Universidade Federal de São Carlos

Centro de Ciências Biológicas e da Saúde
Programa de Pós-Graduação em Ecologia e Recursos Naturais

Gabrielle Cristina Pestana

MECANISMOS DE COEXISTÊNCIA EM ESPÉCIES COM CICLO DE VIDA COMPLEXO: UM ESTUDO SOBRE LIBÉLULAS NEOTROPICAIS

São Carlos
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Mecanismos de coexistência em espécies com ciclo de vida complexo: um estudo sobre libélulas neotropicais

Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais da Universidade Federal de São Carlos, como parte dos requisitos para obtenção do título de DOUTORA em CIÊNCIAS, área de concentração: Ecologia e Recursos Naturais.

Orientador: Prof. Dr. Victor Satoru Saito

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UNIVERSIDADE FEDERAL DE SÃO CARLOS

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Comissão Julgadora:

Prof. Dr. Victor Satoru Saito (UFSCar)

Profa. Dra. Carolina Reigada Montoya (UFSCar)

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O Relatório de Defesa assinado pelos membros da Comissão Julgadora encontra-se arquivado junto ao Programa de Pós-Graduação em Ecologia e Recursos Naturais.

Dedico este trabalho à minha filha Sophia, a qual vem descobrindo as belezas e complexidade da natureza.

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“Mas aconteça o que acontecer, as imperfeições do conceito [de espécie] — e, portanto, do nosso sistema de classificação — refletem a essência idiossincrática da diversidade biológica. São mais um motivo para acalentarmos cada espécie como um mundo em si mesmo, merecedor de várias vidas de estudo.”

Trecho retirado do livro “Diversidade da vida”, de Edward O. Wilson

RESUMO

A ecologia de comunidades busca compreender a manutenção da biodiversidade por meio dos mecanismos que permitem a coexistência das espécies em comunidades locais. A Teoria Moderna da Coexistência (TMC), sintetizada por Chesson (2000), é uma das teorias mais rigorosas para entender como espécies competidoras persistem no mesmo ambiente, ao longo do tempo. De acordo com essa teoria, dois tipos de diferenças interespecíficas determinam a coexistência estável: diferenças de fitness e de nicho. As diferenças de fitness estão relacionadas à variação na capacidade competitiva e reprodutiva das espécies e, quando muito elevadas, podem favorecer a exclusão competitiva das espécies com menor fitness ao longo do tempo. Por outro lado, os mecanismos que aumentam as diferenças de nicho (mecanismos estabilizadores) favorecem uma maior competição intraespecífica do que interespecífica, reduzindo a sobreposição de recursos entre as espécies e, assim, promovendo a coexistência. Por exemplo, interações reprodutivas, como a territorialidade, podem intensificar a competição intraespecífica, atuando como um mecanismo estabilizador. Nas últimas décadas, a TMC tem sido amplamente discutida e aplicada em diversos estudos, tanto teóricos quanto empíricos, para investigar como esses mecanismos operam em diferentes cenários ecológicos. Nesse contexto, insetos da ordem Odonata são excelentes modelos para compreender os mecanismos de coexistência em espécies com ciclo de vida complexo, uma vez que possuem uma fase larval aquática e outra fase adulta alada, caracterizada por comportamentos reprodutivos diversos. Assim, a presente tese teve como objetivo investigar os mecanismos relacionados às interações intra e interespecíficas nos diferentes estágios de vida de libélulas neotropicais. A tese foi estruturada em três capítulos: o Capítulo I apresenta uma introdução aos principais conceitos e mecanismos da TMC, além de uma análise cienciométrica sobre o número de estudos empíricos e teóricos publicados após Chesson (2000), incluindo informações sobre o número de publicações por países, grupos taxonômicos e ecossistemas estudados e metodologias empregadas; O Capítulo II analisa a influência de fatores bióticos e abióticos na variação da mancha alar (atributo relacionado ao sucesso reprodutivo) em *Hetaerina rosea* Selys, 1853, dentro e entre populações. Para isso, foram utilizados dados sobre abundância intraespecífica, abundância total, cobertura vegetal e a localização geográfica em 46 locais na região Centro-Oeste do Brasil; Por fim, o Capítulo III investiga como o efeito das interações intra e interespecíficas varia ao longo do ciclo de vida de espécies de libélulas tropicais. Foi testada a hipótese de que a competição na fase larval é predominantemente neutra, ou seja, independente da identidade das espécies e determinada

pela densidade total de indivíduos, enquanto nos adultos, as interações intraspecíficas são mais intensas devido às interações reprodutivas. Para isso, foram conduzidos experimentos laboratoriais com larvas das espécies *Acanthagrion* (Zygoptera, Coenagrionidae) e *Erythrodiplax* (Anisoptera, Libellulidae), variando a abundância total e a dominância das espécies. Além disso, foram realizadas observações de campo para analisar a coocorrência e a frequência de interações entre adultos de diferentes espécies de Zygoptera e Anisoptera. Deste modo, os resultados desta tese contribuem para a compreensão dos mecanismos ecológicos que sustentam a biodiversidade, integrando a TMC a estudos empíricos com Odonata.

Palavras-chave: Biodiversidade. Comunidades. Coexistência. Interações reprodutivas. Odonata.

ABSTRACT

Community ecology aims to understand the maintenance of biodiversity through the mechanisms that enable species to coexist in local communities. The Modern Coexistence Theory (MCT), synthesized by Chesson (2000), is one of the most rigorous frameworks for understanding how competing species persist in the same environment over time. According to this theory, two types of interspecific differences determine stable coexistence: fitness differences and niche differences. Fitness differences are related to variation in species' competitive and reproductive abilities and, when too large, may lead to the competitive exclusion of lower-fitness species over time. In contrast, mechanisms that increase niche differences (stabilizing mechanisms) promote stronger intraspecific than interspecific competition, reducing resource overlap among species and thus favoring coexistence. For example, reproductive interactions such as territoriality can intensify intraspecific competition, acting as a stabilizing mechanism. Over recent decades, MCT has been widely discussed and applied in both theoretical and empirical studies to investigate how these mechanisms operate across different ecological scenarios. In this context, insects of the order Odonata are excellent models for understanding coexistence mechanisms in species with complex life cycles, as they have an aquatic larval stage and a winged adult stage characterized by diverse reproductive behaviors. Thus, the present thesis aimed to investigate the mechanisms related to intra- and interspecific interactions across different life stages of Neotropical dragonflies. It is structured into three chapters: Chapter I presents an introduction to the main concepts and mechanisms of MCT, along with a scientometric analysis of empirical and theoretical studies published since Chesson (2000), including data on the number of publications by country, taxonomic groups, studied ecosystems, and methodologies employed; Chapter II analyzes the influence of biotic and abiotic factors on the variation in wing spot size (a trait associated with territoriality and male-male sexual competition) in *Hetaerina rosea* Selys, 1853, both within and among populations. For this purpose, data on intraspecific abundance, total abundance, vegetation cover, and site location were collected from 46 sites in the Central-West region of Brazil. Finally, Chapter III investigates how the effects of intra- and interspecific interactions vary across the life cycle of tropical dragonfly species. The hypothesis tested was that larval-stage competition is predominantly neutral, that is, independent of species identity and driven by total individual density, whereas adult-stage interactions are more intense at the intraspecific level due to reproductive behaviors. To test this, laboratory experiments were conducted using larvae of

Acanthagrion (Zygoptera, Coenagrionidae) and *Erythrodiplax* (Anisoptera, Libellulidae), varying both total abundance and species dominance. Additionally, field observations were carried out to analyze co-occurrence and the frequency of interactions among adults of different Zygoptera and Anisoptera species. In this way, the findings of this dissertation contribute to a deeper understanding of the ecological mechanisms that sustain biodiversity by integrating MCT with empirical studies on Odonata.

Keywords: Biodiversity. Communities. Coexistence. Reproductive interactions. Odonata.

SUMÁRIO

Prólogo

A biologia com seus intrigantes questionamentos sempre me cativou. No início, seguir nessa profissão não parecia uma certeza, porém, inspirada por excelentes professores que tive no ensino médio, decidi que, de fato, era a área que eu mais me identificava. Não totalmente. Na verdade, a ideia de estudar animais selvagens me motivava. Assim, antes mesmo de entrar na UFSCar, o plano inicial era cursar biologia e em seguida veterinária. Bem, não preciso dizer que esse plano mudou radicalmente.

O meu primeiro ano no curso de biologia foi um choque. Estudar química e física novamente não estavam nos meus planos. Nada de animais selvagens. Sobrevivi, embora não sem uma boa dose de drama e algumas vezes, repensei se de fato havia feito a escolha certa. No ano seguinte, tive uma oportunidade incrível de participar do programa Ciência sem Fronteiras, e pude estudar durante um ano na Universidade de Pádua, na Itália. E foi no laboratório do professor Dr. Ângelo Bisazza que tive meu primeiro contato com estudos sobre comportamento. Lá pude acompanhar diferentes trabalhos que estavam sendo desenvolvidos com peixes na área de psicobiologia. Retornei ao Brasil com a ideia de buscar orientação na área de comportamento animal. No entanto, uma oportunidade de estágio surgiu e assim, realizei minha primeira iniciação científica na Embrapa Instrumentação – São Carlos, no laboratório do professor Dr. Marcos David, onde desenvolvi um trabalho para conservação de maçãs minimamente processadas. Embora tenham sido dois anos totalmente fora das áreas de comportamento e zoologia, adquiri ampla experiência com método científico, condutas de laboratório e escrita de relatórios científicos. Durante esse período, o professor Dr. Rhainer Guillermo Ferreira se efetivou como professor na UFSCar e ao ter conhecimento da sua área de pesquisa em comportamento animal fui conversar com ele. Prontamente, o professor me recebeu em seu laboratório e, juntamente com o estágio na Embrapa, realizei meu primeiro trabalho com comportamento, em um estudo sobre o impacto da coloração de machos da espécie *Pyrocephalus rubinus* (Príncipe) na taxa de predação de ninhos. Embora a perspectiva de trabalhar com comportamento de aves tenha me encantado, as demandas da área me desmotivaram a continuar (aqui, devo confessar a você que acordar às 4 horas da manhã nunca foi meu ponto forte). E assim, quando terminei meu estágio na Embrapa, iniciei minha segunda IC, pela FAPESP, para estudar seleção sexual em libélulas. Trabalhar com insetos não era, verdadeiramente, o que eu buscava. No fundo, eu alimentava a ingênua ilusão de encontrar uma IC no estilo documentário da vida selvagem. No entanto, com o passar do tempo aprendi a respeitar e admirar imensuravelmente esse grupo, principalmente as libélulas, conforme aprendi sobre sua diversidade taxonômica, ecológica e comportamental. E assim,

finalizei minha iniciação científica juntamente com a minha graduação. Iniciei meu mestrado na mesma área de pesquisa em 2018, quando também me tornei mãe, e até o momento, conciliar a maternidade e a carreira científica tem sido um dos maiores desafios do dia-a-dia. O meu mestrado foi um turbilhão de novidades e desafios, não só pela pesquisa que estava desenvolvendo, mas porque durante este período precisei me reinventar para ocupar dois papeis de extrema importância na minha vida: mãe e pós-graduanda. No entanto, tive o privilégio de contar com uma rede de apoio incrível e, assim, finalizei o mestrado em setembro de 2020, iniciando o doutorado um mês depois.

Alguns meses antes de finalizar meu mestrado, decidi conversar com o professor Dr. Victor Saito sobre a possibilidade de realizar meu doutorado em seu laboratório. A ideia era expandir minha área de conhecimento, combinando os conhecimentos de ecologia com os de seleção sexual e mantendo como modelo de estudo as libélulas. Fui recebida com entusiasmo pelo professor Victor e finalizamos o projeto com o objetivo de investigar os mecanismos reprodutivos na interface da coexistência entre espécies. Assim, nesses últimos anos, surgiram inúmeros desafios - pessoais e acadêmicos. Em relação à área de estudo, muitos conceitos da ecologia emergiram como novidade e compreendê-los demandou muito tempo e paciência. Além disso, me vi sob a necessidade de compreender modelos matemáticos para poder me aprofundar nas teorias que estava estudando – trazendo o arrependimento de um dia ter dito que, seguindo na biologia, eu não precisaria me preocupar com a matemática. Assim, deixo registrado aqui, meus sinceros agradecimentos ao meu orientador, que durante essa jornada, com toda sua paciência e empatia, compartilhou comigo esse conhecimento, tornando esses desafios transponíveis, e possibilitando que este trabalho fosse realizado.

Não foi um caminho fácil, e acho que nunca é. Caminhar pelos trilhos da ciência vai além de produções de artigos, é um ato de resistência, dedicação e amor, ainda mais num cenário de tanto descrédito e desvalorização dessa profissão. No entanto, percorrê-lo tem suas belezas, e me fez admirar e respeitar ainda mais toda complexidade que envolve a natureza. Sem mais delongas, desejo a você, caro leitor, uma viagem intrigante pelas páginas deste trabalho, e que, assim como eu, também possa se encantar com a beleza e complexidade que regem a diversidade da vida.

Introdução Geral

Na natureza podemos observar uma enorme variedade de cores, formas e comportamentos que compõem, de modo singular, cada espécie existente neste planeta. Basta um olhar mais atento ao nosso redor para percebermos a gigantesca diversidade de vida que nos cerca. Assim, o termo biodiversidade foi consolidado por Edward O. Wilson (1988) como referência aos diferentes níveis da diversidade biológica, e sua popularização ajudou a reforçar a importância de compreender os sistemas ecológicos para sua conservação. Dentre as áreas de conhecimento que estudam a biodiversidade, a ecologia de comunidades emerge do interesse em buscar padrões de diversidade e composição de espécies ao longo do tempo e do espaço.

Identificar e explicar padrões é algo intrínseco à ciência. Desta forma, as investigações sobre comunidades ecológicas tiveram início a partir da análise dos padrões de associação entre espécies vegetais. Frederic Clements (1916) foi um dos primeiros a propor uma definição para o termo comunidades, a qual definiu como um "Superorganismo", formando conjuntos previsíveis de espécies integradas funcionalmente. Embora esta ideia de comunidades tenha sido muito influente até meados do século XX, esta também foi criticada por pesquisadores da área, como Henry Gleason (1926) o qual propôs uma visão mais individualista das comunidades, argumentando que as comunidades são, na verdade, resultado da resposta individual de cada espécie a fatores locais. Diante da dicotomia das ideias propostas por Clements e Gleason, o trabalho de Robert Whittaker (1956) foi uma resposta crítica e inovadora na resolução deste problema. Seu estudo sobre gradientes espaciais de vegetação demonstrou que as comunidades não são unidades discretas, mas sim conjuntos de espécies que variam gradualmente ao longo de gradientes ambientais.

Ao longo do tempo, muitas definições foram propostas e o conceito de comunidades passou a ter significados diferentes para diferentes estudiosos da área. Assim, não existe uma única definição para o termo, mas a maioria sintetiza a ideia de que comunidades são um conjunto de espécies encontradas em um determinado lugar (MORIN, 2009). Seguiremos aqui com a ideia de Whittaker (1975) que se refere a comunidade como um:

> *"(...) conjunto de populações de plantas, animais, bactérias e fungos que vivem em um ambiente e interagem entre si, formando juntos um sistema vivo distinto com sua própria composição, estrutura, relações ambientais, desenvolvimento e função"*

Nesta definição o autor aborda não só a ideia de diferentes espécies em um determinado local, mas também a de que estas espécies interagem entre si e com o ambiente, trazendo uma questão fundamental dos estudos mais contemporâneos de ecologia de comunidades.

O surgimento de novas abordagens teóricas e metodológicas possibilitou o avanço científico no estudo das comunidades trazendo uma compreensão mais mecanicista dos padrões de diversidade. É neste cenário que surge o conceito de filtro ambiental, onde as condições ambientais seriam responsáveis por guiar os padrões de diversidade (CODY; DIAMOND, 1975; KEDDY, 1992), além da Teoria de Nicho e Teoria Neutra. Enquanto a teoria de nicho argumenta que as espécies são ecologicamente distintas (HUTCHINSON, 1961) e assim, cada espécie ocupa uma posição diferente nas dimensões de espaço, tempo e tróficas; (*i.e.*, Nichos, PIANKA, 1973), a teoria neutra propõe que as espécies são ecologicamente equivalentes e que eventos estocásticos impulsionam a estruturação da comunidade (ADLER; HILLERISLAMBERS; LEVINE, 2007; HUBBELL, 2001). Por muito tempo estendeu-se um debate sobre qual teoria explicaria os processos de estruturação de uma comunidade, sendo consideradas explicações opostas e dissociadas. Somente após o advento da Teoria Moderna da Coexistência (CHESSON, 2000) é que surgiu uma perspectiva integrada, destacando que a coexistência de espécies resulta de uma combinação de estocasticidade e diferenciação ecológica (ADLER; HILLERISLAMBERS; LEVINE, 2007; LEIBOLD; MCPEEK, 2006; MCPEEK; SIEPIELSKI, 2019).

A Teoria Moderna da Coexistência se desenvolveu no âmbito das interações ecológicas entre e dentro das espécies. As espécies presentes em uma comunidade podem interagir de diferentes formas, competindo por recursos ou compartilhando um predador e, todas essas interações indicam que uma espécie pode impactar positiva ou negativamente outra. Por exemplo, quando duas espécies competem pelo mesmo recurso, a espécie que for melhor competidora pode excluir a outra, num processo denominado exclusão competitiva. Assim, esta teoria propõe que dois tipos de diferenças entre as espécies competidoras

determinam a coexistência estável: diferenças de nicho e de fitness. Enquanto as diferenças de nicho são aquelas que reduzem a sobreposição dos recursos utilizados entre as espécies, as diferenças de fitness estão relacionadas a diferenças na capacidade competitiva e reprodutiva (CHESSON, 2000; HILLERISLAMBERS; ADLER; HARPOLE; LEVINE *et al.*, 2012). A coexistência entre espécies deverá ser, portanto, estável quando as diferenças de nicho forem maiores que as diferenças de fitness. Por exemplo, diferentes espécies de libélulas coexistem, mesmo tendo diferentes habilidades de forregeio (diferenças de fitness), devido a forragearem em horários do dia diferentes (diferenças de nicho). Quanto maiores as diferenças nos horários de forrageio e menores as diferenças nas habilidades competitivas, mais estável é a coexistência entre estas espécies.

Diversos mecanismos podem atuar potencializando as diferenças de nicho e reduzindo as diferenças de fitness. Os mecanismos que aumentam as diferenças de nicho são aqueles que favorecem uma maior competição intraespecífica (dentro da espécie) em detrimento da interespecífica (entre duas ou mais espécies), fazendo com que a espécie regule sua própria taxa de crescimento ao invés de regular a taxa de crescimento da sua competidora (i.e. mecanismos estabilizadores; CHESSON, 2000). Neste contexto, as interações reprodutivas podem atuar como mecanismos estabilizadores (GÓMEZ-LLANO; GERMAIN; KYOGOKU; MCPEEK *et al.*, 2021; YAMAMICHI; KYOGOKU; IRITANI; KOBAYASHI *et al.*, 2020; YAMAMICHI; TSUJI; SAKAI; SVENSSON, 2023). Yamamichi e colaboradores (2020) argumentam que adaptações morfológicas que visam maximizar o sucesso reprodutivo individual (*i.e* intraspecific adaptation load) podem impactar na taxa de crescimento da população e consequentemente, favorecer a coexistência entre as espécies. Por exemplo, a presença de longas genitálias em machos de uma espécie de besouro (*Carabus insulicola*) pode aumentar o sucesso reprodutivo, visto que este traço morfológico traz vantagens ao indivíduo na competição espermática. No entanto, este traço pode reduzir o sucesso reprodutivo da fêmea visto que pode aumentar o descarte dos ovos, afetando a taxa de crescimento da população (TAKAMI; FUKUHARA; YOKOYAMA; KAWATA, 2018). Além disso, comportamentos relacionados à seleção sexual (*i.e.* territorialidade) podem aumentar a competição intraespecífica em detrimento da interespecífica, também contribuindo para que as espécies coexistam (GÓMEZ-LLANO; GERMAIN; KYOGOKU; MCPEEK *et al.*, 2021).

Além disso, as variações na história de vida das espécies podem gerar segregações espaciais e temporais, favorecendo o agrupamento de indivíduos da mesma espécie e a separação entre espécies distintas (AMARASEKARE, 2003; RUDOLF, 2019). Em organismos com ciclo de vida complexo (*i.e.* hemi e holometábolos), como anfíbios e libélulas — cujos estágios imaturos são aquáticos e os adultos, terrestres — essas distinções são particularmente evidentes. Nesses casos, a competição interespecífica pode ser reduzida, uma vez que os indivíduos, em cada fase do desenvolvimento, tendem a interagir predominantemente com conspecíficos devido à sua fenologia (RUDOLF, 2019). A história de vida dessas espécies, por sua vez, pode ser modulada por condições ambientais ou experiências anteriores, como disponibilidade de recursos ou presença de predadores e competidores, influenciando respostas em fases posteriores do ciclo de vida (O'CONNOR; NORRIS; CROSSIN; COOKE, 2014). Evidências empíricas demonstram que, em libélulas, o estresse enfrentado durante a fase larval pode afetar atributos individuais após a metamorfose, como tamanho, massa corporal e resposta imunológica, impactando diretamente o sucesso reprodutivo e a competitividade (ANHOLT, 1990; PLAISTOW; SIVA-JOTHY, 1999; ROLFF; VAN DE MEUTTER; STOKS, 2004; VAN BUSKIRK, 1987). Ainda, as interações reprodutivas presentes na fase adulta podem favorecer a coexistência, em um cenário no qual as espécies são ecologicamente equivalentes na fase juvenil (BROEKMAN; MULLER-LANDAU; VISSER; JONGEJANS *et al.*, 2019), ou serem afetadas pelas condições experimentadas na fase juvenil (SIEPIELSKI; GÓMEZ-LLANO; MCPEEK, 2022). Deste modo, compreender os mecanismos de coexistência em espécies com ciclo de vida complexo pode trazer insights sobre como diferentes processos ecológicos atuam ao longo dos distintos estágios ontogenéticos (GÓMEZ-LLANO; GERMAIN; KYOGOKU; MCPEEK *et al.*, 2021; GÓMEZ-LLANO; BOYS; PING; TYE *et al.*, 2023).

Finalmente, uma gama de fatores podem influenciar a estruturação de uma comunidade e entender os processos pelos quais esses fatores agem no ganho, perda e manutenção da biodiversidade tem sido um grande desafio para os estudiosos da área (HILLERISLAMBERS; ADLER; HARPOLE; LEVINE *et al.*, 2012; VELLEND, 2010). Uma síntese sobre os principais processos que estruturam uma comunidade propõe que as espécies formam subconjuntos, formados por eventos estocásticos e pela limitação da dispersão, que passam por um filtro abiótico (i.e. fatores ambientais) e biótico compondo as comunidades locais (HILLERISLAMBERS; ADLER; HARPOLE; LEVINE *et al.*, 2012). Estas comunidades locais estão sujeitas aos efeitos das interações intra e interespecíficas, que

irão modular os padrões de coexistência entre as diferentes espécies. No entanto, os estudos mais recentes têm mostrado a importância de se adicionar os fatores relacionados à história de vida e as interações reprodutivas em espécies com ciclo complexo (Fig. 1; GÓMEZ-LLANO; GERMAIN; KYOGOKU; MCPEEK *et al.*, 2021; HILLERISLAMBERS; ADLER; HARPOLE; LEVINE *et al.*, 2012; RUDOLF, 2019).

