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Understanding temporal variability across trophic levels and spatial scales in freshwater ecosystems

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Open Research: The LEPAS data set is restricted due to data sharing policies and can be obtained from the Lake Erie Fisheries Program Administrator at the Ohio Department of Natural Resources Division of Wildlife. All other data sets and code (Siqueira et al., 2023) are available in Zenodo at https://doi.org/10.5281/zenodo.8333128.

ABSTRACT

A tenet of ecology is that temporal variability in ecological structure and processes tends to decrease with increasing spatial scales (from locales to regions) and levels of biological organization (from populations to communities). However, patterns in temporal variability across trophic levels and the mechanisms that produce them remain poorly understood. Here we analyzed abundance time series of spatially structured communities (i.e., metacommunities) spanning basal resources to top predators from 355 freshwater sites across three continents. Specifically, we used a hierarchical partitioning method to disentangle the propagation of temporal variability in abundance across spatial scales and trophic levels. We then used structural equation modeling to determine if the strength and direction of relationships between temporal variability, synchrony, biodiversity, and environmental and spatial settings depend on trophic level and spatial scale. We found that temporal variability in abundance decreased from producers to tertiary consumers but did so mainly at the local scale. Species population synchrony within sites increased with trophic level, whereas synchrony among communities decreased. At the local scale, temporal variability in precipitation and species diversity were associated with population variability (linear partial coefficient, $\beta = 0.23$) and population synchrony ($\beta = -0.39$) similarly across trophic levels, respectively. At the regional scale, community synchrony was not related to climatic or spatial predictors, but the strength of relationships between metacommunity variability and community synchrony decreased systematically from top predators ($\beta = 0.73$) to secondary consumers ($\beta = 0.54$), to primary consumers ($\beta = 0.30$) to producers ($\beta =0$). Our results suggest that mobile predators may often stabilize metacommunities by buffering variability that originates at the base of food webs. This finding illustrates that the trophic structure of metacommunities, which integrates variation in organismal body size and its correlates, should be considered when investigating ecological stability in natural systems. More broadly, our work advances the notion that temporal stability is an emergent property of ecosystems that may be threatened in complex ways by biodiversity loss and habitat fragmentation.

Keywords: compensatory dynamics; International long term ecological research (ILTER); metacommunities; mobile consumers; Moran effect; portfolio effect; community synchrony; temporal variability

INTRODUCTION

The temporal variability of ecological attributes (e.g., population biomass) 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 local populations (Schindler et al. 2010). Similarly, organismal abundance at a given patch tends to be more stable at the community than the population level (Doak et al. 1998). However, most previous attempts to understand temporal variability and its drivers have focused on single trophic levels (Kéfi et al. 2019, Danet et al. 2021, Xu et al. 2021), and we cannot yet generalize if these patterns hold across trophic levels. Communities are connected through the spatial flow of organisms in different trophic levels (Leibold and Chase 2018), and the spatial structure of multitrophic-level metacommunities may modulate their temporal variability (Firkowski et al. 2022). For example, mobile consumers may buffer temporal variability of an entire metacommunity if they forage across, and thus link, 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 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 was recently formalized (Wang et al. 2019). 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., correlated fluctuations) that exists across the different populations within local communities (Thibaut and 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 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 scales. 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 (Schindler et al. 2015). Negative covariance in the abundances of different populations caused by biotic and abiotic interactions reduces temporal variation in aggregate ecological properties (Gonzalez and Loreau 2009). Higher diversity can also indirectly increases the chance of compensatory dynamics, unless species are highly functionally redundant – with more species, there will be a broader range of responses to environmental variation (Mori et al. 2013). At the regional scale, ecological attributes (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; Steiner et al. 2013) or via a combination of strong dispersal and predator-prey cycles (Fox et al. 2011). Notably, while organismal trophic position is generally positively associated with body size, lifespan, and dispersal strength (Peters 1983), we cannot yet generalize regarding the relationship between trophic position and environmental variation is mixed. Some have found that species at higher trophic levels are more sensitive to environmental change (Voigt et al. 2003, Thackeray et al. 2016, da Silva et al. 2023), but others have reported the opposite (Hu et al. 2022). 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.

