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Research Report

Community composition as an overlooked driver of spatial population synchrony

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Abstract

Animal populations often display coherent temporal fluctuations in their abundance, with far-ranging implications for species persistence and ecosystem stability. The key mechanisms driving spatial population synchrony include organismal dispersal, spatially correlated environmental dynamics (Moran effect) and concordant consumer–resource dynamics. Disentangling these mechanisms, however, is notoriously difficult in natural systems, and the extent to which the biotic environment (intensity and types of biotic interactions) mediates metapopulation dynamics remains a largely unanswered question. Here, we test the hypothesis that compositional differences among communities (i.e. beta-diversity), used as a proxy of the differences in biotic interactions experienced by separated populations, reduce population synchrony. Using an extensive dataset of fish population abundance time-series across Europe, we provide evidence that higher beta-diversity is associated with reduced spatial population synchrony within river networks and demonstrate that these effects are independent from geographic separation, environmental dissimilarity, and Moran effects. Although beta-diversity is commonly shown to promote metacommunity stability by reducing spatial synchrony in aggregate community attributes (e.g. total biomass), our study indicates that compositional heterogeneity provides a previously overlooked spatial insurance effect that influences metapopulation dynamics by promoting asynchrony between populations separated in space. These findings illustrate how community assembly across different locations within river networks contributes to metapopulation stability and persistence of individual species and further highlights the implications of the loss in beta-diversity over time via biotic homogenization.

Significance Statement

Synchronous dynamics in the abundance of different populations is a widespread phenomenon, having profound implications for ensuring species persistence, influencing ecosystem stability, and modulating disease spread. However, the drivers of spatial synchrony remain notoriously difficult to identify in nature. Here, we use over 30,000 pairs of synchrony estimates between stream fish abundance time series to show that the biotic context, captured through compositional dissimilarity between communities (i.e. beta-diversity), can promote asynchrony in population dynamics of the same species, independently from the effects of geographic separation, environmental dissimilarity, and climate conditions. These results indicate that regional, catchment-scale biotic heterogeneity represents an overlooked dimension of spatial insurance that influences metapopulation dynamics and promotes stability of individual species.

Introduction

Synchronous dynamics in the abundance of geographically distinct populations, defined as spatial population synchrony, is considered a fundamental property of metapopulations (1). Population synchrony has been observed across a range of species, ecosystems, and geographic extents, from microorganisms (2), to invertebrates (3–5), fish, birds, and mammals (6–9). Population synchrony has wide-ranging implications for species ecology, management, and conservation. Subpopulations displaying synchronous fluctuations in abundance often face a higher risk of local extinction due to a lower probability of demographic rescue (10–12), while spatial synchrony can also lead to a widespread increase in the abundance of pests and diseases (13). Research on the causes and consequences of ecological synchrony has grown rapidly (14), including recent recognition of how population and community synchrony underpin the emergence of coordinated dynamics in ecosystem functioning (15).

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Key mechanisms driving spatial synchrony are generalized through three primary pathways. Specifically, spatial synchrony is promoted by: individual dispersal among connected populations; spatially coherent dynamics in external drivers such as climatic factors, also known as the Moran effect (16, 17); and community processes such as consumer–resource interactions. However, estimating the relative importance of synchrony drivers remains a challenge in ecology. This is especially true in natural settings, causing past efforts to favor the use of experimental work and simulations to disentangle the unique and combined contribution of different processes.

Among the aforementioned drivers of spatial synchrony, the role of biotic interactions is particularly difficult to examine in natural settings (18). Theory and some observational studies indicate that trophically linked species can manifest synchronous (sometimes lag-shifted) dynamics when the abundance of separated populations is synchronized by a shared resource or mobile predators (18–20). In addition, the influence of community processes on spatial synchrony may extend beyond direct consumer–resource dynamics. Spatially separated populations may "experience" different types and strengths of biotic interactions (competition, facilitation, predation, etc.) depending on the specific species with which they cooccur. Compositional differences between locations could directly and indirectly affect the strength of density-dependent processes within separated populations—for instance via differences in the effects of competitors and predators (21)—contributing to reduced synchronous fluctuations in local abundances. For a given spatial separation and degree of environmental dissimilarity, two populations of a given species could thus exhibit decreased synchrony when the communities differ with respect to the number and identity of other cooccurring species. Conversely, synchrony may be higher between populations within compositionally similar communities (Fig. 1), as these populations are likely to experience similar interspecific interactions. In other words, compositional dissimilarity may provide an additional (biotic) dimension of spatial diversity that promotes asynchronous dynamics between geographically separated populations. According to this line of reasoning, beta-diversity—quantifying compositional dissimilarity between communities (22)—represents a valuable proxy of the biotic environment whereby higher beta-diversity is expected to decrease population synchrony. However, this hypothesis has yet to be empirically tested.