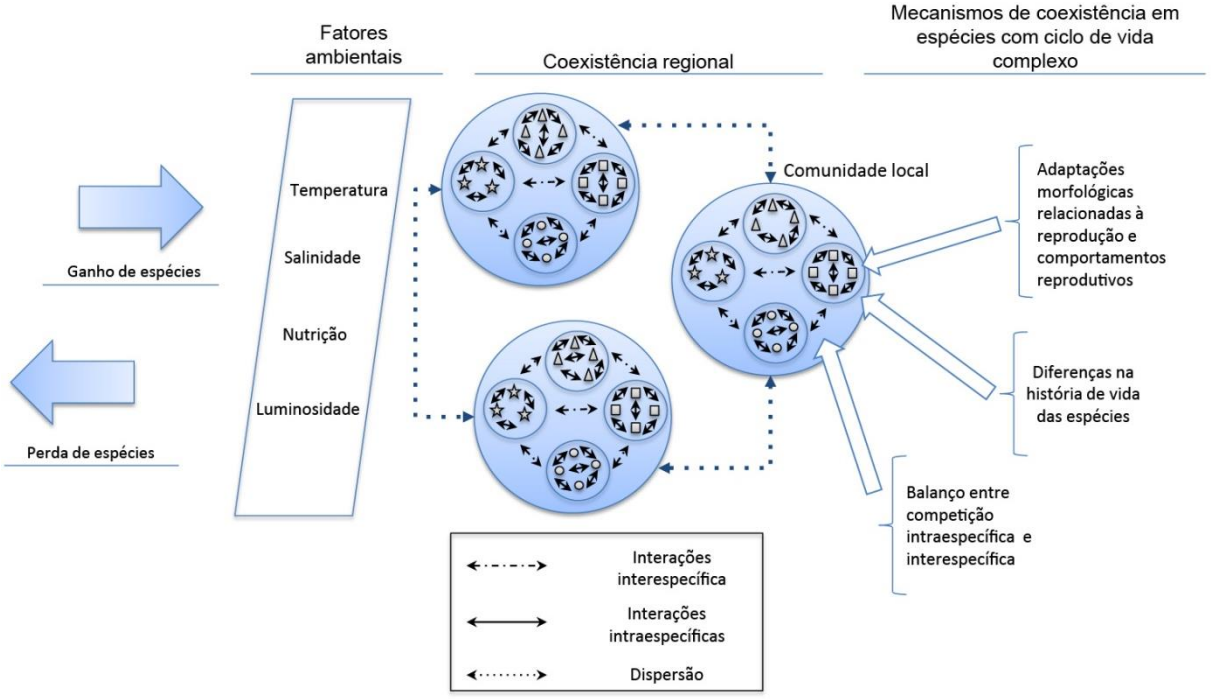

Figura 1. Mecanismos de coexistência em espécies com ciclo de vida complexo. Modificado de HilleRisLambers *et al.* (2012), para a inclusão de mecanismos que devem atuar na coexistência das espécies com ciclo de vida complexo.

Sobre libélulas e donzelinhas

Os insetos da ordem Odonata, comumente conhecidos como libélulas e donzelinhas, são amplamente distribuídos por todo planeta e apresentam uma grande diversidade taxonômica, ecológica e comportamental. As espécies desta ordem estão divididas em três subordens: Zygoptera, Anisoptera e Anisozygoptera, compostas por 48 famílias (BYBEE; KALKMAN; ERICKSON; FRANDSEN *et al.*, 2021). Trata-se de organismos anfibióticos, com ciclo de vida complexo e incompleto (*i.e.* fazem metamorfose, sem fase pupal), que apresentam uma fase larval aquática e uma fase adulta alada (CORBET, 1999).

As larvas de Odonata apresentam uma grande variação morfológica e comportamental entre as famílias deste grupo, principalmente relacionadas à respiração, estratégias de alimentação e seleção de habitat (CORBET, 1999; TAVARES; PESTANA; ROCHA;

SCHIAVONE *et al.*, 2018). Também denominadas de ninfas, estas são predadoras eficientes e generalistas, alimentando-se de alevinos, girinos, outros invertebrados aquáticos e até outras ninfas (HAMADA; NESSIMIAN; QUERINO, 2014). Desta forma, diferentes fatores podem atuar na estruturação de comunidades compostas por ninfas de Odonata, como a partição de nicho, competição intraespecífica, predação intraguilda e o canibalismo, afetando as dinâmicas das populações e, consequentemente, a co-ocorrência das espécies (ANHOLT, 1994; FINCKE, 1994; SUHLING; LEPKOJUS, 2001). Além disso, estudos anteriores demonstraram que dinâmicas neutras também podem guiar os padrões de diversidade em comunidades de libélulas (SIEPIELSKI; HUNG; BEIN; MCPEEK, 2010). As larvas deste grupo também são excelentes bioindicadores, sendo muito utilizadas em estudos sobre impactos antrópicos e qualidade ambiental (LEE FOOTE; RICE HORNUNG, 2005; MIGUEL; OLIVEIRA-JUNIOR; LIGEIRO; JUEN, 2017).

Em relação aos adultos dessa ordem, as distinções morfológicas entre Anisoptera e Zygoptera podem ser visivelmente perceptíveis. Enquanto o primeiro é majoritariamente composto por indivíduos maiores, mais robustos e que pousam com as asas abertas, o segundo é composto por indivíduos menores, com separação entre os olhos e que pousam com as asas fechadas (Fig. 2). Após a emergência das larvas, os adultos de Odonata passam por um período de maturação até entrarem na fase reprodutiva. O comportamento reprodutivo desse grupo pode ser descrito em três etapas (CORBET, 1999): i) Reconhecimento intra e interespecifico; ii) Acasalamento e iii) Oviposição. Na primeira etapa ocorre o reconhecimento/escolha do parceiro reprodutivo, e é composta por uma diversidade de comportamentos que varia de acordo com a espécie. Por exemplo, algumas espécies apresentam comportamentos agonísticos devido a disputas entre machos para defesa de territórios ou comportamento de exibição e corte das fêmeas (GUILLERMO-FERREIRA; BISPO, 2012; GUILLERMO-FERREIRA; DEL-CLARO, 2011). A segunda etapa é composta pela formação do tandem (quando o macho segura a fêmea utilizando seus apêndices anais) e posteriormente a cópula. Um aspecto singular do comportamento desses insetos é a translocação espermática, onde os machos transferem o esperma dos testículos para a vesícula seminal localizada nos primeiros segmentos abdominais antes, durante ou após a cópula, de onde será transferido para a fêmea no momento do acasalamento (RIVAS-TORRES; OUTOMURO; LORENZO-CARBALLA; CORDERO-RIVERA, 2019). Por fim, a etapa de oviposição é composta pela escolha do local de oviposição pela fêmea e deposição dos ovos (dependendo da espécie a oviposição pode ser exofítica - os ovos são depositados

diretamente na água - ou endofítica - os ovos são depositados nos tecidos vegetais) e pode variar em ambientes modificados pela ação antrópica (CALVÃO; SAMWAYS; FARIA; FERREIRA *et al*., 2025). No momento da oviposição, a fêmea pode ou não estar acompanhada do macho, e esse comportamento denominado de "guarda" varia de acordo com a espécie (CÓRDOBA-AGUILAR; CORDERO-RIVERA, 2005).

As libélulas são excelentes modelos para estudos ecológicos e evolutivos devido à sua posição filogenética basal entre os insetos (MISOF; LIU; MEUSEMANN; PETERS *et al*., 2014), aos seus ciclos de vida complexos (STOKS; CORDOBA-AGUILAR, 2012), aos elaborados comportamentos reprodutivos que apresentam (GUILLERMO-FERREIRA; BISPO, 2012;) e à diversidade fenotípica observada no grupo (SCHILDER; MARDEN, 2007). Dentre as características mais marcantes de muitas espécies, tanto de Anisoptera quanto de Zygoptera, destacam-se os padrões conspícuos e frequentemente vistosos de coloração nas asas, desempenhando um papel central no comportamento reprodutivo dessas espécies. A coloração alar pode estar relacionada ás interações agonísticas entre machos (GUILLERMO-FERREIRA; GORB; APPEL; KOVALEV *et al.*, 2015), a escolha de parceiros pelas fêmeas (SIVA-JOTHY, 1999) e o reconhecimento intra e interespecífico (GUILLERMO-FERREIRA; THERÉZIO; GEHLEN; BISPO *et al.*, 2014; SCHULTZ; FINCKE, 2009). Além disso, a presença desse traço sexual está intimamente relacionada com o sucesso reprodutivo individual (CÓRDOBA-AGUILAR; CORDERO-RIVERA, 2005; CÓRDOBA-AGUILAR; GONZÁLEZ-TOKMAN, 2014), podendo afetar as dinâmicas populacionais e de comunidades (GÓMEZ-LLANO; GERMAIN; KYOGOKU; MCPEEK *et al.*, 2021; YAMAMICHI; KYOGOKU; IRITANI; KOBAYASHI *et al.*, 2020). Deste modo, devido a grande importância ecológica deste grupo, estudos recentes têm alertado para a inclusão desta ordem nos modelos de conservação global (SAMWAYS; CÓRDOBA-AGUILAR; DEACON; ALVES-MARTINS *et al*., 2025).

Figura 2. Espécies de Odonata presentes no Horto Municipal de São Carlos, SP, Brasil. Trata-se de três espécies da subordem Anisoptera (conhecidas como libélulas; A,B e C) e uma espécie pertencente à subordem Zygoptera (conhecidas como donzelinhas; D). Fotos de Gabrielle Pestana.

Neste contexto, a presente tese teve por objetivo: i) apresentar uma introdução aos conceitos e mecanismos sintetizados por Chesson (2000) em seu artigo sobre a Teoria Moderna da Coexistência e realizar uma análise cienciométrica sobre os trabalhos que citaram o estudo, de 2000 até 2020; ii) analisar a influência de fatores bióticos e abióticos na variação da mancha alar (um atributo associado ao sucesso reprodutivo) em *Hetaerina rosea*, dentro e entre populações; e finalmente, iii) investigar o efeito das interações intra e interespecíficas ao longo do ciclo de vida de espécies de libélulas tropicais. Os resultados deste trabalho trazem insights sobre os processos que guiam a biodiversidade em comunidades de libélulas neotropicais.

Capítulo I

An introduction to Modern Coexistence Theory for future researchers

Abstract

The Modern Coexistence Theory (MCT), synthesized by Chesson (2000), explains how competing species can coexist in the same environment over time through well-defined theoretical mechanisms. In this study, we provide an overview of MCT, outlining its fundamental concepts and mainly mechanisms through a mathematically friendly synthesis aimed at early-career researchers and newcomers to the field. Additionally, we present a scientometric analysis of studies that cited Chesson's work between 2000 and 2020. A total of 3,093 articles in English were identified and classified into empirical studies, theoretical papers, reviews, meta-analyses, and scientometric works. Empirical and theoretical studies were further categorized based on their use of MCT: (i) articles that apply MCT, (ii) articles that use MCT to hypotheses and discussing results, and (iii) articles that just citing MCT in general. For studies that applied MCT, we gathered additional information including authors' institutional affiliations, study methodology (observational or experimental), model system, and ecosystem type. Our results indicate a notable imbalance between empirical and theoretical studies, as well as a geographic bias, with a predominance of publications from the Northern Hemisphere. Moreover, most empirical applications focused on plant communities and terrestrial ecosystems. These patterns reveal important gaps in the empirical application of MCT and highlight the need for further studies to explore biodiversity maintenance mechanisms across a broader range of taxa and ecosystems.

Keywords: Coexistence. Ecological differences. Fitness. Biodiversity. Stabilizing mechanisms.

Introduction

Modern Coexistence Theory (MCT) has been widely recognized as an integrative framework to understand how competing species persist locally in different ecological contexts, from microorganisms to plants (*i.e.* BAI; QUEENBOROUGH; WANG; ZHANG *et al.*, 2012; GUISLAIN; BEISNER; KÖHLER, 2019; JULIANO; LOUNIBOS; O'MEARA, 2004; NOTO; HUGHES, 2020). Historically, various mechanisms have been proposed to explain community assemblage based on the effects of one competing species on the population growth rates of another. However, empirical studies are still relatively scarce because the theory is based on mathematical models not easily transferable to commonly sampled empirical data, undermining a comprehensive application and understanding by practitioner ecologists (SHOEMAKER; WALTER; GHERARDI; DESIERVO *et al.*, 2021). Therefore, studies that discuss the theory clearly and concisely translating its mathematical language into the empiricists´ vocabulary may boost its application, increasing empirical studies and scientific advances in this fundamental topic of research.

Our aims in this review are 1) to describe a mathematically friendly synthesis of the key concepts of the MCT and 2) present a scientometric analysis of how studies are using MCT. Specifically, we will address what stable coexistence and competitive exclusion are, how the invasibility criteria work and why they can be used to test coexistence, what stabilizing and equalizing mechanisms are, and how fluctuation-dependent and fluctuation-independent coexistence mechanisms can maintain multiple species competing for the same resource.

Early attempts to understand coexistence

Communities are complex systems shaped by the interplay of biotic and abiotic factors, where each species presents unique ecophysiological requirements and interaction patterns with others (SCHOENER, 2009). Over the decades, numerous theories have been proposed to explain how different species assemble within shared habitats. Niche theory proposes that each species in a community occupies a specific position within a multidimensional "niche space," defined by three main dimensions: spatial, temporal, and trophic (PIANKA, 1973). A species' niche is determined by how it influences and responds to each of these dimensions, meaning that species in the same community have distinct ecological roles (HUTCHINSON, 1961; SCHOENER, 2009). On the other hand, the neutral

theory proposes that species are ecologically equivalent and stochastic events drive community assembly (ADLER; HILLERISLAMBERS; LEVINE, 2007; HUBBELL, 2001). For a long time, niche theory and neutral theory were seen as opposing explanations for community structure, as studies provided evidence supporting one or the other. However, the development of modern coexistence theory (MCT) has bridged the gap between these frameworks, demonstrating that both neutral and niche-based processes contribute to community structure at the same time (ADLER, 2007).

This integrative perspective has reshaped community ecology, highlighting that species coexistence results from a combination of stochasticity and ecological differentiation (LEIBOLD; MCPEEK, 2006; MCPEEK; SIEPIELSKI, 2019). In this context, the MCT predicts how competing species are capable of persisting in a given environment in the presence of specific ecological mechanisms (CHESSON, 2000). Persistence refers to a species' ability to increase in abundance when rare. In other words, a species with low abundance exhibits a positive growth rate in the presence of other competing species in equilibrium density. Understanding these concepts is fundamental to grasping the definition of coexistence and the parameters used to assess species coexistence.

Furthermore, it is important to note that not all co-occuring species present in a community are, in fact, coexisting. Four species types may be recognized in a local community, according to its population dynamic: sink, walking dead, neutral and coexisting (GÓMEZ-LLANO; GERMAIN; KYOGOKU; MCPEEK *et al.*, 2021). Some species are occasionally in some local communities for a short period of time and have a negative per capita growth rate in this location (*e.g.* due to harsh environmental conditions), being considered as sink species. These species remain in the community due to the high immigration rate from other local communities (*i.e.* metacommunity) and when this flux is interrupted they quickly become extinct. Walking dead species also have a negative per capita growth rate; however, these species may take a long time to become locally extinct. This could happen for instance, when two species have similar competitive ability (R* values, see below) and so, competitive exclusion due to negative population growth is slow. Neutral species in turn have exactly the same demographic responses to all species present in local communities and to abiotic factors, co-occurring as ecologically identical species. These species are not termed coexisting because there are no mechanisms that rescue species from low densities and stochastic demography may eventually exclude any species (see text and

ADLER; HILLERISLAMBERS; LEVINE, 2007). Finally, coexisting species have a positive per capita growth rate from low densities in the presence and independently of each other's abundance.

A primer of Modern Coexistence Theory

To start framing how different species persist in the same local community, first, we need to understand what factors are involved in setting a community. Community assembly results from the joint effect of dispersal, environmental filters and interactions between species. In this context, species compete for multiple essential resources for their growth. While abiotic environmental factors (*e.g*. temperature, pH, salinity) select which species will be present in a community according to ecophysiological requirements (*e.g.* thermoregulation, body size; DE MARCO JÚNIOR; BATISTA; CABETTE, 2015; SAITO; VALENTE-NETO; RODRIGUES; DE OLIVEIRA ROQUE *et al.*, 2016), species interactions drive the selection of traits related to competitive ability, predator-prey dynamics, and mutualistic relationships. Both processes are virtually inseparable in many situations (*e.g.* when the identity of the best competitor changes in different environmental conditions; HILLERISLAMBERS; ADLER; HARPOLE; LEVINE *et al.*, 2012). Interactions between species can occur in many ways, from widely studied competition for food, or nesting sites, to sharing a common predator, or by mutualistic relationships.

All of these interactions indicate that one species can affect another either positively or negatively. Situations in which one species has a negative effect by competing for shared resources can result in competitive exclusion of the worst competitor. This scenario is the focus of Modern Coexistence Theory. But, how do we know which species is likely to be excluded? The population parameter to assess this attribute is called fitness and allows us to predict which species are expected to persist in the community and which are expected to be competitively excluded (see box 1 for how to calculate the Fitness parameter). To better understand, let's consider a situation where two species compete for a single limiting resource (R). In this case, fitness considers the limiting resource level necessary for the species to maintain a positive growth rate (*i.e.* births surpass deaths, the R* rule; TILMAN, 1982 ; Fig. 1). Thus, the winning species will have greater fitness, being able to grow and reproduce quickly (*i.e*. in order to minimally sustain a constant size population) with lower resource levels, while the losing species would face a negative growth rate at the same resource level. In this context, the fitness of a species can be calculated by the relationship between the per

capita growth rate of the species under optimal resource conditions and the rate at which this per capita growth rate decreases as the resource level decreases due to consumption over time (see Box 1; CHESSON, 2000). For example, two species A and B are competing for the same resource R. The species A has a growth rate of 0.82 when the resource R is at an optimal level in the environment (*i.e.* $\mu_A = 0.82$); and its growth rate decreases by 0.2 (*i.e.* $b_A = 0.2$) (that is, for each level that the resource level decreases it subtracts 0.2 from the growth rate of the species, which is initially 0.82). Thus, the fitness of species A is equal to (0.82/0.2) = 4.1. On the other hand, species B has a per capita growth rate of 0.96 (*i.e.* $\mu_B = 0.96$), and its growth rate decreases by 0.3 (*i.e.* $b_B = 0.3$). Therefore, the fitness of species B will be equal to (0.96/0.3) = 3.2. This example illustrates that although species A has a per capita growth rate in an optimal situation lower than species B, species A is less affected by the decreasing resource abundance and is able to grow and reproduce efficiently even at low resource levels. So, species A would competitively exclude species B, because at a given point, resources would be too low for B, leading to more losses than gains, inevitably being excluded. On the other hand, at this same level of resources, species A is still able to maintain positive growth, sustaining the population despite the low level of resources.

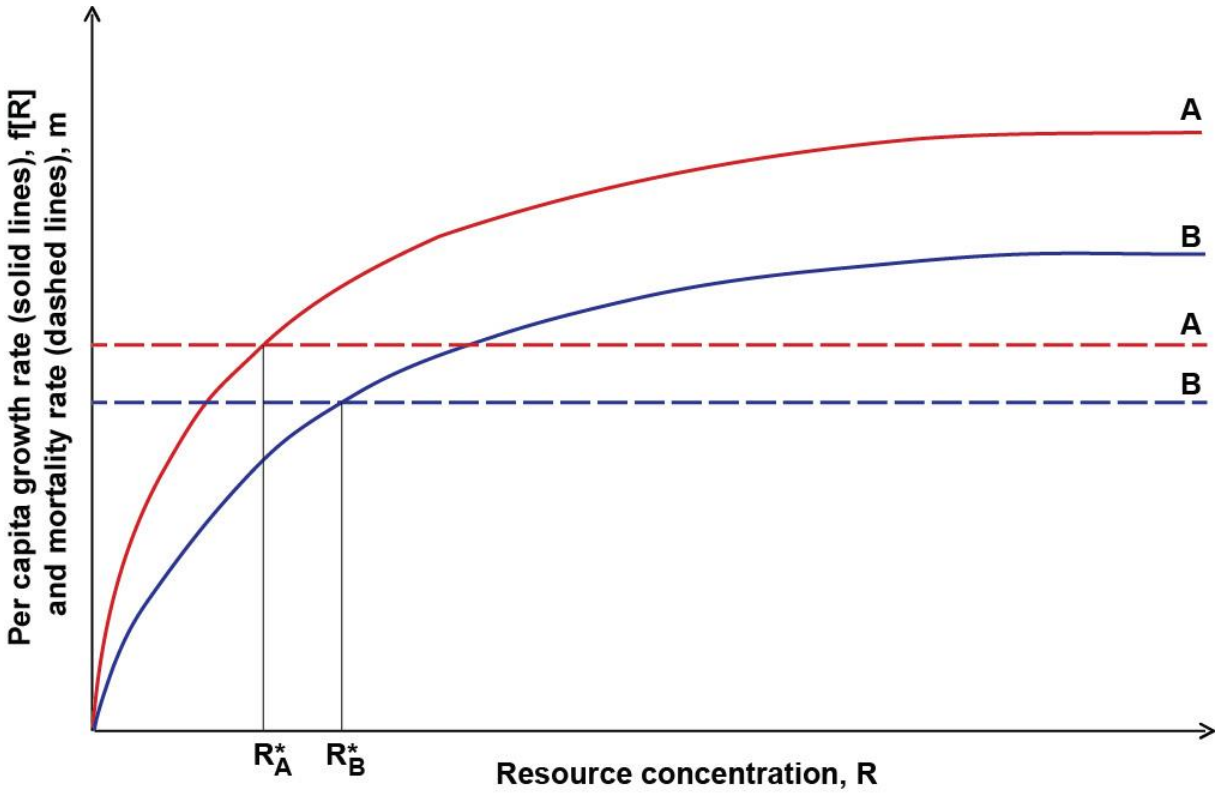

Figure 1. Graphical representation of Tilman's resource competition theory, showing the per capita growth rate as a function of the concentration of an essential resource. Curves A (red) and B (blue) represent the per-capita growth rate of two species with different efficiencies in resource use. The horizontal dashed lines indicate the

mortality rate (m) of each species. The points R^*_A and R^*_B represents the minimum resource concentration required for species A and B, respectively, to maintain a stable population (i.e., where the per capita growth rate equals the mortality rate). According to the theory, the species with the lowest R* (in this case, A) have higher fitness and tend to exclude the other species when competing for a single limiting resource (Adapted from (DYBZINSKI; TILMAN; LEVIN, 2009).

Box 1. The Fitness parameter

Tilman's competition theory (TILMAN, 1982) predicts that species limited by a single resource must follow the R* rule (*i.e.* the resource level required for a species to persist, meaning survive and reproduce). Generally, the species with the lowest R value wins the competition due to its ability to grow and reproduce sufficiently fast at low resource levels, and it will be the species with the greatest fitness.

