UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E BIODIVERSIDADE

EFEITOS DIRETOS E INDIRETOS DE MUDANÇAS AMBIENTAIS SOBRE A ESTRUTURA E ESTABILIDADE DE REDES TRÓFICAS

GEDIMAR PEREIRA BARBOSA

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Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ecologia, Evolução e Biodiversidade.

Orientador: Dr. Tadeu de Siqueira Barros

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2024

B238e

Barbosa, Gedimar Pereira
Efeitos diretos e indiretos de mudanças ambientais sobre a estrutura e estabilidade de redes tróficas / Gedimar Pereira Barbosa. -- Rio Claro, 2024
102 f. : il., tabs., fotos, mapas

Tese (doutorado) - Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro
Orientador: Tadeu de Siqueira Barros

1. redes ecológicas. 2. metacomunidades. 3. mudanças climáticas. 4. uso do solo. 5. modelagem por equações estruturais. I. Título.

Sistema de geração automática de fichas catalográficas da Unesp. Biblioteca do Instituto de Biociências, Rio Claro. Dados fornecidos pelo autor(a).

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TÍTULO DA TESE: EFEITOS DIRETOS E INDIRETOS DE MUDANÇAS AMBIENTAIS SOBRE A ESTRUTURA E ESTABILIDADE DE REDES TRÓFICAS

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Aprovado como parte das exigências para obtenção do Título de Doutor em Ecologia, Evolução e Biodiversidade, área: Biodiversidade pela Comissão Examinadora:

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Rio Claro, 14 de dezembro de 2023

Dedico esta tese aos meus pais, um operário e uma cortadora de cana que, privados da própria educação, lutaram pelos estudos do menino bagunceiro.

Agradecimentos

Ao meu orientador, Tadeu Siqueira, pela paciência, empenho e dedicação com a qual conduziu minha orientação. Obrigado pela imensurável sabedoria que você compartilhou comigo ao longo desses anos, pelos conselhos, conversas e horas dedicadas ao meu desenvolvimento como cientista. Obrigado por confiar em mim, e por me apoiar nos momentos difíceis. Saiba que, para além de todo aprendizado profissional, eu levo comigo a sua capacidade de acreditar no potencial das pessoas e enxergá-las como únicas.

Aos colegas incríveis que eu fiz durante o período de doutorado, Neliton, Ana Carolina, Cristina, Gabriel e Alison, cujos momentos de conversa, risadas e reflexões me ajudaram a transitar pelos momentos difíceis da pós-graduação.

Ao professor Victor Saito (UFSCar), pela parceria ao longo do doutorado, incluindo a possibilidade de experimento que resultou em um dos capítulos desta tese. Agradeço também, pelas conversas e conselhos, tão valiosos para o desenvolvimento desta tese e da minha formação profissional.

Aos professores Gilmar Perbiche Neves e Hugo Sarmento (UFSCar), por abrirem seus laboratórios e compartilharem conhecimentos valiosos, que contribuíram para os capítulos aqui apresentados.

Aos professores Alexandre Colatto (UFScar) e Márcia Pechula (UNESP) que, por meio de conversas sobre ciência, me ajudaram a refletir sobre a minha atuação e contribuíram para minha formação quanto cientista.

Aos professores Mathias Pires (UNICAMP) e Miriam Albrecht (UFRJ), que durante meu exame de qualificação teceram conselhos e considerações relevantes para o desenvolvimento desta tese.

Aos professores Eugenia Zandonà (UERJ) e Raul Costa Pereira (UNICAMP), que teceram comentários valiosos sobre a versão final desta tese e sobre a minha atuação como cientista.

A todas as pessoas que dedicaram seu tempo e esforço, inclusive de forma voluntária, aos perrengues e alegrias dos experimentos: Jorge, Camila, Helen, Aline, Ana, Ana Laura e Fabiana.

Aos servidores do Departamento de Biodiversidade e do Jacarezário, em especial Cristina, Carlinhos e Ailton pelo apoio durante o desenvolvimento dos trabalhos.

Aos servidores da STPG, em especial Ivana e Felipe, que tanto me socorreram em relação às burocracias da pós-graduação.

Aos discentes de graduação que eu tive o prazer de conhecer durante os períodos como docente bolsista. Saibam que a confiança e a contribuição de vocês foi fundamental para a minha carreira.

A Leticia, pela sua competência, profissionalismo e conselhos valiosos que me ajudaram durante o doutorado.

Aos meus pais, Ademar e Maria, aos meus irmãos (de sangue e de afeto), Gismar, Gislene, Márcio e Gisele, e aos meus pequenos Laura, Alice, Pedro, Amora e Ana, pelo apoio incondicional, pelo carinho e por acreditarem em mim. Tem um pedacinho de cada um de vocês em tudo o que eu sou e faço.

A minha humana favorita, Marina, e à nossa família de peninhas, Sol, Bob, Morgana, Lady (*in memoriam*), Manga, Nenê e Paçoca. Obrigado pela paciência e pelo amor, sempre! Dividir esse espaço e tempo com vocês foi a melhor coisa que já me aconteceu.

Por fim, agradeço a todos os cientistas, mulheres e homens, que dedicam suas vidas a explorar a complexidade da natureza. A produção científica de vocês foi o farol que me guiou até aqui.

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001.

Processo nº 2019/06291-3, Fundação de Amparo à Pesquisa do estado de São Paulo (FAPESP).

"Passou vários dias feito um enfeitiçado, repetindo para si mesmo em voz baixa uma fieira de assombrosas conjecturas, sem dar crédito ao próprio entendimento. Finalmente, numa terça-feira de dezembro, na hora do almoço, soltou de um golpe só toda a carga de seu tormento. As crianças haveriam de se recordar pelo resto de sua vida a augusta solenidade com que seu pai sentou-se à cabeceira da mesa, tremendo de febre, devastado pela prolongada vigília e pela ferida aberta de sua imaginação, e revelou a elas sua descoberta:
— A terra é redonda feito uma laranja."

Gabriel García Márquez

Resumo

Em um cenário crescente de mudanças ambientais intensas e imprevisíveis, rastrear como a biodiversidade é afetada se torna uma tarefa cada vez mais difícil e necessária. No entanto, a maioria dos estudos ainda aborda os efeitos de mudanças ambientais sobre aspectos predominantemente taxonômicos, desconsiderando a influência que essas mudanças podem ter na forma como as espécies interagem na natureza. Deste modo, esta tese se propõe a avaliar as relações entre mudanças ambientais e redes tróficas em ecossistemas aquáticos, considerando os caminhos diretos e indiretos pelos quais as mudanças ambientais influenciam a biodiversidade em diferentes escalas. No primeiro capítulo, eu abordei como redes tróficas em lagos e riachos respondem a mudanças climáticas e de uso do solo, considerando diferenças intrínsecas entre esses ecossistemas. Juntando dados disponíveis na literatura, informações geográficas e modelagem por equações estruturais, eu mostrei que a estrutura de redes tróficas é direta e indiretamente influenciada pela intensidade de uso do solo, e por aumentos históricos na temperatura e precipitação. Além disso, mudanças climáticas afetam a estrutura das redes por meio de efeitos negativos na proporção de predadores de topo. Porém, o tipo de ecossistema atua como um importante mediador do tamanho dos efeitos. No segundo capítulo, por meio de uma abordagem experimental com metacomunidades planctônicas, explorei o papel de agroquímicos na estabilidade de produtores e consumidores, ao longo de diferentes escalas (local e regional) e níveis de organização (populações, comunidades e metacomunidades). Novamente, por meio de modelagem por equações estruturais, eu mostrei que a intensificação no uso de agroquímicos altera a forma como a variação temporal se propaga da escala local para a regional, em ecossistemas de água doce. Porém, os resultados dependem da posição trófica dos organismos, do

nível de organização e do tipo de agroquímico considerado. Em suma, os resultados do dois capítulos indicam que as relações entre mudanças ambientais e redes tróficas são complexas e demandam uma análise detalhada dos caminhos (diretos e indiretos) pelos quais elas ocorrem. Diferentes variáveis, como a proporção de predadores, tipo de ecossistema e a sincronia das populações, mediam as respostas observadas na estrutura das redes tróficas e na estabilidade de produtores e consumidores. Dessa forma, além de reforçar a necessidade de se considerar as interações entre as espécies, esta tese sugere que, para avançarmos nosso entendimento sobre como mudanças ambientais influenciam a biodiversidade, se faz necessário investigar a intrincada teia de relações indiretas que ligam preditores ambientais a respostas da biodiversidade.

Palavras-chave: redes ecológicas; metacomunidades; mudanças climáticas; uso do solo; modelagem por equações estruturais.

Abstract

In a growing scenario of intense and unpredictable environmental changes, monitoring how biodiversity is affected becomes an increasingly difficult and necessary task. However, most studies still consider the effects of environmental changes on purely taxonomic aspects, disregarding the influence that these changes might have on how species interact in nature. Thus, this thesis aims to investigate the relationships between environmental changes and food webs in aquatic ecosystems, considering the direct and indirect paths in which environmental changes influence biodiversity at different scales. In the first chapter, I addressed how food webs in lakes and streams respond to climate and land use changes, considering intrinsic differences between these ecosystems. Combining available data, geographic information and structural equation modeling, I showed that food web structure is directly and indirectly influenced by land use intensity, and by historical increases in temperature and precipitation. In addition, effects of climate change on the structure of food webs occurred through negative relationships with the proportion of top predators. However, ecosystem type is an important mediator of effect size. In the second chapter, I explored the role of agrochemicals in the stability of producers and consumers, across different scales (local and regional) and levels of organization (populations, communities and metacommunities), using an experimental approach with planktonic metacommunities. Through structural equation modeling, I showed that agrochemical intensification influences how temporal variability propagates from local to regional scales in freshwater ecosystems. However, the results depend on organism trophic position, level of organization and type of agrochemical considered. Overall, the results of the two chapters indicate that the relationships between environmental changes and food webs are complex and require a detailed analysis of the paths (direct and indirect)

through which they occur. Different variables, such as the fraction of top predators, ecosystem type and population synchrony, mediate the responses of food web structure and the stability of producers and consumers. Thus, besides the need to consider species interactions, this thesis suggests that, to advance our understanding of how environmental changes influence biodiversity, it is necessary to investigate the intricate web of indirect relationships that link environmental predictors to overall biodiversity responses.

Keywords: ecological networks; metacommunities; climate change; land use; structural equation modeling.

Sumário

Apresentação

Aqueles que, de livre e espontânea vontade, optam pela leitura de uma tese, têm uma ideia formada sobre o que encontrarão antes mesmo de ler a primeira linha. Sabem que uma tese é cheia de referências sobre um tema, descrições detalhadas de métodos e processos, dados, imagens e tabelas, que são convertidas em explicações elaboradas e confrontadas com a imensidão (ou, nem tanto!) do que se conhece até o momento. E, tudo isso, geralmente serve a um único objetivo: o avanço do conhecimento sobre um fenômeno complexo e inquietante na vida dos seres humanos. Ainda que, no despertar desse processo, o ser humano em questão seja apenas o solitário autor, que dedica parte da sua existência a acalmar as dúvidas que rondam sua cabeça e que, às vezes, não o deixam dormir. Sim! Eu tenho certeza de que você, que já fez um trabalho científico e está lendo isso, consegue se lembrar de pelo menos um momento em que não tenha conseguido dormir, tentando encontrar sentido nos fragmentos mirabolantes de ideias (dados, dados e mais dados!) que o atazanaram durante o dia. E que, esse sentido tão buscado, veio só meses depois, enquanto seu arroz para o almoço de domingo queimava no fogão. Meu ponto é: o que lemos nas longas páginas brancas, em tamanho 12, espaço duplo, é uma fração muito pequena do que a tese realmente significa para quem a escreveu. E, embora as teses escritas por pessoas (em uma era de *chatGPT*, é bom deixar isso claro) sejam parecidas em sua apresentação, elas são carregadas das mais diversas histórias possíveis. Histórias que são escondidas pelo manto das formalidades e, se você tiver sorte, descobertas científicas mais interessantes ao público. Assim, eu quero usar este espaço para falar sobre como se deu esta tese, principalmente de dois momentos de sua história que, para o bem ou mal, moldaram o que eu apresento

aqui hoje. Prometo não me alongar demais, mas eu não o julgarei, caso você decida avançar para a página 17.

Fazer uma tese é algo trabalhoso e, se você for uma pessoa ansiosa, como este autor que vos fala, aprenderá da pior forma que escrever uma tese requer muita paciência. Transformar desejos e ideias, por vezes desconexas, em um projeto exequível, dentro das condições e prazos estipulados, requer tempo. O projeto que deu origem a esta tese levou quase um ano para ficar pronto, e foi resultado de muito diálogo, estudos e reflexões. E com a valiosa ajuda do meu orientador, chegamos a um projeto que tinha, em sua essência, tudo o que eu acreditava que um projeto de doutorado em Ecologia podia conter para ser legal. Divididos em três capítulos bem robustos, o projeto original desta tese envolvia síntese de dados, dois experimentos bacanas, simulações computacionais, colaborações e intercâmbio. Abordava a ecologia de metacomunidades (ou meta-redes), com ênfase no papel de processos (e.g., dispersão), e em como as mudanças ambientais “bagunçavam” a estrutura das redes de interações em diferentes escalas. Enfim, eu estava bastante feliz com a proposta! Uma professora me disse uma vez, que tem um motivo para os cientistas organizarem as coisas em “projetos”. O projeto caracteriza uma intenção, um desejo, de se realizar algo no futuro. É algo delineado e estruturado, mas que ainda precisa ser realizado. Repare: é a premissa no presente sobre algo que se encontra no futuro. Como você vai concluir, se ler esta tese até o fim, eu consegui entregar apenas dois dos três capítulos, e eles ficaram um pouco diferentes do que foi projetado (embora eu tenha um orgulho enorme de cada linha aqui escrita).

Eu acho que você, que se disponibilizou a ler esta tese e ainda não desistiu desta apresentação, consegue imaginar qual foi o primeiro momento em que meu “projeto dos sonhos” encontrou seu maior obstáculo. Eu vou resumir: os últimos anos

foram bem doidos! Eu iniciei o doutorado no segundo semestre de 2019, e passei quase metade dele longe das atividades presenciais. A pandemia de Covid-19 mudou a nossa forma de viver, nos isolou dentro de casa e, pior de tudo, levou consigo a vida de muitas pessoas (para ser exato, 706.531 pessoas morreram no Brasil, até o momento em que escrevo este texto). As universidades, assim como outros locais de intensa aglomeração de pessoas, foram fechadas, o ensino se tornou remoto (distante), e a pesquisa foi abalada pela impossibilidade de estarmos nos laboratórios. Aquele laboratório, onde a gente discutia ideias e fazia um monte de coisa legal, indispensável para o nosso trabalho. Logo, a única coisa ainda funcionando (e a mil por hora!) eram as nossas cabeças, num *loop* infinito de acordar, ligar a câmera, desligar a câmera, comer, ligar a câmera, "*Fulano, você está falando com o microfone desligado!*". Enfim, minhas amostras coletadas no primeiro experimento (em 2019) ficaram guardadas, e todas as atividades foram adiadas para, como gostávamos de dizer na época, "quando as coisas voltassem a normalidade". A "normalidade" para a minha tese, viria apenas em janeiro de 2022, com a realização de um experimento previsto para ocorrer no primeiro semestre de 2020. Este experimento (de 2022), infelizmente, não chegou a ser incorporado a esta tese.

Assim como os outros alunos de pós-graduação, durante a pandemia, eu me coloquei na tarefa de encontrar algo que fosse plausível e pudesse ser feito para minimizar os impactos do isolamento no meu doutorado. Foi nessa busca que meu capítulo 1 nasceu, nas entranhas do trabalho remoto, e depois de muito diálogo com meu orientador. Neste capítulo, abordo como mudanças climáticas e de uso do solo influenciam indiretamente a estrutura de redes tróficas em ecossistemas aquáticos. Do isolamento, na kitnet 32, rua das Hortênsias, 183, cruzei dados multicontinentais disponíveis na literatura, processamento de informações geográficas e modelagem

por equações estruturais, para mostrar que as relações entre o clima, a conversão de áreas naturais em antrópicas e as redes tróficas nem sempre é direta (*spoiler!*). Ou seja, variáveis como a proporção de predadores mediam a forma como as redes estruturam-se frente a estas mudanças. Ainda, mostramos que as respostas dependem do tipo de ecossistema de água doce estudado, divergindo entre lagos e riachos. Ufa! O resultado de tudo isso foi um manuscrito muito legal que, depois de algumas submissões, rejeições, e reformatações, publicamos esse ano na revista *Global Ecology and Biogeography*.

No início de 2022, ainda sob a influência do Covid-19 e com as faces cobertas pelas máscaras, finalmente retornamos ao laboratório e às atividades presenciais. Eu estava otimista, mas é aqui que entra o segundo momento na história desta tese, e que influenciou profundamente o seu desenvolvimento. Seguindo um movimento crescente na população, o período de isolamento foi muito nocivo para a minha saúde mental. Felizmente, logo que identifiquei os sintomas, busquei ajuda profissional e consegui aliviar bastante a influência disso no trabalho. Porém, foi só na volta ao presencial, que eu realmente tomei consciência do quanto o período de pandemia havia deixado marcas, e o quanto isso havia influenciado e ainda influenciaria a ciência que eu estava tentando produzir. Eu pensei bastante sobre incluir esse trecho aqui, principalmente porque a saúde mental de pós-graduandos ainda é muito ignorada dentro das universidades, mesmo com todas as estatísticas que informam um aumento crônico nos casos de ansiedade e depressão. Mas, além de encarar isso como algo relevante, e que está silenciosamente moldando toda uma geração de pesquisadores, eu não queria que o meu caso fosse apenas mais um para a estatística. Então, se você chegou até esta tese, leu essas linhas e se encontra em uma situação parecida, tenha certeza de que sim, é possível melhorar. E, aqui, eu deixo novamente

um agradecimento especial ao meu orientador, Tadeu, pela compreensão e paciência, ainda que eu nunca tenha discutido isso abertamente com ninguém no trabalho.

Considerando, então, as condições impostas, eu direcionei meu último ano de doutorado a outras atividades acadêmicas, e decidi redigir mais um manuscrito apenas, que é apresentado aqui como capítulo 2. Este capítulo contou com um amplo experimento realizado em 2019, onde metacomunidades planctônicas foram estabelecidas em mesocosmos, para simular efeitos regionais de atividades agrícolas, em especial o uso de agroquímicos, em ecossistemas aquáticos. Nele, eu abordo como a variação temporal se propaga ao longo dos níveis de organização ecológica, em redes tróficas formadas por produtores e consumidores, sob o efeito de um inseticida (fipronil) e um fertilizante (vinhaça). De forma geral, eu mostro os caminhos indiretos pelos quais estes agroquímicos podem influenciar a variabilidade temporal na abundância de metacomunidades multitróficas, indicando de que forma as respostas de produtores e consumidores diferem entre si.

Concluindo esta apresentação, eu gostaria apenas de dizer que esta tese aborda a complexidade das relações entre mudanças ambientais e redes tróficas. É um tema bastante explorado na ecologia, mas que ainda carece de estudos detalhados, principalmente em face de mudanças ambientais cada vez mais intensas e imprevisíveis. Gostaria de dizer também, que esta tese tem um história própria, e que se mistura com a minha história. Por fim, eu sou grato por poder apresentá-la, assim como sou grato a todos aqueles que contribuíram para que ela existisse.

