Ecological stability propagates across spatial scales and trophic levels in freshwater ecosystems

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Tadeu Siqueira[1,2*], Charles P. Hawkins[3], Julian Olden[4], Jonathan Tonkin[5], Lise Comte[6], Victor S. Saito[7], Thomas L. Anderson[8], Gedimar P. Barbosa[1]; Núria Bonada[9], Claudia C. Bonecker[10], Miguel Cañedo-Argüelles[9,11], Thibault Datry[12], Michael B. Flinn[13], Pau Fortuño[9], Gretchen A. Gerrish[14], Peter Haase[15], Matthew J. Hill[16], James M. Hood[17], Kaisa-Leena Huttunen[18], Michael J. Jeffries[19], Timo Muotka[20], Daniel R. O'Donnell[21], Riku Paavola[22], Petr Paril[23], Michael J. Paterson[24], Christopher J. Patrick[25], Gilmar Perbiche-Neves[26], Luzia C. Rodrigues[10], Susanne C. Schneider[27], Michal Straka[23,28], Albert Ruhi[2]

1-Institute of Biosciences, São Paulo State University (UNESP), Rio Claro, SP, Brazil; e-mail: tadeu.siqueira@unesp.br; ORCID: 0000-0001-5069-2904; email: gedimar.barbosa@gmail.com

2- Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA, USA; email: albert.ruhi@berkeley.edu; ORCID: 0000-0003-4011-6457; * Sabbatical Institution where TS was hosted

3-Department of Watershed Sciences and Ecology Center, Utah State University, Logan, UT, USA; e-mail: chuck.hawkins@usu.edu; ORCID: 0000-0003-1247-0248

4-University of Washington, School of Aquatic and Fishery Sciences, WA, USA; e-mail: olden@uw.edu; ORCID: 0000-0003-2143-1187

5-School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand; Te Pūnaha Matatini, Centre of Research Excellence in Complex Systems, New Zealand; Bioprotection Aotearoa, Centre of Research Excellence, New Zealand;
email: jonathan.tonkin@canterbury.ac.nz; ORCID: 0000-0002-6053-291X

6-School of Biological Sciences, Illinois State University, IL 61790 Normal, USA; email: lccomte@ilstu.edu; ORCID: 0000-0001-8030-0019

7- Federal University of São Carlos, Department of Environmental Sciences, Brazil; email: victor.saito@gmail.com; ORCID: 0000-0001-6112-7249

8- Southern Illinois University Edwardsville, USA; email: thander@siue.edu; ORCID: 0000-0001-7479-2192

9- FEHM-Lab (Freshwater Ecology, Hydrology and Management), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), Diagonal 643, 08028 Barcelona, Catalonia, Spain; email: bonada@ub.edu; ORCID: 0000-0002-2983-3335; pfortuno@ub.edu; ORCID: 0000-0002-2198-3486

10- CCB-Nupelia-PEA-PGB, Maringá State University, PR, Brazil; email: bonecker@nupelia.uem.br; ORCID: 0000-0003-4338-9012; email: luziac.rodrigues@gmail.com; ORCID: 0000-0002-0593-0931

11- Freshwater Ecology, Hydrology and Management (FEHM) Research Group, Institute of Environmental Assessment and Water Research (IDAEA), CSIC, Jordi Girona 18, Barcelona, 08034 Catalonia, Spain; email: mcanedo.fem@gmail.com; ORCID: 0000-0003-3864-7451

12- INRAE, UR RiverLy, Centre Lyon-Grenoble Auvergne-Rhône-Alpes, 5 rue de la Doua CS70077, 69626 Villeurbanne Cedex, France; email: thibault.datry@inrae.fr; ORCID: 0000-0003-1390-6736

13- Hancock Biological Station, Biological Sciences, Murray State University, Murray, KY 42071 USA; email: mflinn@murraystate.edu

14- University of Wisconsin Madison, Trout Lake Station, Boulder Junction, WI 54512, USA; email: ggerrish@wisc.edu; ORCID: 0000-0001-6192-5734

15- Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, Gelnhausen, Germany; Faculty of Biology, University of Duisburg-Essen, Essen, Germany; email: peter.haase@senckenberg.de; ORCID: 0000-0002-9340-0438

16- School of Applied Sciences, University of Huddersfield, Queensgate, Huddersfield, HD1 2DH, UK; email: m.hill@hud.ac.uk; ORCID: 0000-0001-8008-2197

17- Aquatic Ecology Laboratory, Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, Ohio, USA; Translational Data Analytics Institute, The Ohio State University, Columbus, Ohio, USA; email: hood.211@osu.edu; ORCID: 0000-0001-6365-0762

18- Ecology and Genetics Research Unit, University of Oulu, Finland; email: kaisa-leena.huttunen@oulu.fi; ORCID: 0000-0003-0488-1274

19- Northumbria University, Newcastle upon Tyne, UK; email: michael.jeffries@northumbria.ac.uk; ORCID: 000 0003 3454 1107

20- University of Oulu, Department of Ecology & Genetics, Finland; email: timo.muotka@oulu.fi; ORCID: 0000-0002-2268-5683
21- Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA 95616, USA; email: drodonnell@ucdavis.edu; ORCID: 000-0003-0452-2888
22- Oulanka Research Station, University of Oulu, Finland; email: riku.paavola@oulu.fi
23- Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlarska 2, 611 37, Brno, Czech Republic; email: paril@sci.muni.cz; ORCID: 0000-0002-7471-997X
24- International Institute for Sustainable Development Experimental Lakes Area, Canada; email: mpaterson@iisd-ela.org; ORCID: 0000-0002-8526-9126
25- Virginia Institute of Marine Science, USA; email: cpatrick@vims.edu; ORCID: 0000-0002-9581-8168
26- Department of Hydrobiology, Federal University of São Carlos, SP, Brazil, 13565-905; email: gpneves@ufscar.br; ORCID: 0000-0002-5025-2703
27- Norwegian Institute for Water Research, Norway; email: susi.schneider@niva.no; ORCID: 0000-0002-9545-3023
28- T.G. Masaryk Water Research Institute p.r.i., Brno Branch Office, Mojmírovo nám. 16, CZ-612 00 Brno, Czech Republic; email: michal.straka@vuv.cz; ORCID: 0000-0002-9949-9555

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Correspondence author: Tadeu Siqueira, Av. 24 A, 1515, UNESP, IB, CEP 13506-900, Rio Claro, SP, Brazil (tadeu.siqueira@unesp.br; +55 19 35264237)

Abstract

The temporal stability of ecological properties increases with spatial scale and levels of biological organization, but how does it propagate across trophic levels? We compiled 35 metacommunity time-series datasets spanning basal resources (e.g., phytoplankton) to top predators (e.g., piscivorous fish) from 384 freshwater sites across three continents. We reveal how stability propagates from populations to metacommunities and across trophic levels through the complementary and opposing contributions of synchrony and variability. Temporal variability in abundance decreased from producers to tertiary consumers mainly at the local scale. Population synchrony within sites increased with trophic level, whereas spatial synchrony among communities decreased. The link between spatial synchrony and metacommunity variability was stronger for top consumers, but the indirect effects of environmental variables and diversity on temporal variability was consistent among spatial scales and trophic levels. We suggest that mobile predators can stabilize metacommunities if they buffer variability originating at the base of food webs. Our findings advance the notion that the trophic structure of metacommunities, which reflects organismal differences in body size, dispersal, and environmental tolerance, should be considered when investigating the propagation of ecological stability.

Introduction

It is well recognized that temporal variability in ecological properties (e.g., population biomass, community richness, ecosystem metabolism) tends to decrease with increasing spatial scale and levels of biological organization (Kéfi *et al.* 2019; Hammond *et al.* 2020). For instance, fluctuations in fishery catch at the metapopulation level are often weaker than in any one of the constituent populations (Schindler *et al.* 2010). Similarly, organismal abundance at a given patch tends to be more stable at the community than at the population level (Doak *et al.* 1998). However, most previous attempts to understand temporal variability and its drivers have done so at single trophic levels (Kéfi *et al.* 2019 ; Xu *et al.* 2021; but see Steiner *et al.* 2005; Danet *et al.* 2021), resulting in a critical knowledge gap. Communities are connected to each other through the spatial flow of organisms that occupy different trophic levels (Leibold & Chase 2018), thus, the hierarchical nature of multitrophic metacommunities may modulate temporal variability (Firkowski *et al.* 2022). For example, top mobile consumers can buffer temporal variability of an entire metacommunity if they move unhindered across the landscape, optimally foraging across heterogeneous resource patches that have asynchronous dynamics (McCann *et al.* 2005). Understanding how temporal variability propagates not only across spatial and organizational scales, but also across trophic levels, would increase realism in our models of metacommunity dynamics and could help identify controls on ecosystem stability.

A hierarchical framework for understanding temporal variability in metacommunities has been formalized only recently (Wang *et al.* 2019). This framework assumes that fluctuations in species populations within sites represent the lowest-level component of temporal variability – i.e., species population variability. The amount of population variability that propagates to the aggregate community level is determined by the amount of synchrony (i.e., coordinated fluctuations) across the different populations in a landscape (Thibaut & Connolly 2013). In turn, metacommunity variability emerges from both aggregate community variability and spatial synchrony among local communities (Wang *et al.* 2019). By virtue of this scaling, temporal variability tends to decrease as ecological properties are aggregated from local populations to regional metacommunities.