Therefore, the fitness parameter can be calculated by the ratio of the average per capita growth rate of species in the absence of limiting resources (u), and the rate of decay of the per capita growth rate as resource abundance decreases (b). Thus, u/b represents the average fitness of species in the studied environment. A species with a higher value of u/b will be a potential competitor with a higher probability of excluding another competing species (Fig. 1).

The Fitness will be used to calculate the low-density growth rate (r) of an invader (i) in the presence of the resident (s) in a competition context (CHESSON, 2000):

$$r_i = b_i \left(\frac{u_i}{b_i} - \frac{u_s}{b_s}\right); \qquad (1)$$

Where *ui/bi* is the average fitness of invader and *us/bs* is the average fitness of resident. This allows us to predict whether the invasive species will be able to persist in the presence of its competitor, thus enabling stable coexistence between them.

The fitness parameter determines which species outcompete the others in a given community if they were to compete solely for the same resource - in other words, if they overlapped completely in their niche. However, species with some levels of fitness differences can still coexist if they also present some ecological differences that lead to species occupying different niches in the environment. These ecological differences can occur in relation to the resources used, how they respond to shared predators and natural enemies,

the space, or even the time of activity, allowing two species to persist in the same location even with fitness differences between them (AMARASEKARE, 2013). At this point, we can understand that the equilibrium between fitness differences and niche differences will determine which species can coexist.

Stable coexistence is the indeterminate persistence of competing species in the same local community. In MCT, this is commonly quantified using the "mutual invasion criterion" (with some exceptions, see BARABÁS; D'ANDREA; STUMP, 2018; PANDE; FUNG; CHISHOLM; SHNERB, 2020) which is the dynamic when two species can have positive population growth rates (births surpass deaths) when invading each other populations at their equilibrium density. To illustrate, let us first set one species to be the "invader" and remove it from the community. We next calculate the abundance of all other species, which we call the "residents" at their equilibrium (*i.e.* point at which the growth rate remains constant). We can then invade this resident community, calculating the invader's low-density growth rate (also called it's growth rate when rare). If this rate is positive, we expect the invader to persist with the resident community; if this growth rate is negative, we would instead expect this species to be driven towards competitive exclusion by the residents. To evaluate if two species stably coexist it is necessary that both species are able to sustain positive population growths when invaders are in the presence of the residents.

We return now to the factors discussed above: fitness differences and niche differences. The balance of these two factors determines the growth rate of an invader species, therefore determining if both species can grow from low densities. Considering that species A will be the invader and species B the resident, we have the growth rate of species A equal (from Chesson 2000):

$$r_A = b_A\left(\frac{u_A}{b_A} - \frac{u_B}{b_B}\right) + b_A(1 - \mathrm{p})\frac{u_B}{b_B} \qquad (2)$$

Where μ/b is the fitness of each species (A and B) and 1-*p* is the ecological differences between them (Eq. 3 of CHESSON, 2000). The fitness of both species was calculated previously (see Box 1), so we will now focus on niche differences. To better understand how the two factors affect the growth rate, we will consider two extreme situations, first when ecological differences are maximum and second when minimum, that is, $p = 1$ (no niche differences between species) and $p = 0$ (complete niche differences). With $p = 1$ we will have:

$$r_A = 0.2\left(\frac{0.82}{0.2} - \frac{0.96}{0.3}\right) + \frac{0.2(1-1)0.96}{0.3} \qquad (3)$$

$$r_A = 0.18 + 0$$

$$r_A = 0.18$$

Therefore, species A has a positive growth rate when invading a population of species B at equilibrium density. But, for both species to coexist, species B also needs to have a positive growth rate when invading. Considering B as an invader and A as a resident we have:

$$r_B = 0.3\left(\frac{0.96}{0.3} - \frac{0.82}{0.2}\right) + \frac{0.3(1-1)0.82}{0.2} \qquad (4)$$

$$r_B = -0{,}27$$

For species B we noticed that the growth rate will be negative (-0.27) due solely to fitness differences. Thus, we conclude that in the absence of niche differences, these species will not coexist, but that species A (which has greater fitness) will competitively exclude species B. Now, let's assess the situation in which niche differences are maximum (p=0). Defining A as invader and B as resident:

$$r_A = 0.2\left(\frac{0.82}{0.2} - \frac{0{,}96}{0{,}3}\right) + \frac{0.2(1-0)0.96}{0.3} \qquad (5)$$

$$r_A = 0{,}18 + 0{,}64$$

$$r_A = 0{,}82$$

Again, we have that the growth rate of species A will be positive. Now, calculating the growth rate of species B as invader and A as resident:

$$r_B = 0.3\left(\frac{0.96}{0.3} - \frac{0.82}{0.2}\right) + \frac{0.3(1-0)0.82}{0.2} \qquad (6)$$

$$r_B = 0.96$$

In the presence of maximum ecological differences, the per capita growth rate of species B as invaders will also be positive. This means that species B will be able to grow when recovering from low densities.

Based on these two hypothetical examples, we can understand how each of these two factors acts to drive coexistence (Fig. 2). In the absence of ecological differences, fitness differences inhibit the coexistence between species. If we imagine a situation in which the

fitness of both species is identical (*e.g.* in Neutral models; ADLER; HILLERISLAMBERS; LEVINE, 2007; HUBBELL, 2001), we still have that, for the two species in the invader condition, the growth rate will be close to 0 in the absence of niche differences. Thus, the magnitude of fitness differences between species can accelerate or delay competitive exclusion, but cannot prevent exclusion from occurring by itself. However, in the presence of sufficient ecological differences, high fitness differences may still allow stable coexistence. The smaller the fitness differences between species, the greater the chance that growth rates will be positive in the presence of niche differences, even if these are small (Fig 2.).

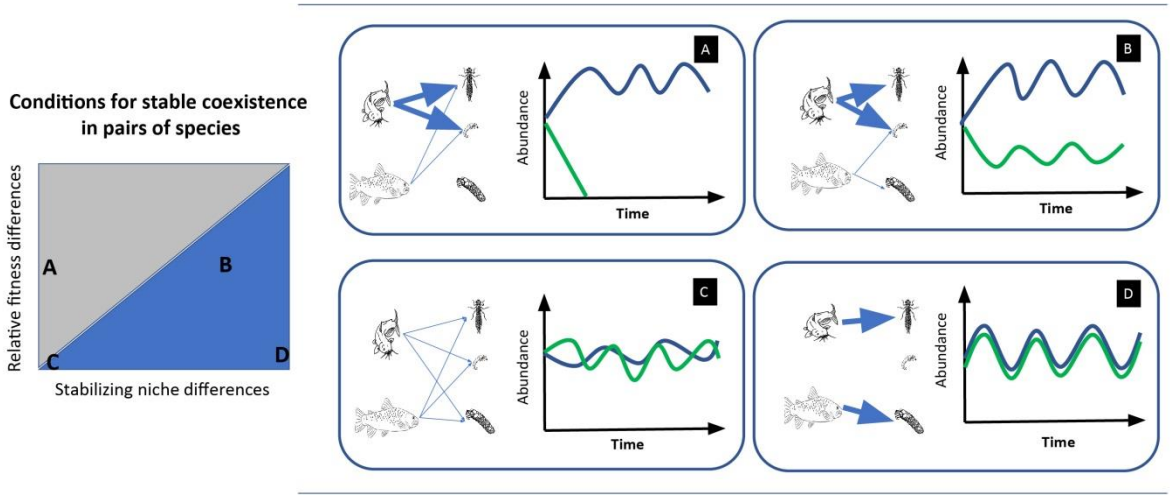

Figura 2. Scenarios of coexistence and competitive exclusion in pairs of species according to the balance between relative fitness differences (RFD) and stabilizing niche differences (SND). Arrows represent the resources used by species, in this case, prey identity. Thickness of arrows represent the species ability to compete for a given resource. (A) The species pair has a large RFD and a small SND preventing them from coexisting. The large overlap in their niches means that they will compete for the same resources and are limited by the same factors. Because they have distinct competitive abilities, one of them will quickly outcompete the other. (B) This species pair has a large RFD, but also a sufficient SND, enabling them to coexist. The sufficient SND make the strongest competitor to control its own population before it excludes the other species. This can be seen at the beginning of the time scale when the blue species grow to a certain point but decrease after that. At this point the green species can recover from low density. (C) The two species have zero RFD and SND and thus the impact of intra and interspecific competition is the same and populations drift in time. Because there is no SND, one species will eventually be excluded by chance, since equalizing mechanisms can only delay competitive exclusion. (D) The two species have little RFD and a large SND enabling them to stably coexist with little interference from one population on another. Note that both populations fluctuate synchronously only to represent how density from one species have no influence on the growth rate of the other species.

Although fitness similarity alone may not promote coexistence, smaller differences can equalize competition for the species with lower fitness, allowing it to present a positive growth rate. Therefore, fitness differences are called the equalizing term. Considering that the amplitude of fitness differences can vary, there are mechanisms that act to minimize these differences and are called equalizing mechanisms. On the other hand, niche differences are fundamental for coexistence between species, and in the absence of these, competitive exclusion is inevitable. Niche differences can also vary in magnitude, and higher niche

differences enhance the chances for species to coexist. So, mechanisms that increase niche differences are termed stabilizing mechanisms.

Now that we understand how important niche differences are to the stable coexistence of species, we need to explain how these differences operate. In summary, niche differences will make individuals of a species have a stronger effect on its own per capita growth rate (*i.e.* the species self-regulates) regarding the effect on the per capita growth rate of the other species in a community. This means that niche differences enhance the magnitude of **intraspecific** (within species) competition in contrast to **interspecific** (among species) competition. In other words, stabilizing mechanisms act so that the species regulates its growth rate more intensely than the growth rate of the other competitor, favoring coexistence. Below we describe and synthesize (see Table 1) some of the key mechanisms that can stabilize coexistence minimizing the effect of the fitness differences and maximizing niche differences (AMARASEKARE, 2013; CHESSON, 2000).

Intraspecific interference

Intraspecific interference mechanisms are widespread in nature and can vary according to the species (especially in animals, AMARASEKARE, 2013). They operate in a simple way: they make species regulate their per capita growth rate with more intensity than the growth rate of their competitors, regardless of the levels of shared resources. It is an intraspecific density-dependent mechanism and therefore when the population is small, the effect of this mechanism will also be low or null. When the population density is higher, the effect of this mechanism will be stronger, making intraspecific competition stronger in comparison to the interspecific one. This happens because the mechanism is not regulated by a shared resource, but on intraspecific interactions that are density-dependent. An example would be dragonflies where males have territoriality over other males (CÓRDOBA-AGUILAR; CORDERO-RIVERA, 2005). Regardless of the levels of resources shared with other species, this mechanism works by decreasing the per capita reproductive success of the population itself when abundant, as individuals of the same species interfere (*e.g.* with disputes or exhibitions) in the reproductive success of conspecifics and not heterospecific ones (AMARASEKARE, 2013; YAMAMICHI; KYOGOKU; IRITANI; KOBAYASHI *et al.*, 2020, GÓMEZ-LLANO; GERMAIN; KYOGOKU; MCPEEK *et al.*, 2021).

Nonlinear response

For this mechanism to operate, there must be variations over time in the limiting factor. Coexistence can result from different responses (linear or nonlinear) to these variations (Fig. 3), which will be interpreted as the ecological differences mentioned above. A limiting factor can be interpreted as a resource that directly influences the per capita growth rate of species (*e.g.* food, nests). Nonlinear responses indicate that a species stabilizes its per capita growth at a certain point in the response to the limiting factor, that is, at a given point in the environmental response, the per capita growth rate does not increase with the increase in the limiting factor (*e.g.* due to response type II, species cannot feed infinitely due to the time processing preys). Thus, this can be an equalizing mechanism, as it can reduce the impact of the fitness difference on the per capita growth rates. If the species with greater fitness presents a more nonlinear response, this means that this species will be more affected by the fluctuation of the limiting factor in terms of a reduction in the per capita growth rate. When the limiting factor is high (*e.g.* many resources), the species with more nonlinear response will have a lower per capita growth rate, due to the stabilization point. This disadvantage balances the advantage the species already have due to the high fitness value (the species grows quickly with few resources due to the curvature of the non-linear response) and allows species coexistence. The intensity of a nonlinear response presented by a species can be measured by the rate of change in the slope of the curvature (τ [tau]; CHESSON, 1994), where $\tau = 0$, when the species presents a linear response and $\tau > 0$, when the response is nonlinear). Two species with different τ values can coexist in a stable way, given that: (1) The species with the highest τ value has greater fitness in the absence of limiting factor fluctuation and, (2) The species with the highest τ faces lower fluctuations when it is an invasive compared to when it is a resident. An empirical example of how nonlinear responses allow species to coexist is desert plants competing for water that can be divided into drought-resistant and opportunistic (VERHULST; MONTANA; MANDUJANO; FRANCO, 2008). Drought-resistant species have a more linear response to the amount of water in the system, being better competitors in wet years. In contrast, opportunistic species grow rapidly in drier years, where a small increase in humidity allows rapid population growth.

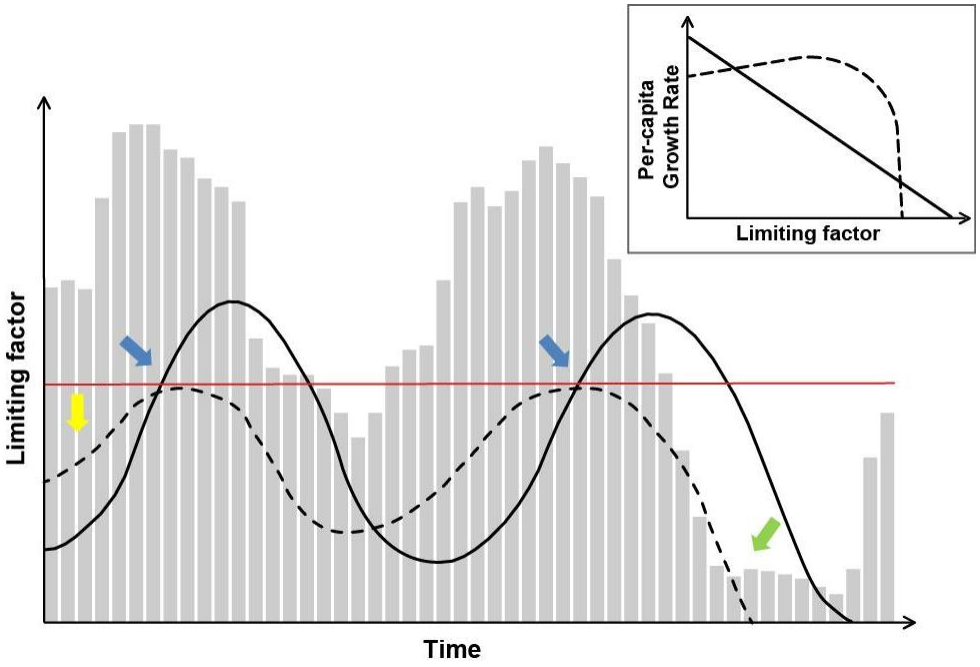

Figura 3. Example of variation in the per capita growth rate of two species due to different responses to limiting factor fluctuations. The gray bars represent the fluctuation of the limiting factor; the solid black line represents the growth rate of the species with a linear response ($\tau = 0$), and the dashed black line represents the growth rate of the species with a nonlinear response ($\tau > 0$); the red line represents the stabilization point of the growth rate for the species with a nonlinear response. The species with a nonlinear response exhibits a higher growth rate than the species with a linear response in the absence of limiting factor fluctuations due to its greater fitness (yellow arrow). However, stronger fluctuations in the limiting factor negatively affect the species with a nonlinear response due to a stabilization point of its growth rate (blue arrows). In this scenario, the species with a linear response achieves a higher growth rate than the species with a nonlinear response, and this difference in growth rates allows for the coexistence of both species. A severe reduction in the availability of the limiting factor (green arrow) could drive both species to extinction. (Adapted from Chesson, 2000).

Trade-off in multiple resources

Unlike the mechanisms described above, this mechanism works with more than one limiting resource. Considering two species, A and B. Species A relies heavily on a resource r1, showing a strong response to the availability of this resource in terms of its per capita growth rate. However, variation in the resource r1 used by species A also has a strong effect on its own per capita growth rate, reducing its abundance when at low levels. On the other hand, species B relies heavily on resource r2, also showing a strong feedback loop with this resource. Thus, although species A also uses resource r2, and species B uses resource r1, both have a weak relationship with the resources cited. Thereby, the strongest relationship (A with r1 and B with r2) will regulate the population growth of the species through competition between individuals of the same species for the resources. In this sense, the trade-off mechanism will act by reducing interspecific competition through the dependence of each

species on different resources reinforcing the intraspecific density-dependent feedback loop (Fig. 1).

The Storage effect

Environmental variables beyond those considered resources can indirectly affect community dynamics by changing population growth rates and consequently affecting intra and interspecific competition intensity. This environmental variation effect can act as a stabilizing mechanism, allowing different competing species to coexist under some specific conditions. The summed criteria and specific combinations needed for that is called the Storage effect (WARNER; CHESSON, 1985).

The first criterion is the existence of differential responses to the environment by competing species. For example, increases in pH can affect the per capita growth rate of two competing species in different ways, positively for one and negatively for the other. Therefore, when one species has an increased growth rate, the other has a decrease. This in turn, increases the population and intraspecific competition of one species, while decreasing for the other (with low abundance intraspecific competition will be low). So, responses to environmental variations can have opposite effects on the per capita growth rate of the species, which will reduce competition when in unfavorable conditions. Thus, the intraspecific competition effect can vary along with the effect of environmental responses (in terms of population density), in what Chesson (2000) called covariance between environment and competition.

For the covariance between environmental response and competition strength to result in coexistence between species, the species in low density (as invader) must be favored by the environment, that is, the response to the environment has a positive effect on the per capita growth rate. Otherwise, if the resident (more abundant) is favored, interspecific competition will lead to competitive exclusion. In situations like this, a third mechanism must operate for coexistence. Buffered population growth can minimize the negative environmental effect on the invader species and, combined with the covariance criteria, rescue populations from low densities. This buffered population growth can result from species life-history traits that inhibit species from competing when in unfavorable conditions and rescue them when the environment changes, such as seed banks in annual plants or eggs dormancy in freshwater zooplankton (CÁCERES, 1997; VENABLE; BROWN, 1988; WARNER; CHESSON, 1985).

To better understand how the combination of these three criteria can result in coexistence, let us imagine two competing species in a scenario of temperature variation. Temperature is an abiotic factor that varies over time, generating different responses from species present in a community. Thus, in this example, the reduction in temperature implies a reduction in the population density of both species, due to the negative effect on the per capita growth rate. The variation in population density is followed by a variation in intraspecific competition, which means that a decrease in density also reduces intraspecific competition intensity in both species. In this case, species A has a greater reduction in population density, which means that the negative effect of the response to the environment is greater in this species. Therefore, for two species to coexist, species A must have a buffered population growth that will favor its growth when it is in a situation of low abundance (Fig 4).

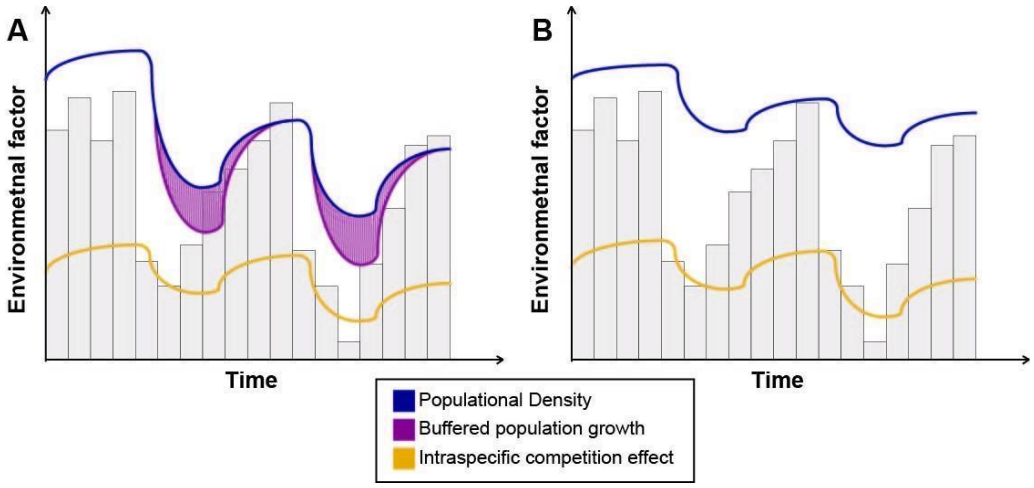

Figure 4. Covariance between effect of response to environment and intraspecific competition. Hypothetical example of two species that showed a decrease in population abundance in response to the environmental factor variation. Species A showed a greater decrease in its abundance (blue line), so the negative effect of the environmental response on the per capita growth rate was stronger for this species. On the other hand, species B showed a smaller decrease in population density (blue line), due to the negative effect of the response to the environment . Every decrease in population density implies a decrease of intraspecific competition effect. The two species can only coexist if species A has some buffered population growth to reduce the negative effect of the response to the environment on its abundance (purple area).

The Storage effect can also act in space and is classified as a spatial niche mechanism. In this context, the dynamics between the three criteria above will be based on differences in environmental quality, which can favor or disfavor the same species, increasing or decreasing intraspecific competition. This spatial mechanism can act by varying the fitness of different species and the variation in dispersion in different habitats. Concerning fitness variation, we have that: (1) when a species is favored by spatial variation, having a positive environmental

effect on its per capita growth rate, the result will be greater intraspecific competition, as its competitors will be disadvantaged by spatial variation; (2) when the environment is unfavorable for the species and, therefore, favorable to its competitors, interspecific competition will be more intense. Again, buffered population growth can minimize the environmental negative effect on the species. On the other hand, dispersal between locations allows individuals of a species present in a favorable location (with higher population abundance and positive per capita growth rate) to migrate to unfavorable locations (with smaller population abundance and negative per capita growth rate) preventing the species from exclusion from the lowest quality environment.

Table 1. A synthesis of the mechanisms of stable coexistence (Based on Chesson, 2000 and Amaresekare, 2009). *It can also occur in situations involving multiple shared resources.