The notion that beta-diversity could promote asynchrony among local communities is not new, but past investigations have focused on higher organization levels. Communities composed of more homogeneous species memberships are more likely to respond similarly to environmental fluctuations relative to communities of heterogeneous compositions. It follows that metacommunity composition or beta-diversity is expected to affect ecological synchrony by providing a sort of insurance, or portfolio effect, reducing spatial synchrony of aggregate community properties such as total biomass and richness (14, 23, 24).

The present study is the first to test the hypothesis that beta-diversity can influence metapopulation dynamics and buffers spatial synchrony among separated populations. To do so, we use species-specific synchrony estimates for 48 species from an extensive time-series database comprising >33,000 pairs of stream fish species populations across Europe. We present multiple lines of evidence based on multimembership random effects, null models, and structural equations, indicating that similarity in community composition regulates spatial population synchrony with effects that are independent of geographic separation, climatic Moran driver, and environmental dissimilarity. The results shed light on an overlooked aspect of biotic mechanisms able to influence metapopulation dynamics, reinforcing the importance of biotic heterogeneity at catchment scales for the local persistence of species. Our findings bolster ongoing concerns regarding the implications of global biotic homogenization (25) and point to the fundamental importance of maintaining beta-diversity in contemporary conservation efforts (26).

Results

Our results support the hypothesis that increasing community dissimilarity limits the degree of spatial population synchrony within river basins.

Using Akaike Information Criterion (AIC) model selection among a set of multimembership random-effects models that account for the pairwise nature of the data, we found that the most supported and parsimonious model for predicting population synchrony included watercourse distance, community dissimilarity, and the interaction between these two factors (conditional $R^2 = 0.112$; $P < 0.0001$; $n = 33{,}807$; pairs = 1,045; Table 1). Inclusion of an environmental (Moran) driver based on synchrony in local air temperature as well as environmental dissimilarity between sites (based on air temperature, elevation, stream order, and mean discharge) received weaker support (delta AIC > 4; Table S1).

For a given spatial separation and climatic dynamic, separated populations in communities with higher compositional dissimilarity show lower overall spatial synchrony than populations within more similar communities (Fig. 2). An additional null-model-based approach, comparing observed and expected synchrony values while controlling for other covarying factors, further supported the results from the multimembership models: low compositional dissimilarity between communities was associated with higher than expected spatial population synchrony (z-score = 4.07); conversely, populations in more heterogeneous communities displayed lower than expected synchrony (z-score = −4.01; Fig. S1).

We constructed two additional multimembership models—replacing the overall community dissimilarity (Bray–Curtis distance between communities) with either the species-replacement (actual turnover of species between communities) or the species richness-difference component of beta-diversity. Comparison of these two models indicates that the species-replacement component was a stronger predictor of population synchrony compared with the richness-difference component (delta AIC = ~25).

To further account for the expected interrelationships between watercourse distance, climatic Moran driver, beta-diversity, and population synchrony, we developed a piecewise structural equation model (SEM). The final SEM was satisfactory with global nonsignificant Fisher's C test, indicating that no important paths were excluded from the analysis. A relatively large range variation in both beta-diversity and population synchrony was explained by the random-effects components of basin and species identity (conditional R^2; Fig. 3). Both watercourse distance and community dissimilarity (beta-diversity) had negative effects on spatial population synchrony (standardized path coefficients: −0.081 and −0.077), whereas Moran forcing based on air temperature had a positive—albeit weaker—effect (0.16). In addition, both environmental dissimilarity (0.003) and watercourse distance (0.23) were positively associated with beta-diversity. Finally, the residual of the overall model indicated that—after accounting for the direct and indirect effects of the other variables—spatial population synchrony declined with increasing community dissimilarity (Fig. 3, inset).