The propagation of temporal variability across spatial scales and levels of organization has been explained, thus far, by mechanisms operating either at local or regional scale. At local scales, aggregate ecological properties tend to be more stable in more diverse communities due to statistical averaging among species that fluctuate independently through time (portfolio effects; Schindler *et al.* 2015). Negative covariance in the abundance of different populations due to biotic and abiotic interactions also reduces temporal variation in aggregate ecological properties (compensatory dynamics; Gonzalez & Loreau 2009). Higher diversity also indirectly increases the chance of compensatory dynamics unless species are highly functionally redundant. With more species, there will likely be a broader range of responses to environmental variation (Mori *et al.* 2013). At the regional scale, ecological properties (e.g., metacommunity total biomass) will vary more if spatially separated communities are synchronized, either via correlated fluctuations in the environment (Moran effect; Steiner *et al.* 2013) or via a combination of strong dispersal and predator-prey cycles (phase locking; Fox *et al.* 2011). Notably, organismal trophic position is generally associated with body size, dispersal strength, and response to environmental variation (Woodward *et al.* 2005; Jenkins *et al.* 2007).

Thus, the trophic structure of a metacommunity may determine the magnitude and drivers of its temporal variability—a hypothesis that has not been robustly tested, to our knowledge.

High-level mobile consumers can also stabilize the temporal dynamics of metacommunities by coupling heterogeneous local food webs in space (McCann *et al.* 2005; Rooney *et al.* 2008). This hierarchical framework assumes that larger organisms tend to be at higher trophic levels, and demonstrate high mobility across the landscape, leaving low prey density patches for more profitable high-density patches ("the bird feeder effect"; Eveleigh *et al.* 2007). Within a large ecosystem, the spatial coupling of heterogeneous local food webs guarantees a continuous supply of resources of different quality to mobile predators, making their temporal dynamics more stable relative to organisms at lower trophic levels. Merging these two views (Rooney *et al.* 2008; Wang *et al.* 2019) offers new opportunities to test hypotheses about how diversity, environmental fluctuations, and spatial fluxes interact with trophic levels to influence the propagation of temporal variability across space and across levels of organization (Danet *et al.* 2021).

Here we compiled 35 temporal data sets on metacommunity dynamics spanning basal resources (e.g., phytoplankton) to top predators (e.g., piscivorous fish), comprising spatially replicated interannual time series sampled from 384 freshwater sites across three continents. Merging the two hierarchical frameworks of temporal variability, we tested the following hypotheses: (H1) Temporal variability in abundance decreases with trophic position, as top consumers may buffer variability originating at the base of the food web. (H2) Species population synchrony within sites increases with trophic level, whereas spatial synchrony among communities decreases, as top mobile consumers may flock in heterogeneous resource patches through time. This hypothesis is supported by the idea that tracking heterogeneous resources should increase variability in the time that top consumers spend in a patch, which should decrease spatial synchrony in resources at the regional scale but increase local predator synchrony (Vasseur & Fox 2009). Finally, we tested if the strength and direction of relationships between temporal variability, synchrony, diversity, and environmental and spatial predictors depend on trophic level and spatial scale. We hypothesized (H3a) a stronger role of environmental control in primary producer population variability and synchrony at the local scale, as their dynamics would be less affected by the spatial coupling of mobile top consumers (Fig. 1), and (H3b) a stronger role of spatial connectivity on top consumer spatial synchrony and metacommunity variability at the regional scale. We found that temporal variability in abundance decreases from producers to top consumers in freshwater ecosystems, especially at the local scale, because of the complementary and opposing contributions of different trophic levels to synchrony and variability within and across localities.

Material and methods

We compiled and reorganized metacommunity temporal data sets comprising spatially replicated time series of species spanning different trophic levels. We then used the hierarchical partitioning framework proposed by Wang et al. (2019) applied to metacommunities to test hypotheses H1 and H2. Next, we used structural equation modelling (SEM) applied to variability and synchrony components measured at two spatial scales (sites and metacommunities) to test hypothesis H3. We articulate each analytical step below.

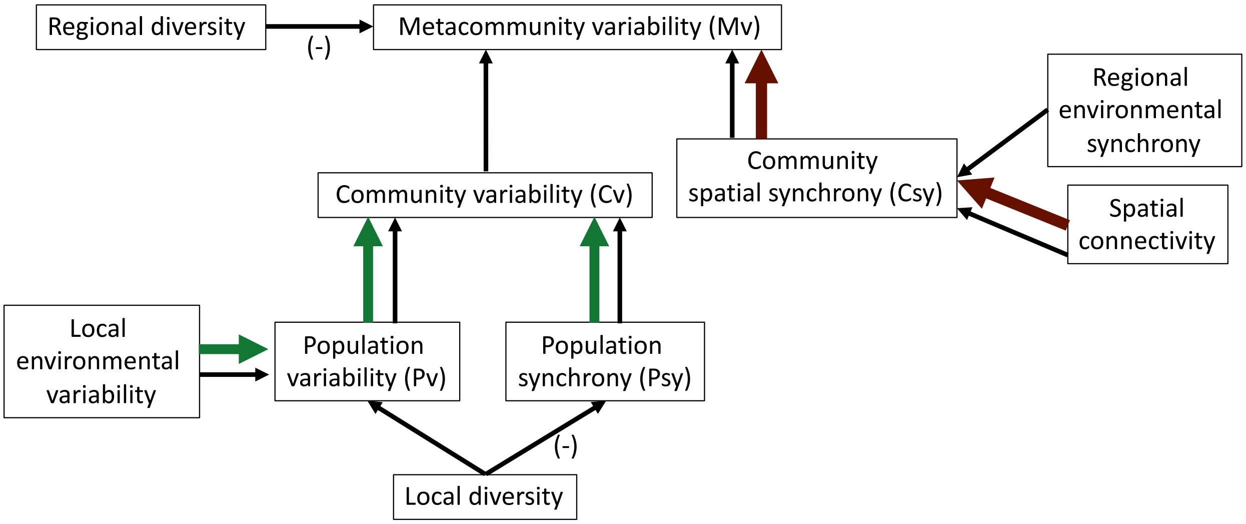

Figure 1. Hypothesized propagation of temporal variability and synchrony (from populations to metacommunities) and their relationships with diversity, environmental variability and synchrony, and spatial connectivity. Directions of the arrows represent directions of each hypothesized causal relationship, and arrow widths represent their strength. Expected influences are positive unless indicated otherwise (with a “(-)”). Arrow colors represent relationships that are expected to be specific to a particular trophic level: green for primary producers, dark red for tertiary consumers. Black arrows indicate relationships that are expected to be similar across trophic levels.

Data sets

We collated 35 independent metacommunity data sets, comprising spatially replicated time series of counts of individual species (or genera) spanning those representing basal resources (e.g., phytoplankton) to top predators (e.g., piscivorous fish) across different geographies and climates of the globe (Fig. S1). A summary of each data set as well as a general description of data reorganization can be found in the supporting information.

Our data included 10 metacommunities in lentic systems (ponds and lakes) and 25 in lotic systems (streams and rivers). Each data set contained at least 4 sites (max. = 30; mean =

11.35; median = 10) sampled for at least 5 years (max. = 36; mean = 12.8; median = 10). When the original data included multiple sampling events per year, we chose the summer month with the highest number of sites sampled.

Each species was assigned to one trophic category: producers (including stream benthic algae, macrophytes, and phytoplankton; 53 site-level time series after filtering, see below), primary consumers (zooplankton [Cladocera and Copepoda], macroinvertebrates, and fish; 115 site-level time series), secondary consumers (macroinvertebrates and fish; 208 site-level time series), and tertiary consumers (piscivorous fish; 173 site-level time series). We then reorganized the original data sets into trophic-level-specific metacommunities. For example, an original data set on fish could be subdivided into three data tables, one with primary consumers only, one with secondary, and another with tertiary consumers. This reorganization of data resulted in 59 data tables (producers = 5; primary consumers = 17; secondary = 22; tertiary = 15). Finally, we removed sites with only 1 species, resulting in 549 sites (the same site could be part of more than one data table) and 54 trophic-level-specific metacommunities for analysis. Importantly, none of the original 35 data sets included information on all trophic levels. Thus, our inferences are based on analyses of trophic levels that were represented by different data sets. We recognize the simplification of trophic level categorization as we do not consider omnivory or variation in feeding strategies within a particular group. However, failing to simplify the data in this manner would have resulted in many combinations of metacommunities and trophic levels, most without any replication or temporal and spatial sampling completeness. As we aimed to investigate relationships that are theoretically expected along a complex gradient of trophic levels (Vander Zanden & Fetzer 2007) and dispersal capacity (Rooney *et al.* 2008), we believe our strategy represents a useful compromise.

We explicitly considered variation inherent to the original data by using two strategies. First, we estimated all variables (e.g., local diversity, population synchrony) used in our analysis within each of the 59 metacommunity-trophic level data sets. Second, we used mixed-effects models to quantify the relationships between these variables (see details below).

Metacommunity variability partitions across scales and levels

To test hypotheses H1 and H2, we first partitioned temporal variability in total metacommunity abundance into its lower-level components for each of the 54 trophic-level-specific metacommunities. For this, we used the framework proposed by Wang *et al.* (2019) that allows partitioning the variability of total metacommunity abundance (Mv) into two components – temporal variability of local community abundance (Cv) and spatial synchrony among those local communities (Csy). Cv was further partitioned into the variability of individual population abundances within sites (Pv) and synchrony among those local populations (Psy; Fig. 1). Thus, Mv = Cv x Csy = (Pv x Psy) x Csy. Temporal variability at a given level was defined as the coefficient of variation in abundance across years, where Cv was expressed as the weighted (by the temporal mean) average of community variability across sites and Pv was expressed as the weighted average of local population variability across species and patches. Csy was calculated as the annual variance of metacommunity abundance divided by the sum of temporal standard deviations of local community abundance. Species population synchrony was calculated as the annual variance of community abundance divided by the squared sum of the standard deviations of the constituent species' abundances. Psy was expressed as the weighted average of species synchrony across patches (see Wang *et al*. 2019 for equations). Thus, there was one value of Mv, Cv, Pv, Csy, and Psy per each of the 54 trophic-level-specific metacommunities.