		Mechanism	**Type**	**Empirical studies**	**Literature about mechanisms of stable coexistence**
Single limiting factor	**Fluctuation-dependent**	Non-linear competitive response*	Temporal and Spatial fluctuation	Letten *et al.* (2018) Zepeda & Martore (2019)	Chesson, 2000; Amarasekare, 2003; Hillerislambers *et al.*, 2012; Amarasekare, 2013; Barabás *et al.*, 2018;
		Storage effect	Temporal and Spatial fluctuation	Cáceres (1997) Angert *et al.* (2009) Brooks *et al.* (2023)	
	Fluctuation-independent	Intraspecific interference	-	Svensson *et al.* (2018)	
Multiple limiting factors		Trade-offs in multiple resource	-	McPeek (1996) Amarasekare (2007)	

Bibliometric analyses

After twenty-five years of Chesson's (2000) work, several studies were conducted to understand how the described mechanisms apply in different contexts. To analyze the available literature on Coexistence theory, we compiled literature data citing Chesson (2000) between 2000 and 2020. The data was collected from Scopus (Elsevier) and Web of Science (Thomson-Reuters) databases and only articles in English were considered. The search retrieved 3,443 works from the Web of Science and 3,551 from the Scopus database. These

works were then screened and filtered to remove duplicates, book chapters, theses, and articles in other languages. At this stage, 399 articles from 2016 to 2018 had not yet been filtered (to be finalized), resulting in a final dataset of 3,093 works, of which 2,863 were articles in English and proceeded to the classification stage. We conducted a criteria-based analysis that involved reading and initially classifying the articles according to manuscript type (*i.e.* empirical, theoretical, review, meta-analyses and scientometrics). Only articles identified as empirical or theoretical studies were further classified based on their study proposals (Fig. 5). Additionally, for theoretical and empirical studies classified as category 1. (those applying MCT), we recorded further details, including the authors' location, methodology (observational/experimental), study model, and studied ecosystem.

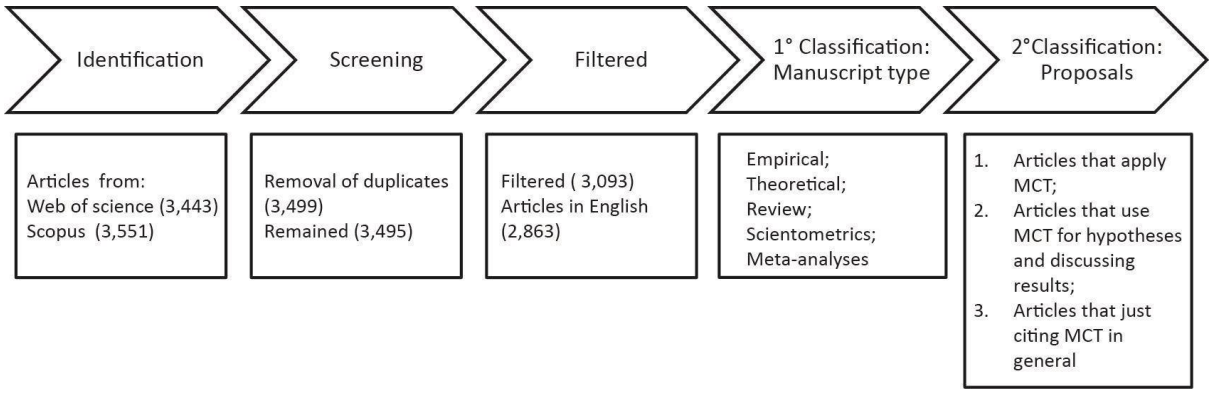

Figure 5. Fluxogram of the stages of identification, screening, filtering, and classification of articles that cite Chesson (2000) between 2000 and 2020.

Our classification of manuscript types identified 1,789 empirical studies, 671 theoretical studies, 418 review articles, 24 meta-analyses, and 2 scientometric studies, with 41 articles classified as both theoretical and empirical (Fig. 6A). Subsequently, a second classification was conducted exclusively for theoretical and empirical studies, yielding the following results: 343 empirical studies that explicitly applied MCT, 639 empirical studies that used MCT to formulate hypotheses and discuss results, and 804 empirical studies that only referenced MCT in a general manner. Similarly, 376 theoretical studies explicitly applied MCT, 138 theoretical studies used MCT for hypotheses and discussion, and 157 theoretical studies only cited MCT without direct application (Fig. 6B).

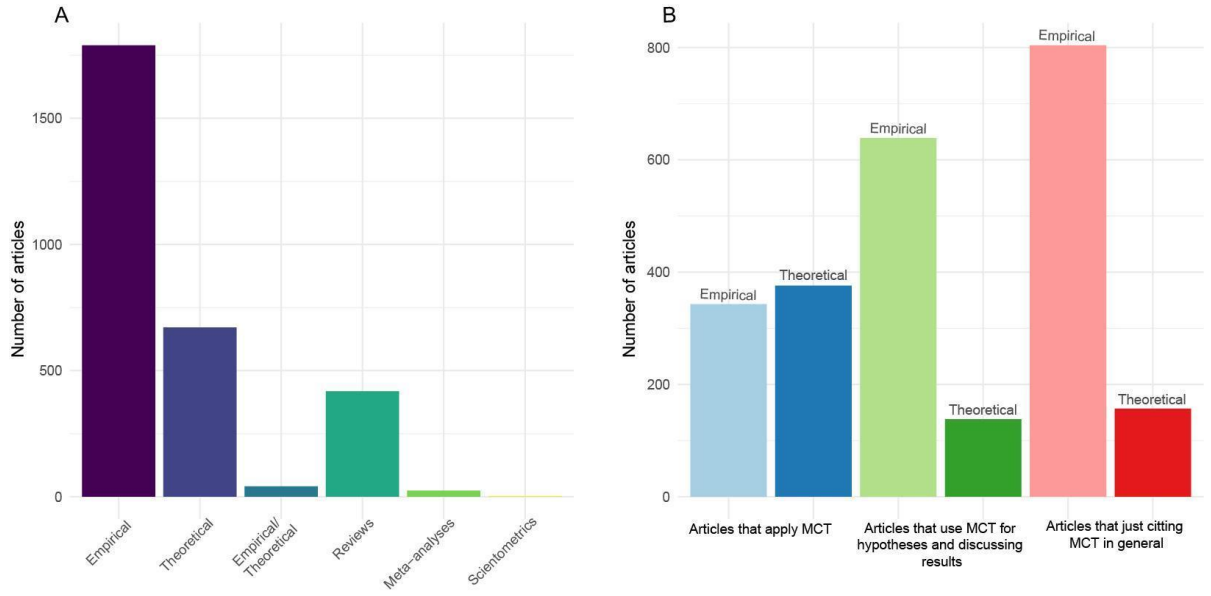

Figure 6. Number of published articles classified by: A) type (empirical, theoretical, review, meta-analysis, scientometrics) and, B) proposals (articles applying MCT, articles that use MCT for hypotheses and discussing results, and articles that just citting MCT in general).

Additional information on the authors' affiliation countries revealed that 58 countries have at least one theoretical or empirical study applying MCT. The United States was the leading contributor, with 352 publications, followed by Canada with 78 and Germany with 75 (Fig. 7). Among empirical studies, plants were the most commonly used study model (Fig. 8A), and the majority of studies were conducted in terrestrial ecosystems (Fig. 8B). Regarding methodology, the proportion of observational and experimental studies was similar, with some studies incorporating both approaches (Fig. 8C).

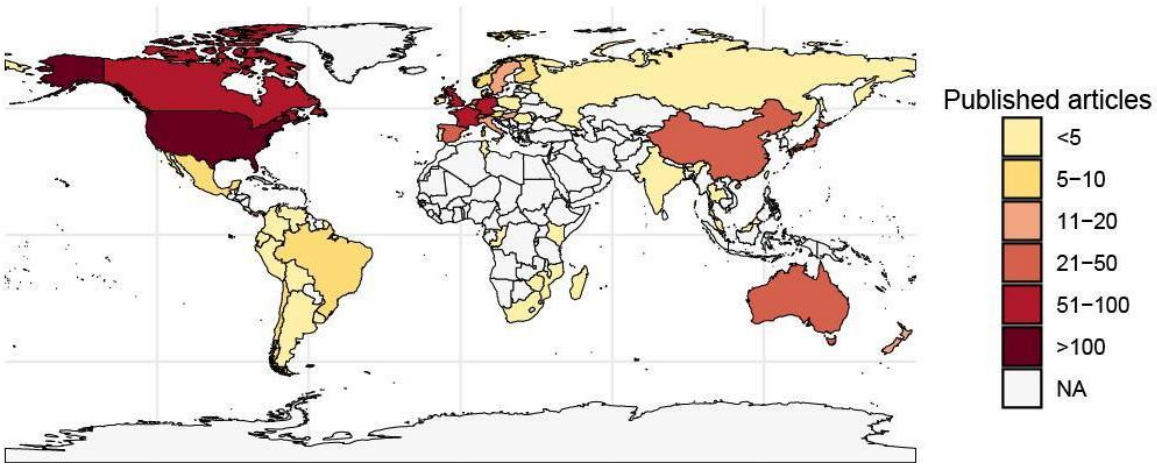

Figure 7. Map of countries that have published at least one theoretical and/or empirical studies applying MCT.

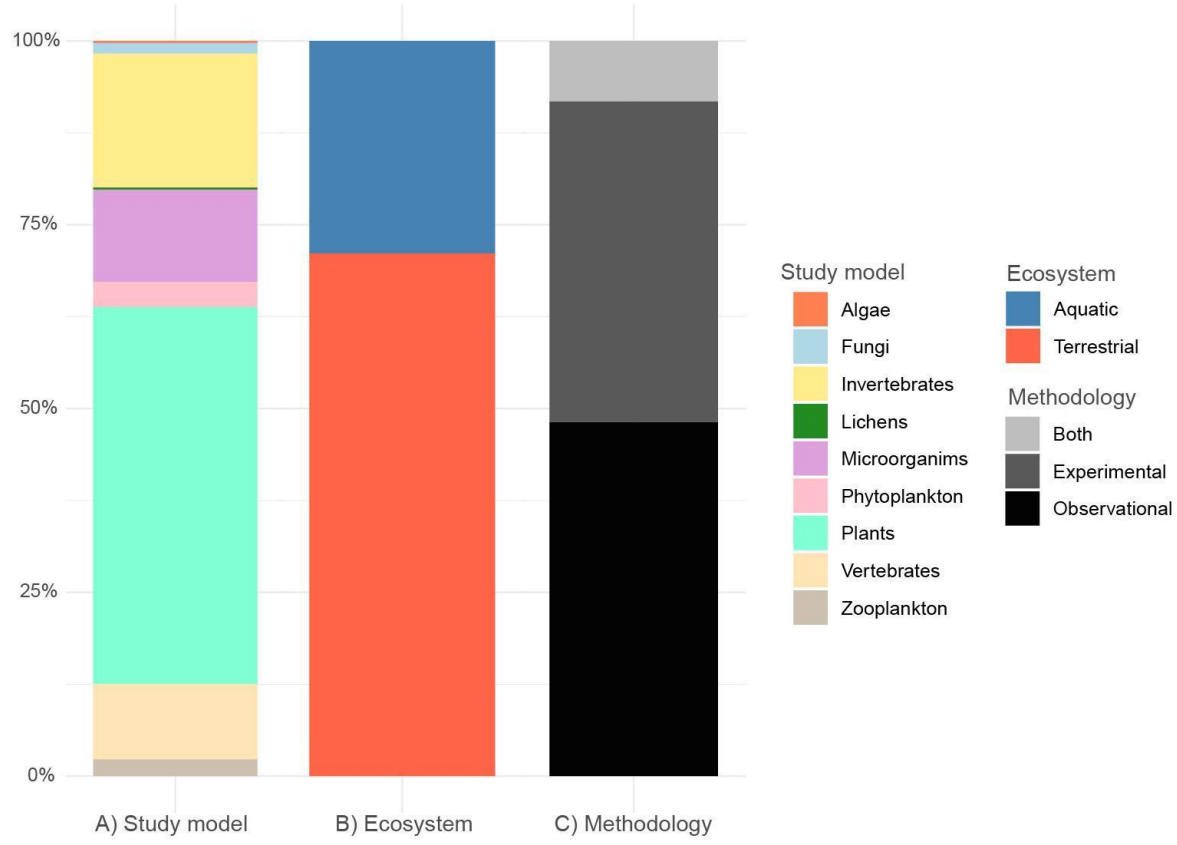

Figure 8. Percentage of published empirical studies applying MCT using: A) Study models; B) Ecosystems; and C) Study methodologies.

Discussion

The scientometric analysis of studies citing Chesson (2000) between 2000 and 2020 demonstrates that over the past two decades, this theory has been widely disseminated and applied across various ecological contexts. The predominance of empirical articles over theoretical ones indicates that the MCT has been extensively used as a foundation for experimental and observational investigations. However, the relatively low number of published empirical studies applying MCT may reflect the complexity of the theory and the challenges associated with integrating its mathematical models into empirical data. While studies based on mathematical models are undeniably crucial for advancing ecology, limitations in understanding and applying these models can impact the number of studies in the field (SHOEMAKER; WALTER; GHERARDI; DESIERVO *et al.*, 2021).

Regarding the geographical distribution of published studies, the concentration of scientific knowledge in Northern Hemisphere countries underscores disparities in funding and

research infrastructure compared to tropical regions (PATELLI; NAPOLITANO; CIMINI; GABRIELLI, 2023). Moreover, the underrepresentation of studies conducted in tropical and subtropical areas, where biodiversity and ecological mechanisms may exhibit distinct patterns (SAITO et al., 2021; NASHet al., 2024), highlights a significant knowledge gap regarding the processes promoting biodiversity. This issue is particularly relevant as tropical ecosystems, characterized by warmer climates, are expected to harbor species with higher metabolic rates. Higher metabolic rates can influence community assembly dynamics by increasing stochasticity, as populations in these environments tend to be smaller and more affected by demographic fluctuations, dispersal processes, and intrinsic mortality linked to oxidative stress, regardless of species identity (SAITO; PERKINS; KRATINA, 2021; SAITO; STOPPA; SHIMABUKURO; CAÑEDO-ARGÜELLES *et al.*, 2021; SIQUEIRA; SAITO; BINI; MELO *et al.*, 2020). Furthermore, the most rapid and intense environmental changes are currently occurring in tropical regions (FRANÇA; BENKWITT; PERALTA; ROBINSON *et al.*, 2020; THOMPSON; MOSLEY-THOMPSON; BRECHER; DAVIS *et al.*, 2006; TREW; EDWARDS; LEES; KLINGES *et al.*, 2024) which reinforces the urgency and importance of conducting studies in these areas to improve our understanding of biodiversity loss and gain under changing environmental conditions. Thus, fostering international collaborations and strengthening research in underrepresented regions is essential to expand the scope of MCT applications.

Finally, the predominance of studies focusing on plants and terrestrial ecosystems (*e.g.* ADLER; HILLERISLAMBERS; LEVINE, 2009; EPPINGA; BAUDENA; JOHNSON; JIANG *et al.*, 2018; WANG; CHI; TANG; JIANG, 2019; WANG; HU; WANG; LIU *et al.*, 2019) suggests a potential bias in the application of MCT, likely due to the methodological feasibility of observing and experimenting with these organisms and environments. While the relatively balanced distribution between observational and experimental studies demonstrates the theory's flexibility across different methodological approaches, the lower representation of aquatic ecosystems and other taxonomic groups raises concerns about potential gaps in understanding coexistence mechanisms across diverse communities. In conclusion, these findings point to significant gaps in the empirical application of MCT and emphasize the need for more research across a broader diversity of taxa, ecosystems, and especially in tropical regions, to better understand the mechanisms that maintain biodiversity.

Capítulo II

Intraspecific density and abiotic factors affect fitness-related phenotype in a neotropical damselfly

Abstract

Sexual ornaments can play a key role in individual reproductive success. In Odonata, some species exhibit wing pigmentation, as seen in the genus *Hetaerina*. This trait may be associated with fertility, territory defense, female attraction, and increased mating opportunities. While some hypotheses suggest that the elaboration of sexual ornaments at the individual level may be linked to physiological factors such as immunity and nutrition, little is known about the effects of biotic and abiotic interactions on ornament variation within and between populations. So, this study aimed to investigate how biotic factors (i.e., co-occurrence patterns and abundance) and abiotic factors (*i.e.* vegetation cover and spatial scales) influence the variation in wing pigmentation in *Hetaerina rosea* Selys within populations and across populations in different communities. To achieve this, we collected data on abundance and species richness in 46 sites, as well as vegetation cover and geographic data, which were converted to spatial variables. To assess sexual ornament variation, we measured the wing spot ratio by dividing the pigmented area by the wing area. We calculated the mean wing spot across the four wings for each individual. Within each population, we determined the mean and standard deviation of the wing spot ratio. To investigate co-occurrence patterns, we conducted a Checkerboard score analysis. Using Structural Equation Modeling, we examined the effects of vegetation cover, intraspecific abundance, total abundance, and spatial scale on the mean and standard deviation of wing spot ratio. Our results revealed a co-occurrence pattern among species greater than expected by chance, with 12 Odonata species positively co-occurring with one or more species, and only one species negatively co-occurring with another. For *H. rosea*, no significant co-occurrence patterns were observed. The analyses of structural equation modeling indicated that intraspecific abundance and vegetation cover had a significant positive and negative effect, respectively, on the standard deviation of wing spot ratio within populations. Additionally, we observed a significant spatial signature on the mean wing spot ratio across sites from different watersheds/micro basins. Our findings provide important insights into the drivers of wing spot variation in *H. rosea*, emphasizing the influence of intraspecific interactions and environmental factors in shaping fitness-related phenotypic variation both within and among populations.

Keywords: Sexual traits. Density-dependence. Environmental factors. Biotic interactions.

Introduction

Sexual ornaments play a crucial role in individual reproductive success with potential consequences for population growth and persistence. Coloration patterns observed in males of different species are well-known examples linked to reproductive success. In Odonata, wing pigmentation is common in several families, particularly those showing territorial behaviour, like Calopterygidae, Polythoridae, Pseudolestidae, and Euphaeidae (among others). In the calopterygid genus *Hetaerina*, wing pigmentation is associated with territoriality, since males with larger pigmented areas win more territorial disputes (GUILLERMO-FERREIRA; DEL-CLARO, 2011), show higher fertility (i.e., produce more sperm; PESTANA, 2020) and obtain more mating opportunities (CÓRDOBA-AGUILAR, 1995; GRETHER, 1996). While these studies hypothesized that the elaboration of sexual ornaments at the individual level is mostly driven by physiological traits such as those involving immunity (RANTALA; KOSKIMÌKI; TASKINEN; TYNKKYNEN *et al.*, 2000) and fertility (PESTANA, 2020), little is known about the influence of drivers on the population (*e.g.* intra-specific abundance), and community levels (co-occurring species) and the environment itself (suitable habitats) on ornament size variation within and between populations.

Two main opposing hypotheses can be formulated regarding the effect of intraspecific density on ornament size variation in Odonata. First, previous research suggests that intraspecific competition can lead to disruptive selection of sexual traits (BOLNICK, 2004), favoring individuals with extreme phenotypes in a bimodal distribution. This pattern may reflect the coexistence of alternative reproductive strategies, such as territorial males with larger phenotypes and non-territorial males with smaller ones (SERRANO-MENESES; CÓRDOBA-AGUILAR; MÉNDEZ; LAYEN et al., 2007). In *Hetaerina*, where males compete for reproductive territories, intense competition under high male density could promote the maintenance of distinct strategies linked to differences in wing spot size. According to the Disruptive Selection Hypothesis, high-density populations would exhibit greater intrapopulation variation in wing spot size without affecting the population mean, suggesting the coexistence of both reproductive strategies. For example, the highly pigmented (territorial) or hyaline-winged (non-territorial) males observed in *Mnais* damselflies (WATANABE; TAGUCHI, 1990) (Fig. 1A).

Second, however, in Odonata species with resource-defense mating systems, selection on fitness-related traits can also be directional, favoring individuals with more pronounced sexual ornaments (FINCKE; WAAGE; KOENIG, 1997). This pattern is especially expected in high-density populations, where exaggerated traits—such as larger wing spots—may quickly determine territorial dominance, thereby reducing the energetic costs of prolonged male-male contests (ANDERSSON, 1994). In *Hetaerina*, male competition over territories has been shown to drive directional selection for increased wing pigmentation (GRETHER, 1996), with evidence suggesting that this effect intensifies as male density increases (CÓRDOBA-AGUILAR; GONZÁLEZ-TOKMAN, 2014b). Under this scenario, the Directional Selection Hypothesis predicts that males with larger wing spots will be more successful in high-density environments, leading to reduced intrapopulation variation and a positive correlation between male abundance and mean wing spot size (Fig. 1B).

High-density populations may also impact community structure. Since the intensity of intraspecific competition is density-dependent, populations of *Hetaerina* with high density of males presumably will experience a higher intraspecific territorial competition. (CÓRDOBA-AGUILAR; GONZÁLEZ-TOKMAN, 2014a). Theory predicts that intraspecific competition must be higher than interspecific one for two or more species to coexist (CHESSON, 2000). Reproductive mechanisms may promote such differences, (YAMAMICHI; KYOGOKU; IRITANI; KOBAYASHI *et al.*, 2020) as territorial Odonata species interact more frequently with conspecifics than with heterospecifics, suggesting that territoriality enhances energy expenses on intraspecific interactions (PESTANA; ZANATTA; SACILOTI; SAITO, 2024).

Concerning interspecific interactions, when several similar species locally co-occur, interspecific interference can affect the expression of wing pigmentation, and produce reproductive character displacement (HASSALL, 2014; TYNKKYNEN; RANTALA; SUHONEN, 2004) mediated by agonistic encounters (IYENGAR; CASTLE; MULLEN, 2014). In Odonata, agonistic encounters can happen due to mistaken species recognition and may lead to negative selection on sexual traits, reducing wing spot size in the population (TYNKKYNEN; KOTIAHO; LUOJUMÄKI; SUHONEN, 2005; TYNKKYNEN; RANTALA; SUHONEN, 2004). For *Hetaerina*, variation in wing spot size has also been observed in the presence of congeners due to differences in the intensity of interspecific aggression, which can result in either an increase or decrease in wing spot size depending on the observed species (ANDERSON; GRETHER, 2010a; b; DRURY; GRETHER, 2014).

Furthermore, the high frequency of agonistic encounters due to harder recognition of similar species can intensify interspecific competition, negatively impacting the coexistence of closely related species (AMARASEKARE, 2002; DRURY; GRETHER, 2014; GRETHER; LOSIN; ANDERSON; OKAMOTO, 2009).

Environmental gradients also play a crucial role in Odonata community assemblages. Thus, environmental differences can influence the species composition of a community according to their ecophysiological requirements (*e.g.* thermoregulation, body size), driving the presence of phylogenetic clusters of similar species along environmental gradients (DE MARCO JÚNIOR; BATISTA; CABETTE, 2015; SAITO; VALENTE-NETO; RODRIGUES; DE OLIVEIRA ROQUE *et al.*, 2016). Additionally, variation in resource availability across sites may mitigate the effects of competition on intrapopulation variation in fitness-related traits, as demonstrated for *Hetaerina americana* regarding body size variation (CONTRERAS-GARDUNO; CANALES-LAZCANO; JIMENEZ-CORTES; JUAREZ-VALDEZ *et al.*, 2009). This suggests that environmental effects may outweigh intra- and interspecific ones, driving variation in fitness-related phenotypes across environmental gradients. However, studies that investigate how these dynamics unfold are essential for a deeper understanding of the mechanisms involved.

In this regard, our study aimed to investigate the biotic and abiotic effects on wing spot size variation (a fitness associated trait) within and between populations of a damselfly, *Hetaerina rosea* Selys, 1853. We investigated the potential effects of intra- and interspecific interaction via species density variation (intraspecific abundance of *H. rosea* and the abundance of all species), as well as abiotic factors (vegetation cover and geographical distribution) on wing spot variation within and between populations. Additionally, we examined whether there was a co-occurrence pattern between *H. rosea* and other species and whether this pattern could be explained by variation in the mean proportion of wing spot size among communities.

