the metanetwork? We expect species' ecological and functional traits to be related to species' role and centrality. For instance, parasite prevalence and abundance, as well as host body size are measures already related to centrality (Pilosof et al., 2015; Romano et al., 2016). We hope to answer these questions based on a distinguish metanetwork approach that accounts for both local and regional structures of interactions.

Methods

Study area and data sample

The Guaraguaçu River is one of the main rivers in the Coastal Basin of the Paraná State, South Brazil. Its source is located in pristine mountains fragments of the Atlantic Forest, and its mouth is located in the Paranaguá Bay, characterized by an extensive and well preserved Mangrove (Silva, 2008; Galvanese et al., 2022). The river is part of the Atlantic forest set of estuaries considered a Biosphere Reserve and World Heritage Site, named Lagamar. The river has a total length of 60 km, with the normal flow during ebb tide and counterflow during high tide. This pattern brings an inverted flow dynamic to the river twice a day, depending on the tide table. Due to the river's environmental characteristics and human pressures, we were able to categorize the river in four clear distinct sectors, following the continuous distance of the river.

The 1st sector, located in the upstream part, has a very conserved and pristine environment. Its margins are characterized by the dominance of the tree species Tabebuia cassinoides (Lam.) DC., and an average width of 10-15 m (Galvanese et al., 2022). The following sectors have a higher influence of the counterflow. The 2nd sector is strongly influenced by anthropogenic impacts. Two rectified channels, one for water supply capturing and the other (quite paradoxically) for sewage effluent. The 3rd sector is located inside the Guraguaçu River Ecological Station, thus representing a restoration zone given that human pressures described in the second sector are still reflected. Biotic and abiotic measures showed that both sectors has a sign of eutrophication (*e.g.* Galvanese et al., 2022). Sector 4th is near the mouth of the river, with an extensive and well preserved mangrove ecosystem, high tidal influence, and greater salinity (Silva, 2008; Galvanese et al., 2022) (Figure 1). Abiotic traits were measured during the project sample, in order to confirm and better relate the sectors distinctions (Appendix A). Sectors' minimum linear distance from each other was 4 km, and the maximum linear distance between the first and last sector is 13 km.

The fish sampling was carried out by the Guaraguacu River Monitoring project. Ichthyofauna sampling survey was made with the use of 10 gillnets of 20 meters (2, 4, 6 and 8 mm) and 10 traps (drum nets) in each sector, to capture individuals of all sizes. The method was the same between the four sectors of the river, according to the heterogeneity of the spatial gradient and covering practically all its extension. Nets were arranged in a paired fashion - used to sample associated fauna from native and non-native macrophyte banks. For the sectors where non-native banks did not occur (i.e. sectors 1 and 4) traps and gillnets were paired in native macrophytes banks and the closer structured microhabitat. Fish sampled were identified, measured (total and standard length), weighed, and their sex and gonadal maturation were identified. After taking biometric data, all the individuals' organs were removed and separated. The gills, visceral cavity, and each organ were examined under a stereoscopic microscope to collect parasites. The methodology for fixing the parasites followed the protocol established by Eiras et al. (2006). Parasites were identified using the following works: Kohn et al. (2006, 2007), Thatcher and Boeger (1984b,a), Thatcher and Varella (1981), Thatcher (2006), Moravec et al. (1998). A total of 159 individuals, summarized in 12 fish species, and 68 different species of parasites (36 species of ectoparasites and 32 species of endoparasites) were sampled in the Guaraguaçu river. Of those, 32 fishes were sampled in sector 1, 42 in sector 2, 38 in sector 3, and 47 in sector 4 (Appendix A).

Fish and parasite traits

Fish information of order, family, trophic class and level, habitat, schooling behavior, and migration category were gathered from the fishbase.org database (Froese and Pauly, 2000). The number of individuals sampled, the number of individuals infected, mean length and weight of each species sampled were also calculated. Parasite species were categorized by their parasitism form, taxonomy group, development stage, and mode of transmission. Ecological traits of each parasite species were also calculated: the number of host individuals infected by each parasite species, total and maximum prevalence, mean intensity of infection, and mean abundance.

The total prevalence of each species was calculated by host infected individuals divided by the total number of host individuals sampled in the river (Bush et al., 1997). Maximum prevalence took into account only the total number of individuals of the host species infected by the parasite in question. Mean intensity of infection was calculated by the total abundance of the parasite divided by the number of host individuals infected by it, and mean abundance was the total abundance of the parasite divided by the total number of host individuals sampled, also taking into account only the individuals of the species infected by the parasite in question (Bush et al., 1997).

Metanetwork structure and analyses

We construct our metanetwork based on two approaches. First, we looked at the network of each sector separately, with host and parasite species connected by parasite abundance. These networks were used to calculate species centrality values for all sectors and to calculate the species' role - described below. The second approach was a binary matrix that related fish species, categorized by the sector they were found, to parasite species abundance. Fish were classified in a way that species occurring in more than one sector appeared more than one time in the interaction matrix. Parasite abundance that makes up the interaction link refers to the sum of parasite individuals found in a host species, in a specific river sector. We may have a better visualization of the process through the network framework in figure 2. This metanetwork was used to calculate centrality values.

In order to verify the different responses of each measure to species connectivity, we looked into two different measures of centrality: betweenness and eigenvector (Rushmore et al., 2017; Dallas, Han, Nunn, Park, Stephens and Drake, 2019). Betweenness centrality measures how many paths (the link between two nodes) go through a node, consequently, species with higher betweenness usually connect different interaction groups. In our case, parasite species with higher betweenness would combine different host species or river sectors. Further, hosts with higher betweenness may have a higher spatial distribution or higher probability of maintaining parasite diversity along the river (Jordán et al., 2006; Dallas, Han, Nunn, Park, Stephens and Drake, 2019). Eigenvector centrality measures the importance of a node by its link with highly connected nodes, relating interaction flow inside a network, associated to a measure of indirect species' importance (Allesina and Pascual, 2009). Parasites with higher eigenvector may infect hosts with a higher diversity of parasites or have a wide range of distribution. Hosts with higher eigenvector can be sharing parasites with wide-distributed hosts (Dallas, Han, Nunn, Park, Stephens and

Drake, 2019). Centrality values were measured with “igraph” (Csardi and Csardi, 2007) in the software R (Team et al., 2020).

We also looked at species’ role among sectors, mainly for contrasting species centrality values with their role categorization in the metanetwork. To do this we based on the species’ role proposed by Guimera and Amaral (2005) and modified by Hackett et al. (2019). In which we calculated within sector connectivity z_i and among sector connectivity c_i:

$$z_i = \sum tb_{it}z_{it},$$

and

$$c = 1 - \sum (k.it/k.i)^2,$$

b_{it} is a belonging coefficient calculated by the ratio of species interaction weight in the sector over the total weight of species in the river, and z_i the z-score of species weight in sector t. In c_i case, $k.it$ is the mean weight of species i to sector t, divided by $k.i$, the mean weight of species i in all rivers. To categorize species roles, we used two threshold values: z_i 1.64 and c_i of 0.55. These values were based on the confidence interval of 95% in relation to null model’s with fixed row and column margin, calculated with the "Bipartite" package (Dormann et al., 2008) in the software R (Team et al., 2020). Species with z and c values above the thresholds were categorized as “River hubs”, and species with values below, as “Peripherals”. Species with z higher and c below were categorized as “Sector hubs” and with c higher and z below, as “River connectors”.

Fish’s connectivity metrics were related to their traits by generalized linear models. Parasites were related with traits by generalized linear and additive models, once some factors showed a nonlinear tendency. We first made a correlation analysis plot between host and parasite predictor variables (Figures 11 and 12). After, we generate a model selection table using the “MuMIn”(Barton and Barton 2015) package. The best model for each metric was chosen by its weight and AIC values. Model validation was made with the “Dharma” package (Hartig and Hartig, 2017), using the function “simulateResiduals” and “testDispersion”. Model analyses were calculated by the packages “lme4” (Bates et al., 2011), “mgcv” (Wood and Wood, 2015), all in the software R (Team et al., 2020).