We modeled partition values as a function of trophic and organizational levels with linear models. Because we were more interested in differences among trophic levels, when there was a relationship between variability or synchrony with trophic levels (global model with $P < 0.05$), we used estimated marginal means and specific pairwise contrasts corrected for multiple comparisons (Holm adjustment) to compare trophic levels. To do that we used the package emmeans (Lenth *et al.* 2022) in the R (v4.1.0; R Core Team 2021).

Two-scale structural equation modelling

Based on hypotheses H3a-b, we used local estimation structural equation modeling (SEM; Shipley 2000) to test the direct and indirect relationships among diversity, environmental and spatial predictors, variability and synchrony, and trophic levels at two spatial scales. We used two independent SEMs to maximize the statistical power of our test. First, we applied SEM to metacommunity partitions (regional-scale SEM; $n = 54$ trophic-level-specific metacommunities). Then, we applied SEM to variability and synchrony metrics estimated at the local scale, i.e., for individual sites within the trophic-level-specific metacommunities (local-scale SEM; $n = 549$).

To estimate variability and synchrony metrics at the local scale, we used the same equations as in Wang *et al.* (2019), but without averaging variability or synchrony across sites.

Therefore, the temporal variability of aggregate community abundance at each site (Cv_local) was defined as the coefficient of variation of summed species abundance within the site. We estimated Cv_local independently for each of the 54 trophic-level-specific metacommunities and obtained one value of Cv_local per site. For the local scale, we also partitioned community variability into its lower components, population variability within sites (Pv_local), defined as the weighted average CV of population abundance of the species present within the local community, and synchrony among those local populations within sites (Psy_local), defined as the synchrony in abundance among the species present within the local community. The two SEMs were conceptually linked by community variability. However, for the local-scale SEM community variability was estimated for each site (Cv_local), whereas for the regional-scale SEM, it was averaged within each metacommunity (Cv).

We built each SEM following our conceptual model (Fig. 1). We then fitted different models following that structure but using different variables to represent the direct and indirect relationships. For example, we represented the direct path between local environmental variability and population variability by using temperature seasonality in one candidate model, and precipitation seasonality in another. We used AICc, model weight, and delta AICc to compare alternative models. When different models were equally plausible (i.e., delta AIC < 2), we chose the one with the highest total R^2 value and with residuals that did not show strong patterns.

For the regional-scale SEM, we fitted Gaussian linear mixed models with the response and predictor variables as described in Figure 1, and with metacommunity identity as a random effect. Local diversity, variability and synchrony were log-transformed prior to analyses to improve model fit. For the local-scale SEM, we fitted Gaussian linear mixed effects models with the response and predictor variables as described in Figure 1, and with metacommunity identity and a variable identifying the trophic-level-specific metacommunity as random effects. The fit and evaluation of the model followed the same procedures described for regional-scale SEM.

We performed multigroup SEM analysis (Lefcheck 2016) to test whether the relationships among predictor and response variables varied between trophic groups. That is, we tested which paths had similar strength and direction, and which varied between trophic groups. The goodness of fit of each SEM was evaluated with a test of directed separation (Fisher's C statistic; alpha ≥ 0.05). The SEMs were fitted with lme4 (Bates *et al.* 2015) and piecewiseSEM (Lefcheck 2016) in R.

Environmental and spatial predictors

Two measures of spatial synchrony in mean maximum and mean minimum temperature and precipitation were used as predictors in the regional-scale SEM. Local, direct measures of thermal and hydrologic regimes would have been ideal, but these data were not available. We therefore used ~4 km resolution temperature and precipitation data from the TerraClimate database, a monthly generated product of climate and climatic water balance for global terrestrial surfaces for the period 1958 – 2015 (Abatzoglou *et al.* 2018). We extracted monthly mean values at the spatial coordinates of the sampling sites, from 1958 to the last year in which data was sampled within each data set. Spatial synchrony in temperature and in precipitation was then estimated as the mean Kendall rank correlation between each pair of sites. One metacommunity had all values of spatial synchrony set to 1 because its spatial extent was lower than 4 km^2. We decided to include seven decades of data instead of restricting the data to the study period of each data set to get a broad and comparable characterization of environmental variation across sites.

For the regional-scale SEM, we estimated one metric of spatial connectivity, network closeness centrality (Erős *et al.* 2012), and used it as a predictor of community spatial synchrony. Closeness centrality was calculated for each site within a metacommunity as the sum of the length of the shortest paths between the site and all other sites in the metacommunity. The more central a site is, the closer it is to all other sites. Considering that our data were heterogeneous with regards to Euclidean vs watercourse connectivity (connected river networks vs. isolated lakes), all sites within a metacommunity were considered connected and only the Euclidean spatial distance between them was included as a weight between each pair of sites. This procedure resulted in one value of distance-weighted closeness for each site within each metacommunity, which were averaged so that we had a value of closeness for each metacommunity. Thus, metacommunities with higher values of closeness centrality had shorter Euclidean paths among their sites.

For the local-scale SEM, we used measures of temperature and precipitation seasonality as predictors of population variability. We expected that more seasonal sites would have lower levels of population variability across years, as species may be more tolerant to the wider environmental fluctuations present in any given year and because we only used summer months. We gathered data on average temperature and precipitation seasonality (bio4 and bio15, respectively) data from the WorldClim database (Fick & Hijmans 2017).

Results

Metacommunity variability partitions across scales and levels

Temporal variability decreased with increasing trophic level (F = 22.16, df = 11, $p < 0.001$, $R^2 = 0.62$; Figure 2A), as hypothesized (H1). Pairwise contrasts indicated that population variability at the regional scale differed among all trophic levels; community variability of producers and primary consumers was higher than that of tertiary consumers; and metacommunity variability of producers was higher than that of secondary and tertiary consumers (Table S1). Thus, temporal variability of tertiary consumers was lower than that of producers and primary consumers—from local populations to regional metacommunities.

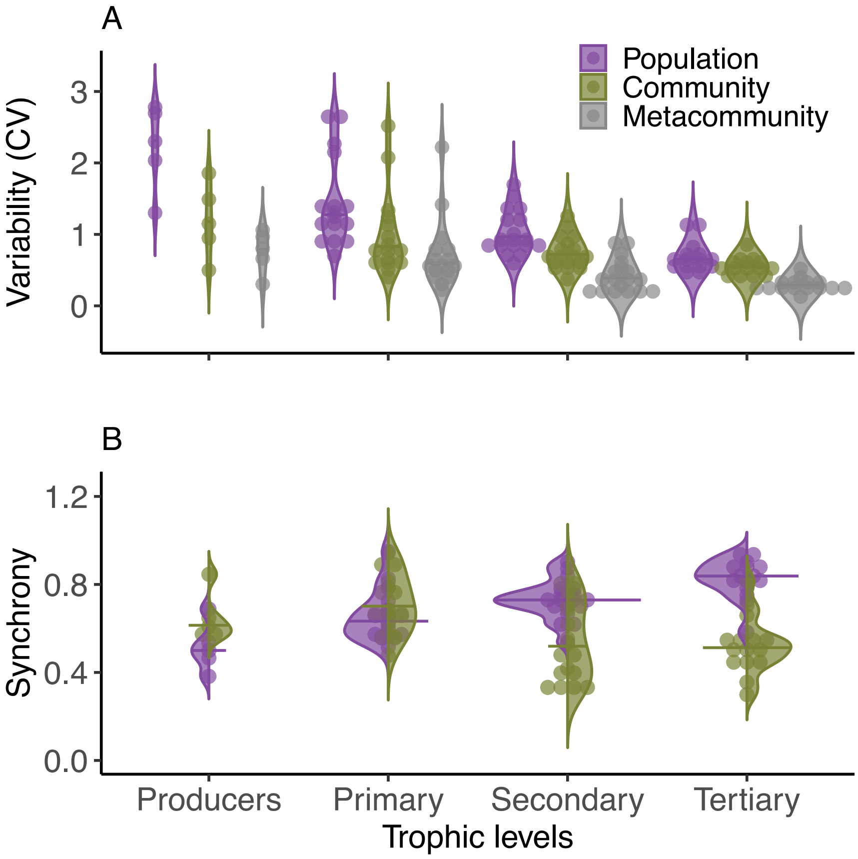

Figure 2. The spatial and trophic scaling of temporal variability (A) and synchrony (B). Plots with different colors represent the distribution of values as a density shape of aggregated variability or synchrony at the population, community and metacommunity levels. The overall average value per plot is represented by the solid line. Raw data values are shown inside each density shape. Statistics describing specific pairwise contrasts corrected for multiple comparisons to compare trophic levels are available in Table S2. Trophic levels include producers and primary, secondary, and tertiary consumers.

We observed an interaction between trophic level and type of synchrony (F = 13.8, df = 3, $P < 0.001$). Specifically, while population synchrony increased from producers to tertiary consumers (all pairwise contrasts differed from each other, Table S2), community spatial synchrony decreased from primary to tertiary consumers (Fig. 2B), partially supporting hypothesis H2. None of the relationships described above, either for temporal variability or synchrony, differed among ecosystem types (lotic vs. lentic), nor depended on time series length or number of sites within the metacommunity (Fig. S2-S5).

The propagation of temporal variability from populations to metacommunities varied among trophic levels (Figure 3A-C). The amount of Pv that was propagated to Cv increased from producers to tertiary consumers (Table 1). On average, 51.4% of producer population variability was propagated to community variability (Pv/Cv ratio), compared to 82.6% for top consumers (Table 1). This trend was due to increasing levels of species population synchrony from producers to tertiary consumers (Figure 2B), which increased the similarity of Cv and Pv estimates for tertiary consumers (Figure 3C; tertiary consumers are very close to the population-community variability identity line).