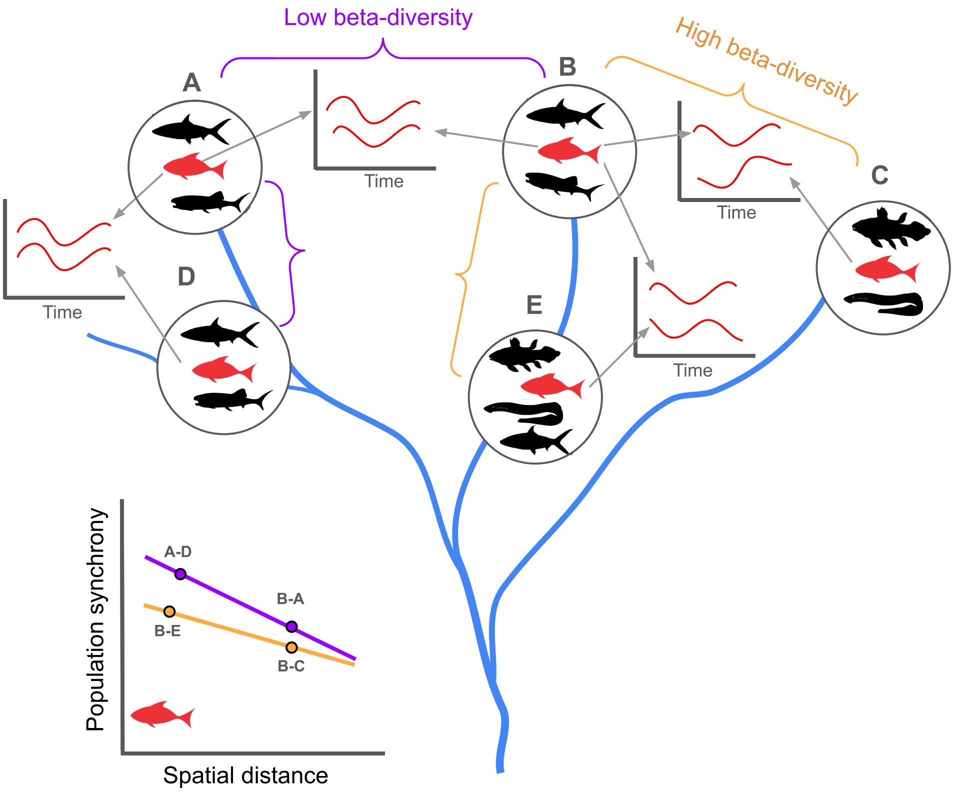

Fig. 1. Conceptual diagram illustrating five fish communities within a river network, with relatively different species composition. Communities A–B and A–D display very low beta-diversity, while communities B–C and B–E are characterized by high beta-diversity. Patterns of population synchrony for the focal species (in the center of the community circles) are shown. Among pairs of populations with the same level of geographic separation and environmental dissimilarity, we hypothesize that populations within dissimilar communities would exhibit lower synchrony, as each population is subject to different types and intensity of interspecific biotic interactions.

Table 1. Parameters from the top-ranking multimembership random-effects model explaining pairwise spatial population synchrony.

Model terms	Estimate	SE	χ^2	P-value
Watercourse distance	−0.041	0.003	111.43	2.2e−16
Beta-diversity (mean)	−0.027	0.002	105.14	2.2e−16
Watercourse distance × beta-diversity (mean)	0.015	0.002	37.74	8.1e−10

Discussion

Multiple lines of evidence indicated that differences in community composition, reflected in higher overall catchment beta-diversity, influence metapopulation dynamics across river networks with potential implications for the local persistence of species and overall stability. Evidence reported here shows that higher compositional dissimilarity between communities is associated with lower spatial synchrony in the abundance of separated populations, thus supporting the key hypothesis of the study.

