






RESEARCH ARTICLE

Climatic effects on the synchrony and stability of temperate headwater invertebrates over four decades

Stefano Larsen¹  | Fiona Joyce² | Ian P. Vaughan²  | Isabelle Durance²  | Jonathan A. Walter^{3,4}  | Steve J. Ormerod² 

¹Research and Innovation Centre, Fondazione Edmund Mach, San Michele all' Adige, Italy

²Water Research Institute, Cardiff School of Biosciences, Cardiff University, Cardiff, UK

³Center for Watershed Sciences, University of California, Davis, California, USA

⁴Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia, USA

Correspondence

Stefano Larsen, Research and Innovation Centre, Fondazione Edmund Mach, via E. Mach 1, San Michele all' Adige 38010, Italy.

Email: stefano.larsen@fmach.it

Funding information

Esmee Fairbairn Foundation; Natural Environment Research Council, Grant/Award Number: NE/J014818/1; Seventh Framework Programme, Grant/Award Number: 603378

Abstract

Important clues about the ecological effects of climate change can arise from understanding the influence of other Earth-system processes on ecosystem dynamics but few studies span the inter-decadal timescales required. We, therefore, examined how variation in annual weather patterns associated with the North Atlantic Oscillation (NAO) over four decades was linked to synchrony and stability in a metacommunity of stream invertebrates across multiple, contrasting headwaters in central Wales (UK). Prolonged warmer and wetter conditions during positive NAO winters appeared to synchronize variations in population and community composition among and within streams thereby reducing stability across levels of ecological organization. This climatically mediated synchronization occurred in all streams irrespective of acid–base status and land use, but was weaker where invertebrate communities were more functionally diverse. Wavelet linear models indicated that variation in the NAO explained up to 50% of overall synchrony in species abundances at a timescale of 4–6 years. The NAO appeared to affect ecological dynamics through local variations in temperature, precipitation and discharge, but increasing hydrochemical variability within sites during wetter winters might have contributed. Our findings illustrate how large-scale climatic fluctuations generated over the North Atlantic can affect population persistence and dynamics in inland freshwater ecosystems in ways that transcend local catchment character. Protecting and restoring functional diversity in stream communities might increase their stability against warmer, wetter conditions that are analogues of ongoing climate change. Catchment management could also dampen impacts and provide options for climate change adaptation.

KEYWORDS

benthic invertebrates, ecological synchrony, metacommunity, North Atlantic Oscillation, Wales

1 | INTRODUCTION

Streams and rivers are affected profoundly by climate through variations in global heat budgets, atmospheric temperature and precipitation (Durance & Ormerod, 2007; Tonkin et al., 2019; Woodward

et al., 2016). Effects include changes in water temperatures that track those in the atmosphere, variations in discharge, and variations in solute or pollutant concentrations that reflect dilution or mobilization under different flows (Ruhi et al., 2018; Vaughan & Gotelli, 2019). The solubility of important gasses such as oxygen and carbon dioxide also

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. *Global Change Biology* published by John Wiley & Sons Ltd.

changes with temperature, while basic ecological processes such as production, decomposition and respiration respond to both warming and changing flow (Lauerwald et al., 2015; Verberk & Bilton, 2013). Climatic effects on freshwater communities include changes in geographical distribution, variations in population size and effects on emergent properties such as community stability (Colombano et al., 2022; Knouft & Ficklin, 2017; Markovic et al., 2014). However, the exact processes that link ecological dynamics to climatic variability are challenging to identify over the inter-decadal timescales involved, in particular where they interact with local catchment character.

As well as progressive global warming, stream ecosystems respond to climatic variations linked to large-scale phenomena such as the El Niño–Southern Oscillation (ENSO), the North Atlantic Oscillation (NAO) and the position of the Jet Stream. Among these, the NAO has extensive effects around the North Atlantic reflecting cyclical variations in atmospheric pressure between the Azores and Iceland with an approximate periodicity of 6–8 years (Hurrell, 1995; Stenseth et al., 2003). In western Europe, positive and negative phases of the winter NAO respectively bring either mild, wet and stormy winters or cold, dry and calm winters as oceanic westerlies give way to northerly air masses of continental origin (Visbeck et al., 2001). These contrasting conditions affect both temperature and discharge in European rivers and are sufficient to influence the growth, persistence, and phenology of stream organisms (Briers et al., 2004; Durance & Ormerod, 2007; Elliott et al., 2000). Potential effects on stream invertebrate communities first attracted interest in the late 1980s (Weatherley & Ormerod, 1990). NAO signals were subsequently identified in community resilience, variations in invertebrate abundance and even local species extirpation (Bradley & Ormerod, 2001; Durance & Ormerod, 2007, 2010).

As well as being intrinsically important in ecosystem processes, the NAO offers a valuable proxy of overall climate conditions over areas surrounding the north Atlantic as a synoptic 'package of weather' that could predict population or ecosystem dynamics (Stenseth et al., 2003). Potentially even more important, variations in the NAO provide an analog of developing climate-change effects over western Europe, and in particular an ongoing shift toward warmer, wetter winters combined with hotter, drier summers (Otttersen et al., 2001; Visbeck et al., 2001). The NAO could thus offer an opportunity within manageable timescales to assess the extent to which climatic conditions affect ecological dynamics in stream ecosystems at regional scales in ways that transcend more local, catchment-scale variations. Important clues about climate-change impacts over longer timescales would result.

One of the possible approaches to assessing the effects of regional climatic effects on stream organisms is through patterns of synchrony in population and community dynamics (Post & Forchhammer, 2002). Synchronized dynamics have been detected increasingly across ecosystems, taxonomic groups and levels of organization (Liebhold et al., 2004; Valencia et al., 2020; Wilcox et al., 2017). For example, coherent temporal fluctuations in the abundance of spatially separated populations (spatial synchrony) are considered a fundamental property of metapopulations but could also increase local extinction

risk by lowering the chance of demographic rescue (Heino et al., 1997; Yeakel et al., 2014). Spatial synchrony also enhances variance in species abundances, for example among pests (Peltonen et al., 2002; Vindstad et al., 2019; Walter et al., 2020) and diseases (Moustakas et al., 2018; Viboud et al., 2006). Synchronous variations can also link spatiotemporal patterns in dispersal, richness and diversity, all of which can have larger effects on ecosystem stability than richness alone (Lande et al., 1999; Moran, 1953; Walter et al., 2021). As well as having spatial dimensions, correlated dynamics in the abundances of multiple species within single locations can give rise to community synchrony as species respond coherently to environmental drivers. In contrast, more stable communities are maintained where species fluctuate independently or covary negatively through compensatory dynamics which maintain total abundance or biomass (Loreau & de Mazancourt, 2008; Wang et al., 2019). Independent or compensatory dynamics are more likely among species differing in their functional traits, in turn engendering increased temporal stability in functionally diverse communities (de Bello et al., 2021; Wayne Polley et al., 2020).

While the integration of spatial and community synchrony within a unified framework has provided insight into metacommunity dynamics and stability (Lamy et al., 2021; Wang et al., 2019; Wilcox et al., 2017), less is known about the synchronizing effects of environmental and climate changes through time. This is despite the well-recognized effects of climate change on population dynamics and evidence for the synchronizing effect of other environmental drivers (Bogdziewicz et al., 2021; Grenfell et al., 1998). Changes in the mean, extreme, and variability of climate under global warming are all likely to influence spatial and community synchrony, but the extent and direction of these effects are unclear (Post & Forchhammer, 2002). For example, increasing synchrony in vertebrate populations at continental scales in the northern hemisphere has been linked to recent climate trends and spatial autocorrelation in temperature (Black et al., 2018; Koenig & Liebhold, 2016; Post & Forchhammer, 2004). However, the extent to which climate variation affects synchrony and stability in metapopulations and metacommunities, particularly in freshwater ecosystems at local or catchment scales, is poorly understood.

Among freshwater organisms, invertebrates are an ideal group for appraising the effects of climatic variation on metacommunity dynamics. First, as ectothermic organisms with relatively short generation times, their communities respond rapidly to changes in temperature, flow regime and dissolved oxygen (Vaughan & Gotelli, 2019). Second, they are taxonomically and functionally diverse, allowing tests of hypotheses about diversity–stability relationships across communities that are well-characterized over large areas of the world. Finally, along with many freshwater organisms, they are at risk from a range of habitat impairments (Haase et al., 2023; Tickner et al., 2020). Effort to understand how climate variation may affect synchrony and stability in these systems is clearly needed, but consistent long-term observations are still scarce, especially from remote catchments where other global change effects are limited.

In this paper, we quantify spatial population synchrony as well as community synchrony and stability among stream invertebrates using a globally unique dataset where their abundances have been monitored consistently for four decades in a spatially replicated set of headwaters.

We focus on a set of 10 streams from the Llyn Brianne Stream Observatory in central Wales (UK), a long-term ecological research (LTER) site where the influence of the NAO on regional and local dynamics was first documented over 20 years ago (Bradley & Ormerod, 2001), and where other influences on taxonomic and functional diversity are well-understood from over 40 years of research (Durance & Ormerod, 2007; Larsen et al., 2018; Ormerod & Durance, 2009).

Based on our previous observation and knowledge of the effects on the NAO in Western Europe, we hypothesized that

- (i) positive phases of the NAO would bring increased precipitation and temperature to the Llyn Brianne catchments.
- (ii) prolonged positive NAO phases with warmer, wetter winters would bring more coherent dynamics across species and locations, thus increasing synchrony and reducing inter-annual stability in invertebrate populations and communities across the Llyn Brianne streams.
- (iii) streams or time periods with greater functional diversity would buffer communities against the synchronizing effects of the NAO. This is because communities supporting a range of functional traits are more likely to have internal community dynamics that are resilient to environmental variation (Feio et al., 2015).

2 | METHODS

2.1 | Study area

The headwaters that form the Llyn Brianne Stream Observatory (Figure 1) were first sampled in 1981 thus initiating one of the world's longest running investigations of global change effects on stream

ecosystems (Stoner et al., 1984). Established initially to investigate the combined role of land use and acid rain in surface water acidification and recovery (Ormerod & Durance, 2009), long-term data collection has since revealed climatic influences on stream community dynamics as well as possible strategies for climate change adaptation (Durance & Ormerod, 2007, 2010; Pye et al., 2022). As a result, the study area has been described extensively. In outline, the Observatory is situated in Central Wales (UK) on the maritime north-western fringes of Europe (52°8'N 3°45'W) where 14–16 second-third order streams drain catchments of 15–253 Ha at altitudes of 215–410 m above sea level spread over approximately 300 km² in the upland reaches of the Afon Tywi. As well as variations in local land cover ranging from native deciduous woodlands and plantation forestry to open sheep-walk, the streams vary in acid base status in part reflecting historical acid deposition over base-poor rocks and soils, and in part reflecting local geological variations where calcite veins running through Ordovician shales and mudstones increase concentrations of base cations (Weatherley & Ormerod, 1987). From this broader array, streams with the longest and most complete runs of data were selected for analysis, respectively: (i) 'acid forest': conifer plantations of Sitka spruce *Picea sitchensis* and lodgepole pine *Pinus contorta* (LI1, LI2, LI4, and LI8 < 10–12 mg/L CaCO₃); (ii) sheep-grazed 'acid moorland' (CI1, CI2, CI4, CI5 < 10–12 mg L⁻¹ CaCO₃) or (iii) 'circumneutral moorland' (LI6, LI7; 15–19 mg/L CaCO₃). These catchment types are representative of larger areas of Wales, reflected also in consistent ecological responses to declining acid deposition between Llyn Brianne and other Welsh headwaters (Carr et al., unpubl. data). The regional climate is temperate with mean monthly stream temperatures within the range 0.5–16°C and mean precipitation of 1900 mm/year. The streams are dominantly perennial despite inter-annual variations in discharge of around 350%.