By contrast, the amount of Cv that was propagated to Mv generally decreased from producers to tertiary consumers (Table 1). On average, 70.9% of the variability in producer communities was propagated to metacommunity variability (Cv/Mv ratio), compared to 52.5% observed for tertiary consumers (Table 1). In support of hypothesis H2, this trend was due to higher ratio of community spatial synchrony to population synchrony of organisms in lower trophic levels (Figure 3B). Consequently, the general differences in variability among trophic levels were reduced at the metacommunity level – i.e., all trophic levels are more equally distant to the community-metacommunity variability identity line (Figure 3A). Together, these results indicate that decreasing variability from populations to metacommunities across trophic levels was mediated by a contrasting contribution of synchrony among populations and among communities.

Table 1. Average amount of variability scaled up from lower- to upper-levels of organization (e.g., Pv/Cv ratio). Pv = variability of population abundance; Cv = variability of total community abundance; Mv = variability of total metacommunity abundance.

Trophic level	Pv/Cv ratio	Cv/Mv ratio	Pv/Mv ratio
Producers	0.514	0.650	0.331
Primary consumers	0.657	0.709	0.468
Secondary consumers	0.730	0.540	0.392
Tertiary consumers	0.826	0.525	0.435

Connecting and uncovering the drivers of temporal variability

As hypothesized (H3), the local-scale SEM indicated that the strength of the positive relationship between community variability and both population variability and species population synchrony varied among trophic levels (Fig. 4). As we are not aware of any statistical method that compares multigroup coefficients in SEM *a posteriori*, we interpret these relationships qualitatively. Secondary consumers displayed the highest coefficient (0.43) for the path linking population to community variability, while the other trophic levels showed little differences (0.34-0.39). We also found that the path coefficient linking species population synchrony to community variability was highest for secondary consumers (0.76) and lowest for tertiary consumers (0.33), with producers and primary consumers being similarly high (0.64 and 0.60, respectively). Overall, the standard linear coefficients for each trophic level were higher for the population synchrony-community variability path. Additionally, we found the expected negative relationship between local species richness and species population synchrony, which did not vary among trophic levels (Fig. 4). However, contrary to our predictions, the positive relationship between population variability and precipitation seasonality did not vary among trophic levels (Fig. 4).

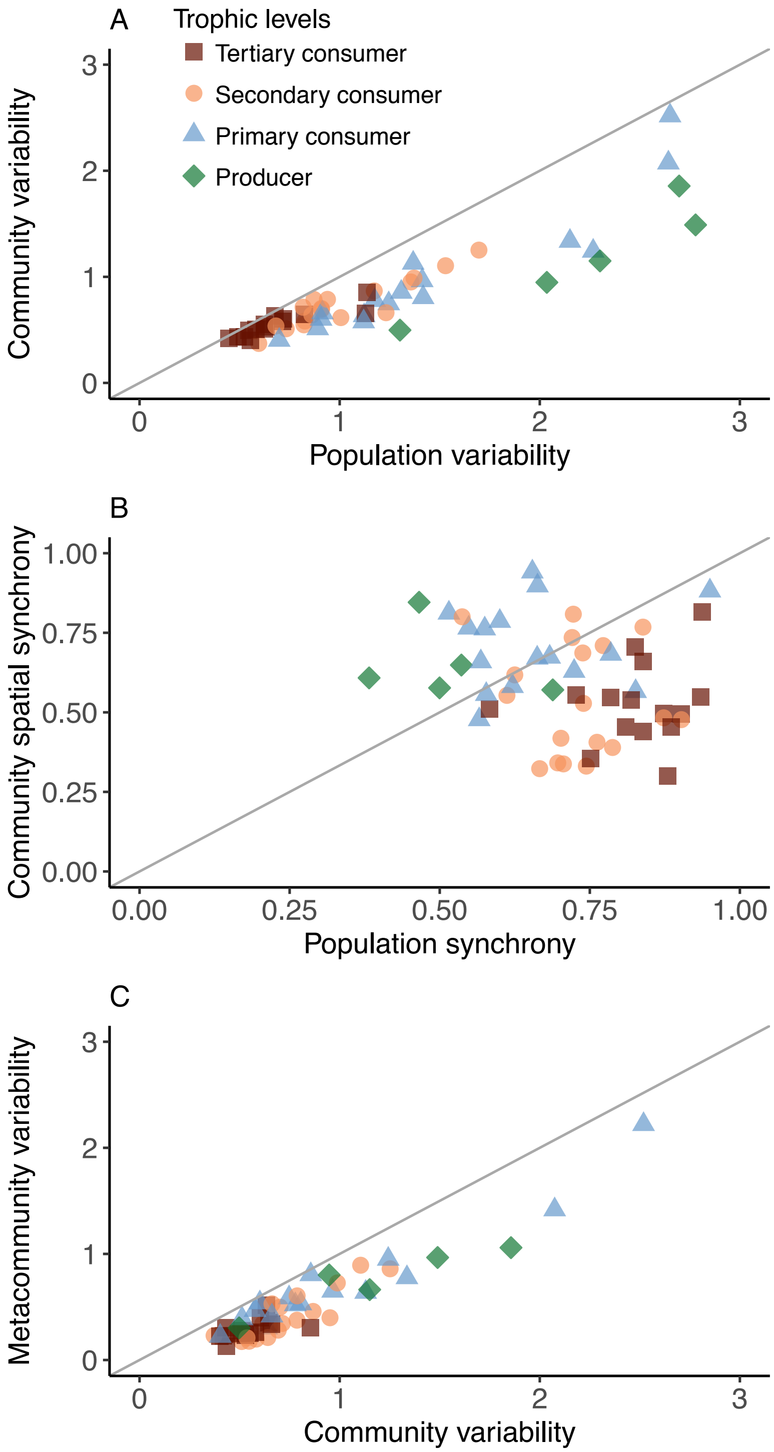

Figure 3. Temporal variability (A, C) and synchrony (B) scaling relationships among different levels of biological organization and trophic levels, from populations to metacommunities.

Finally, the regional-scale SEM also indicated that the strength of the positive relationships between metacommunity variability and community variability, and between metacommunity variability and spatial synchrony, varied among trophic levels, and in both cases were null for producers (Fig. 4). While the strength of the relationship between metacommunity and community variability decreased with trophic levels (0.77 to 0.55), the relationship between metacommunity variability and community spatial synchrony strongly increased with trophic levels (0.27 to 0.73). Thus, in agreement with hypothesis H3b, the relationship between temporal variation in metacommunity aggregate abundance and community spatial synchrony was strongest for predators. This result confirmed the expectation that communities that are more spatially synchronous tend to also be more temporally variable at the regional scale—but notably, the strength of this relationship depends on the trophic level being analyzed.

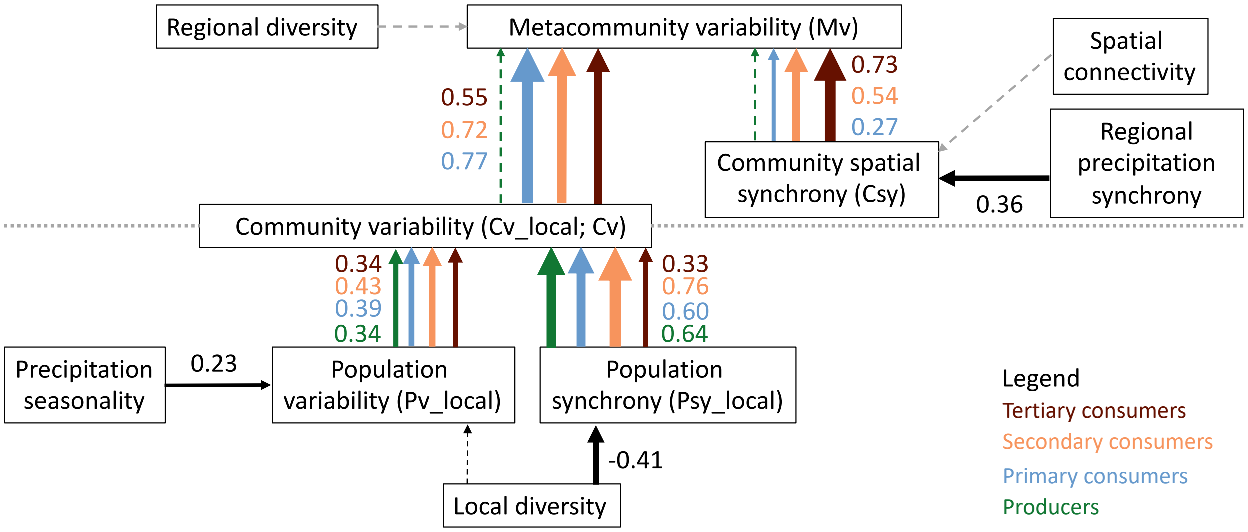

Figure 4. Results of multigroup structural equation models (SEM) at local and regional scales (separated by the horizontal gray dashed line). Dashed and solid arrows indicate relationships associated with $p < 0.05$ and > 0.05, respectively. Colored lines represent relationships that

varied among trophic groups. The numbers associated with the lines represent SEM linear standardized coefficients. Local-scale SEM (n = 549; Fisher's C = 11.65; P-value = 0.17; df = 8). Regional-scale SEM (n = 54; Fisher's C = 11.86; P-value = 0.16; df = 8). Detailed description of all statistics is given in Table S3 and S4.