1. Introdução geral

1.1. Um novo olhar para um problema atemporal

Entender como mudanças ambientais moldam a biodiversidade é um dos objetivos que transpassa gerações na pesquisa em ecologia de comunidades. Dada a importância e a complexidade desse assunto, cientistas têm se esforçado para desvendar o papel de mudanças ambientais na estrutura de diferentes grupos biológicos (Dornelas *et al.* 2014; Flynn *et al.* 2009; Newbold *et al.* 2020), ecossistemas (Hautier *et al.* 2020; Jackson *et al.* 2016; Magurran *et al.* 2015), e escalas espaciais e temporais diversas (Dornelas *et al.* 2014; Petsch *et al.* 2021; Siqueira *et al.* 2015a). Evidências sugerem alterações substanciais nas comunidades, que transitam entre a perda de diversidade, medida de diferentes formas (Flynn *et al.* 2009; Schürings *et al.* 2022), e modificações na composição temporal e espacial das comunidades (Dornelas *et al.* 2014; Leão *et al.* 2020; Siqueira *et al.* 2015a), com fortes indícios de homogeneização biótica (Jia *et al.* 2020; Olden 2006; Peoples *et al.* 2020). No entanto, a maioria dos estudos ainda é centrada apenas em descritores relacionados às espécies (e.g., utilizando riqueza de espécies como variável resposta; Siqueira *et al.* 2015b), e que talvez não revelem respostas consistentes sobre como mudanças ambientais afetam a biodiversidade. Por exemplo, apesar de intensas mudanças ambientais nos ecossistemas aquáticos e terrestres ao longo dos anos, a diversidade alfa de espécies parece não se alterar sistematicamente em series temporais longas (Dornelas *et al.* 2014). Em contrapartida, valores de diversidade beta em metacomunidades expostas a mudanças ambientais, como uso do solo, variam consideravelmente entre diferentes regiões e táxons (Leão *et al.* 2020; Petsch *et al.* 2021; Schneck *et al.* 2022). Dessa forma, grande atenção têm sido dada para meios alternativos de se medir os efeitos de mudanças ambientais sobre a biodiversidade, e

um exemplo significativo é o entendimento do papel que as interações entre as espécies (e.g. tróficas e mutualísticas) têm na manutenção das comunidades (Poisot *et al.* 2016) e, possivelmente, na regulação de como elas respondem a mudanças ambientais (Tylianakis & Morris 2017).

1.2. Redes ecológicas e mudanças ambientais

De forma geral, redes ecológicas descrevem sistemas complexos onde unidades (e.g., indivíduos e espécies), conectam-se entre si por links que denotam as interações entre elas. Redes ecológicas fornecem informações valiosas sobre a estrutura dos ecossistemas, e são comumente utilizadas para representar interações como presa-predador (tróficas), animal-planta (mutualísticas e de herbivoria) e parasita-hospedeiro (parasitárias) (Guimarães 2020). No nível de comunidades, redes são utilizadas para investigar os mecanismos que regulam as interações entre espécies (Allesina *et al.* 2008; Brose *et al.* 2019), propriedades emergentes em sua estrutura (ou arquitetura) (Bascompte 2009; Dunne *et al.* 2002b), e de que forma essa estrutura pode ser associada a fatores ambientais (Thompson & Gonzalez 2017; Tylianakis & Morris 2017). Ao longo dos anos, uma série de métodos e métricas foram desenvolvidas para se quantificar a estrutura e complexidade de redes ecológicas (Delmas *et al.* 2019; Guimarães 2020). Destacam-se métricas bastante utilizadas, como riqueza (número de espécies), tamanho da rede (número de links), densidade de links (número médio de links por espécie), conectância (proporção de interações observadas em relação ao número máximo possível), nível de aninhamento (interações estabelecidas por especialistas formam um subconjunto daquelas realizadas por generalistas), modularidade (formação e compartimentos dentro da rede), e centralidade (mede o quão “influente” – e.g., mais conectada – as espécies são dentro da rede) (Delmas *et al.* 2019).

Estudos sobre alterações na estrutura de redes ecológicas são populares também, devido a relação entre estrutura, complexidade e estabilidade dos ecossistemas (Dunne *et al.* 2002b; Landi *et al.* 2018; Thebault & Fontaine 2010). A relação entre complexidade e estabilidade é um debate antigo na ecologia (Landi *et al.* 2018), e o principal argumento a favor dessa tese foi, de certa forma, proposto por MacArthur (1955), que sugeriu que a estabilidade aumenta com o número de espécies e interações entre elas (e.g., maior conectância). Mais tarde, Robert Paine (1966) complementou esse argumento, mostrando que a diversidade de espécies, e consequentemente a estabilidade em uma rede trófica, está ligada com o número de predadores na rede. Estas ideias iniciais foram desafiadas por Robert May (1972), que demonstrou matematicamente que sistemas mais diversos tendem a apresentar comportamento mais instável, conforme o número de espécies aumenta. O trabalho de Robert May (1972) foi bastante criticado, principalmente pelo argumento de que as comunidades aleatórias utilizadas por ele não simulavam ecossistemas reais, ignorando, por exemplo, diferenças observadas entre níveis tróficos (Landi *et al.* 2018). Além disso, estudos posteriores sobre a arquitetura de redes tróficas indicaram que a estrutura dos ecossistemas não é aleatória (Dunne *et al.* 2002b, a), reforçando a ideia de que mais realismo ecológico era preciso para o entendimento da relação entre complexidade e estabilidade (Landi *et al.* 2018). Assim, outras variáveis, além da diversidade, passaram a ser consideradas, como por exemplo, a força das interações presa – predador, que podem levar ao aumento da estabilidade em redes pequenas, mas apresenta um efeito inverso em redes maiores (Gross *et al.* 2009).

Mudanças ambientais, como as causadas por intervenções humanas, podem influenciar a estrutura das redes ecológicas por meio de três mecanismos principais: modificações na composição das espécies, na probabilidade ou frequência de

interações, e em processos evolutivos (Tylianakis & Morris 2017). Modificações na composição de espécies são resultados diretos de dinâmicas de invasões e extinções (Wardle *et al.* 2011), o que faz com que as interações variem devido à separação ou sobreposição de espécies no espaço (Poisot *et al.* 2015; Tylianakis & Morris 2017). Em contrapartida, mudanças na frequência de interações dependem da probabilidade de encontro das espécies no espaço (Tylianakis & Morris 2017). Por exemplo, o consumo de presas é fortemente afetado por flutuações ambientais (Penn *et al.* 2017), principalmente devido à sensibilidade de predadores a distúrbios, inclusive espécies generalistas (Wimp *et al.* 2019). Esse efeito na população de predadores pode alterar a razão presa – predador (Ryall & Fahrig 2005), o que levaria a redução na probabilidade de encontro entre as espécies. Por fim, mudanças ambientais causadas por intervenções humanas influenciam características intrínsecas da história de vida das espécies, alterando traços fundamentais para que as interações ocorram (e.g., tamanho corporal e fenologia; Brose *et al.* 2019; Loeuille 2019). Tais mudanças também podem resultar em perdas ou ganhos de interações, mesmo que a co-ocorrência e abundância favoreçam a associação entre as espécies (Tylianakis & Morris 2017).

Independente do mecanismo associado à modificação, a escala analisada exerce grande influência na forma como as redes respondem às variações ambientais (Tylianakis & Morris 2017). Localmente, espera-se que mudanças ambientais influenciem a complexidade das redes por meio de alterações na abundância e na ocorrência de espécies (Sabatino *et al.* 2010), na taxa de consumo de presas por predadores (Penn *et al.* 2017) e na realização de potenciais interações (Laliberté & Tylianakis 2010). Na escala regional (e.g., metacomunidades), mudanças ambientais podem levar a modificações estruturais severas nas redes (Thompson & Gonzalez

2017), podendo acarretar num processo de homogeneização espacial das redes de interações (Laliberté & Tylianakis 2010). Porém, respostas das redes a mudanças ambientais no nível de metacomunidades (ou meta-redes) dependem de outros processos atuando em conjunto. Por exemplo, modelos preveem que, ainda que as comunidades sejam afetadas por processos exclusivamente locais, como a presença de distúrbio, resposta das redes ecológicas dependerão da capacidade de dispersão dos organismos entre as manchas (Galiana *et al.* 2018; Pillai *et al.* 2010; Thompson & Gonzalez 2017). Ou seja, quando a dispersão é alta, a estrutura local da rede de interação se mantem, graças a capacidade que alguns consumidores (e.g., predadores de topo) tem de se deslocar no espaço, explorando recursos em diferentes manchas e garantindo a coexistência regional (Pillai *et al.* 2010).

1.3. Os ecossistemas de água doce

Os ecossistemas de água doce figuram entre os ecossistemas mais afetados por mudanças antrópicas ao redor do mundo (Reid *et al.* 2019; Vörösmarty *et al.* 2010). O crescimento desordenado da população humana e o aumento do consumo isolam corpos d'água em paisagens urbanas e agrícolas, e afetam faces distintas de sua biodiversidade por meio da destruição de habitats, escassez de recursos e poluição (Foley 2005; Vörösmarty *et al.* 2010). No entanto, ainda que uma atenção crescente seja dada a forma como redes tróficas são afetas por mudanças ambientais em ecossistemas dulcícolas (Chen *et al.* 2021; Ho *et al.* 2022; Jackson *et al.* 2020; O'Gorman *et al.* 2019), estudos ainda carecem de um entendimento detalhado sobre aspectos fundamentais. Por exemplo, de que forma diferenças intrínsecas entre lagos e riachos influenciam na resposta das redes tróficas a mudanças climáticas globais e de uso do solo. Ou ainda, como agrotóxicos utilizados de forma sistemática na

produção agrícola influenciam aspectos como a estabilidade de redes tróficas, em corpos d'água ao longo de paisagens agrícolas.

Mudanças climáticas e de uso do solo influenciam redes tróficas em ecossistemas dulcícolas por diferentes caminhos. Ao passo em que áreas de vegetação natural são convertidas em paisagens agrícolas, a complexidade das redes tróficas é reduzida por alterações na composição de espécies e interações (Jackson *et al.* 2020; Wilkinson *et al.* 2018), dominância de espécies generalistas (Schürings *et al.* 2022; Wilkinson *et al.* 2018), e efeitos em cascata (e.g., aumento de herbivoria em face da extinção de predadores de topo; Estes *et al.* 2011). Como resultado, redes tróficas em regiões com intenso uso do solo são simplificadas, com redução de níveis tróficos e de sua diversidade funcional (Chen *et al.* 2021; Jackson *et al.* 2020; Price *et al.* 2019). Mudanças climáticas, por sua vez, podem levar redes ao colapso por conta de limitações impostas ao fluxo de biomassa entre níveis tróficos (Ledger *et al.* 2013; Rosset *et al.* 2017), extinções de espécies sensíveis, como predadores de topo com alta demanda energética (Jackson *et al.* 2020; Wootton 2017), e alterações na conectividade hidrológica, que pode levar manchas ao isolamento geográfico (Palmer & Ruhi 2019).

Além da simplificação da paisagem, atividades agrícolas também influenciam redes tróficas por meio da contaminação por agroquímicos, utilizados de forma indiscriminada para aumento da produção agrícola (Hayasaka *et al.* 2012; Mello *et al.* 2019; Rumschlag *et al.* 2020). Evidências empíricas mostram que a contaminação de corpos d'água por inseticidas (e.g., fipronil) levam a modificações no tamanho corporal, na abundância e na composição de espécies não-alvo, principalmente invertebrados (Hayasaka *et al.* 2012; Hébert *et al.* 2021). Tais mudanças, consequentemente, refletirão na forma como consumidores e recursos interagem, podendo levar redes

tróficas a colapsarem. Em contrapartida, fertilizantes químicos podem levar corpos d'água a eutrofização, modificando a base de redes tróficas por meio do crescimento excessivo de espécies dominantes, como cianobactérias (Burford & O'Donohue 2006). Além disso, apesar destes compostos geralmente afetarem determinados grupos biológicos, seus efeitos podem ser detectados em grupos diversos, ao longo das cadeias tróficas, por meio de efeitos cascata (Rumschlag *et al.* 2020).

1.4. Como esta tese aborda o tema

Em um cenário crescente de mudanças ambientais globais (Guiden *et al.* 2019; Johnson *et al.* 2017), os ecossistemas estão expostos a condições cada vez mais intensas e imprevisíveis (Potapov *et al.* 2021). Isso dificulta nossa capacidade rastrear os efeitos na biodiversidade, e investigar como as interações entre as espécies são afetadas é fundamental para uma real compreensão da natureza. Além disso, esforços recentes têm mostrado que as respostas de redes tróficas a mudanças ambientais não são diretas, e dissolvem-se numa intrincada teia de relações entre variáveis (Gibert 2019; Ho *et al.* 2022; Rumschlag *et al.* 2020), formando um sistema complexo e que demanda um olhar mais holístico sobre este fenômeno. Deste modo, esta tese se propõe a aventurar-se na complexidade das relações entre redes tróficas e mudanças ambientais em ecossistemas aquáticos, considerando os caminhos diretos e indiretos pelos quais as mudanças ambientais influenciam comunidades multitróficas em diferentes escalas. Dividida em dois capítulos independentes, esta tese primeiro aborda como redes tróficas em lagos e riachos respondem a mudanças climáticas e de uso do solo, considerando diferenças intrínsecas entre esses ecossistemas (capítulo 1). Depois, por meio de uma abordagem experimental com metacomunidades planctônicas, explorei o papel de agroquímicos (inseticidas e fertilizantes) na sincronia e variação temporal de produtores e consumidores (capítulo

2), ao longo de diferentes escalas (local e regional) e níveis de organização (populações, comunidades e metacomunidades).

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2. Direct and indirect relationships of climate and land use change with food webs in lakes and streams

Abstract

Climate and land use change can independently affect food web structure. However, their direct and indirect relationships with food webs are not well understood. This is particularly relevant for freshwater ecosystems, which are strongly affected by global threats and differ substantially in attributes and functioning. Here, we investigated direct and indirect relationships between climate and land use changes and freshwater food web structure, while considering the differences between lakes and streams. We compiled 51 food webs, spanning 12 countries and six continents to investigate the direct and indirect relationships between land use intensity, changes in air temperature and precipitation, and food web structure, using structural equation modelling (SEM). We further tested how lake and stream food webs differ in their responses to environmental change by applying a multigroup analysis to our SEM. We found that connectance was positively related to both land use intensity and increases in air temperature and precipitation in stream food webs, whereas in lakes it was only related to temperature. These findings suggest a dominance of generalists where conversion to agriculture and urbanization has been intensified, and temperature has increased. Food web vertical structure was negatively related to land use and increases in air temperature and precipitation, but climatic predictors were only linked to network structure through a negative relationship with the fraction of top consumers. While land use intensity was directly related to food web structure, complex relationships between changes in climate and network topology were mediated by the fraction of top consumers. Also, as food webs in lakes and streams responded differently to land use and climate change, we suggest that their intrinsic characteristics

must be explicitly considered to fully understand the effects of global changes on freshwater biodiversity.

Keywords: connectance, freshwater, networks, precipitation, structural equation modeling, temperature, trophic interactions

2.1. Introduction

Food webs tend to respond fast to environmental change (Estes et al., 2011; Tylianakis & Morris, 2017). Empirical evidence shows that land use change affects food web specialization, trophic chain length and functional diversity (Chen, Dudgeon, & Liew, 2021; Jackson et al., 2020; Price, Sertić Perić, Romero, & Kratina, 2019). Model predictions suggest that climate change might simplify food webs, with loss of interactions and dominance of generalist species (Ledger, Brown, Edwards, Milner, & Woodward, 2013; O'Gorman et al., 2019). Although some progress has been done recently (e.g., Hayden et al., 2019; Sánchez-Hernández, Hayden, Harrod, & Kahilainen, 2021), the direct and indirect effects of both climate and land use change on food webs are still far from being fully understood. In addition, inherent properties of ecosystems, such as physical, biogeochemical, and biological aspects, influence the response of communities to environmental change, as already shown in lakes and rivers (Rosset, Ruhi, Bogan, & Datry, 2017). As freshwater ecosystems are among the most affected ecosystems by land use intensification and climate change (Reid et al., 2019; Schürings, Feld, Kail, & Hering, 2022; Vörösmarty et al., 2010), understanding how food webs respond to these major global threats could help identify what controls food web stability in lakes and streams, as well as inform ecosystem management based on food web structure monitoring (Thompson, Dunne, & Woodward, 2012).

The conversion of natural to agricultural and urban landscapes affects freshwater food webs through changes in species composition and interactions (Jackson et al., 2020; Wilkinson, Yeo, Tan, Fikri, & Ewers, 2018). As ecosystems are simplified, species composition changes due to the extinction of more sensitive species and the dominance of generalists (Schürings et al., 2022; Wilkinson et al., 2018). Once consumers with broader feeding range dominate community assembly (Schürings et al., 2022), food web structure reorganizes due to changes on connectance (Riede et al., 2010). Food web structure also changes in face of cascading effects caused by agricultural and urban practices. For instance, while algae and invertebrates are directly influenced by agricultural pollution (Dubey & Dutta, 2020; Rumschlag et al., 2020), species at higher trophic levels experience bottom-up effects, which may contribute to shortening food chain length due to the exclusion of more sensitive predators (Jackson et al., 2020; Price et al., 2019; Rumschlag et al., 2020). On the other hand, predator extinction leads to top-down effects in food webs, such as enhanced herbivory (Estes et al., 2011) and increased presence of omnivores, who can survive where specialist predators cannot (Wootton, 2017).

Food web structure also changes with altered temperature and precipitation regimes (Jackson et al., 2020; O'Gorman et al., 2019). For instance, warming can increase the demand for food resources and thus increase herbivory and predator-prey interactions (Hunt, Galatowitsch, & McIntosh, 2017; O'Connor, 2009). As resources are depleted due to consumption, top predators should be negatively affected or even replaced by omnivores or species at lower trophic levels, because large consumers struggle to keep up with their metabolic demands (Jackson et al., 2020; Rosenblatt, Smith-Ramesh, & Schmitz, 2017; Wootton, 2017). However, the effects of warming on food web structure may also depend on the predator's ability to

find and handle prey, in which more time spent searching and less time handling usually indicates consumer generalism, and thus, increased food web connectance (Petchey, Brose, & Rall, 2010).

Changes in precipitation regimes influence food web structure by limiting the flux of biomass across trophic levels, and by reducing species and interactions, particularly involving predators (Ledger et al., 2013; Pires, Marino, Srivastava, & Farjalla, 2016; Rosset et al., 2017). Altered precipitation also affects hydrological connectivity in freshwater ecosystems, which in turn disrupt community composition through changes in water flow and spatial flux of organisms among stream sites (Palmer & Ruhi, 2019). On the other hand, drying conditions show more pronounced effects in alpha diversity in lakes than in streams, as lakes are comparatively less connected to each other (Rosset et al., 2017). These ecosystem-based responses indicate that the influence of altered precipitation patterns on food webs might also depend on physical aspects of ecosystems (Rosset et al., 2017).

Lakes and streams differ profoundly regarding to their physical, biogeochemical, and biological aspects. One of the main differences between lakes and rivers is their hydrodynamics: lakes are relatively stagnant (Wetzel, 2001), while streams are more dynamic (Allan & Castillo, 2009). This affects their physicochemical properties, such as salinity and pH, which tend to be more variable in lakes and more stable in rivers (Allan & Castillo, 2009; Wetzel, 2001). Another difference is their geological history: lakes can have diverse origins and ages, while rivers are more uniform in their formation and evolution (Allan & Castillo, 2009; Wetzel, 2001). These differences have implications for the ecology and biodiversity of these systems and influence how communities respond to environmental changes (Ho et al., 2022; Merz et al., 2023; Rosset et al., 2017).

Most research on freshwater biodiversity is still centered around community descriptors (e.g., species richness as a response variable; Siqueira, Bini, Thomaz, & Fontaneto, 2015), which might not show consistent responses to environmental change. For example, previous studies have shown that species richness might not systematically change through time (Dornelas et al., 2014) and varying responses of beta-diversity to land use intensity across different regions and taxa (Leão, Siqueira, Torres, & Montag, 2020; Petsch, Blowes, Melo, & Chase, 2021; Schneck et al., 2022). By focusing on food webs, we expected to understand how drivers of environmental change affect species interactions, and their influence on emergent properties of interacting multispecies communities.

Here, we expand the understanding about how environmental drivers influence freshwater food webs, including multicontinental distributed data and considering the differences between lake and stream ecosystems. We first tested the hypothesis that (H1) land use intensification favors generalist consumers in freshwater food webs due to ecosystem homogenization (Estes et al., 2011; Schürings et al., 2022). We expected a decrease in the number of top specialist consumers (Ho et al., 2022; Merz et al., 2023) and, consequently, an increase in herbivory and omnivory (Wootton, 2017), decrease in mean trophic levels, and higher connectance values in both lake and streams, as generalists concentrate a higher number of links within few species (Riede et al., 2010; Tylianakis & Morris, 2017). However, (H2) the exclusion of top predators could also reduce connectance, as in cases where environmental changes caused the extinction of generalist top consumers with relatively broader diets in lakes (Merz et al., 2023) and streams (Ho et al., 2022).

