Temporal variability declines with increasing trophic levels and spatial scales in freshwater ecosystems

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Abstract

The temporal variability of ecological properties tends to decrease with spatial scale and levels of biological organization, but how does it propagate across trophic levels? We compiled metacommunity time-series datasets spanning basal resources to top predators from 355 freshwater sites across three continents. 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. While climate and diversity controlled temporal variability similarly across trophic levels, the relationship between metacommunity variability and spatial synchrony was stronger for top consumers. Our results suggest that mobile predators can stabilize metacommunities by buffering variability originating at the base of food webs. This finding demonstrates that the trophic structure of metacommunities, which integrates variation in organismal body size, dispersal, and environmental tolerance, should be considered when investigating ecological stability.

Introduction

The temporal variability of ecological properties (e.g., population biomass) tends to decrease with increasing spatial scale and levels of biological organization [1,2]. For instance, fluctuations in fishery catch at the metapopulation level are often weaker than in any one of the constituent populations [3]. Similarly, organismal abundance at a given patch tends to be more stable at the community than at the population level [4]. However, most previous attempts to understand temporal variability and its drivers have done so at single trophic levels [1,5–7], resulting in a critical knowledge gap. Communities are connected to each other through the spatial flow of organisms in different trophic levels [8]; thus, the spatial structure of multitrophic metacommunities may modulate temporal variability [9]. For example, mobile top 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 [10]. Understanding how temporal variability propagates not only across spatial and organizational scales, but also along trophic levels, would increase realism in 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 [11]. This framework assumes that fluctuations in species populations within sites represent the lowest-level component of temporal variability – i.e., 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 [12]. In turn, metacommunity variability emerges from both aggregate community variability and spatial synchrony among local communities [11].

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 [13]. Negative covariance in the abundance of different populations due to biotic and abiotic interactions reduces temporal variation in aggregate ecological properties [14]. 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 [15]. 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 (i.e., Moran effect [16]) or via a combination of strong dispersal and predator-prey cycles [17]. Notably, organismal trophic position is generally associated with body size, dispersal strength, and response to environmental variation [18,19]. 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.

High-level mobile consumers can stabilize the temporal dynamics of metacommunities by coupling heterogeneous local food webs in space [10,20]. This second 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 [21]. Within a large ecosystem or metacommunity, 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. Such dynamics can also promote regional stability of resources as spatial heterogeneity in predation pressure can reduce spatial synchrony of organisms at lower trophic levels[22]. Merging these two views [11,20] may offer 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 [6].

Here we compiled 30 temporal datasets on metacommunity dynamics spanning basal resources (e.g., phytoplankton) to top predators (e.g., piscivorous fish), comprising spatially replicated interannual time series sampled from 355 freshwater sites across three continents (Fig. S1). 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. This hypothesis is based on the idea that top mobile consumers couple alternate among local food webs characterized by fast energy channels comprised mostly of strong interactions and slow channels mostly comprised of weak interactions [23]. An alternative plausible expectation would be for higher trophic levels to exhibit higher population fluctuations due to environmental and demographic stochasticity affecting disproportionally taxa with larger body size and smaller population sizes [24]. (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 [25]. 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 (Fig. S2). 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, and (H3b) a stronger role of spatial connectivity on top consumer spatial synchrony and metacommunity variability at the regional scale (Fig. S2). We used the hierarchical partitioning framework proposed by Wang et al. [11] 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 to test hypothesis H3.

Results

Metacommunity variability partitions across scales and levels

Temporal variability in abundance decreased with increasing trophic level ($F = 27.18$, df $= 11$, $p < 0.001$, $R^2 = 0.69$; Fig. 1A), as hypothesized (H1). Pairwise contrasts indicated that population variability (Pv) differed among all trophic levels; community variability (Cv) differed among all trophic levels, except between producers and primary consumers; and metacommunity variability (Mv) 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. This same pattern was observed when we analyzed temporal variability and synchrony only within datasets that included more than one trophic level (22 datasets encompassing a total of 300 sites; Fig. 2A).

These results indicate that the amount of population variability that propagated to community variability (i.e., Pv/Cv ratio) increased from producers to tertiary consumers: 54.7% of producer's Pv propagated to the community level, compared to 82.6% for top consumers. In contrast, the amount of Cv propagating to metacommunity variability (i.e., Cv/Mv ratio) generally decreased from producers to tertiary consumers, with 66% of producer's Cv (but only 52.5% of tertiary consumers' CV) propagating to the metacommunity level.

In support of hypothesis H2, these propagation trends were due to an interaction between trophic level and type of synchrony ($F = 9.67$, $df = 3$, $P < 0.001$). This result suggests that the scaling of variability observed across trophic levels was likely explained by a divergence or increasing gap between synchrony at the population level (i.e., synchrony among populations within sites) and at the community level (i.e., among communities across sites) (Fig. 1B). While population synchrony generally increased from producers to tertiary consumers (all pairwise contrasts differed from each other, except between primary and secondary consumers; Table S3), community spatial synchrony decreased from primary to secondary and tertiary consumers (Fig. 1B; Table S3). Consequently, the general differences in variability among trophic levels were reduced at the metacommunity level. We note this general pattern was also observed when focusing on datasets that included more than one trophic level (Fig. 2B).

Sensitivity analyses

Because individual datasets differed in number of sites and years sampled, and previous studies showed these aspects can affect population variability estimates [26], we tested the strength of our inferences. First, we examined if variation in time series length and site replication could have influenced the observed patterns. Although variability and synchrony metrics were often positively related to time series length and negatively related to the site replication, none of these relationships showed a statistical interaction with trophic level (Fig. S5 and S6). This observation suggests that sampling heterogeneity effects were consistent across trophic levels, and thus unlikely to generate a spurious “propagation effect”. Second, to further examine if results would have differed under a reduced number of sites or years, we developed two sensitivity analyses that resampled sites (Fig. S7 and S8) or reduced time steps in the time series (Fig. S9) and ran the same set of analyses on those datasets (see Methods for details). We obtained the same patterns described above (see Figs. S7-S9 for details), confirming that variation in time series length or site replication did not drive propagation patterns.

Connecting and uncovering the drivers of temporal variability

The local-scale structural equation model (local-scale SEM) indicated that the strength of the positive relationship between community variability and population variability varied among trophic levels, partially supporting H3 (Fig. 3). As we are not aware of any statistical method that compares multigroup coefficients in SEM *a posteriori*, we interpret these differences among trophic levels qualitatively. Producers displayed the highest coefficient (0.98) for the path linking population to community variability, while consumers showed little differences (0.34-0.45). The path coefficient linking species population synchrony to community variability did not vary among trophic levels (0.58). Additionally, we found the expected negative relationship between species population synchrony and local species richness, which did not vary among trophic levels (Fig. 3). However, contrary to our predictions, the positive relationship between population variability and precipitation seasonality did not vary among trophic levels (Fig. 3). Precipitation seasonality influenced slightly secondary and tertiary consumers in opposite ways, but we note this direct path was not part of our conceptual model (Fig. S2) and was included *a posteriori* to improve model fit.

The regional-scale SEM 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. 3). While the strength of the relationship between metacommunity and community variability decreased with trophic levels (0.75 to 0.54), the relationship between metacommunity variability and community spatial synchrony increased with trophic levels (0.30 to 0.73). Thus, in agreement with hypothesis H3b, the relationship between community spatial synchrony and temporal variability in metacommunity aggregate abundance 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.

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 or absent at the regional metacommunity scale. These patterns were consistent when we analyzed all datasets together and within datasets, suggesting that they were due to the complementary and opposing contributions of different trophic levels to variability and synchrony within and across localities (H2). While synchrony among populations within localities increased from producers to tertiary consumers, spatial synchrony across localities 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 on temporal variability at both local and regional scales were generally 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 [18,19], should be more explicitly accounted for when attempting to understand the propagation of temporal ecological stability.