Discussion

Our broad-scale investigation suggests that temporal variability in abundance decreases from producers to top consumers in freshwater ecosystems (H1), but that differences in temporal variability among trophic levels are smaller at the regional metacommunity scale. These patterns were due to the complementary and opposing contributions of different trophic levels to synchrony and variability within and across localities (H2). While synchrony among local populations increased from producers to tertiary consumers, spatial synchrony among separated communities decreased. Our analyses also confirmed that the associations between community spatial synchrony and metacommunity variability was strongest for top consumers (H3b). However, in contrast to our expectation (H3a), the indirect effects of environmental variables and diversity on temporal variability at both local and regional scales were consistent among trophic levels. Our results thus indicate that the trophic structure of metacommunities, which generally reflects organismal differences in body size, dispersal strength, and response to environmental variation (Woodward *et al.* 2005; Jenkins *et al.* 2007), should be more explicitly accounted for when attempting to understand the propagation of temporal ecological stability.

Metacommunity variability partitions across scales and levels

The decrease in temporal variability from producers to tertiary consumers was not consistent from local populations to regional metacommunities; a result of variability and synchrony differing among trophic levels across the local and regional scales. At the local scale, the amount of variability propagated from the population to the community level was higher for tertiary consumers because fluctuations in abundances of tertiary species were highly synchronized, while the opposite manifested at the regional scale. Populations of higher trophic levels tend to congregate together on specific resource patches within the metacommunity while they are profitable (Eveleigh *et al.* 2007), which explains the highest levels of local population synchrony among tertiary and secondary consumers, a result also supported by microcosm research (Firkowski *et al.* 2022). The local synchronizing effect of top consumers appears to weaken along the trophic chain within communities, leading to lower population synchrony within primary consumers and producers.

In contrast to species population synchrony, secondary and tertiary consumers exhibited the lowest levels of community spatial synchrony. That is, temporal fluctuations in aggregate community abundance of top consumers were more desynchronized across localities. Top consumers will likely have asynchronous spatial dynamics at increasing spatial extents because the coupling of spatially separated resource patches by mobile predators occurs in response to spatial-temporal variation in resource densities (Rooney *et al.* 2008). Spatial coupling by top consumers should also promote more spatially asynchronous fluctuations in their prey – an effect that should decrease with decreasing trophic levels. Recent experimental evidence suggests that the extinction of a top predator led to more unstable communities due to a decrease in asynchrony of lower trophic levels caused by mesopredator pressure (Rezende *et al.* 2021). We thus suggest that top mobile consumers can be seen as stabilizers of their abundances and of entire metacommunities.

Connecting and uncovering the drivers of temporal variability

The local-scale SEM showed that community diversity moderately dampened population synchrony and that this relationship was consistent among trophic levels. A recent meta-analysis reported strong support for the negative indirect effect of local diversity on community variability through population synchrony (Xu *et al.* 2021). More diverse communities tend to be more temporally stable due to two non-exclusive mechanisms, which our analysis cannot resolve. First, fluctuations in the abundance of some species can be compensated for by fluctuations of other species due to biotic interactions or opposing responses to environmental variation, maintaining aggregate ecological properties more stable through time (compensatory dynamics; Gonzalez & Loreau 2009). Second, statistical averaging among species that fluctuate independently through time may also lead to a similar pattern of 'risk dampening' (portfolio effects; Schindler *et al.* 2015). Although the direct relationship between diversity and population synchrony varied little among trophic levels, we suggest that this is not the case for the indirect relationship between diversity and aggregate community variability. We found that the strength of path linking population synchrony to community variability was relatively similar among producers, primary and secondary consumers (0.64, 0.60, 0.76, respectively), but was clearly weaker for tertiary consumers (0.33). Thus, by considering both direct and indirect paths, we suggest that community variability of tertiary consumers might depend less on their diversity than other trophic levels.

In contrast to the indirect relationship between community variability and diversity, the paths linking precipitation seasonality to population (direct) and to community (indirect) variability were similar among trophic levels. Precipitation seasonality weakly increased population variability. Although the path linking population variability to community variability was statistically different among trophic levels, the standardized coefficients did not differ strongly (ranged from 0.34 to 0.43). More seasonal environments may have species more adjusted to the timing of environmental events compared to locations with less predictable seasonality (Tonkin *et al.* 2017). Fluctuations in per capita population growth tend to be affected by the short-term effects of environmental forcing (Loreau & de Mazancourt 2008). Thus, our results suggest that populations are more temporally variable among years in seasonal environments. The degree to which this result applies equally to all trophic levels needs to be further investigated, as organisms with different lifespans should evolve different life history strategies to cope with the frequency of environmental fluctuations (Lytle 2001).

Our results lend support to hypothesis H3b, as we found that the strength of the relationship between metacommunity variability and community spatial synchrony increased from producers to tertiary consumers. In contrast to the hypothesis, however, only synchrony in precipitation but not spatial connectivity played a role as a driver of community spatial synchrony. This relationship indicates that fluctuations in community abundance can be determined by regional environmental forcing (Moran effect), independently of the overall spatial connectivity within the metacommunity. Evidence supporting the influence of the Moran effect on the dynamics of freshwater ecosystems has been accumulating recently. For example, flow management for hydropower can spatially synchronize invertebrate metacommunities along regulated sections of dammed rivers, benefiting species better adapted to fast flows (Ruhi *et al.* 2018). Similarly, drought can lead to regional quasi-extinction of species with lower resistance and resilience abilities by synchronizing stream metapopulations (Sarremejane *et al.* 2021). Considering results both from metacommunity partitioning analyses and two-scale SEMs, we suggest that the ability of mobile consumers to move across patches may sometimes counteracts the effects of environmental variability on population variability, and of environmental synchrony on community spatial synchrony (Rooney *et al.* 2008). Also, the stronger relationship between community spatial synchrony and metacommunity variability for secondary and tertiary consumers indicates that the lowest levels of community spatial synchrony were essential to maintain the decreasing trend of temporal variability from producers to top consumers.

Our SEMs did not include all paths seen in previous studies. For example, we did not link metacommunity variability, indirectly through community spatial synchrony, or directly to spatial beta-diversity. While some previous studies have suggested that high beta-diversity can cause low spatial synchrony (e.g., Wang & Loreau 2016; Hautier *et al.* 2020), others have suggested that it is temporal turnover (a form of temporal variability) that drives beta-diversity (Steiner & Leibold 2004), and others suggested this relationship may be due to pure sampling effects (Stegen *et al.* 2013). We think spatial and temporal turnover and spatial synchrony are all consequences of an interaction among environmental forcing, the various forms of stochasticity, and dispersal (Leibold & Chase 2018), and that they likely represent different facets of temporal stability (Lamy *et al.* 2021). Thus, we built our conceptual model focusing on paths supported by theory as representations of causal relationships. A second potential caveat is the chosen frequency of observations (annual). Organisms in different trophic levels differ in life-span and generation times—from days or weeks (e.g., phytoplanktonic and zooplanktonic organisms) to years (fishes). Although it is challenging to completely rule out this caveat, most data on fish temporal variability spanned at least 10 years, which we deem long enough to represent trends across generations and relative to environmental cycles.

Our study has implications for the understanding of temporal stability in multitrophic metacommunities, as well as for how stability is influenced by environmental change. We showed that temporal variability in abundance, one of the facets of temporal stability, decreases from producers to top predators across levels of biological organization. Given that species at higher trophic levels are more susceptible to extinction than species at lower trophic levels (Estes *et al.* 2011) and that environmental change tends to increase environmental homogeneity (Ellis 2021), the propagation of stability across spatial scales and trophic levels cannot be taken for granted. Our work advances the notion that temporal stability is an emergent property of ecosystems that may be threatened in complex ways by both human and climate-driven biodiversity loss.

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Supplementary information 1. The propagation of stability across spatial scales, organizational, and trophic levels in freshwater ecosystems (Siqueira et al.).

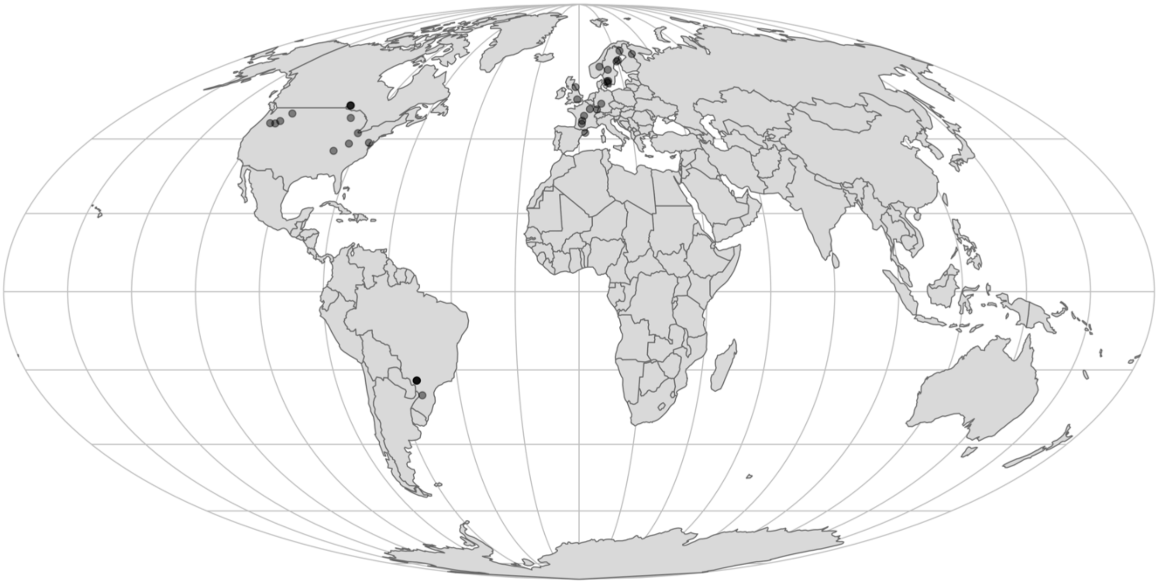

Fig. S1. Geographical distribution of the 35 metacommunities used in this study. Dots indicating the position of metacommunities are of the same color, but due to superimposing of spatially closed sites, some of them appear darker.