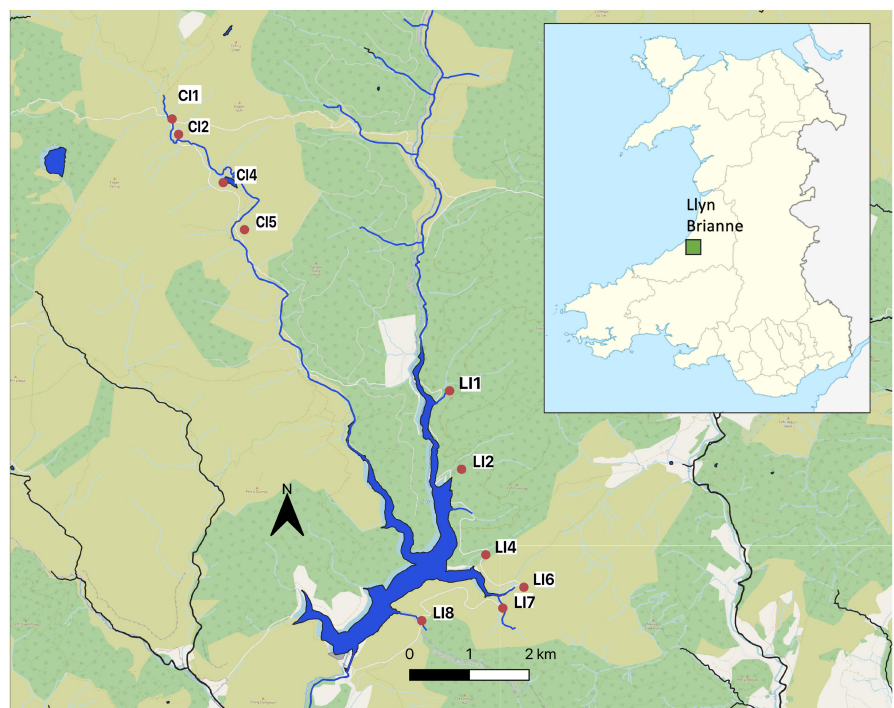


FIGURE 1 Map of the Llyn Brianne Reservoir in mid-Wales (inset) and the 10 streams included in the study. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

2.2 | Invertebrate sampling

Macroinvertebrates were first sampled from selected streams at Llyn Brienne in 1981, but more consistently from 1985 onwards in all years except 1991 when there was a funding hiatus. Data for 1994 (LI6, LI7, LI8), 2009 (CI2, CI4, LI4), and 2011 (CI2, CI4, LI4, LI8) were incomplete for the indicated streams. Data for this paper came from 1985 to 2018 and involved a quality-assured and standardized procedure involving kick-sampling for 3-min duration (Freshwater Biological Association handnet 0.9 mm mesh size) aggregated between marginal (1 min) and riffle habitats (2 min). This approach has been validated directly, and also has proven reliable in detecting differences in abundance and composition among streams and years (Bradley & Ormerod, 2002). Samples were collected in April each year. Invertebrates were preserved on-site in 70% ethanol prior to subsequent sorting and identification to species (~70% of taxa) except for Diptera, Oligochaetes and some Coleoptera. We used keys published by the Freshwater Biological Association and maintained taxonomic consistency throughout all years of the study. Further details are provided in previous papers (Bradley & Ormerod, 2001; Durance & Ormerod, 2007; Ormerod & Durance, 2009; Weatherley & Ormerod, 1990).

2.3 | Physico-chemistry

Chemical data were first collected from the streams at Llyn Brienne in 1981–1982 (Stoner et al., 1984), and water samples have since been collected at weekly–monthly intervals and analysed using accredited methods in the laboratories of Natural Resources Wales. The exact length of the data runs varied across sites such that LI1, LI2, LI8, and LI6 have been sampled since 1981 while sampling at the other sites began in 1984. Briefly, pH was measured on samples returned to the laboratory by combination glass electrode while cations were measured using atomic absorption spectrophotometry after acidification and filtration at 0.45 μm and anions using colorimetry (see Weatherley & Ormerod, 1987). Determinands included pH, conductivity, total oxidized nitrogen, hardness, alkalinity, and concentration of multiple ions including Cl^- , Na^+ , K^+ , Mg^{++} , Ca^{++} , Al^{3+} and other metals. Mean winter values (October–March, i.e., before macroinvertebrate sampling) were derived for each year and included in subsequent analyses.

A principal components analysis (PCA) based on correlation was used to extract the main axes of spatiotemporal variability in hydrochemical data across streams. Six streams offered the most complete data series (LI1, LI4, LI5, LI6, CI2, CI4). These were included in a PCA and the first principal component (PC) was used to assign a synthetic score to each year and stream. Scores were then used to calculate spatial synchrony between streams and temporal variance within stream.

2.4 | NAO and climate data

Our climate variables comprised the winter NAO index (December–March inclusive), mean daily winter rainfall, mean winter discharge,

and mean winter air temperature for the region, each calculated from October–March prior to spring macroinvertebrate sampling. NAO data were obtained from the National Centre for Atmospheric Research after Hurrell (1995). This NAO model was chosen for consistency with previous studies (e.g., Bradley & Ormerod, 2001; Ottersen et al., 2001) and the proven correlation with weather and stream variables in UK (Ness et al., 2004). Moreover, we considered the modes of the NAO a stronger potential analog of future climate change effects on winter weather patterns than other Atlantic weather systems such as the East Atlantic or Scandinavian patterns.

Rainfall and air temperature data were derived from Met Office HadUK-Grid datasets (Hollis et al., 2019). For these, HadUK-grid data for the UK (1980 to 2019) were obtained at the highest available temporal resolution—daily rainfall and monthly temperature—at 5 km grid spatial resolution. The 10 study streams fell within three spatial grids.

Climate data for each grid within which streams were located were subsequently extracted using *ncdf4* (Pierce, 2019), *raster* (Hijmans, 2020) and *rgdal* (Bivand et al., 2023) packages in R. Discharge data at 15-min intervals (April 1996 to June 2020) were available from Natural Resources Wales (NRW, 2020) from the flume at LI1 within the Llyn Brienne Observatory. Values were standardized by dividing by catchment area (km^2) above the LI1 monitoring station. To confirm that the available environmental data from Llyn Brienne were representative of local conditions, cross-checks were performed against nearby rain gauge, air temperature, and discharge gauging sites, located between 11 and 40 km from the study area ($R \geq .9$; Table S1 and Table S2). In addition, during the 1980s, discharge and temperature were measured continuously in the majority of the Llyn Brienne streams (15-min intervals), providing confidence in the representativeness of our longer-term data (Edwards et al., 1990).

The influence of the NAO on local rainfall and temperature was quantified using a linear mixed-effect model including stream identity as random effect (using the R function `nlme::lme`).

2.5 | Synchrony analysis

Our data analysis involved two aspects respectively involving synchrony among locations (spatial synchrony) and synchrony among species' populations within locations (community synchrony).

2.5.1 | Spatial synchrony

Only species occurring in more than five streams and observed in more than seven individual years were included in the analyses to reduce the chance effects of scarcer species on detectable patterns. In order to have a complete biological data series for the analyses, we imputed any missing abundance data for each species using a simple moving average with a 4-year window expanding before and after the missing year. Imputation of the few missing

data did not affect the estimates of population synchrony ($R^2 = .96$; correlation between original and imputed synchrony values). For each species, spatial synchrony was expressed as the Spearman correlation in abundance between each pair of streams (e.g., Larsen et al., 2021). We also calculated spatial synchrony in overall community abundance across each stream (Walter et al., 2021). In order to examine temporal changes in spatial synchrony of population and community abundance, synchrony values were also calculated using a 6-year moving window which provided a good compromise between individual series length and number of windows while also matching the longest periodicity in the NAO over the 6–8 year timescale (see Results and Stenseth et al., 2003). In the analyses, we limited the overlap of time windows by excluding every second window (hence, $N = 15$). Autoregressive first-order generalized least square (gls) models (`cor = corAR1`) were used to account for serial non-independence of time-series data. When necessary, multiple observations per stream were accounted for using mixed effect models with stream identity as random factor (`nlme::lme` function).

To assess how different NAO phases influenced the decay in population synchrony with spatial distance, we modelled mean population synchrony as a function of Euclidean geographic distance between streams. We separated observations over five quantiles of increasing NAO values (with equal number of observations), which were included as a random factor in a linear mixed model. This also allowed us to estimate whether the NAO affected the mean synchrony (i.e., random intercept) and/or also the rate of decay with distance across locations (random slope).

2.5.2 | Community synchrony and variability

We next calculated variability (as coefficient of variation, CV) and community (inter-specific) synchrony across levels of organization (population, metapopulations, community, metacommunity) following the hierarchical decomposition approach and the associated R function (`var.partition`) of Wang et al. (2019); see also Erős et al. (2020). The specific mathematical definition for each hierarchical component is given in Wang et al. (2019) and additional conceptual diagrams are given in Erős et al. (2020) and Wilcox et al. (2017). Metrics used in this study are given below.

We define $X_{i,s(t)}$ the abundance of species i in stream s in year t , and use the subscripts P and C to represent ‘population-level’ and ‘community-level’, respectively, and the subscript R (regional) to define catchment scale variables (across the 10 streams in Llyn Brienne). At the local site scale, we calculated ‘population CV’ as the weighted average of local population abundance variability ($CV_{i,s}$) across species and streams:

$$\text{Population CV} = CV_{P,S} = \frac{\sum CV_{i,s} \times \mu_{i,s}}{\mu_{\Sigma\Sigma}}, \quad (1)$$

where $CV_{i,s} = \sqrt{V_{i,ss}} / \mu_{i,s}$, with $V_{i,ss}$ and $\mu_{i,s}$ being the temporal variance and mean of population abundances, respectively, while $\mu_{\Sigma\Sigma}$ is the

temporal mean of total metacommunity abundance (sum across species and streams).

