

Research article

Agrochemical effects on plankton temporal variability are buffered at larger spatial scales

Gedimar Pereira Barbosa^{1,2}, Camila B. Vieira^{1,3}, Ana Carolina dos Santos⁴, Neliton Lara¹, Erick Mateus-Barros^{5,6}, Jorge L. Portinho^{1,7}, Hugo Sarmiento⁶, Gilmar Perbiche-Neves⁷, Bianca Veloso⁸, Cassiana Montagner⁸, Luis Schiesari⁹, Victor S. Saito¹⁰ and Tadeu Siqueira^{1,11}

¹Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, SP, Brasil

²Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas (UNICAMP), Campinas, SP, Brasil

³Instituto de Desenvolvimento Sustentável Mamirauá, Projeto Providence, Tefé, Amazonas, Brasil

⁴Programa de Pós-Graduação em Ciências Ambientais, Universidade Federal de São Carlos, São Carlos, SP, Brasil

⁵Programa de Pós-Graduação em Ecologia e Recursos Naturais, Universidade Federal de São Carlos, São Carlos, SP, Brasil

⁶Departamento de Hidrobiologia, Universidade Federal de São Carlos, São Carlos, SP, Brasil

⁷Departamento de Ciências Biológicas, Universidade Estadual Paulista (UNESP), Assis, SP, Brasil

⁸Instituto de Química, Universidade Estadual de Campinas (UNICAMP), Campinas, SP, Brasil

⁹Escola de Artes, Ciências e Humanidades, Universidade de São Paulo, SP, Brasil

¹⁰Departamento de Ciências Ambientais, Universidade Federal de São Carlos, São Carlos, SP, Brasil

¹¹School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

Correspondence: Gedimar Pereira Barbosa (gedimar.barbosa@gmail.com)

Oikos

2025: e11436

doi: 10.1002/oik.11436

Subject Editor: Benoit Gauzens

Editor-in-Chief: Pedro Peres-Neto

Accepted 14 July 2025

Agricultural expansion affects ecosystem dynamics both locally and through regional-scale processes. However, the way local and regional effects interact to influence temporal dynamics is not well understood. We conducted an outdoor freshwater mesocosm experiment to examine how localized agrochemical contamination, across different landscape compositions, influences the temporal variability of producers and consumers in planktonic food webs. We found that localized agrochemical contamination changed the temporal variability of local populations, but its effects varied across trophic levels. Insecticide contamination both increased the variability of consumers and reduced that of producer populations through cascading effects. Fertilizer contamination increased the variability of producer populations, but its effects on consumers were less pronounced. Temporal variability originating at the population level was buffered at higher levels of biological organization and spatial scales (communities and metacommunities). These results indicate that more complex systems, comprising interacting species and embedded in spatial dynamics, play an important role in reducing temporal variability, regardless of landscape composition and spatial heterogeneity. Our study reinforces the destabilizing effects of agrochemicals on freshwater planktonic food webs, and suggests that sustaining complex, spatially connected ecological systems could be crucial to biodiversity stability in highly modified agricultural landscapes.

Keywords: freshwater, mesocosms, metacommunity, stability, synchrony, trophic levels



Introduction

Changes in natural land cover due to agricultural expansion are a continuing threat to biodiversity and ecosystem functioning (Vörösmarty et al. 2010, Newbold et al. 2015). The hierarchical, interconnected nature of freshwater ecosystems makes them receivers of matter coming from the terrestrial catchment in which they are embedded (Dudgeon 2019, Patrick et al. 2021). This spatial structure of freshwater ecosystems means that intensive agricultural practices that usually result in run-off into rivers and lakes change the dynamics of these ecosystems (Allan 2004, Rumschlag et al. 2020, Schiesari et al. 2023). Recent progress has been made on how land use expansion influences the local dynamics of freshwater biota (Barbosa and Siqueira 2023, Schiesari et al. 2023), yet evidence on how these localized effects interact with wider regional-scale effects associated with landscape composition is still lacking.

Agrochemicals such as fertilizers and insecticides have a variety of effects on freshwater ecosystems, frequently resulting in unequal responses of food web compartments (Hayasaka et al. 2012, Rumschlag et al. 2020). Crop fertilizers are high-nutrient compounds used to boost productivity, with high potential of causing eutrophication of freshwater ecosystems (Khan et al. 2014). Although increased nutrient availability could level up the biomass of primary producers, such as phytoplankton, allowing different species to persist, the exposure of pristine water bodies to fertilizer run-off is more likely to result in excessive growth and dominance of a few species (Burford and O'Donohue 2006). Insecticides, on the other hand, usually reduce the abundance of non-target primary and secondary consumers (Hayasaka et al. 2012, Rumschlag et al. 2020, Hébert et al. 2021). Given their toxic potential for all zooplankton components (Hayasaka et al. 2012), insecticides commonly act as an unequivocal habitat filter on most species. Despite the existence of interspecific differences in sensitivity, the overall negative effect of insecticides increases the chances of larger predators with smaller populations being prone to extinction (Schiesari et al. 2023).

Because agrochemicals influence the temporal dynamics of producers and consumers (Burford and O'Donohue 2006, Rumschlag et al. 2020), they will inevitably affect how species fluctuate temporally within and across sites. Local species synchrony describes the degree to which population fluctuations of different species within a patch are correlated (Wang et al. 2019). After agrochemical contamination events, local species synchrony can either decrease if agrochemicals select for more tolerant species (Rumschlag et al. 2020, Hébert et al. 2021), or increase, as in cases in which most species respond similarly to contamination events (e.g. high toxic potential for all zooplankton; Hayasaka et al. 2012). According to a hierarchical framework of temporal stability (Wang et al. 2019), local species synchrony determines the amount of population variability that propagates to the aggregate community level (i.e. community variability; Thibaut and Connolly 2013, Wang et al. 2019). For example, synchronized population fluctuations within sites reduce

the chance of compensatory dynamics because the selected species will respond similarly to environmental conditions (Loreau and De Mazancourt 2013). This will increase community temporal variability and make the whole community less stable (Thibaut and Connolly 2013, Wang et al. 2019).

Synchrony can also be measured across multiple sites. Community-level spatial synchrony refers to the degree of correlation in total community biomass across patches (Wang et al. 2019). High spatial synchrony arises mainly from two factors: a combination of high dispersal rates among local patches and strong predator–prey cycles (Fox et al. 2011), and spatially synchronous environmental fluctuations, known as the Moran effect (Ranta et al. 1997). Community-level spatial synchrony and the aggregate temporal variability of local communities will determine the amount of variability that propagates to the metacommunity level (i.e. metacommunity variability; Wang et al. 2019). Because synchrony acts as the scaling factor in this hierarchical framework, temporal stability is expected to increase (or at least remain constant) from local populations to regional metacommunities.