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. Temporal variability can be expected to decrease with increasing organism body size in aquatic food webs at the local scale [27]. This is because while primary consumers tend to obtain most of their resources from either phytoplankton or detritus in freshwater ecosystems, consumers at higher trophic levels tend to derive carbon from both local webs [23]. These coupled heterogeneous webs differ in the amount of energy entering through basal resources and interaction strengths, which guarantees that top consumers have access to asynchronous dynamics originating at the base of local food webs [23] – a mechanism widely recognized as a driver of stability [13]. However, an increase in temporal variability from producers to tertiary consumers could also be expected. The high growth rates of small organisms at lower trophic levels and their larger population sizes could also counter the effects of perturbations and demographic stochasticity[24]. We thus think these alternative hypotheses deserve future investigation through a combination of modelling and appropriate observational data.

Interestingly, 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 locally, 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 [21], which explains the highest levels of local population synchrony among tertiary consumers, a result also supported by microcosm research [9]. 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, 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 switching among spatially separated resource patches by mobile predators occurs in response to spatial-temporal variation in resource densities [20]. The movement of top consumers from low prey density patches for more profitable high-density patches should also promote more spatially asynchronous fluctuations in resources, which should in turn decrease prey variability at the regional scale. Recent experimental evidence suggests that the extinction of a top predator led to more unstable communities due to an increase in synchrony of lower trophic levels caused by mesopredator pressure [28]. We thus suggest that top mobile consumers can be seen as stabilizers of their abundances and of entire metacommunities.

The local-scale SEM showed that community diversity 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 [7]. 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 [14]. Second, statistical averaging among species that fluctuate independently through time may also lead to a similar pattern of 'risk dampening' [13]. Interestingly, the positive relationship between population synchrony and aggregate community variability, which mediated the indirect relationship between diversity and community variability, was also consistent among trophic levels. Thus, by considering both direct and indirect paths, we suggest that the influence of diversity on aggregate community variability at the local scale holds even if the number of species within trophic levels varies.

Similarly, the path linking precipitation seasonality to population variability was consistent among trophic levels. Precipitation seasonality weakly increased population variability. However, the path linking population variability to community variability was statistically different among trophic levels. While the standardized coefficients did not differ strongly among consumers (ranged from 0.34 to 0.45), the relationship was clearly stronger for producers (0.98). More seasonal environments may have species more adjusted to the timing of environmental events compared to locations with less predictable seasonality [29]. Fluctuations in per capita population growth tend to be affected by the short-term effects of environmental forcing [30], especially among smaller organisms. Thus, our results suggest that populations are more temporally variable among years in seasonal environments and that this relationship might vary across trophic levels, as organisms with different lifespans should evolve different life history strategies to cope with the frequency of environmental fluctuations [31].

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. The stronger relationship between community spatial synchrony and metacommunity variability for 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. In contrast to hypothesis H3b, however, neither synchrony in precipitation nor spatial connectivity played a role as a driver of community spatial synchrony. This result is surprisingly because 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 [32]. Similarly, drought can lead to regional quasi-extinction of species with lower resistance and resilience abilities by synchronizing stream metapopulations [33]. We cannot discard, however, that the lack of relationship between community spatial synchrony and environmental predictors was due to the use of climatic variables only. For example, ecosystem productivity is one of the key drivers of ecological stability (i.e., paradox of enrichment[34]). Even though, 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 [20].

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 [35,36], others have suggested that it is temporal turnover (a form of temporal variability) that drives beta-diversity [37], and others suggested this relationship may be due to pure sampling effects [38]. 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 [8], and that they likely represent different facets of temporal stability [39]. 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 lifespan 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. Also, measurements of temporal variability are not biased if sampling rates are slow relative to system dynamics [40]. A third potential caveat is the scarcity of datasets comprising three or more trophic levels. We addressed this caveat by analyzing temporal variability and synchrony within datasets that included more than one trophic level and found that the general patterns observed with the full data hold. Thus, these relationships seem to be real, and not an artifact resulting from variation in sampling methods. We urge, however, efforts to prioritize sampling or collation of time-series data on complete food webs.

Our study has implications for the understanding of temporal variability in multitrophic metacommunities, as well as for how it 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, but that differences among trophic levels tend to equalize at the regional scale. Given that species at higher trophic levels are more susceptible to extinction than species at lower trophic levels [41] and that environmental change tends to increase environmental homogeneity [42], 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.

Methods

Datasets

We collated 30 independent metacommunity datasets, 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 dataset can be found in the supporting information.

Our data included 5 metacommunities in lentic systems (lakes) and 25 in lotic systems (streams and rivers). We only used data on metacommunities in which local communities were physically connected – i.e., stream networks and sites within lakes. None of the relationships described for temporal variability or synchrony differed among ecosystem types (lotic vs. lentic; Fig. S3 and S4). Each dataset contained at least 4 sites (max. = 30; mean = 11.83; median = 11.50) sampled for at least 5 years (max. = 30; mean = 11.93; median = 10). When the original data included multiple sampling events per year, we chose the summer month with the highest number of sites sampled. We removed unidentified taxa and taxa identified at higher than genus level from all datasets.

Within each dataset, 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. Within each metacommunity, 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. [11] code to allow for missing data – i.e., average population, community and metacommunity variability were estimated with incomplete time series (for more details, see Supp. Material). 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.

Each species was assigned to one trophic category: producers (including stream benthic algae, macrophytes, and phytoplankton; 23 site-level time series after filtering, see below), primary consumers (zooplankton [Cladocera and Copepoda], macroinvertebrates, and fish; 97 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 datasets into trophic-level-specific metacommunities. For example, an original dataset 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 54 data tables (producers = 4; primary consumers = 13; secondary = 22; tertiary = 15). Finally, we removed sites with only 1 species, resulting in 501 sites (the same site could be part of more than one data table) and 49 trophic-level-specific metacommunities for analysis.

Importantly, none of the original datasets included information on all trophic levels. Thus, our inferences are based on analyses of trophic levels that were represented by different datasets – e.g., producers from dataset A and tertiary consumers from dataset B. 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 [43] and dispersal capacity [20], we believe our strategy represents a useful compromise.

We explicitly considered variation inherent to the original data by using four strategies. First, we estimated all variables (e.g., local diversity, population synchrony) within each of the 49 metacommunity-trophic level datasets. Second, we used mixed-effects models to quantify the relationships between these and potential confounding variables (e.g., length of the time series; see details below). Third, we estimated and analyzed variability and synchrony metrics for datasets that included more than one trophic level. Two datasets included information on primary to tertiary consumers, while seven and thirteen datasets included information on primary to secondary and secondary to tertiary consumers, respectively. Fourth, we ran a sensitivity analysis to investigate the potential effect of the number of sites per metacommunity and time series length on variability and synchrony metrics (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 49 trophic-level-specific metacommunities. For this, we used the framework proposed by [11] 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). 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 [11] for equations). Thus, there was one value of Mv, Cv, Pv, Csy, and Psy per each of the 49 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 [44] in the R [45].

Sensitivity analysis

Our exploratory analyses indicated that that some of the variability metrics were negatively related to the number of sites sampled – although there was no interaction between the number of sites and trophic groups (Fig. S6). To investigate the potential effect of site replication and time series length further, we ran two sensitivity analyses in which variability and synchrony were estimated for metacommunity with only 8 sites and with only 11 years. First, we got all datasets with more than 7 sites (the maximum number of sites of the trophic group [producers] with the minimum number of sites) and sampled 8 sites randomly from each one of them. We repeated this process 1000 times, and each time we estimated the variability and synchrony metrics. We averaged these 1000 values and compared these "rarefied" estimates with the estimates obtained using the full data. To investigate the potential effect of time series length, we used a standardized reduced time series – 11 years only (the maximum number of years of the trophic group [tertiary consumers] with the minimum number of years). We did not rarefy time series length (but rather truncated raw time series), as we wanted to preserve the time series nature of the population and community data (ignoring temporal autocorrelation would have likely affected variability estimates).