Interactions and species beta-diversity

Beta diversity between the different sectors of the river was calculated based on Poisot et al. (2012) index, $\beta_{WN} = \beta_{ST} + \beta_{OS}$, been β_{WN} the total dissimilarity in the network. It uses β_{ST}, dissimilarity in interaction structure introduced by dissimilarity in species composition- turnover; and β_{OS} dissimilarity of interactions of shared species- rewiring.

To test if beta values were different from randomly expected, they were contrasted with null models with. Which were constructed by reshuffling the sector identity of each interaction. After, their difference was validated with variance analysis. Indexes were calculated using "betalink" package (Poisot, 2019), and their relation with geographical distance was tested with a linear model with permutation test, found in "lmPerm" package (Wheeler et al., 2016), all in software R (Team et al., 2020).

Results

Metanetwork structure and species centrality

Concerning local networks, we had 4 fishes interacting with 21 parasites in sector one, 5 with 22 in sector two, 7 with 29 in sector three, and 9 with 47 in sector four. When combining fish species with the sectors they were found we had a metanetwork of 25 fish, belonging to different species or different sectors, interacting with 68 parasite species, as we can see in Figure 2.

All sectors and metanetwork metric values showed the same parasite and fish species as being the most central. Although parasite's species were the same, their values oscillated over sectors, with a big amplitude of variation (figure 3 and 4). The copepod *Ergasilus sp.* Nordman, 1832 had the highest mean values of the two metrics and was classified as a river hub. The fish *Geophagus iporangensis* Haseman, 1911 also showed the highest mean values, followed by *Hoplias malabaricus* (Bloch, 1794) and *Rhamdia quelen* (Quoy & Gaimard, 1824), between sectors and in the metanetwork. All three species were classified as river connectors (figure 5).

When contrasted parasite's traits with metrics of metanetwork connection, we found relation mostly with ecological traits. Parasites with highest eigenvector were the ones with a higher mean abundance (GAM F = 12.57, $p < 0.001$). The highest betweenness centralities were related to parasites in an intermediary stage, which had the highest total prevalence (GLM t-value = 2.82 and 2.5, both $p<0.001$). Looking at species roles, connectivity values were related to the number of host individuals infected and development stage (GAM F = 5.18, p = 0.03; t-value=2, p = 0.05), figure 7.

Apart from betweenness centrality, fish's traits were not related to any connectivity metrics. Fish betweenness centrality was related to fish location, being fishes sampled in sector 2 the ones with higher values. This centrality also showed a slight relation with fish's mean length, although it was a location-dependent relation. In this case, fish with higher mean length had a higher betweenness in sector 1, and lower betweenness in sector 2 (figure 8)(Table1).

Table 1: General linear model results for fishes' centralities in the metanetwork. We provide slope estimates, standard errors and p-values for the best model's effects. Betweenness = betweenness centrality, Aic= -71.34.

		Slope	Std. Error	p
Betweenness	Mean lenght	0.00	0.00	0.06
	Siluriformes	0.06	0.03	0.07
	Gymnotiformes	-0.04	0.06	0.57
	Characiformes	0.03	0.03	0.25
	Mugiliformes	0.11	0.06	0.08
	Sector 2	0.09	0.03	0.02
	Sector 3	0.01	0.03	0.61
	Sector 4	0.04	0.03	0.13

Beta diversity of interactions

The turnover component β_{ST} of pairwise dissimilarity was different from randomly expected (F= 101.9, p-value < 0.001), but not rewiring β_{OS} (figure 9). This shows that the beta diversity of host and parasites interactions through the river is based on species turnover over the sectors (F= 4.764, p-value= 0.03) (figure 10).

Discussion

Our results indicate a high turnover of species and interactions along the river gradient. Even so, differently from our expectations, species with the highest centrality values were the same in all river sectors. Concerning the metanetwork, not surprising, fishes with higher centrality values were distributed in all four sectors of the river, which are also classified as river connectors. The same pattern was observed for parasite species. Interestingly, just 4 of the 68 parasite species found in the river were central to the metanetwork connectivity of the river. These were the ones with the highest infection rates, between prevalence and abundance. In addition, taking into account the sampling sectors, the highest betweenness values were found in sector 2. This is a central sector and also the one with the highest anthropogenic pressure.

Host and parasite's centrality measures have different ecological meanings. When accounting for parasites metrics, we expected to distinguish which were the parasites connecting different host species and sectors in the metanetwork. Relatedly, we also expected that high host centrality would be observed for species sharing more parasites throughout the river (Rushmore et al., 2017). Further, we were expecting different relations to different metrics, however, most results were ecologically equivalent. Indeed, studies accounting for host-parasite centrality had found a conservatism among different metric predictors (Gómez et al., 2013; Dallas, Han, Nunn, Park, Stephens and Drake, 2019). Besides most metrics were related to ecological predictors, host and parasite's betweenness had a unique ecological relation Gómez et al. (2013). Betweenness properties indicated the importance of a species in connecting distinctive groups (Delmas et al., 2018; Dallas, Han, Nunn, Park, Stephens and Drake, 2019), what can indeed classified this centrality as a better predictor of spatial differences over the river.

We also changed the measured of species' role inside modular networks by using it inside a metanetwork perspective (Hackett et al., 2019; Li et al., 2020). Species within and among sectors' contribution values allowed us to see further and categorized their roles inside the metanetwork (Hackett et al., 2019). However, only among sector values related to parasite traits was related to parasite's traits. It should be noted that both parasite betweenness centrality and parasite among sectors contribution were correlated to parasite development stage. In this case, non-adult forms, that use fishes as intermediate hosts, presented higher relative values. Non-adult stages have a myriad of strategies for getting to their final hosts, which increases distribution across host species and populations, what increases their ability of connecting different parasite faunas, being it by different host species or parasite faunas of the same species in different sectors (Bellay et al., 2013).

Apart from development stages, parasites with higher infection rates (measured by their prevalence, mean abundance, or the number of specimens infected) were the ones with high connectivity values. Looking at their taxonomic identity, it is possible to note mostly ectoparasites infecting fish species widely distributed across the river. So, we can first conclude that parasite centrality in the metanetwork is extremely connected to host centrality, but not exclusively. Just a few species among the ones infecting central hosts were classified as sector hubs or river connectors. Besides, high infection rates can be related to a high fitness performance (Felix et al., 2022) and suggest a parasite's ability of host and environment exploitation, mostly for ectoparasites, that are directly affected by both (Costa et al., 2021). Ectoparasite infections were already related to host distribution (Berkhout et al., 2020). But their performance is usually explained by environmental variation (Lafferty, 2008; Jerônimo et al., 2022). In this study, we found that (disregarding non-adults) monogeneans and copepods species act as river hubs and connectors. We can relate such a pattern to the river's environmental natural gradient or human-impacted sectors. For instance, an increase in organic nutrient load generates an initial opportunity of increasing species fitness and performance, in each, species with a higher capacity for exploitation increase its abundance and distribution (Brooks et al., 2019).

Between ectoparasites, the species *Ergasilus sp.* had the highest centrality values, which can be interpreted as a river hub connecting the network within and among sectors. This can be related to its higher prevalence in the host with higher frequency in all sectors: *H. malabaricus*. This copepod was also found infecting other host species along the river, but with a lower prevalence. Copepods from the Ergasilidae family have a unique life form in which parasites are just fertilized adult females, being male and juvenile free-living individuals (Kvach et al., 2021). This family also has an extensive gradient of host specificity, with some species registered in 15 different families of fishes, although most Ergasilidae species seem to have a host preference (Kvach et al., 2021). Indeed, *Ergasilus sp.* was the only copepod infecting other host species. This event is evidence of host switching, possibly occurring to the species' environmental adaptation capacity, increasing its performance and consequently, the opportunity to infect other host species (Brooks et al., 2019).

The ecosystem focus of our study has two main gradients driven species distribution, the increase in salinity levels with the river flow; and the eutrophication due to anthropogenic pressure in the intermediate sectors of the river. These two regions of disturbance were the ones with higher host betweenness centrality (sectors 2 and 4, figure 4). Host high betweenness can indicate a pathway of parasite sharing (Dallas, Han, Nunn, Park, Stephens and Drake, 2019). In the case of this study, hosts found in sectors with clear environmental disturbance were the ones that allowed a higher opportunity for parasite sharing. Therefore, we may hypothesize that environmental changes across the river are driving the increase in the performance of opportunistic parasite species, which in turn, increases their host switching opportunity.