Similarly, we calculated ‘metapopulation CV’ as the catchment scale (the 10 streams) weighted average of metapopulation abundance variability ($CV_{P,R}$):

$$\text{Metapopulation CV} = CV_{P,R} = \frac{\sum CV_{i,R} \times \mu_{i,\Sigma}}{\mu_{\Sigma\Sigma}}, \quad (2)$$

where $CV_{i,R} = \sqrt{V_{i,\Sigma}} / \mu_{i,\Sigma}$, with $V_{i,\Sigma}$ and $\mu_{i,\Sigma}$ being the temporal variance and mean of metapopulation abundances.

Finally, we define ‘metacommunity CV’, the variability of total metacommunity abundance of the species present across the 10 streams as:

$$\text{Metacommunity CV} = CV_{C,R} = \frac{\sqrt{V_{\Sigma\Sigma}}}{\mu_{\Sigma\Sigma}}, \quad (3)$$

where $\sqrt{V_{\Sigma\Sigma}}$ is the temporal variance in total metacommunity abundance across all streams.

We then defined local scale (within-stream, s) community synchrony as in Loreau and de Mazancourt (2008), but in a square-root version:

$$\text{Local community synchrony } (\varphi_s) = \frac{\sqrt{V_{\Sigma,ss}}}{\sum \sqrt{V_{i,ss}}}, \quad (4)$$

where $\sqrt{V_{\Sigma,ss}}$ is the temporal variance in community abundance, and the denominator is the sum of individual population variances.

Similarly, regional synchrony is defined as the synchrony among different metapopulation:

$$\text{Regional community synchrony } (\varphi_R) = \frac{\sqrt{V_{\Sigma\Sigma}}}{\sum \sqrt{V_{i,\Sigma}}}, \quad (5)$$

Community synchrony ranges between 0 (perfect asynchrony) to 1 (perfect synchrony), the latter indicating that all populations within a site, or all metapopulations within the region, are correlated through time. Measures of variability and synchrony were also calculated for each 6-years moving window as described above. An autoregressive function of order 1 was used to model the effect of NAO on measures of community synchrony and variability.

As well as assessing patterns for organisms, spatial synchrony and variance in stream hydrochemical data series were also calculated over the 6-year window, using the scores of streams over the first axis from the PCA as synthetic values reflecting overall water quality variables. Using the moving window approach, we examined whether higher synchrony or variability in hydrochemistry across streams was linked to positive NAO phases.

2.6 | Wavelet analyses

We used wavelet analyses—a method that identifies any periodic oscillations in time-series data—to examine the temporal scales of

climate variability and timescale-specific spatial synchrony in the stream invertebrate metacommunity. Specifically, wavelet transforms were used to decompose the temporal scales of variability in the winter NAO series, as well as winter air temperature for each site and for the discharge series from LI1. This allowed the visualization of similarities in the main scales of variability between NAO and the available environmental data.

To study the timescale specificity of spatial synchrony in the stream invertebrate community, we examined the wavelet phasor mean field of community abundance (Sheppard et al., 2016). The wavelet phasor mean field ranges from 0 to 1, with values of 1 indicating perfect phase alignment (synchrony) among a set of data series at a given time and timescale. Statistical significance was assessed by comparing empirical synchrony magnitudes to those of 10,000 sets of $n=10$ (for 10 streams used in the analyses) random phasors; empirical synchrony was considered statistically significant when it exceeded 95% of surrogates.

To further explore the extent and timescales at which winter NAO influenced spatial synchrony in community abundances, we used a wavelet linear model (Sheppard et al., 2019). Wavelet linear models are analogous to linear regression models but use the normalized wavelet transforms of predictor and response variables to quantify the degree to which spatial synchrony in the predictor variable(s) explain spatial synchrony in the response variable. In combination with the wavelet Moran theorem (Sheppard et al., 2016), wavelet linear models permit quantification of the fraction of synchrony in the response variable explained by predictors as a function of timescale, similar to the coefficient of determination (R^2) in linear regression analysis.

Before wavelet analyses, all data series were Box-Cox transformed to improve normality and standardized (demeaned, detrended, with unit variances). All wavelet analyses used the continuous complex Morlet wavelet transform. Wavelet analyses were performed in R using the 'wsyn' package (Reuman et al., 2021).

2.6.1 | Functional traits

To estimate community functional diversity, we gathered information on species affinity for multiple ecological and biological traits, including river zonation, temperature preference, feeding habits, body size, and locomotion (Table S3). These traits were selected based on availability, and because they reflect the sensitivity of the species to temperature and flow dynamics while also describing key ecological functions. Available trait information was obtained from the online database provided in www.freshwaterecology.info. The affinity of each species for each trait category was fuzzy coded and values were standardized between 0 and 1 to represent the relative preference of each taxon for the different trait categories (Chevenet et al., 1994). Trait information was available, on average, for about 70% of taxa, ranging from 80% (river zonation, feeding habits) to 40% (temperature preference). Most missing trait information was limited to taxa classified at the family or genus level.

Functional diversity, for each stream, year, and 6-year window, was expressed as Rao's quadratic entropy:

$$Q = \sum_i \sum_j d_{ij} p_i p_j.$$

Based on species relative abundances p and their functional distance d_{ij} calculated as the square root of Gower trait dissimilarity index. Two approaches were used with missing trait information when calculating functional distance between taxa. Missing values were either excluded, or substituted with the mean trait profile of the other taxa, as obtained from the `prep.fuzzy.var` function of the Ade4 R package. Qualitative similar results were obtained, and we present results based on the second approach.

Functional diversity was calculated using the `SYNCSA::rao.diversity` function in R.

To control for the potential influence of taxonomic richness on functional diversity, we also calculated *functional deviation* by shuffling the names of the species in the trait matrix (999 times), keeping the observed abundance distribution, thus deriving the expected mean functional diversity. Functional deviations were expressed as: (observed functional diversity)–(mean expected functional diversity).

The influence of local functional diversity on community synchrony and stability was modelled including stream identity as random effect.

3 | RESULTS

3.1 | NAO and local environmental conditions

As expected, the normalized wavelet transform of the winter NAO index displayed consistently strong variation over a timescale of 6–8 years, as well as a temporary strong signal at an approximate 3-year timescale after 2005 (Figure 2). The wavelet transform of monthly winter rain for an example stream (LI8) over the same period showed similar features, while winter discharge from LI1 showed a clear signal over the 6–8 year timescale. These analyses indicated clear similarity in the temporal variation of the NAO and local hydro-climatic condition in the catchment. As expected, positive NAO phases were accompanied by increasing mean winter rainfall (lme slope=0.37; $p<.001$) and air temperature (slope=0.40; $p<.001$) across the streams, as well as increasing variability (Figure 3).

Turning to relationships between the NAO and hydrochemical patterns, the first principal component (PC1) of hydrochemical data explained about 40% of the variation and reflected a strong gradient in acid–base status as expected from previous studies at Llyn Brianne (Figure S1). There was no evidence for greater spatial synchrony in scores on this PC across streams during positive NAO phases (slope=0.20; $p=.2$; Figure S2), but there was an increase in variance in PC1 scores within each stream (lme slope= $1.26 \pm 0.35E$; $p<.004$; Figure S3). In other words, streams across the Brianne catchments were not systematically more or less acidic during warmer, wetter NAO periods, but chemistry was more variable within streams during positive NAO phases.

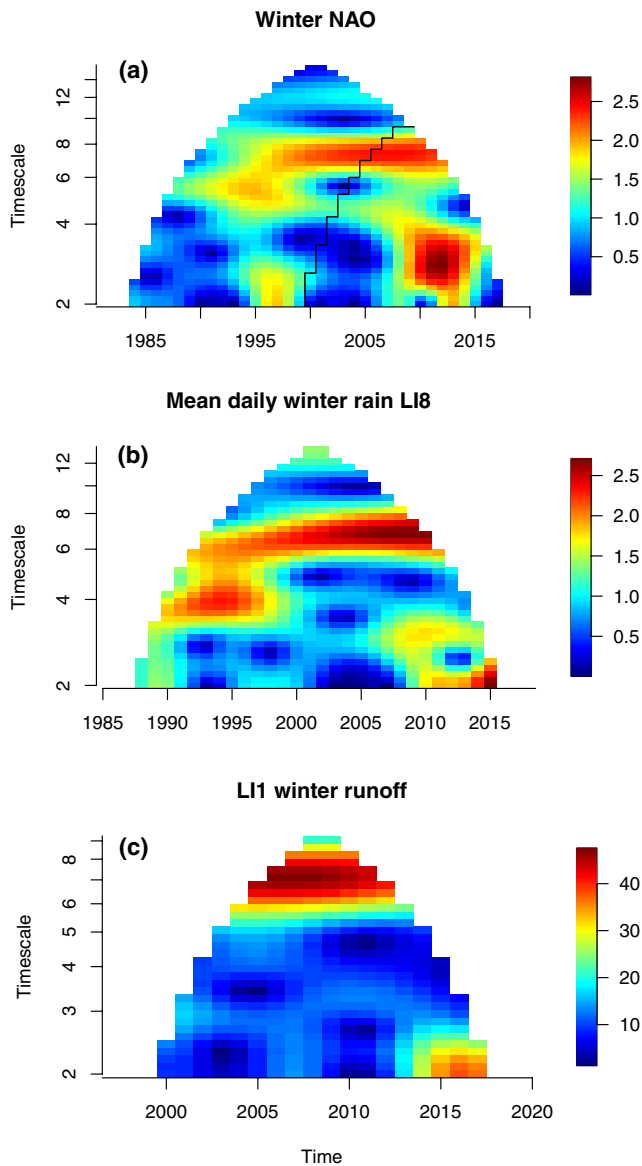


FIGURE 2 Wavelet transform of winter NAO (a), mean monthly rain at stream LI8 (b), and winter discharge at stream LI1 (c) revealing variations at comparable 6–8 years timescale and at shorter timescale between 2010 and 2015. These data come from the Llyn Brianne Stream Observatory in central Wales.

3.2 | NAO and spatial synchrony

Overall mean spatial synchrony in invertebrate populations among streams—calculated for 6-years moving windows—decayed with distance between them (Figure 4). This distance effect occurred across all phases of the NAO, but with far stronger overall synchrony when the NAO was more positive. This effect was clearly visible from the linear fits of population synchrony-decay for the five quantiles of increasing NAO values: a linear mixed effect model of decay in mean population synchrony including the NAO quantile groups as random components supported the inclusion of a random NAO intercept (slope = $-9.33e-06$; $p < .001$; AIC = -905), and to a lesser extent a random slope (AIC = -902). In other

words, positive NAO phases were accompanied by higher mean synchrony in population abundances but relatively similar decay with distance. Overall, the inclusion of a random NAO model was clearly supported over a model which ignored it (AIC = -810), indicating that the NAO had detectable effects on population spatial synchrony.

Irrespective of distance between streams, fluctuations in invertebrate abundance were more synchronous during positive NAO phases (Figure 5a), increasing by $\sim 100\%$ for each unit increase in average NAO values (gls model slope = 0.35 ± 01 SE; $p = .006$).