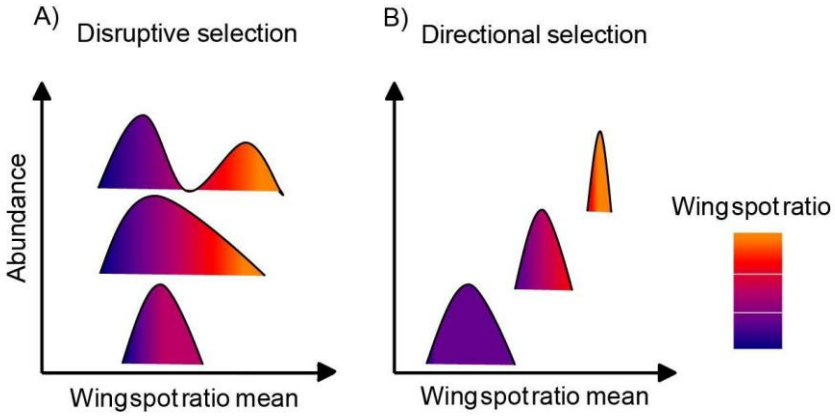

Figure 1. Predictions of the effects of abundance on wing spot ratio variation. (A) Disruptive selection: populations exhibit a bimodal pattern, where both large and small wing spots are favored in high-density populations, leading to increased intrapopulation variation in wing spot size. (B) Directional selection: populations exhibit a unimodal pattern, with a decrease in intrapopulation variation of wing spot size as population density increases. The color gradient represents the wing spot ratio, ranging from lower (purple) to higher (orange) values.

Methods

Fieldwork was carried out in 46 sites in the Central-West region of Brazil between April 2011 and October 2013 (Fig. 2). The climate in this region is humid tropical, with well-defined rainy and dry seasons. The vegetation exhibits transitional characteristics between savanna (Cerrado) and forest formations of the Atlantic Forest.

Adults dragonflies and damselflies were collected using an entomological net along a 100-m transect parallel to the stream banks. Samplings were carried out for 1 hour between 10 am and 3 pm, the period in which individuals are most active. Posteriorly, individuals were identified using taxonomic keys (GARRISON; ELLENRIEDER; LOUTON, 2010; GARRISON; VON ELLENRIEDER; LOUTON, 2006).

To estimate vegetation cover, a circular buffer of 250 m was used from the middle of each sampling point. To describe spatial variables, we applied Principal Coordinates of Neighbor Matrices (PCNM) to the sampling location data using the Vegan Community Ecology Package (version 2.6-8). First, we calculated an Euclidean distance matrix based on latitude and longitude values. We then applied a Principal Coordinates Analysis (PCoA) to this distance matrix and extracted eigenvectors with positive eigenvalues. To refine the analysis, we performed an additional selection step to identify the eigenvectors that

significantly explained spatial variation, and only these were used as spatial predictors in our structural equations model (BORCARD; LEGENDRE, 2002).

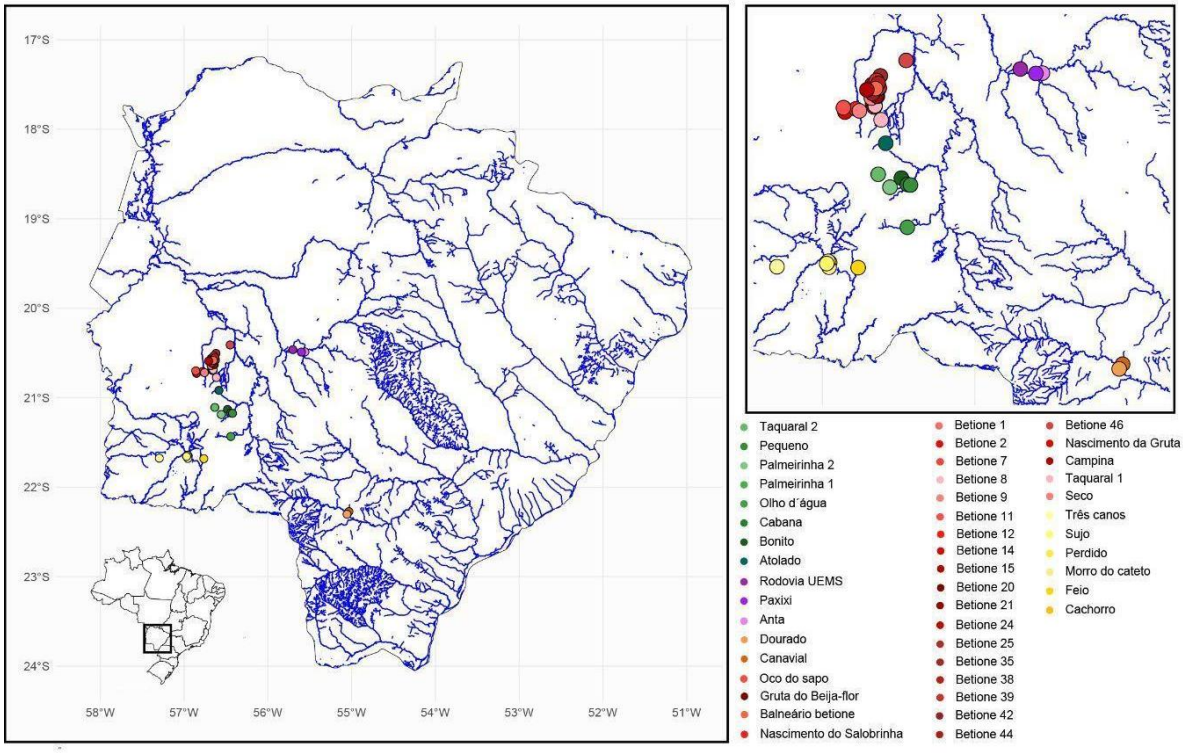

Figure 2. Map of the sampling sites. The sites are divided into groups according to their geographic proximity. Points with the same color scale indicate nearby sampling sites.

Wing pigmentation

Wing pigmentation was measured by removing the hindwings and forewings of all individuals of *Hetaerina rosea* and taking digital pictures with a Canon EOS 70D digital camera with a macro lens. The ratio of wing spot was analyzed using Adobe Photoshop CS6 Extended® by dividing the pigmented area by the total area of the wing (Fig. S1). The average value for all four wings was used for each individual to assess the individual wing spot ratio (GUILLERMO-FERREIRA; GORB; APPEL; KOVALEV *et al.*, 2015). Within each population, we determined the mean and standard deviation of the wing spot ratio.

Data analyses

Wing spot ratio variation

To investigate whether there is variation in the wing spot ratio among the studied streams, we performed an analysis of variance (ANOVA). In this analysis, the wing spot ratio

of individuals from each population was used as the dependent variable and the streams were used as the grouping factor. Subsequently, the percentage of total variance attributed to the variation in the mean wing spot proportion among different populations (variance among populations) and the variation in wing spot proportion among individuals within the same population (variance within populations) were calculated. The variance among populations was represented by the mean square between groups, while the variance within populations was represented by the mean square within groups.

Biotic and abiotic effects

The effects of vegetation cover, spatial, and biological variables (intra- and interspecific abundances) on wing spot ratio were assessed using structural equation modeling (SEM). We built a model with mean and standard deviation as endogenous variables, while vegetation cover, geographic distances, intraspecific abundance, and total abundance were included as exogenous variables. For the spatial variables, PCNMs with significant results were used. We calculated the standardized direct coefficients for each pathway in the model. To determine the indirect effects of exogenous variables, we multiplied the standardized coefficients along each indirect path. A bootstrapping significance test was conducted to assess the significance of indirect effects. Model fit was evaluated using the following parameters: 1. Root Mean Square Error of Approximation (RMSEA), 2. Comparative Fit Index (CFI), 3. Tucker-Lewis Index (TLI) and 4. Standardized Root Mean Square Residual (SRMR).

Species co-occurrence

To assess species co-occurrence patterns, we performed a checkerboard score analysis (C-score; STONE; ROBERTS, 1990). Using a presence/absence matrix of species at each studied site, this analysis calculates the segregation index for each species pair. Based on 1000 randomizations, both the observed and expected indices were calculated. If the observed index was higher than the expected index, it indicated that the species co-occurred less often than expected by chance. Conversely, if the observed index was lower than the simulated index, it indicated that the species co-occurred more often than expected by chance. Using the *cooccur* R package we generated a heatmap of species co-occurrence.

Results

A total of 58 species were identified, distributed across seven families, with 29 species belonging to the suborder Zygoptera and 29 to the suborder Anisoptera (Fig. 3). Among the Zygoptera, *Hetaerina rosea* was the most abundant species (273 individuals), followed by *Argia chapada* (116 individuals) and *Oxyagrion sulmatogrossense* (102 individuals). Among the Anisoptera, *Dythemis multipunctata* was the most abundant species (47 individuals), followed by *Erythrodiplax fusca* (33 individuals) and *Elasmothemis cannacrioides* (13 individuals). The most widespread Zygoptera species were *Hetaerina rosea* (present at all sites; Fig. 5), *Argia reclusa* (33 sites), and *Oxyagrion sulmatogrossense* (29 sites). The most widely distributed Anisoptera were *Dythemis multipunctata* (20 sites), *Erythrodiplax fusca* (12 sites), *Elasmothemis cannacrioides* (6 sites), and *Progomphus* sp2 (6 sites) (Fig. 4).

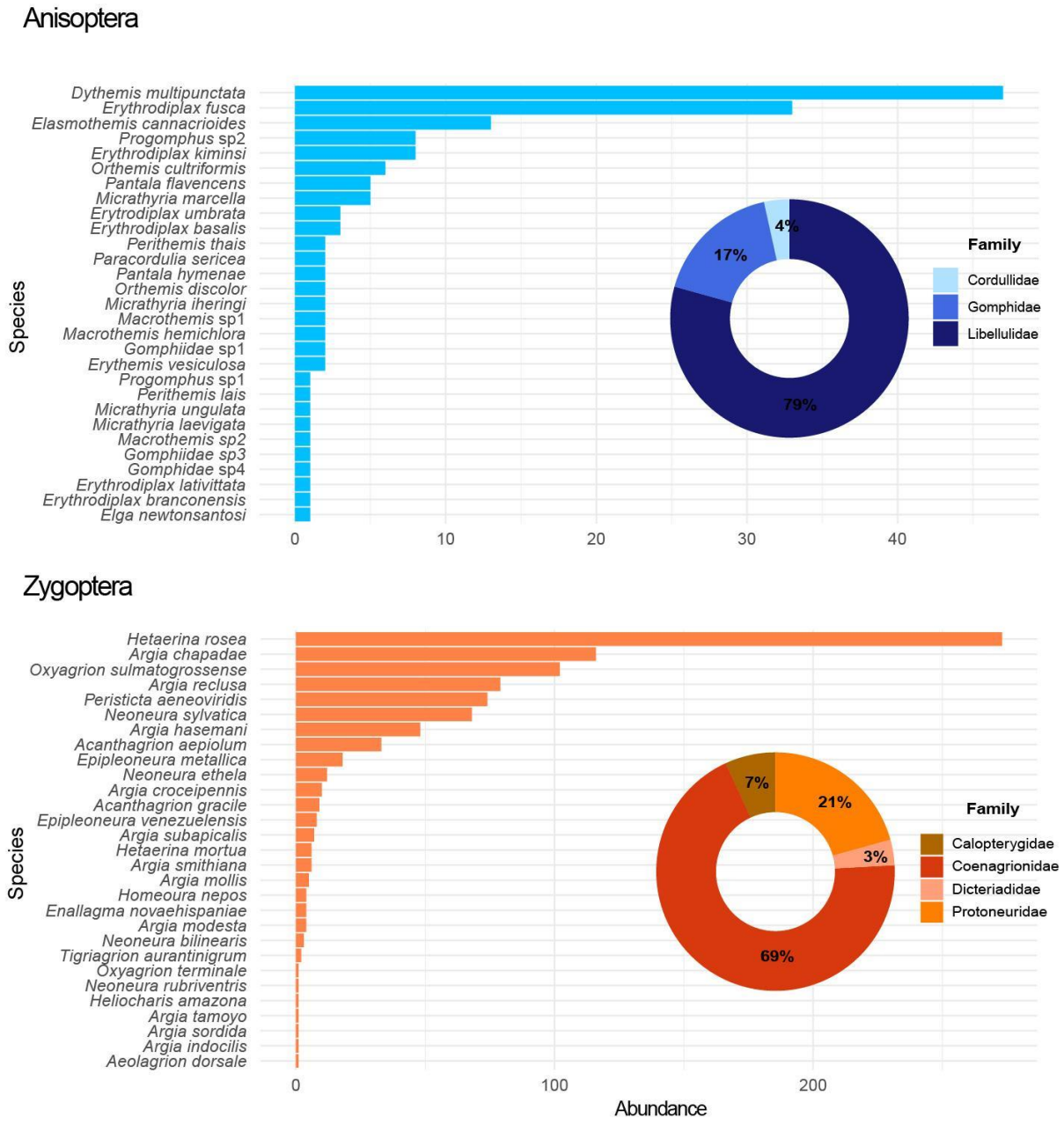

Figure 3. Abundance of species identified at the 46 sampling sites and the percentage of species belonging to each family of Anisoptera and Zygoptera (doughnut chart).

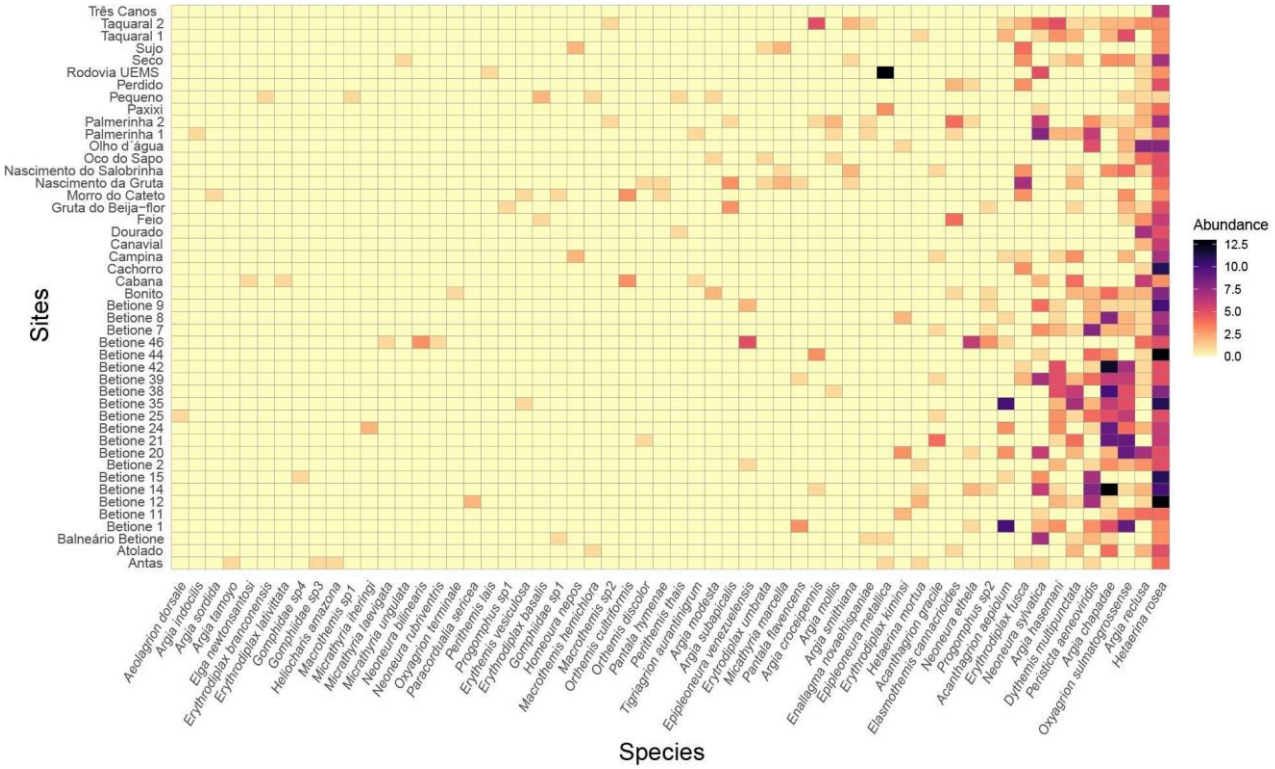

Figure 4. Heatmap of occurrence and abundance of each species in each site.

Wing spot ratio variation

The ANOVA indicated a significant variation in wing spot ratio among the studied streams ($F = 2.21$; $df = 45$; $p = 0.00024$). This indicates that the wing spot ratio of individuals in at least one pair of *H. rosea* communities varies between the studied sites more than within the same population (Fig. 5). Moreover, the analysis showed that most of the variance in wing spot proportion (~60%) was associated with variation within populations, while the remaining ~40% was explained by differences among populations.

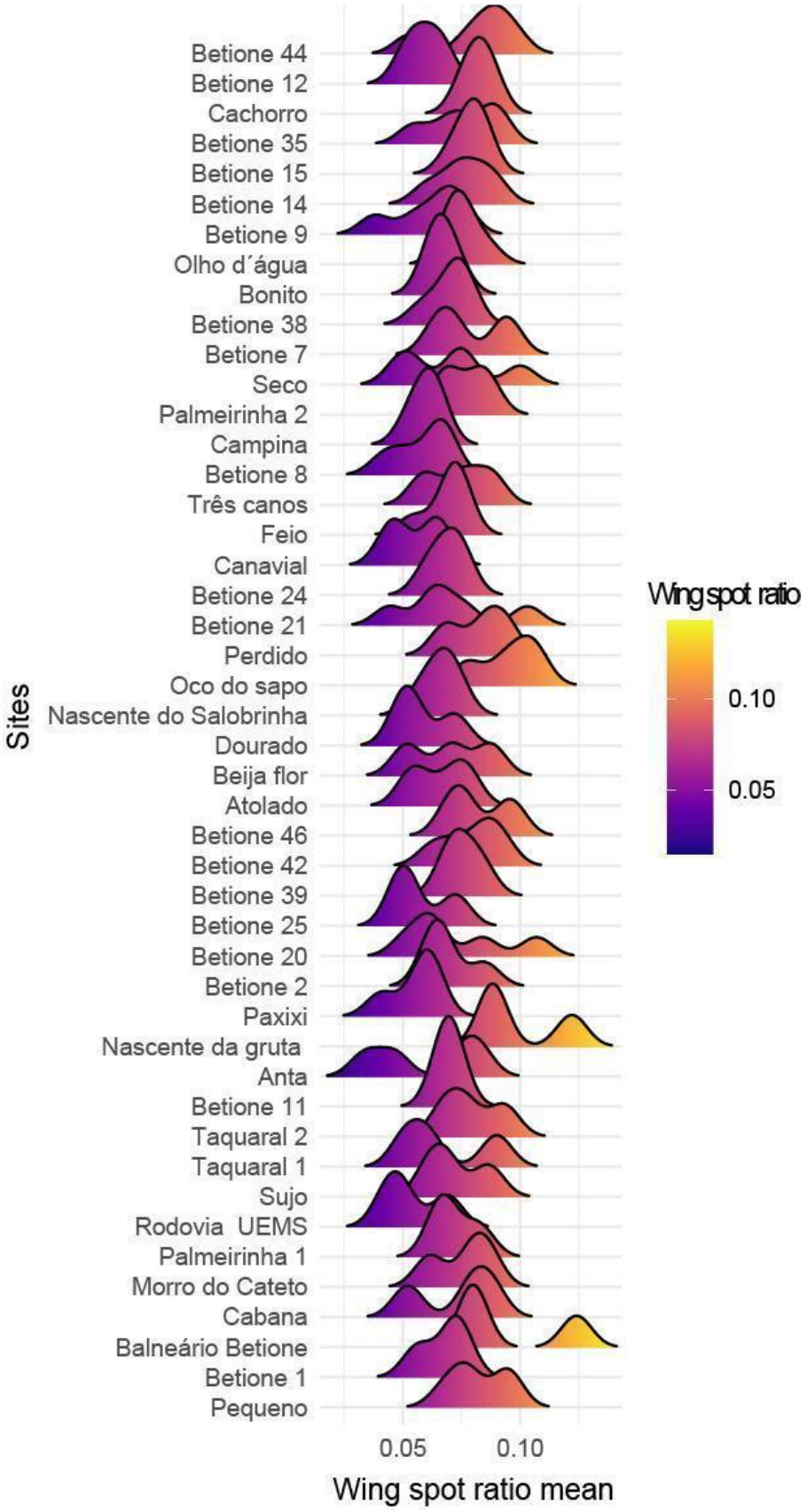

Figure 5. Wing spot ratio variation for each *H. rosea* population at each sampled site (y-axis). The sampling sites are organized in ascending order of *H. rosea* intraspecific abundance, with the "Pequeno" stream having the lowest abundance and the "Betione 44" stream having the highest abundance. The figure was generated using the

the "ggridges" package in R software. This function plots ridgelines and ridgeline plots with fill gradients along the x-axis and calculates densities from the point data mapped onto the x-axis.

Biotic and abiotic effects

The SEM showed a good fit as indicated by the CFI (1.00), TLI (1.00), RMSEA (0.00), and SRMR (0.00) indices. Our model was significant for the following variables: vegetation cover, spatial scale and intraspecific abundance (Table 1, Fig. 6). In this way, we found direct positive effects of vegetation cover and direct negative effects of intraspecific abundance on wing spot ratio standard deviation, indicating that higher wing size ratio variation was found in sites with high vegetation cover and low intraspecific densities. Spatial variables associated with large scales (PCNM1) had direct positive effects on the wing spot ratio mean. No significant indirect effects of observed variables were found. The covariance between wing spot ratio local variation and mean variation was not significant.

Table 1. Results of the structural equation model (SEM) analysis showing the effects of intraspecific abundance, total abundance, vegetation cover, and spatial predictors (PCNM variables) on the mean and local variation of wing spot ratio in *Hetaerina rosea*. Standard errors (Std. Err.), *z*-values, and *p*-values are provided for each predictor. Significant relationships ($p < 0.05$) are highlighted in bold.