At the scale of entire catchments, the influence of agrochemicals on the temporal fluctuation of metacommunities is less known, as it depends on landscape composition, spatial flow of agrochemicals and organisms between sites and the extent of agrochemical impacts (Clements et al. 2012, Thompson et al. 2017). For example, the conversion of natural land cover into agricultural land creates landscape mosaics consisting of some habitat patches that are exposed and others that are unexposed to agrochemical run-off. This heterogeneous combination means that landscape mosaics will comprise separated local patches with communities that fluctuate asynchronously, following their local environmental conditions (Steiner et al. 2013). This spatial asynchrony among local patches tends to decrease variability, thus making the entire region more temporally stable (Thibaut and Connolly 2013, Wang et al. 2019). However, agriculture expansion can also create homogenous landscapes when land cover changes are widespread and persistent. Agrochemical run-off in these landscapes should affect individual patches similarly, leading to increased spatial synchrony among geographically separated communities. Moreover, dispersal of organisms among patches can itself act as a synchronizing mechanism, since movement of individuals couples local population fluctuations across space (Ranta et al. 1997). High connectivity and frequent dispersal thus increase spatial synchrony, potentially compounding the effects of environmental forcing. These synchronized dynamics increase temporal variability and make the entire region less temporally stable (Thibaut and Connolly 2013, Wang et al. 2019).

Here, we investigated the interactions between the localized impacts of agrochemicals and the larger regional-scale effects of landscape composition, aiming to understand the combined influence of these factors on the temporal dynamics of freshwater producers and consumers. To do that, we experimentally simulated planktonic metacommunities along a gradient of agricultural expansion, including pristine, mosaic and agricultural landscapes (Fig. 1A). To simulate

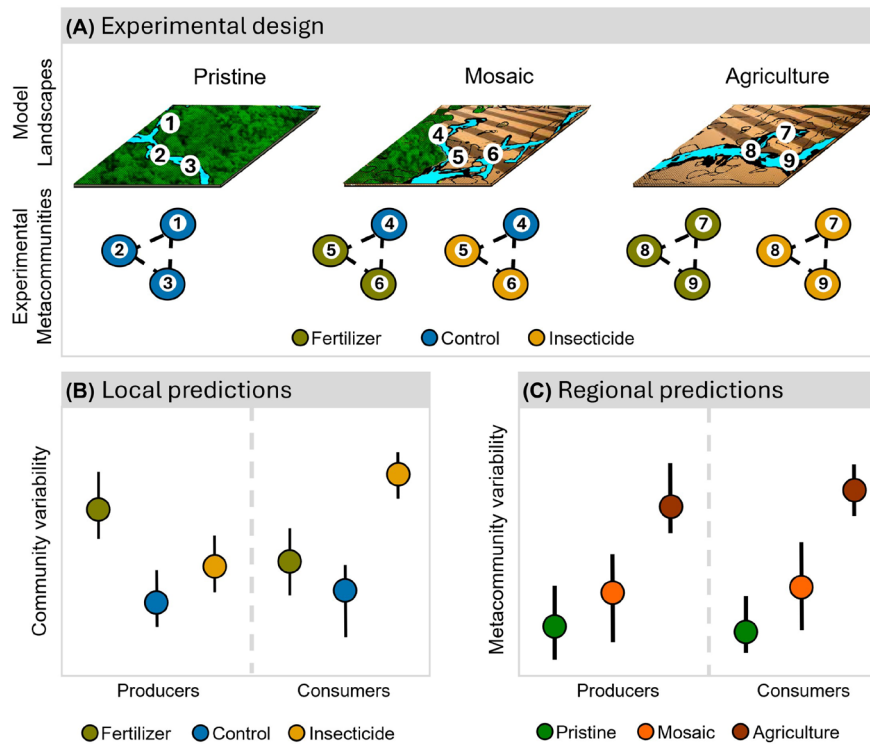


Figure 1. Theoretical expectations for the influence of agrochemicals and landscape composition on the temporal variability of producers and consumers under agricultural expansion, illustrated with our experiment. (A) Each experimental metacommunity mimics a model landscape composition (pristine, mosaic and agriculture) with varying localized agrochemical effects (control, fertilizer and insecticide). (B) At the local scale, the dominance of few species due to fertilizer exposure might increase local variability of producers, while high mortality caused by insecticide is expected to increase local variability of consumers. (C) Metacommunity variability should increase in agricultural landscapes, but the presence of uncontaminated patches within mosaic landscapes is expected to counterbalance the effects of agriculture expansion, buffering temporal variability at the regional scale.

localized effects of agrochemical contamination, we exposed local patches to either fertilizer or insecticide, commonly used compounds in agricultural practices known to influence natural ecosystem dynamics (Sharma et al. 2019). Then, we used the hierarchical framework proposed by Wang et al. (2019) applied to metacommunities to test our hypotheses.

We hypothesized that (H_1) local synchrony among consumer species is higher under insecticide exposure (e.g. high mortality caused by target insecticides; Rumschlag et al. 2020, Hébert et al. 2021), leading to increased temporal variability of local consumer communities (Fig. 1B). Similarly, local synchrony among producer species is higher in face of fertilizer contamination (e.g. dominance of few species due to fertilizer exposure; Burford and O'Donohue 2006), increasing temporal variability of producers at the local scale (Fig. 1B). On the other hand, because local dynamics might depend on landscape composition, we hypothesized that (H_2) uncontaminated patches within mosaic landscapes counterbalance the effects of agrochemicals on producers and consumers. More specifically, we predicted that the presence of contaminated and uncontaminated patches would decrease community spatial synchrony, making the regional dynamics of mosaic landscapes more stable and similar to the dynamics of pristine ones (Fig. 1C). Finally, although temporal variability usually decreases with the increase of levels of organization

(local populations vary more than entire metacommunities; Kéfi et al. 2019, Siqueira et al. 2024), we hypothesized (H_3) this pattern to be less evident in agricultural metacommunities, when compared to pristine ones. This is expected because patches in agricultural landscapes tend to be more similar to each other, so temporal variability at the metacommunity level should more closely reflect variability observed at local scales.