Still analyzing host metanetwork betweenness, not only the host location was important, but also the mean length of the host species. Interestingly, opposite patterns were revealed in sectors 1 and 2: in which sector 1, centrality was positively related to host mean length, and sector 2 negatively related. Body size was already related to the parasite richness, and even centrality when looking at an individual-based/multi-species network (Pilosof et al., 2015). But the main discussion concerning body size and parasite diversity depends on parasite transmission strategy (Poulin and Leung, 2011a). For example, fish length can be related to predation susceptibility, with small fishes having a higher probability of being predated. This vulnerability can increase the parasite's chances of infecting final hosts, resulting in a higher proportion of larval or non-adult parasite infections (Poulin and Leung, 2011a). In another context, hosts with higher body size are more related to contact transmission, for being more exposed to infection (Downs et al., 2019).

Additionally, host-parasite interactions over the river were affected by a high turnover of species, with few central species. Of the 12 species sampled along the river, just three fish species were widely distributed: *H. malabaricus*, *G. iporangensis*, and *R. quelen*. While central parasite species were only the ones infecting central hosts and with high performance. This pattern is in line with a clear environmental filter that selects species and increases parasite abundance along the river, a tendency of community simplification. This is not the first study showing an increase in dominant species and a loss of diversity in the Guaraguaçu river, Galvanese et al. (2022) already related this event to macrophyte composition patterns. Coastal rivers usually has a strong pattern related to species turnover and increase of species richness along their longitudinal gradient (Vannote et al., 1980; Winemiller and Leslie, 1992). While we were already expecting a turnover of species and interactions along the river, it is important to highlight that there were no changes in the centrality over river stretches.

A high gradient of salinity, water transparency, and temperature likely select tolerant species and may disrupt community distribution patterns along the river (Matthews, 2012). In the Guraguaçu river, the natural salinity gradient can be related to species and interaction turnover. Indeed, there is a known pattern of species succession along a river continuum (Vannote et al., 1980). However, the eutrophication in the central part of the river may be filtering central species, maintaining few dominant fish species, apart from species turnover. Studies accounting for environmental changes along river stretches already related parasite abundance and prevalence in host populations, which tends to increase downstream (Falke and Preston, 2021; Blasco-Costa et al., 2013). More than that, species centrality is also reflected by parasite interactions, with a few opportunistic species increasing their infection and probability of host switching along the river. Our results acknowledge the necessity of increasing the river monitoring program, mostly to reaffirm the pattern addressed in this study.

Here we also saw the use of beta diversity and centralization measures as complementary, as well as species role analysis (Dallas, Han, Nunn, Park, Stephens and Drake, 2019). Shifts in the turnover or rewiring of interactions do not account for species importance inside each local community. Looking at those aspects together may lead to a more accurate analysis of community response to environmental or spatial gradients. Shifts in host-parasite interactions across gradients are an extremely important topic, once we are now facing an increase in emergent zoonotic diseases, that is putting at risk the health of humans and wildlife species (Brooks et al., 2019). Indeed, our results do reinforce that anthropic changes can lead to an increase in parasite performance and the probability of host switching. We conclude by showing the relevance of monitoring host-parasite interactions, mostly in ecosystems with a high environmental gradient, to prevent new pathogen emergence that could lead to increased virulent interactions.

Figures

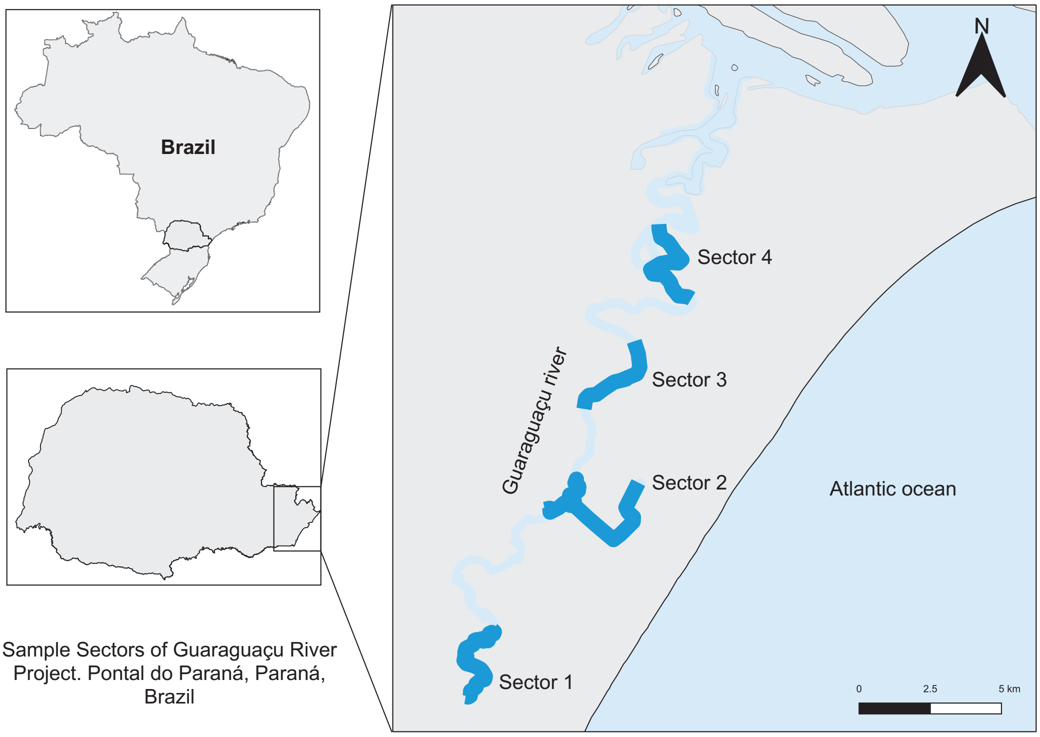


Figure 1: Map of the Guaraguaçu River, Parana, Brazil. Sectors where fishs were sampled correspond to the highlighted parts of the river

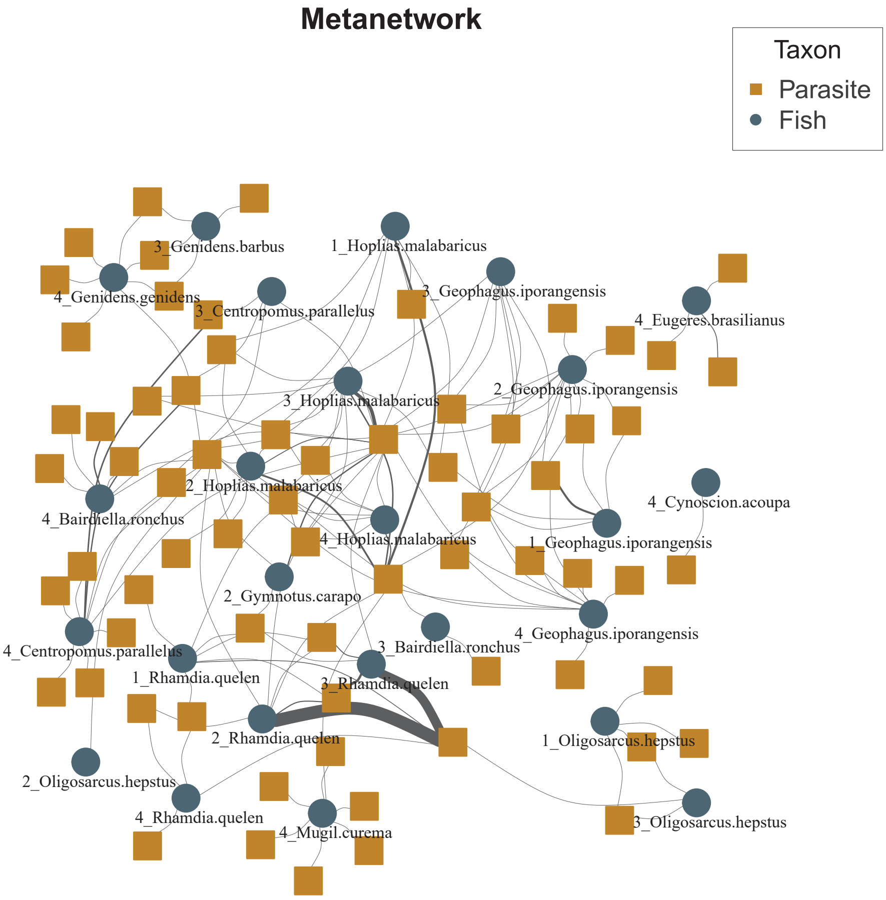


Figure 2: River metanetwork structure based on fish species categorized by sector. Sector/Fish are represented by the blue circles and parasite species by the orange squares