The wavelet model allowed us to quantify the extent and timescale with which the NAO apparently influenced synchrony in invertebrates abundance across streams (Figure 5b). The apparent effect of the NAO was evident over the 4–6 year timescale, with up to 50% of variation in abundance synchrony explained by the model. However, the wavelet phasor mean field of the observed spatial synchrony in abundance (Figure 5c) indicated that strong synchrony also occurred at shorter timescales, especially around the year 2000.

3.3 | NAO and community synchrony and variability

As well as apparently affecting the synchrony of invertebrate populations among streams, there were also strong relationships between NAO phases and community synchrony across levels of organization from streams to the whole Llyn Brianne region. In particular, community synchrony increased during positive NAO phases (Figure 6a), with effects strongest at the regional scale (Equation 5; gls model slope = 0.24 ± 0.07 SE; $p = .007$), and weaker at local stream scales (Equation 4; slope = 0.12 ± 0.05 SE; $p = .03$). Greater synchrony among species during positive NAO phases was associated with increasing variability in abundances, with trends significant at the metapopulation (Equation 2; weighted average of metapopulations CV; gls model slope = 0.29 ± 0.09 SE; $p = .007$) and metacommunity levels (Equation 3; CV of total metacommunity abundance; gls slope = 0.30 ± 0.08 SE; $p = .004$; Figure 6b). In other words, community synchrony increased instability during positive NAO phases, with effects particularly evident at the metacommunity level.

3.4 | The influence of community functional diversity

Stream-scale community synchrony declined significantly with increasing functional diversity (Figure 7; lme slope = -1.86 ; $p < .01$; $n = 150$). This trend was relatively consistent across streams except for CI2 and LI6, which display rather opposite patterns, but had narrow variation in values of functional diversity. The relationship between local population variability and functional diversity was

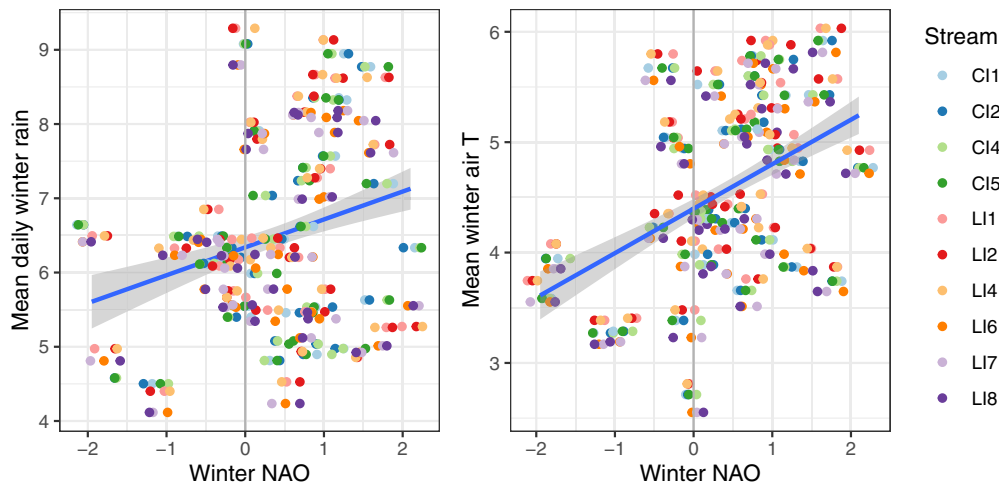


FIGURE 3 Mean daily rainfall (mm) and air temperature (°C) over sub-catchments from the Llyn Brianne Stream Observatory in relation to the winter index of the NAO. A small displacement has been added to reveal the position of each stream where values overlapped. Model fit and SE are shown.

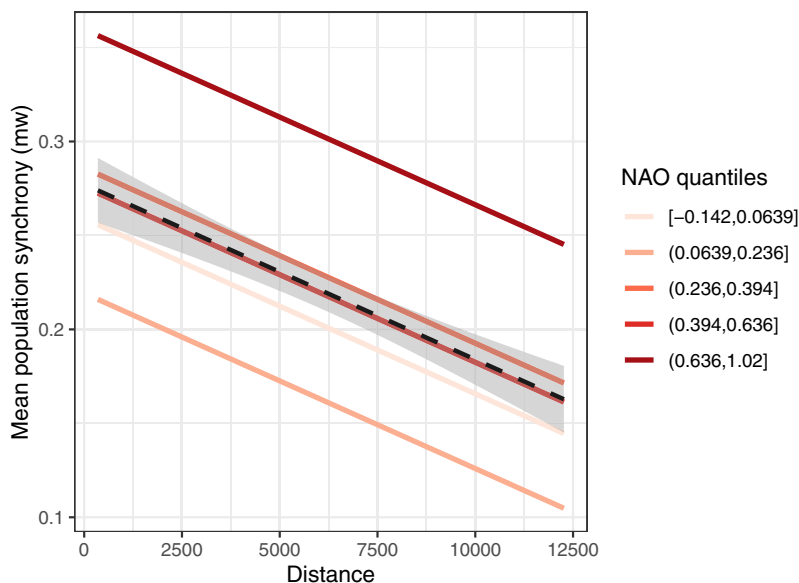


FIGURE 4 Population spatial synchrony with increasing distance (m) among the Llyn Brianne streams calculated from a moving window (mw) of 6 years. The colored lines illustrate model fits for different NAO quantiles as random intercept. Dashed line shows the fit (\pm SE) of the synchrony pattern for all NAO phases. Positive winter NAO phases were accompanied by greater population spatial synchrony across species' populations.

weaker (lme $p = .06$). The patterns were similar when functional deviation was used to control for the effect of taxonomic richness on functional diversity, albeit non-significant (Figure S4; $p = .09$).

4 | DISCUSSION

We aimed to test three hypotheses that (i) positive phases of the NAO would bring warmer, wetter conditions to the Llyn Brianne catchments—reflecting their maritime position in western Europe; (ii) prolonged warmer, wetter conditions induced by the NAO would increase population synchrony among species and locations, thus reducing inter-annual stability among Llyn Brianne's stream invertebrates; and (iii) streams or time periods with more functionally diverse communities would be buffered against the synchronizing effects of the NAO through internal community

dynamics that were more resilient to climatic variation. The first hypothesis was supported clearly by variations in rainfall and temperature that match the well-known effects of the NAO across Europe. Hypotheses (ii) and (iii) were also supported: first, synchrony and variability in population abundances increased markedly with each unit increase in the NAO index, with these effects scaling up also to affect community and regional metacommunity synchrony across the Llyn Brianne catchments. Second, synchrony declined at sites and times with the most functionally diverse communities. Our previous work at Llyn Brianne had hinted at some of these effects, and evidence has strengthened over the last four decades. Already by 1990, Weatherley and Ormerod (1990) had detected developing changes in the stability of invertebrate communities in the study streams but were unaware of the cause. Bradley and Ormerod (2001) subsequently linked inter-annual and region-wide variations in community composition and population

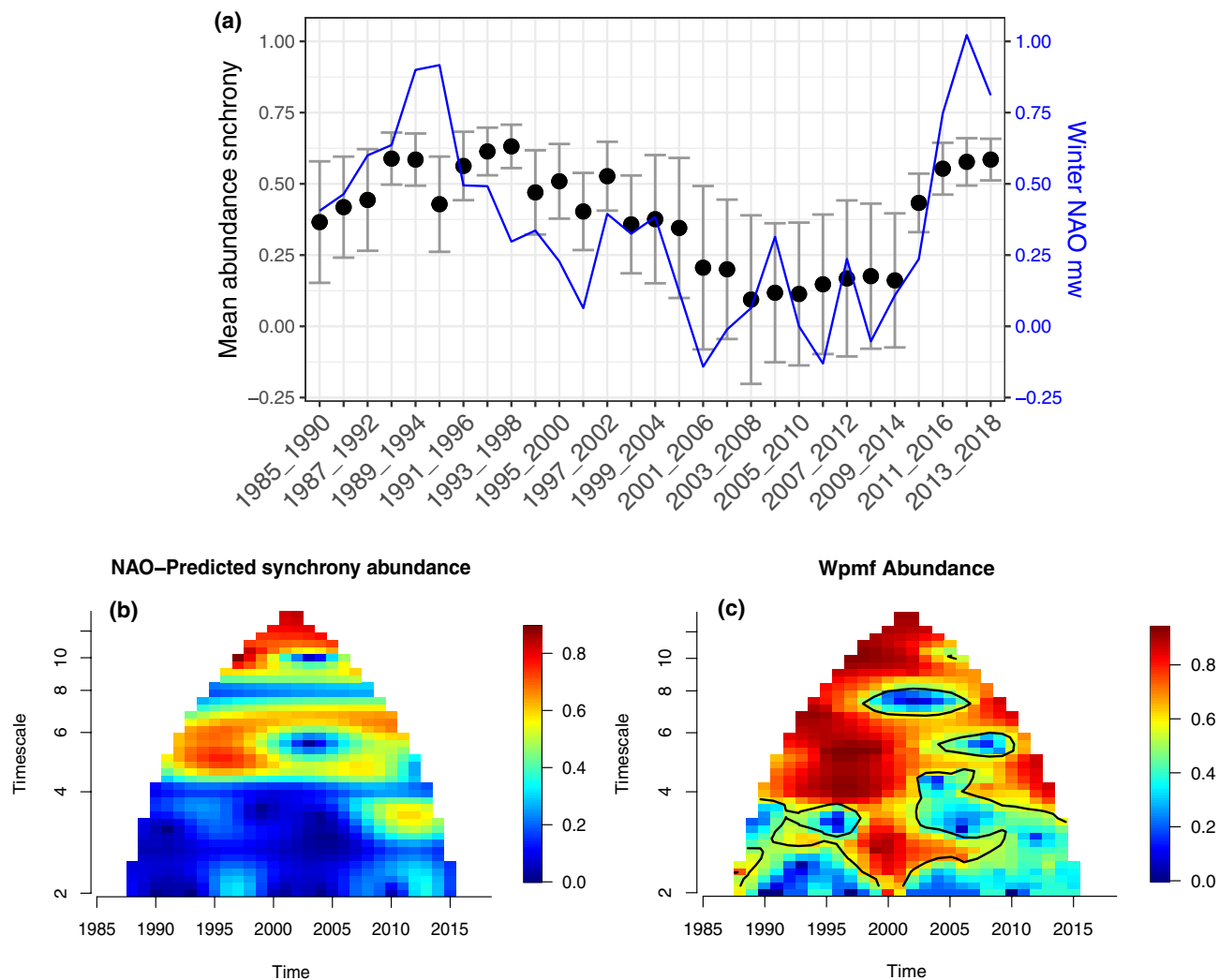


FIGURE 5 (a) Spatial synchrony in the overall (mean \pm variance) community abundance of invertebrates at the Llyn Brienne Stream Observatory plotted alongside values of the winter NAO over a moving window of 6 years during the study period; (b) Wavelet phasor mean field (Wpmf) of spatial synchrony in community abundances as predicted if the NAO was the only driver of synchrony. The plot indicates the time and timescale-specific spatial synchrony in abundance as predicted by the wavelet linear model using the NAO as the only predictor. Color ramp indicates magnitude of wavelet meanfield. (c) Wavelet phasor mean field of the observed spatial synchrony in community abundances. color ramp indicates magnitude of wavelet phasor mean field. Continuous contour black lines indicate significant synchrony based on random phasor.