Mobile consumers at higher trophic levels can stabilize the temporal dynamics of metacommunities by coupling heterogeneous local food webs in space (McCann et al. 2005, Rooney et al. 2008). This second hierarchical framework assumes that larger organisms tend to be at higher trophic levels, are highly mobile across the landscape, and leave low prey density patches for more profitable high-density patches (Eveleigh et al. 2007). 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 synchrony across space of organisms at lower trophic levels (Howeth and Leibold 2013). Merging these two views (Rooney et al. 2008, Wang et al. 2019) may offer new opportunities to test hypotheses about how diversity, environmental fluctuations, and dispersal interact with trophic levels to influence the propagation of temporal variability across space and across levels of ecological organization (Danet et al. 2021).

We compiled 30 temporal datasets on annual metacommunity dynamics spanning four trophic levels, from 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 (Appendix S1: Figure S1). Based on temporal variability properties of both hierarchical frameworks of temporal variability, we hypothesized that (H1) temporal variability in abundance decreases with trophic position, as top consumers should buffer variability originating at the base of the food web. This hypothesis is based on the idea that top mobile consumers may couple different local food webs characterized by both fast energy channels exhibiting mostly of strong interactions and slow channels exhibiting mostly weak interactions (Rooney et al. 2006). Alternatively (H1'), higher trophic levels could exhibit stronger fluctuations in population abundance if environmental and demographic stochasticity disproportionally affect taxa with larger body size—a pattern that is also plausible given larger-bodied taxa tend to have relatively smaller population sizes and longer generation times (and thus, lower capacity to recover quickly after disturbance) (Sousa 1984, Lande 1993).

Additionally, we hypothesized that (H2) species population synchrony within sites increases with trophic level, whereas spatial synchrony among communities decreases, as top mobile consumers may aggregate 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 occupy a patch, which should decrease spatial synchrony in resources at the regional scale and increase local predator synchrony (Vasseur and Fox 2009). Alternatively (H2'), if top-down rather than bottom-up forces predominate, a high abundance of mobile, top consumers could synchronize fluctuations in their resources, leading to an increased, rather than decreased, population synchrony levels at the base of the food web (relative to its top).

Finally, we tested if the strength and direction of relationships between temporal variability, synchrony, diversity, and environmental and spatial settings depend on trophic level and spatial scale (Appendix S1: Figure 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. Alternatively, (H3a') environmental controls could operate mostly at large spatial scales, synchronizing spatially-structured patches across regions (e.g., via flooding or regional drought; (Ruhi et al. 2018, Sarremejane et al. 2021)); and

(H3b') strong dispersal in the lower trophic levels could maintain resource synchrony even if patches are isolated (e.g., via mass effects; Vanschoenwinkel et al. 2008, Abbott 2011).

We 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 to test hypothesis H3.

METHODS

Datasets

We collated 30 independent metacommunity datasets, comprising spatially replicated annual 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 (Appendix S1: Figure S1). When the original data included multiple sampling events per year, we selected the summer month with the highest number of sites sampled. Each dataset contained one sample per year from 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). We only used data on metacommunities in which local communities were physically connected (e.g., multiple sites per lake; multiple streams within a catchment). Our data included a mix of 5 lentic (lakes) and 25 in lotic (streams and rivers) metacommunities, but none of the relationships differed between lotic and lentic ecosystems (Appendix S1: Figure S3 and S4). A summary of each dataset and a detailed description of the procedures used in data filtering can be found in Appendix S1. Data and code are available in Siqueira et al. (2023).