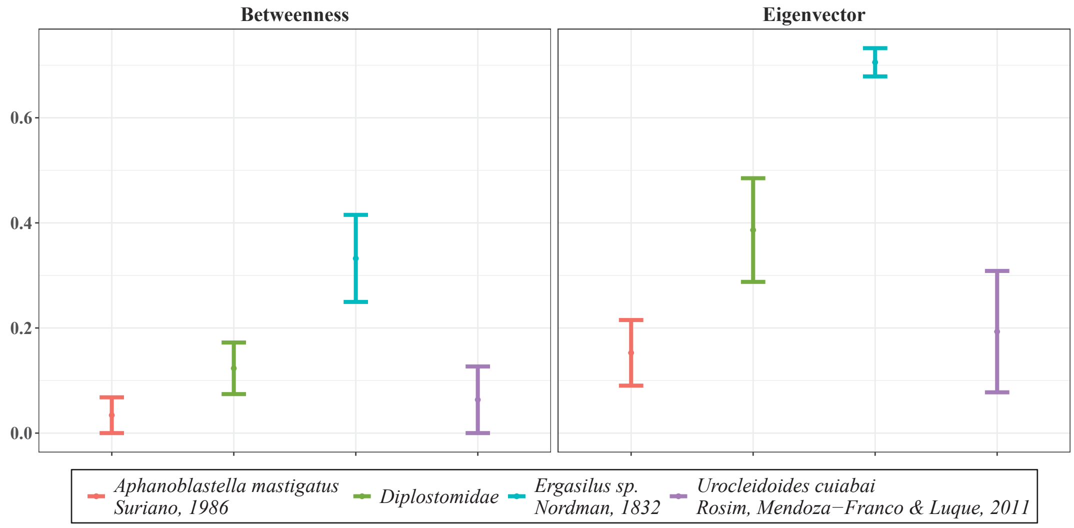


Figure 3: Parasite centrality values calculated for each sector network. Only the 4 parasite species with highest values are represented in the plot. Each color represents a different species.

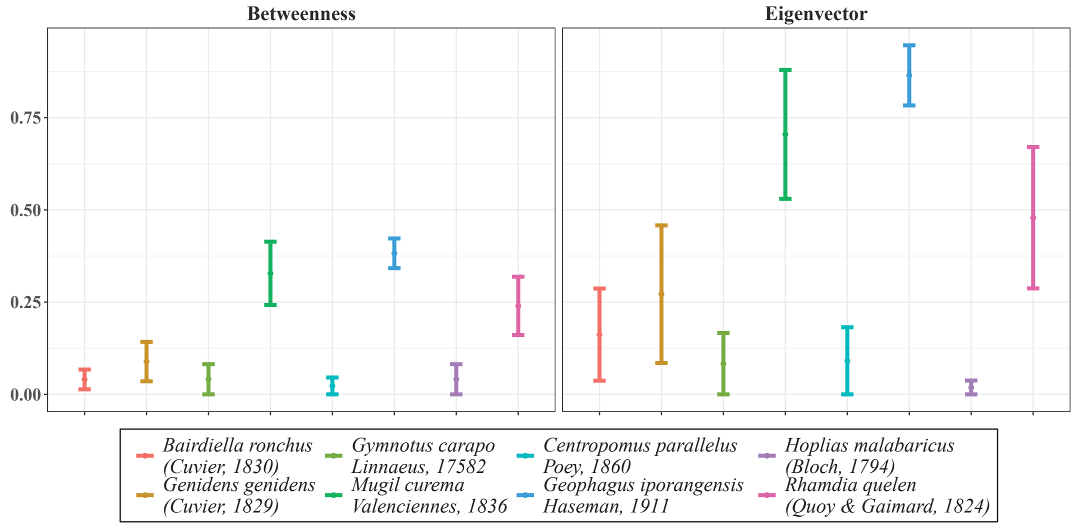


Figure 4: Fish centrality values calculated for each sector network. Each color represents a different species. Fishes with centrality values lower than 0 were removed from the plot.

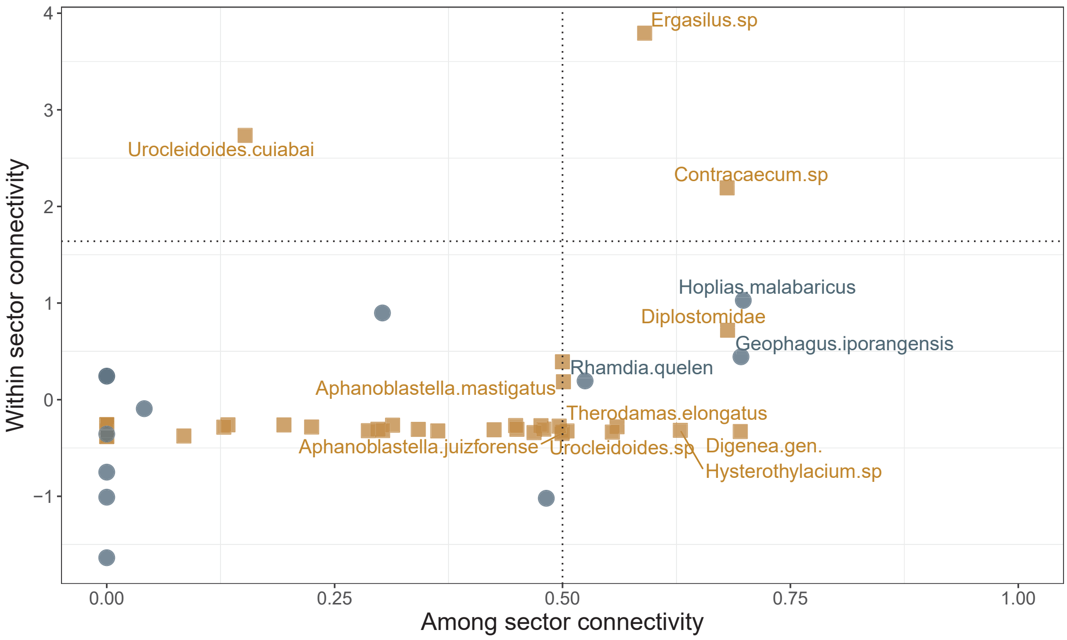


Figure 5: Plot showing parasite and fish species among sector connectivity versus within sectors connectivity. The dashed line is the threshold classifying the species role. Blue circles are fish species and orange squares parasite species. Species names were disposed of sector hubs, river hubs, and connectors.