abundance to the NAO, which also increased stream discharge locally. Durance and Ormerod (2007) then illustrated how climate change and positive phases of the NAO acted in concert to increase stream temperatures at Llyn Brienne, in turn driving down invertebrate abundances in circumneutral streams. Here, using a larger set of streams, we found that positive NAO phases were associated with increasing synchrony across streams, although effects on overall invertebrate abundance were less consistent among streams. Elsewhere in upland Britain, contemporaneous studies had linked the phenology of stream organisms and the NAO (Briers et al., 2004; Elliott et al., 2000). Our expanded data set from four decades confirms further that variations in atmospheric pressure systems and associated teleconnections over the North Atlantic combine with weather systems to influence stream ecosystem dynamics in maritime Britain. Moreover, the detection

of common NAO effects across replicate streams with contrasting chemistry and land use at Llyn Brienne reveals how region-wide climatic variation takes precedence over local factors in influencing important aspects of ecological variability. Not only do these effects in freshwaters augment established links between the NAO and the dynamics of European terrestrial and marine systems (Ottersen et al., 2001), they also provide the first evidence that NAO-induced climatic variations affect synchrony and stability in freshwater organisms across populations, communities and ultimately the regional metacommunity. Classical explanations on spatial ecological synchrony cite three likely mechanisms that involve (i) congruence between population dynamics linked to environmental factors such as temperature, rainfall; (ii) biotic interactions among species whose dynamics are synchronized and (iii) dispersal among populations (Liebhold et al., 2004). The role of

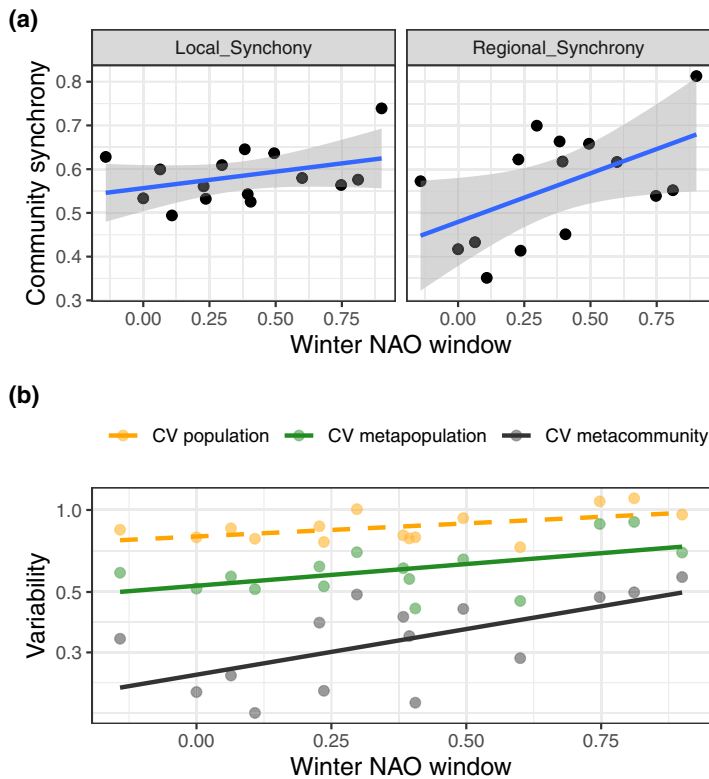


FIGURE 6 Community synchrony and variability across levels of organization as derived from the hierarchical community decomposition. (a) Mean community synchrony (i.e., inter-specific) at the local scale (synchrony among species in a stream averaged across each stream; see Equation 4) and regional scale (combining all populations; Equation 5) increased during positive NAO phases. (b) Community variability (as CV) also increases during positive NAO phases, with significant effect at the metapopulation (Equation 3) and metacommunity levels (Equation 4).

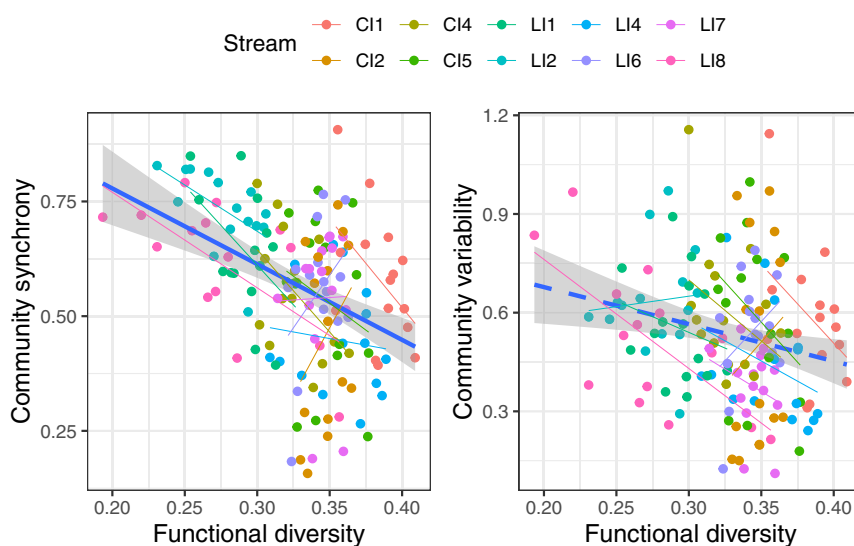


FIGURE 7 Patterns of local community synchrony and variability (for each stream and moving window) in relation to community functional diversity (as Rao index). Models indicate that higher functional diversity may limit synchrony and to a lesser extent variability.

the NAO in synchrony demonstrated here is consistent with these perspectives, but in reality, all of these effects could interact, and we cannot separate them. We expand on these points below.

Among the NAO effects recorded during our long-term study, those related to stream temperature and discharge are readily explained. Atmospheric pressure differences between the Azores and Iceland during positive NAO phases in winter act to draw warmer, wetter air masses eastwards from the Atlantic across Europe (Hurrell, 1995). These increases in precipitation and atmospheric temperature in turn increasing river discharge and water temperature widely across northern, central and southern Europe (Arora et al., 2016; Trigo et al., 2004; Webb & Nobilis, 2007). The

consequences are remarkably consistent across western Britain, where mean stream temperatures in winter increase by around 2.5°C between the most negative and positive phases (Durance & Ormerod, 2007; Elliott et al., 2000). Winter discharge in the Llyn Brianne streams increases on average by at least 15%–20% as this switch occurs (Bradley & Ormerod, 2001).

Although these climatically induced effects are almost certainly involved either directly or indirectly in the invertebrate dynamics we observed, there are several possible mechanisms that range from hydrological response, altered thermal regimes, hydrochemical change and resource depletion. From a thermal perspective, changes of the magnitude detected during different NAO phases

are sufficient to affect invertebrate phenology in temperate streams (Briers et al., 2004), but might also approach or exceed thermal tolerances in cool-water invertebrates, for example by increasing metabolic costs or reducing competitiveness (Durance & Ormerod, 2010; Shah et al., 2023). Warmer, wetter periods during positive NAO years also increase the downstream export of particulate organic matter through the Llyn Brianne streams, depleting benthic stocks except where maintained by litterfall from riparian broadleaves (Pye et al., 2022). This is important given the role of organic leaf litter in stream macronutrient dynamics, food-web energetics and population maintenance as shown in adjacent catchments (Thomas et al., 2016). Notably, however, the NAO can also influence precipitation and stream discharge in summer, for example through effects on drought, which complicates assessments of subsequent changes among stream organisms. Further complications also arise through interactions between the NAO, stream discharge and water quality. In upland catchments like those at Llyn Brianne, this includes effects on acid–base dynamics, metals (specifically aluminum), dissolved organic carbon, base cations and nitrate which respond variously to precipitation, chemistry, soil hydrology and thermodynamic influences on mobilization (Hindar et al., 2004; Monteith et al., 2000; Ness et al., 2004). At Llyn Brianne, most chemical variation across the streams and through time reflects acid–base dynamics (see Figures S1 and S2), but we found no synchronous, linear relationships between chemistry and the NAO as reflected in principal component analysis. However, temporal variability in hydrochemistry increased during positive phases of the NAO. This is consistent with the occurrence of acid episodes at the least buffered streams at Llyn Brianne during hydrological events that dilute base-cations, reduce pH and mobilize aluminium at potentially toxic concentrations (Kowalik et al., 2007; Ormerod & Durance, 2009). These effects are diminishing with progressive recovery from the past effects of acid deposition, but will still have affected stream invertebrates over the time period covered by the present assessment. For all of these reasons, we cannot yet offer an unequivocal view of which aspects of stream variability link the NAO to stream invertebrate dynamics either alone or in combination. Moreover, uncovering the exact mechanisms is always likely to be challenging because very long-term studies like ours are beyond the scope of conventional, manipulative experiments and so rely on weak inference through correlation. This perspective is consistent with assessments elsewhere (Ottersen et al., 2001).

Similar uncertainties exist around the complex interactions between climate change, weather patterns and ecological dynamics that affect ecological synchrony and stability (García-Palacios et al., 2018; Sabater et al., 2022; Sheppard et al., 2016). While some long-term assessments of ecological synchrony are emerging (Wang et al., 2019; Wilcox et al., 2017), they are scarce especially at decadal timescales similar to ours. Wavelet modelling indicated that the synchronizing effect of the NAO on overall invertebrate abundance across streams was significant at long time-scales, but weaker at shorter scales. Although wavelet models are a relatively novel technique, these results are in line with recent investigations in showing

how ecological responses to large-scale climate oscillations mostly manifest at longer timescales (Castorani et al., 2022; Sheppard et al., 2016). One small caveat was that we also found that the dynamics in abundance were relatively synchronous also at shorter timescales (<4 years), implying that other processes, not directly linked to variation in the NAO, could be involved. Nevertheless, growing evidence suggests that changes in the mean and variance of climate variables are linked to greater spatial autocorrelation between the weather and other environmental variations (Black et al., 2018; Hansen et al., 2020). These, in turn, can promote spatial synchrony in population fluctuations (Koenig & Liebhold, 2016). The effects on population dynamics of large-scale climatic variation, such as the ENSO, are well documented and can reflect ecological synchrony through spatially correlated regional effects on weather, even at continental scales (Koenig & Liebhold, 2016; Post & Forchhammer, 2002). Anthropogenic forcing of climate is also changing the frequency of extreme events and likely to induce ecological synchrony at regional and continental scales (Post & Forchhammer, 2004). Evidence for similar effects at the hierarchy of scales in our study, involving metacommunity, community and population patterns, is scarcer and likely to be complicated by local factors such as habitat heterogeneity, dispersal limitation and functional difference among species. In addition, the effects of the NAO might depend on the intensity of environmental fluctuation involved. Evidence elsewhere shows that synchrony in ecological dynamics can be induced by changes in environmental variability, either as extreme events or increasing variance (Dallas et al., 2020; Hansen et al., 2020), without necessarily involving changes in spatial correlation.