Regarding temperature change, we tested the following hypothesis: (H3) warming increases the demand for food resources, selecting against large top

predators and favoring omnivores and species at lower trophic levels (Jackson et al., 2020; Wootton, 2017). Thus, for both lakes and streams, we expected warming to decrease top consumer occurrence (Ho et al., 2022; Merz et al., 2023), increase herbivory and omnivory (O'Connor, 2009; Wootton, 2017), and reduce mean trophic levels within food webs (Jackson et al., 2020; O'Gorman et al., 2019). As in freshwater ecosystems top predators can be large consumers with wider niche breadth (Ho et al., 2022), we expected connectance to decrease with warming in lakes (Merz et al., 2023) and streams (Ho et al., 2022; O'Gorman et al., 2019). However, (H4) warming can also select for more generalist species (Ho et al., 2022). This could lead to an increase in the number of interactions per node, consequently, increasing connectance (Gibert, 2019; Petchey et al., 2010).

Regarding precipitation change, we tested the following hypothesis: (H5) water limits the flux of biomass across trophic levels and regulate the loss of species and interactions (Ledger et al., 2013; Rosenblatt et al., 2017). Thus, we expected reduced precipitation to decrease top consumers, mean trophic level and connectance in lakes and streams (Ho et al., 2022; Merz et al., 2023). However, (H6) physical aspects of ecosystems govern how precipitation change influences freshwater communities (Rosset et al., 2017). Therefore, we expected a stronger effect of precipitation change in stream food webs, because of intrinsic hydrological connectivity of stream networks (Palmer & Ruhi, 2019). In this sense, reduced precipitation would isolate food webs, decreasing the number of species and interactions.

2.2. Methods

2.2.1. Food web data

We obtained data from three sources: the Mangal interaction database, using the 'rmangal' package in R (Poisot, Baiser, et al., 2016), the GlobAl databasE of traits and food Web Architecture (GATEWAY) version 1.0 (Brose et al., 2019), and the Interaction Web Data Base (IWDB, 2020). Food webs in these repositories were included in our analysis only if 1) sampling was designed to target community interactions instead of single species diet; 2) data were available as matrix, edge list or network graphic formats; 3) methods to infer species interactions were described; 4) data included predation, herbivory and detritivory interactions; 5) the precise geographical coordinates of the sites were available; and 6) sampling year was available. We checked the original publications for geographical location, sampling date and methods, when information was not available in the databases. In cases where sites were sampled more than once, resulting in replicated data for the same location, we selected samples with the highest number of nodes. As lake food webs meeting our criteria were rarely found in the databases, we also performed a search in the Web of Science Core Collection (see Supporting Information for searched terms). Because the land use database we used contained data from 1992 to 2015 (see section bellow), we selected only food webs sampled within this period. We considered the sampling date as the year in which the researchers concluded field sampling. To calculate food web metrics (section 2.3. bellow), we transformed original data into adjacency matrices ($A = [i, j]$), in which i represented the resources and j represented consumers. After filtering the data, we ended up with 51 freshwater food webs sampled in 12 countries and six continents (Fig. S1, Table S1). A list of the food web sources can be found in Appendix 1.

2.2.2. Environmental variables

To test the relationship between food web properties and land use intensity, we first characterized land use on the surroundings of the sites where food webs were originally sampled. We did that by extracting land cover information from the global ESA CCI database (ESA, 2017), an annually generated land cover product at 300 m resolution for the period 1992 – 2015. The data set comprises 38 land cover categories, following the classification system developed by the United States Food and Agricultural Organization (ESA, 2017). To extract cell values, we established a 1 km buffer around the locations where food webs were sampled. In cases of food webs sampled in large water bodies, such as lakes, we extended the 1 km buffer to the total surrounding area of the water body (see Fig. S2 in the Supporting Information for an example). To estimate land use intensity, we modified an earlier approach (van Klink et al., 2020) and attributed a value of 1.0 to cells falling into cropland areas (categories 10, 11, 12, 30, and 40 in the ESA CCI database), 1.5 to urban areas (category 190), and 0.0 to cells pertaining to other categories (e.g., forest and grassland areas). Because categories 30 and 40 are mixed cropland and natural vegetation (30 – mosaic (>50%) cropland and (<50%) natural vegetation, and 40 - mosaic (>50%) natural vegetation and (<50%) cropland), their cell values were down-weighted to 0.75 and 0.25, respectively. The values reported in the analysis represent the average of land use within the 1 km buffer.

To quantify local changes on climate conditions, we gathered maximum air temperature and precipitation data from the TerraClimate database, a monthly generated product for climate and climatic water balance for global terrestrial surfaces at ~ 4 km for the period 1958 – 2015 (Abatzoglou, Dobrowski, Parks, & Hegewisch, 2018). We extracted monthly values that represented means of daily maximum

temperature and precipitation at the exact cell coordinates where food webs were sampled, following a timeframe of 30 years past to the sampling year. So, for each food web location we had 360 records of maximum temperature and precipitation (12 per year, each representing a monthly mean value). Then, we modeled temporal climatic data as a function of time using generalized additive models, with a temporally autocorrelated structure (AR of order 1) using the R package 'mgcv' (Wood, 2017). Finally, we extracted the time coefficients of the model, which summarized the estimated long-term trend for maximum temperature and precipitation at each site location (see Table S2 and Fig. S3 in the Supporting Information for examples). We selected maximum temperature and precipitation because these variables are better representations of the warming and water deficit conditions considered in our hypothesis.

2.2.3. Food web variables

Although a variety of metrics to describe the structure of food webs are available (Delmas et al., 2019), here we measured only aspects related to our hypotheses. We calculated food web variables separately for each one of the 51 food webs, and only then used these variables in our model (section below). We quantified properties related to the number of nodes and interactions within the food web, as fraction of top consumers (nodes that are not consumed by other nodes in the food web), and fraction of herbivory (proportion of interactions between primary consumers and basal resources). For each food web, we also calculated network level responses, such as mean omnivory index (the average value of the omnivory index calculated for each node within the food web), mean trophic level index (the average value of species trophic levels for each node within the food web), and connectance (as the residuals from a linear regression between the number of realized interactions and the number

of possible ones, both log-transformed). We decided to represent connectance as residual connectance to control for the negative relationship between food web size (i.e., number of nodes) and connectance (Dunne, Williams, & Martinez, 2002). This approach allows us to compare distinct food webs in terms of higher or lower connectance than expected by their size. Omnivory and trophic level indexes were calculated using the package 'NetIndices' (Kones, Soetaert, van Oevelen, & Owino, 2009).

2.2.4. Data analysis

Because environmental change might influence food web structure through direct and indirect pathways, we used structural equation modeling (SEM) to test our hypotheses. Structural equation models provide means to link multiple predictor and response variables in a single casual network, in which paths indicate hypothesized relationships between variables (Lefcheck, 2016). SEMs are especially useful when response variables can also act as predictor variables of another response variable – i.e., when they mediate an indirect relationship. For example, land use intensity is expected to reduce the number of top consumers in a food web, which is expected to affect connectance.

We opted for a SEM based on local estimation to analyze our data. Different from global estimation SEM, which treats variables as arising from the same data generating process, SEM based on local estimation is a more flexible option because the assumptions pertaining to each response are evaluated individually (Lefcheck, 2016; Shipley, 2000). Thus, endogenous variables are addressed and estimated separately, and the model is then pieced together (Lefcheck, 2016; Shipley, 2000). SEM based on local estimation also has other advantages compared to SEM based on global estimation, such as the option of fitting generalized and mixed-effects models,

the incorporation of non-independence, and the need of only enough samples to fit the individual regressions, which relaxes many of the assumptions associated with global estimation (Lefcheck, 2016).

The paths in our model represented hypothesized casual relationships among explanatory and response variables (Supporting Fig. S4). We fit linear mixed-effects models to decompose the relative contribution of explanatory variables to the quantified metrics of food webs to land use and climate, both direct and indirect (see the Supporting Information for model description). The term “direct” here means a relationship not mediated by other variables in the SEM, but that can rely on mechanisms or variables not included in this work. In our SEM, exogenous variables included land use intensity, maximum temperature change and precipitation change. Mean trophic level index was considered only as an endogenous variable, while fraction of top consumers, mean omnivory index, fraction of herbivory and connectance were considered both as exogenous and endogenous variables (Supporting Fig. S4). In our model, connectance is also considered as an inverse of food web overall interaction specialization. In this sense, the higher the connectance, the lower the specialization of predator prey interactions.

To account for variation among food webs caused by differences in methodological procedures, we incorporated the sampling method (modeling, gut-content, and gut-isotope analysis) used in each of the original studies in our dataset as a random factor within the mixed models (Brimacombe, Bodner, Michalska-Smith, Poisot, & Fortin, 2023). Modeling refers to food webs in which species interactions were determined through modeling procedures, such as the Ecopath modeling approach (Christensen & Pauly, 1992), which is based on empirical data. Gut-content refers to food webs in which predator-prey interactions were determined through an

evaluation of predator gut content analysis. The gut-isotope category represents food webs in which trophic interactions were record through a combination of gut content and isotope signature analysis.

To check if the relationships between environmental predictors (e.g., land use) and food web metrics (e.g., connectance) differ between lakes and streams, we ran the so-called multi-group SEM. By using this approach, we followed the same principle of a linear model that includes an interaction between a numerical (e.g., change in temperature) and a categorical (ecosystem type) predictor variable – i.e., Analysis of Covariance. However, instead of focusing on a single response variable, the interaction term is applied through the entire SEM. Thus, we were able to test how all linear coefficients representing the relationships between the response and the numerical predictor variables varied among ecosystem types. Overall model fit was evaluated using Shipley d-separation test, a method that evaluates the assumption of all variables being conditionally independent. This procedure identifies the sets of missing relationships in the model, and tests whether the effect is not different from zero ($P > 0.05$). The test of d-separation produces a Fisher's C statistic that can be described by a chi-square distribution (Shipley, 2000). To test for differences in food web metrics between lakes and streams, we fitted generalized linear models with gaussian distribution for fraction of top consumers, fraction of herbivory and connectance (t-test; $P < 0.05$), and gamma distribution for mean trophic level index (t-test; $P < 0.05$) and mean omnivory index (z-test; $P < 0.05$). We set dispersion parameter = 1, for mean omnivory index model.

To ensure that differences in the number of lake and stream food webs would not affect our model results, we performed a sensitivity analysis by randomly subsampling 14 out of 37 stream food webs and running the model with the 14

available lake food webs. This process was then repeated 999 times (see the Supporting Information for details). We conducted the piecewise SEM using the R package ‘piecewiseSEM’ (Lefcheck, 2016), and for the linear mixed models, we used the function ‘lme’ in the R package ‘nlme’ (Pinheiro, Bates, DebRoy, Sarkar & R Core Team, 2021). All data and codes used to run the analysis are freely available at Zenodo (Barbosa & Siqueira, 2022).

2.3. Results

We found that food web structure differed between lakes and streams (Fig. 1). This happened especially regarding the fraction of herbivory interactions, which was higher in stream than in lake food webs ($t = 4.959$, $P < 0.0001$, Fig. 1b). Lake food webs had higher average values of omnivory ($z = 2.071$, $P = 0.0384$) and higher trophic level indexes ($t = 3.568$, $P = 0.0008$) than stream food webs (Fig.1c and Fig.1e, respectively). On the other hand, the fraction of top consumers ($t = 0.146$, $P = 0.885$) and the residual connectance ($t = - 1.215$, $P = 0.230$) did not vary statistically between ecosystem types (Fig. 1a and Fig.1d, respectively). As expected, rivers and streams accounted for most of the food webs in our dataset ($n = 37$, against 14 in lakes). However, differences in the number of lake and stream food webs did not affect model results, as demonstrated by our sensitivity analysis (Fig. S5 – S9 in Supporting Information).

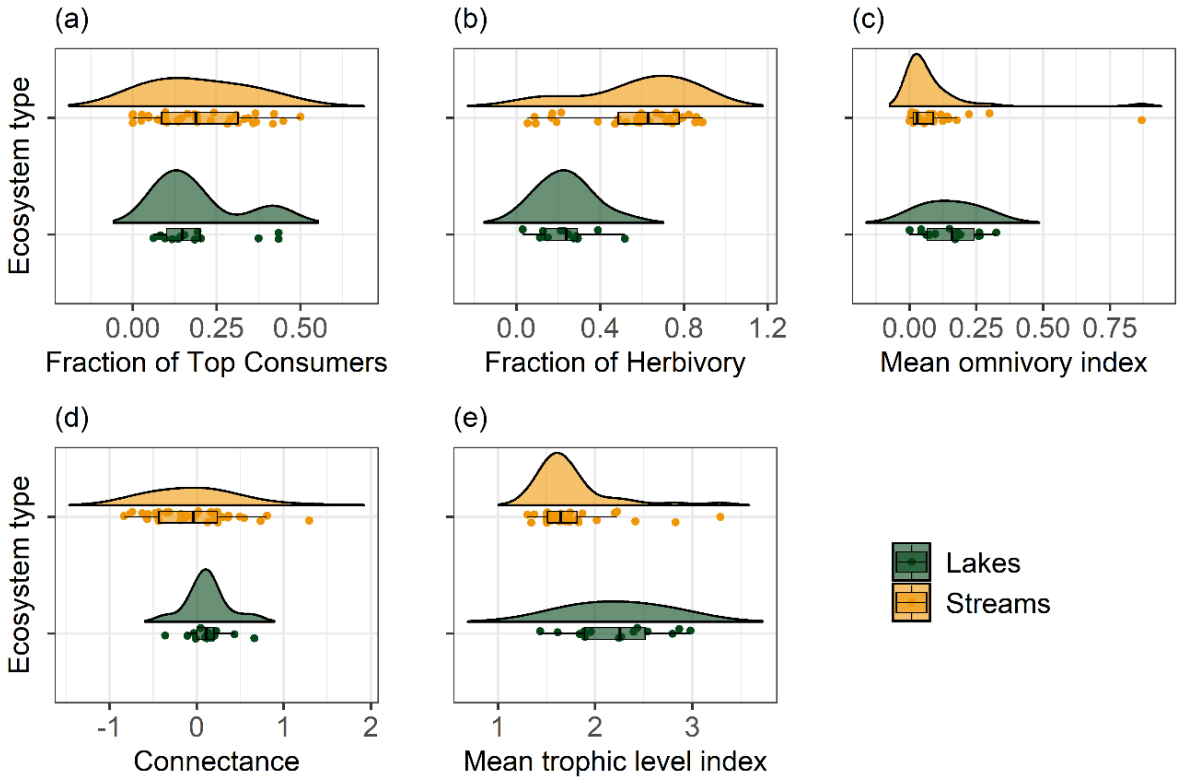

Figure 1. Raincloud plots of food web metrics calculated for lakes and streams in our multicontinental data set. Half-violin diagrams show adjusted density estimates, and boxplots show observed data variation in the fraction of top consumers (a), fraction of herbivory (b), mean omnivory index (c), connectance (d) and mean trophic level index (e), among both ecosystems.

Overall, multi-group SEM fitted the data well (C_4 = 4.631, P = 0.327, Fig. 2), and revealed interesting associations of freshwater food webs to environmental predictors. While food web metrics were directly linked to land use intensity, relationships with climate change variables occurred through indirect paths mediated by the fraction of top consumers within the food web (Fig. 2). The model also showed how some of the relationships between food webs and environmental changes differed between lakes and streams, particularly those involving land use intensity and temporal trends in

precipitation. In total, five relationships differed among ecosystem types: land use intensity and connectance, land use intensity and mean trophic level index, fraction of top consumers and connectance, precipitation change and fraction of top consumers, and fraction of herbivory and mean trophic level index (Fig. 2).

While there was no relationship between land use intensity and connectance in lakes, connectance in streams was positively related to land use intensity through a direct path, partially supporting H1 (Fig. 2). On the other hand, temperature and precipitation trends were positively related to connectance on streams through changes in the fraction of top consumers, partially supporting H3 (Fig. 2). We also found that land use intensity was negatively related to mean trophic level index in streams (H1), and climate change was negatively related to mean trophic level through changes on the fraction of top consumers (H3; H5; Fig. 2). Contrary to our hypothesis (H1; H3), food web omnivory and herbivory were not related to either climate change or land use intensity (Fig. 2).

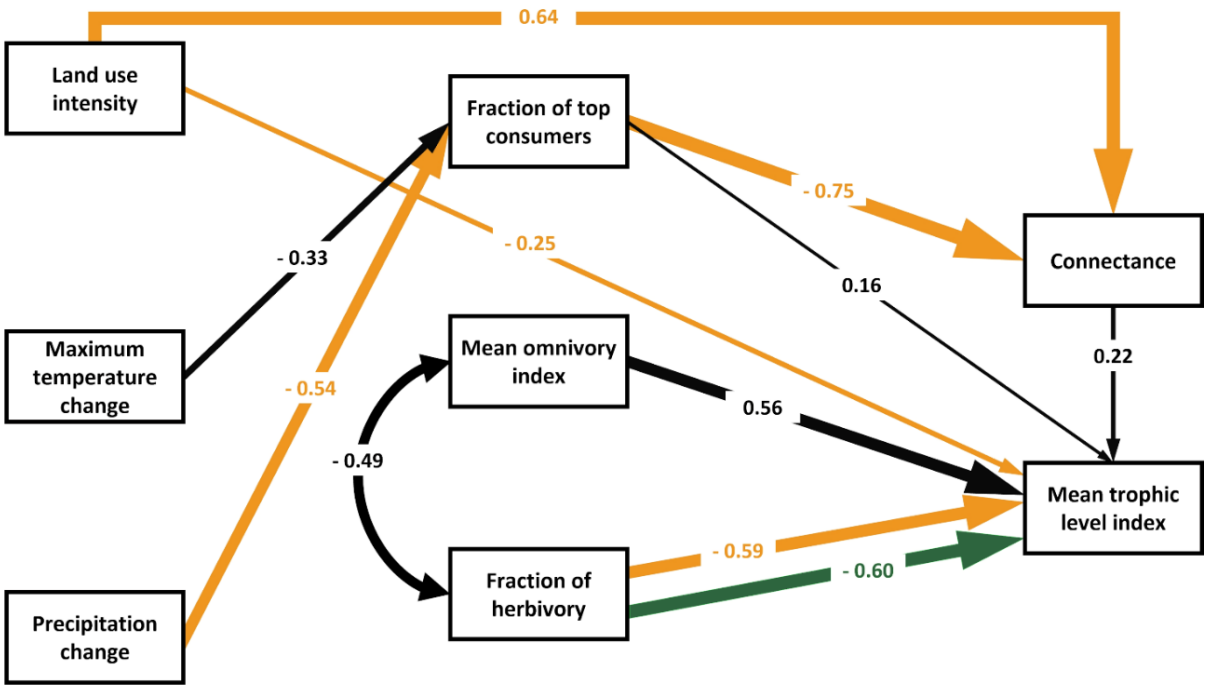

Figure 2. Multi-group SEM that relates land use intensity and climate change to the structure of lake and stream food webs across continents. Green, orange and black arrows represent significant relationships among variables in lakes, streams and in both ecosystems, respectively. Arrow width represents relationship magnitude, following standardized coefficients (*β*) reported along the connections. Non-significant relationships were hidden for clarity (see Supporting Fig. S4 for full model).

The exogenous variables explained a large portion of the variation in some food web metrics (Table 1). As shown by marginal and conditional R^2 values, food web inference methods (modeling, gut-content, and gut-isotope analysis), which were included in the SEM as random effects, did not affect the relationships between predictors and connectance. On the other hand, the sampling method used to infer trophic interactions explained a great amount of the variation in the fraction of herbivory (Table 1).

Table 1. Marginal and Conditional R^2 values obtained for individual endogenous variables, following the multi-group SEM that relates lake and stream food webs to land use intensity and climate change.