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 only secondary consumers, and another with only tertiary consumers. This reorganization of data resulted in 54 data tables representing individual metacommunities (producers = 4; primary consumers = 13; secondary = 22; tertiary = 15). We removed unidentified taxa and taxa identified at a level higher than genus from all datasets. 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.

We recognize our trophic level categorizations are somewhat simplistic as we did 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 full representation of temporal and spatial sampling. As we aimed to investigate relationships that are theoretically expected along a complex gradient of trophic levels (Vander Zanden and Fetzer 2007) and dispersal capacity (Rooney et al. 2008), we believe our strategy represents a useful compromise.

The original metacommunity datasets differed in in terms of what and how many trophic levels were included, with 22 datasets including information on more than one trophic level. We explicitly considered potential artifacts associated with variation inherent to the original data by pursuing four strategies. First, we estimated all variables relevant to our analyses (e.g., local diversity, population synchrony) for each of the 49 trophic-level-specific metacommunities. Second, we used mixed-effects models both to quantify the relationships between response and predictor variables in structural equation modeling (details below), and to test the effect of potential confounding variables on variability and synchrony (e.g., number of sites; details below). Third, we compared variability and synchrony metrics among trophic levels for a subset of the data that included more than one trophic level, by conducting paired t-tests in which dataset identity was used as a blocking factor. In this case, paired t-tests are equivalent to both a linear mixed model with random intercepts and a simple linear fixed effects model with varying intercepts – i.e., they result in the same treatment test statistic. 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 assess the potential effect of the number of sites per metacommunity and time series length on estimates of variability and synchrony metrics (see details below). Because the number of generations represented in each time-series differed among trophic levels (particularly between producers and the consumer groups), we included the median number of generations sampled as a predictor in structural equation models (see details below) and in individual mixed effects models (one per response variable; Appendix S1).

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 analysis, 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 synchrony across those local communities (Csy). Cv was further partitioned into the variability of individual population abundances within sites (Pv) and synchrony across those local populations (Psy). Thus, $Mv = Cv \times Csy = (Pv \times Psy) \times Csy$. 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 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 49 trophic-level-specific metacommunities.

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

Sensitivity analysis

Because individual datasets differed in number of sites and years sampled, and previous studies showed these differences can affect population variability estimates, we tested if variation in time series length, average number of generations per trophic level (see Appendix S1), and site replication could have influenced the observed patterns. We ran two sensitivity analyses in which variability and synchrony were estimated for metacommunities with only 8 sites and with only 11 years. First, we selected all datasets with more than 7 sites (the maximum number of sites for the trophic group with the minimum number of sites) and sampled 8 sites randomly from each one of them. We repeated this process 1000 times and estimated the variability and synchrony metrics each time. We averaged these 1000 values and compared these "rarefied" estimates with the estimates obtained based on the full data. To assess the potential effect of time series length on variability and synchrony estimates, we used a standardized reduced time series – 11 years only (the maximum number of years for the trophic group with the minimum number of years). We did not rarefy time series length (but truncated raw time series), as we wanted to preserve the time series nature of the population and community data.

Two-scale structural equation modelling

We used local estimation structural equation modeling (SEM) (Shipley 2000) to test if the direct and indirect relationships among diversity, environmental and spatial predictors, variability and synchrony, trophic levels at two spatial scales were consistent with H3a-b. 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 (see explanation and justification of environmental and spatial predictors below). 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 higher total R^2 value and more randomly distributed residuals.

We performed multigroup SEM analysis (Lefcheck 2016) 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, consider the following model: population synchrony ~ local diversity * trophic level. If there is an interaction between the two predictor variables, we should interpret the relationship between population synchrony and local diversity (standardized coefficient) separately for each trophic level. When that was the case, we represented the graphed multiple pathways with distinct colors to indicate that the relationship between a response and a predictor variable depended on trophic level.