Material and methods

Experimental design

We studied the influence of landscape composition and agrochemicals on the temporal variability of phyto and zooplankton through a mesocosm experiment in which we simulated metacommunities along a gradient of agricultural expansion (Fig. 1). For this, we manipulated two variables, one at the regional scale and another at the local scale (Supporting information). Landscape composition was defined as a regional-scale categorical variable with three levels: pristine, mosaic and agricultural landscapes. Within each of these levels, we manipulated a second categorical variable to represent the potential effects of local land management. Local agrochemical contamination was defined as a local-scale categorical

variable with three levels: control (no agrochemical), fertilizer contamination and insecticide contamination. Pristine landscapes included three local patches free from agrochemicals. Mosaic landscapes included two local patches exposed to either fertilizer or insecticide contamination and one patch free from agrochemicals. Agricultural landscapes included three local patches exposed to either fertilizer or insecticide contamination.

Due to the complexity of the experimental design, replication was unbalanced at both scales (Supporting information). At the regional scale, pristine landscapes were replicated three times, while mosaic and agricultural landscapes were replicated six times each ($3 + 6 + 6 = 15$ landscapes). The six replicates of mosaic and agricultural landscapes included three that were contaminated with fertilizer and three with insecticide. Thus, at the local scale, the control treatment was replicated 15 times: nine local communities within pristine landscapes; six local communities within mosaic landscapes. The fertilizer and insecticide treatments were replicated 15 times each. For more details on replication, see the Supporting information.

Experimental setup

The experiment was conducted between August and November 2019, at the Federal University of São Carlos campus in southeast, Brazil. We used 45 polypropylene water tanks (filled with 400 l of water) to represent local patches (local communities from now on) and arranged them as 15 landscapes (metacommunities from now on), so each metacommunity was composed of three local communities. Metacommunity dynamics were simulated by actively manipulating dispersal among local communities. For this, we removed 4 l (1%) of water from each tank within the three tank metacommunity and placed them together in a 12 l container. Then, we homogenized the 12 l volume and returned 4 l to each one of the initial tanks (Gianuca et al. 2017). The dispersal procedure was repeated twice for all metacommunities over the 18-day experiment.

Tanks were colonized with phytoplankton and zooplankton samples, collected at two well-studied nearby reservoirs known to have high density and diversity of phytoplankton and zooplankton (Angelini and Petrere 2000, Matsumura-Tundisi and Tundisi 2005, Sendacz et al. 2006). Phytoplankton samples were collected using 20 μm mesh nets, through 8 vertical trawls starting at a depth of 5 m, resulting in approximately 706 l of water filtered for each tank. We inoculated phytoplankton samples into tanks on the same day they were collected, and added nutrients (2.5 ml of fertilizer N:P:K; nitrogen, phosphorus and potassium in a 10:10:10 ratio) to allow population growth.

After adding phytoplankton, we homogenized the experimental tanks to keep similar phytoplankton species composition before adding zooplankton. For this, we filtered 30 l from each one of the 45 tanks, using a 20 μm mesh net, mixed the filtered volume in a single container, and redistributed the solution equally back to each tank. This procedure occurred three times: on the 2nd, 8th, and 13th days after phytoplankton inoculation. On the 15th, we sampled

zooplankton from the natural reservoir and added it to the tanks. Zooplankton was sampled using 68 μm mesh nets, through 10 vertical drags starting at a depth of 5 m, resulting in approximately 883 l of water filtered for each tank. Then, we conducted two more homogenization events to ensure similar planktonic communities before starting the experiment. This pre-experimental phase lasted for 28 days.

Agrochemical contamination

Agrochemical contamination was simulated by exposing experimental tanks to two widely used compounds that can affect non-target freshwater biodiversity (Hayasaka et al. 2012, Christofolletti et al. 2013, Sharma et al. 2019). To simulate fertilizer effects, local communities were contaminated with 125 ml of vinasse, a compound commonly used in fertilization of sugarcane fields (Christofolletti et al. 2013). The raw vinasse was composed of 0.353 g l⁻¹ of nitrogen and 5.2 g l⁻¹ of phosphorous, as shown by analysis conducted using 99 NKT Hatch method. After adding the vinasse to the experiment, the final concentration was approximately 0.11 mg l⁻¹ of nitrogen and 1.62 mg l⁻¹ of phosphorus in each tank.

For insecticide effects, we inoculated local communities with 2 μg l⁻¹ of Regent 800 WG (BASF; active ingredient fipronil 80%), a broad-spectrum phenylpyrazole insecticide applied across several plantations in Brazil (Gonçalves et al. 2022). For this, we prepared a solution of fipronil at a concentration of 2 mg l⁻¹ through the dilution of Regent in water, of which 200 ml was diluted in each tank. To ensure that each experimental tank would have the aimed final concentration (2 μg l⁻¹), we quantified the concentration of fipronil in water tanks using liquid chromatography coupled to tandem mass spectrometry (LC-MS/MS). An Agilent model 1200 chromatograph was used. Contaminant concentrations were defined after a pilot experiment, which tested for the effects of fipronil and vinasse on plankton abundance across a range of concentrations.

Plankton sampling, identification and quantification

Plankton were sampled four times during the experimental period. To sample phytoplankton, we collected 1 l of water from each tank using plastic bottles, and preserved 250 ml with a 3 ml Lugol solution. For zooplankton, we filtered 30 l of water from each tank with a 20 μm mesh net, concentrated into 5 ml samples, and preserved with a 4% formaldehyde solution. The first sampling event (T1) occurred three days after the last homogenization event. The second sampling event (T2) occurred three days later, one day after carrying out the agrochemical contamination procedure. The local communities were exposed to either fipronil or vinasse, following the concentrations and the experimental design described above (Supporting information). Four days after T2, we conducted the first dispersal event (D1) among the three communities within each metacommunity, followed by a new sampling event (T3) three days after the dispersal. Then, we repeated the same procedure, conducting a second dispersal event (D2) four days after T3, and the last sampling event (T4) three days after that. The experiment lasted for 18

days. As plankton organisms have relatively short generation times (Allan 1976, Dokulil 2024), particularly tropical species, the four sampling events conducted in our experiment allowed us to capture variation across distinct generations of zooplankton and phytoplankton populations.

We identified and counted a minimum of 300 individuals of phytoplankton using a 2 ml sedimentation chamber and an inverted microscope. For zooplankton, we identified and counted a minimum of 50 individuals from each group (Cladocera, Copepoda and Rotifera), using a 1 ml Sedgewick–Rafter chamber and an optic microscope. For juvenile and adult copepods and cladocerans we also used an acrylic chamber and a stereomicroscopy. Plankton samples collected during the experiment were identified to the lowest taxonomic resolution when possible, using the available literature (Elmoor-Loureiro 1997, Perbiche-Neves et al. 2015, Bicudo and Menezes 2017). Based on quantified and unquantified sample volumes, we estimated phytoplankton density as the number of individuals per ml, and zooplankton density as the number of individuals per liter.