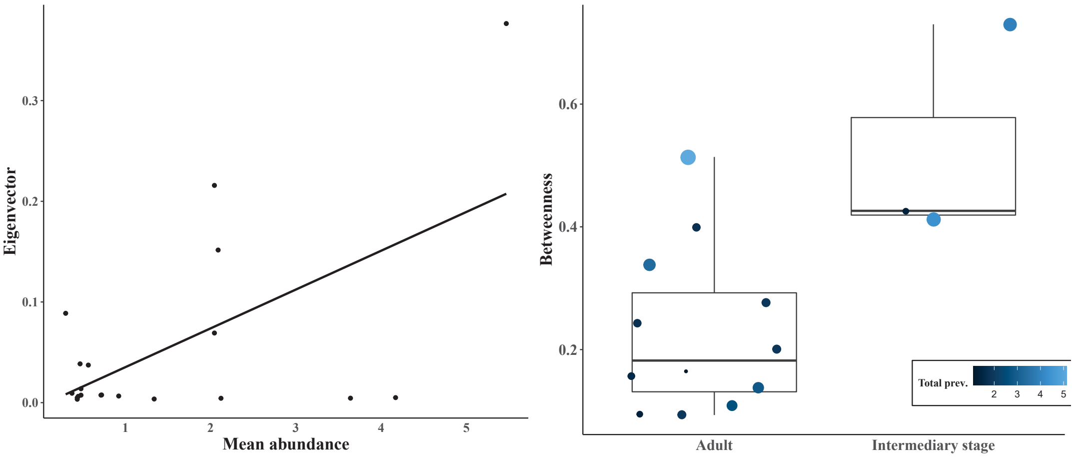


Figure 6: Parasite centrality values and interaction strength related to their main drivers. Betwwennes relation to parasite total prevalence, parasite degree relation to the number of individuals infected, eigenvector centrality relation to the parasite development stage, with color and size representing the number of individuals infected, and interaction strength relation to total prevalence with parasite maximum prevalence represented by color and size.

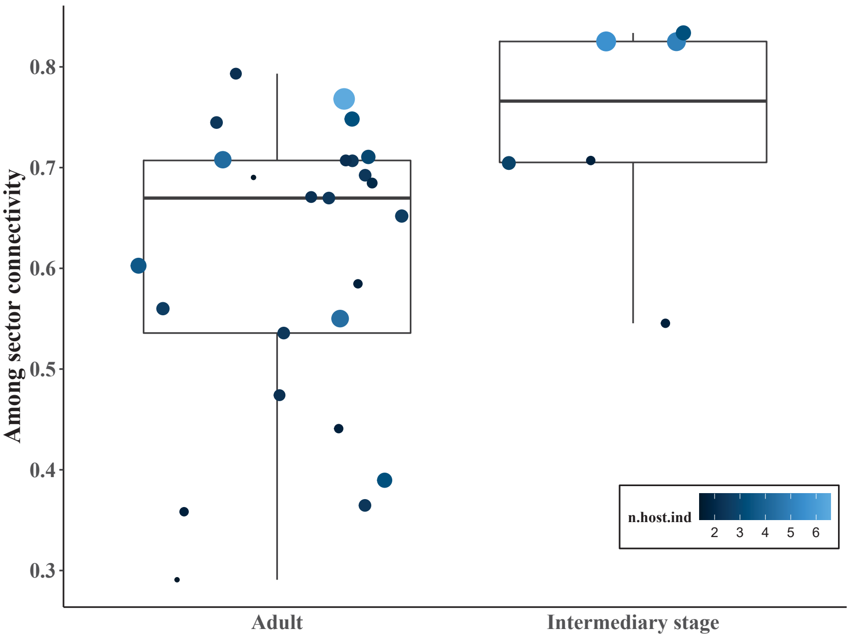


Figure 7: Parasite within sector connectivity values relation to number of individuals infected and among sector connectivity relation to parasite development stage, with color representing number of individuals infected.

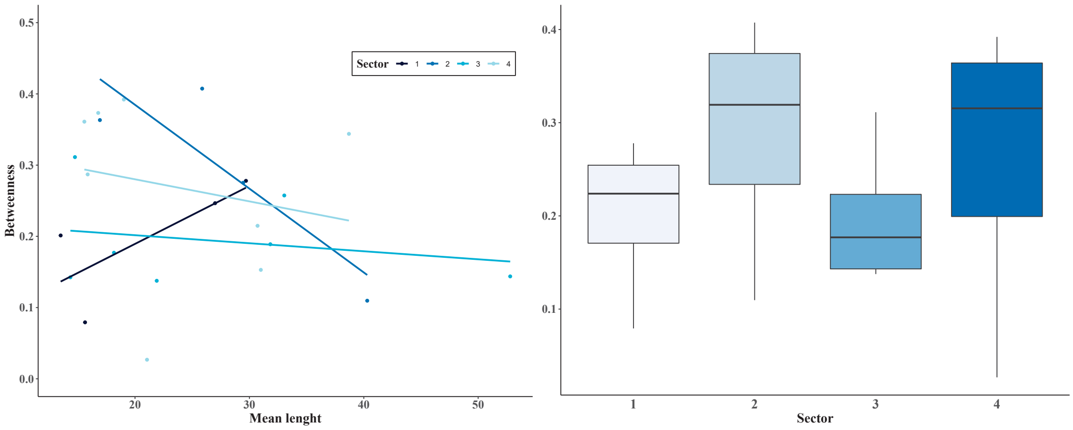


Figure 8: Fish betweenness relation to their mean lenght, categorized by sector sampled, and the relation just with sector sampled.

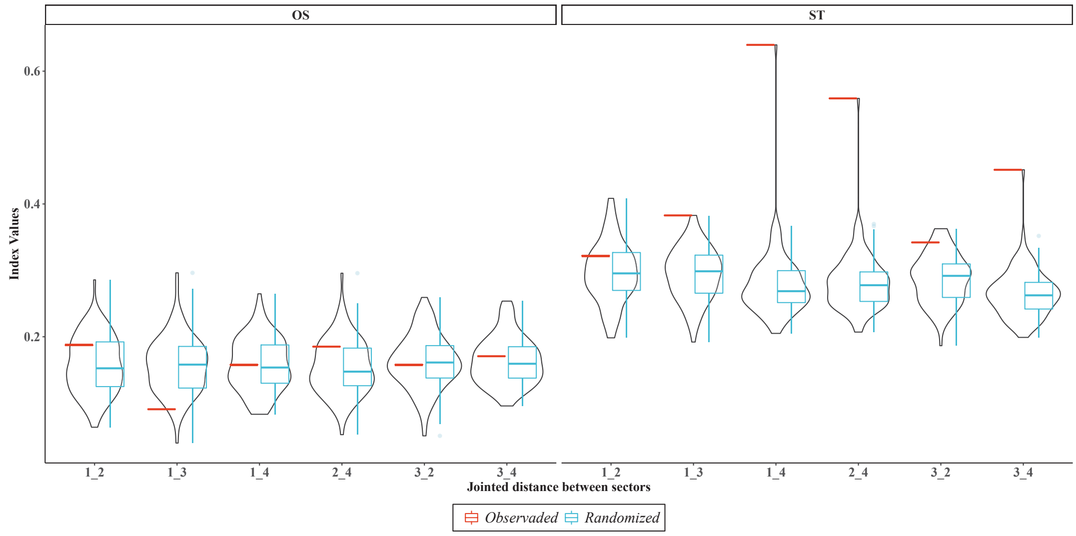


Figure 9: Observated vs randomized values of OS (rewiring) and ST (turnover) beta diversity by sector pairwise analyses. Red line represents observated value and blue box randomized median values.

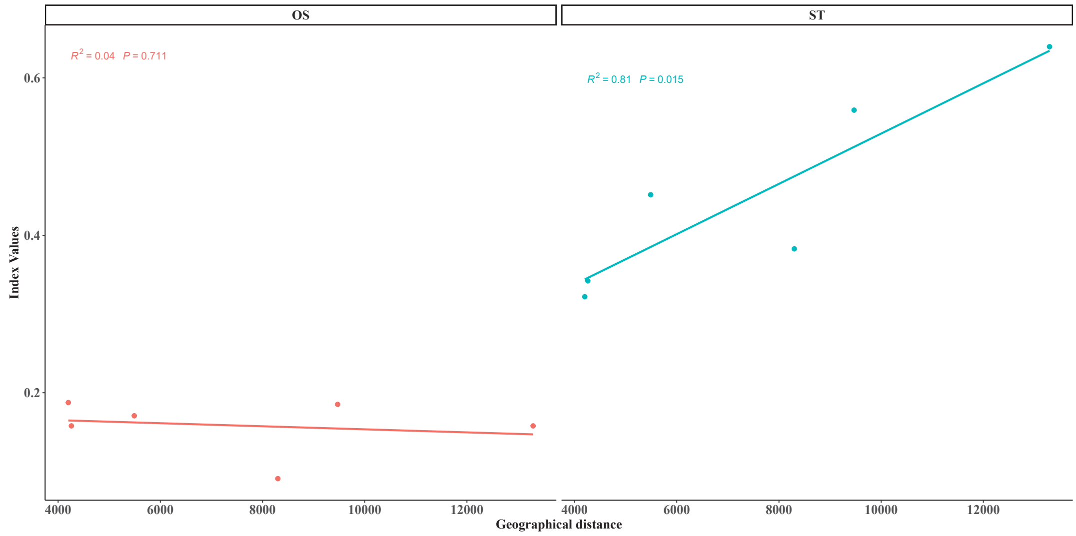


Figure 10: Observated values of OS (rewiring) and ST (turnover) beta diversity in relation to geographical distance along river sectors