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 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 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 better approximate linear relationships. For the local-scale SEM, we fitted the response and predictor variables with Gaussian linear mixed effects models and considered metacommunity identity and a variable identifying the trophic-level-specific metacommunity as random effects. Model fit and evaluation followed the same procedures as for the regional-scale SEM. For the local-scale SEM, we also included average number of generations sampled per site as an explanatory variable for population variability because exploratory analyses indicated that the number of generations sampled differed between producers and the other levels (Appendix S1: Table S1) and that variability metrics were sensitive to it (Appendix S1: Figure 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 (Bates et al. 2015) and piecewiseSEM (Lefcheck 2016) in R.

Environmental and spatial predictors

For the local-scale SEM, we used measures of overall temporal variability in temperature and precipitation as predictors of population variability. We expected that more variable 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 biological data from summer months. Local, direct measures of thermal and hydrologic regimes would have been ideal, but these data were not universally available. We therefore gathered data on average variability in temperature and precipitation (bio4 and bio15, respectively) data from the WorldClim database (Fick and Hijmans 2017). Variability in temperature is calculated as the standard deviation of monthly temperatures within a year × 100, whereas variability in precipitation is the coefficient of variation of monthly 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 (Stefan and Preud'homme 1993, Mohseni and Stefan 1999). Differences in air temperature can potentially affect food web dynamics, by for example, affecting metabolic rates and the demand for food resources (Hunt et al. 2017). Similarly, precipitation is a primary predictor of stream flow or lake volume, and differences in flooding and drying can also affect food webs (e.g., Greig et al. 2013, Jellyman and McIntosh 2020). For example, floods mediate the strength of stream trophic cascades by decreasing algal abundance and removing defended herbivores (McIntosh 2022). Also, under scenarios of reduced precipitation, lotic systems might suffer from reduced hydrological connectivity, which can influence food-web structure via decreases in species diversity (Rosset et al. 2017).

Two measures of the synchrony among sites 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 (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 communities were sampled within each dataset. Spatial synchrony in temperature and in precipitation was then estimated as the mean Kendall rank correlation across years 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 ensure we accurately characterized temporal environmental variation across sites.

For the regional-scale SEM, we also estimated one metric of spatial connectivity, network closeness centrality (Erős et al. 2012) and used it as a predictor of community 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 distances between them were included as weights 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.

RESULTS

Metacommunity variability partitions across scales and levels

Temporal variability in abundance generally decreased with increasing trophic level ($F_{3,135} = 47.69$, $p = 2.2e\text{-}16$, Figure 1a) and with spatial scale ($F_{2,135} = 75.47$, $p = 2.2e\text{-}16$; R^2 of the global model = 0.69), as hypothesized (H1). However, pairwise contrasts indicated that while population variability differed among all trophic levels, community variability did not differ between producers and primary consumers, and metacommunity variability of producers was higher than that of secondary and tertiary consumers (Appendix S1: Table S2). Thus, in general, temporal variability of tertiary consumers was lower than that of producers and primary consumers—from local populations to regional metacommunities. These general patterns were similar but weaker when we analyzed temporal variability only within datasets that included more than one trophic level (22 datasets encompassing 300 sites; Figure 2a). When we used dataset identity in paired t-tests, both population and community variability decreased only from secondary to tertiary consumers (Appendix S1: Table S3).

In support of hypothesis H2, we found that synchrony depended on an interaction between trophic level and spatial scale ($F_{3,90} = 9.67$, $P = 0.000013$). While population synchrony (i.e., synchrony among populations within sites) generally increased from producers to tertiary consumers (all pairwise contrasts differed from each other, except between primary and secondary consumers; Appendix S1: Table S4), community spatial synchrony (i.e., among communities across sites) decreased from primary to secondary and tertiary consumers (Figure 1b; Appendix S1: Table S4). Paired t-tests, which blocked dataset identity, partially confirmed these general results (Figure 2b). While there was no difference between population and community synchrony for primary consumers, population synchrony was higher than community synchrony for both secondary and tertiary consumers (Appendix S1: Table S3).