Two-scale structural equation modelling

Based on hypotheses H3a-b (Fig. S2), we used local estimation structural equation modeling (SEM) [46] to test the direct and indirect relationships among diversity, environmental and spatial predictors, variability and synchrony, trophic levels at two spatial scales. We fitted different models following our hypotheses 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.

We performed multigroup SEM analysis [47] to test whether the relationships among predictor and response variables varied between trophic groups. Multigroup SEM can be thought as an Analysis of Covariance (ANCOVA). For example, let's consider the following model: population synchrony ~ local diversity * trophic level. If there is an interaction between the two predictor variables, one should interpret the relationship between population synchrony and local diversity (standardized coefficient) for each trophic level. When that was the case, we represented the multiple pathways with different colors to indicate that the relationship between a response and a predictor variable depended on trophic level (Fig 3).

We used two independent SEMs to maximize the statistical power of our test. First, we applied SEM to metacommunity partitions (regional-scale SEM; n = 49 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 = 501).

To estimate variability and synchrony metrics at the local scale, we used the same equations as in [11], 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 49 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).

For the regional-scale SEM, we fitted Gaussian linear mixed models with the response and predictor variables, with metacommunity identity as a random effect. Regional diversity was dropped from the model, and 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, 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. For this SEM, we also included time series length as an explanatory variable for population variability because exploratory analyses indicated that variability metrics were sensitive to it (Fig. S5). 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 [48] and piecewiseSEM [47] in R.

Environmental and spatial predictors

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. Local, direct measures of thermal and hydrologic regimes would have been ideal, but these data were not available. We therefore gathered data on average temperature and precipitation seasonality (bio4 and bio15, respectively) data from the WorldClim database [49]. Temperature seasonality is calculated as the standard deviation of month temperature within a year * 100, whereas precipitation seasonality is the coefficient of variation of month precipitation within a year.

Air temperature has been shown to be a good proxy for water temperature – particularly in systems not strongly affected by snowmelt [50,51]. Thus, changes in air temperature can affect food web dynamics, by for example, increasing the demand for food resources and thus leveling the rates of herbivory and predator-prey interactions [52]. With regards to precipitation, food webs are strongly influenced by changes in precipitation amounts and regimes, because water limits the flux of biomass across trophic levels and govern the loss of species and interactions, particularly among predators [53]. Also, under scenarios of reduced precipitation and increased drying conditions, lakes might suffer from reduced hydrological connectivity, which in turn influences food web structure due to changes on species diversity [54].

Two measures of spatial synchrony in mean maximum and mean minimum temperature and precipitation were used as predictors in the regional-scale SEM. We 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 [55]. We extracted monthly mean values at the spatial coordinates of the sampling sites, from 1958 to the last year in which community was sampled within each dataset. 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 dataset to get a broad and comparable characterization of environmental variation across sites.

For the regional-scale SEM, we also estimated one metric of spatial connectivity, network closeness centrality [56], 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. sites within 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.

Data availability: The data and code supporting the results are archived in Zenodo (10.5281/zenodo.6591419).

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Figures

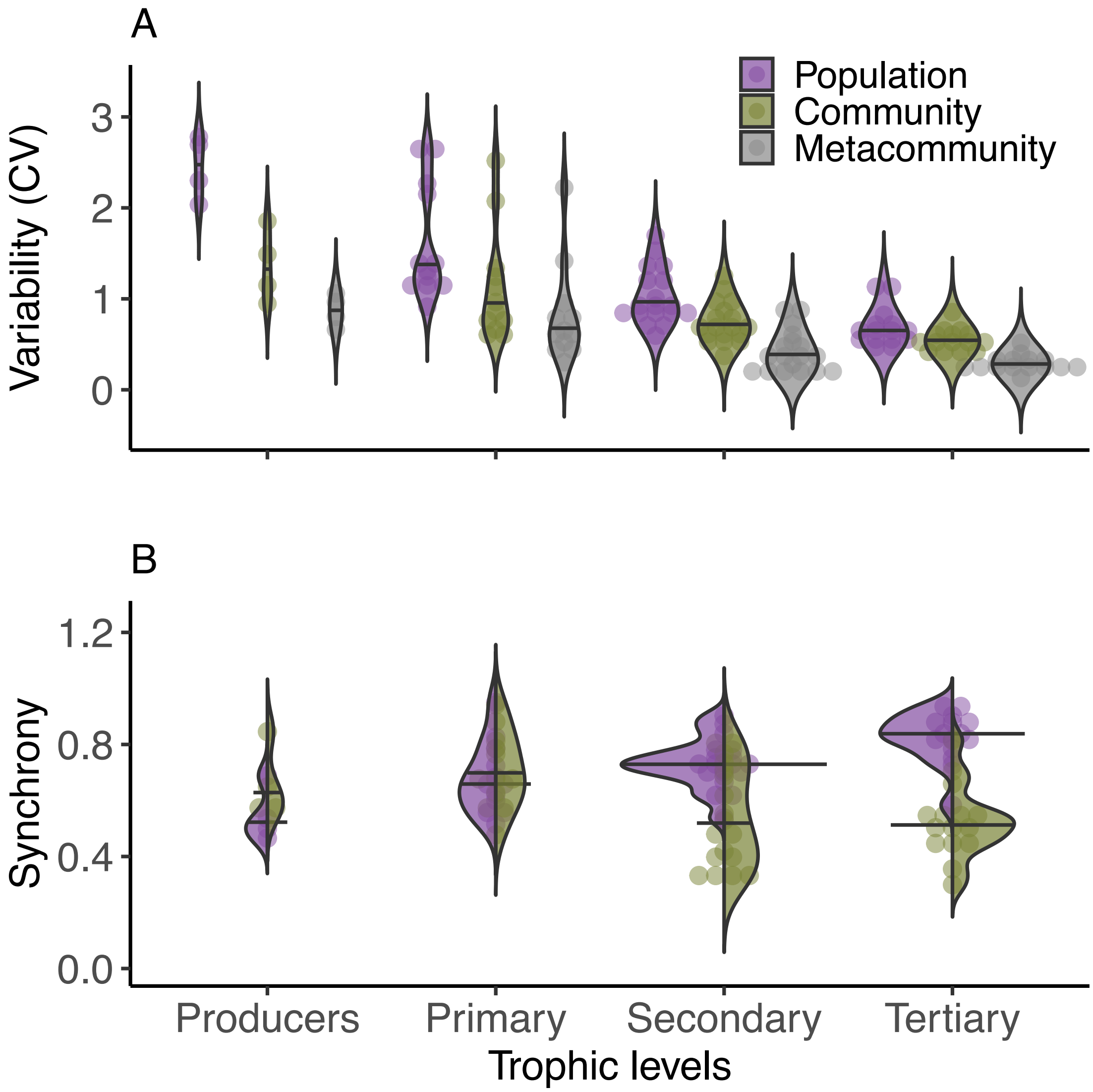

Figure 1. Spatial and trophic scaling of temporal variability (A) and synchrony (B). Plots with different colors represent the distribution of values as a density shape of aggregated variability or synchrony at the population, community and metacommunity levels. The overall median value per plot is represented 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 S1 and S3. Trophic levels include producers and primary, secondary, and tertiary consumers.