Endogenous variables	Marginal R^2	Conditional R^2
Mean omnivory index	0.09	0.17
Fraction of top consumers	0.23	0.33
Fraction of herbivory	0.14	0.39
Connectance	0.47	0.47
Mean trophic level index	0.70	0.90

2.4. Discussion

Our analysis of multi-continental data indicates that freshwater food webs are strongly related to land use intensity and changes in temperature and precipitation that occurred in the last 30 years. Most of the relationships between land use and climate change and food web structure were mediated by the fraction of top consumers, meaning that they were indirect, and differed between lakes and streams. More specifically, whereas connectance and mean trophic level in stream food webs were related to all predictors used to represent environmental change, in lake food webs, only mean trophic level was affected, and only by increases in temperature.

Land use change tends to impose novel, more severe conditions to communities (Schürings et al., 2022; Tylianakis & Morris, 2017; Wilkinson et al., 2018). These conditions can affect food webs substantially, from loss of species and interactions (Jackson et al., 2020; Price et al., 2019; Wilkinson et al., 2018) to reduced trophic levels and simplification of overall food web structure (Estes et al., 2011; Jackson et al., 2020). Because connectance is related to food web robustness to extinction (Dunne et al., 2002), it is considered a good metric to describe how communities respond to environmental change. Although lower connectance is expected in freshwater food webs under land use intensification, due to the extinction of large consumers with broader diets (Ho et al., 2022; Merz et al., 2023), our model indicates an increase in connectance with increasing land use intensity. This result suggests that as land use change simplifies habitats, it selects for more generalist consumers (Chen et al., 2021; Schürings et al., 2022) and, consequently, increases the number of links per species in the network. However, we also found that connectance was only related to land use intensity in stream food webs, which

reinforces the idea of intrinsic ecosystem characteristics driving community responses to disturbances (Rosset et al., 2017).

Although connectance is expected to decrease with warming in freshwater ecosystems (Merz et al., 2023; O'Gorman et al., 2019), potentially due to the loss of top predators with wider niche breadth (Ho et al., 2022), our results indicate that food webs were more connected in sites where temperature has increased in the past 30 years (Gibert, 2019; Petchey et al., 2010). Higher connectance under warming conditions could be attributed to an increase in the strength of realized interactions within food webs (O'Connor, 2009). Such scenario can lead to depletion of resources and, consequently, to local extinction of functional feeding groups, such as carnivores (Rosenblatt et al., 2017). Our findings indicate that this might be the case but only in streams, as warming was related to reduced fraction of top consumers, and lower fraction of top consumers was related to higher connectance in our model.

Stream food webs were more influenced by changes in precipitation than those in lakes. This can be attributed to the effects of increasing precipitation on water flow in streams, as flow regimes alter community composition due to changes in the spatial flux of organisms among sites (Palmer & Ruhi, 2019). Contrary to streams, lake food webs were not influenced by precipitation change, which reinforces the role of physical structures inherent to ecosystems as mediators of how biodiversity is affected by environmental change (Rosset et al., 2017). However, future work is needed to elucidate the actual mechanisms behind how ecosystem differences govern how precipitation reorganizes food webs.

Overall, mean trophic level was negatively related to land use intensity in stream food webs, but contrary to our hypotheses, this relationship was not mediated by the loss of top predators, increase in generalist consumers (i.e., higher connectance), or

herbivory and omnivory (Riede et al., 2010; Wootton, 2017). Thus, these results suggest that other aspects not included in our model, such as changes in species composition and interactions, and cascading effects, might affect how food chain length is influenced by land use intensity (Price et al., 2019; Rumschlag et al., 2020; Tylianakis & Morris, 2017). On the other hand, the loss of top consumers mediated negative relationships between warming and mean trophic level in both ecosystems, and precipitation and mean trophic level in streams. This is expected because warming might influence top consumers due to metabolic constraints (Rosenblatt et al., 2017), while precipitation might affect stream consumers due to changes in flow regimes (Palmer & Ruhi, 2019).

Although we carefully selected the data included in this study, some caveats need to be considered. First, although we consider the data to be reasonably well distributed in terms of spatial coverage, the number of food webs per region was unbalanced and specifically low for some regions. If there are important drivers of food web structure operating at the regional scale, we might have missed them. Second, we used maximum air temperature to estimate warming trends, instead of water temperature, which was not available for most sampling locations in our data set. Even though species interactions could be more related to variables describing their local environment, air temperature can be considered a good proxy for water temperature (Mohseni & Stefan, 1999; Stefan & Preud'homme, 1993). Third, even though we are confident that our data analysis is robust for identifying whether the detected relationships are due to the predictors or to confounding variation in the way interactions were inferred, large-scale analysis, spanning across continents, can be affected by some co-variates that are difficult, if not impossible, to consider. For example, although we recognize that local, direct measures of physical and chemical

characteristics (stream width, lake depth, pH, conductivity) would have been ideal, these data were not universally available. Fourth, we modelled static responses (food web structure metrics) as a function of dynamic predictors (climate trends). Although new insights could arise from modeling dynamic responses of food web structure in function of dynamic environmental change, such data are extremely rare, even more so at the spatial scale we focused on this study. In addition, changes in food web structure are the consequence of both dynamic and static process. Finally, as food web sampling methods differ largely among primary studies, and even though we statistically considered some of the variability by including sampling method as random effects in our model (Brimacombe et al., 2023), potential biases might have persisted in variables we could not control, such as sampling period and taxonomic resolution. This could be solved in the future, with approaches that intend to standardize how species interactions data are collected and organized (Poisot, Baiser, et al., 2016). Despite these caveats, considering the strength of the relationships we found, we consider that our results help advancing our understanding of the effects of environmental change on the structure of freshwater food webs.

Our study reveals that fundamental aspects of food web structure, such as connectance and the number of trophic levels, are related with climate and land use changes. This is alarming because the conversion of natural to modified landscapes has been happening rapidly and potentially reaching points of no return (Ellis et al., 2021). We also found that the fraction of top consumers in a food web plays a major role linking the drivers of environmental change and food web structure. This is in consonance with previous findings that indicate the importance of predator diversity to food web structure and dynamics (Estes et al., 2011). Although environmental predictors were not related to herbivory and omnivory in our analyses, we show that

such interactions are strongly related to the vertical structure of food webs and help to explain a great portion of the variation in the number of trophic levels in food webs. This strengthens the necessity of considering species interactions to understand and predict past and current biodiversity changes (Poisot, Stouffer, & Kéfi, 2016). Finally, as our results implicitly show, the way freshwater food webs are structured under environmental disturbances depend on intrinsic aspects of ecosystems and, thus, must be considered to fully understand the effects of environmental change on freshwater biodiversity.

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2.6. Data availability

The data and code that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.6501834

2.7. Appendix 1: Data Sources

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2.8. Supporting information

2.8.1. Food web data

The final data set included 51 freshwater food webs, averaging 59 nodes and 196 links, sampled in 12 countries and six continents. See main text for information on how food webs were acquired and selected for this study.

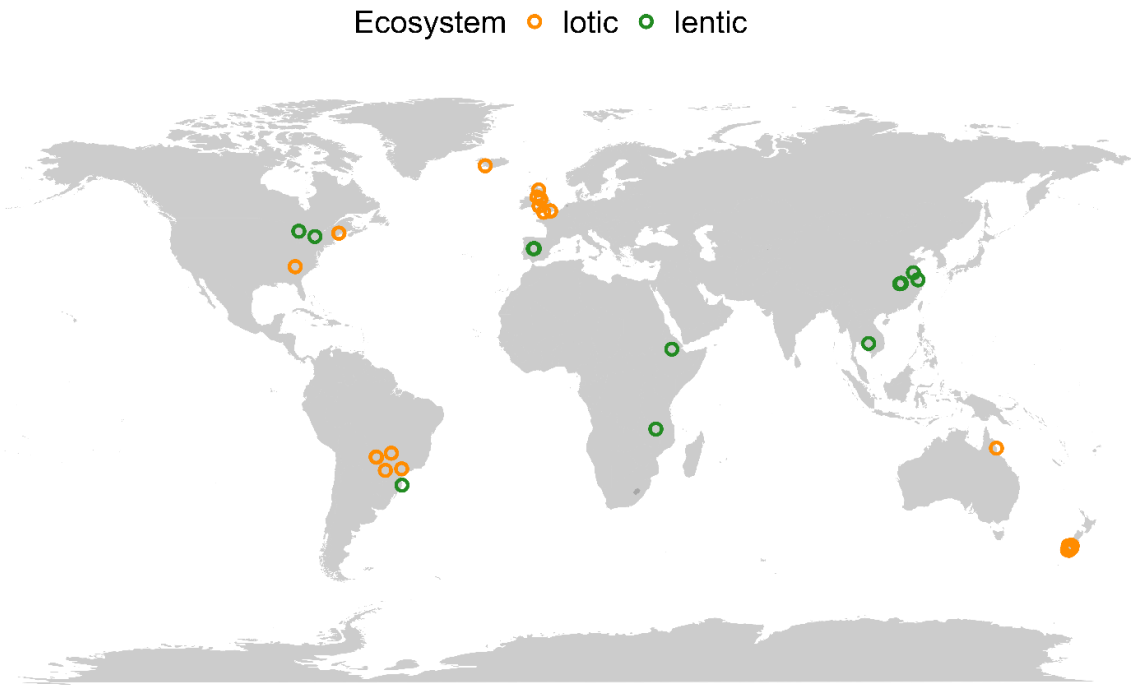

Fig. S1. Geographical distribution of the freshwater food webs used in this study. Green and orange circles indicate lake and stream food webs, respectively. Coordinates are based on data set meta-data and original publications. Central points are considered for large water bodies (e.g., Lake Ontario). Sites in China, New Zealand and Spain are indistinguishable at this map scale. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Table S1: Detailed information on the food webs filtered and used for the local SEM analysis.

Food Web	Country	Continent	Ecosystem	Type	Method	Author
Afon Hafren 2005	United Kingdom	Europe	Stream	Lotic	Gut-isotope	Layer et al. [2]
Akatore A	New Zealand	Oceania	River	Lotic	Gut-content	Thompson & Townsend [3]
Allt a Mharcaidh	United Kingdom	Europe	Stream	Lotic	Gut-isotope	Layer et al. [2]
Baoan Lake	China	Asia	Lake	Lentic	Modeling	Guo et al. [4]
Berwick	New Zealand	Oceania	Stream	Lotic	Gut-content	Thompson & Townsend [5]
Blackrock Stream	New Zealand	Oceania	Stream	Lotic	Gut-content	Townsend et al. [6]
Broad Stream	New Zealand	Oceania	Stream	Lotic	Gut-content	Townsend et al. [6]
Broadstone Stream	United Kingdom	Europe	Stream	Lotic	Gut-isotope	Layer et al. [2]
Caballeros	Spain	Europe	Lake	Lentic	Gut-content	Sánchez-Hernández [7]
Canton Creek	New Zealand	Oceania	Stream	Lotic	Gut-content	Townsend et al. [6]
Catlins Stream	New Zealand	Oceania	Stream	Lotic	Gut-content	Thompson & Townsend [3]
Cimera	Spain	Europe	Lake	Lentic	Gut-content	Sánchez-Hernández [7]
Corrente River	Brazil	South America	River	Lotic	Modeling	Angelini et al. [8]
Coweeta1	United states	North America	Stream	Lotic	Gut-content	Thompson & Townsend [5]
Coweeta17	United states	North America	Stream	Lotic	Gut-content	Thompson & Townsend [5]
Dargall Lane	United Kingdom	Europe	Stream	Lotic	Gut-isotope	Layer et al. [2]
Dempsters Stream	New Zealand	Oceania	Stream	Lotic	Gut-content	Townsend et al. [6]
Duddon Pike Beck	United Kingdom	Europe	Stream	Lotic	Gut-isotope	Layer et al. [2]
German Creek	New Zealand	Oceania	Stream	Lotic	Gut-content	Townsend et al. [6]
Grande De Gredos	Spain	Europe	Lake	Lentic	Gut-content	Sánchez-Hernández [7]
Hardknott Gill	United Kingdom	Europe	Stream	Lotic	Gut-isotope	Layer et al. [2]
Healy Creek	New Zealand	Oceania	Stream	Lotic	Gut-content	Townsend et al. [6]
Hongze Lake	China	Asia	Lake	Lentic	Modeling	Guo [9]
Iceland Stream Is7 Aug 2008	Iceland	Europe	Stream	Lotic	Gut-content	O'Gorman et al. [10]
Iceland Stream Is8 Aug 2008	Iceland	Europe	Stream	Lotic	Gut-content	O'Gorman et al. [10]
Kye Burn	New Zealand	Oceania	Stream	Lotic	Gut-content	Townsend et al. [6]

Lake Biandantang	China	Asia	Lake	Lentic	Gut-content	Liu [11]
Lake Hayq	Ethiopia	Africa	Lake	Lentic	Modeling	Fetahi et al. [12]
Lake Huron	Canada	North America	Lake	Lentic	Modeling	Langseth et al. [13]
Lake Malawi	Tanzania	Africa	Lake	Lentic	Modeling	Nsiku et al. [14]
Lake Ontario	Canada	North America	Lake	Lentic	Modeling	Stewart & Sprules [15]
Lake Shangshe	China	Asia	Lake	Lentic	Modeling	Li et al. [16]
Lake Taihu	China	Asia	Lake	Lentic	Modeling	Xu et al. [17]
Little Kye Burn	New Zealand	Oceania	Stream	Lotic	Gut-content	Townsend et al. [6]
Martins	United states	North America	Stream	Lotic	Gut-content	Thompson & Townsend [5]
Mill Stream	United Kingdom	Europe	Stream	Lotic	Gut-isotope	Layer et al. [2]
Mosendale Beck	United Kingdom	Europe	Stream	Lotic	Gut-isotope	Layer et al. [2]
Mulgrave River	Australia	Oceania	River	Lotic	Gut-isotope	Rayner et al. [18]
Northcol	New Zealand	Oceania	Stream	Lotic	Gut-content	Thompson & Townsend [5]
Old Lodge	United Kingdom	Europe	Stream	Lotic	Gut-isotope	Layer et al. [2]
Paraguay River Bm Abaixo	Brazil	South America	River	Lotic	Modeling	Angelini et al. [19]
Paraguay River Bm Acima	Brazil	South America	River	Lotic	Modeling	Angelini et al. [19]
Parana River	Brazil	South America	River	Lotic	Modeling	Angelini & Agostinho [20]
Peri Lake	Brazil	South America	Lake	Lentic	Gut-content	Peralta-Maraver [21]
Potreirinho Creek	Brazil	South America	Stream	Lotic	Gut-content	Motta & Uieda [22]
Powder	New Zealand	Oceania	Stream	Lotic	Gut-content	Thompson & Townsend [5]
Stony Stream	New Zealand	Oceania	Stream	Lotic	Gut-content	Townsend et al. [6]
Sutton Stream	New Zealand	Oceania	Stream	Lotic	Gut-content	Townsend et al. [6]
Tonle Sap Lake	Cambodia	Asia	Lake	Lentic	Modeling	Chea et al. [23]
Troy	United states	North America	Stream	Lotic	Gut-content	Thompson & Townsend [5]
Venlaw	New Zealand	Oceania	Stream	Lotic	Gut-content	Thompson & Townsend [5]

Web of science searched keyword for lake food webs:

TI = (lake OR lakes OR pond OR ponds) AND TI = (food web OR food webs OR foodweb OR foodwebs OR food-web OR food-webs OR network OR networks) AND TI = (ecopath OR ecosim OR connectance OR topology OR structure OR architecture).

2.8.2. Land use intensity data for large waterbodies

Different from streams, which were buffered 1km around the exact location where researchers informed sampled, large lakes were buffered 1km surrounding their total waterbody extension.

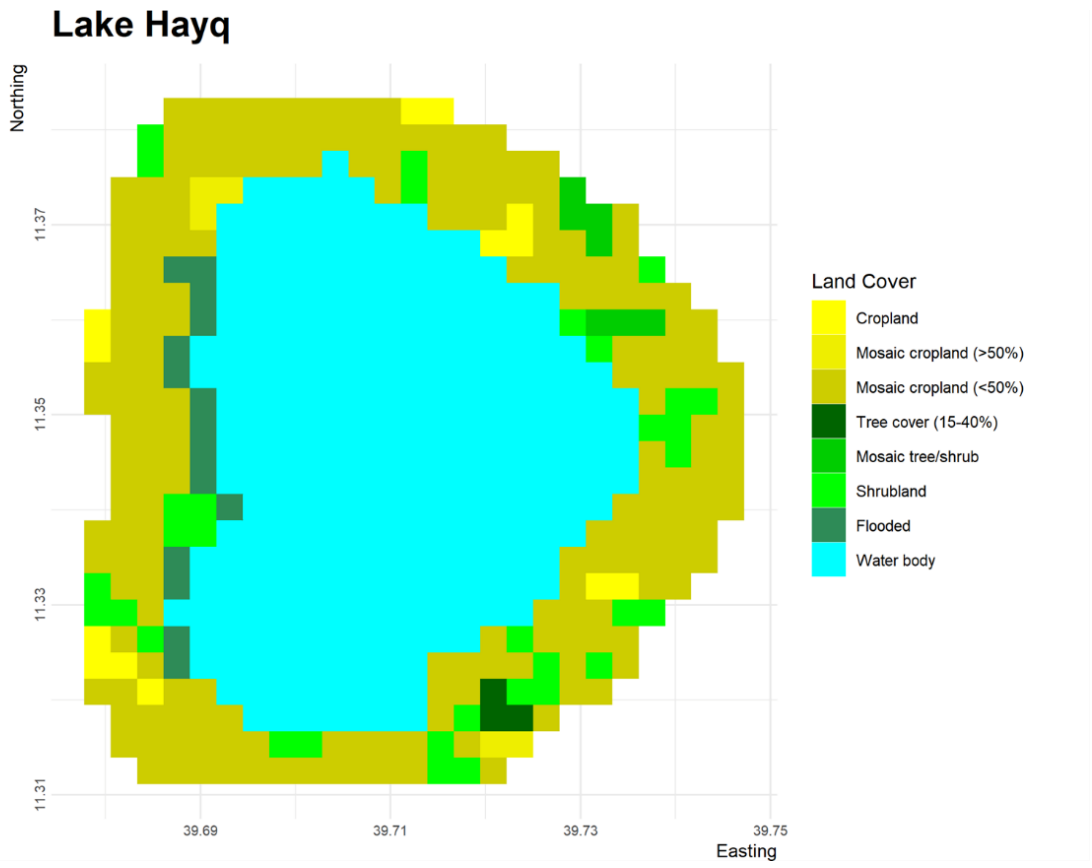

Fig. S2: Example of how land use intensity was obtained for large waterbodies. In this case, we considered all pixels surrounding lake extension under 1km for the measurement of land use intensity (see main text for a description of calculation methods, land use classes and attributed pixel values).

2.8.3. Climate data

To obtain a measurement of how climate changed over the past 30 years, we estimated long term trends of maximum temperature and precipitation at each food

web location, following Wood (2017). For this, we ran Generalized Additive Models, accounting for a temporally autocorrelated structure (AR of order 1) for each location and variable, with the R package *mgcv* (Wood, 2017). This allowed us to detect whether there was any increase in average maximum temperature and precipitation over time. From the model results (Table S2), we extracted linear coefficients that represents the estimated long-term trends, indicating the extent of increase/ decrease in the climate variable across the 30-year period. An example of how the coefficients were obtained is illustrated in Figure S4.