Whatever environmental drivers link the NAO and its associated climatic variability to synchrony in stream communities, the biological processes involved are also elusive. Emergent patterns at community and metacommunity levels are likely to emerge from cumulative effects on individuals and populations, for example from effects on species metabolism, growth rate, phenology, behaviour, resource availability and interspecific interactions. Evidence for climatic effects on resource availability and inter-specific competition in stream communities at Llyn Brianne is already available (Durance & Ormerod, 2010; Pye et al., 2022). Direct physiological effects on individuals are less well evidenced, but potentially important in ectothermic organisms such as stream insects. Higher water temperature increases metabolic rate, accelerates development and alters the allocation of internal resources between somatic growth and reproduction with consequences for fitness. Even small thermal changes can affect cool-water organisms (Shah et al., 2023) and occur alongside other constraints such as declining oxygen concentration as temperature increases (Rubalcaba et al., 2020). Whether these effects on individuals translate into increasing biotic synchrony is unclear, but altered fitness at higher air temperature could influence both the aquatic stages of insects as well as the fecundity and dispersal of adult aquatic insects among streams (Briers et al., 2004; Wonglersak et al., 2020). Our data revealed major

NAO variations over a 6–8 year timescale, which may be enough to cause dispersal-driven spatial synchrony, even in univoltine species. However, our data showed that the NAO did not alter the rate of synchrony decay with distance and moreover movement data from Llyn Brienne suggest that inter-basin dispersal events in invertebrates are less likely than longer-distance movements (Masters et al., 2007; Petersen et al., 2004). The biological and ecological dimensions for synchrony of the types we detected is likely to be a fertile area for further research both to unpick the mechanisms and understand the consequences.

4.1 | Implications: Climate change, catchment management, and biodiversity conservation

As well as its fundamental importance, synchrony in ecological dynamics is recognized as a widespread phenomenon with strategic implications for the management and conservation of ecosystems (Heino et al., 1997; Liebhold et al., 2004). This stems from the growing understanding of the multiple dimensions of synchrony in different ecosystems (e.g., Larsen et al., 2021; Walter et al., 2021) and the scaling relationship with ecological stability across organizational levels (Wang et al., 2019). Based on our results, we draw attention to three implications relevant to climate change, catchment management and biodiversity conservation.

First, the interdecadal community dynamics at Llyn Brienne add to the increasing evidence for time-dependent biotic synchrony linked to timescales relevant to climate change and fluctuation (Allstadt et al., 2015; Koenig & Liebhold, 2016; Post & Forchhammer, 2004). Of particular importance is that the NAO is not just a synoptic 'package of weather' (Ottersen et al., 2001; Stenseth et al., 2003), but also a potential analog of developing climate change. Specifically, warmer, wetter, and more stormy winters brought by positive phases of the NAO match some climate change effects over temperate western Europe. Importantly, these conditions appear to destabilize invertebrate populations communities in temperate streams by synchronizing biotic dynamics. Similar effects at Llyn Brienne were documented in previous analyses, but not with such marked effects at the population, community and metapopulation scales (Bradley & Ormerod, 2001). Clarifying the extent to which spatial and community synchrony in species abundances determine compositional stability is an important research area (Lamy et al., 2021), but so too is the need to assess the consequences for ecological function, food-web energetics, population persistence and ecosystem resilience.

Secondly, as a corollary to potential climatic effects on invertebrate community stability, the scale of the mechanisms hints at catchment management options that could obviate the effects. Specifically, if warmer, wetter winters destabilize upland invertebrate communities through combined effects of discharge, resource depletion, temperature and hydrochemical variability—for example acid episodes—then catchment management aimed at flood-risk management, resource enhancement, thermal damping and reduced

pollution would be beneficial. Judiciously expanding the cover of natural deciduous woodlands on temperate catchments is already known to have benefits in some of these respects as a key aspect of climate change adaptation (Pye et al., 2022; Thomas et al., 2016). For thermal damping in winter and natural flood management, the evidence is still equivocal, but considered as an opportunity for landscape-scale interventions (Cooper et al., 2021).

Thirdly, the apparent effects of increased functional diversity in reducing synchrony argues for biodiversity conservation aimed at retaining or restoring composition in stream communities. Communities supporting more diverse functional traits are more likely to display independent or compensatory dynamics among species which respond differently to environmental variation (Feio et al., 2015). One small caveat from our work is that the reduction in community synchrony brought by higher functional diversity was partly driven by the underlying increase in taxonomic richness, which is known to limit synchrony among species. Nevertheless, factors that promote synchrony and variability at the metacommunity scale have key conservation implications as they are likely to hinder both demographic rescue among subpopulations as well compensatory dynamics within communities (Heino et al., 1997; Liebhold et al., 2004; Wilcox et al., 2017). These effects are still poorly understood in biodiversity conservation generally, and nor are they recognized widely.

In summary, we offer this work and its strategic implications as one of the longest assessments so far of ecological synchrony in streams and rivers, and the first to reveal the synchronizing effects of NAO-induced climatic variations on freshwater organisms across populations, communities and metacommunities.

AUTHOR CONTRIBUTIONS

Stefano Larsen: Conceptualization; formal analysis; methodology; writing – original draft. **Fiona Joyce:** Data curation; formal analysis; writing – review and editing. **Ian P. Vaughan:** Methodology; supervision; writing – review and editing. **Isabelle Durance:** Data curation; funding acquisition; investigation; project administration; resources. **Jonathan A. Walter:** Formal analysis; methodology; writing – review and editing. **Steve J. Ormerod:** Funding acquisition; investigation; project administration; resources; supervision; writing – original draft; writing – review and editing.

ACKNOWLEDGEMENTS

Many individuals have contributed to the collection of these data over the last 40 years over which time the Llyn Brienne Stream Observatory has been funded variously by the Esmee Fairbairn Foundation, the NERC Dures project (NE/J014818/1), the EU MARS project under the 7th Framework Programme (contract no. 603378) and earlier grants from Defra and the Welsh Government. FJ was supported by a NERC FRESH studentship. Natural Resource Wales provided the water quality data. We are grateful to Lise Comte and Albert Ruhi for their comments on earlier drafts. We thank two anonymous reviewers for their constructive comments and suggestions. Yog Sothoth provided support during data analysis.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Biological, climatic and water quality data used in this study are available from the Dryad repository with <https://doi.org/10.5061/dryad.1ns1rn90w>. Codes used for the processing and analysis of the data are available on https://github.com/stefanolarsen/LB_synchrony.