Causal mechanisms are impossible to discern from correlative, large-scale field data; however, we expect that multiple, nonmutually exclusive processes are likely contributing to the results reported here. Separated populations may experience different types and intensities of interspecific biotic interactions depending on the specific species and their abundances in the communities with which they cooccur. Everything else being equal (i.e. spatial separation and environmental dynamics and dissimilarity), differences in the type and intensity of biotic interactions experienced by two populations may contribute to desynchronize their local dynamics. Local differences in density-dependent processes may also affect the extent to which dispersal and environmental dynamics result in synchrony (1, 27, 28). Beta-diversity could thus reflect this spatial dimension of biotic variability.

Alternatively—or in combination with the aforementioned mechanism—the influence of compositional dissimilarity on population dynamics may reflect environmental differences across locations that were not accounted for in our analyses, such as physical habitat and water quality. However, air temperature, elevation, stream order, and discharge were included, are considered valuable proxies for local habitat features (29), and should capture most of the ecologically relevant variability at the catchment scale. Our estimates of population synchrony were limited to within-basin and included basin and species identity in the models, thus excluding the effects of larger-scale factors such as historical legacies, while also limiting the influence of genetic differences among populations.

The link between biodiversity and stability is of both fundamental and practical importance and has been the focus of numerous studies (10, 30–33). Recent frameworks allowed decomposing metacommunity variability across the ecological hierarchy and highlighted the stabilizing role of beta-diversity that provides spatial insurance and promotes asynchrony in the dynamics of aggregate community metrics, such as biomass and richness (14, 23, 34). The results from our analyses suggest an additional pathway by which beta-diversity can contribute to

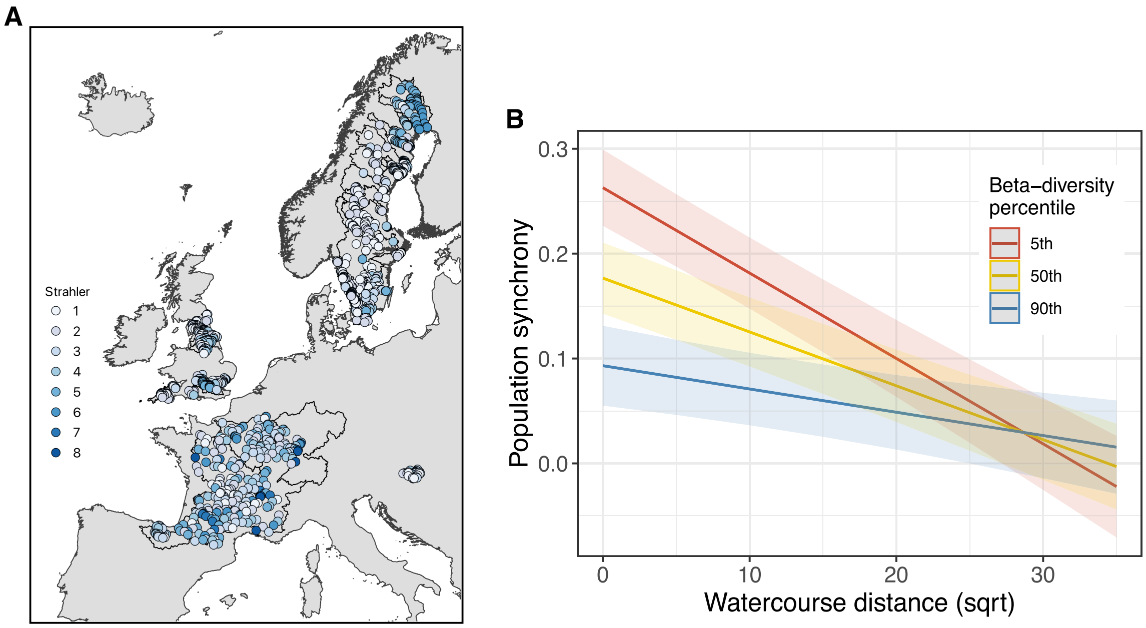

Fig. 2. A) Map of the stream sites included in the study; color intensity is proportional to the stream Strahler order. B) Prediction from the multimembership random-effects model showing population synchrony as a function of watercourse distance and beta-diversity (Bray–Curtis dissimilarity) between communities. Fits are shown for the 5th, 50th, and 90th percentiles of beta-diversity values.