	Mean (wing spot ratio)			**Standard deviation (wing spot ratio)**		
	Std. Err.	z-value	p-value	Std. Err.	z-value	p-value
Intraspecific abundance	0.001	-1.296	0.195	0.000	-2.525	**0.012**
Total abundance	0.000	0.935	0.350	0.000	-0.031	0.975
Vegetation cover	0.000	1.416	0.157	0.000	2.412	**0.016**
PCNM1	0.009	3.619	**0.000**	0.005	-1.102	0.270
PCNM 2	0.009	-0.760	0.447	0.005	-0.425	0.671
PCNM 5	0.010	-0.676	0.499	0.005	-1.800	0.072
PCNM 6	0.009	0.907	0.365	0.005	0.751	0.453

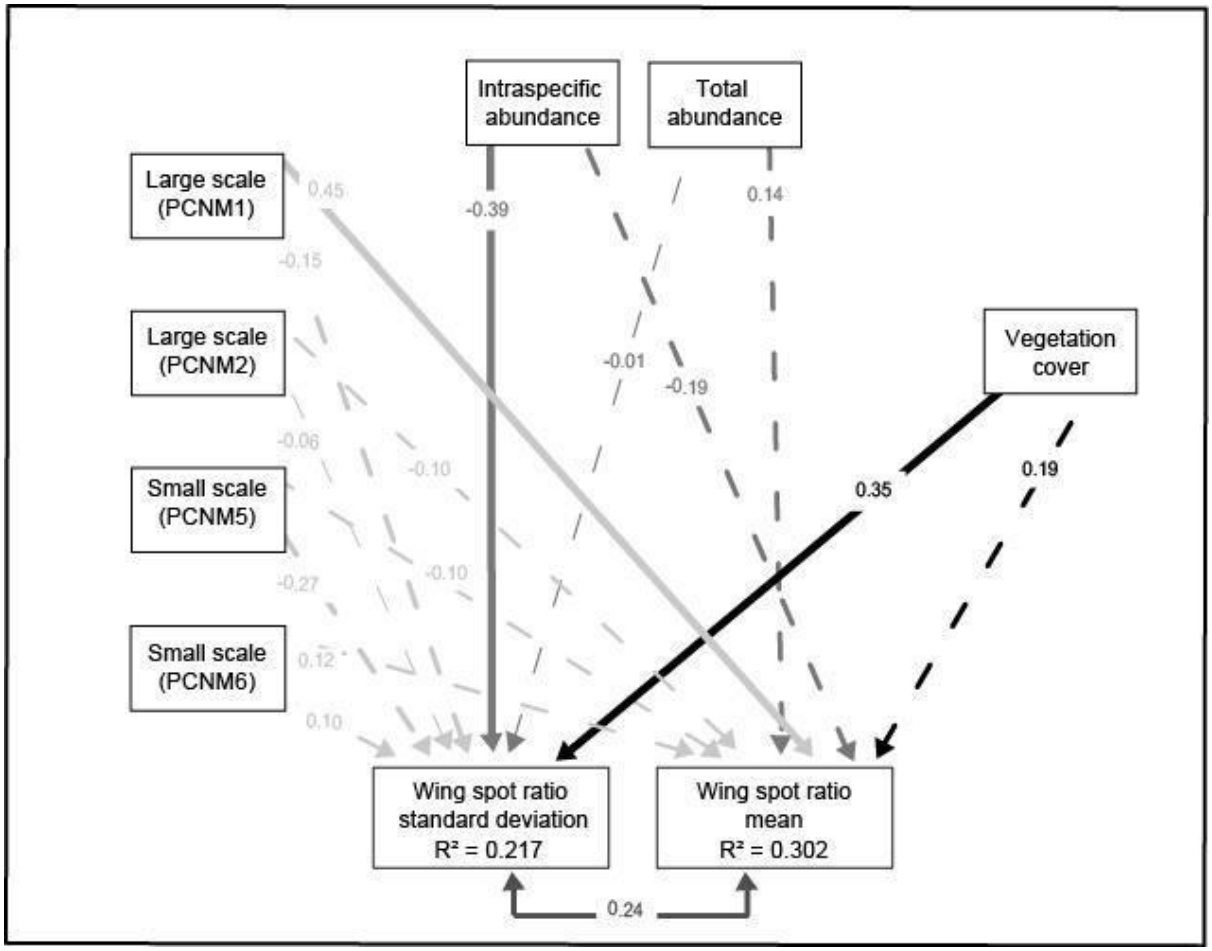

Figure 6. Diagram representing the results of the structural equation model (SEM) assessing the effects of intraspecific abundance, total abundance, vegetation cover, and spatial predictors (PCNM variables) on the mean and local variation of wing spot ratio in Hetaerina rosea.. Arrows indicate relationships between variables, with thickness proportional to the strength of the standardized effect. Solid arrows represent significant relationships ($p < 0.05$), while dashed arrows indicate non-significant relationships. The values along the arrows correspond to the standardized path coefficients.

Species co-occurrence

In the C-score analysis no co-occurrence pattern was found for *Hetaerina rósea.* The observed index was 11.222, while the mean of the simulated index was 15.648, with the limits of variation between 15.182 and 16.477. Thus, the observed species co-occurrence was higher than expected by chance. The species co-occurrence matrix (Fig. 7) showed that only 13 Odonata species co-occur positively or negatively with at least one other species, with 9 belonging to the family Coenagrionidae (Zygoptera), 2 to the family Protoneuridae (Zygoptera), and 2 to the family Libellulidae (Anisoptera). A total of 18 positive co-occurrences and 1 negative co-occurrence were observed.

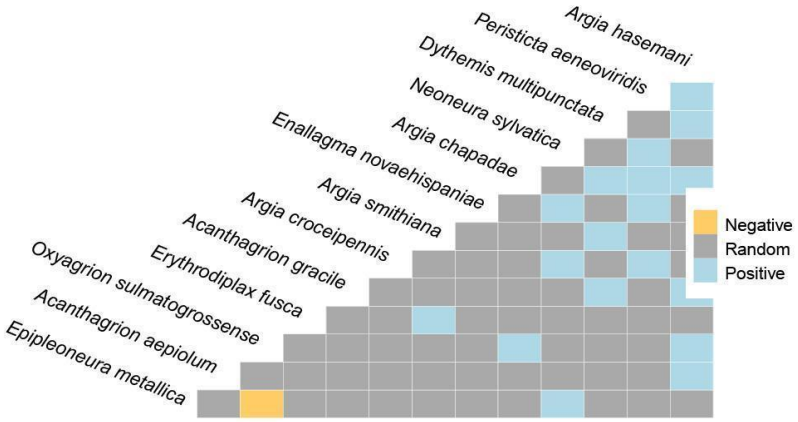

Figure 7. Species co-occurrence matrix. Yellow squares indicate a negative co-occurrence between a pair of species, indicating that these species co-occur less frequently than expected by chance. Blue squares indicate a positive co-occurrence patterns, greater than expected by chance, between species pairs. Finally, grey squares indicate random co-occurrence patterns. The figure was generated using the *cooccur* R package.

Discussion

Sexual selection can drive the evolution of elaborate phenotypic traits that enhance individual reproductive success (DARWIN, 1871). However, various biotic and abiotic factors can influence the variation of fitness-related traits within and among populations. Such variation may arise due to strong competitive or selective pressures that either constrain or promote phenotypic variability. Our results indicate that the magnitude of variation in the wing spot ratio of *Hetaerina rosea* is similar within and between-populations, mostly associated with changes in vegetation cover and intraspecific abundance. Specifically, higher phenotypic variation was associated with smaller populations and locations with higher vegetation cover, indicating that population and environmental factors drive individual fitness variation in *Hetaerina rosea*. In contrast to that, we found no evidence that the wing spot size ratio is controlled by interspecific interactions.

Within populations, intraspecific interactions can play a crucial role in shaping the variation of sexually selected traits. We hypothesized two ways to explain wing spot variation. While the Directional Selection Hypothesis argues that high-density populations favor males with more extreme fitness-related phenotypes, as these individuals may have a competitive advantage improving reproductive success, the disruptive selection hypothesis predicts that individuals with extreme phenotypes are favored in a bimodal distribution pattern. Our findings reveal that intraspecific abundance negatively affects intrapopulation variation in *H. rosea*, suggesting that higher population densities are associated with reduced

variability in wing spot ratio. Surprisingly, these results do not support any of the proposed hypotheses. A possible explanation may involve stabilizing selection, in which an intermediate wing spot pattern is favored. Intermediate wing spot size might reduce physiological and ecological costs without significantly compromising individual reproductive success (ANDERSSON, 1994; COTTON; FOWLER; POMIANKOWSKI, 2004) Supporting this interpretation, complementary results show that higher abundance is associated with smaller wing spot sizes. Furthermore, physiological conditions can also contribute to within-population variation in sexually selected traits. For example, in *Calopteryx splendens*, wing spot size is positively correlated with immunocompetence, and males with greater asymmetry exhibit smaller wing spots, indicating a potential link between ornamentation and male quality (RANTALA; KOSKIMÌKI; TASKINEN; TYNKKYNEN *et al.*, 2000).

Concerning environmental factors, we found that variation in vegetation cover positively influenced within-population variation in wing pigmentation, suggesting that environments with higher vegetation cover promote greater variation in wing spot size within populations. Vegetation is an important factor driving Odonata communities structure, as it provides food resources and territory for male defense and female oviposition (GUILLERMO-FERREIRA; DEL-CLARO, 2011; PERRON; RICHMOND; PICK, 2021). Since environments with greater vegetation cover may be considered heterogeneous habitats, this may support the coexistence of alternative reproductive strategies, such as territorial and non-territorial individuals, promoting higher wing spot size variation (LARISON, 2007). Supporting this idea, our findings indicate that spatial variables significantly explained variation in wing spot ratio among streams, highlighting a geographic signature in this fitness-related trait of *H. rosea*. Notably, 41.66% of the total variance in wing spot ratio occurred among populations, suggesting that local environmental conditions may be contributing to this pattern. Importantly, the spatial variable included in our models may reflect unmeasured environmental variation or, alternatively, historical processes related to dispersal, whereby individuals from high-fitness populations (e.g., those with larger wing spots) colonize nearby sites, leaving a spatial imprint on phenotypic traits (STANDRING; SÁNCHEZ-HERRERA; GUILLERMO-FERREIRA; WARE et al., 2022).

Finally, species co-occurrence patterns can provide insights into fundamental mechanisms underlying community structuring and species coexistence. While our results

revealed significant non-random co-occurrence patterns for some species, *H. rosea* did not exhibit any significant co-occurrence patterns. This finding suggests that its widespread presence is not primarily driven by interspecific interactions but rather by its ecological flexibility and ability to thrive under diverse environmental conditions (CÓRDOBA-AGUILAR; CORDERO-RIVERA, 2005). Moreover, the absence of interspecific effects may result from the species pool present in the community. Significant effects were presumably in the presence of congenerics (HASSALL, 2014; TYNKKYNEN; RANTALA; SUHONEN, 2004). Although individuals of *Hetaerina mortua* Hagen in Selys, 1853 were found in some of the studied communities, the low density of this species may have prevented any detectable effects from emerging. In conclusion, our results offer valuable insights into the factors influencing wing spot variation in *H. rosea*, highlighting the predominant role of intraspecific interactions and environmental variables to shape fitness-related phenotype variation between and within populations.

Supplementary material

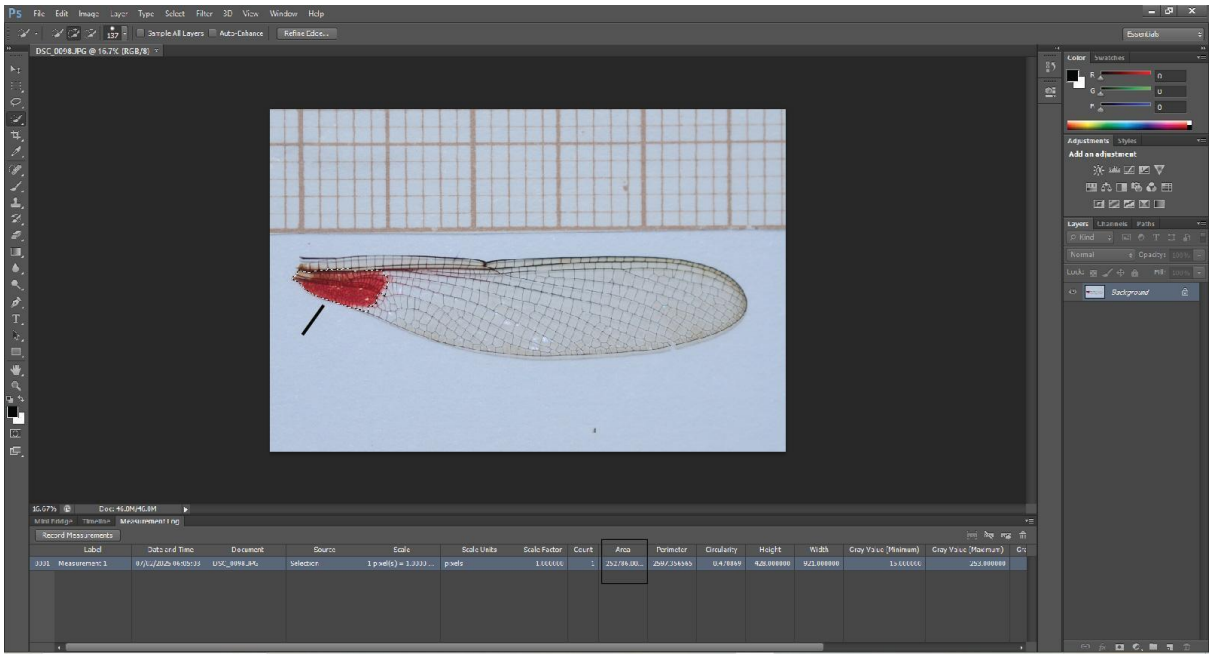

Figure S1. Photo of the *H. rosea* wing used to measure the wing spot area and wing area in Adobe Photoshop CS6 Extended®.

Capítulo III

Intraspecific competition along different life stages can stabilize coexistence among dragonflies and damselflies

Abstract

In this study we aimed to understand how intra and interspecific interference may vary according to the life stage in tropical Odonata species. We hypothesized that competition in the larval stages is mostly responsive to total densities due to high diet overlap among different groups, while in adults, intraspecific interference may be more intense due to sexual selection mechanisms operating as deterministic stabilizing processes. Therefore, the study integrated two approaches, focusing on: 1. Laboratory experiments, where larvae of *Acanthagrion* (Zygoptera, Coenagrionidae) and *Erythrodiplax* (Anisoptera, Libellulidae) were allocated to four different treatments, with variation in total abundance and dominance of species; 2. Field observations, where we assessed adult co-occurrences and species interactions. Our results suggested a stronger intraspecific interference in both life stages. We found a spatial segregation in the larval stage decreasing interspecific interference. Whereas adults were spatially segregated at a fine scale, increasing the frequency of intraspecific interactions, especially in species with prominent territoriality. This study provided novel results on how intraspecific competition acts during both the larval and adult stages of the Odonata life cycle, and how coexistence mechanisms could be consistent along ontogenetic development, broadening our understanding of processes sustaining biodiversity in tropical ecosystems.

Keywords: neotropical species, niche partitioning, ontogenetic development, reproductive interactions, species interaction

Introduction

Community ecology seeks to understand how species are able to coexist sharing limited resources, yielding our current and past patterns of biodiversity. Because biodiversity is the main actor of ecosystem processes that translate into services for human society (*e.g.*, nutrient cycling, clean water, and fisheries), understanding how species coexist is pivotal to forecasting and avoiding undesirable changes that may lead to negative environmental and societal consequences (CARDINALE; DUFFY; GONZALEZ; HOOPER *et al.*, 2012; HOOPER; ADAIR; CARDINALE; BYRNES *et al.*, 2012). Species can interact in both

positive and negative ways. In this context, competition emerges as an important mechanism in shaping community composition, potentially leading to the competitive exclusion of the worst competitor. While competition among species has been studied for more than a century (LOTKA, 1914), theoretical and empirical advances are shedding new light on this important process regulating biodiversity (CHESSON, 2000; HÜLSMANN; CHISHOLM; COMITA; VISSER *et al*., 2024; KRAFT; GODOY; LEVINE, 2015; SAITO; LAROCHE; SIQUEIRA; PAVOINE, 2018).

Previous studies have demonstrated the effects of competition on the maintenance of biodiversity (*e.g.* KRAFT; GODOY; LEVINE, 2015) and the importance of a variety of mechanisms that reduce the impacts of competition and avoid exclusions. For instance, stabilizing mechanisms (CHESSON, 2000) are those that increase intraspecific competition, making species regulate their per capita growth rate more intensely than the growth rate of their competitors. Traditionally, such stabilizing mechanisms are linked to resource competition and the ways which species partition resources. For example, some pairs of bark beetles have a clear niche segregation in the height they occupy within the trees. In this example, the smaller, weaker competitor species occupy the top of the trees, avoiding direct competition for food with larger, better competitor species, reducing interspecific interference, and favoring their local coexistence in the same tree (SCHLYTER; ANDERBRANT, 1993).

Although trophic resources (*e.g*., prey and nutrients) have traditionally been the most studied, non-trophic resources can also mediate stabilizing processes. For instance, reproductive interactions may impact intraspecific competition, through either male-male or male-female interactions (*e.g.* GÓMEZ-LLANO; GERMAIN; KYOGOKU; MCPEEK et al., 2021; YAMAMICHI; KYOGOKU; IRITANI; KOBAYASHI *et al*., 2020). As an example, territoriality can affect community dynamics directly or indirectly, as studies have shown that this behavior increases intraspecific competition and can negatively affect the survival rate of males and mating success (PINTO; DE MARCO; MOURA, 2022; SVENSSON; GÓMEZ-LLANO; TORRES; BENSCH, 2018). Additionally, behaviors involved in sexual conflict, such as male harassment may have negative effects on female's survival rate and fecundity (GOMEZ-LLANO; BENSCH; SVENSSON, 2018; TAKAHASHI; WATANABE, 2010). Both situations may control population growth as densities rise, enhancing the chances of

intraspecific self-regulation and species coexistence (KOBAYASHI, 2019; M'GONIGLE; MAZZUCCO; OTTO; DIECKMANN, 2012).

Despite the potential impacts of reproductive behaviors on species coexistence, most of the theoretical and empirical studies are focused on organisms with relatively simple life cycles, such as annual plants (KRAFT; GODOY; LEVINE, 2015) and phytoplankton (NARWANI; ALEXANDROU; OAKLEY; CARROLL *et al.,* 2013), while studies in groups with complex life cycles (*i.e.* holometabolous and hemimetabolous) are rare (GÓMEZ-LLANO; GERMAIN; KYOGOKU; MCPEEK *et al*., 2021). Dragonflies and damselflies are optimal organisms to be studied in this regard as they are hemimetabolous organisms with aquatic larvae and winged terrestrial adults. Larvae of several groups can behave as generalist predators with efficient foraging strategies (CORBET, 1999). In this stage, competition for food should be intense, driving extreme competitive outcomes such as intraguild predation and cannibalism, potentially resulting in similar intra- and interspecific effects on population densities. In contrast, adults exhibit markedly different ecological and behavioral dynamics: they are aerial and dispersive, and often engage in complex intraspecific sexual interactions, such as territoriality, that could increase intraspecific interactions, stabilizing species coexistence (deterministic coexistence, YAMAMICHI; KYOGOKU; IRITANI; KOBAYASHI *et al*., 2020; YAMAMICHI; TSUJI; SAKAI; SVENSSON, 2023). Therefore, in organisms with complex life cycles, mechanisms of coexistence could vary along with ontogenetic development, potentially impacting broad patterns of coexistence and community patterns.

Furthermore, empirical studies on species coexistence are mostly done in temperate regions, while studies in tropical ecosystems are lacking. In these ecosystems, tropical Odonata species may present differences in stages of development and an increased number of generations per year (*i.e.* voltinism), as demonstrated by Libellulidae and Coenagrionidae families, due to environmental factors, such as temperature and photoperiod in tropical ecosystems (CORBET, 1999; CORBET; SUHLING; SOENDGERATH, 2006). This should increase the chances that overlapping generations of different species co-occur at the same time, adding a layer of complexity to these species interactions. Moreover, the higher metabolic demand of living in a higher temperature in the tropics could decrease the species' feeding selectivity, reinforcing larval competition and the overlap in the use of food resources (SAITO; PERKINS; KRATINA, 2021). In this sense, studies on organisms with complex life

cycles in tropical ecosystems can help us elucidate competition patterns in communities with highly dynamic interactions.

We aimed to understand how intra- and interspecific interference varies according to the life stages in tropical Odonata to identify the stabilizing mechanisms that may promote coexistence. We hypothesized that competition in the larval stage is determined by total densities, as intra- and interspecific effects on mortality would be similar, given the high metabolic demands imposed by high temperatures. While in adults, intraspecific interference should be more intense due to sexual selection mechanisms (*i.e.*, territoriality) operating as deterministic stabilizing processes. The study integrated two approaches, focusing on: 1) laboratory experiments with larvae of two taxa, Acanthagrion (Zygoptera, Coenagrionidae) and Erythrodiplax (Anisoptera, Libellulidae), to assess total mortality rate, predation ratio, and dead larvae ratio under different abundance conditions (high and medium) and dominance scenarios; and 2) field observations with adults, to evaluate Odonata adult abundance and species-specific antagonistic and sexual interactions in a community composed of five different species—two Zygoptera and three Anisoptera. In the experimental approach, significant effects of total abundances on demographic properties would represent taxa-independent density-dependent effects, indicating neutrality; on the other hand, a dominance effect (whether by *Acanthagrion* or *Erythrodiplax*) would suggest that intra- and interspecific interactions have different impacts on mortality. For the observational approach, a higher frequency of intraspecific than interspecific interactions with increasing density would be interpreted as stronger intraspecific rather than interspecific negative density-dependence, a mechanism for potential stable coexistence.

Methods

Observational approach

We conducted field observations in a headwater stream in São Carlos (São Paulo State, Brazil, 21° 59' 15.749" S 47° 52' 32.428" W). Previously, to determine adult Odonata community composition in this site, we sampled individuals freely and identified them to genus level using taxonomic keys (GARRISON; ELLENRIEDER; LOUTON, 2010; GARRISON; VON ELLENRIEDER; LOUTON, 2006). After, to assess adult abundance and species interactions we used the fixed area scanning method as it minimizes double counting individuals, as short time intervals cover small sections (DE MARCO JÚNIOR; BATISTA;

CABETTE, 2015). As such, the local stream was divided into 16 five-meter sections and each section was observed for two minutes by two trained researchers to account for the abundance of each species. After that, we selected the five-meter sections with the highest total abundances and we observed intra and interspecific interactions for five minutes, separated in three categories: 1) interspecific (individuals of one species displacing or chasing individuals of another species); 2) Intraspecific male-male (contests between males of the same species); 3) Intraspecific male-female (mating behavior, *i.e.* tandem, post-copulatory guarding). When any species was not recorded during the abundance survey, but was later observed interacting, we adopted the following protocol: if the species was interacting with another species, we recorded its abundance as one (minimum abundance for that interaction to occur at least once); if it was interacting with another individual of the same species, we recorded its abundance as two (minimum abundance for the interaction to occur at least once). Field observations were carried out weekly, between November, 2022 and March, 2023, totaling 15 samplings.

We also measured environmental variables in each sampling date. Air temperature was measured using an electronic thermometer. Rainfall data for the previous 3 days and on the day of sampling were compiled from the INPE website (https://clima.cptec.inpe.br/monitoramentobrasil/pt).