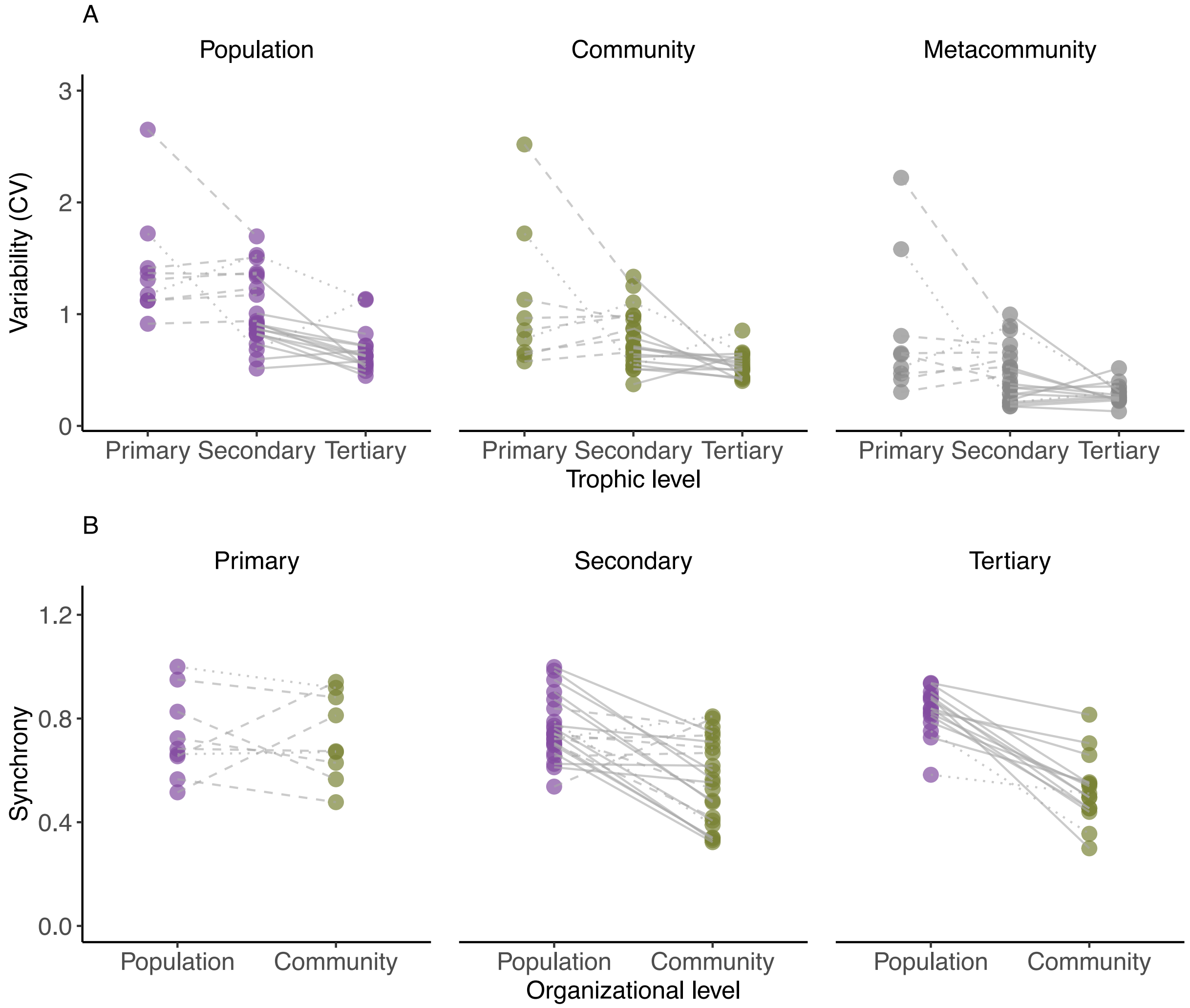

Figure 2. Spatial and trophic scaling of temporal variability (A) and synchrony (B) within metacommunities with more than one trophic level. Dots represent average variability or synchrony per metacommunity. Line types indicate the number of trophic levels monitored in each metacommunity: dotted lines indicate metacommunities with primary to tertiary consumers (n = 2); dashed lines indicate metacommunities with primary to secondary consumers (n = 7); and solid lines indicate metacommunities with secondary to tertiary consumers (n = 13). Paired t-tests indicated that (A) temporal variability of secondary consumers was higher than that of tertiary consumers, but only at the population and community levels, and (B) population synchrony was higher than community spatial synchrony for both secondary and tertiary consumers (Table S2). Color legend is as in Figure 1.

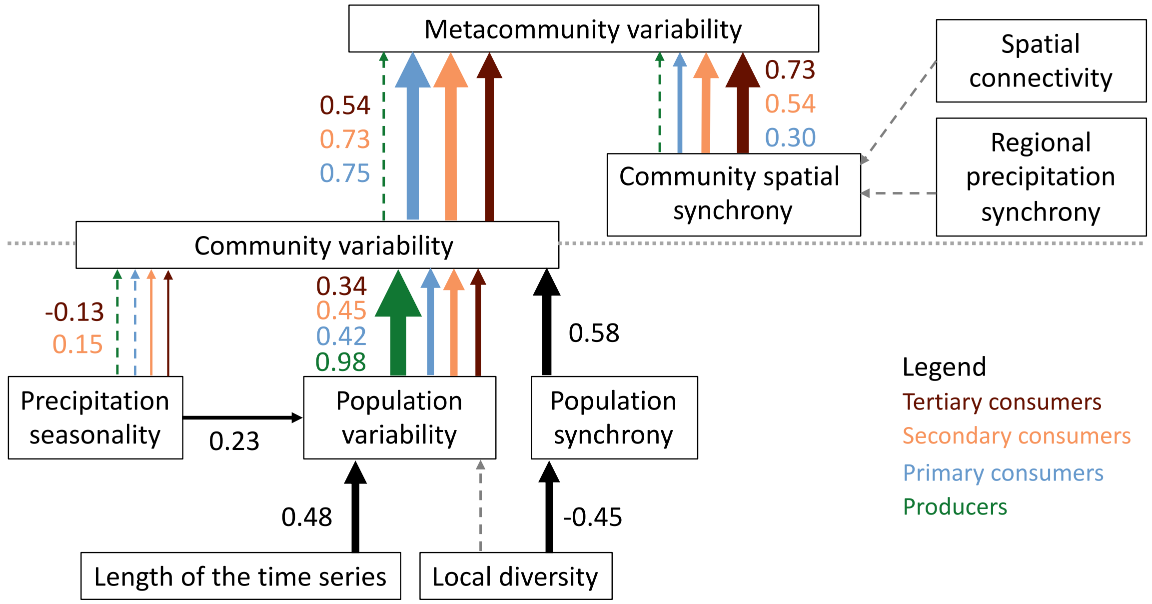

Figure 3. Results of multigroup structural equation models (SEM) at local and regional scales (separated by the horizontal gray dashed line). Dashed and solid arrows indicate relationships associated with $p < 0.05$ and > 0.05, respectively. Colored lines represent relationships that varied among trophic groups. The numbers associated with the lines represent SEM linear standardized coefficients. Local-scale SEM (n = 501; Fisher's C = 9.65; P-value = 0.14; df = 6). Regional-scale SEM (n = 49; Fisher's C = 9.31; P-value = 0.16; df = 6). Detailed description of all statistics is given in Table S4 and S5.

Supplementary Information for

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

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Supplementary Information Text

Methods

Dealing with missing data

The code used to run Wang’s partitioning approach requires by default that the time series is complete for all sites. That is, all sites need to be sampled during all sampling events (but does not require yearly spacing). Some of the datasets we used did not conform to this requirement (but all had >70% sample completeness). We note that sample completeness is a requirement of the R function, not the partitioning method per se, and no publications (to our knowledge) have examined sample completeness may influence temporal variability and synchrony estimates. Thus, we proceeded to modify the R function to allow missing values. To illustrate what we did, let’s consider a vector of values describing the temporal variability of species A at a given site along 9 years: A = {10, 14, 12, 18, 20, 14, 12, 18, 20}. Now let’s consider that one of these values went missing A’ = {10, NA, 12, 18, 20, 14, 12, 18, 20}. CV is calculated by diving the standard deviation by the mean of this vector: CV_A = sd(A) / mean(A) = 0.244. In R, to calculate CV_A’, one would need to allow for missing values: CV_A’ = sd(A’, na.rm = TRUE) / mean(A’, na.rm = TRUE) = 0.256. These values would be then averaged per site and then across sites to produce a value of population variability.

Our second approach to deal with missing values was to impute a median value to replace the “NA” in A’. In R, this would look like this: median (A’, na.rm = TRUE) = 16. Thus, the new vector would look like this A’’ = {10, 16, 12, 18, 20, 14, 12, 18, 20}. And thus, CV_A’’ = sd(A’’) / mean(A’’) = 0.239.