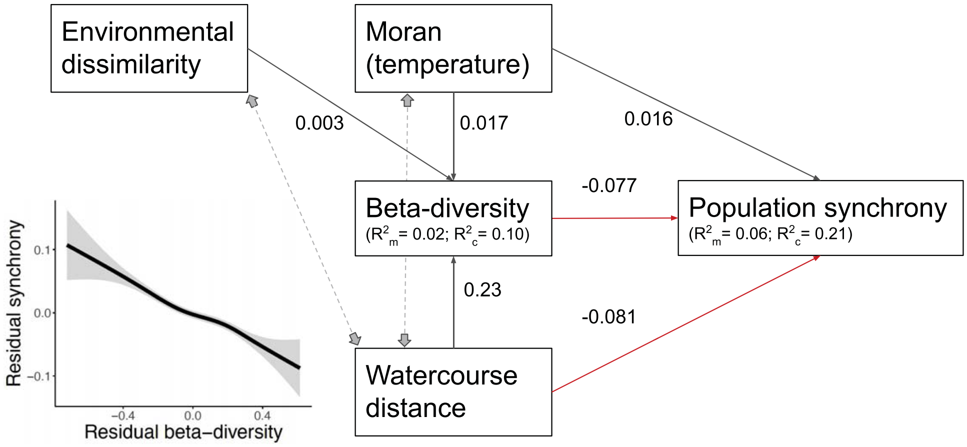

Fig. 3. SEM diagram showing standardized path coefficients. Marginal and conditional effect sizes are shown for beta-diversity and synchrony. Inset shows the relationship between population synchrony and beta-diversity after accounting for the effect of the other variables. Dashed double-arrow lines indicate the inclusion of correlated errors between variables.

stability. Across a wide latitudinal gradient and multiple river types, beta-diversity appeared to reduce the spatial synchrony in the abundance of fish populations within river networks, with effects independent from spatial separation and environmental dynamics (Moran forcing and key abiotic characteristics). This suggests that compositional dissimilarity not only provides spatial insurance for aggregate community properties (i.e. communities with different species are likely to respond differently to environmental changes), but may reflect an additional dimension of biotic heterogeneity that influences population dynamics. The results are noteworthy as the relationship between beta-diversity and population dynamics is less direct than between the portfolio effect regulating spatial synchrony in aggregate metrics at the metacommunity scale (24, 35). This opens the possibility that the desynchronizing effect of beta-diversity on aggregate community metrics—as observed in previous studies—may in part reflect overlooked responses at the population level. We recognize that estimates of population synchrony are conceptually linked to beta-diversity to the extent that the number of pairwise synchrony values included in the analyses reflects the number of species shared between locations (i.e. when beta-diversity = 1, no species are shared between locations and no population synchrony is obtained). However, the number of population synchrony values does not—per se—influence the degree of pairwise synchrony. Similarly, the extent to which beta-diversity reflects the number of shared species depends on the overall species richness of the communities. In Fig. S2, we demonstrate that our results are robust to differences in species richness using beta-diversity estimates based on null-model procedures. The need to include compositional variability in the assessment of metacommunity stability is clear, particularly with respect to both aggregate and compositional variability through time at local and regional scales (35). Past efforts have focused on temporal changes in beta-diversity and aggregate variability and not considered relationships with spatial population synchrony as we do here. However, a recent study across multiple taxonomic groups (36) indicated that spatial compositional synchrony (i.e. spatially coherent compositional trajectory across locations) appears generally limited by beta-diversity, supporting to the notion that spatial population dynamics are influenced by compositional heterogeneity at regional scales.

In addition, Walter et al. (23) highlighted how spatial synchrony in species richness is a common phenomenon across ecosystems, tightly linked to biomass stability. Their work discussed how richness synchrony necessarily emerges from local population extinction and colonization dynamics and hence may be regulated by the same mechanisms underpinning population synchrony, including dispersal, Moran effect, and biotic interactions. Furthemore, although beta-diversity had limited effects on richness synchrony, Walter et al. (23) observed that the replacement component—the actual turnover of species between communities—had a negative effect on synchrony. The results presented here also indicate that the turnover of species among locations reduces population synchrony more effectively than richness differences. Whether this reflects differences in the range of biotic interactions, the degree of interspecific competition or density-dependent processes regulating separated populations, is ripe for additional, preferably experimental, investigation.