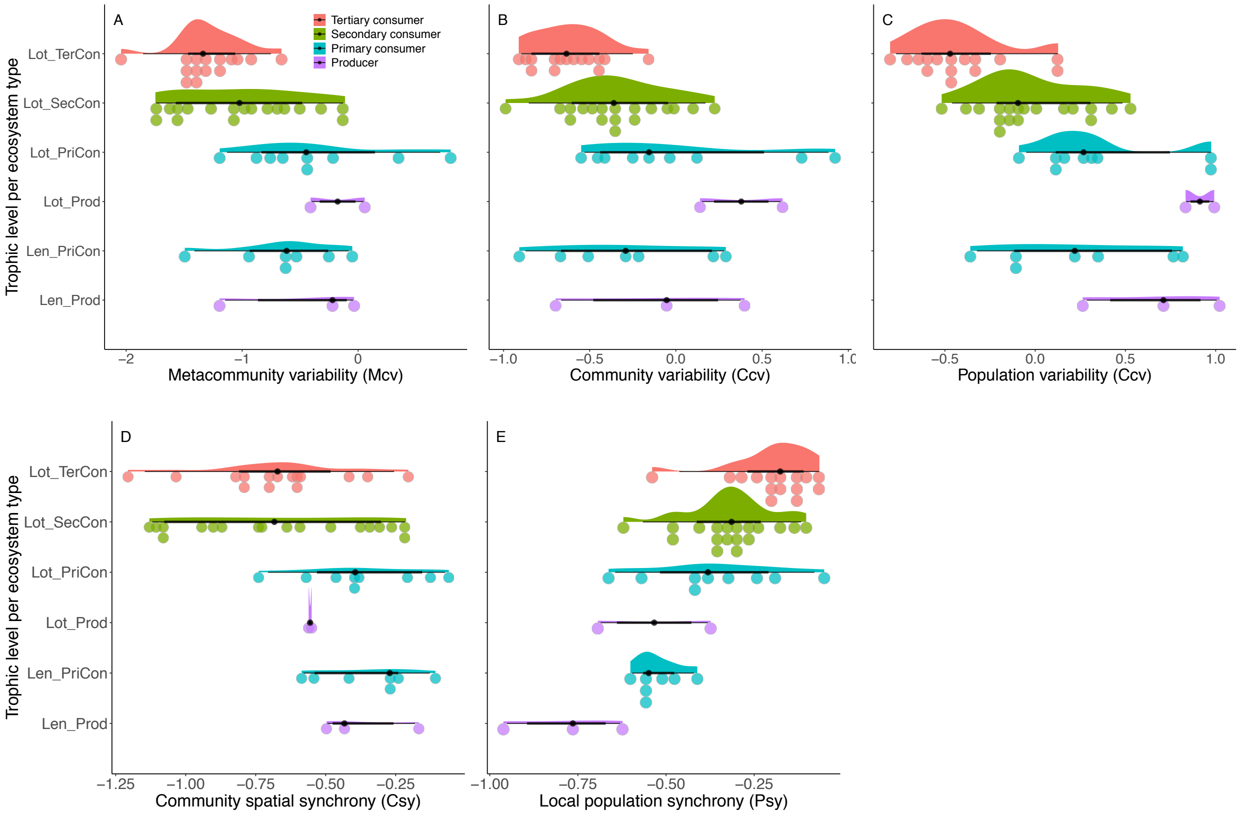

Fig S2. Metacommunity-level estimates of temporal variability (A to C) and synchrony (D-E) across levels of organization and in lotic and lentic systems. Key to y-axis: Len = lentic; Lot = lotic; Pri = primary; Sec = secondary; Ter = tertiary; Prod = producers; Con = consumers.

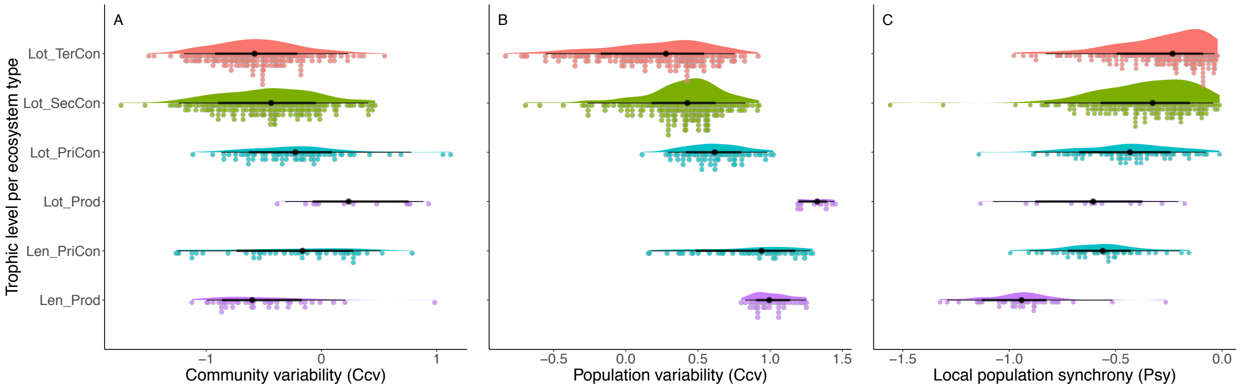

Fig S3. Site-level estimates of temporal variability (A-B) and synchrony (C) across levels of organization and in lotic and lentic systems. Colors and codes as in Fig. S1.

Table S1. Specific pairwise contrasts corrected for multiple comparisons (Holm adjustment) to compare temporal variability components among trophic levels…

group1	**group2**	**df**	**statistic**	**p.adj**	**part**
Producers	Primary	50	0.5422	0.5901	Mcv
Producers	Secondary	50	2.6320	0.0338	Mcv
Producers	Tertiary	50	3.6856	0.0028	Mcv
Primary	Secondary	50	3.0638	0.0141	Mcv
Primary	Tertiary	50	4.5226	0.0002	Mcv
Secondary	Tertiary	50	1.6381	0.2153	Mcv
Producers	Primary	50	1.1472	0.2568	Ccv
Producers	Secondary	50	2.2773	0.1083	Ccv
Producers	Tertiary	50	3.6689	0.0035	Ccv
Primary	Secondary	50	1.6399	0.2146	Ccv
Primary	Tertiary	50	3.6362	0.0035	Ccv
Secondary	Tertiary	50	2.1264	0.1153	Ccv
Producers	Primary	50	2.8230	0.0119	Pcv
Producers	Secondary	50	4.8140	0.0001	Pcv
Producers	Tertiary	50	7.0999	0.0000	Pcv
Primary	Secondary	50	2.8734	0.0119	Pcv
Primary	Tertiary	50	6.1771	0.0000	Pcv
Secondary	Tertiary	50	3.5262	0.0027	Pcv

Table S2. Specific pairwise contrasts corrected for multiple comparisons (Holm adjustment) to compare synchrony components among trophic levels…

group1	**group2**	**df**	**statistic**	**p.adj**	**part**
Producers	Primary	50	-3.353	0.005	Psyn
Producers	Secondary	50	-4.907	0.000	Psyn
Producers	Tertiary	50	-6.452	0.000	Psyn
Primary	Secondary	50	-2.219	0.037	Psyn
Primary	Tertiary	50	-4.490	0.000	Psyn
Secondary	Tertiary	50	-2.435	0.037	Psyn
Producers	Primary	50	-0.607	1.000	Csyn
Producers	Secondary	50	1.717	0.363	Csyn
Producers	Tertiary	50	1.724	0.363	Csyn
Primary	Secondary	50	3.431	0.007	Csyn
Primary	Tertiary	50	3.343	0.008	Csyn
Secondary	Tertiary	50	0.064	1.000	Csyn