Sensitivity analyses

Although variability metrics were often positively related to the number of generations sampled and negatively related to the number of site replicates, none of these relationships showed a statistical interaction with trophic level (Appendix S1: Figure S5 and S6). This observation suggests that sampling heterogeneity effects were consistent across trophic levels and thus unlikely to generate a spurious "propagation effect". The sensitivity analyses with resampled sites and reduced time steps in the time series resulted in the same patterns described above for the whole dataset (see Appendix S1: Figure S7 – S9 for details), confirming that variation in time series length or site replication did not drive propagation patterns.

Drivers of temporal variability

Only one local-scale structural equation model (local-scale SEM) had a good fit in multigroup analysis (Fisher's C = 3.376, df = 4, p-value = 0.49) and thus no model selection was necessary. This local-scale SEM indicated that the strength of the positive relationship between community variability and population variability varied among trophic levels, partially supporting H3 (Figure 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 standardized coefficient (0.71; see Appendix S1: Table S4 for detailed model statistics) for the path linking population to community variability. The coefficients for this same path were much lower and more similar among consumers (0.34-0.45). The path coefficient linking species population synchrony to community variability (0.58) did not vary among trophic levels (Appendix S1: Table S5). Additionally, we observed the expected negative relationship between species population synchrony and local species richness, which did not vary among trophic levels (-0.39; Figure 3). However, contrary to our predictions, the positive relationship between population variability and variability in precipitation did not vary among trophic levels (0.23; Figure 3). Variability in precipitation slightly influenced secondary and tertiary consumers in opposite ways, but we note this direct path was not part of our conceptual model and was included *a posteriori* to improve model fit. The number of generations sampled was positively related to population variability (0.30; Figure 3) and negatively related to population synchrony (-0.20; Figure 3). Although these relationships did not vary among trophic levels (Appendix S1: Table S5), for community variability, the interaction between number of generations and trophic levels was associated with a p-value close to 5% (0.067). We thus further investigated this potential issue by using an Akaike information criterion corrected for small sample size (AICc) to compare models with and without an interaction between number of generations sampled and trophic levels. This exercise indicated that in all cases (population variability, population synchrony, and community variability), models without the interaction (i.e., 'additive' models) were substantially better supported than models with the interaction (Appendix S1: Table S6).

Three regional-scale SEMs fitted the data well, and two of them had delta AIC values smaller than 2 (Appendix S1: Table S7). We interpreted the one with the highest R^2 values. This 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 (Figure 3). While the strength of the relationship between metacommunity and community variability decreased with trophic levels (0.75 to 0.54; see Appendix S1: Table S8 for detailed model statistics), the relationship between metacommunity variability and community synchrony increased with increasing trophic level (0.30 to 0.73). Thus, in agreement with hypothesis H3b, the relationship between community synchrony and temporal variability in metacommunity aggregate abundance was strongest for predators. This result confirmed the expectation that communities that are more synchronous with one another 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 clear when we analyzed all datasets together but less consistent within datasets. These results suggest that the propagation of temporal variability across trophic levels was caused by a contrasting contribution of synchrony among populations within sites (local scale measure of synchrony) compared to the synchrony among communities across sites (regional scale measure of synchrony; H2). Because population synchrony generally increased from producers to tertiary consumers whereas community synchrony decreased from primary to secondary and tertiary consumers, general differences in variability among trophic levels were diminished from populations to metacommunities. While synchrony among populations within localities increased from producers to tertiary consumers, synchrony across localities decreased. Our analyses also confirmed that the associations between community 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 and dispersal strength (Peters 1983), should be more explicitly accounted for when attempting to understand 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 (Rip and McCann 2011). This decrease could occur if primary consumers tend to obtain most of their resources from either algae or detritus in freshwater ecosystems, whereas consumers at higher trophic levels tend to derive carbon from both sources, as suggested by Rooney et al. (2006). These coupled heterogeneous food webs differ in the amount of energy entering through basal resources and interaction strengths, which guarantees that top consumers have access to heterogeneous resources associated with asynchronous temporal dynamics originating at the base of local food webs (Rooney et al. 2006) – a mechanism widely recognized as a driver of stability (Schindler et al. 2015). However, an increase in temporal variability from producers to tertiary consumers is also expected (as described in our alternative H1'). For example, 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 (Lande 1993). These alternative hypotheses deserve future investigation through a combination of modeling and appropriate observational data.