Experimental approach

We sampled Odonata larvae using a D net in the same stream where we conducted the observational method (21° 59' 15.749" S 47° 52' 32.428" W) and additionally, in a second stream of similar dimensions (21°58'26.3"S 47°52'14.4"W), also in São Carlos, Brazil. Species of the genus *Acanthagrion* (Zygoptera, Coenagrionidae) and *Erythrodiplax* (Anisoptera, Libellulidae), were found in large quantities at these sites, therefore, we selected them for the experiment. We observed two species of *Erythrodiplax* and one of *Acanthagrion* in the adult community present in this area. However, one of the *Erythrodiplax* species was significantly more abundant than the other, which increases the likelihood that the larvae collected belonged to this dominant species. Posteriorly, we took the collected larvae to the laboratory for screening and identification of genera using taxonomic keys (HAMADA; THORP; ROGERS, 2018). Subsequently, larvae were measured from the top of the head to the end of the last abdominal segment using a millimeter scale to select individuals of similar sizes. Larval size was selected based on its abundance, and differences among experimental

replicates were due to variation in larval developmental stages at the time of collection (Table S1). No pharate larvae were used. We used body size data to estimate biomass according to the length-mass equations for Calopterygidae (Benke (BENKE; HURYN; SMOCK; WALLACE, 1999) and Libellulidae (DEKANOVÁ; VENARSKY; BUNN, 2022). To evaluate whether the larvae biomass varied between treatments at the beginning of the experiments, we performed a three-way ANOVA, with biomass as the response variable and species identity, total abundances, and dominance as independent variables.

The selected larvae were placed into sterilized polypropylene boxes containing 6 liters of dechlorinated water, properly oxygenated, with 6 polypropylene black straws (a refuge simulating a plant root), in environmental temperature and lightness conditions. During the experimental period, temperatures ranged from 15 °C to 29 °C in spring and summer, and from 15 °C to 28 °C in autumn and winter, with a natural photoperiod averaging 9 to 10 hours per day depending on the season. The setup followed an orthogonal experimental design with two levels of total abundance (high abundance with 12 individuals and medium abundance with 6 individuals in total) and two levels of relative density, alternating the dominant species (66% of one species and 33% of the other). The boxes measured 20 × 40 cm, and based on these dimensions and the water volume, larval density corresponded to approximately 1 individual per liter (or 0.75 larvae per 100 cm^2) in the medium-density treatment, and 2 individuals per liter (or 1.5 larvae per 100 cm^2) in the high-density treatment. A total of four treatments were outlined (Fig. 1): 1) high abundance and dominance of Acanthagrion, 2) medium abundance and low dominance of *Acanthagrion*, 3) high abundance and dominance of Erythrodiplax and 4) medium abundance and low dominance of *Erythrodiplax*. The individuals were fed daily with six larvae of other aquatic insects highly abundant in the sampling sites (mostly Chironomidae and Simuliidae) per box. This meant that each Odonata on the medium-density treatments had a potential prey per day. Data on mortality, remaining larvae and spatial distribution (larvae in straws) were collected daily, for 10 consecutive days, between December, 2022 and January, 2024, totaling 6 replicates for each treatment.

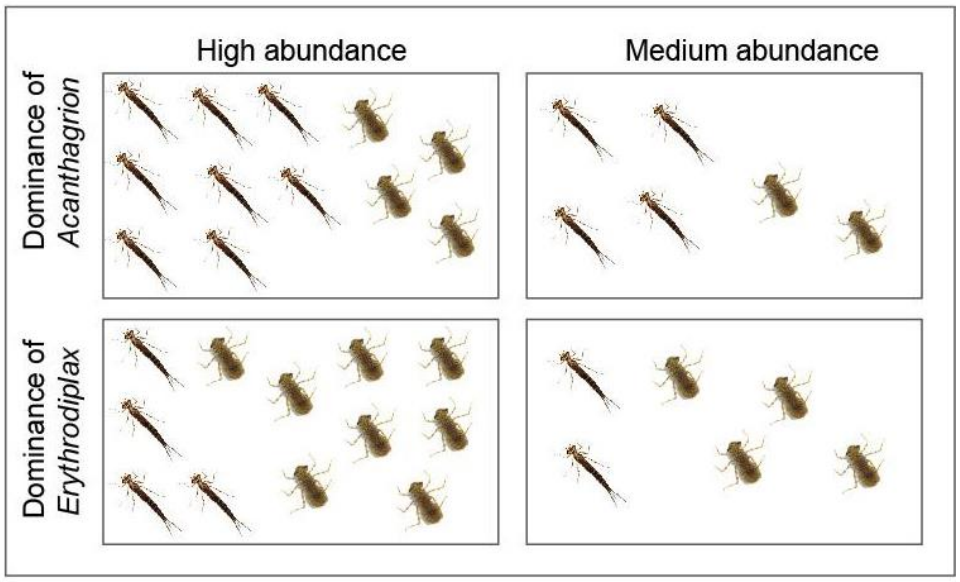

Figure 1. Experimental design for a pair of dragonfly and damselfly species. The scheme configures a 2x2 crossed orthogonal design, with two levels of total densities and alternation in the relative density of species. The number of replicates was six for each pair of species.

Data analyzes

Observational approach

Species in a community can share their niches temporally and spatially. In the observational approach, we considered the diel activity as a temporal niche and the sections occupied by species in each day as a spatio-temporal niche. To determine the temporal and spatio-temporal niche overlap of Odonata adults we applied the Pianka overlap index, using a matrix of abundance per section and sampling dates. This index is calculated by the following equation:

$$O_{jk} = O_{kj} = \frac{\Sigma P_{ji} \times P_{kj}}{\sqrt{\Sigma(P_{ji}^2) \times (P_{ik}^2)}} \quad (1)$$

where, O_{jk} is Pianka's measure of niche overlap between species *j* and *k*; P_{ji} is the proportion of resource *i* in the total resources used by species *j*; P_{ik} is the proportion of resource *i* in the total items used by species *k*. Values range from 0 to 1, with 0 being completely separated niches and 1 being complete niche overlap (PIANKA, 1973). For the temporal analysis, the summed abundance in all sections were used for each date (15 temporal replicates) and for the

spatio-temporal scale, the abundance in each section and on each date (75 spatial-temporal replicates) were used. We compared the Pianka's index to a randomized null model, where 5,000 randomizations were performed using the Ra3 algorithm (shuffle the resource utilization of each species holding species niche breadth and zero states, WINEMILLER; PIANKA, 1990). This is the null model algorithm recommended for discrete resources and analyses of niche overlap (GOTELLI; HART; ELLISON; HART, 2015). We then estimated the effect size of the index as the difference between the empirical means and the simulated means divided by the null model standard deviations. Positive values were interpreted as a tendency towards niche overlap, and negative values as a tendency towards niche differentiation.

We performed analyses of covariance (Ancova) to compare the effects of intra- and interspecific densities on species interactions. Specifically, we compared the number of total interactions observed (n=75, 15 days x 5 stretches per day) (response variable) among intra and interspecific interaction (explanatory variable), using the abundance of the respective intraspecific and interspecific individuals per observation as a covariate. We run individual Ancovas for each taxon separately.

To assess whether species distribution could be influenced by environmental variables related to water and air parameters, we performed a Redundancy Analysis (RDA). The RDA is a multivariate extension of a multiple regression to estimate the linear relationships between an explanatory matrix and a response matrix based on minimum squares and residual calculations. We performed this analysis twice with different explanatory matrices, but with the same species abundance matrix: 1) RDA with the water parameters matrix containing the variables water temperature, dissolved O2, % dissolved O2 and pH as matrix explanatory. 2) RDA with the air parameters matrix containing the variables air temperature, average rainfall for the 3 days prior to collection and the sum of rainfall up to 12pm on the day of collection.

Experimental approach

To compare the differences of larvae competition and spatial distribution in each treatment, the total mortality ratio per species and spatial distribution ratio per species were used. The total mortality ratio of each species and the spatial distribution ratio were calculated using the following formula:

$$Total\ Mortality\ ratio = \frac{n\ larvae\ initial\ -\ n\ remaining\ larvae}{n\ larvae\ initial} \quad (2)$$

$$Spatial\ distribution\ ratio = \frac{n\ total\ larvae\ on\ straws}{n\ larvae\ initial} \quad (3)$$

Within total mortality, two categories were recorded: the dead larvae ratio (number or larvae found whole and dead in each treatment in relation to initial number of larvae) and the preyed larvae ratio (number of missing larvae in each treatment in relation to initial number of larvae). The average of these variables for each treatment (total mortality ratio, spatial distribution ratio, dead larvae ratio and preyed larvae ratio) were analyzed using a three-way ANOVA, with the genus identity, total abundances (medium and high total abundance) and dominance (*Acanthagrion* and *Erythrodiplax*) as independent variables (SIEPIELSKI; HUNG; BEIN; MCPEEK, 2010). In every Anova that returned a significant result, we tested for pairwise differences in treatments using Tukey HSD (Honestly Significant Difference) test.

All analyzes were performed using R software (TEAM, 2013) and the packages EcoSimR and vegan.

Results

Observational Approach

We identified 5 morphotypes in adult Odonata communities, separated into four genera: *Acanthagrion* sp. (Zygoptera, Coenagrionidae), *Oxyagrion* sp. (Zygoptera, Coenagrionidae), *Erythrodiplax* sp.1 (Anisoptera, Libellulidae), *Erythrodiplax* sp.2 (Anisoptera, Libellulidae) and *Micrathyria* sp. (Anisoptera, Libellulidae). *Acanthagrion* sp. and *Erythrodiplax* sp.2 were the most abundant, with 466 and 116 records, respectively. The other species were recorded 63 times (*Oxyagrion* sp.), 19 times (*Micrathyria* sp.) and 9 times (*Erythrodiplax* sp1.). Moreover, we recorded 691 interactions spread between interspecific interactions, male-male intraspecific interactions and male-female intraspecific interactions (Fig. S1). *Acanthagrion* sp. interacted 65 times with others species and 124 times with individuals of the same species, where 86 times there were male-male interactions and 38 male-female interactions; *Erythrodiplax* sp.2 interacted 122 times with others species and 183 times with individuals of the same species, where 177 times there were male-male interactions and 6 male-female interactions; *Erythrodiplax* sp.1 interacted 99 times with

others species and 8 times with individuals of the same species, where 8 times there were male-male interactions and zero male-female interactions; *Oxyagrion* sp. interacted 66 times with others species and 6 times with individuals of the same species, where 5 times there were male-male interactions and 1 male-female interactions; *Micrathyria* sp. interacted 17 times with others species and 1 times with individuals of the same species, where 1 times there were male-male interactions and 0 male-female interactions. All interspecific interactions occurred between males.

Pianka's index for temporal niche overlap (15 replicates) resulted in a mean value for all pairwise comparisons of 0.68. In the null model, the mean of the simulated index, that is, the overlap rate expected by chance, is 0.53, while the limits of variation were 0.48 to 0.60. Thus, the observed temporal overlap was higher than expected by chance (Standardized Effect Size=4.32, p=0.0002). Similarly, in the spatio-temporal comparison, the observed index was 0.31, higher than expected by chance in comparison with the null model which had threshold values of 0.22 and 0.27 (Standardized Effect Size=4.59, p=0.0002). The results for the pairwise Pianka's niche overlap indices (Table 1) showed that on the temporal scale, all species presented positive values, indicating a tendency for temporal niche overlap, while on the spatio-temporal scale the species pairs *Acanthagrion* sp. and *Oxyagrion* sp., and *Erythrodiplax* sp.1 and *Micrathyria* sp. showed negative effects, indicating that these pairs tend to avoid each other in the finer spatial scale. Thus, the results indicate a tendency towards high overlap in the use of temporal and spatio-temporal resources, with the exception of the pairs *Acanthagrion* sp. and *Oxyagrion* sp. and *Erythrodiplax* sp.1 and *Micrathyria* sp. which tend to occur on the same day, but occupying different sections.

Table 1. Standardized effect size of Pianka index of niche overlap in comparison to null models. Positive values were interpreted as a tendency towards niche overlap, and negative values as a tendency towards niche differentiation.

Genus 1	Genus 2	Temporal scale	Spatio-temporal scale
Acanthagrion sp.	*Erythrodiplax* sp.2	1.7394	1.1912
Acanthagrion sp.	*Erythrodiplax* sp.1	0.9084	0.1660
Acanthagrion sp.	*Micrathyria* sp.	1.2530	0.2525
Acanthagrion sp.	*Oxyagrion* sp.	2.5922	-1.2758
Erythrodiplax sp.2	*Erythrodiplax* sp.1	0.3581	2.0381
Erythrodiplax sp.2	*Micrathyria* sp.	2.0255	4.1782
Erythrodiplax sp.2	*Oxyagrion* sp.	2.1485	4.3892
Erythrodiplax sp.1	*Micrathyria* sp.	2.1007	-0.9157
Erythrodiplax sp.1	*Oxyagrion* sp.	0.9807	1.2749
Micrathyria sp.	*Oxyagrion* sp.	1.2302	1.4705

The analyses of covariance indicated differences in the frequencies of intra- and interspecific interactions, as well as a significant effect of the covariate of intra- and interspecific abundance, for all species (Table 2, Fig. 2). In other words, the frequencies of intra- or interspecific interactions differ and are related to their respective abundance. Furthermore, the frequency of interactions differed between the types of interaction (intra and inter), with a higher frequency of interspecific interaction for the species *Oxyagrion* sp., *Micrathyria* sp. and *Erythrodiplax* sp.1 (rare species throughout the study), and a higher frequency of intraspecific interactions for the species *Acanthagrion* sp. and *Erythrodiplax* sp.2 (most abundant species). Despite this higher intraspecific interaction frequency for *Acanthagrion* sp., interactions increased with abundance at a similar rate between inter and

intra (equal slopes but different intercepts). However, the statistical interaction between abundance and type of interaction was significant for *Erythrodiplax* sp.2, indicating different slope between the intra- and interspecific interactions, with a marked increase in intraspecific interactions with increasing population density (Table 2 , Fig. 2). It is also worth noting that for the three rarest species (*Oxyagrion* sp., *Micrathyria* sp. and *Erythrodiplax* sp.1), the intraspecific slope showed accentuated trends, but with non-significant results.

Table 2. Results of the Ancova test showing the F value and P value for each species. Values in bold represent significant results ($p < 0.05$).

		Acanthagrion sp.		*Mycrathiria* sp.		*Erythrodiplax* sp.1		*Erythrodiplax* sp.2		*Oxyagrion* sp.	
	DF	F value	P	F value	P	F value	P	F value	P	F value	P
Abundance	1	8.522	**0.004**	14.244	**0.001**	31.819	**<0.001**	4.382	**0.039**	14.088	**<0.001**
Interaction type	1	9.103	**0.003**	5.043	**0.038**	5.718	**0.021**	14.872	**<0.001**	12.554	**<0.001**
Abundance:interaction type	1	0.342	0.560	0.828	0.375	1.292	0.261	56.911	**<0.001**	1.119	0.295

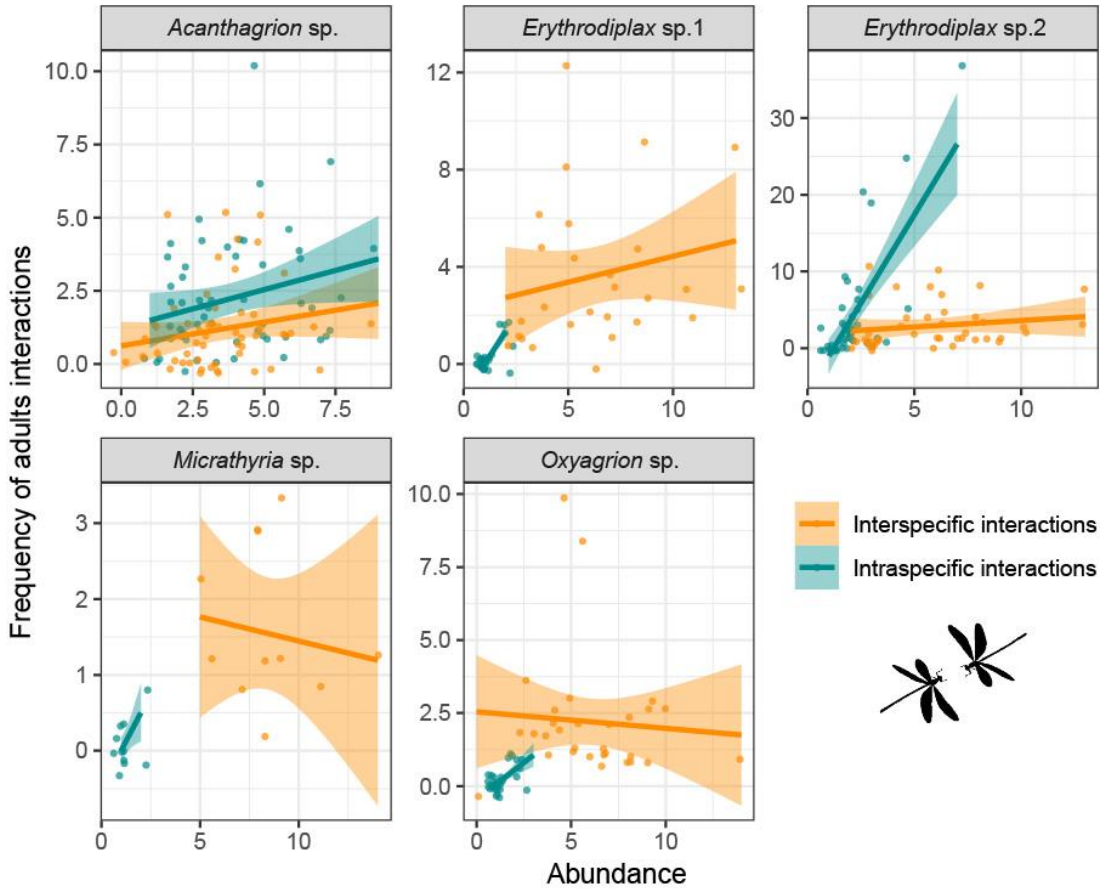

Figure 2. Linear regression showing differences between intra- and interspecific interactions. The x-axis represents intraspecific abundance, and the y-axis represents the frequency of interactions with conspecific individuals (in blue) and with heterospecific individuals (in orange).

The RDA with the air temperature, average rainfall of the 3 days preceding the observations and the accumulated rainfall until the beginning of the observations did not show significant associations with community composition.

Experimental approach

The analysis of variance indicated differences between treatments for the total mortality ratio (Table 3). Specifically, the total mortality ratio of *Acanthagrion* in treatments with *Acanthagrion* dominance was marginally higher in relation to the mortality ratio of *Erythrodiplax* in treatments with *Acanthagrion* dominance (Figure 3; ad hoc Tukey, p= 0.08), regardless of abundance. For the dead larvae ratio and preyed larvae ratio no significant differences were found.

We found that the spatial distribution ratio was different among genera (Table 3), with *Acanthagrion* larvae occupying more the straws during the experiment for all treatments

(Figure S2). Finally, we observed significant differences in the individual biomass based on genus and dominance. Specifically, *Acanthagrion* were larger than *Erythrodiplax* and treatments with *Erythrodiplax* dominance exhibited higher biomass of both taxa (Table 3, Figure S3).

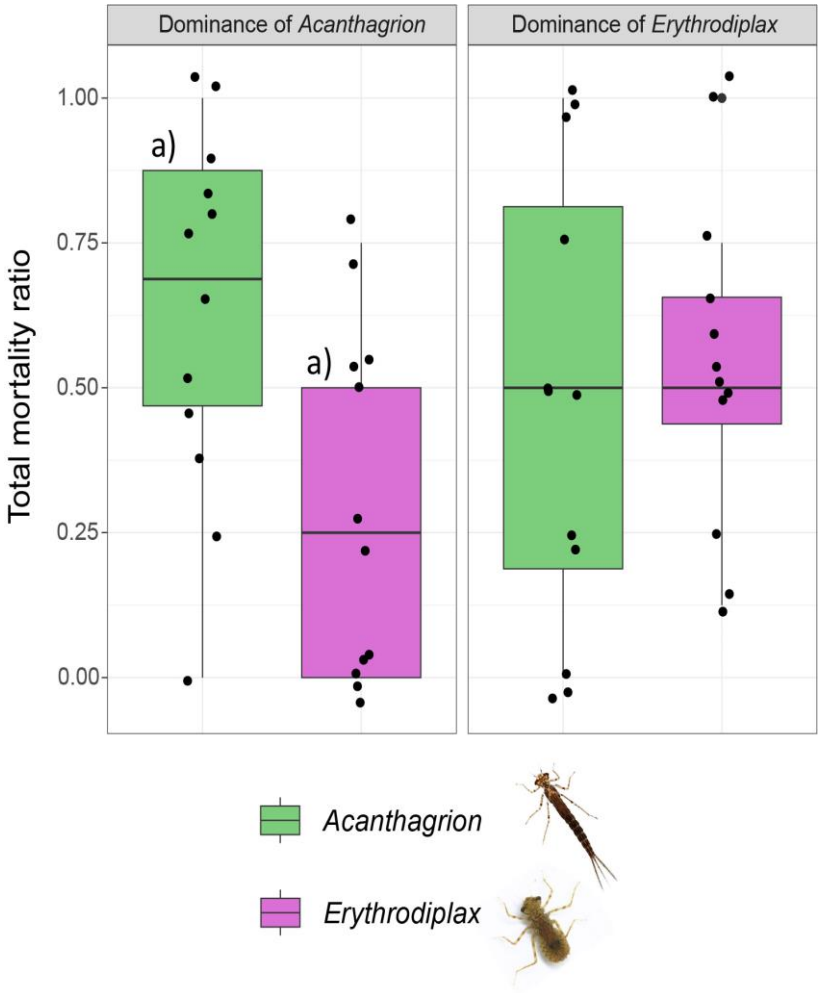

Figure 3. Boxplot showing significant differences for the total mortality ratio. A statistically significant difference was observed for Acanthagrion ($p < 0.05$), with a higher total mortality ratio when it was the dominant species, compared to Erythrodiplax, as indicated by the letter (a).

Tabela 3. Results of the Anova test showing the F value and P value of total mortality rate, preyed larvae, death larvae, spatial distribution rate and biomass. Values in bold represent significant results ($p < 0.05$).

		Total mortality ratio		Preyed larvae ratio		Dead larvae ratio		Spatial distribution ratio		Individual biomass	
	DF	F	P	F	P	F	P	F	P	F	P
Genus	1	2.0233	0.1602	2.7502	0.1051	0.0826	0.7753	64.45	**< 0.001**	19.5672	**< 0.001**
Abundance	1	0.9666	0.3314	2.0438	0.1606	0.4495	0.5064	0.741	0.3945	1.3955	0.24446
Dominance	1	0.2983	0.5879	0.0033	0.9547	1.1101	0.2984	0.3774	0.5425	23.1879	**< 0.001**
Genus: Abundance	1	0.0119	0.9135	0.0818	0.7764	0.0826	0.7753	0.4715	0.4963	0.4508	0.50582
Genus: Dominance	1	4.3144	**0.0444**	1.4210	0.2369	2.6514	0.1113	0.3848	0.5386	3.7510	0.05986
Abundance: Dominance	1	0.5847	0.4489	0.2649	0.6096	0.2294	0.6346	0.4781	0.4933	0.7175	0.40200
Genus: Abundance: Dominance	1	0.9666	0.3314	1.1805	0.2838	0.0092	0.9242	0.0814	0.7768	0.2388	0.62778

Discussion

One of the main goals of community ecology is to understand the maintenance of biodiversity through mechanisms that enable species to coexist in local communities. Whereas competition may imply competitive exclusion of the weaker competing species, stabilizing mechanisms balance this equation increasing intraspecific competition in relation to interspecific (CHESSON, 2000). Although some empirical studies have been conducted in light of the Modern Coexistence Theory, there is a scarcity of studies carried out with species with a complex life cycle aiming at understanding how the ecological differences surrounding these stages may promote species coexistence (GÓMEZ-LLANO; GERMAIN; KYOGOKU; MCPEEK *et al*., 2021). While in the larval stage individuals focus on competition for resources and survival (*i.e*. increasing feeding and avoiding predators), in the adult stage the main goal is to maximize individual reproductive success through different reproductive strategies, such as territoriality. Our results suggest that different mechanisms decrease interspecific interference and control population densities in both life stages. In the larval stage, intraspecific competition was found to be density-dependent, while in adults, a higher rate of intraspecific interactions associated with sexual selection may act as a stabilizing mechanism, increasing intraspecific regulation. Spatial niche segregation should reinforce such mechanisms and was observed for both life stages due to differences in habitat preferences in larval stage, while in the adult community it occurred within streams at fine spatial scale for *Acanthagrion* sp. and *Oxyagrion* sp., and also for *Erythrodiplax* sp.1 and *Micrathyria* sp. Our study adds another piece to the complex puzzle of tropical biodiversity, indicating that at fine resolutions, stabilizing deterministic mechanisms can indeed maintain high biodiversity even in dynamic tropical ecosystems.