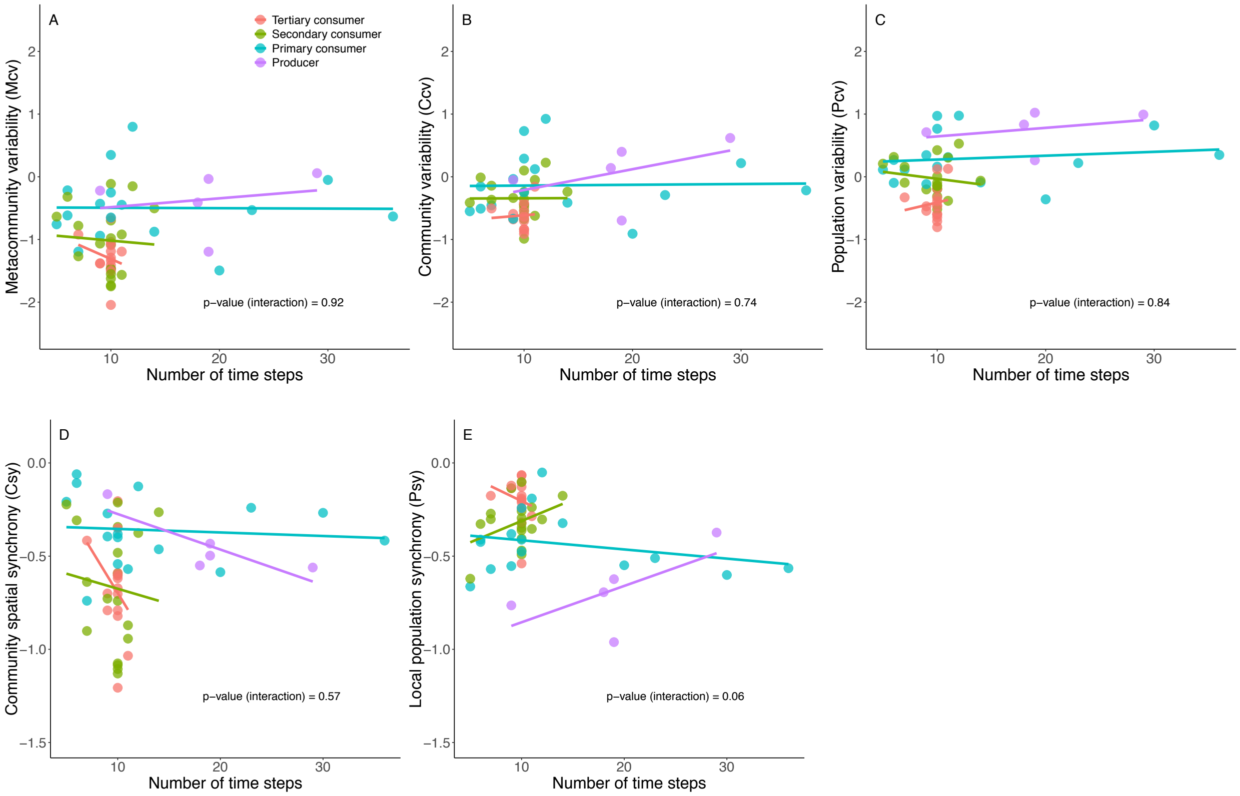

Fig S4. Relationship of temporal variability (A-C) and synchrony (D-E) with the length of the time series in years (number of time steps) in each data set. The p-value refers to a linear relationship between the response variable and an interaction between trophic level and number of time steps.

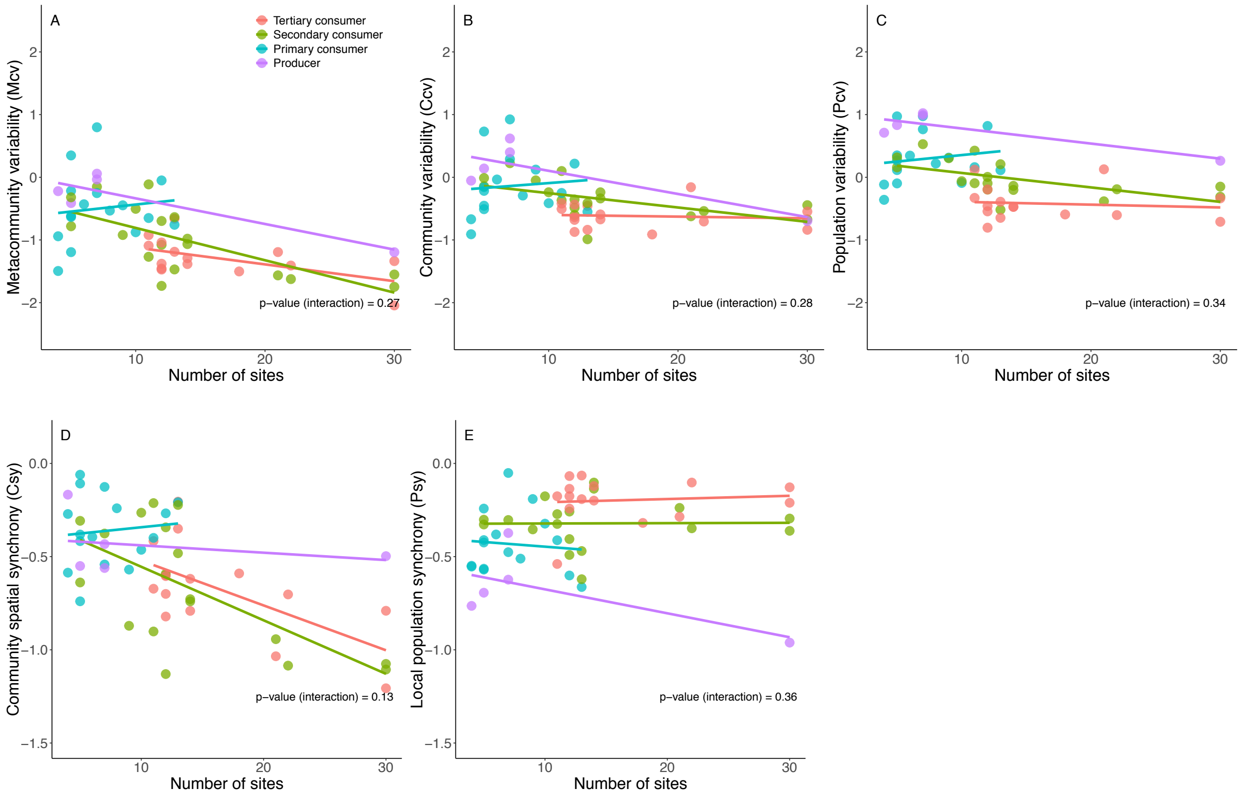

Fig S5. Relationship of temporal variability (A-C) and synchrony (D-E) with number of sites in each data set. The p-value refers to a linear relationship between the response variable and an interaction between trophic level and number of time steps.

Table S3. Model summary statistics of the local-scale SEM (n = 549; Fisher's C = 11.65; P-value = 0.17; df = 8). Psyn_local = population synchrony within sites; Pcv_local = population variability within sites; Ccv_local = aggregated community variability within sites; S = species richness; PS = precipitation seasonality.

Constrained to the global model							
Response	**Predictor**	**Estimate**	**Std.Error**	**DF**	**Crit.Value**	**P.Value**	**Std.Est.**
Psyn_local	S	-0.173	0.022	494	-7.814	< 0.0001	-0.408
Pcv_local	S	-0.052	0.030	493	-1.748	0.081	-0.085
Pcv_local	PS	0.010	0.003	493	3.038	0.003	0.232
Model-wide interactions							
Producers							
Ccv_local	Psyn_local	1.166	0.142	46	8.223	< 0.0001	0.636
Ccv_local	Pcv_local	1.095	0.313	46	3.501	0.001	0.338
Primary consumers							
Ccv_local	Psyn_local	1.274	0.090	97	14.160	< 0.0001	0.604
Ccv_local	Pcv_local	0.789	0.112	97	7.065	< 0.0001	0.392
Secondary consumers							
Ccv_local	Psyn_local	1.067	0.086	188	12.441	< 0.0001	0.757
Ccv_local	Pcv_local	0.585	0.074	188	7.932	< 0.0001	0.434
Tertiary consumers							
Ccv_local	Psyn_local	0.737	0.120	156	6.152	< 0.0001	0.345
Ccv_local	Pcv_local	0.405	0.071	156	5.681	< 0.0001	0.328

Table S4. Model summary statistics of the regional-scale SEM (n = 54; Fisher's C = 11.86; P-value = 0.16; df = 8). Psyn = average population synchrony within the metacommunity; Pcv = average population variability within the metacommunity; Csyn = avegare community spatial synchrony within the metacommunity; Ccv = avegare community variability within the metacommunity; Mcv = metacommunity variability; S gamma = regional species richness; RPS = regional precipitation seasonality.

Constrained to the global model

Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P.Value	Std.Est.
Mcv	S gamma	-0.006	0.026	16	-0.226	0.824	-0.007
Csyn	Closeness	0.000	0.000	18	-0.355	0.727	-0.048
Csyn	RPS	0.412	0.185	33	2.230	0.033	0.361
Model-wide interactions							
Producers							
Mcv	Csyn	1.899	0.736	1	2.581	0.235	0.417
Mcv	Ccv	0.936	0.192	1	4.878	0.129	1.015
Primary consumers							
Mcv	Csyn	1.351	0.289	12	4.680	0.001	0.274
Mcv	Ccv	0.836	0.066	12	12.586	< 0.0001	0.772
Secondary consumers							
Mcv	Csyn	1.821	0.107	14	17.095	< 0.0001	0.541
Mcv	Ccv	1.330	0.085	14	15.736	< 0.0001	0.716
Tertiary consumers							
Mcv	Csyn	1.948	0.139	11	14.037	< 0.0001	0.726
Mcv	Ccv	1.673	0.155	11	10.829	< 0.0001	0.546

Supplementary information 2. The propagation of stability across spatial scales, organizational, and trophic levels in freshwater ecosystems (Siqueira et al.).

Methods used in data cleaning

Within each data set, we only retained sites that were sampled at least 70% of all years and years that included at least 70% of all sites. We tried higher percentages of site and time completeness and found that 70% maximized the number of sites, years and metacommunities retained.

We removed unidentified taxa and taxa identified at higher than genus level from all data sets.

Years with missing data were imputed with the median of species abundance for the respective year or site. We also estimated stability metrics by modifying Wang et al. (2019) code to allow for missing data. We compared matrices containing estimates of variability and synchrony (trophic-level-specific metacommunity by variability and synchrony metrics matrix) from these two approaches (median vs. missing data allowed) with a Procrustes analysis and found they were highly correlated (r = 0.99). We thus concluded that the median-based imputation was robust.

Data set description

The numbers are related with the data set used in the R code.

DS. 5-18. These data sets correspond to basins 2080020590, 2080020620, 2080021030, 2080022150, 2080023010, 2080030100, 2080030610, 2080030710, 2080031490, 2080033020, 2080033080, 2080033120, 2080053790, 7080047060 in the data base RivFishTIME (Comte et al. 2021).

These data sets were chosen based on their availability at the time of data analysis and considering both spatial and temporal completeness.
Data set owners: Public available
Additional information about the dataset can be found here: Comte, L., Carvajal-Quintero, J., Tedesco, P. A., Giam, X., Brose, U., Erős, T., ... & Olden, J. D. (2021). RivFishTIME: A global database of fish time-series to study global change ecology in riverine systems. Global Ecology and Biogeography, 30(1), 38-50.

DS. 19. The data set consists of 28 wadable streams from a Maryland, USA. In these sites, stream fish were quantified annually, from 2000 through 2012, as sentinel sites within the larger Maryland Biological Stream Survey. Full details regarding sampling methods can be found below.