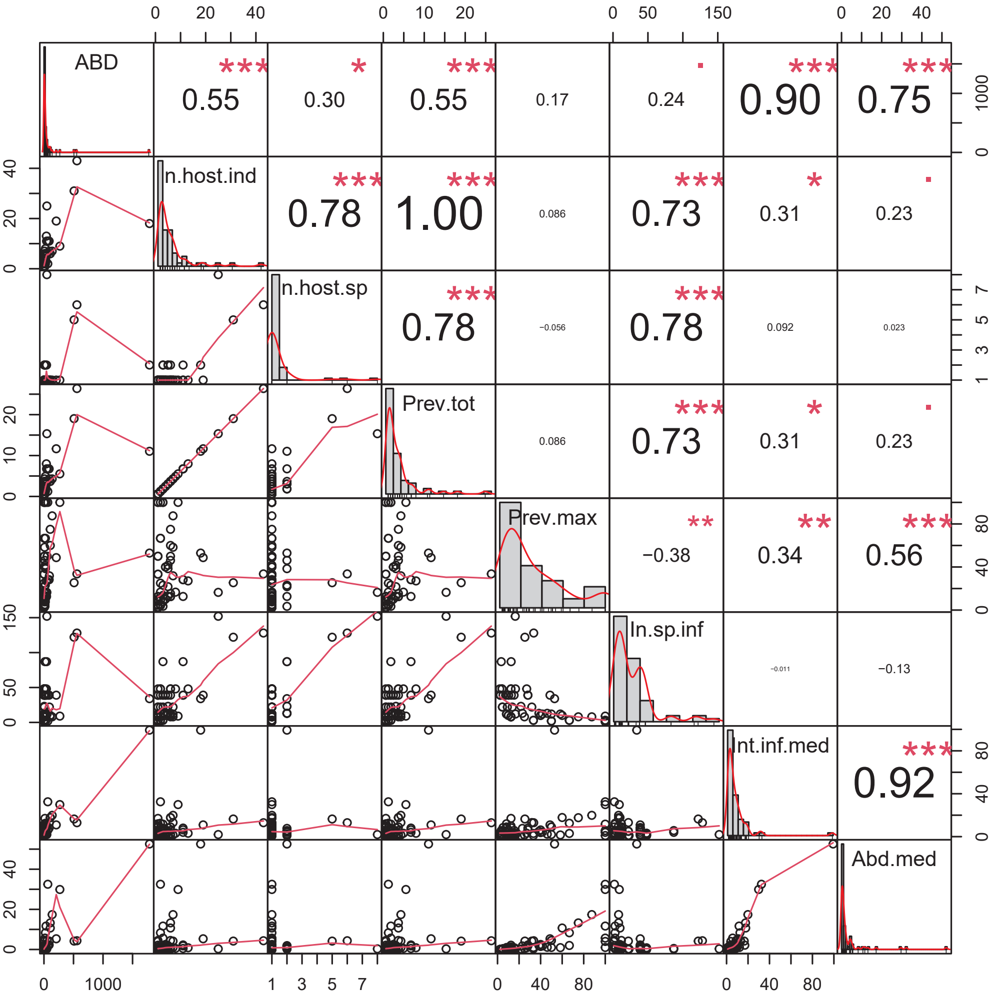


Figure 11: Chart correlation between parasite' traits

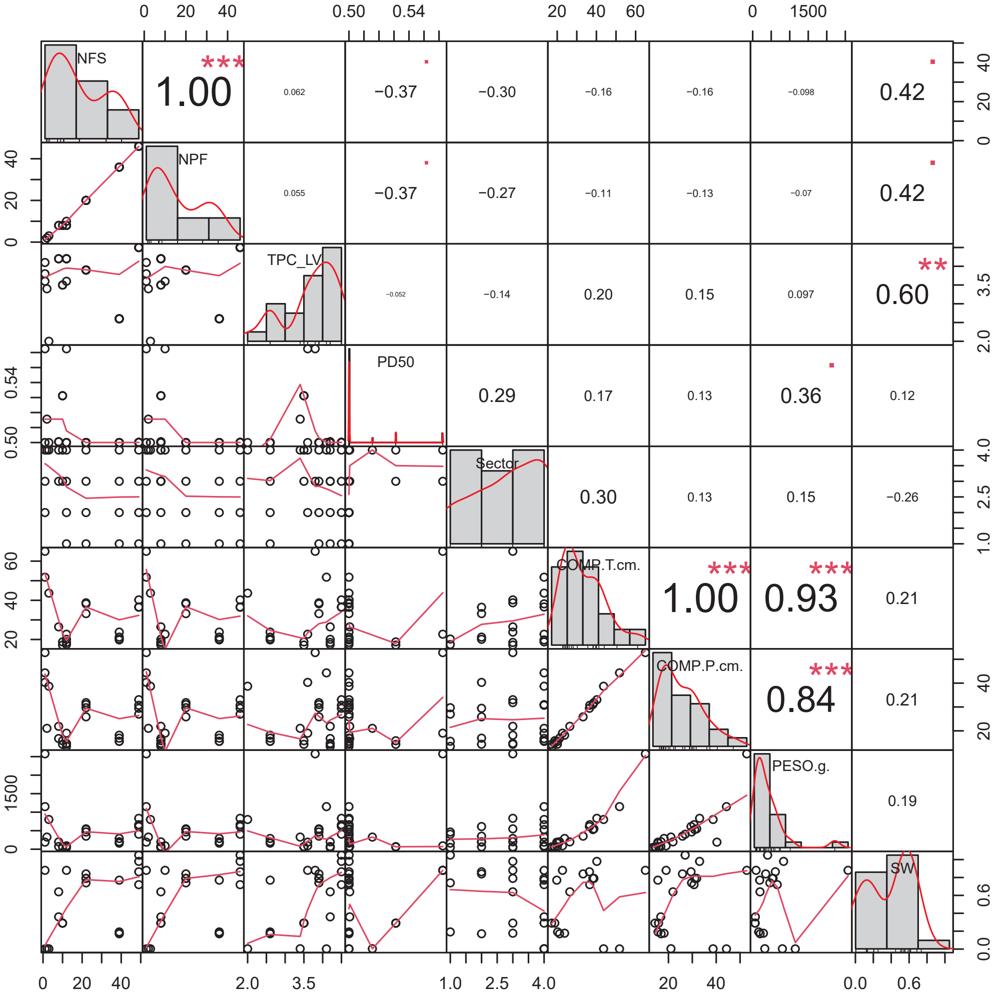
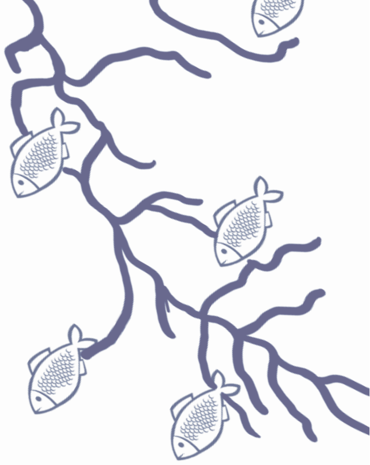


Figure 12: Chart correlation between hosts' traits



Conclusões gerais

Nothing in life is to be feared, it is only to be understood. Now is the time to understand more, so that we may fear less

— Marie Curie

Esta tese foi construída a partir da necessidade de aumentar o conhecimento sobre os padrões e mecanismos estruturantes das interações parasito-hospedeiro. Neste sentido, o fator propulsor deste trabalho foi criar ferramentas e informações que aumentem nosso potencial científico na elaboração e corroboração de teorias ecológicas. Além disso, com o monitoramento do Rio Guaraguaçu, também notamos a necessidade de registrar as espécies parasitas deste rio, assim como seus padrões de distribuição. Os resultados descritos nesta tese conseguiram ir além dos objetivos propostos. A partir dos estudos apresentados aqui como capítulos, foi possível trazer informações não só sobre os mecanismos propulsores da distribuição parasitária em diferentes escalas organizacionais, como também sobre fatores críticos ligados a perturbações antrópicas. De fato, nossos resultados mostraram o quanto a interação parasito-hospedeiro é sensível a mudanças ambientais, e o quanto a persistência das redes dependem do monitoramento e manutenção dos impactos antrópicos. A emergência de novas interações parasíticas é a primeira fase para um aumento da intensidade das interações, medidas pela abundância dos parasitos. Esperamos que esta tese consiga trazer recursos que evidenciem este fato, além de ser base de mais estudos sobre o tema.