We estimated variability and synchrony metrics following the two approaches described above. The matrix the resulted from these analyses was a metacommunity (row) per metric (column). We compared the matrices obtained with the median versus missing values allowed with a Procrustes analysis and found that the Procrustes correlation coefficient between them was R=0.99 ($p < 0.001$). Thus, we concluded that either approach could be used.

Dataset description

The numbers identifying each dataset (DS) correspond to the ID of the datasets used in the R code “01_Siqueira_etal_dataprep_stability_metrics.R”.

DS. 5-18. These datasets 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 datasets were chosen based on their availability at the time of data analysis and considering both spatial and temporal completeness.
Dataset owners: Public available
Additional information about the dataset can be found here: Comte et al. (2021).

DS. 19. The dataset 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.

Dataset 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 datasets 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.

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

Additional information about the dataset can be found here: Bonecker et al. (2020).

DS. 22-24. (Removed from analysis after peer review). These datasets 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.

Dataset 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 dataset 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.

Dataset owners: Hancock Biological Station, Watershed Studies Institute, Murray State University, Murray, KY, USA.

Additional information about the dataset can be found here: Yurista et al. (2001); Yurista et al. (2004).

DS. 26-27. These datasets 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.

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

Additional information about the dataset can be found here: Rodrigues et al. (2015); Pineda et al. (2019).

DS. 28. (Removed from analysis after peer review). This dataset 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.

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

Additional information about the dataset can be found here: Jeffries (2010).

DS. 29. This dataset 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.

Dataset owner: Norwegian Institute for Water Research.

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

DS. 30. (Removed from analysis after peer review). This dataset 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.

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

Additional information about the dataset can be found here: Lead et al. (2018). https://doi.org/10.6073/pasta/8d5e19d0e9680fddc3402e148e377c1a (Accessed 1/17/2020).

DS. 31. This dataset 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 dataset 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.

Dataset 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 dataset 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.

Dataset 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 dataset 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.

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

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

DS. 34. This dataset 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.

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

Additional information about the dataset can be found here: Nilsson et al. (2022).

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

Dataset 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.

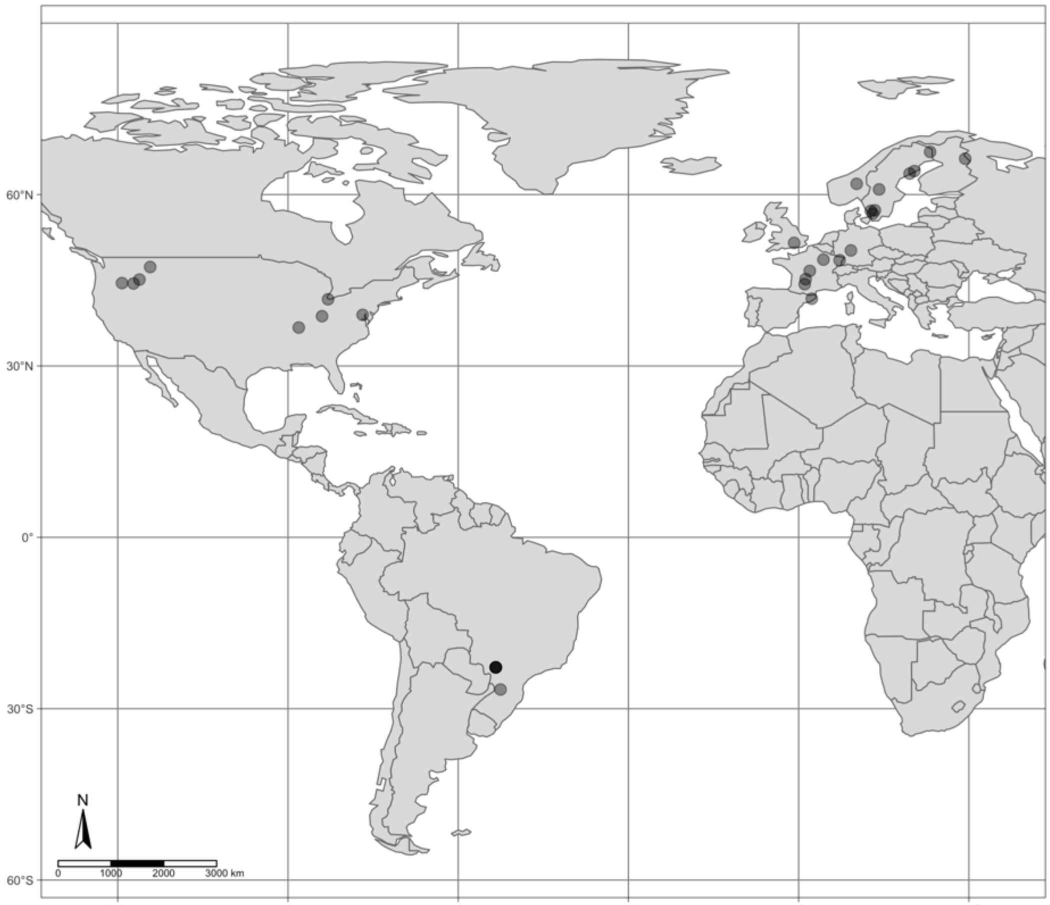

Fig. S1. Geographical distribution of the 30 metacommunities used in this study. Dots indicating the position of metacommunities are of the same color, but due to superimposing of spatially closed sites, some of them appear darker.

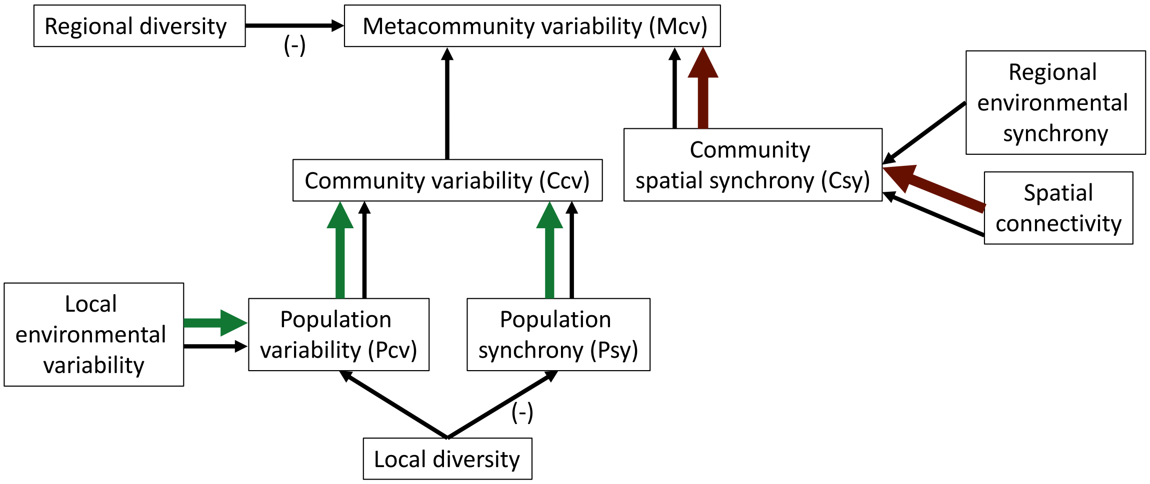

Fig. S2. Hypothesized propagation of temporal variability and synchrony (from populations to metacommunities) and their relationships with diversity, environmental variability and synchrony, and spatial connectivity. Directions of the arrows represent directions of each hypothesized causal relationship, 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.