Data set owners: Maryland Department of Natural Resources
Data may be requested here: https://dnr.maryland.gov/streams/Pages/dataRequest.aspx

Additional information about the dataset can be found here:
https://dnr.maryland.gov/streams/Pages/mbss.aspx

DS. 20-21. These data sets consist of 7 lakes (DS. 20) and 5 riverine systems (DS. 21) in Upper Paraná River basin, northwest of the state of Paraná State. In these sites, zooplankton was quantified annually, from 2000 through 2010.

Data set owner: Claudia Costa Bonecker (Nupelia, Maringá State University).

Additional information about the dataset can be found here: Bonecker, C.C., Diniz, L.P., Souza, L. De, Braghin, M., Moi, A., Deosti, S., Naomi, G., Aparecido, D., Julya, A., Machado, D.M., Felipe, L., Velho, M., 2020. Synergistic effects of natural and anthropogenic impacts on zooplankton diversity in a subtropical floodplain: a long-term study. Oecologia Australis 24, 524–537. https://doi.org/10.4257/oeco.2020.2402.20

DS. 22-24. These data sets consist of Cladoceran and Copepod abundances from 13 lakes (DS. 22 = 4 lakes; DS. 23 = 4 lakes; DS. 24 = 5 lakes;) in the Experimental Lakes Area, Ontario, Canada. In these sites, zooplankton have been quantified on multiple dates in various years between 1969 and 2018.

Data set owners: International Institute for Sustainable Development Experimental Lakes Area, https://www.iisd.org/ela/.

Additional information about the dataset can be found here: https://www.iisd.org/ela/our-data/metadata/zooplankton/. Contact mpaterson@iid-ela.org.

DS. 25. This data set consists of samples collected from the central region of Kentucky Lake, the last of eight impoundments on the Tennessee River system near Murray, KY, USA. The Kentucky Lake Long-term monitoring program collects samples every 16 days in conjunction with LANDSAT TM overflights at approximately 8-12 sites measuring a suite of approximately 40 limnological parameters. In these sites, zooplankton samples were quantified annually from 1988 until present.
Data set owners: Hancock Biological Station, Watershed Studies Institute, Murray State University, Murray, KY, USA.

Additional information about the dataset can be found here:

Yurista, P. M., D. S. White, G. W. Kipphut, K. Johnston, G. Rice, and S. P. Hendricks. 2004. Nutrient patterns in a mainstem reservoir, Kentucky Lake, USA, over a 10-year period. Lake and Reservoir Management 20:148-163. https://doi.org/10.1080/07438140409354359

Yurista, P.M., K. Johnston, G. Rice, G.W. Kipphut and D.S. White. 2001. Particulate organic carbon patterns in a mainstem reservoir, Kentucky Lake, USA. Lake and Reservoir Management. 17:330-340. DOI: 10.1080/07438140109354139

DS. 26-27. These data sets consist of seven lakes (DS. 26) and five riverine systems (DS. 27) in Upper Paraná River basin, northwest of the state of Paraná State. Phytoplankton was sampled quarterly from 2000 to 2018.

Data set owner: Luzia Cleide Rodrigues (Nupelia, Maringá State University).

Additional information about the dataset can be found here:
Pineda A, Peláez Ó, Dias JD, et al (2019) The El Niño Southern Oscillation (ENSO) is the main source of variation for the gamma diversity of plankton communities in subtropical shallow lakes. Aquat Sci 81:49. https://doi.org/https://doi.org/10.1007/s00027-019-0646-z

Rodrigues LC, Simões NR, Bovo-scomparin VMVM, et al (2015) Phytoplankton alpha diversity as an indicator of environmental changes in a neotropical floodplain. Ecol Indic 48:334–341. https://doi.org/10.1016/j.ecolind.2014.08.009

DS. 28. This data set consists of 30 small ponds, 1m2, dug in the autumn of 1994 at Hauxley Nature Reserve, in Northumberland, North-east England. The ponds are arranged across a hydrological gradient, most ponds drying out for a period most years, but not always, and also linked by winter inundation flooding the field some years. The hydrological patterns were very dependent on variability in local weather. The animals (mostly invertebrates but very occasional amphibia) and plants were sampled every year from 1995 to 2014. The animals were recorded every late winter (January/February) and early summer (May/June), occasionally more often. Animals were recorded as presence/absence, all taxa including smaller crustacea such as Ostracoda and Cladocera, most identified to species, a few to just genus or Family. Plants were recorded to species, by quadrat point counts.

Data set owner: Dr Michael Jeffries, Department of Geography & Environmental Sciences, Northumbria University

Additional information about the dataset can be found here: Jeffries, M.J., (2010). The temporal dynamics of temporary pond macroinvertebrate communities over a 10-year period. Hydrobiologia, 661, 391-405.

DS. 29. This data set consists of 7 sites along the Atna river watershed in Norway. Non-diatom benthic algae were quantified (percent cover) annually (with few exceptions) at each site in autumn (end of August/September) since 1988. The sampled material was determined to the lowest taxonomic level possible, usually species. The Atna watershed is one of the few unaffected larger catchments in Norway and is used as unimpacted reference in many national and international projects.

Data set owner: Norwegian Institute for Water Research.

Additional information about the dataset can be found here: http://doi.org/10.23728/b2share.177a0aedcfee4f3d82537bc3b72a3cc7

DS. 30. This data set consists of Cladoceran and Copepod abundances from 5 lakes in the Northern Highlands Lake District, Wisconsin, USA. In these sites, zooplankton are quantified on multiple dates each year since 1982. Data used here are from 1982 through 2017.

Data set owners: North Temperate Lakes Long-Term Ecological Research program, lter.wisc.edu

Additional information about the dataset can be found here: Lead PI N., J. Magnuson, S. Carpenter, E. Stanley. 2010. North Temperate Lakes LTER: Zooplankton - Trout Lake Area 1982 - current. Environmental Data Initiative. https://doi.org/10.6073/pasta/8d5e19d0e9680fddc3402e148e377c1a. Dataset accessed 1/17/2020

DS. 31. This data set consists of macroinvertebrate counts from 14 reference sites scattered along in 4 catchments of the Barcelona (Spain) region and located in Natural Parks: Llobregat, Besòs, Ter, and Tordera. Macroinvertebrates were collected two times per year (spring and summer) from 2013 to 2017 and using a multihabitat kick sampling. This data set was extracted from the research contract “CARIMED: Effects of Environmental Change on Biological Communities in Mediterranean Rivers” (www.ub.edu/barcelonarius) funded by the regional administration “Diputació de Barcelona”. The main objective of CARIMED is to examine whether global environmental changes are affecting biological communities in Mediterranean ecosystems. This contract is the continuation of the first river quality monitoring studies in the region that started back in 1979.

Data set owners: Núria Bonada and Pau Fortuño. FEHM-Lab (Freshwater Ecology, Hydrology and Management), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Barcelona, Catalonia/Spain

Additional information about the dataset can be found here: https://doi.org/10.15470/yt2uex

DS. 32. This data set consists of 5 locations along the Kinzig river within the eLTER site Rhine-Main-Observatory as part of the Main-Kinzig district, state of Hesse, Germany. In these locations, macroinvertebrates were quantified annually, from 2010 through 2019.

Data set owners: Peter Haase (Department of River Ecology and Conservation, Senckenberg Society for Nature Research & University of Duisburg-Essen)

Additional information about the dataset can be found here: DEIMS ID: https://deims.org/9f9ba137-342d-4813-ae58-a60911c3abc1

DS. 33. This data set consists of four sites in the Quebra-Queixo reservoir, Uruguay basin, state of Santa Catarina, Brazil. Phytoplankton was sampled at least twice a year in the low-water season (July) and high-water season (January), from 2006 to 2016.

Data set owner: Luzia Cleide Rodrigues (Nupelia, Maringá State University).

Additional information about the dataset can be found here: unpublished data.

DS. 34. This data set consists of benthic macroinvertebrate samples from ten 1st-to-3rd order reference sites in the Koutajoki catchment in northeastern Finland close to the Polar Circle (for more information, see Nilsson et al. 2022). Macroinvertebrates were collected once a year (autumn; September to early October) from 2000 to 2014, using multihabitat kick sampling. Sampling and species identification work has been supported by Oulanka Research Station and several consecutive grants by the Academy of Finland. The main objective of the project is to examine long-term variability of benthic invertebrate populations and communities in near-pristine reference streams in a north boreal river system.

Data set owners: Timo Muotka and Kaisa-Leena Huttunen (Ecology and Genetics, University of Oulu, Finland).

Additional information about the dataset can be found here: Nilsson, C., Muotka, T., Malmqvist, B. & Timm, H. 2022. The Fennoscandian shield. In: Tockner, K. et al. (eds). Rivers of Europe. Elsevier.

DS. 35. This data dataset consists of zooplankton samples collected from sixteen sites in the western and central basins of Lake Erie (U.S. and Canada). At these sites, zooplankton was collected approximately biweekly between May and September.

A protocol for sampling can be found here under methodology and data access: https://ael.osu.edu/researchprojects/lake-erie-plankton-abundance-study-lepas

Data set owner: Ohio Department of Natural Resources – Division of Wildlife, managed by Jim Hood, Dept. of Evolution, Ecology, and Organismal Biology, The Ohio State University

Additional information about the dataset can be found here: Conroy, J.D., Kane, D.D., Dolan, D.M., Edwards, W.J., Charlton, M.N., Culver, D.A., 2005. Temporal trends in Lake Erie plankton biomass: role of external phosphorus loading and dreissenid mussels. Journal of Great Lakes Research 31(Suppl.2), 89-110. Data are available upon reasonable request to Jim Hood.