ORCID

Stefano Larsen  <https://orcid.org/0000-0002-6774-1407>

Ian P. Vaughan  <https://orcid.org/0000-0002-7263-3822>

Isabelle Durance  <https://orcid.org/0000-0002-4138-3349>

Jonathan A. Walter  <https://orcid.org/0000-0003-2983-751X>

Steve J. Ormerod  <https://orcid.org/0000-0002-8174-302X>

REFERENCES

- Allstadt, A. J., Liebhold, A. M., Johnson, D. M., Davis, R. E., & Haynes, K. J. (2015). Temporal variation in the synchrony of weather and its consequences for spatiotemporal population dynamics. *Ecology*, 96(11), 2935–2946. <https://doi.org/10.1890/14-1497.1>
- Arora, R., Tockner, K., & Venohr, M. (2016). Changing river temperatures in northern Germany: Trends and drivers of change. *Hydrological Processes*, 30(17), 3084–3096. <https://doi.org/10.1002/hyp.10849>
- Bivand, R., Keitt, T., Rowlingson, B., Pebesma, E., Sumner, M., Hijmans, R., Baston, D., Rouault, E., Warmerdam, F., Ooms, J., & Rundel, C. (2023). *rgdal: Bindings for the "Geospatial" Data Abstraction Library (1.6-6)*. <https://cran.r-project.org/web/packages/rgdal/index.html>
- Black, B. A., van der Sleen, P., Di Lorenzo, E., Griffin, D., Sydeman, W. J., Dunham, J. B., Rykaczewski, R. R., García-Reyes, M., Safeeq, M., Arismendi, I., & Bograd, S. J. (2018). Rising synchrony controls western North American ecosystems. *Global Change Biology*, 24(6), 2305–2314. <https://doi.org/10.1111/gcb.14128>
- Bogdziewicz, M., Hackett-Pain, A., Ascoli, D., & Szymkowiak, J. (2021). Environmental variation drives continental-scale synchrony of European beech reproduction. *Ecology*, 102(7), e03384. <https://doi.org/10.1002/ecy.3384>
- Bradley, D. C., & Ormerod, S. J. (2001). Community persistence among stream invertebrates tracks the North Atlantic Oscillation. *Journal of Animal Ecology*, 70(6), 987–996. <https://doi.org/10.1046/j.0021-8790.2001.00551.x>
- Bradley, D. C., & Ormerod, S. J. (2002). Evaluating the precision of kick-sampling in upland streams for assessment of long-term change: The effects of sampling effort, habitat and rarity. *Archiv fuer Hydrobiologie*, 155(2), 199–221.
- Briers, R. A., Gee, J. H. R., & Geoghegan, R. (2004). Effects of the North Atlantic Oscillation on growth and phenology of stream insects. *Ecography*, 27(6), 811–817. <https://doi.org/10.1111/j.0906-7590.2004.04005.x>
- Castorani, M. C. N., Bell, T. W., Walter, J. A., Reuman, D. C., Cavanaugh, K. C., & Sheppard, L. W. (2022). Disturbance and nutrients synchronise kelp forests across scales through interacting Moran effects. *Ecology Letters*, 25(8), 1854–1868. <https://doi.org/10.1111/ele.14066>
- Chevenet, F., Dolédec, S., & Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, 31(3), 295–309. <https://doi.org/10.1111/j.1365-2427.1994.tb01742.x>
- Colombano, D. D., Carlson, S. M., Hobbs, J. A., & Ruhi, A. (2022). Four decades of climatic fluctuations and fish recruitment stability across a marine-freshwater gradient. *Global Change Biology*, 28(17), 5104–5120. <https://doi.org/10.1111/gcb.16266>
- Cooper, M. M. D., Patil, S. D., Nisbet, T. R., Thomas, H., Smith, A. R., & McDonald, M. A. (2021). Role of forested land for natural flood management in the UK: A review. *WIREs Water*, 8(5), e1541. <https://doi.org/10.1002/wat2.1541>
- Dallas, T. A., Antão, L. H., Pöyry, J., Leinonen, R., & Ovaskainen, O. (2020). Spatial synchrony is related to environmental change in Finnish moth communities. *Proceedings of the Royal Society B: Biological Sciences*, 287(1927), 20200684. <https://doi.org/10.1098/rspb.2020.0684>
- de Bello, F., Lavorel, S., Hallett, L. M., Valencia, E., Garnier, E., Roscher, C., Conti, L., Galland, T., Goberna, M., Májeková, M., Montesinos-Navarro, A., Pausas, J. G., Verdú, M., E-Vojtkó, A., Götzenberger, L., & Lepš, J. (2021). Functional trait effects on ecosystem stability: Assembling the jigsaw puzzle. *Trends in Ecology & Evolution*, 36(9), 822–836. <https://doi.org/10.1016/j.tree.2021.05.001>
- Durance, I., & Ormerod, S. J. (2007). Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology*, 13(5), 942–957. <https://doi.org/10.1111/j.1365-2486.2007.01340.x>
- Durance, I., & Ormerod, S. J. (2010). Evidence for the role of climate in the local extinction of a cool-water trichopteran. *Journal of the North American Benthological Society*, 29(4), 1367–1378. <https://doi.org/10.1899/09-159.1>
- Edwards, R. W., Stoner, J. H., & Gee, A. S. (Eds.). (1990). *Acid waters in Wales*. Kluwer.
- Elliott, J. M., Hurley, M. A., & Maberly, S. C. (2000). The emergence period of sea trout fry in a Lake District stream correlates with the North Atlantic Oscillation. *Journal of Fish Biology*, 56(1), 208–210. <https://doi.org/10.1111/j.1095-8649.2000.tb02096.x>
- Erős, T., Comte, L., Filipe, A. F., Ruhi, A., Tedesco, P. A., Brose, U., Fortin, M.-J., Giam, X., Irving, K., Jacquet, C., Larsen, S., Sharma, S., & Olden, J. D. (2020). Effects of nonnative species on the stability of riverine fish communities. *Ecography*, 43(8), 1156–1166. <https://doi.org/10.1111/ecog.04985>
- Feio, M. J., Doledec, S., & Graca, M. A. S. (2015). Human disturbance affects the long-term spatial synchrony of freshwater invertebrate communities. *Environmental Pollution*, 196, 300–308. <https://doi.org/10.1016/j.envpol.2014.09.026>
- García-Palacios, P., Gross, N., Gaitán, J., & Maestre, F. T. (2018). Climate mediates the biodiversity–ecosystem stability relationship globally. *Proceedings of the National Academy of Sciences of the United States of America*, 115(33), 8400–8405. <https://doi.org/10.1073/pnas.1800425115>
- Grenfell, B. T., Wilson, K., Finkenstädt, B. F., Coulson, T. N., Murray, S., Albon, S. D., Pemberton, J. M., Clutton-Brock, T. H., & Crawley, M. J. (1998). Noise and determinism in synchronized sheep dynamics. *Nature*, 394(6694), 6694. <https://doi.org/10.1038/29291>
- Haase, P., Bowler, D. E., Baker, N. J., Bonada, N., Domisch, S., Garcia Marquez, J. R., Heino, J., Hering, D., Jähnig, S. C., Schmidt-Kloiber, A., Stubbington, R., Altermatt, F., Álvarez-Cabria, M., Amatulli, G., Angeler, D. G., Archambaud-Suard, G., Jorrín, I. A., Aspin, T., Azpiroz, I., ... Welti, E. A. R. (2023). The recovery of European freshwater biodiversity has come to a halt. *Nature*, 620, 582–588. <https://doi.org/10.1038/s41586-023-06400-1>
- Hansen, B. B., Grøtan, V., Herfindal, I., & Lee, A. M. (2020). The Moran effect revisited: Spatial population synchrony under global warming. *Ecography*, 43(11), 1591–1602. <https://doi.org/10.1111/ecog.04962>
- Heino, M., Kaitala, V., Ranta, E., & Lindström, J. (1997). Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 264(1381), 481–486. <https://doi.org/10.1098/rspb.1997.0069>
- Hijmans, R. J. (2020). *Raster: Geographic data analysis and modeling*. R package version 3.4-5.

- Hindar, A., Tørseth, K., Henriksen, A., & Orsolini, Y. (2004). The significance of the North Atlantic Oscillation (NAO) for sea-salt episodes and acidification-related effects in Norwegian Rivers. *Environmental Science & Technology*, 38(1), 26–33. <https://doi.org/10.1021/es030065c>
- Hollis, D., McCarthy, M., Kendon, M., Legg, T., & Simpson, I. (2019). HadUK-grid—A new UK dataset of gridded climate observations. *Geoscience Data Journal*, 6(2), 151–159. <https://doi.org/10.1002/gdj3.78>
- Hurrell, J. W. (1995). Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science*, 269(5224), 676–679. <https://doi.org/10.1126/science.269.5224.676>
- Knouft, J. H., & Ficklin, D. L. (2017). The potential impacts of climate change on biodiversity in flowing freshwater systems. *Annual Review of Ecology, Evolution, and Systematics*, 48(1), 111–133. <https://doi.org/10.1146/annurev-ecolsys-110316-022803>
- Koenig, W. D., & Liebhold, A. M. (2016). Temporally increasing spatial synchrony of north American temperature and bird populations. *Nature Climate Change*, 6(6), 614–617. <https://doi.org/10.1038/nclimate2933>
- Kowalik, R. A., Cooper, D. M., Evans, C. D., & Ormerod, S. J. (2007). Acidic episodes retard the biological recovery of upland British streams from chronic acidification. *Global Change Biology*, 13(11), 2439–2452. <https://doi.org/10.1111/j.1365-2486.2007.01437.x>
- Lamy, T., Wisnoski, N. I., Andrade, R., Castorani, M. C. N., Compagnoni, A., Lany, N., Marazzi, L., Record, S., Swan, C. M., Tonkin, J. D., Voelker, N., Wang, S., Zarnetske, P. L., & Sokol, E. R. (2021). The dual nature of metacommunity variability. *Oikos*, 130(12), 2078–2092. <https://doi.org/10.1111/oik.08517>
- Lande, R., Engen, S., & Sæther, B. (1999). Spatial scale of population synchrony: Environmental correlation versus dispersal and density regulation. *The American Naturalist*, 154(3), 271–281. <https://doi.org/10.1086/303240>
- Larsen, S., Chase, J. M., Durance, I., & Ormerod, S. J. (2018). Lifting the veil: Richness measurements fail to detect systematic biodiversity change over three decades. *Ecology*, 99(6), 1316–1326. <https://doi.org/10.1002/ecy.2213>
- Larsen, S., Comte, L., Filipa Filipe, A., Fortin, M.-J., Jacquet, C., Ryser, R., Tedesco, P. A., Brose, U., Erős, T., Giam, X., Irving, K., Ruhi, A., Sharma, S., & Olden, J. D. (2021). The geography of metapopulation synchrony in dendritic river networks. *Ecology Letters*, 24(4), 791–801. <https://doi.org/10.1111/ele.13699>
- Lauerwald, R., Laruelle, G. G., Hartmann, J., Ciais, P., & Regnier, P. A. G. (2015). Spatial patterns in CO₂ evasion from the global river network. *Global Biogeochemical Cycles*, 29(5), 534–554. <https://doi.org/10.1002/2014GB004941>
- Liebhold, A., Koenig, W. D., & Bjørnstad, O. N. (2004). Spatial synchrony in population dynamics. *Annual Review of Ecology, Evolution, and Systematics*, 35(1), 467–490. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132516>
- Loreau, M., & de Mazancourt, C. (2008). Species synchrony and its drivers: Neutral and nonneutral community dynamics in fluctuating environments. *The American Naturalist*, 172(2), E48–E66. <https://doi.org/10.1086/589746>
- Markovic, D., Carrizo, S., Freyhof, J., Cid, N., Lengyel, S., Scholz, M., Kasperdus, H., & Darwall, W. (2014). Europe's freshwater biodiversity under climate change: Distribution shifts and conservation needs. *Diversity and Distributions*, 20(9), 1097–1107. <https://doi.org/10.1111/ddi.12232>
- Masters, Z., Peteresen, I., Hildrew, A. G., & Ormerod, S. J. (2007). Insect dispersal does not limit the biological recovery of streams from acidification. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 17(4), 375–383. <https://doi.org/10.1002/aqc.794>
- Monteith, D. T., Evans, C. D., & Reynolds, B. (2000). Are temporal variations in the nitrate content of UK upland freshwaters linked to the North Atlantic Oscillation? *Hydrological Processes*, 14(10), 1745–1749. [https://doi.org/10.1002/1099-1085\(200007\)14:10<1745::AID-HYP116>3.0.CO;2-O](https://doi.org/10.1002/1099-1085(200007)14:10<1745::AID-HYP116>3.0.CO;2-O)
- Moran, P. A. P. (1953). The statistical analysis of the Canadian Lynx cycle. *Australian Journal of Zoology*, 1(3), 291–298. <https://doi.org/10.1071/zo9530291>
- Moustakas, A., Evans, M. R., Daliakopoulos, I. N., & Markonis, Y. (2018). Abrupt events and population synchrony in the dynamics of bovine tuberculosis. *Nature Communications*, 9(1), 1. <https://doi.org/10.1038/s41467-018-04915-0>
- Ness, L., Neal, C., Davies, T. D., & Reynolds, B. (2004). Impacts of the North Atlantic Oscillation on stream water chemistry in mid-Wales. *Hydrology and Earth System Sciences*, 8(3), 409–421. <https://doi.org/10.5194/hess-8-409-2004>
- NRW. (2020). ATI-20064a: Rainfall data Nant Y Maen and Brianne Flume flow data [Data set].
- Ormerod, S. J., & Durance, I. (2009). Restoration and recovery from acidification in upland Welsh streams over 25 years. *Journal of Applied Ecology*, 46(1), 164–174. <https://doi.org/10.1111/j.1365-2664.2008.01587.x>
- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C., & Stenseth, N. C. (2001). Ecological effects of the North Atlantic Oscillation. *Oecologia*, 128(1), 1–14. <https://doi.org/10.1007/s004420100655>
- Peltonen, M., Liebhold, A. M., Bjørnstad, O. N., & Williams, D. W. (2002). Spatial synchrony in Forest insect outbreaks: Roles of regional stochasticity and dispersal. *Ecology*, 83(11), 3120–3129. <https://doi.org/10.2307/3071847>
- Petersen, I., Masters, Z., Hildrew, A. G., & Ormerod, S. J. (2004). Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology*, 41(5), 934–950.
- Pierce, D. (2019). ncd4: Interface to unidata netCDF (version 4 or earlier) format data files. R package version 1.17 <https://CRAN.R-project.org/package=ncdf4>
- Post, E., & Forchhammer, M. C. (2002). Synchronization of animal population dynamics by large-scale climate. *Nature*, 420(6912), 168–171. <https://doi.org/10.1038/nature01064>
- Post, E., & Forchhammer, M. C. (2004). Spatial synchrony of local populations has increased in association with the recent Northern Hemisphere climate trend. *Proceedings of the National Academy of Sciences of the United States of America*, 101(25), 9286–9290. <https://doi.org/10.1073/pnas.0305029101>
- Pye, M. C., Vaughan, I. P., Ormerod, S. J., & Durance, I. (2022). Organic litter dynamics in headwater streams draining contrasting land uses. *Hydrobiologia*, 850, 3375–3390. <https://doi.org/10.1007/s10750-022-05084-4>
- Reuman, D. C., Anderson, T., Walter, J. A., Zhao, L., & Sheppard, L. W. (2021). *wsyn: Wavelet approaches to studies of synchrony in ecology and other fields* (R package 1.0.4).
- Rubalcaba, J. G., Verberk, W. C. E. P., Hendriks, A. J., Saris, B., & Woods, H. A. (2020). Oxygen limitation may affect the temperature and size dependence of metabolism in aquatic ectotherms. *Proceedings of the National Academy of Sciences of the United States of America*, 117(50), 31963–31968. <https://doi.org/10.1073/pnas.2003292117>
- Ruhi, A., Dong, X., McDaniel, C. H., Batzer, D. P., & Sabo, J. L. (2018). Detrimental effects of a novel flow regime on the functional trajectory of an aquatic invertebrate metacommunity. *Global Change Biology*, 24(8), 3749–3765. <https://doi.org/10.1111/gcb.14133>
- Sabater, S., Freixa, A., Jiménez, L., López-Doval, J., Pace, G., Pascoal, C., Perujo, N., Craven, D., & González-Trujillo, J. D. (2022). Extreme weather events threaten biodiversity and functions of river ecosystems: Evidence from a meta-analysis. *Biological Reviews*, 98(2), 450–461. <https://doi.org/10.1111/brv.12914>
- Shah, A. A., Hotaling, S., Lapsansky, A. B., Malison, R. L., Birrell, J. H., Keeley, T., Giersch, J. J., Tronstad, L. M., & Woods, H. A. (2023). Warming undermines emergence success in a threatened alpine stonefly: A multi-trait perspective on vulnerability to climate change. *Functional Ecology*, 37(4), 1033–1043. <https://doi.org/10.1111/1365-2435.14284>