Table S2: Example of stats table from Generalized Additive Models of maximum temperature over time. Each model number represents a site where food webs were sampled, and the coefficients from the parameter time were used as a measure of temporal trend over a 30-year period for each site.

model	parameter	coef	se	CI_lower	CI_upper	pvalue
1	(Intercept)	10.15	0.17	9.817	10.483	-
1	time	0.003	0.001	0.002	0.005	0.0001
2	(Intercept)	14.577	0.124	14.334	14.82	-
2	time	-0.001	0.001	-0.002	0	0.2269
3	(Intercept)	8.843	0.14	8.568	9.118	-
3	time	0.003	0.001	0.002	0.004	<.0001
4	(Intercept)	21.251	0.175	20.908	21.593	-
4	time	0	0.001	-0.002	0.002	0.9474
5	(Intercept)	14.056	0.131	13.799	14.312	-
5	time	-0.001	0.001	-0.002	0	0.0985
6	(Intercept)	14.576	0.12	14.341	14.811	-
6	time	-0.001	0.001	-0.002	0	0.1053
7	(Intercept)	14.576	0.12	14.341	14.811	-
7	time	-0.001	0.001	-0.002	0	0.1053
8	(Intercept)	13.112	0.19	12.739	13.484	-
8	time	0.004	0.001	0.002	0.006	<.0001
9	(Intercept)	12.009	0.188	11.639	12.378	-
9	time	0.003	0.001	0.001	0.004	0.0027
10	(Intercept)	14.576	0.12	14.341	14.811	-

10	time	-0.001	0.001	-0.002	0	0.1053
11	(Intercept)	14.375	0.123	14.133	14.617	-
11	time	-0.001	0.001	-0.002	0.001	0.2992
12	(Intercept)	13.312	0.188	12.943	13.681	-
12	time	0.003	0.001	0.001	0.005	0.0012
13	(Intercept)	28.136	0.096	27.947	28.325	-
13	time	0.003	0	0.002	0.004	<.0001
14	(Intercept)	18.522	0.229	18.072	18.972	-
14	time	0.001	0.001	-0.001	0.003	0.1958
15	(Intercept)	18.522	0.229	18.072	18.972	-
15	time	0.001	0.001	-0.001	0.003	0.1958
16	(Intercept)	10.288	0.151	9.993	10.584	-
16	time	0.003	0.001	0.002	0.004	<.0001
17	(Intercept)	13.499	0.137	13.231	13.768	-
17	time	-0.001	0.001	-0.002	0	0.0676
18	(Intercept)	10.371	0.164	10.049	10.693	-
18	time	0.003	0.001	0.002	0.005	<.0001
19	(Intercept)	13.28	0.133	13.02	13.54	-
19	time	-0.001	0.001	-0.002	0	0.0786
20	(Intercept)	13.015	0.188	12.646	13.383	-
20	time	0.003	0.001	0.001	0.005	0.0011
21	(Intercept)	10.371	0.164	10.049	10.693	-
21	time	0.003	0.001	0.002	0.005	<.0001
22	(Intercept)	13.499	0.137	13.231	13.768	-
22	time	-0.001	0.001	-0.002	0	0.0676
23	(Intercept)	18.809	0.177	18.462	19.155	-
23	time	0.002	0.001	0	0.004	0.0173
24	(Intercept)	4.177	0.158	3.867	4.487	-
24	time	0.006	0.001	0.004	0.007	<.0001
25	(Intercept)	4.177	0.158	3.867	4.487	-
25	time	0.006	0.001	0.004	0.007	<.0001
26	(Intercept)	13.499	0.137	13.231	13.768	-
26	time	-0.001	0.001	-0.002	0	0.0676
27	(Intercept)	20.986	0.181	20.632	21.34	-
27	time	0.002	0.001	0.001	0.004	0.0082
28	(Intercept)	25.383	0.137	25.115	25.65	-
28	time	0.004	0.001	0.003	0.005	<.0001
29	(Intercept)	10.555	0.249	10.068	11.042	-
29	time	0.003	0.001	0.001	0.005	0.0071
30	(Intercept)	28.028	0.106	27.82	28.236	-
30	time	0.002	0	0.001	0.003	<.0001
31	(Intercept)	13.526	0.249	13.039	14.014	-
31	time	0.002	0.001	0	0.004	0.0636
32	(Intercept)	21.198	0.181	20.843	21.554	-
32	time	0.002	0.001	0.001	0.004	0.0081

33	(Intercept)	19.054	0.174	18.713	19.395	-
33	time	0.003	0.001	0.001	0.005	0.0002
34	(Intercept)	13.499	0.137	13.231	13.768	-
34	time	-0.001	0.001	-0.002	0	0.0676
35	(Intercept)	11.521	0.185	11.159	11.884	-
35	time	0.002	0.001	0	0.003	0.036
36	(Intercept)	13.506	0.182	13.149	13.862	-
36	time	0.004	0.001	0.002	0.005	<.0001
37	(Intercept)	9.943	0.164	9.622	10.265	-
37	time	0.003	0.001	0.002	0.005	<.0001
38	(Intercept)	27.857	0.106	27.648	28.065	-
38	time	0.002	0	0.001	0.003	0.0009
39	(Intercept)	13.425	0.131	13.168	13.683	-
39	time	-0.001	0.001	-0.002	0	0.1921
40	(Intercept)	13.309	0.19	12.938	13.681	-
40	time	0.004	0.001	0.002	0.006	<.0001
41	(Intercept)	30.614	0.135	30.349	30.879	-
41	time	0.001	0.001	0	0.002	0.1224
42	(Intercept)	30.503	0.142	30.224	30.781	-
42	time	0.001	0.001	0	0.002	0.2026
43	(Intercept)	28.154	0.139	27.881	28.426	-
43	time	-0.002	0.001	-0.003	-0.001	0.0044
44	(Intercept)	22.869	0.12	22.634	23.104	-
44	time	0.001	0.001	0	0.002	0.0196
45	(Intercept)	24.925	0.129	24.671	25.179	-
45	time	0.002	0.001	0.001	0.003	0.002
46	(Intercept)	13.776	0.128	13.524	14.027	-
46	time	-0.001	0.001	-0.002	0	0.1874
47	(Intercept)	15.033	0.125	14.787	15.278	-
47	time	-0.001	0.001	-0.002	0	0.1226
48	(Intercept)	15.033	0.125	14.787	15.278	-
48	time	-0.001	0.001	-0.002	0	0.1226
49	(Intercept)	31.648	0.132	31.388	31.907	-
49	time	0.002	0.001	0.001	0.003	0.0032
50	(Intercept)	11.639	0.186	11.275	12.004	-
50	time	0.002	0.001	0	0.004	0.0337
51	(Intercept)	14.061	0.126	13.813	14.308	-
51	time	-0.001	0.001	-0.002	0	0.1169

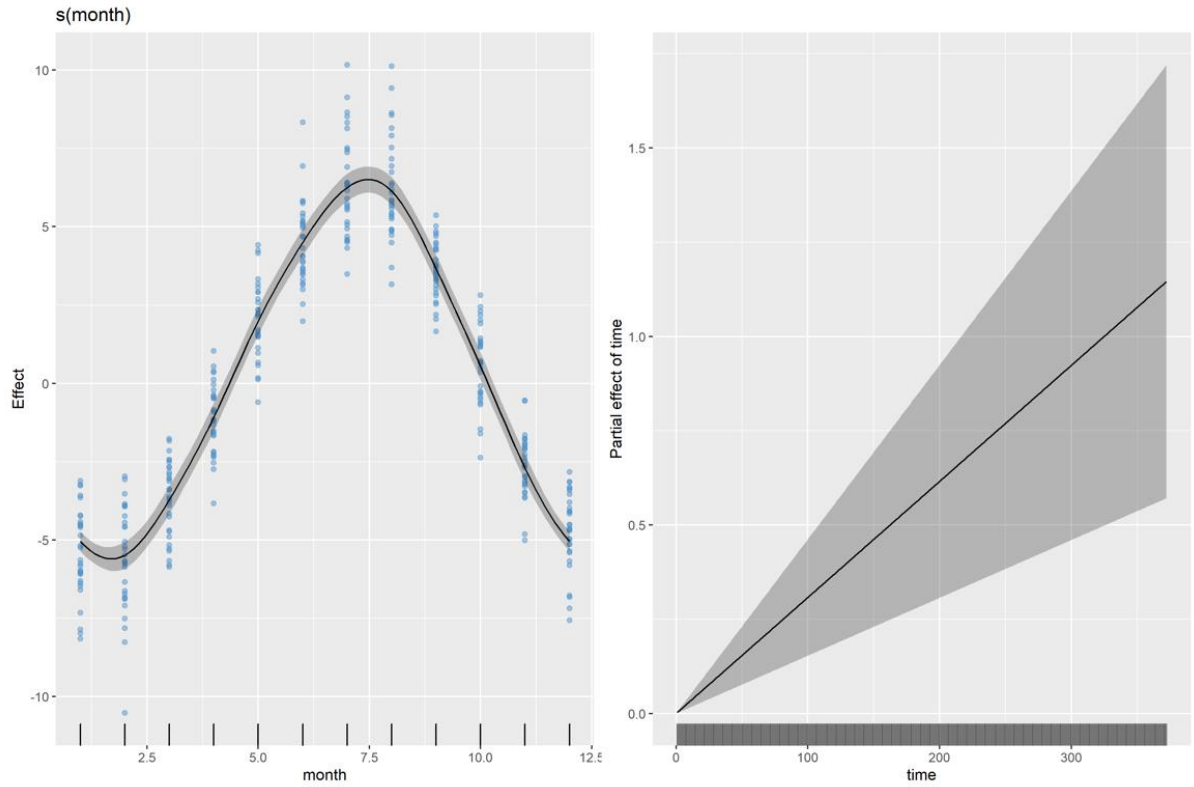

Fig. S3: Example of GAM terms for monthly maximum temperature at food web sampling location. The left panel is the estimated annual cycle for this location, and the right panel is the estimated long-term trend across the entire 30-year period (based on model fit).

2.8.4. Model description

We used a hypothetical model to evaluate the effects of land use intensity and climate change on the structure of food webs (Fig. S4). Food web sampling method (modeling, gut-content, and gut-isotope analysis) was considered as random effect within the model.

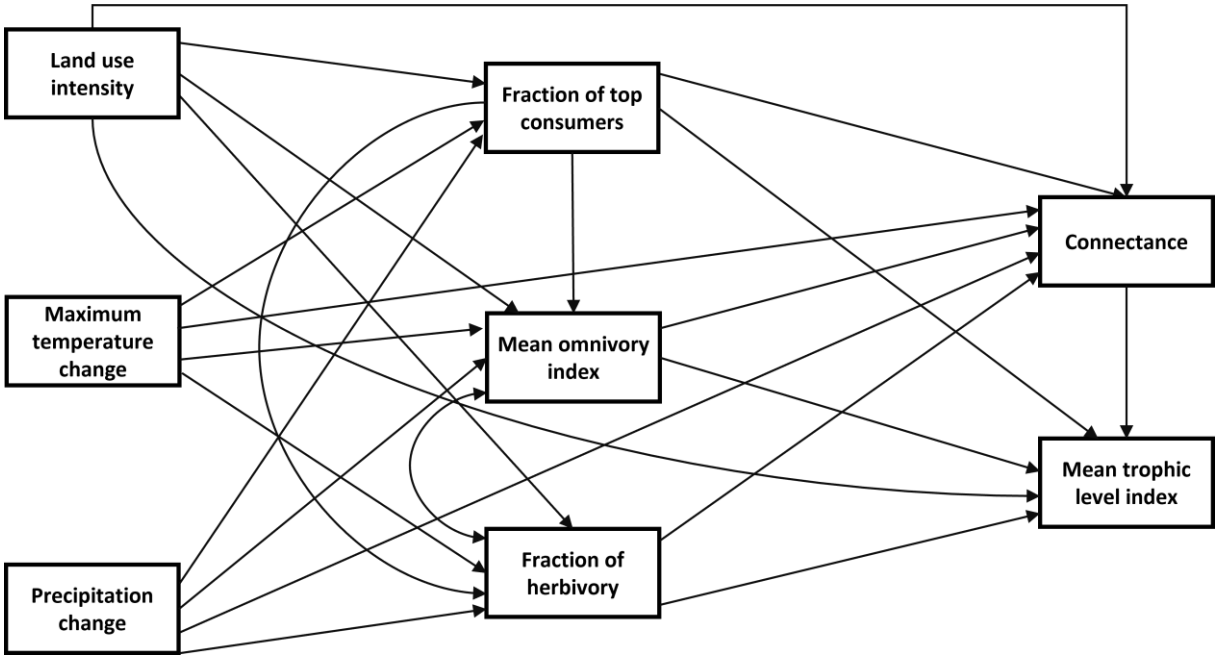

Fig. S4. Hypothetical model for the effects of land use intensity and climate change on the structure of lake and stream food webs**.** A standard regression coefficient (*β*) was retrieved for each relationship between exogenous and endogenous variables, using *piecewiseSEM* [1].

2.8.5. Sensitivity analysis

To ensure that differences in the number of lentic and lotic food webs compiled would not affect our model, we performed a sensitivity analysis in which we used the same number of lentic and lotic food webs by fitting the model on 999 networks randomly selected from our dataset.

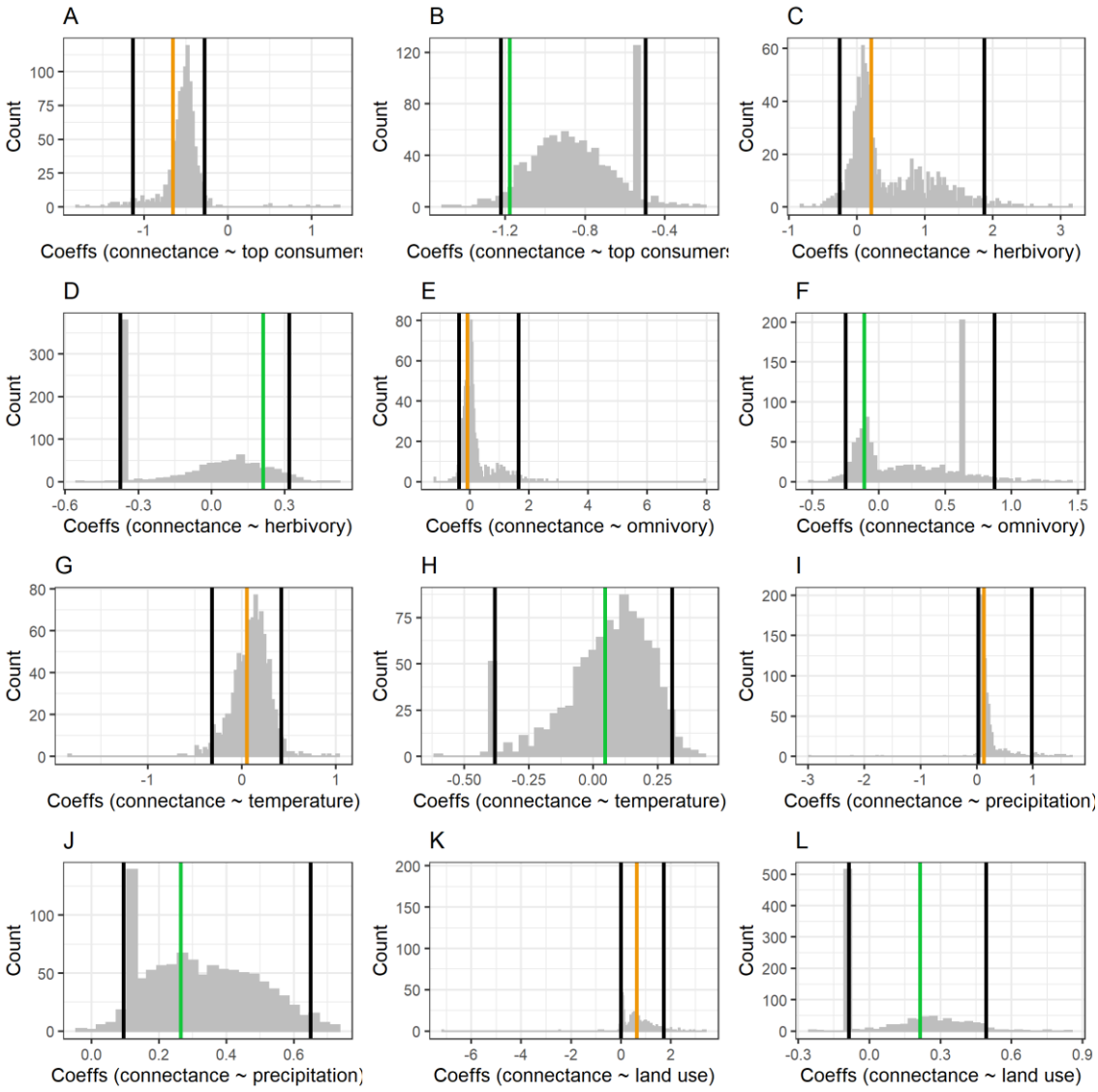

Fig. S5: Results of the sensitivity analysis performed with 999 lake and stream food webs randomly selected from our dataset. Green and orange lines indicate observed coefficients for the relationship between connectance and exogenous variables for lakes and streams, respectively.

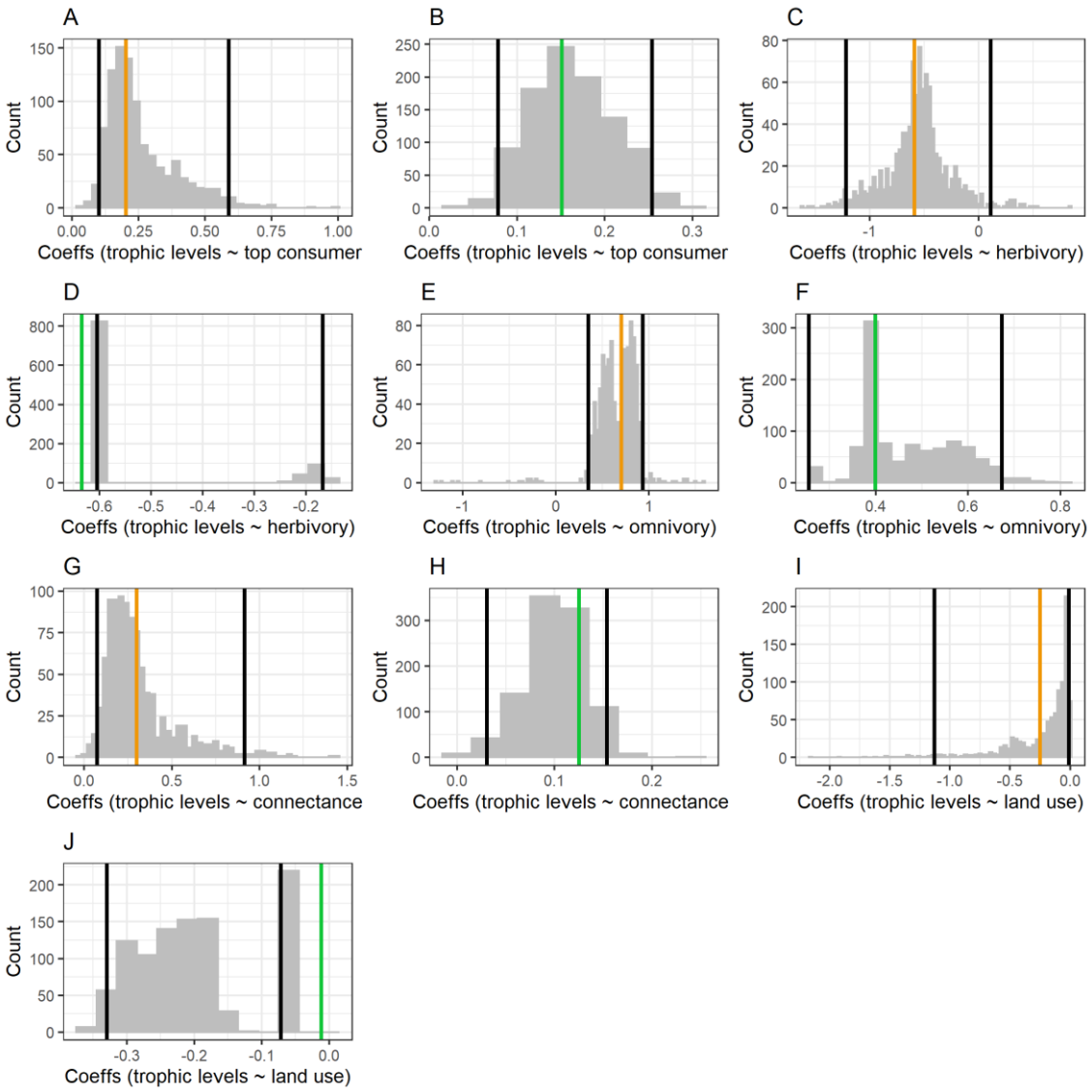

Fig. S6: Results of the sensitivity analysis performed with 999 lake and stream food webs randomly selected from our dataset. Green and orange lines indicate observed coefficients for the relationship between mean trophic level index and exogenous variables for lakes and streams, respectively.