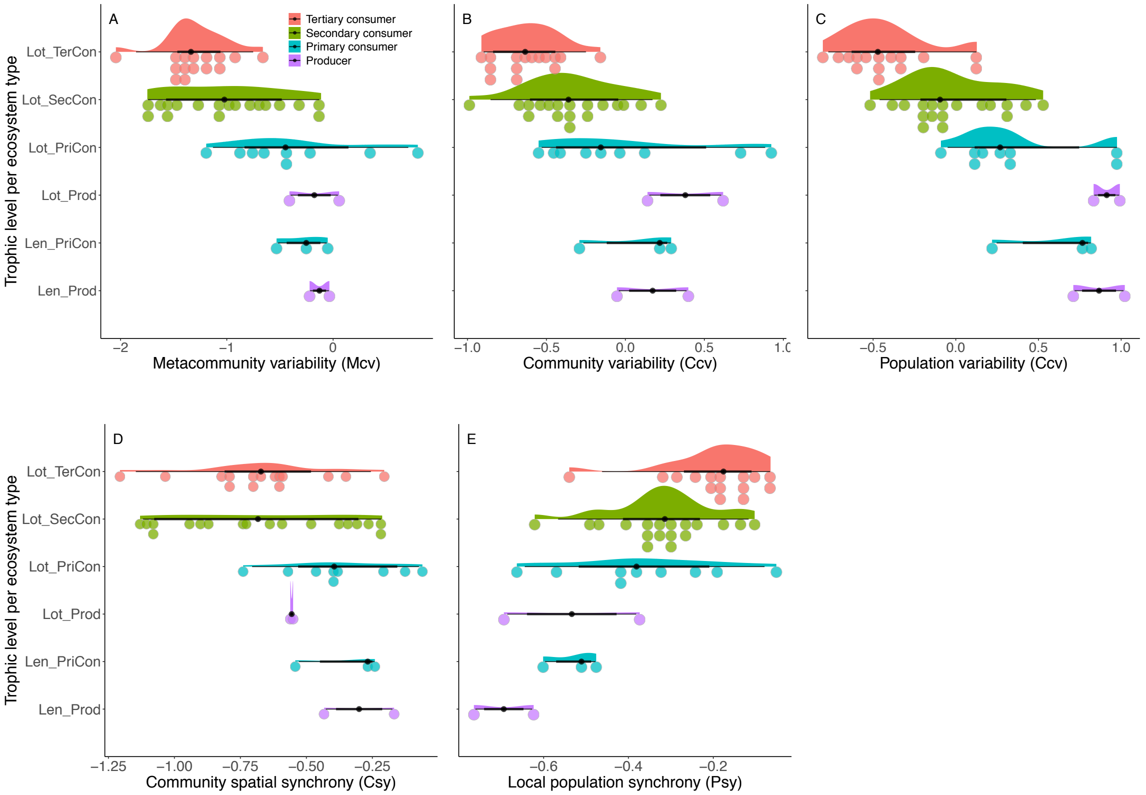

Fig S3. Metacommunity-level estimates of temporal variability (A to C) and synchrony (D-E) across levels of organization and in lotic and lentic systems. Key to y-axis: Len = lentic; Lot = lotic; Pri = primary; Sec = secondary; Ter = tertiary; Prod = producers; Con = consumers.

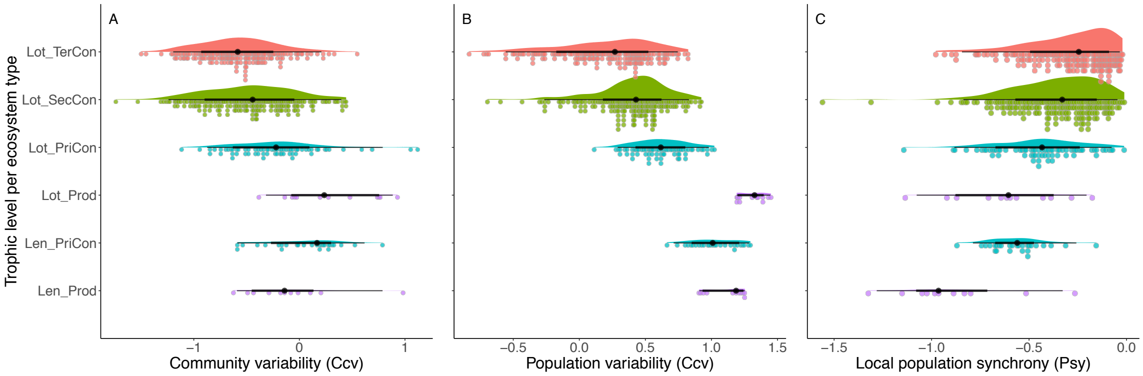

Fig S4. Site-level estimates of temporal variability (A-B) and synchrony (C) across levels of organization and in lotic and lentic systems. Colors and codes as in Fig. S3.

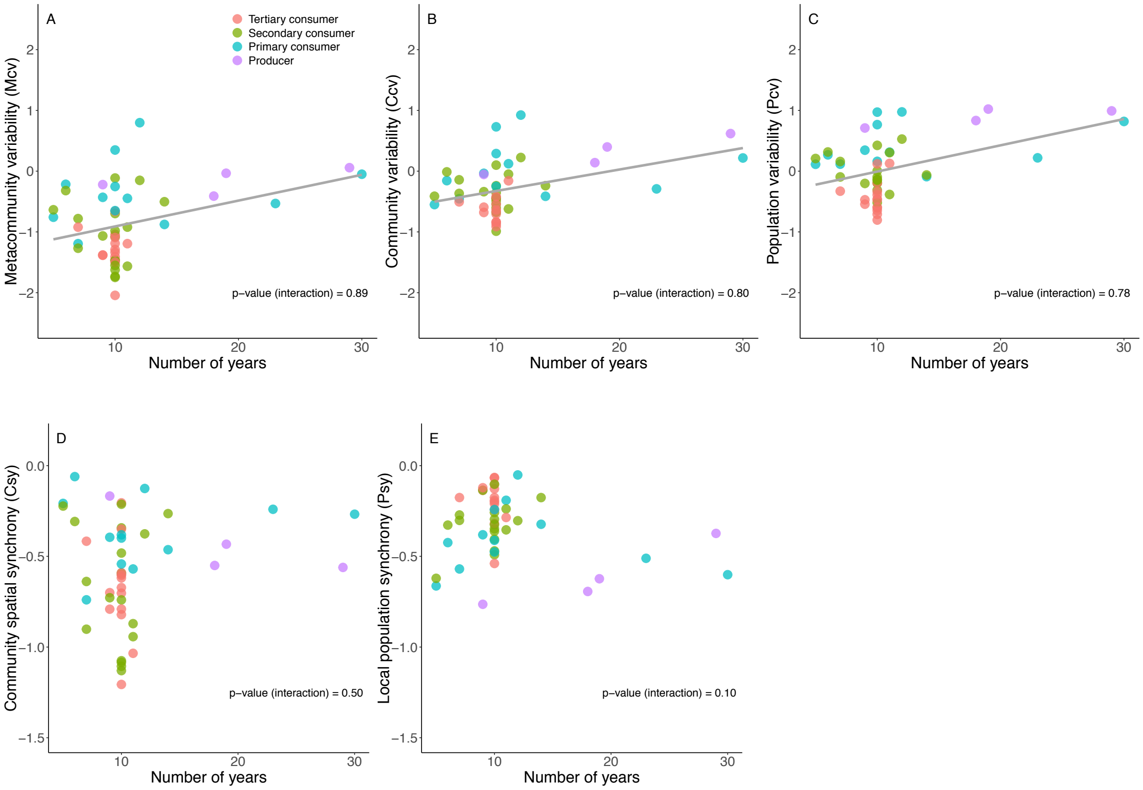

Fig S5. Relationship of temporal variability (A-C) and synchrony (D-E) with the length of the time series in years (number of time steps) in each dataset. The p-value refers to a linear relationship between the response variable and an interaction between trophic level and number of time years. The grey regression line indicates a relationship between the response variable in the y-axis and number of years.