Diante disso, esses objetivos e resultados fazem parte dos três capítulos que compõem esta tese. No PRIMEIRO CAPÍTULO foi investigado como uma metacomunidade parasita é estruturada em uma metapopulação de hospedeiros em um rio de planície de inundação com constantes mudanças hidrológicas, marcadas por regimes de seca e cheia. Foi encontrada uma estrutura marcada pelo determinismo, com variados fatores estruturantes para diferentes grupos de parasitos. Ectoparasitos sofrem maior pressão do ambiente, enquanto a estrutura de endoparasitos é influenciada pelos atributos funcionais de seus hospedeiros. Por fim, averiguou-se o quanto a dinâmica hidrológica do rio é chave na distribuição da diversidade de parasitos dentro de uma metapopulação hospedeira, ditando seu fluxo e mantendo o equilíbrio estrutural das interações parasito-hospedeiro.

Doravante, o SEGUNDO capítulo investigou a estrutura das interações parasíticas em uma metacomunidade de hospedeiros presente em um rio costeiro de elevado impacto antrópico, focando nos fatores que influenciam mudanças nas infracomunidades parasíticas. Com base na análise de uma rede mista, formada por indivíduos de hospedeiros se relacionando com espécies de parasitos, foi possível observar mais uma vez quão diferente ecto e endoparasitos se estruturam diante de um gradiente ambiental. Ectoparasitos apresentaram uma resposta maior em setores de maior impacto do rio, formando redes mais modulares em relação a outros setores. Já endoparasitos, apesar de apresentarem redes significantemente modulares, não responderam ao gradiente de pressão. Contudo, ambos os grupos mostraram relação entre sua estrutura e a intensidade média de parasitismo. Esse fator, junto com a performance dos hospedeiros foram elementos chave na formação de agrupamentos que constituíram os módulos dentro das redes. Aqui foi possível mostrar a importância da variação intraespecífica e da performance dos hospedeiros na estrutura das redes parasitárias, além de relacionar a modularidade das redes com a manutenção da estabilidade das interações em vista de ambientes com alto impacto antrópico.

Por fim, O TERCEIRO CAPÍTULO teve como objetivo delimitar como a diversidade de interações parasito-hospedeiro estava estruturada ainda dentro do rio costeiro e quais eram as espécies centrais e o seu papel na conectividade desta rede de interações. Com base na construção de uma metarede, foi possível analisar quais aspectos ecológicos e funcionais dos parasitos e biológicos ou espaciais dos hospedeiros estão relacionados ao papel e centralidade das espécies dentro do rio. A prevalência e abundância dos parasitos foram os principais fatores relacionados a maiores valores de centralidade. Já para espécies hospedeiras, o tamanho foi importante, mas de forma contrastante, a depender do local em que a espécie foi encontrada no rio. Ainda, pela análise da beta diversidade de interações, foi possível ver que o turnover de interações corresponde de fato ao gradiente do rio, mas a mudança na composição de espécies não corresponde a mudança na centralidade de espécies, que continuam iguais entre setores. Este capítulo destacou tanto um padrão de turnover de espécies quanto um conservatismo no papel delas em relação a conectividade da metarede, sendo este último possivelmente relacionado a uma filtragem antrópica na comunidade de parasitos e hospedeiros.

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Apêndice A

Tabela 1: Environmental variables of each sector of the Guaraguaçu river, Paraná, Brazil. Sec: Sector; Lat: Latitude; Long: Longitude; RW: River Width; HS: Human Structures; U.p: presence of *Urochloa arrecta* (Hack. ex T. Durand & Schinz) Morrone Zuloaga; Cond: Conductivity; Sec.disck: Secchi disk (cm); Temp: temperature (Celsius degree).

Sec	Lat	Long	RW	HS	U.p	Cond	Sec.disk	Temp
1	-25.7498	-48.5517	10.65	0	0	47.76	115.8	19.36
2	-25.6942	-48.5164	25.84	0.197	1	82.48	88.2	21.54
3	-25.6517	-48.5053	39.33	0.097	1	90.86	93.33	21.43
4	-25.612	-48.4866	85.9	0.03	0.33	5186.66	117.66	22.76

Tabela 2: Fish and parasite species sampled in each sector of the Guaraguaçu river, Paraná, Brazil. Inf rate: total abundance of parasites found in the fish species. NIS: Number of fish individuals sampled in the sector. NIF: number of fish individuals sampled that was infected by at list one parasite. Abd: total abundance of each parasite species.

Fish species	**Parasite species**	**Inf Rate**	**NIS**	**NIF**	**Abd**
	Sector 1				
Geophagus iporangensis		199	9	9	
	Digenea gen				22
	Neoechinorhynchus sp				15
	Procamallanus sp1				4
	Sciadicleithrum frequens				157
	Urocleidoides cuiabai				1
Hoplias malabaricus		268	12	11	
	Contracaecum sp				4
	Cystidicoloides izecksohni				7

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Tabela 2 – *Continued from previous page*

Fish species	**Parasite species**	**Inf Rate**	**NIS**	**NIF**	**Abd**
	Diplostomidae				168
	Ergasilus sp				18
	Urocleidoides brasiliensis				29
	Urocleidoides cuiabai				37
	Urocleidoides malabaricusi				5
Oligosarcus hepstus		48	4	4	
	Characithecium chascomusensis				11
	Characithecium longianchoratum				25
	Heliconema sp				9
	Nematoda gen sp				3
Rhamdia quelen		74	7	6	
	Aphanoblastella juizforense				5
	Aphanoblastella mastigatus				58
	Aphanoblastella sp				5
	Ergasilus sp				1
	Ergasilus thatcheri				2
	Hysterothylacium sp				1
	Nematoda gen1 sp				2
	Sector 2				
Geophagus iporangensis		108	13	11	
	Digenea gen				30
	Diplostomidae				3
	Ergasilus sp				4
	Lobatostoma sp				1
	Neoechinorhynchus sp				20
	Procamallanus sp1				3
	Procamallanus sp2				1
	Rhabdochona sp1				4
	Sciadicleithrum frequens				22
	Sciadicleithrum guanduense				17
	Therodamas elongatus				3
Gymnotus carapo		102	1	1	
	Contracaecum sp				1
	Ergasilus sp				100
	Hysterothylacium sp				1

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Tabela 2 – *Continued from previous page*

Fish species	**Parasite species**	**Inf Rate**	**NIS**	**NIF**	**Abd**
Hoplias malabaricus		236	15	14	
	Contracaecum sp				15
	Cystidicoloides izecksohni				1
	Diplostomidae				140
	Ergasilus sp				66
	Eustrongylides sp				2
	Thometrema overstreeti				1
	Urocleidoides brasiliensis				7
	Urocleidoides sp				4
Oligosarcus hepstus		1	6	2	
	Contracaecum sp				1
Rhamdia quelen		1129	7	6	
	Acanthostomum gnerii				12
	Aphanoblastella juizforense				83
	Aphanoblastella mastigatus				998
	Contracaecum sp				2
	Diplostomidae				6
	Ergasilus sp				10
	Ergasilus thatcheri				18
	Sector 3				
Bairdiella ronchus		2	2	1	
	Blastocyst				1
	Diplostomidae				1
Centropomus parallelus		38	2		
	Acusicola sp				6
	Anakohnia brasiliana				1
	Ergasilus sp				9
	Rhabdosynchus sp				22
Genidens barbus		47	1	1	
	Chauhanellus boegeri				21
	Chauhanellus neotropicalis				21
	Ergasilus jaraquensis				4
	Therodamas sp				1
Geophagus iporangensis		109	10	9	
	Digenea gen.				26
	Ergasilus leporinidis				2