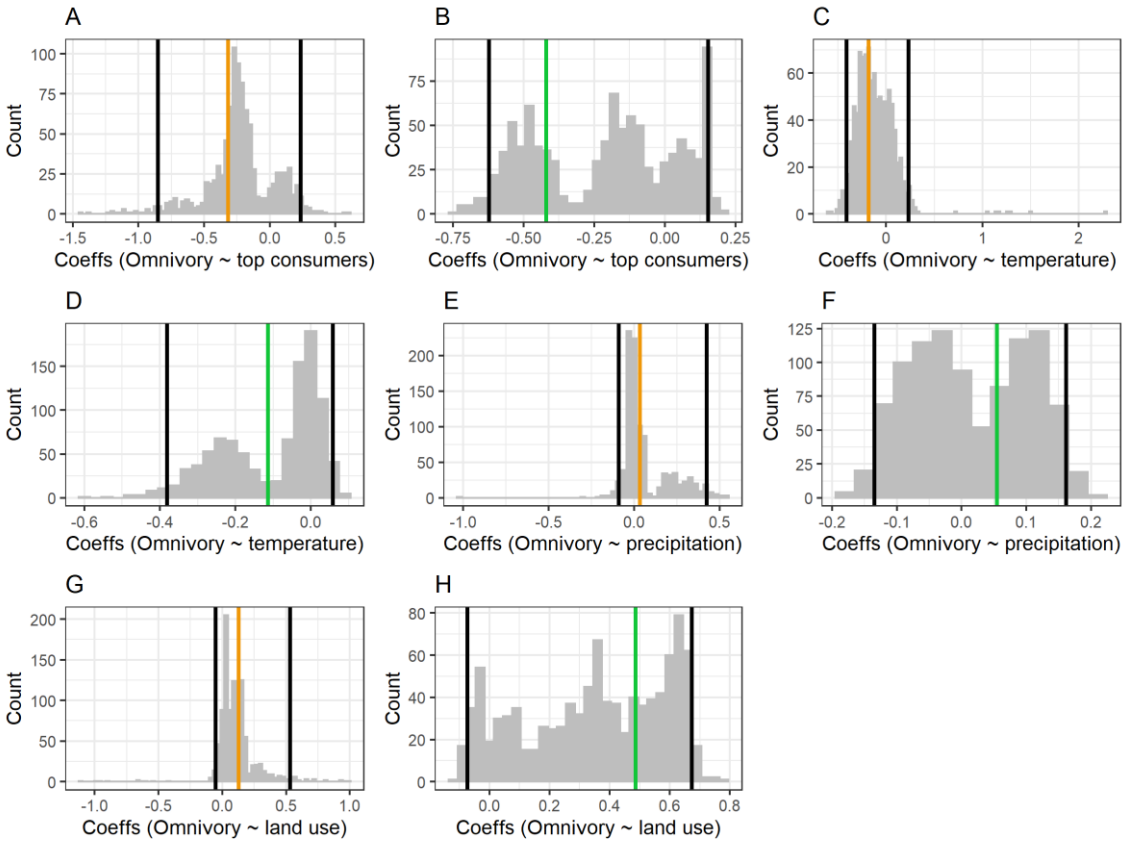

Fig. S7: Results of the sensitivity analysis performed with 999 lake and stream food webs randomly selected from our dataset. Green and orange lines indicate observed coefficients for the relationship between mean omnivory index and exogenous variables for lakes and streams, respectively.

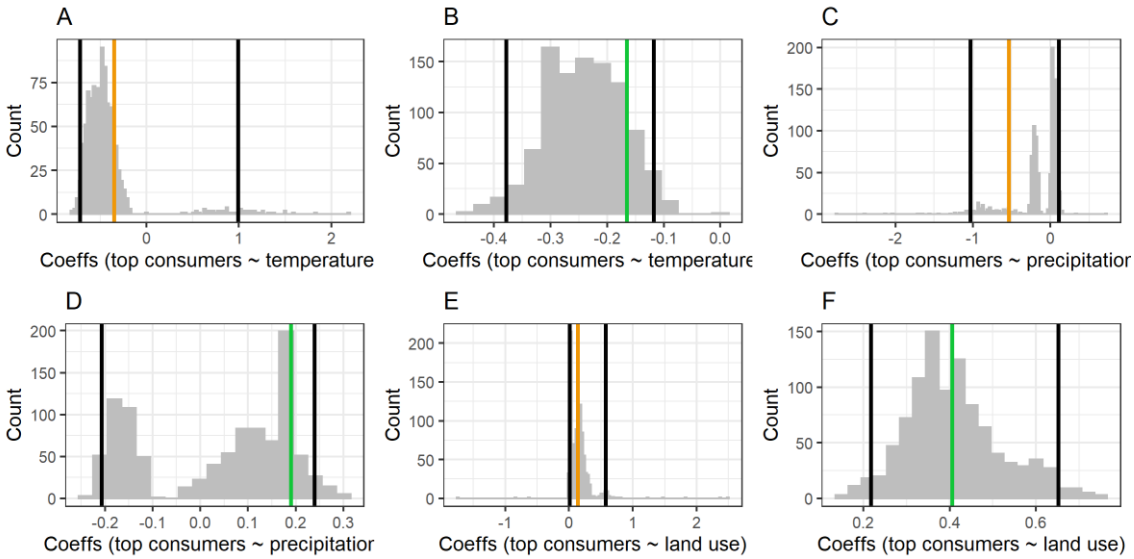

Fig. S8: Results of the sensitivity analysis performed with 999 lake and stream food webs randomly selected from our dataset. Green and orange lines indicate observed coefficients for the relationship between fraction of top consumers and exogenous variables for lakes and streams, respectively.

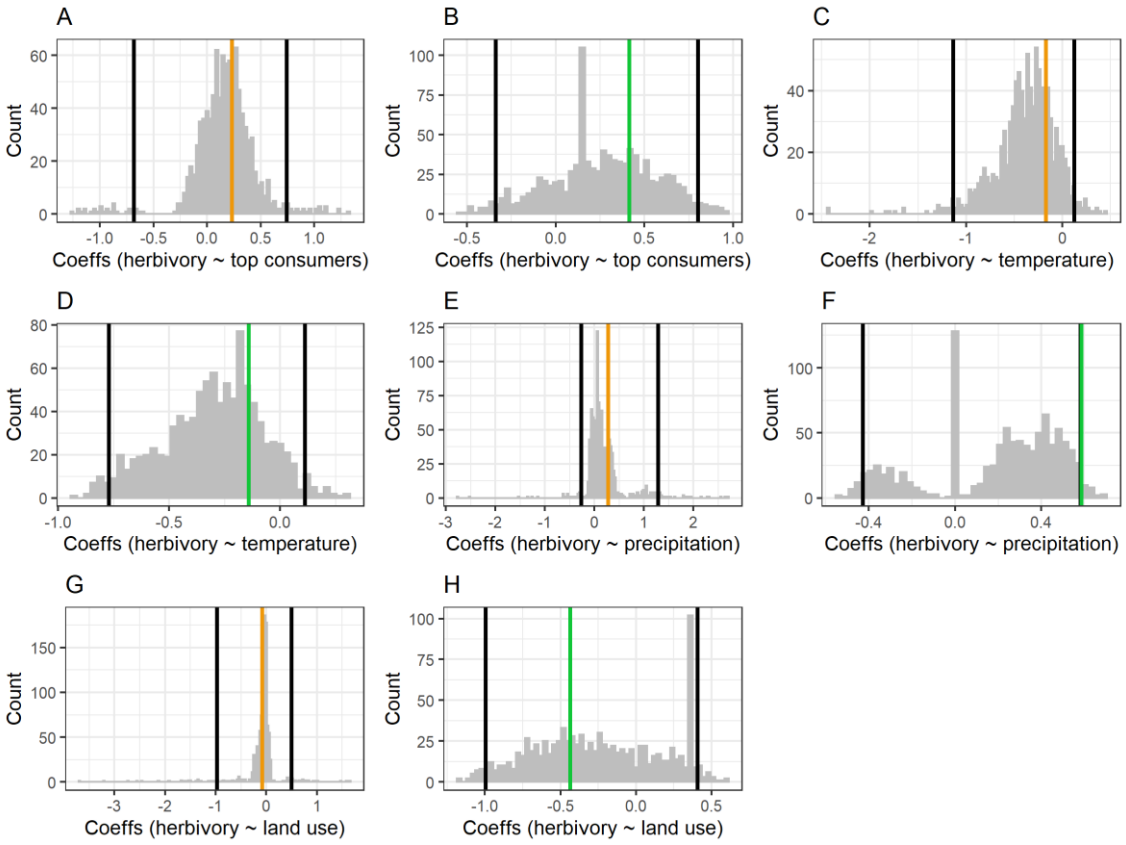

Fig. S9: Results of the sensitivity analysis performed with 999 lake and stream food webs randomly selected from our dataset. Green and orange lines indicate observed coefficients for the relationship between fraction of herbivory and exogenous variables for lakes and streams, respectively.

2.8.6. Supporting information references

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3. Agrochemical intensification induces contrasting responses on temporal variability of planktonic producers and consumers across scales

Abstract

Agrochemicals are widely used to increase crop production, both through nutrient enrichment (fertilizers) and control of pest populations (pesticides). When these compounds reach freshwater ecosystems, they affect non-target organisms and drive substantial changes to aquatic biota, disrupting ecosystem function and stability. However, information is still scarce, and we do not know how the exposure to agrochemicals influences stability of producers and consumers across scales. Here, we experimentally simulated agricultural landscapes to investigate how temporal variability in abundances of producers and consumers propagates across scales, under varying levels of regional exposure to insecticide and fertilizer compounds. Using structural equation modeling, we showed that insecticide exposure increases temporal variability in consumer populations, showing a clear influence on the frequency and magnitude of abundance fluctuations. However, variability did not propagate to communities, and overall community variability of consumers decreased because insecticide exposure also desynchronized populations. At regional scale, metacommunity exposure to fertilizer was positively related to reduced community spatial synchrony, thus decreasing metacommunity variability of consumers and producers. On the other hand, local diversity was positively related to temporal variability of consumer communities, indicating that, although fertilization did not influence local variability directly, it might have made species functionally redundant and susceptible to future perturbations. In summary, our results suggests that agrochemical intensification changes how temporal variability propagates from local to

regional scales in freshwater ecosystems, but results are contrasting and depend on organism trophic position, level of organization and type of agrochemical considered.

Keywords: fertilizer, insecticide, metacommunity, plankton, stability, structural equation modelling, synchrony.

3.1. Introduction

Agrochemicals are employed to increase crop production worldwide (Sharma et al., 2019), but their overuse represent a considerable source of diffuse contamination to freshwater biodiversity (Hayasaka et al., 2012; Mello, Cardoso, Colombo-Corbi, & Corbi, 2019; Rumschlag et al., 2020). For instance, empirical evidence shows that insecticide contamination disrupts aquatic communities, changing body size, abundance and composition of non-target consumers, such as zooplankton (Hayasaka et al., 2012; Hébert et al., 2021), macroinvertebrates (Cothran, Radarian, & Relyea, 2011; Hayasaka et al., 2012), fish and other vertebrates (Gibbons, Morrissey, & Mineau, 2015; Hayasaka et al., 2012). In contrast, crop fertilizers can cause eutrophication of natural water bodies (Khan et al., 2014), fostering the excessive growth and dominance of more resistant primary producers, such as cyanobacteria (Burford & O'Donohue, 2006). Such contrasting effects on producers and consumer populations may directly influence how stable these aquatic communities are in agricultural landscapes (Schiesari et al., 2023). In addition, as cropland intensification drives biotic homogenization in space (Siqueira, Lacerda, & Saito, 2015), cross-community synchrony is also expected to increase among patches (Wang & Loreau, 2016). Despite recent progress, we do not know how temporal variability propagates across ecological hierarchies (Wang, Lamy, Hallett, & Loreau, 2019), under insecticide and fertilizer exposure. Here, we simulated agricultural landscapes to investigate how

temporal variability in abundances of producers and consumers propagates across scales, under varying levels of regional exposure to insecticide and fertilizer agrochemicals.

As agrochemicals can both increase (fertilizers) and decrease (insecticides) species abundance and biomass (Burford & O'Donohue, 2006; Rumschlag et al., 2020), they will inevitability influence temporal variability of ecological properties across spatial and organizational scales. Starting at local scale, populations are expected to become more synchronized (abundances will fluctuate similarly), as agrochemicals might drive the selection of tolerant species, similar in functionality (e.g., feeding habits and mobility) (Hébert et al., 2021; Rumschlag et al., 2020). Positive covariance in the abundance of local populations reduces the chance of compensatory dynamics because correlated species will respond similarly to the novel environmental condition (Loreau & De Mazancourt, 2013), increasing population temporal variability. Thus, temporal variability (i.e., the amount of total abundance variation in time) at community level will be a consequence of the amount of synchrony and temporal variability arising from local populations (Siqueira et al., 2022; Thibaut & Connolly, 2013; Wang et al., 2019).

At metacommunity scale, the influence of agrochemicals on temporal variability of aggregated properties might vary according to connectivity and spatial configuration of metacommunities (Clements & Rohr, 2009; Thompson, Rayfield, & Gonzalez, 2017). The process of converting natural vegetation into arable fields strongly modifies the landscape, placing metacommunities across extensive agricultural-pristine mosaics (Siqueira et al., 2015). In mosaic landscapes, unexposed communities (i.e., those where agrochemical effects are less severe) could function as keystone due to its potential to maintain metacommunity structure under environmental change (Mouquet

& Loreau, 2003; Siqueira, Durães, & De Oliveira Roque, 2014). This combination of exposed and unexposed patches within the metacommunity should reduce community spatial synchrony, as spatially distributed populations will fluctuate more independently, following local environmental conditions (Steiner, Stockwell, Kalaimani, & Aqel, 2013). In the same way, in homogeneous landscapes, when all communities are exposed equally (the entire metacommunity relies within a cropland domain), populations are expected to be spatially synchronized because fluctuations across environments are now correlated (i.e., Moran effect) (Steiner et al., 2013), increasing overall metacommunity variability (Siqueira et al., 2022; Wang et al., 2019).

Insecticides might influence temporal variability across scales via effects on consumer populations (Hayasaka et al., 2012). Top consumers are usually large, high-mobile organisms that move from low to high prey density patches, coupling heterogeneous food webs across landscapes through trophic interactions (McCann, Rasmussen, & Umbanhowar, 2005). Such dynamics promote spatial heterogeneity in predation pressure and can reduce spatial synchrony at lower trophic levels (Howeth & Leibold, 2013, but see Quévreux et al., 2023, for another perspective). When patches are exposed to insecticides, consumer abundance, body size and individual mobility are expected to be negatively affected (e.g., zooplankton) (Hanazato, 2001; Hayasaka et al., 2012; Pereira et al., 2009). Under these circumstances, not only predator ability to disperse could be reduced, but also changes in abundance and body size could disrupt previous established trophic interactions (Hanazato, 2001). This would, in turn, prevent predator stabilizing effect, increasing community spatial synchrony and metacommunity temporal variability.

Fertilizers are high-nutrient compounds applied to boost crop productivity, with high potential of causing eutrophication in freshwater ecosystems (Khan et al., 2014).

Although increased nutrient availability could level up the biomass of producers and consumers through bottom-up effects, allowing different species to persist (Bini, Landeiro, Padial, Siqueira, & Heino, 2014; Chase, 2010), the exposure of pristine water bodies to cropland fertilization is more likely to result in excessive growth and dominance of more resistant species, such as cyanobacteria (Burford & O'Donohue, 2006). At local scale, dominance of resistant organisms and loss of species at the bottom of food webs could boost temporal variability of producers (Guelzow, Dirks, & Hillebrand, 2014) and consumers through bottom-up effects (Rumschlag et al., 2020). Such a scenario would, in turn, lead to increased variability at the regional scale (Wang et al., 2019).

Here, we experimentally simulated multitrophic metacommunities under three levels of insecticide and fertilizer exposure: pristine (entire metacommunity unexposed), mosaic (exposed and unexposed patches) and agriculture (entire metacommunity exposed) (Figure 1). Then, we measured temporal variability in abundance of consumers and producers across levels of biological organization (population, community and metacommunity) to test the following hypotheses. H1) Temporal variability of consumers increases in local communities exposed to insecticide, as this compound enhances population variability and synchrony through negative effects on consumer abundance, body size and mobility (Hanazato, 2001; Hayasaka et al., 2012; Hébert et al., 2021; Rumschlag et al., 2020). H2) The negative effects of insecticides on consumer populations should decrease grazing pressure on producers, thus allowing growth of dominant, more efficient competitors, and increasing community variability of producers through top-down effects (Guelzow et al., 2014; Rumschlag et al., 2020). H3) Dominant producer species should also prevail under fertilizer exposure (Burford & O'Donohue, 2006), thus synchronizing local

populations of producers and increasing overall community variability. H4) Consequently, the selection filter imposed on producer communities by fertilizer exposure should also influence trophic interactions, and thus increase variability of consumer communities through bottom-up effects. Increasing the level of metacommunity exposure to agrochemicals (insecticide and fertilizers) should synchronize communities in space, because patches become more environmentally correlated, thus increasing metacommunity variability (Steiner et al., 2013). In this sense, (H5) regional exposure to insecticide should increase spatial synchrony among consumers and, thus, producers through top down-effects (Rumschlag et al., 2020), while (H6) regional exposure to fertilizers should increase spatial synchrony of producers and, thus, consumers through bottom-up effects.

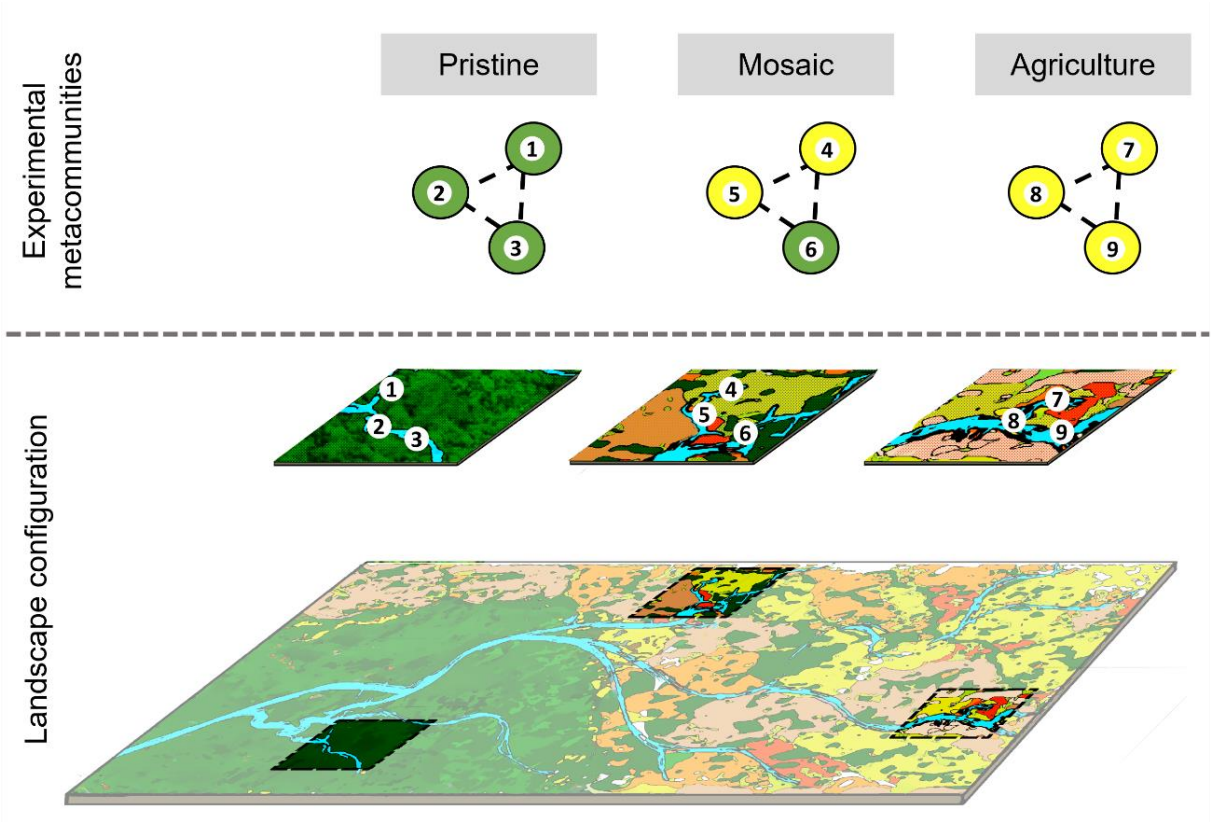

Figure 1. Experimental design of metacommunities exposed to agrochemical intensification across landscapes. In pristine environments, metacommunities are free from agrochemicals (green patches), in mosaics placed between pristine areas and croplands, patches are both free and exposed to agrochemicals (yellow patches), and in agricultural environments, all patches within metacommunity are exposed. In our experiments, yellow patches represent mesocosms exposed to insecticide or fertilizer solutions.