Temporal variability and synchrony across scales

To measure variability across levels of organization, we followed a hierarchical framework in which metacommunity variability (Mv) is partitioned into its lower-level components (Wang et al. 2019). We partitioned Mv into two components – temporal variability of local communities (Cv), and spatial synchrony among local communities (Csy), as $Mv = Cv \times Csy$. We then further partitioned Cv into local population variability (Pv) and synchrony among local populations (Psy), as $Cv = Pv \times Psy$. Temporal variability and synchrony were measured for both producers and consumers separately.

We defined temporal variability at a given level of organization as the coefficient of variation (temporal variance divided by temporal mean) in plankton density across sampling surveys (Wang et al. 2019). At local scale (single patch), Pv was obtained for each population, dividing the temporal variance by the temporal mean of species density. At community level, we used the temporal variance and temporal mean of the total community (aggregated species density) to obtain Cv for each local patch. Similarly, Mv was defined as the coefficient of variation of total metacommunity density, and calculated dividing the temporal variance by the temporal mean of total density across the three-patch metacommunity. Pv and Cv were calculated as inverse measures of stability, obtained with the *community_stability* function in the R package ‘codyn’ (Hallett et al. 2016), while Mv was obtained with the associated R function *var.partition* of Wang et al. (2019).

For each local community, we defined synchrony among local populations (Psy) following Loreau and De Mazancourt (2008), as:

$$Psy = \frac{\sigma_{x_T}^2}{\left(\sum_i \sigma_{x_i}\right)^2}, \quad (1)$$

where $\sigma_{x_T}^2$ denotes the temporal variance in community density, and $\left(\sum_i \sigma_{x_i}\right)^2$ represents the sum of individual population variances. This measure of synchrony is standardized between 0 (perfect asynchrony) and 1 (perfect synchrony) and was obtained with the *synchrony* function in the package ‘codyn’ (Hallett et al. 2016).

At metacommunity scale, we defined spatial synchrony among local communities (Csy) as the spatial synchrony of total community density across local patches, following Wang et al. (2019), as:

$$Csy = \frac{\sqrt{V_{\Sigma,\Sigma}}}{\sum_k \sqrt{V_{\Sigma,kk}}}, \quad (2)$$

where $\sqrt{V_{\Sigma,\Sigma}}$ is the temporal variance of total metacommunity density, and $\sum_k \sqrt{V_{\Sigma,kk}}$ represents the sum of local community variances. This measure of synchrony is also standardized between 0 (perfect asynchrony) and 1 (perfect synchrony) and was obtained with the associated R function *var.partition* of Wang et al. (2019).

Data analysis

We assessed how landscape agrochemical contamination affected temporal variability in density of plankton producers (phytoplankton) and consumers (zooplankton) at local and regional scales. To do that, we fitted generalized linear models (GLM), and generalized linear mixed models (GLMM), with gaussian distribution, for local and regional response variables. We fitted one model for each temporal variability (Pv, Cv and Mv) and synchrony (Psy and Csy) metric, as response variables. Local scale responses (Pv, Cv and Psy) were modelled against an interaction between three fixed effects (local agrochemical contamination \times landscape composition \times trophic level). Cv and Psy GLMMs included metacommunity identity as a random factor, while the Pv GLMM included patch identity nested with metacommunity identity as random factors. Temporal variability at the metacommunity level (Mv) and community spatial synchrony (Csy) were modelled against an interaction between two fixed effects (landscape composition \times trophic level). For the metacommunity model, landscape composition was defined as a categorical variable that encompassed both regional and local agrochemical contamination, with five levels: pristine, fertilizer-mosaic, insecticide-mosaic, fertilizer-agriculture and insecticide-agriculture. More information on model description can be found in the Supporting information. Model analyses were conducted using the R package ‘lme4’ (Bates et al. 2015), and model assumptions examined with the ‘DHARMA’ package (Hartig 2024). All computational work and analyses were performed in R ver. 4.2.1 (www.r-project.org). Data and code used in this research are freely available at Zenodo (Barbosa et al. 2025).

Results

Local agrochemical contamination strongly influenced population temporal variability, and its effects depended on trophic level (Fig. 2A). As expected, the temporal variability of producer populations increased with fertilizer contamination, but it was reduced under insecticide effects (Fig. 2A), partially supporting hypothesis H1. Similarly, the temporal variability of consumer populations increased substantially with insecticide contamination (H1), but it was not influenced by the fertilizer treatment (Fig. 2A). Contrary to expectations (H2), local contamination effects did not depend on larger regional-scale effects of landscape (Supporting information), and landscape composition alone did not influence population variability (Fig. 2B).

At the community level, our model showed that the temporal variability of producer and consumer communities were not affected by local agrochemical contamination, landscape composition or their interaction (Supporting information). Similarly, we found no relationship between landscape contamination and the variability of producers or consumers at the metacommunity level (Supporting information). Neither local agrochemical contamination nor landscape composition influenced population synchrony or spatial synchrony among communities (Supporting information). All model results and detailed information can be found in Supporting information.

When we partitioned temporal variability of producers and consumers into their lower hierarchical levels (Fig. 3), we found that variability scaled up similarly under all combinations of localized agrochemical contamination (control, fertilizer and insecticide) and spatial composition of the landscape (pristine, mosaic and agriculture), not supporting hypothesis H3. Overall, and in accordance with our models, the high variability generated at the population level was buffered at the community and metacommunity levels. Visual representation of the data also indicated that this pattern of decreasing variability at higher levels and scales was similar for both producers and consumers, independently of fertilizer and insecticide contamination effects (Fig. 3).

Discussion

We experimentally investigated how localized anthropogenic effects interact with regional landscape composition to shape the temporal dynamics of freshwater food webs across spatial scales. Our results indicate that localized agrochemical contamination changed the temporal variability of local populations, but its effects varied in signal and magnitude across trophic levels. Local contamination played a major role in shaping the dynamics of planktonic producers and consumers in agricultural landscapes, but its influence on temporal variability and synchrony remained similar across