Future work should investigate the extent to which the findings of this study are generalizable to other systems. River networks are characterized by a unique dendritic geometry that promotes spatial patterns of synchrony linked to flow direction, degree of network branching, and dispersal directionality (37–39). Low-order, headwater reaches are typically highly heterogeneous across the basin and appear to contribute the most to maintain asynchrony among populations (40, 41). Whether and under which circumstances the influence of beta-diversity on metapopulation dynamics may in part reflect the contribution of headwater streams and the geometry of the riverscape (42, 43) deserves further attention.

Although the causes and consequences of ecological synchrony have been investigated for decades (1, 3, 44), empirical assessments at large spatial and temporal scales have emerged only in recent years as datasets became available (14, 34). These assessments have shown, for instance, how examining spatial patterns (geography) of synchrony (40, 45), species life-history traits (6, 10), and large-scale climate drivers (4, 7) can inform on the potential mechanisms underpinning population synchrony. Nonetheless, the inferences that can be made are inherently limited from survey data. To our knowledge, a clear link between metacommunity beta-diversity and spatial population synchrony in an extensive abundance time-series dataset has not been presented so far.

Many of the conservation challenges facing society necessitate broadening our science from understanding individual species loss to anticipating multifaceted changes to biodiversity (Socolar et al. (26)). As ecosystems are facing substantial changes in biodiversity, the ecological implications of local reduction in species richness and changes in composition have been widely documented (46–49). Yet, erosion of biodiversity at regional and catchment scales generally occurs through biotic homogenization, that is, a reduction in spatial beta-diversity. Although ongoing homogenization has been observed across multiple taxonomic groups (50), the consequences for ecosystems are only recently being investigated, highlighting the implications for ecological stability (e.g. 24). Our findings add worrying evidence that the deterioration of beta-diversity through the process of biotic homogenization can also influence metapopulation dynamics and affect local species persistence.

Data and methods

Biotic and environmental data

We gathered long-term (>10 years) fish populations time series for 61 basins across Sweden, the UK, France, Spain, and Hungary—providing the most continuous and consistent data series—from the RivFishTIME database (51). Sampling occurred during low flows and standard protocols were maintained through time. We included basins with at least eight sites (i.e. stream reaches; range = 8–63) and two species (range = 2–27 species/basin). In addition, to limit the influence of zeros and low means when estimating synchrony, only species occurring in more than 80% of sampling events were included for a total of 48 species (Table S2). Overall, more than 34,000 pairs of fish population time series across 1,180 sites were included in the analyses (see 40).

Environmental data included yearly time series of mean air temperature and streamflow for each river reach. Monthly minimum and maximum air temperatures at ~4 km in NetCDF format were derived from the global monthly climate dataset TerraClimate (52). We computed annual means of minimum and maximum monthly values and then calculated the mean of those values to get the annual mean air temperature for every site. The mean annual streamflow data were derived directly from FLO1K (53), which is available at 1-km spatial resolution.

We used R packages `ncdf4` (54), `sp` (55), and `raster` (56). Strahler order and elevation were also gathered for each stream reach from HydroATLAS (57).

Statistical modeling

Synchrony between the abundance of population pairs within the same basin was expressed as Spearman's correlation through time (40). Geographic distance between populations was calculated based on hydrologic (watercourse) distance from HydroRIVERS (58), as this is more relevant to fish dispersal than Euclidean distances. The mean compositional dissimilarity between communities was estimated using Bray–Curtis distances between communities using the time-averaged species abundances. Overall beta-diversity was also decomposed into the replacement (turnover) and richness-difference (nestedness) components following the framework implemented in the BAT package (59).

To estimate the contribution of coherent environmental dynamics to spatial synchrony (Moran effect), we calculated spatial synchrony between reaches in monthly air temperature and streamflow (both maximum and mean) using Spearman's correlations. Preliminary analysis indicated that population synchrony was influenced by temperature synchrony (lme model, $P < 0.001$), but not by streamflow metrics ($P > 0.1$). Therefore, we subsequently included only temperature synchrony as a proxy for climatic Moran driver.