3.2. Methods

3.2.1. Experimental design and sampling

We studied the effects of insecticide and fertilizer exposure on propagation of temporal variability in a planktonic metacommunity experiment. For this, we built an experimental facility to mimic the landscape configuration described in Figure 1, using 45 pond mesocosm made of plastic containers (500 L each), to represent local communities of consumers (zooplankton) and producers (phytoplankton). Then, we arranged local communities as 15 independent metacommunities, each composed of three randomly chosen mesocosms. To establish initial communities within the mesocosms, we inoculated phytoplankton samples collected using a plankton net (mesh size: 20 µm) from an artificial reservoir located next to the experimental facility (22°11'33.1"S, 47°53'16.8"W). At this stage, we also added nutrients at a low concentration (2.5 mL of NPK fertilizer; Nitrogen, Phosphorus and Potassium at concentration 10:10:10) to secure phytoplankton growth in the mesocosms. After phytoplankton establishment, we inoculated zooplankton samples collected using a plankton net (mesh size: 68 µm) from another artificial reservoir located next to the experimental facility (21°59'05.0" S, 45°53'06.1" W). We ensured that containers would

have similar initial species composition, by carrying out homogenization events twice a week (see Supporting information for details on methods).

The first sampling event was conducted ten days after zooplankton inoculation, and before exposing the metacommunities to agrochemicals. To sample phytoplankton, we used individual plastic bottles to collect a 250 ml volume in the subsurface from each container, which was immediately preserved in a 1.5 ml lugol solution. For zooplankton sampling, we filtered a 15 L volume from each mesocosm, also in the subsurface using a short vertical haul plankton net (mesh size: 68 µm) and preserved it in a 4% formaldehyde solution. We also measured some water variables from the mesocosms using a Horiba Multiprobe MODEL, including water temperature (°C), pH, conductivity (mS/cm), turbidity (NTU), salinity (PPT), and dissolved oxygen (mg/L).

Two days after the first sample, we exposed metacommunities to either insecticide or fertilizer solutions, following the landscape configuration in Figure 1. Pristine metacommunities (n = 3) were not manipulated, and all local communities (n = 9) remained free from agrochemicals. In agricultural metacommunities, all local communities were exposed to either insecticide (n = 9), in cases of insecticide metacommunity exposure (n = 3), or fertilizer (n = 9), in fertilizer metacommunity exposure (n = 3). In mosaic metacommunities, where local patches are in the intersection of pristine and agricultural landscapes(Figure 1), metacommunities were partially exposed to insecticide (n = 3) or fertilizer solution (n = 3). In this configuration, one mesocosm is free from agrochemicals, and two are exposed in each metacommunity. For insecticide exposure, we inoculated 200 ml of a 2 µg/L final solution of fipronil, a broad-spectrum phenylpyrazole insecticide (Singh, Sharma, Singh, & Singh, 2021) known to affect aquatic communities in agricultural environments (Hayasaka et al., 2012). For fertilizer exposure, we inoculated 125 ml of

vinasse, a nutrient rich compound used in the fertigation of sugarcane fields, with potential to cause eutrophication in aquatic environments (Christofoletti, Escher, Correia, Marinho, & Fontanetti, 2013). Check the Supporting information, for more detailed information on how agrochemicals were used in the experiments. A new sampling event was conducted the day after metacommunities were exposed to agrochemicals.

The first dispersal event was conducted three days after agrochemical exposure, by manually exchanging water among mesocosms within each metacommunity. For this, we collected 1% volume from each of the three mesocosms that comprised the metacommunity and the pooled volume was redistributed equally over all mesocosms (Gianuca, Declerck, Lemmens, & De Meester, 2017). With this approach we expected to simulate dispersal by passive dispersers in natural metacommunities, where relative abundances within the mesocosms drive species dispersal rates. We carried out one more dispersal event one week after, following the same procedures described above.

Plankton samples collected during the experiment were analyzed and identified to the lowest taxonomic level when possible, using the available literature (Elmoor-Loureiro, 1997; Koste, 1978a, Koste, 1978b, Perbiche-Neves, Boxshall, Previattelli, Nogueira & da Rocha; Reid, 1985; Ueda & Reid, 2003). We identified and counted a minimum of 300 hundred individuals of phytoplankton preserved in the lugol's solution using an inverted optic microscope. For zooplankton, we divided each sample in three major groups: Copepods, Cyclopoids and Rotifers, in which a minimum of 50 individuals were counted for each group under an optical microscope Olympus CX, using a Sedgwick-Rafter chamber. To calculate response variables (section below), density estimates were then calculated for both producers (phytoplankton, ind.ml-1) and consumers (zooplankton, ind.m3).

3.2.2. Predictor and response variables

Predictor variables were based on the level of community and metacommunity exposure to agrochemicals. Local exposure (LE) is a binary predictor that measures communities free from agrochemicals (LE = 0), and communities that were exposed to insecticide or fertilizer (LE = 1), independently of metacommunity configuration. On the other hand, regional exposure (RE) is a three-level numerical variable representing metacommunity exposure to agrochemicals (Figure 1). In pristine landscapes (RE = 0.0), communities are embedded in natural vegetation with no exposure to agrochemicals; in mosaic landscapes (RE = 0.5), local communities are distributed across pristine areas and croplands (according to Figure 1); and in agricultural landscapes (RE = 1.0), the entire metacommunity is within the agricultural domain, exposed to either insecticide or fertilizer compounds. In addition, we also included spatial synchrony in temperature as a predictor variable in our analysis. Spatial synchrony in temperature was estimated as the mean Kendall rank correlation between each pair of local communities within the metacommunity.

To measure how variability propagates across scales, we followed a hierarchical framework on temporal variability in metacommunities (Wang et al., 2019). For this, we partitioned the variability of total metacommunity abundance (Mv) in two components – temporal variability of local communities (Cv), and spatial synchrony among local communities (Csy). Cv was further partitioned into local population variability (Pv), and synchrony among local populations (Psy). For the local scale model, Psy was calculated following Loreau & De Mazancourt (2008), using the function ‘synchrony’, and Cv and Pv were calculated as an inverse measure of stability, using the function ‘community_stability’, both functions are included in the package ‘codyn’ (Hallett et al., 2016). For the regional scale model, Cv, Csy and Mv were obtained according to the

functions present in Wang et al. (2019). We also computed diversity at local scale (alpha), as the species richness per community at each time. For the analysis, we included diversity as temporal means.

3.2.3. Data analysis

We modeled how temporal variability propagates under agrochemical exposure using Structural Equation Modeling - SEM (Lefcheck, 2016). To account for temporal variability across scales in producers and consumers, we followed a recent work of Siqueira *et al.* (2022), and built joint SEM's, representing local and regional scales, for each agrochemical. The paths in our models were hypothesized causual relationships among explanatory and response variables (see Figure S2 for hypothetical model). We fit linear mixed-effects models to decompose the relative contribution of agrochemical exposure to propagation of temporal variability, both direct and indirect (e.g., through synchrony). To account for variation across experimental metacommunities, we incorporated metacommunity ID as a random factor within the mixed models. To check if the relationships between predictors and responses differed between producers and consumers, both at local and regional scales, we ran a multi-group analysis on our SEM's. This approach resembles a linear model that includes an interaction between a numerical (e.g., population variability) and a categorical (trophic position) predictor variable. However, in the multigroup analysis, the interaction term is applied through the entire SEM, allowing us to test how linear coefficients vary between producers and consumers. We evaluated model fit through the Shipley d-separation test, a method that identifies the sets of missing relationships in the model, and tests whether the effect is not different from zero ($P > 0.05$). The test of d-separation produces a Fisher's C statistic that can be described by a chi-square distribution (Shipley, 2000). We conducted the piecewise SEM using the R package 'piecewiseSEM' (Lefcheck, 2016),

and for the linear mixed models, we used the function ‘lme’ in the R package ‘nlme’ (Pinheiro, Bates, DebRoy, Sarkar & R Core Team, 2021).

3.3. Results

Overall temporal variability (Figure 2) and synchrony (Figure 3) of producer and consumer abundances differed across scales and levels of insecticide and fertilizer exposure. Metacommunity models under agrochemical intensification fit the data well (Figure 4). Exogenous variables explained almost the entire variation in temporal variability in our models, as shown by marginal and conditional R^2 values (Supplementary Table S1). In both experiments, temporal variability of producers and consumers increased hierarchically from populations to communities and metacommunities. Also, local and spatial synchrony contributed to community and metacommunity variability, respectively. Alpha diversity was negatively related to temporal variability of producer populations in both insecticide and fertilizer experiments (Figure 4). On the other hand, while population variability of consumers decreased with alpha diversity under insecticide exposure (Figure 4a), it increased under fertilizer exposure (Figure 4b). Alpha diversity also contributed to decrease the synchrony of both producers and consumers, but only in the fertilizer experiment (Figure 4b).

At local scale, our results showed contrasting associations between temporal variability and local exposure to agrochemicals (Figure 4). As expected, population variability of consumers increased in patches exposed to insecticide, which in turn contributed to increased community variability (H1). However, local insecticide exposure was negatively related to population synchrony of consumers, decreasing overall local variability of consumer communities (Figure 4a). Insecticide exposure did not influence population variability and synchrony of producers, but overall community

variability was positively related to local exposure to insecticides through a direct path (Figure 4a), as expected (H2). Contrary to our hypotheses (H3 and H4), our model for fertilizer exposure showed no relationships between local exposure and temporal variability of producers and consumers (Figure 4b).

At regional scale, our models showed that increasing patch exposure to insecticides did not influence metacommunity variability through changes in community spatial synchrony (Figure 4a), contradicting H5. Similarly, increased regional exposure to fertilizers was negatively related to community spatial synchrony, reducing metacommunity variability of both producers and consumers through an indirect path (Figure 4b), contradicting H6. However, although consumer models showed reduced metacommunity variability under agrochemical intensification, either through propagation across scales (insecticide exposure), or reduced community spatial synchrony (fertilizers), metacommunity variability of producers increased with insecticide exposure. This happened through an indirect path, propagated from local effects of insecticide exposure on community variability of producers, partially supporting hypothesis H5 (Figure 4a).

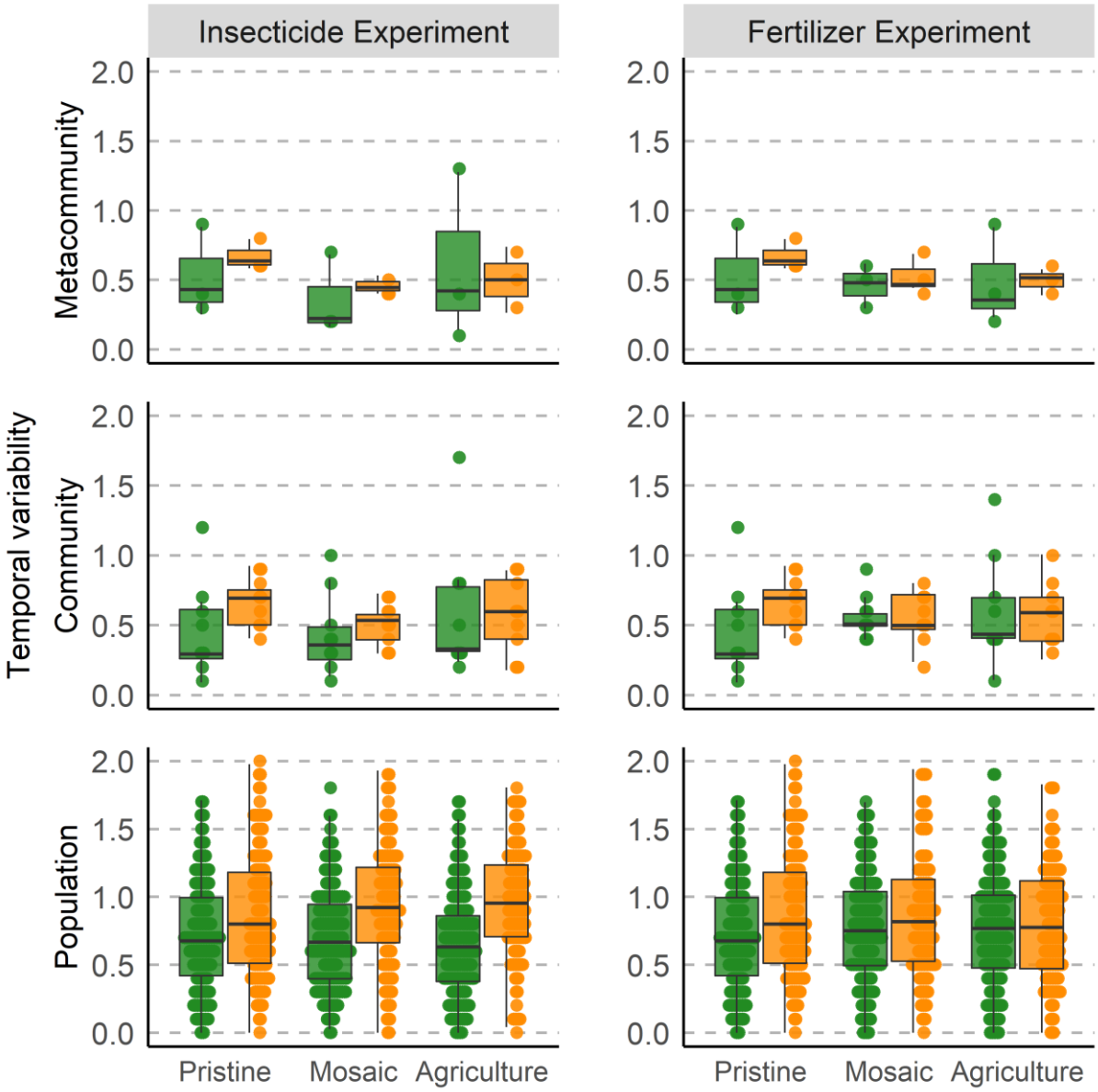

Figure 2: Effects of agrochemical intensification on temporal variability of producers and consumers across scales. Boxplots show observed data variation in population, community and metacommunity temporal variability of producers (green) and consumers (orange), under insecticide (left) and fertilizer (right) exposure.

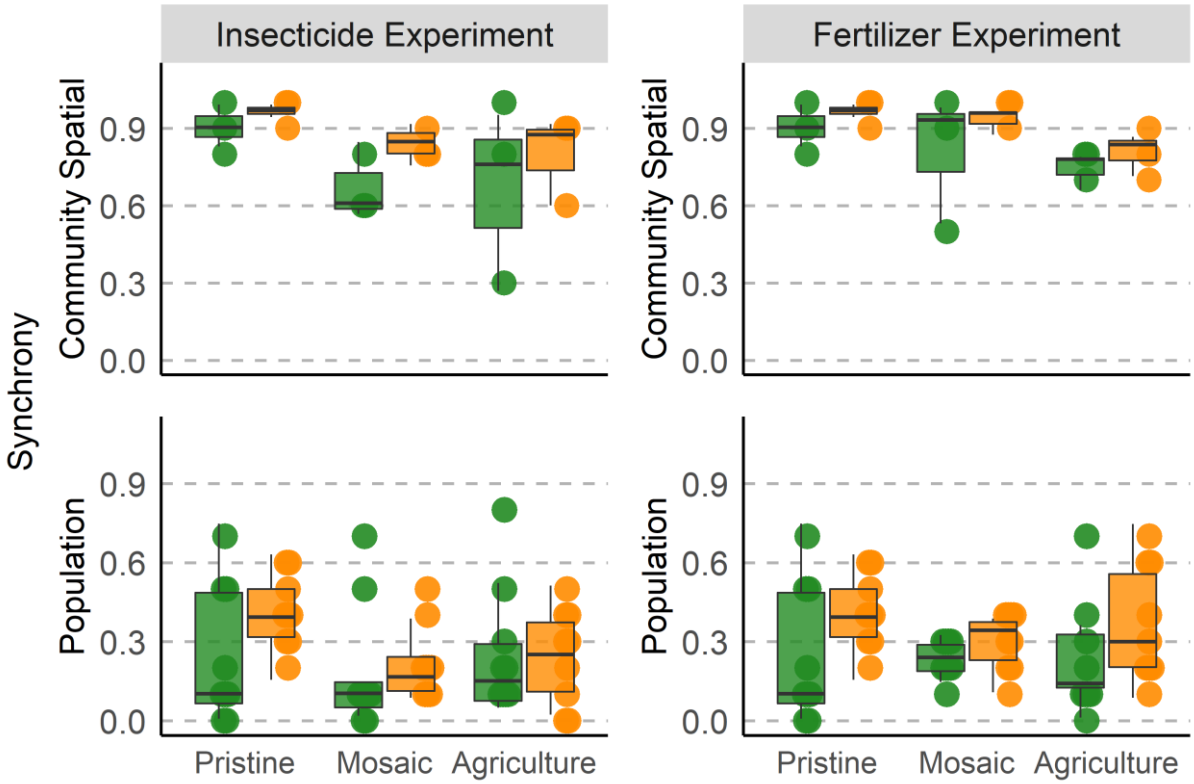

Figure 3: Effects of agrochemical intensification on synchrony of producers and consumers across scales. Boxplots show observed data variation in population and community spatial synchrony of producers (green) and consumers (orange), under insecticide (left) and fertilizer (right) exposure.

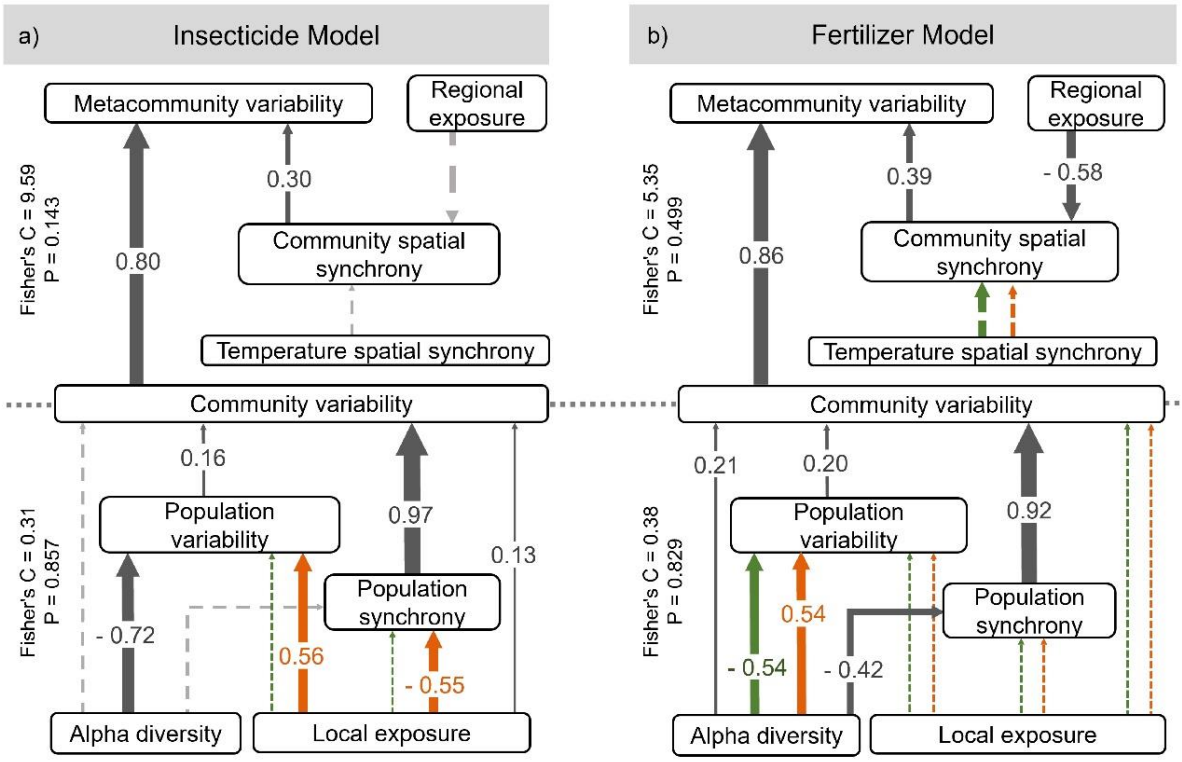

Figure 4: Structural equation models for propagation of temporal variability in producers and consumers exposed to insecticides (a) and fertilizers (b), across scales and levels of organization. Solid arrows represent significant relationships between exogenous and endogenous variables, and dashed arrows are non-significant paths (P value < 0.05). Arrow widths are scaled to represent standard estimates calculated by the model. Green, orange and dark gray colors indicate relationships across producers, consumers and both trophic levels, respectively.