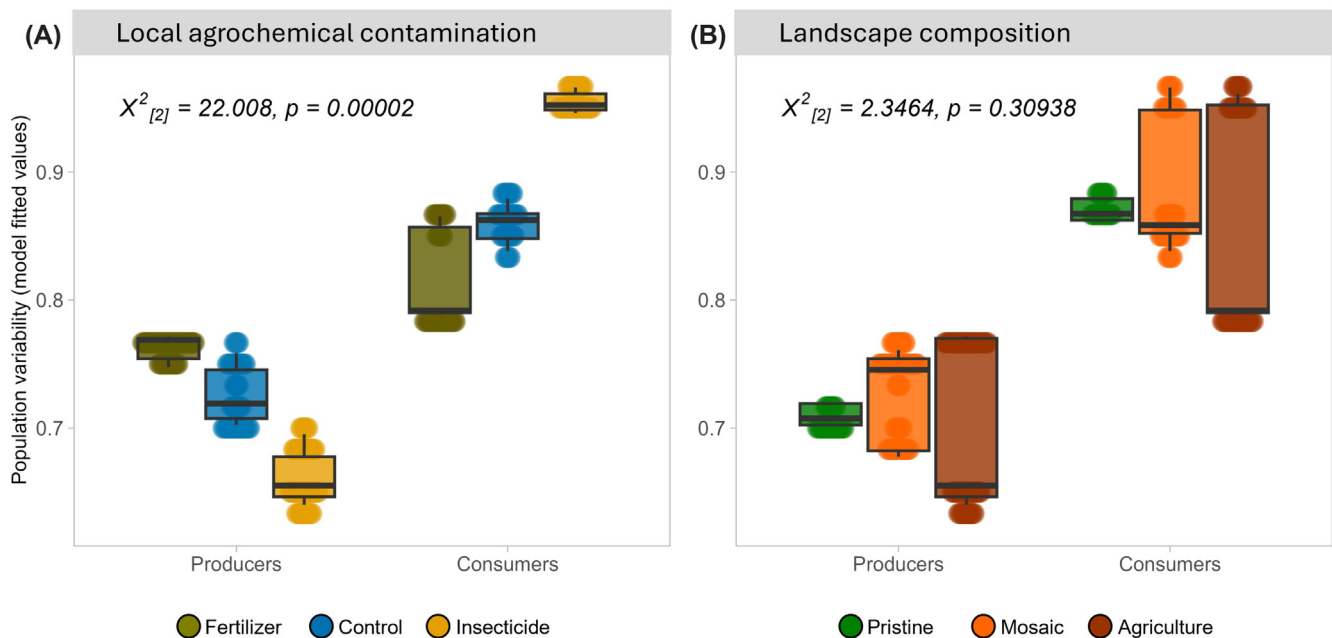


Figure 2. Temporal variability in density of plankton populations under agricultural expansion. (A) Population variability was influenced by local agrochemical contamination, but effects were distinct between producers and consumers. While insecticide contamination strongly increased consumer variability, it also decreased the variability of producer populations. The opposite was observed for fertilizer contamination, although the effects were less prominent. (B) On the other hand, landscape composition did not influence population variability of producers or consumers, either through its interaction with the local treatment or with trophic level. Model results within graphs indicate the interaction between local agrochemical contamination and trophic level in (A), and between landscape composition and trophic level in (B).

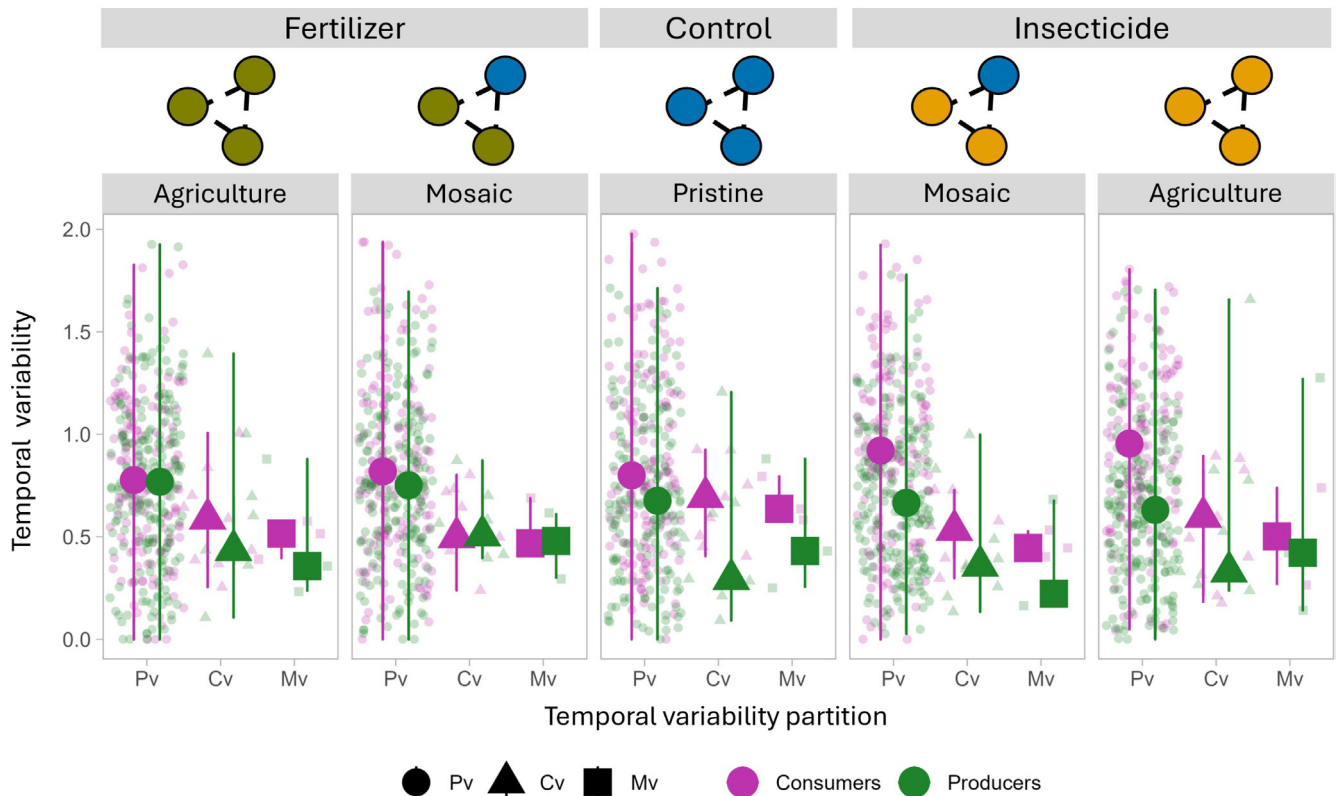


Figure 3. Partitioning the metacommunity variability (Mv) of producers and consumers into their lower hierarchical levels, community variability (Cv) and population variability (Pv), across varying landscape composition. The central points (Pv, Cv and Mv) within the picture represent the median of each temporal variability partition, for both producers and consumers, under an interaction of localized agrochemical contamination and landscape composition.

different landscape compositions. We also showed that temporal variability originating at the population level was buffered at higher levels of biological organization and spatial scales. Overall, our findings highlight the crucial role of local anthropogenic factors in destabilizing biodiversity within agricultural landscapes. However, they also suggest that more complex systems, comprising interacting species and embedded in spatial dynamics, may have greater resilience to agrochemical contamination, a growing threat to freshwater biodiversity.