To quantify dissimilarity between stream reaches in local conditions (i.e. environmental distance), we calculated the Euclidean distance matrix based on mean annual air temperature, mean annual streamflow, elevation, and river Strahler order, all centered and scaled to mean = 0 and sd = 1, to make them comparable in their contributions to the overall Euclidean distance metric.

We used a combination of analytical approaches to provide multiple lines of evidence for the effect of community dissimilarity on spatial population synchrony. First, we used a multiple membership random-effects approach implemented in `lmerMultiMember` (60) to model pairwise population synchrony as a function of watercourse distance, mean compositional dissimilarity (or beta-diversity) between communities (Bray–Curtis distance), environmental distance, and Moran driver (synchrony in mean air temperature). This analytic framework thus accounted for all the key synchrony mechanisms within a coherent pairwise analytical framework. The multiple membership model allowed including site pairs as random components as this is a peculiar feature of pairwise data whereby a given site belongs to multiple pairs. In addition, we included basin and species identity as random components. Model selection based on AIC was then used to identify the most supported and parsimonious model. Similarly, additional models were developed to compare the contribution of species-replacement and richness-difference components of beta-diversity (59). Predictor variables were centered and scaled before analysis.

To specifically test whether compositional dissimilarity promoted population asynchrony while controlling for other covarying factors, we developed a null-model procedure. Specifically, we randomized the Bray–Curtis beta-diversity values (999 times) within basins, while maintaining the population synchrony estimates and watercourse distances. This procedure broke the association between beta-diversity and population synchrony within each basin but preserved the overall data structure, spatial distance, number of population pairs, and species richness. We thus obtained a null distribution of spatial synchrony values within basins decoupled from community beta-diversity. Using multiple membership random-effects models, we then extracted the intercept of synchrony decay with distance for low and high beta-diversity as represented by the first and third quantiles of Bray–Curtis distance, respectively. This generated the null distribution of expected model intercept for low and high beta-diversity, which we then compared with the observed (i.e. nonrandomized) values.

For both low and high beta-diversity quantile groups, difference between observed and expected (null) intercept values for synchrony-decay models was expressed as z-scores:

$$z - score = [observed - mean(null)]/sd(null),$$

with $|\text{z-score}| > 1.96$ indicating significance deviation from null expectations.

Third, we used SEMs based on local estimation (package `piecewiseSEM`) to better characterize the complex relationships between the predictor and response variables. Piecewise SEM allows for flexibility in evaluating each response path individually and then developing the overall interaction structure. We considered this necessary as both population synchrony and communities beta-diversity are expected to show different degrees of codependence with Moran driver, spatial, and environmental distance across river networks, which need to be accounted for. Specifically we modeled population synchrony as a function of Moran driver (temperature), watercourse distance, and communities beta-diversity, while separately modeling beta-diversity as a function of environmental distance and watercourse distance. An initial test of direct separation indicated that the Moran driver also had a direct influence on beta-diversity, which we then included in the model. Test of direct separation (`dSep` function) was used to evaluate whether important paths were overlooked in the model structure, and the global Fisher test (C-statistics) was used to assess the overall SEM fit. Linear mixed-effect models were used to build the SEM, with basin identity included as a random factor when modeling beta-diversity, and both basin and species as random factors in the population synchrony model.

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Supplementary Material

Supplementary material is available at PNAS Nexus online.

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Author Contributions

Stefano Larsen (Conceptualization, Formal Analysis, Writing—original draft), Lise Comte (Conceptualization, Data curation, Funding acquisition, Writing—review & editing), Xingli Giam (Data curation, Investigation, Writing—review & editing), Katie Irving (Formal Analysis, Writing—review & editing), Pablo A. Tedesco (Conceptualization, Writing—review & editing), and Julian D. Olden (Conceptualization, Data curation, Funding acquisition, Writing—review & editing).

Data Availability

All data used to generate the analysis and plots presented in this work are available in the Dryad repository (10.5061/dryad.n2z34tn6x). Raw species abundance time series are available in Comte et al. 2021 (51). Data were analyzed in R. All codes are provided in GitHub (https://github.com/stefanolarsen/Synchrony_Betadiversity).

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