3.4. Discussion

Our mesocosm experiment suggests that agrochemical intensification influences how temporal variability propagates from local to regional scales, but results are contrasting and depend on organism's trophic position (Siqueira et al., 2022), level of organization (Wang et al., 2019), and type of agrochemical considered (Hébert et al., 2021; Rumschlag et al., 2020). Cropland Insecticides are known to influence aquatic non-target organisms, especially through body size, abundance, and composition changes (Hanazato, 2001; Hayasaka et al., 2012; Hébert et al., 2021). We found that insecticide exposure increases temporal variability in consumer populations, showing a clear influence on the frequency and magnitude of abundance fluctuations. However, although a portion of this variability propagated from populations to communities, as predicted by literature (Siqueira et al., 2022; Wang et al., 2019), overall community variability of consumers decreased because insecticide exposure led to more asynchronous populations. This finding suggests that even though insecticides are expected to impose a selection filter to zooplankton consumers, favoring dominant species (Hébert et al., 2021), populations that overcame habitat alteration may respond asynchronously to perturbation. On the other hand, population asynchrony could also be a result of dispersal (which was kept constant in our experiments), providing colonizers through source-sink dynamics (Mouquet & Loreau, 2003; Siqueira et al., 2014). In this sense, besides governing food web structure under regional environmental change (Thompson et al., 2017), dispersal could also be fundamental to maintain stability in agricultural landscapes.

Evidence suggests that environmental correlation should lead to spatial synchrony among patches (Steiner et al., 2013). As agrochemicals might select species that respond similarly to induced environmental change (Rumschlag et al.,

2020), we expected communities to be spatially synchronized in metacommunities where patches were equally exposed to agrochemicals, thus increasing overall metacommunity variability (Wang et al., 2019). Our model showed that synchrony among communities indeed contributed to increase temporal variability in abundance of consumers and producers at regional scale, but it was not driven by regional exposure to insecticide. We highlight to main reasons for this outcome. First, although spatially connected communities undergo a similar process of insecticide perturbation, their response might have been influenced by other processes, such as historical contingency and priority effects (Fukami, 2015). Given that, in our experimental design, dispersal among patches occurred after the exposure to insecticide, it is possible that prior independent community assembly had modulated local responses to insecticide, desynchronizing patches (Fukami, 2015). Even though we tried to control for initial variation among communities, inoculating colonizers from the same species pool and homogenizing communities prior to the experiment, it is possible that community assembly differed among mesocosms. The second reason could be attributed to the insecticide we used in our experiment. Fipronil has a variable half-life in aquatic environments, ranging from hours to days and depending on water physical and chemical attributes (Singh et al., 2021). Thus, it is possible that mesocosm's internal condition (e.g., random variation caused by mesocosm's location within experimental facility) influenced insecticide fate in water, generating asynchronous environmental fluctuations and reducing community spatial synchrony.

Because exposure to agrochemical fertilizers can lead to eutrophication in freshwater ecosystems (Khan et al., 2014), we hypothesized excessive growth, dominance of few species (Burford & O'Donohue, 2006), and positive effect of fertilizers on local producer synchrony and temporal variability. However, abundance

fluctuation of producers and consumers did not change between exposed and unexposed communities, suggesting that, at local scale, fertilization has no influence on the temporal variability in our mesocosm. On the other hand, our model showed that increasing the number of patches under fertilizer exposure led to reduced spatial synchrony among communities, thus decreasing metacommunity variability of consumers and producers. This finding suggests that the fertilizer solution in our experiment might have favored producers in some communities, allowing them to persist and differentiate at the regional scale (Bini et al., 2014; Chase, 2010). Consequently, through bottom-up effects, consumers might also have benefited from increased nutrient availability, promoting spatial heterogeneity in grazing pressure and also contributing to spatial asynchrony of producers (Howeth & Leibold, 2013).

In our hypotheses, we considered agrochemicals to be a precursor of metacommunity variability, as they were expected to disrupt abundances of non-target aquatic organisms (Hébert et al., 2021; Rumschlag et al., 2020), prevent compensatory dynamics (Loreau & De Mazancourt, 2013), and synchronize communities at regional scale. However, a recent study has shown that local perturbations can induce contrasting changes in lower trophic levels, and the stability of entire metacommunity may depend on how fast energy channels within perturbed patches (Quévreux et al., 2023). The authors showed that, as asymmetry in energy flow is generated by varying the strength of trophic interactions (Rooney, McCann, Gellner, & Moore, 2006), perturbing prey in slow patches (where energy flows more slowly), decreases the synchrony of prey communities, and contribute to stabilize predator dynamics (Quévreux et al., 2023). These differences in how perturbation drives spatial synchrony could help to explain why regional exposure to fertilizers decreased synchrony in our experiment.

Diverse communities are expected to be more stable, as more species should increase the chances of asynchronous populations through time (Schindler, Armstrong, & Reed, 2015) and favor a broader range of responses to environmental change (Moi et al., 2023). Our models for insecticide exposure corroborated these ideas, and local diversity was negatively related to temporal variability of both producers and consumers across scales. However, under fertilizer exposure, diversity was positively related to temporal variability of consumers at population and community levels, consequently propagating to the metacommunity. These results are interesting and might suggest that even when communities are taxonomically diverse, species can fluctuate similarly, indicating functional redundancy. Thus, although fertilizer exposure did not influence temporal variability of consumer abundances directly, it might have changed functional traits within species (e.g., body size, feeding habits), making them more functionally similar and less stable to future perturbations.

Overall, our study reveals complex relationships between stability and agrochemical intensification, showing that insecticide and fertilizer exposure strongly influence how temporal variability in abundances propagates across scales and levels of organization. Producers and consumers fluctuated independently under insecticide exposure at local scale, changing how variability propagated to the metacommunity level. Altering the configuration of metacommunities, going from pristine (free from agrochemicals) to fully exposed agricultural landscapes, desynchronized communities under fertilizer exposure, indicating that other aspects not considered in our models, such as energy flow within patches (Quévreux et al., 2023), might influence stability under fertilizer perturbation. Our model also showed a positive relationship between diversity and temporal variability of consumers under fertilizer exposure, indicating that, although fertilization did not influence local variability directly, it might have made

species functionally redundant and susceptible to future perturbations. Lastly, as agriculture has advanced fast in the last century (Potapov et al., 2021), our work contributes to unveil the complexity behind stability and how it emerges in ecosystems under anthropogenic changes.

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3.6. Supporting information

3.6.1. Details on experimental methods

Our experimental facility was built using 45 pond mesocosm made of plastic containers (500 L each). We filled each container with filtered water, using an activated carbon filter (Fig. S1a), before assembling initial communities. To establish initial communities within the mesocosms, we inoculated phytoplankton samples collected using a plankton net (mesh size: 20 µm) from an artificial reservoir located next to the experimental facility (22°11'33.1"S, 47°53'16.8"W) (Fig. S1b). Then, we homogenized the entire material filtered from the artificial reservoir and distributed equal volumes among the containers (Fig. S1c). To secure initial similar phytoplankton communities among the mesocosms, we conducted homogenization events, in which we filtered a chosen volume of phytoplankton from the containers, using a plankton net (mesh size: 20 µm). Then, the filtered volume from each container was mixed and redistributed back to the containers. After phytoplankton establishment, we collected zooplankton samples using a plankton net (mesh size: 68 µm), from another artificial reservoir located next to the experimental facility (21°59'05.0" S, 45°53'06.1" W) (Fig. S1d). The, we conducted the same homogenization processes described for phytoplankton, to secure that all mesocosms would have similar initial communities.

After establishing initial communities, we arranged local communities as 15 independent metacommunities, each composed of three randomly chosen mesocosms (Fig. S1e). To sample phytoplankton, we used individual plastic bottles to collect a 250 ml volume in the subsurface from each container, which was immediately preserved in a 1.5 ml lugol solution (Fig. S1f and S1g). For zooplankton sampling, we filtered a 15 L volume from each mesocosm, also in the subsurface using a short vertical haul plankton net (mesh size: 68 µm) and preserved it in a 4% formaldehyde

solution (Fig. S1h). Water variables from the mesocosms were measured using a Horiba Multiprobe MODEL, including water temperature (°C), pH, conductivity (mS/cm), turbidity (NTU), salinity (PPT), and dissolved oxygen (mg/L) (Fig. S1i).

Two days after the first sample, we exposed metacommunities to either insecticide or fertilizer solutions. For the insecticide experiment, we prepared 4 L of a 2 mg/L solution of fipronil, using the Regent® 800 WG product, manufactured by BASF, with 80% of fipronil in its composition (Fig S1j and k). Then, we diluted 200 ml of the 4 L solution in the chosen mesocosms within the insecticide experiment (check the description in the section Methods of the main text). The fipronil final concentration (mean = 2.0 µg/L) of fipronil in each mesocosm was obtained through liquid chromatography mass spectrometry (LC-MS/MS). For fertilizer exposure, we inoculated 125 ml of vinasse in each mesocosm for the fertilizer experiment, a nutrient rich compound used in the fertigation of sugarcane fields. The addition of 125 mL of vinasse resulted in 0.11 mg/L of nitrogen and 1.62 mg/L of phosphorus, for each mesocosm.

Plankton samples collected during the experiment were analyzed and identified to the lowest taxonomic level when possible, using the available literature (Fig. S1l). We identified and counted a minimum of 300 hundred individuals of phytoplankton preserved in the lugol's solution using an inverted optic microscope. For zooplankton, we divided each sample in three major groups: Copepods, Cyclopoids and Rotifers, in which a minimum of 50 individuals were counted for each group under an optical microscope Olympus CX, using a Sedgwick-Rafter chamber. To calculate response variables (section below), density estimates were then calculated for both producers (phytoplankton, ind.ml-1) and consumers (zooplankton, ind.m3).

Figure S1. Procedures and steps adopted in our experimental simulation of metacommunities exposed to agrochemicals: a) plastic containers used as mesocosms with filtered water, b-d) sampling and assembling of initial communities, e) metacommunities within the experimental facility, f-i) experimental data sampling procedures, j-k) laboratory methods to handle agrochemicals, and l) counting and identification of plankton samples collected during experimental period.

3.6.2. Model description

We used a hypothetical model to evaluate the effects of agrochemicals on propagation of temporal variability across scales, for both consumers and producers, in our planktonic mesocosm experiment (Fig. S2). Check the main text for information on how the variables were calculated. Metacommunity identity was considered as random effect within the model.

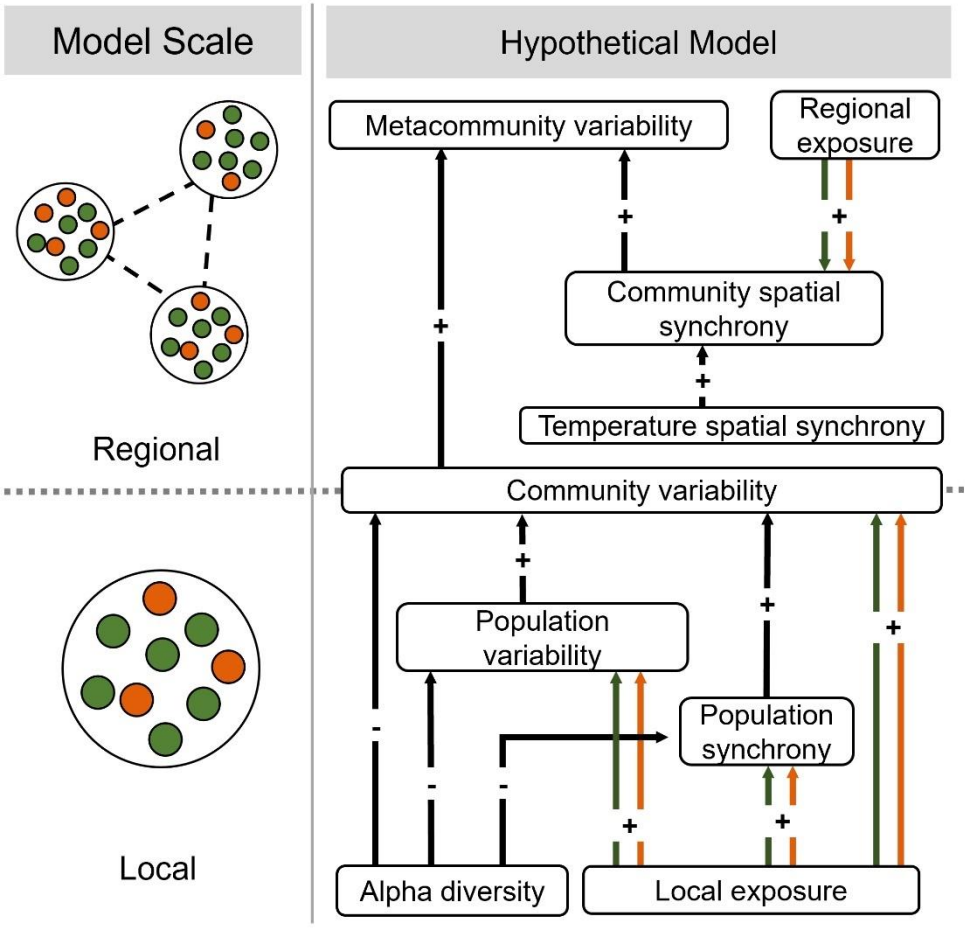

Figure S2. Hypothetical model for the effects of agrochemicals on propagation of temporal variability across scales and trophic positions, in our planktonic mesocosm experiment. At the left, the figure denotes the scale of the variables considered in the model (local and regional), and at the right, the hypothetical expectations. Green and orange arrows represent paths in which the coefficients are expected to differ between producers and consumers, according to the type of agrochemical considered (insecticide or fertilizer). Signals denote increase (+) or decrease (-) from exogenous to endogenous variables. A standard regression coefficient (β) was retrieved for each relationship, using *piecewiseSEM* [1].

3.6.3. Supplementary results

The exogenous variables explained a large portion of the variation in producers and consumers metrics (Table S1). As shown by marginal and conditional R^2 values, metacommunity identity, which were included in the joint SEMs as random effects, did not affect the relationships between predictors and responses.

Table S1. Marginal and Conditional R^2 values obtained for individual endogenous variables, following the joint SEMs that relates agrochemical exposure to food web temporal variability.

Model	Scale	Endogenous variables	Marginal R^2	Conditional R^2
Insecticide	Local	Community variability	0.88	0.90
Insecticide	Local	Population variability	0.52	0.52
Insecticide	Local	Population synchrony	0.11	0.11
Insecticide	Regional	Metacommunity variability	0.99	0.99
Insecticide	Regional	Community spatial synchrony	0.22	0.22
Fertilizer	Local	Community variability	0.79	0.82
Fertilizer	Local	Population variability	0.17	0.17
Fertilizer	Local	Population synchrony	0.17	0.17
Fertilizer	Regional	Metacommunity variability	0.99	0.99
Fertilizer	Regional	Community spatial synchrony	0.30	0.30

3.6.4. Supporting information references

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4. Considerações finais

Mudanças ambientais, principalmente causadas por intervenções humanas nos ecossistemas, influenciam diferentes aspectos da biodiversidade. Utilizando diferentes abordagens de pesquisa, esta tese dedicou-se a explorar as relações diretas e indiretas entre mudanças ambientais e redes tróficas em ecossistemas aquáticos dulcícolas. Os dois estudos aqui apresentados trazem importantes contribuições para o entendimento dos caminhos pelos quais modificações no ambiente, em especial mudanças climáticas, de uso do solo, e exposição a agrotóxicos, afetam a estrutura e a estabilidade de comunidades multitróficas.

No primeiro estudo, eu mostrei que aspectos fundamentais da estrutura de redes tróficas, como a conectância e o número de níveis tróficos foram direta e indiretamente influenciados por mudanças climáticas (temperatura e precipitação) e de uso do solo. No entanto, a forma como os preditores afetam a estrutura das redes depende de características intrínsecas dos ecossistemas. Enquanto redes tróficas em lagos não demonstraram alterações na conectância, em riachos a relação entre conectância, intensidade do uso do solo e mudanças climáticas foi positiva, sugerindo dominância de espécies generalistas onde a urbanização e a conversão em agricultura foram mais intensas. Já a estrutura vertical das redes tróficas foi negativamente relacionada com mudanças climáticas e de uso do solo em riachos, e negativamente relacionada com aumento da temperatura em riachos, indicando simplificação das redes frente a estas mudanças. Além disso, o primeiro estudo mostrou ainda que a proporção de predadores de topo na comunidade exerce um papel importante, mediando os efeitos de mudanças climáticas na estrutura das redes tróficas.

No segundo estudo, meus esforços foram direcionados a entender como efeitos indiretos da expansão agrícola, mais especificamente a exposição de ecossistemas aquáticos a agrotóxicos, influencia a estabilidade de produtores e consumidores em comunidades multitróficas. Por meio de uma abordagem experimental consistente, eu mostrei que inseticidas e fertilizantes tem o potencial de modificar a forma como a variação temporal na abundância se propaga ao longo de escalas e níveis de organização. A exposição a inseticidas foi relacionada com alta variação temporal na população de consumidores. Porém, ao nível de comunidade, a variação temporal na abundância foi reduzida devido a um efeito negativo do fipronil na sincronia populacional. Esse resultado sugere que, ainda que inseticidas imponham filtros de seleção a consumidores em ecossistemas aquáticos, outros processos podem estar atuando para manutenção da estabilidade em níveis hierárquicos superiores (e.g., dispersão). Por outro lado, modelos investigando os efeitos de fertilizantes na variação temporal de produtores e consumidores mostraram que, ao passo em que as manchas que compõem a metacomunidade são expostas a vinhaça, a sincronia espacial entre comunidades é reduzida. Esse resultado sugere que o fertilizante possa ter favorecido a produtividade primária em algumas comunidades, permitindo que estas se diferenciassem na escala regional.

Por fim, é possível concluir que mudanças ambientais influenciam fortemente a estrutura e estabilidade de redes tróficas em ecossistemas aquáticos. Porém, as relações entre preditores ambientais e variáveis resposta são complexas e demandam uma análise detalhada dos caminhos (diretos e indiretos) pelos quais as mudanças ocorrem. Para que possamos compreender melhor como mudanças climáticas e de uso do solo influenciam a estrutura de redes tróficas, é crucial que se considere as características intrínsecas dos ecossistemas dulcícolas (e.g., lagos e

riachos), visto que as relações entre preditores e respostas mudam entre eles. Por outro lado, é necessário que aumentemos os esforços para investigar a influência de agrotóxicos nas comunidades aquáticas, visto que os efeitos de inseticidas e fertilizantes transpassam níveis de organização e escalas, afetando diferentemente produtores e consumidores.