Insecticides and fertilizers are widely used compounds in agricultural practices (Sharma et al. 2019), and they both changed the temporal variability of freshwater planktonic populations, even though local species synchrony remained unchanged. Insecticide contamination both increased the temporal variability of consumer and reduced that of producer populations. Recent literature has shown that insecticides have the potential not only to alter species density and cause direct mortality of zooplankton (Hayasaka et al. 2012, Hébert et al. 2021), but also to increase phytoplankton abundance and alter community composition via top-down cascading effects (Rumschlag et al. 2022). Our results extend these findings, revealing that insecticides can also influence phytoplankton stability via top-down effects, by increasing the temporal variability of zooplankton populations.

In contrast, fertilizer contamination increased the temporal variability of phytoplankton populations, though its effects on zooplankton were less pronounced. Mobile consumers can stabilize their own temporal dynamics by shifting among asynchronous resource patches (McCann et al. 2005). However, this explanation should be considered with caution in our experimental context, given our simplified representation of the freshwater food web (focusing only on producers and consumers) and limited scale of dispersal. Nevertheless, our findings underscore the role of trophic structure in influencing the magnitude of temporal variability (Siqueira et al. 2024), though this outcome may vary with the organizational level examined and the type of perturbation experienced by the ecosystem.

Spatial heterogeneity has been widely recognized as a major driver of temporal variability in natural ecosystems (Brown 2003, Wilcox et al. 2017, Collins et al. 2018, Larsen et al. 2021). Spatial heterogeneity promotes asynchronous dynamics among local communities (Wilcox et al. 2017, Larsen et al. 2021), influencing many ecological properties, such as population dynamics (Steiner et al. 2013), resource distribution (Tilman et al. 2014), and predator-prey interactions (McCann et al. 2005). Agricultural landscapes tend to homogenize local freshwater communities in space (Siqueira et al. 2015), exposing them to similar environmental

fluctuations, consequently enhancing community spatial synchrony (Steiner et al. 2013, Larsen et al. 2021) and temporal variability. Our results showed that variations in landscape composition, and consequently spatial heterogeneity, did not affect planktonic temporal variability or synchrony across spatial scales and organizational levels. These findings suggest two main explanations: first, that consistent dispersal within metacommunities may have buffered spatial heterogeneity in our experiment, synchronizing local populations and distinct communities across metacommunities and exerting a destabilizing influence, even in pristine (uncontaminated) landscapes (Steiner et al. 2013). Second, the effects of agrochemical contamination may have been highly restricted to the local scale only, with minimal detectable impact at larger spatial scales. If this explanation is more plausible, dispersal could have had a stabilizing effect on ecosystem dynamics (Steiner et al. 2013, Anderson and Fahimipour 2021).

Support for the hypothesis of restricted local effects of agrochemicals on plankton temporal variability is further evident in the partitioning of variability across scales within our experimental metacommunities. Although temporal variability tends to decrease with increasing spatial scale and levels of organization (Kéfi et al. 2019, Wang et al. 2019, Siqueira et al. 2024), we expected this pattern to be less prominent in metacommunities in which patches were exposed to agrochemicals. Instead, our models indicate that landscape composition did not influence the partition of temporal variability, as pristine landscapes behave similarly to mosaic and agricultural ones. Even though a visual examination suggested distinct partitioning patterns between plankton producers and consumers, the effects of landscape composition on temporal variability were also consistent across trophic levels. This result suggests that maintaining spatial fluxes of individuals can be important for buffering variability and maintaining ecosystem stability at broad spatial scales, regardless of land use change or trophic level.

Although our experimental approach contemplated distinct landscape compositions (e.g. mosaics with contaminated and uncontaminated connected patches), real world landscapes present a more complex manifestation of anthropogenic effects. Our local communities were exposed to either fertilizer or insecticide, but freshwater communities in agricultural domain are concomitantly exposed to distinct agrochemicals, which interact to produce observed changes in biotic dynamics (Barmantlo et al. 2018, Rumschlag et al. 2020). Also, given the magnitude and complexity of ways in which freshwater organisms can disperse (Bilton et al. 2001, Altermatt et al. 2011, Anderson and Fahimipour 2021), our experimental metacommunity dynamics are a very small simplification of how local communities are connected in nature. Therefore, future studies considering more complex landscape compositions, the interaction between insecticide and fertilizer contaminants, and distinct dispersal dynamics can be useful to fully understand how temporal variability changes across scales under agricultural expansion.

Despite certain limitations inherent to experimental manipulations of complex systems, our study demonstrates

that agrochemical contamination alters the temporal variability of planktonic producers and consumers in agricultural landscapes, but these effects are observed only at the population level. When we increase spatial scales and levels of organization (i.e. from populations to communities and metacommunities), the magnitude and signal of agrochemical effects disappear, and temporal variability in planktonic density is buffered, independently of landscape composition, suggesting strict localized effects of agrochemical contamination in agricultural landscapes. We also showed that the density of producers and consumers fluctuate differently according to agrochemicals, with insecticides having cascading effects on phytoplankton variability, while directly increasing the temporal variability of zooplankton consumers. As agriculture expansion constitutes a major driver of natural ecosystem change (Vörösmarty et al. 2010, Newbold et al. 2015, Barbosa and Siqueira 2023), our findings shed light on how local effects of agriculture perturbations interact with large-scale effects to influence temporal variability. It also suggests that, in the case of agrochemical contamination, sustaining complex, spatially connected ecological systems could be fundamental to maintaining biodiversity and stability in highly modified agricultural landscapes.

Acknowledgements – We thank Anne McLeod and Holly Harris for providing valuable comments on an earlier version of the manuscript.

Funding – Financial support was provided by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) – Funding code 001, for PhD and Master students during the realization of this study. Financial support was also provided by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), grant no. 19/06291-3, 21/00619-7 and 15/18790-3; Rufford Foundation 26823-1, and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), grant no. 409215/2018-0, 309496/2021-7, 310333/2022-9 and 303906/2021-9. TS is supported by funding from the Centre for Research on Biodiversity Dynamics and Climate Change, FAPESP no. 2021/10639-5 and JLP was funded by PNPd/CAPES (no. 88887.473604/2020-00).