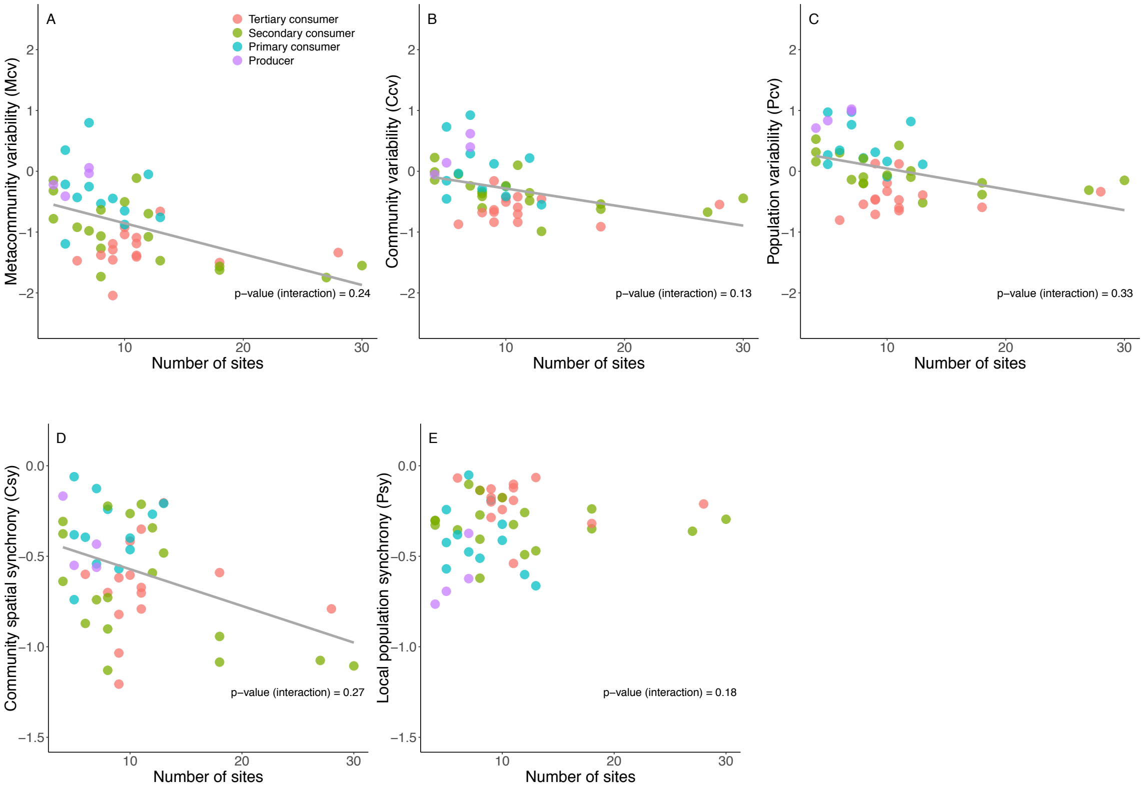

Fig S6. Relationship of temporal variability (A-C) and synchrony (D-E) with number of sites in each dataset. The p-value refers to a linear relationship between the response variable and an interaction between trophic level and number of sites. The grey regression line indicates a relationship between the response variable in the y-axis and number of sites.

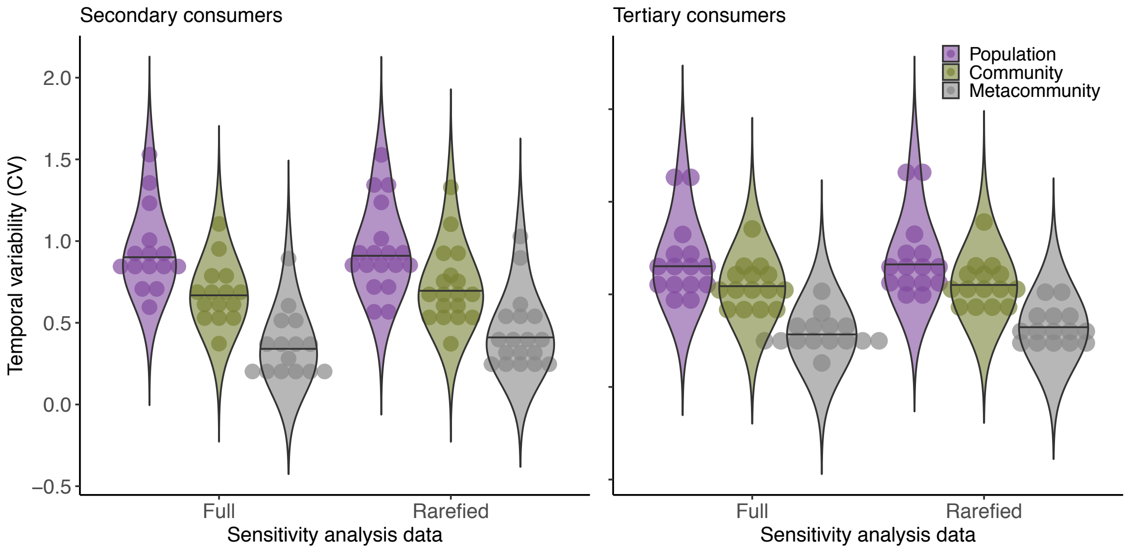

Fig S7. Assessing potential site replication effects on temporal variability metrics (sensitivity analysis 1). The spatial scaling of temporal variability in the full dataset (Full) and in datasets with rarefied number of sites (Rarefied; maximum number of sites = 8) for secondary and tertiary consumers. Plots with different colors represent the distribution of values as a density shape of aggregated variability at the population, community and metacommunity levels. The median value per distribution is represented by the solid line. Raw data values are shown inside each density shape. **Pearson's correlation coefficient among full and rarefied data averaged r=0.95 (range: 0.87-0.99), confirming that inferences on variability components across trophic levels are not influenced by variation in site replication.**

Fig S8. Assessing potential site replication effects on synchrony metrics (sensitivity analysis 1). The spatial scaling of synchrony in the full dataset (Full) and in datasets with rarefied number of sites (Rarefied; maximum number of sites = 8) for secondary and tertiary consumers. Plots with different colors (key as described in Fig. 1) represent the distribution of values as a density shape of synchrony at the population and community. The median value per distribution is represented by the solid line. Raw data values are shown inside each density shape. **Pearson's correlation coefficient among full and rarefied data averaged r=0.96 (range: 0.92-0.99), confirming that inferences on synchrony components across trophic levels are not influenced by variation in site replication.**