For adult dragonflies and damselflies, our results showed that both intra and interspecific interactions can be density-dependent. We found higher male-male and male-female intraspecific interactions for the two most abundant species *Acanthagrion* sp. and *Erythrodiplax* sp.2, suggesting a higher intraspecific interference for these species. For Odonata, this effect is magnified with reproductive intraspecific interactions. Regarding *Acanthagrion*, studies have shown that males are non-territorial, adopting sit-and-wait or actively searching for females as mating strategies. Thus, male-male interactions occur when one male chases the other or faces off against the other (DE ALMEIDA; SALOMONI; VILELA; GUILLERMO-FERREIRA, 2022; GUILLERMO-FERREIRA; DEL-CLARO, 2012). Male-female interactions can occur before, during and after copulation. For this group oviposition guard can be frequent, when males hold the female during oviposition to prevent

them from copulating with other males (GUILLERMO-FERREIRA; DEL-CLARO, 2012). Considering this complex reproductive system, the energetic cost for both males and females to increase individual reproductive success can be enormous, reducing the time and frequency of interaction with other species. Thus, our results indicate that reproductive interactions may act as stabilizing mechanisms, increasing intraspecific interactions in relation to interspecific interaction and potentially enhancing coexistence with other species. Furthermore, in the absence of courtship behaviors male harassment negatively affect females survival rate and fecundity (GOMEZ-LLANO; BENSCH; SVENSSON, 2018; TAKAHASHI; WATANABE, 2010). Such effects may control population growth at the expense of higher individual success, increasing the chances of intraspecific self-regulation and species coexistence (YAMAMICHI; KYOGOKU; IRITANI; KOBAYASHI *et al*., 2020).

Additionally, *Erythrodiplax* sp.2 also presented higher male-male interactions, showing a pronounced increase with increasing population density in relation to interspecific interactions. Species of the *Erythrodiplax* genus are mostly territorialists, where males defend a mating area from other males to attract females (PINTO; DE MARCO; MOURA, 2022). This behavior was observed during field samplings, where males pursued and chased other males that approached their area, and then returned to the same spot. Previous studies have demonstrated that male-male contests can reduce the lifespan of males or limit access to females, which can, directly or indirectly, affect the per capita growth rate (PINTO; DE MARCO; MOURA, 2022; SVENSSON; GÓMEZ-LLANO; TORRES; BENSCH, 2018). However, more studies are needed to understand whether the negative effects of territoriality on the per capita growth rate are sufficient to control population growth, and thus promote coexistence. On a different perspective, territoriality could influence coexistence by generating a spatial separation, where males are more aggressive towards conspecifics invading their territories, increasing the distance between conspecifics neighbors and allowing heterospecifics to occupy territories between conspecifics (MIKAMI; KOHDA; KAWATA, 2004). This may be a possible explanation for the co-occurrence of two morphotypes of the genus *Erythrodiplax*, given that both species exhibit territorial behavior. However, *Erythrodiplax* sp.1 did not presented a high frequency of intraspecific interactions even though it showed territoriality behavior. This may occur due to the low abundance of the species and, therefore, lower probability of encountering conspecifics, which may mean that sexual selection mechanisms also operate depending on density.

In addition to reproductive behaviors, niche partitioning may reduce interspecific competition and promote species coexistence. According to Pianka (1973), species may partition their niches along three main dimensions: trophic, temporal, and spatial. In this context, our results revealed spatial niche segregation between two pairs of species in the adult community, which may be explained by environmental differences, such as vegetation structure and light availability, that influence species distribution according to their ecophysiological requirements (*e.g*., thermoregulation, body size DE MARCO JÚNIOR; BATISTA; CABETTE, 2015; OSBORN; SAMWAYS, 1996; RESENDE, 2002). Although species–environment correlations are often stronger at broader spatial scales (SAMWAYS; CALDWELL; OSBORN, 1996), spatial segregation at the microhabitat level may also be related to phylogeny, enabling closely related species to coexist (KHELIFA; ZEBSA; MOUSSAOUI; KAHALERRAS *et al*., 2013).

While for Odonata adults mechanisms related to sexual selection can affect the intensity of interactions, in the larval stage these mechanisms are absent. In this sense, our results showed a strong influence of dominance (the identity of the most abundant species) in larvae mortality, regardless of the abundances. Our findings indicate a tendency towards greater intensity in the intraspecific competition of *Acanthagrion* larvae, since their total mortality ratio was higher when dominant. Regarding *Erythrodiplax*, the total mortality ratio was higher, although not statistically significant, when dominant than when rare (in dominance of *Acanthagrion*). This result may also signal a higher intraspecific effect on population density for *Erythrodiplax*. According to McPeeck (2012) competition model, intraspecific density-dependence may promote species coexistence, even though these species share the same resources. This occurs because each species controls its own population density, preventing just one species from dominating resources (MCPEEK, 2012). Although our results did not show statistically significant differences between high and medium abundance treatments, density-dependent competition remains an important ecological factor that can influence species distribution and community structure, particularly in larval Odonata (MCPEEK, 1990b). Increased density may elevate the frequency of aggressive encounters and are also mediated by species-specific behavioral strategies. For instance, some species may reduce movement in the presence of dominant competitors, thereby decreasing encounter rates and mitigating the direct effects of competition (MCPEEK, 1990a; MCPEEK; CROWLEY, 1987). Such behavioral differences suggest that the effects of density may not

manifest directly through individual survival. Instead, various biotic and abiotic factors must be considered when interpreting density effects in experimental settings.

In addition to strong intraspecific competition, the presence of spatial niche segregation also may explain the coexistence between the pair of studied species. Our results showed that *Acanthagrion* larvae and *Erythrodiplax* larvae occupied different locations in the experimental arenas. While *Erythrodiplax* larvae were found more frequently at the bottom of the boxes, *Acanthagrion* larvae were found predominantly in the straws. Previous studies have shown that there is a difference in habitat preference between larvae of the Coenagrionidae family and the Libellulidae family, with Coenagrionidae larvae (including the genus *Acanthagrion*) preferring more complex environments, with the presence of structures such as macrophytes (TAVARES; PESTANA; ROCHA; SCHIAVONE et al., 2018). Our results indicate that these habitat preferences are not only associated with an environmental selection, but also with reducing interspecific interference.

Additionally, several factors can influence Odonata larval mortality and regulate population density, including competition, intraguild predation, and cannibalism (FINCKE, 1994). Intraspecific resource competition is a strong driver of population dynamics, enhancing conspecific mortality through stress or starvation until densities stabilize (FINCKE, 1994). Certain conditions, such as limited food availability (WILDY; CHIVERS; KIESECKER; BLAUSTEIN, 2001) and low habitat heterogeneity (BLOCK; STOKS, 2004), can further intensify competitive interactions among larvae. Although our results did not reveal statistically significant treatment effects on the ratio of predated larvae, we observed evidence of intraguild predation or cannibalism, including missing individuals and partially consumed larvae. These observations suggest that trophic interactions occurred during the experiment but were not fully reflected in survival metrics. Cannibalism can contribute to population persistence by enhancing predator growth, allowing cannibals to survive under adverse ecological conditions, and by reducing direct competition for resources (DE BLOCK; STOKS, 2004). Previous studies have suggested that cannibalism is a significant density-dependent factor affecting Odonata mortality, particularly under conditions of high conspecific density (CLARK; HOSSIE; BERESFORD, 2021; VAN BUSKIRK, 1989; WILDY; CHIVERS; KIESECKER; BLAUSTEIN, 2001). It also tends to be more frequent when there are substantial size differences between individuals, as larger larvae can prey on smaller conspecifics, potentially reducing size variation within populations (VAN BUSKIRK,

1989). In our study, we found significant differences in biomass between the genera *Acanthagrion* and *Erythrodiplax*, as well as treatment effects associated with *Erythrodiplax* dominance. While such biomass differences could facilitate intraguild predation via size-dependent mechanisms, they did not significantly affect larval mortality in our study. One possible explanation is that the observed biomass variation was relatively small, thereby limiting size-based asymmetries and preserving similar competitive capacities across genera (WOODIE; ANDERSON, 2024). Intraguild predation is shaped by multiple factors, including body size, density, temperature, behavioral responses to predators, species-specific developmental rates, and priority effects - each of which can alter both the direction and strength of predator-prey interactions (FRANCES; MCCAULEY, 2018; MCPEEK, 1990b; PADEFFKE; SUHLING, 2003; RASMUSSEN; VAN ALLEN; RUDOLF, 2014). For instance, survival may depend on early oviposition and faster development, as individuals that hatch earlier can gain a size advantage and outcompete or prey upon later-arriving larvae (PADEFFKE; SUHLING, 2003; RASMUSSEN; VAN ALLEN; RUDOLF, 2014). Moreover, behavioral differences such as movement reduction in the presence of predators — like fish or other Odonata larvae — may reduce predation risk (*e.g.*, decreased larval activity in response to predator cues; MCPEEK 1990b). Although intraguild predation may not always lead to reduced survival, it can still influence size structure within populations and mediate competitive dynamics and distribution in larval communities (MCPEEK 1990b).

Despite the clear evidence we have about the stronger intra than interspecific effects on Odonata competition, defining if species are able to coexist is a daunting quest. Empirical studies that seek to understand how interactions can affect the coexistence of species generally use the per capita growth rate as the fitness component. Here, we analyzed mortality ratio as the main population parameter to evaluate competition patterns in the larval stage, however we cannot estimate the impact of this competition on per capita growth rate. Furthermore, for the adult community we have the frequencies of interactions, but not their consequences on population growth. We estimate that high frequency interactions represent more time and energy spent on that type of interaction, which would consequently reduce interspecific interactions. Moreover, although our results present evidence of intraspecific density-dependence in the larval stage, our sampling design disregards the impact of predation by other species. Previous studies have shown that fish are one of the main predators of Odonata larvae and predation can have a stabilizing effect on the population growth rate,

impacting population density and consequently reducing interspecific competition for resources (CHASE; ABRAMS; GROVER; DIEHL *et al*., 2002).

Conclusion

The presence of stabilizing mechanisms can favor the coexistence of competing species, balancing inter and intraspecific effects. Higher intraspecific competition proved to be an important mechanism to decrease interspecific interactions and control population density in both larval and adult stages of Odonata species, which may occur due to spatial niche segregation or the presence of behaviors related to sexual selection. We conclude that several mechanisms may act together to structure the Odonata community in both life stages. Our study provided novel results on how coexistence mechanisms could vary along with ontogenetic development broadening our understanding of processes sustaining biodiversity in tropical ecosystems.

Supplementary material

Table S1. Mean and standard deviation of larval body size used in each experimental replicate.

Genus	Replicate	Mean (cm)	Standard deviation
Acanthagrion	1	0.863	0.014
	2	0.547	0.041
	3	0.863	0.014
	4	0.947	0.082
	5	0.753	0.232
	6	0.828	0.048
Erythrodiplax	1	0.628	0.036
	2	0.358	0.014
	3	0.628	0.036
	4	0.672	0.026
	5	0.606	0.113
	6	0.728	0.021

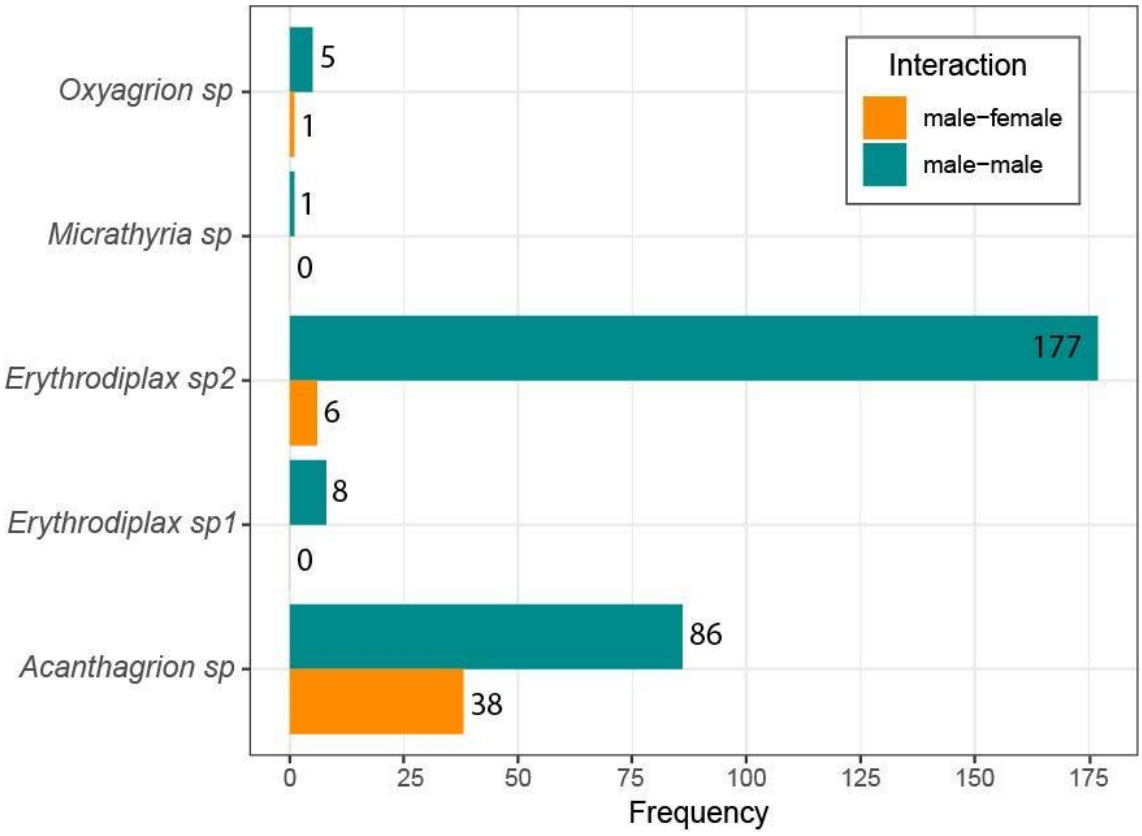

Figure S1. Number of intraspecific male-male and male-female interactions between Odonata adults.

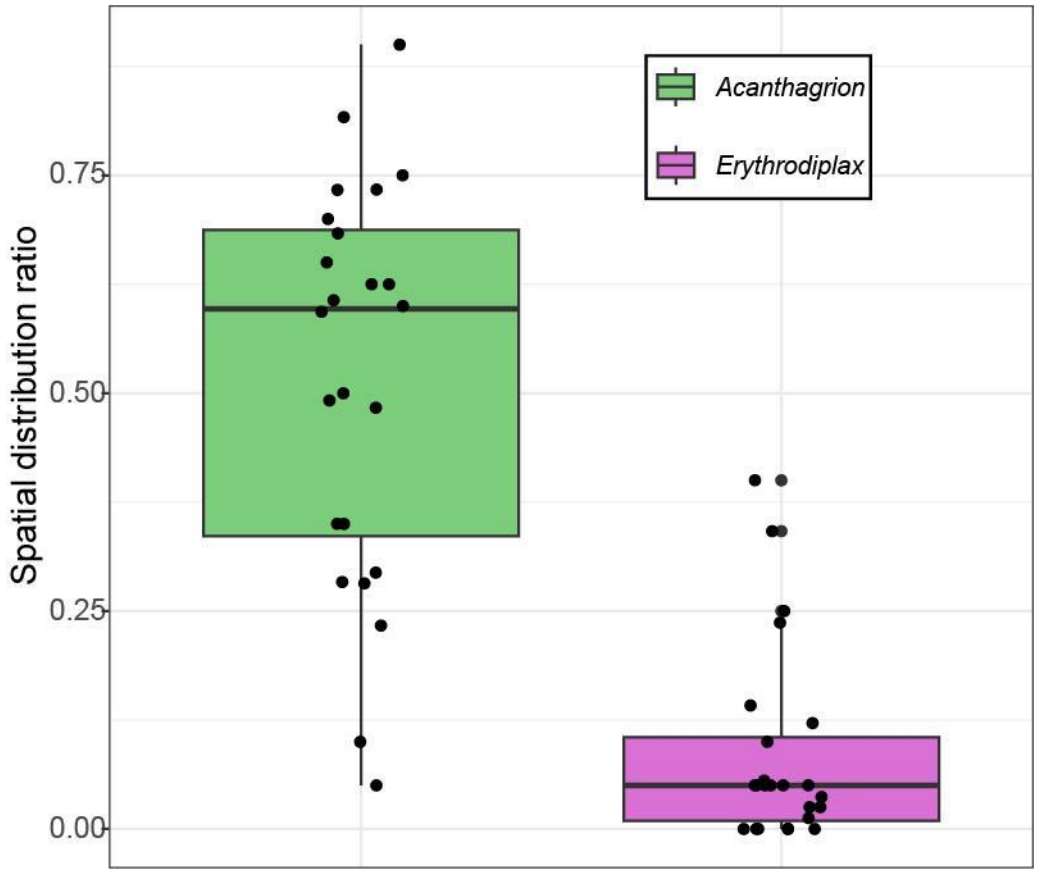

Figure S2. Spatial distribution ratio among Acanthagrion and Erythrodiplax larvae.

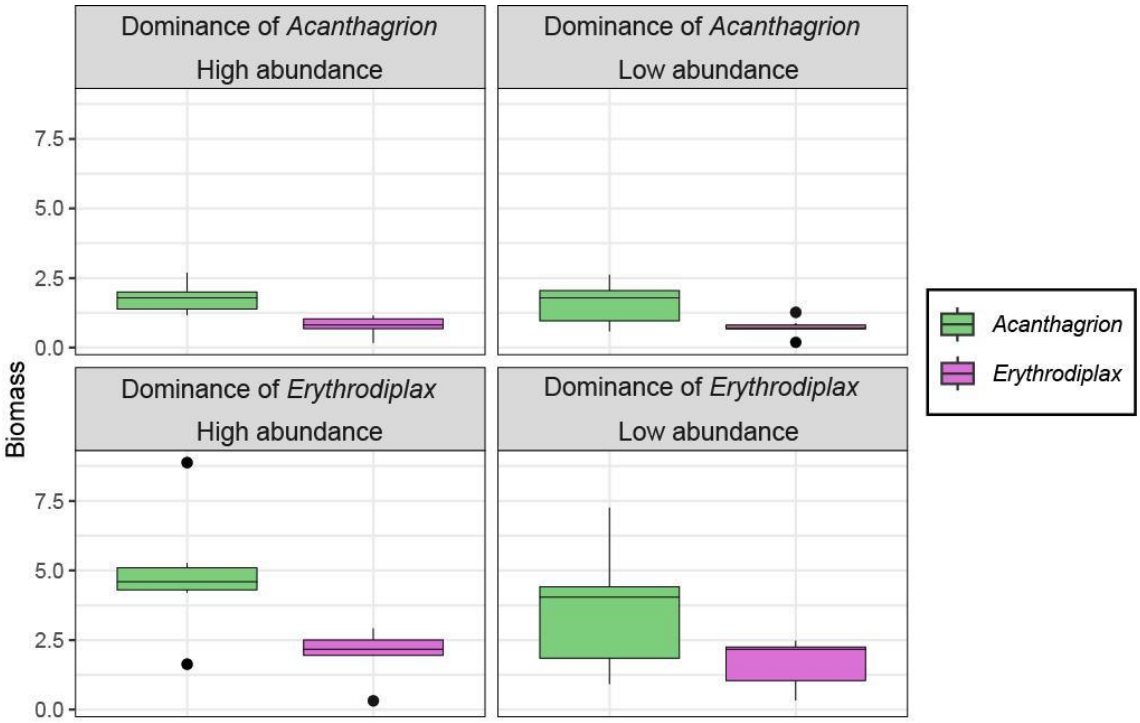

Figure S3. Acanthagrion and Erythrodiplax biomass for each treatment.

Considerações finais

Compreender os mecanismos que estruturam comunidades biológicas e sustentam a biodiversidade continua sendo um dos principais desafios da ecologia contemporânea. Entre as propostas teóricas voltadas a essa questão, a Teoria Moderna da Coexistência tem se destacado por oferecer explicações robustas sobre como espécies competidoras persistem no mesmo ambiente ao longo do tempo. Embora esta teoria tenha sido amplamente utilizada nos últimos 20 anos, sua reduzida aplicação em trabalhos empíricos demonstra uma limitação devido à utilização de modelos matemáticos complexos. Assim, o primeiro capítulo desta tese trouxe uma introdução aos principais conceitos envolvendo a coexistência de espécies, assim como seus mecanismos e modelos matemáticos, com o objetivo de simplificar esses termos para aqueles que estão iniciando nessa área de pesquisa.

Além disso, ao longo desta tese foram desenvolvidos dois trabalhos empíricos utilizando como modelos de estudo o grupo Odonata. O trabalho descrito no capítulo dois sobre os efeitos de fatores bióticos e abióticos na variação da mancha alar em *Hetaerina rosea*, sugere que este traço sexual, intimamente relacionado ao sucesso reprodutivo individual, pode ser afetado por diferentes fatores ambientais e interações intraespecíficas. Assim, este trabalho abre novos questionamentos para futuros estudos sobre como esses efeitos podem extrapolar no âmbito da co-ocorrência de espécies. Ademais, o terceiro capítulo evidencia a importância das interações intraespecíficas tanto na fase larval como na fase adulta de libélulas e donzelinhas, fornecendo insights sobre os mecanismos que atuam na estruturação de comunidades de libélulas nos diferentes estágios do ciclo de vida.

Por fim, os resultados aqui apresentados demonstram que diferentes fatores podem atuar afetando as dinâmicas nos diferentes níveis de organização. Esses trabalhos ressaltam a importância de considerar tanto os aspectos ambientais quanto as interações biológicas para uma compreensão mais ampla sobre os processos que envolvem as populações e comunidades. Além disso, esta tese reforça o valor das libélulas como um modelo eficiente para o estudo da ecologia de comunidades, devido sua diversidade taxonômica, ecológica e comportamental que permite estudar diferentes mecanismos inerentes aos sistemas ecológicos.

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