Interestingly, population and community variability of tertiary consumers was similar because fluctuations in abundances of tertiary species were highly synchronized. Populations of higher trophic levels tend to congregate together on specific resource patches within metacommunities while they are profitable (Eveleigh et al. 2007), which may explain why we observed the highest levels of local population synchrony among tertiary 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 among primary consumers and producers.

In contrast to species population synchrony, tertiary consumers exhibited the lowest levels of community 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 switching among spatially separated resource patches by mobile predators occurs in response to spatial-temporal variation in resource densities (Rooney et al. 2008). The movement of top consumers from low prey density patches to 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 (Rezende et al. 2021). We thus suggest that top mobile predators can be seen as stabilizers 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 (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, ensuring aggregate ecological properties are more stable through time (Gonzalez and Loreau 2009). Second, statistical averaging among species that fluctuate independently through time may also lead to a similar pattern of 'risk dampening' (Schindler et al. 2015). Interestingly, the positive relationship between population synchrony and aggregate community variability, which mediated the indirect negative 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 total local diversity on aggregate community variability may be independent of horizontal diversity (i.e., diversity within trophic levels).

Similarly, the path linking variability in precipitation to population variability was consistent among trophic levels. Variability in precipitation weakly increased population variability. 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). However, the path linking variability in precipitation to community variability varied among trophic levels. While there was no apparent relationship between those variables for producers and primary consumers, there was a modest relationship for top consumers. Thus, our results suggest that populations are more temporally variable among years in more variable environments, but that the manner in which variability in precipitation indirectly and directly relates to community-level variability depends on species trophic level. The range of responses of different trophic levels is likely explained by the fact that the life histories of organisms are shaped by the frequencies of environmental fluctuations that roughly match, but are not much longer than, organismal generation times (Lytle 2001).

Our results are consistent with hypothesis H3b, as we found that the strength of the relationship between metacommunity variability and community synchrony increased from producers to tertiary consumers. Synchrony across sites is the scaling factor that determines the amount of variability that propagates from the community to the metacommunity level (Mv = Cv x Csy; Wang et al. 2019). Thus, the stronger relationship between metacommunity variability and community synchrony for tertiary consumers indicates their variability at the regional level was more strongly influenced by synchrony than for other trophic levels. This result could also explain why differences in temporal variability among trophic levels at the local scale almost disappeared at the regional scale. In contrast to hypothesis H3b, however, neither synchrony in precipitation nor spatial connectivity played a role as a driver of community synchrony. This result is surprising 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 (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). We cannot discard, however, that the lack of relationship between community synchrony and environmental predictors was due to the use of coarse climatic variables only. For example, ecosystem productivity is a key driver of ecological stability (i.e., paradox of enrichment; Rosenzweig 1971). Overall, 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 counteract the effects of environmental variation on population variability, and of environmental synchrony on community synchrony (Rooney et al. 2008).