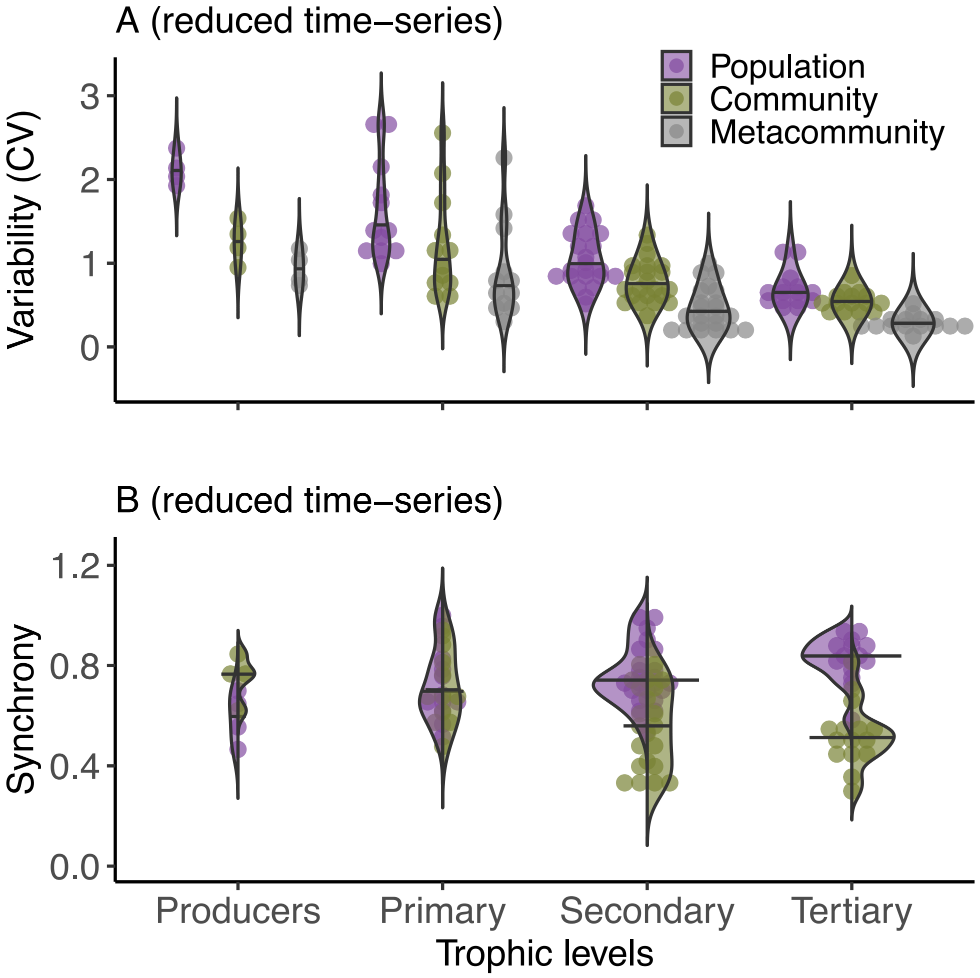

Fig S9. Assessing potential time series length effects on temporal variability and synchrony metrics (sensitivity analysis 2). The spatial and trophic scaling of temporal variability (A) and synchrony (B) estimated with datasets with less than 11 years of observations. Plots with different colors represent the distribution of values as a density shape of aggregated variability or synchrony at the population, community and metacommunity levels. The median value per distribution is represented by the solid line. Raw data values are shown inside each density shape. Trophic levels include producers and primary, secondary, and tertiary consumers. **Pearson's correlation coefficient among full and reduced time series within variability and synchrony components were all higher than r=0.98, confirming that inferences on synchrony and variability across trophic levels are not influenced by time series length.**

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	45	0.7603	0.4511	Mcv
Producers	Secondary	45	3.3627	0.0048	Mcv
Producers	Tertiary	45	4.3797	0.0004	Mcv
Primary	Secondary	45	3.8099	0.0017	Mcv
Primary	Tertiary	45	5.2302	0.0000	Mcv
Secondary	Tertiary	45	1.7328	0.1800	Mcv
Producers	Primary	45	1.4110	0.1651	Ccv
Producers	Secondary	45	3.4469	0.0050	Ccv
Producers	Tertiary	45	4.8847	0.0001	Ccv
Primary	Secondary	45	2.9266	0.0161	Ccv
Primary	Tertiary	45	4.9938	0.0001	Ccv
Secondary	Tertiary	45	2.4125	0.0400	Ccv
Producers	Primary	45	2.7656	0.0082	Pcv
Producers	Secondary	45	5.5455	0.0000	Pcv
Producers	Tertiary	45	7.8276	0.0000	Pcv
Primary	Secondary	45	3.9409	0.0008	Pcv
Primary	Tertiary	45	7.2506	0.0000	Pcv
Secondary	Tertiary	45	3.8314	0.0008	Pcv

Table S2. Specific paired comparisons (paired t-tests) between the temporal variability of secondary and tertiary consumers at the population, community and metacommunity levels, and between population and community synchrony of producers, and secondary and tertiary consumers. These analyses were done on datasets (n =13; # of sites = 213) that included both secondary and tertiary consumers. Df = degrees of freedom; t = t statistic; p = p-value.

Metric	**Paired comparison**	**Condition**	**Mean of the differences**	**df**	**t**	**p**
Variability (CV)	Secondary vs. Tertiary	Population	0.243	12	3.988	0.001
Variability (CV)	Secondary vs. Tertiary	Community	0.164	12	2.128	0.027
Variability (CV)	Secondary vs. Tertiary	Metacommunity	0.074	12	1.111	0.144
Synchrony	Population vs. Community	Primary	-0.001	8	-0.020	0.492
Synchrony	Population vs. Community	Secondary	-0.202	21	-4.703	<0.001
Synchrony	Population vs. Community	Tertiary	-0.301	14	-8.064	<0.001

Table S3. 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	45	-2.557	0.042	Psyn
Producers	Secondary	45	-3.716	0.003	Psyn
Producers	Tertiary	45	-5.202	0.000	Psyn
Primary	Secondary	45	-1.551	0.128	Psyn
Primary	Tertiary	45	-3.746	0.003	Psyn
Secondary	Tertiary	45	-2.497	0.042	Psyn
Producers	Primary	45	-0.399	1.000	Csyn
Producers	Secondary	45	1.612	0.447	Csyn
Producers	Tertiary	45	1.622	0.447	Csyn
Primary	Secondary	45	3.009	0.026	Csyn
Primary	Tertiary	45	2.952	0.026	Csyn
Secondary	Tertiary	45	0.062	1.000	Csyn

Table S4. Model summary statistics of the local-scale SEM (n = 501; Fisher's C = 9.65; P-value = 0.14; df = 6). 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; LTS = length of the time series.

Constrained to the global model							
Response	**Predictor**	**Estimate**	**Std.Error**	**DF**	**Crit.Value**	**P.Value**	**Std.Est.**
Psyn_local	S	-0.1668	0.0212	451	-7.8804	0	-0.4522
Pcv_local	S	-0.0212	0.03	450	-0.7061	0.4805	-0.0361
Pcv_local	PS	0.0104	0.0032	450	3.2849	0.0011	0.2315
Pcv_local	LTS	0.0413	0.0082	28	5.0242	< 0.0001	0.4801
Ccv_local	Psyn_local	1.0408	0.0596	448	17.4515	< 0.0001	0.5765
Model-wide interactions							
Producers							
Ccv_local	PS	-0.011	0.006	15	-1.764	0.098	-0.218
Ccv_local	Pcv_local	2.883	0.860	15	3.351	0.004	0.978
Primary consumers							
Ccv_local	PS	0.003	0.005	81	0.733	0.466	0.043
Ccv_local	Pcv_local	0.801	0.149	81	5.383	< 0.0001	0.424
Secondary consumers							
Ccv_local	PS	0.011	0.004	186	2.396	0.017	0.151
Ccv_local	Pcv_local	0.604	0.073	186	8.302	< 0.0001	0.449
Tertiary consumers							
Ccv_local	PS	-0.010	0.005	154	-2.019	0.045	-0.128
Ccv_local	Pcv_local	0.424	0.070	154	6.039	< 0.0001	0.344

Table S5. Model summary statistics of the regional-scale SEM (n = 49; Fisher's C = 9.31; P-value = 0.16; df = 6). Psyn = average population synchrony within the metacommunity; Pcv = average population variability within the metacommunity; Csyn = average community spatial synchrony within the metacommunity; Ccv = average community variability within the metacommunity; Mcv = metacommunity variability; RPS = regional precipitation synchrony.

Constrained to the global model							
Response	**Predictor**	**Estimate**	**Std.Error**	**DF**	**Crit.Value**	**P.Value**	**Std.Est.**
Csyn	Closeness	0.0112	0.0065	18	1.7222	0.1022	0.2996
Csyn	RPS	0.1225	0.2352	28	0.5209	0.6065	0.1058
Model-wide interactions							
Producers							
Mcv	Csyn	1.2478	0.3124	1	3.9943	0.1562	0.7341
Mcv	Ccv	0.6979	0.1007	1	6.9295	0.0912	1.355
Primary consumers							
Mcv	Csyn	1.2749	0.2565	9	4.9699	0.0008	0.2971
Mcv	Ccv	0.7648	0.0578	9	13.2424	< 0.0001	0.7456
Secondary consumers							
Mcv	Csyn	1.8069	0.1096	15	16.4845	< 0.0001	0.5365
Mcv	Ccv	1.3531	0.0858	15	15.7736	< 0.0001	0.7282
Tertiary consumers							
Mcv	Csyn	1.9499	0.1233	12	15.8131	< 0.0001	0.7265
Mcv	Ccv	1.6704	0.1346	12	12.407	< 0.0001	0.5452

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