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Tabela 2 – *Continued from previous page*

Fish species	Parasite species	Inf Rate	NIS	NIF	Abd
	Ergasilus sp				5
	Lobatostoma sp				5
	Sciadicleithrum frequens				17
	Sciadicleithrum guanduense				24
	Therodamas elongatus				30
Hoplias malabaricus		425	14	14	
	Contracaecum sp				12
	Cystidicoloides izecksohni				1
	Diplostomidae				110
	Ergasilus sp				270
	Polyacanthorhynchus cf				8
	Pseudoterranova sp				12
	Urocleidoides brasiliensis				2
	Urocleidoides cuiabai				6
	Urocleidoides sp				4
Oligosarcus hepstus		40	2	2	
	Aphanoblastella mastigatus				1
	Characithecium chascomusensis				10
	Characithecium longianchoratum				29
Rhamdia quelen		1000	7	7	
	Aphanoblastella juizforense				181
	Aphanoblastella mastigatus				713
	Ergasilus sp				31
	Ergasilus thatcheri				72
	Hysterothylacium sp				3
	Sector 4				
Bairdiella ronchus		151	8	7	
	Acanthochepala sp3				15
	Acusicola sp1				1
	Contracaecum sp				2
	Ergasilus sp				1
	Rhamnocercus margaritae				107
	Rhamnocercus rhamnocercus				25
Centropomus parallelus		270	6	6	
	Acanthocollaritrema umbilicatum				2
	Acusicola sp				100

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Tabela 2 – *Continued from previous page*

Fish species	**Parasite species**	**Inf Rate**	**NIS**	**NIF**	**Abd**
	Allocreadium centropomi				10
	Anakohnia brasiliana				2
	Contracaecum sp				8
	Ergasilus sp				12
	Microcotylidae pos larval				17
	Parahemiurus sp				1
	Pseudocryptogonemus sp				1
	Rhabdosynchus sp				117
Cynoscion acoupa		4	1	1	
	Diplectanum sp				4
Eugeres brasilianus		76	2	2	
	Aristocleidus sp				9
	Cucullanus sp1				2
	Neodiplectanum sp				65
Genidens genidens		41	12	10	
	Chauhanellus boegeri				4
	Chauhanellus neotropicalis				2
	Contracaecum sp				1
	Echinorhynchus sp				1
	Ergasilus jaraquensis				10
	Hysterothylacium sp1				11
	Pseudoacanthostomum floridense				12
Geophagus iporangensis		148	7	7	
	Contracaecum sp				1
	Crassicutis sp				17
	Digenea gen				10
	Ergasilus leporinidis				21
	Ergasilus sp				19
	Ergasilus sp1				25
	Gauchergasilus sp				2
	Polyacanthorhynchus cf				2
	Sciadicleithrum frequens				12
	Sciadicleithrum juruparii				2
	Therodamas elongatus				37
Hoplias malabaricus		119	7	6	
	Contracaecum sp				2

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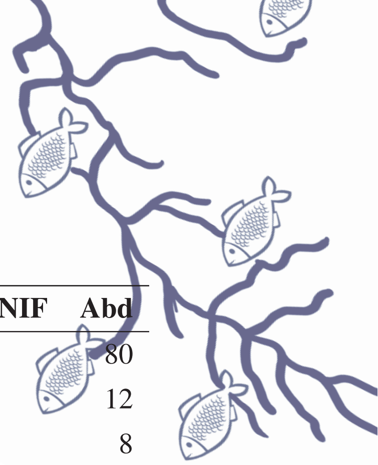

Tabela 2 – *Continued from previous page*

Fish species	**Parasite species**	**Inf Rate**	**NIS**	**NIF**	**Abd**
	Diplostomidae				80
	Ergasilus sp				12
	Polyacanthorhynchus cf				8
	Pseudoterranova sp				13
	Urocleidoides brasiliensis				3
	Urocleidoides sp				1
Mugil curema		92	3	3	
	Cucullanus sp2				3
	Diplostomidae				2
	Ergasilus atafonensis				17
	Ergasilus caraguatatubensis				6
	Ligophorus sp				25
	Sacoccoloides sp				4
	Therodamas frontalis				35
Rhamdia quelen		24	1	1	
	Acanthostomum gnerii				1
	Aphanoblastella mastigatus				17
	Crocodilicola pseudostoma				5
	Nematoda gen1 sp				1

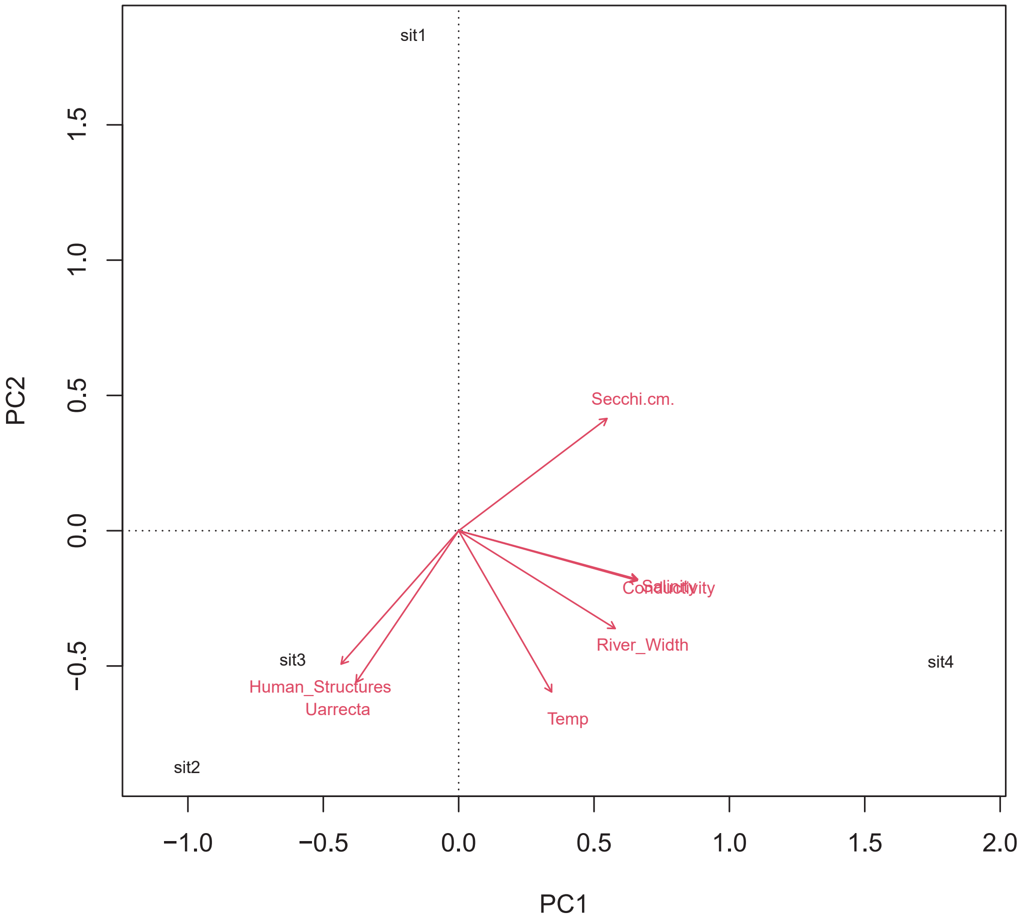

Figura 1: PCA plot of the environmental variables sampled in each sector of the Guaraguaçu river, Paraná, Brazil. sit1: sector 1, sit2: sector 2, sit3: sector3, sit4: sector 4.