Author contributions

Victor S. Saito and **Tadeu Siqueira** share last authorship. **Gedimar Pereira Barbosa**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (equal); Writing – original draft (equal). **Camila B. Vieira**: Data curation (equal); Methodology (equal); Writing – review and editing (equal). **Ana Carolina dos Santos**: Data curation (equal); Methodology (equal); Writing – review and editing (equal). **Neliton Lara**: Methodology (equal); Writing – review and editing (equal). **Erick Mateus-Barros**: Methodology (equal); Writing – review and editing (equal). **Jorge L. Portinho**: Data curation (equal); Methodology (equal); Writing – review and editing (equal). **Hugo Sarmento**: Methodology (equal); Resources (equal); Writing – review and editing (equal).

Gilmar Perbiche-Neves: Methodology (equal); Resources (equal); Writing – review and editing (equal). **Bianca Veloso:** Methodology (equal); Writing – review and editing (equal). **Cassiana Montagner:** Methodology (equal); Resources (equal); Writing – review and editing (equal). **Luis Schiesari:** Resources (equal); Writing – review and editing (equal). **Victor S. Saito:** Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal). **Tadeu Siqueira:** Conceptualization (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Zenodo repository: <https://doi.org/10.5281/zenodo.15802512> (Barbosa et al 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Allan, J. D. 1976. Life history patterns in zooplankton. – *Am. Nat.* 110: 165–180.
- Allan, J. D. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. – *Annu. Rev. Ecol. Syst.* 35: 257–284.
- Altermatt, F., Schreiber, S. and Holyoak, M. 2011. Interactive effects of disturbance and dispersal directionality on species richness and composition in metacommunities. – *Ecology* 92: 859–870.
- Anderson, K. E. and Fahimipour, A. K. 2021. Body size dependent dispersal influences stability in heterogeneous metacommunities. – *Sci. Rep.* 11: 17410.
- Angelini, R. and Petrere, M. 2000. A model for the plankton system of the Broa reservoir, São Carlos, Brazil. – *Ecol. Modell.* 126: 131–137.
- Barbosa, G. P. and Siqueira, T. 2023. Direct and indirect relationships of climate and land use change with food webs in lakes and streams. – *Global Ecol. Biogeogr.* 32: 2153–2163.
- Barbosa, G. P., Vieira, C. B., dos Santos, A. C., Lara, N., Mateus-Barros, E., Portinho, J. L., Sarmiento, H., Perbiche-Neves, G., Veloso, B., Montagner, C., Schiesari, L., Saito, V. and Siqueira, T. 2025. Data and code from: Agrochemical effects on plankton temporal variability are buffered at larger spatial scales [Dataset]. – Zenodo Repository, <https://doi.org/10.5281/zenodo.15802512>.
- Barmantlo, S. H., Schrama, M., Hunting, E. R., Heutink, R., van Bodegom, P. M., de Snoo, G. R. and Vijver, M. G. 2018. Assessing combined impacts of agrochemicals: aquatic macroinvertebrate population responses in outdoor mesocosms. – *Sci. Total Environ.* 631–632: 341–347.
- Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.
- Bicudo, C. E. de and Menezes, M. (eds) 2017. Gêneros de algas de águas continentais do Brasil: chave para identificação e descrições (Terceira edição [revista e ampliada]). – RiMa.
- Bilton, D. T., Freeland, J. R. and Okamura, B. 2001. Dispersal in freshwater invertebrates. – *Annu. Rev. Ecol. Syst.* 32: 159–181.
- Brown, B. L. 2003. Spatial heterogeneity reduces temporal variability in stream insect communities. – *Ecol. Lett.* 6: 316–325.
- Burford, M. A. and O'Donohue, M. J. 2006. A comparison of phytoplankton community assemblages in artificially and naturally mixed subtropical water reservoirs. – *Freshw. Biol.* 51: 973–982.
- Christoforetti, C. A., Escher, J. P., Correia, J. E., Marinho, J. F. U. and Fontanetti, C. S. 2013. Sugarcane vinasse: environmental implications of its use. – *Waste Manage.* 33: 2752–2761.
- Clements, W. H., Hickey, C. W. and Kidd, K. A. 2012. How do aquatic communities respond to contaminants? It depends on the ecological context. – *Environ. Toxicol. Chem.* 31: 1932–1940.
- Collins, S. L., Avolio, M. L., Gries, C., Hallett, L. M., Koerner, S. E., La Pierre, K. J., Rypel, A. L., Sokol, E. R., Fey, S. B., Flynn, D. F. B., Jones, S. K., Ladwig, L. M., Ripplinger, J. and Jones, M. B. 2018. Temporal heterogeneity increases with spatial heterogeneity in ecological communities. – *Ecology* 99: 858–865.
- Dokulil, M. T. 2024. Long-term adjustment of phytoplankton structure to environmental traits at timescales during lifetime development and over generations. – *Hydrobiologia* 851: 823–847.
- Dudgeon, D. 2019. Multiple threats imperil freshwater biodiversity in the Anthropocene. – *Curr. Biol.* 29: R960–R967.
- Elmoor-Loureiro, L. M. A. 1997. Manual de identificação de cladóceros límnicos do Brasil. – Ed. Universa.
- Fox, J. W., Vasseur, D. A., Hausch, S. and Roberts, J. 2011. Phase locking, the Moran effect and distance decay of synchrony: experimental tests in a model system. – *Ecol. Lett.* 14: 163–168.
- Gianuca, A. T., Declerck, S. A. J., Lemmens, P. and De Meester, L. 2017. Effects of dispersal and environmental heterogeneity on the replacement and nestedness components of β -diversity. – *Ecology* 98: 525–533.
- Gonçalves, S., Vasconcelos, M. W., Mota, T. F. M., Lopes, J. M. H., Guimaraes, L. J., Miglioranza, K. S. B. and Ghisi, N. C. 2022. Identifying global trends and gaps in research on pesticide fipronil: a scientometric review. – *Environ. Sci. Pollut. Res.* 29: 79111–79125.
- Hallett, L. M., Jones, S. K., MacDonald, A. A. M., Jones, M. B., Flynn, D. F. B., Ripplinger, J., Slaughter, P., Gries, C. and Collins, S. L. 2016. CODYN: an R package of community dynamics metrics. – *Methods Ecol. Evol.* 7: 1146–1151.
- Hartig, F. 2024. Dharma: residual diagnostics for hierarchical (multi-level/mixed) regression models. – R ver. 0.4.7, <https://florianhartig.github.io/DHARMA/>.
- Hayasaka, D., Korenaga, T., Suzuki, K., Saito, F., Sánchez-Bayo, F. and Goka, K. 2012. Cumulative ecological impacts of two successive annual treatments of Imidacloprid and fipronil on aquatic communities of paddy mesocosms. – *Ecotoxicol. Environ. Saf.* 80: 355–362.
- Hébert, M., Fugère, V., Beisner, B. E., Barbosa Da Costa, N., Barrett, R. D. H., Bell, G., Shapiro, B. J., Yargeau, V., Gonzalez, A. and Fussmann, G. F. 2021. Widespread agrochemicals differentially affect zooplankton biomass and community structure. – *Ecol. Appl.* 31: e02423.
- Kéfi, S., Domínguez-García, V., Donohue, I., Fontaine, C., Thébault, E. and Dakos, V. 2019. Advancing our understanding of ecological stability. – *Ecol. Lett.* 22: 1349–1356.
- Khan, F. A., Naushin, F., Rehman, F., Masoodi, A., Irfan, M., Hashmi, F. and Ansari, A. A. 2014. Eutrophication: global scenario and local threat to dynamics of aquatic ecosystems. – In:

- Ansari, A. A. and Gill, S. S. (eds), Eutrophication: causes, consequences and control. – Springer, pp. 17–27.
- Larsen, S., Comte, L., Filipa Filipe, A., Fortin, M.-J., Jacquet, C., Ryser, R., Tedesco, P. A., Brose, U., Erős, T., Giam, X., Irving, K., Ruhi, A., Sharma, S. and Olden, J. D. 2021. The geography of metapopulation synchrony in dendritic river networks. – *Ecol. Lett.* 24: 791–801.
- Loreau, M. and De Mazancourt, C. 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. – *Am. Nat.* 172: E48–E66.
- Loreau, M. and De Mazancourt, C. 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. – *Ecol. Lett.* 16: 106–115.
- Matsumura-Tundisi, T. and Tundisi, J. G. 2005. Plankton richness in a eutrophic reservoir (Barra Bonita Reservoir, SP, Brazil). – *Hydrobiologia* 542: 367–378.
- McCann, K. S., Rasmussen, J. B. and Umbanhowar, J. 2005. The dynamics of spatially coupled food webs. – *Ecol. Lett.* 8: 513–523.
- Newbold, T. et al. 2015. Global effects of land use on local terrestrial biodiversity. – *Nature* 520: 45–50.
- Patrick, C. J., Anderson, K. E., Brown, B. L., Hawkins, C. P., Metcalfe, A., Saffarinia, P., Siqueira, T., Swan, C. M., Tonkin, J. D. and Yuan, L. L. 2021. The application of metacommunity theory to the management of riverine ecosystems. – *WIREs Water* 8: 1–21.
- Perbiche-Neves, G., Boxshall, G. A., Previattelli, D., Nogueira, M. G. and Da Rocha, C. E. F. 2015. Identification guide to some Diaptomid species (Crustacea, Copepoda, Calanoida, Diaptomidae) of “de la Plata” River Basin (South America). – *ZooKeys* 497: 1–111.
- Ranta, E., Kaitala, V., Lindström, J. and Helle, E. 1997. The Moran effect and synchrony in population dynamics. – *Oikos* 78: 136–142.
- Rumschlag, S. L., Casamatta, D. A., Mahon, M. B., Hoverman, J. T., Raffel, T. R., Carrick, H. J., Hudson, P. J. and Rohr, J. R. 2022. Pesticides alter ecosystem respiration via phytoplankton abundance and community structure: effects on the carbon cycle? – *Global Change Biol.* 28: 1091–1102.
- Rumschlag, S. L., Mahon, M. B., Hoverman, J. T., Raffel, T. R., Carrick, H. J., Hudson, P. J. and Rohr, J. R. 2020. Consistent effects of pesticides on community structure and ecosystem function in freshwater systems. – *Nat. Commun.* 11: 6333.
- Schiesari, L., Saito, V., Ferreira, J., Freitas, L. S., Goebels, A. J., Leite, J. P. C. B., Oliveira, J. C., Pelinson, R. M., Querido, B. B., Carmo, J., Espíndola, E. L. G., Guedes-Munin, N. C., Montagner, C., Rossetto, R., Taniwaki, R. and Martinelli, L. A. 2023. Community reorganization stabilizes freshwater ecosystems in intensively managed agricultural fields. – *J. Appl. Ecol.* 60: 1327–1339.
- Sendacz, S., Caleffi, S. and Santos-Soares, J. 2006. Zooplankton biomass of reservoirs in different trophic conditions in the State of São Paulo, Brazil. – *Braz. J. Biol.* 66: 337–350.
- Sharma, A., Kumar, V., Shahzad, B., Tanveer, M., Sidhu, G. P. S., Handa, N., Kohli, S. K., Yadav, P., Bali, A. S., Parihar, R. D., Dar, O. I., Singh, K., Jasrotia, S., Bakshi, P., Ramakrishnan, M., Kumar, S., Bhardwaj, R. and Thukral, A. K. 2019. Worldwide pesticide usage and its impacts on ecosystem. – *S.N. Appl. Sci.* 1: 1446.
- Siqueira, T., Lacerda, C. G.-L. T. and Saito, V. S. 2015. How does landscape modification induce biological homogenization in tropical stream metacommunities? – *Biotropica* 47: 509–516.
- Siqueira, T. et al. 2024. Understanding temporal variability across trophic levels and spatial scales in freshwater ecosystems. – *Ecology* 105: e4219.
- Steiner, C. F., Stockwell, R. D., Kalaimani, V. and Aqel, Z. 2013. Population synchrony and stability in environmentally forced metacommunities. – *Oikos* 122: 1195–1206.
- Thibaut, L. M. and Connolly, S. R. 2013. Understanding diversity–stability relationships: towards a unified model of portfolio effects. – *Ecol. Lett.* 16: 140–150.
- Thompson, P. L., Rayfield, B. and Gonzalez, A. 2017. Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. – *Ecography* 40: 98–108.
- Tilman, D., Isbell, F. and Cowles, J. M. 2014. Biodiversity and ecosystem functioning. – *Annu. Rev. Ecol. Evol. Syst.* 45: 471–493.
- Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S. E., Sullivan, C. A., Liermann, C. R. and Davies, P. M. 2010. Global threats to human water security and river biodiversity. – *Nature* 467: 555–561.
- Wang, S., Lamy, T., Hallett, L. M. and Loreau, M. 2019. Stability and synchrony across ecological hierarchies in heterogeneous metacommunities: linking theory to data. – *Ecography* 42: 1200–1211.
- Wilcox, K. R. et al. 2017. Asynchrony among local communities stabilises ecosystem function of metacommunities. – *Ecol. Lett.* 20: 1534–1545.