- Sheppard, L. W., Bell, J. R., Harrington, R., & Reuman, D. C. (2016). Changes in large-scale climate alter spatial synchrony of aphid pests. *Nature Climate Change*, 6(6), 610–613. <https://doi.org/10.1038/nclimate2881>
- Sheppard, L. W., Defriez, E. J., Reid, P. C., & Reuman, D. C. (2019). Synchrony is more than its top-down and climatic parts: Interacting Moran effects on phytoplankton in British seas. *PLoS Computational Biology*, 15(3), e1006744. <https://doi.org/10.1371/journal.pcbi.1006744>
- Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K., Yoccoz, N. G., & Åndlandsvik, B. (2003). Studying climate effects on ecology through the use of climate indices: The North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1529), 2087–2096. <https://doi.org/10.1098/rspb.2003.2415>
- Stoner, J. H., Gee, A. S., & Wade, K. R. (1984). The effects of acidification on the ecology of streams in the upper Tywi catchment in West Wales. *Environmental Pollution*, 35(2), 125–157. [https://doi.org/10.1016/0143-1471\(84\)90135-1](https://doi.org/10.1016/0143-1471(84)90135-1)
- Thomas, S. M., Griffiths, S. W., & Ormerod, S. J. (2016). Beyond cool: Adapting upland streams for climate change using riparian woodlands. *Global Change Biology*, 22(1), 310–324. <https://doi.org/10.1111/gcb.13103>
- Tickner, D., Opperman, J. J., Abell, R., Acreman, M., Arthington, A. H., Bunn, S. E., Cooke, S. J., Dalton, J., Darwall, W., Edwards, G., Harrison, I., Hughes, K., Jones, T., Leclère, D., Lynch, A. J., Leonard, P., McClain, M. E., Muruven, D., Olden, J. D., ... Young, L. (2020). Bending the curve of global freshwater biodiversity loss: An emergency recovery plan. *Bioscience*, 70(4), 330–342. <https://doi.org/10.1093/biosci/biaa002>
- Tonkin, J. D., Poff, N. L., Bond, N. R., Horne, A., Merritt, D. M., Reynolds, L. V., Olden, J. D., Ruhi, A., & Lytle, D. A. (2019). Prepare river ecosystems for an uncertain future. *Nature*, 570(7761), 301–303. <https://doi.org/10.1038/d41586-019-01877-1>
- Trigo, R. M., Pozo-Vázquez, D., Osborn, T. J., Castro-Díez, Y., Gámiz-Fortis, S., & Esteban-Parra, M. J. (2004). North Atlantic Oscillation influence on precipitation, river flow and water resources in the Iberian Peninsula. *International Journal of Climatology*, 24(8), 925–944. <https://doi.org/10.1002/joc.1048>
- Valencia, E., de Bello, F., Galland, T., Adler, P. B., Lepš, J., E-Vojtkó, T., Van Klink, R., Carmona, C. P., Danihelka, J., Dengler, J., Eldridge, D. J., Estiarte, M., García-González, R., Garnier, E., Gómez-García, D., Harrison, S. P., Herben, T., Ibáñez, R., Jentsch, A., ... Götzenberger, L. (2020). Synchrony matters more than species richness in plant community stability at a global scale. *Proceedings of the National Academy of Sciences of the United States of America*, 117(39), 24345–24351. <https://doi.org/10.1073/pnas.1920405117>
- Vaughan, I. P., & Gotelli, N. J. (2019). Water quality improvements offset the climatic debt for stream macroinvertebrates over twenty years. *Nature Communications*, 10(1), 1956. <https://doi.org/10.1038/s41467-019-09736-3>
- Verberk, W. C. E. P., & Bilton, D. T. (2013). Respiratory control in aquatic insects dictates their vulnerability to global warming. *Biology Letters*, 9(5), 20130473. <https://doi.org/10.1098/rsbl.2013.0473>
- Viboud, C., Bjørnstad, O. N., Smith, D. L., Simonsen, L., Miller, M. A., & Grenfell, B. T. (2006). Synchrony, waves, and spatial hierarchies in the spread of influenza. *Science*, 312(5772), 447–451. <https://doi.org/10.1126/science.1125237>
- Vindstad, O. P. L., Jepsen, J. U., Yoccoz, N. G., Bjørnstad, O. N., Mesquita, M. D. S., & Ims, R. A. (2019). Spatial synchrony in sub-arctic geometrid moth outbreaks reflects dispersal in larval and adult life cycle stages. *Journal of Animal Ecology*, 88(8), 1134–1145. <https://doi.org/10.1111/1365-2656.12959>
- Visbeck, M. H., Hurrell, J. W., Polvani, L., & Cullen, H. M. (2001). The North Atlantic Oscillation: Past, present, and future. *Proceedings of the National Academy of Sciences of the United States of America*, 98(23), 12876–12877. <https://doi.org/10.1073/pnas.231391598>
- Walter, J. A., Sheppard, L. W., Venugopal, P. D., Reuman, D. C., Dively, G., Tooker, J. F., & Johnson, D. M. (2020). Weather and regional crop composition variation drive spatial synchrony of lepidopteran agricultural pests. *Ecological Entomology*, 45(3), 573–582. <https://doi.org/10.1111/een.12830>
- Walter, J. A., Shoemaker, L. G., Lany, N. K., Castorani, M. C. N., Fey, S. B., Dudney, J. C., Gherardi, L., Portales-Reyes, C., Rypel, A. L., Cottingham, K. L., Suding, K. N., Reuman, D. C., & Hallett, L. M. (2021). The spatial synchrony of species richness and its relationship to ecosystem stability. *Ecology*, 102(11), e03486. <https://doi.org/10.1002/ecy.3486>
- Wang, S., Lamy, T., Hallett, L. M., & Loreau, M. (2019). Stability and synchrony across ecological hierarchies in heterogeneous metacommunities: Linking theory to data. *Ecography*, 42(6), 1200–1211. <https://doi.org/10.1111/ecog.04290>
- Wayne Polley, H., Yang, C., Wilsey, B. J., & Fay, P. A. (2020). Temporal stability of grassland metacommunities is regulated more by community functional traits than species diversity. *Ecosphere*, 11(7), e03178. <https://doi.org/10.1002/ecs2.3178>
- Weatherley, N. S., & Ormerod, S. J. (1987). The impact of acidification on macroinvertebrate assemblages in Welsh streams: towards an empirical model. *Environmental Pollution*, 46, 223–240.
- Weatherley, N. S., & Ormerod, S. J. (1990). The constancy of invertebrate assemblages in soft-water streams: Implications for the prediction and detection of environmental change. *Journal of Applied Ecology*, 27(3), 952–964. <https://doi.org/10.2307/2404389>
- Webb, B. W., & Nobilis, F. (2007). Long-term changes in river temperature and the influence of climatic and hydrological factors. *Hydrological Sciences Journal*, 52(1), 74–85. <https://doi.org/10.1623/hysj.52.1.74>
- Wilcox, K. R., Tredennick, A. T., Koerner, S. E., Grman, E., Hallett, L. M., Avolio, M. L., La Pierre, K. J., Houseman, G. R., Isbell, F., Johnson, D. S., Alatalo, J. M., Baldwin, A. H., Bork, E. W., Boughton, E. H., Bowman, W. D., Britton, A. J., Cahill, J. F., Collins, S. L., Du, G., ... Zhang, Y. (2017). Asynchrony among local communities stabilises ecosystem function of metacommunities. *Ecology Letters*, 20(12), 1534–1545. <https://doi.org/10.1111/ele.12861>
- Wonglersak, R., Fenberg, P. B., Langdon, P. G., Brooks, S. J., & Price, B. W. (2020). Temperature-body size responses in insects: A case study of British Odonata. *Ecological Entomology*, 45(4), 795–805. <https://doi.org/10.1111/een.12853>
- Woodward, G., Bonada, N., Brown, L. E., Death, R. G., Durance, I., Gray, C., Hladzy, S., Ledger, M. E., Milner, A. M., Ormerod, S. J., Thompson, R. M., & Pawar, S. (2016). The effects of climatic fluctuations and extreme events on running water ecosystems. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences*, 371(1694), 20150274. <https://doi.org/10.1098/rstb.2015.0274>
- Yeakel, J. D., Moore, J. W., Guimarães, P. R., & de Aguiar, M. A. M. (2014). Synchronisation and stability in river metapopulation networks. *Ecology Letters*, 17(3), 273–283. <https://doi.org/10.1111/ele.12228>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Larsen, S., Joyce, F., Vaughan, I. P., Durance, I., Walter, J. A., & Ormerod, S. J. (2023). Climatic effects on the synchrony and stability of temperate headwater invertebrates over four decades. *Global Change Biology*, 00, e17017. <https://doi.org/10.1111/gcb.17017>