We built our conceptual model focusing on paths supported by theory as representations of causal relationships. For example, we did not link metacommunity variability, indirectly through community synchrony, or directly, to spatial beta-diversity. While some previous studies have suggested that high beta-diversity can cause low synchrony among communities (Wang and Loreau 2016), others have suggested that temporal turnover (a form of temporal variability) drives spatial beta-diversity (Steiner and Leibold 2004). Others have suggested this relationship may be caused by pure sampling effects (Stegen et al. 2013). We suspect spatial and temporal turnover and community synchrony are all consequences of an interaction among environmental forcing, the various forms of stochasticity, and dispersal (Leibold and 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 caveat is that our analyses were based on annual observations only, and organisms in different trophic levels tend to differ in lifespan and generation times—from days or weeks (e.g., planktonic organisms) to years (fishes). Even though there was no statistical interaction between number of generations and trophic levels as determinants of variability and synchrony metrics at any scale, the number of time series for producers was low compared to the other trophic groups, and some time series were short. Thus, given that generation time and trophic position are generally correlated, we cannot completely rule out that temporal variability was not underestimated for species with long generation times relative to the data series. 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 understanding temporal variability in multitrophic metacommunities and for how ecological stability may be 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 (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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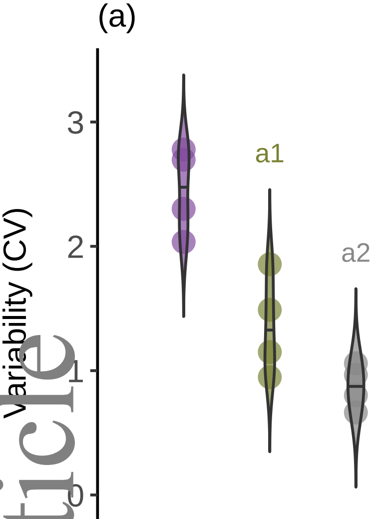
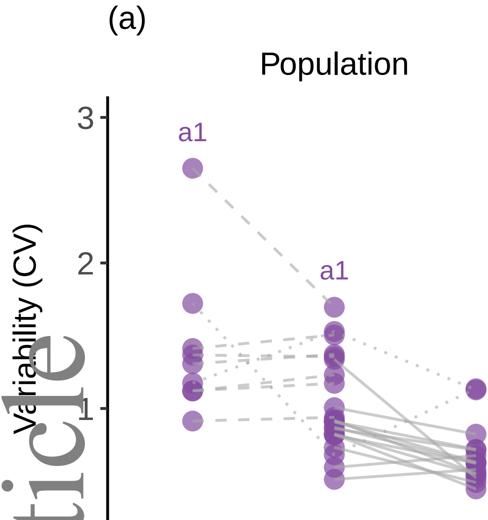
Figure captions

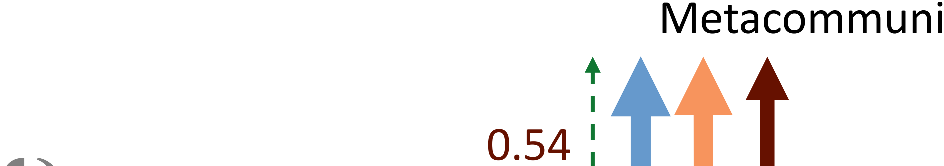
Figure 1. Spatial and trophic propagation of temporal variability (a) and synchrony (b). Plots with distinct colors represent the distribution of values as a density shape of aggregated variability or synchrony at the population, community and metacommunity levels. The overall median value per plot is 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 Appendix S1: Table S2 and S4. Specific pairwise contrasts that do not differ are indicated by colored numbered letters (e.g., a1, a2, etc.). Plots not associated with numbered letters are statistically different from each other and from those associated with numbered letters. Trophic levels include producers and primary, secondary, and tertiary consumers.

Figure 2. Spatial and trophic propagation 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 do not differ are indicated by colored numbered letters (e.g., b1, b2, etc.; Appendix S1: Table S3). Plots not associated with numbered letters are statistically different from each other and from those associated with numbered letters. 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 $C = 3.376$, $df = 4$, P-value $= 0.49$). Regional-scale SEM ($n = 49$; Fisher's $C = 9.31$; P-value $= 0.16$; $df = 6$). Detailed description of all statistics is given in Appendix S1: Table S5 and S7.


(a)
Variability (CV)
3
2
1
0
a1
a2


(a)
Population
3
2
1
Variability (CV)
a1
a1


Metacommuni
0.54