


# Freshwater eutrophication drives sharp reductions in temporal beta diversity

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**Abstract.** Eutrophication has become one of the most widespread anthropogenic forces impacting freshwater biological diversity. One potentially important mechanism driving biodiversity changes in response to eutrophication is the alteration of seasonal patterns of succession, particularly among species with short, synchronous, life cycles. We tested the hypothesis that eutrophication reduces seasonally driven variation in species assemblages by focusing on an understudied aspect of biodiversity: temporal beta diversity ( $\beta_t$ ). We estimated the effect of eutrophication on  $\beta_t$  by sampling benthic macroinvertebrate assemblages bimonthly for two years across 35 streams spanning a steep gradient of total phosphorus (P) and benthic algal biomass (as chlorophyll *a* [chl *a*]). Two widely used metrics of  $\beta$  diversity both declined sharply in response to increasing P and chl *a*, regardless of covariates. The most parsimonious explanatory model for  $\beta_t$  included an interaction between P and macroinvertebrate biomass, which revealed that  $\beta_t$  was lower when macroinvertebrate biomass was relatively high. Macroinvertebrate biomass explained a greater amount of deviance in  $\beta_t$  at lower to moderate concentrations of P, providing additional explanatory power where P concentration alone was unable to fully explain declines in  $\beta_t$ . Chl *a* explained similar amounts of deviance in  $\beta_t$  in comparison to the best P model, but only when temperature variability, which was positively related to  $\beta_t$ , also was included in the model. Declines in  $\beta_t$  suggest that nutrient enrichment decreases the competitive advantage that specialists gain by occupying particular temporal niches, which leads to assemblages dominated by generalists that exhibit little seasonal turnover. The collapse of seasonal variation in assemblage composition we observed in our study suggests that treating dynamic communities as static assemblages is a simplification that may fail to detect the full impact of anthropogenic stressors. Our results show that eutrophication leads to more temporally homogenous communities and therefore degrades a fundamental facet of biodiversity.

**Key words:** diversity; eutrophication; macroinvertebrate; productivity; seasonality; stream; temporal beta; temporal homogenization.

## INTRODUCTION

Cultural eutrophication of lotic systems is leading to widespread declines in water quality, biodiversity, and valuable ecosystem services (Carpenter et al. 1998, Smith et al. 2006, Paulsen et al. 2008). Nutrient concentrations have increased over reference conditions in most ecoregions of North America (Dodds and Smith 2016), and have the capacity to increase algal biomass and primary production (Elser et al. 2007). Alteration of nutrient regimes in ecosystems limited by nitrogen (N) or phosphorus (P) dramatically shifts the competitive balance of organisms in basal compartments, which in turn elicits changes in higher trophic levels (Carpenter et al. 1998, Nelson et al. 2013). As the prevalence of cultural eutrophication continues to expand, so too does the potential for eutrophication to result in unforeseen,

deleterious alterations to ecosystem structure and function (Dodds et al. 2010, Radeloff et al. 2015).

Freshwater assemblages respond strongly to increases in productivity associated with nutrient enrichment (Smith et al. 1999). Beta diversity ( $\beta$ ), which is generally defined as the compositional dissimilarity in species assemblages across space or time (Whittaker 1972, reviewed by Tuomisto 2010 and Anderson et al. 2011), provides a conceptual and mathematical link between diversity at a particular locality (alpha diversity,  $\alpha$ ) and the regional species pool (gamma diversity,  $\gamma$ ). Declines in the compositional heterogeneity of aquatic communities (or spatial beta diversity;  $\beta_{\text{spat}}$ ) exposed to nutrient enrichment indicate that eutrophication can act as a strong ecological filter, and increase the importance of species sorting mechanisms (Passy and Blanchet 2007, Donohue et al. 2009, McGoff et al. 2013, Goldenberg Vilar et al. 2014). The most striking direct effect of eutrophication on animal communities stems from large increases in benthic biomass, which in turn can lead to precipitous declines in dissolved oxygen concentrations following senescence and decomposition in the basal

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compartment (Carpenter et al. 1998). Even relatively low levels of nutrient enrichment can elicit shifts in producer community composition and alter the relative concentrations of nutrients in the basal compartments (Rosemond et al. 1993, Cross et al. 2006, Evans-White et al. 2009, Taylor et al. 2014), which can indirectly affect the ability of some consumers to effectively compete. While spatial beta diversity ( $\beta_{\text{spat}}$ ) has been examined in response to eutrophication and a wide range of other ecological questions (Qian and Ricklefs 2007, Chase 2010, Bini et al. 2014, Heino et al. 2015a), comparatively little study has been devoted to the underlying factors that influence temporal patterns in community composition (but see Mykrä et al. 2011, Hatosy et al. 2013, Steiner 2014, Heino et al. 2015b, and Magurran et al. 2015). Specifically, we do not have a clear understanding of how eutrophication impacts the temporal variability of community composition.

Seasonal oscillations in environmental conditions, and in turn the availability and quality of food resources, exert a controlling influence on communities (Tonkin et al. 2017). As a result, organisms have evolved unique life-history strategies to exploit seasonally generated niches (Bêche et al. 2006, Bonada and Resh 2013). Benthic macroinvertebrates have evolved to time periods of peak growth and maturation at different times of the year to coincide with advantageous conditions (Wolda 1988), which can cause streams to harbor higher biodiversity than can be observed at a single point in time. Moreover, meta-analysis across a variety of aquatic ecosystems found that intra-annual variability was much higher than interannual variability (Korhonen et al. 2010), which suggests that seasonally driven variation in community composition could generate a large portion of biodiversity in aquatic systems.

Given the high degree of seasonal variation inherent in these assemblages, examining the effects of eutrophication at a single time point across a spatial metacommunity (i.e., a watershed) may be insufficient to fully explain the impact of nutrient enrichment on aquatic communities (Heino et al. 2015b). If eutrophication negatively impacts the competitive ability of species that have evolved to utilize specific temporal niches, then this could cause significant declines in the temporal variation in community composition (or temporal beta diversity;  $\beta_t$ ). Thus, spatiotemporally explicit studies are needed to examine the effects of nutrient enrichment on the temporal assembly process, as focusing on the spatial effects of eutrophication alone may mask important declines in biodiversity.

We examined benthic communities among stream reaches that spanned a wide range of P and benthic chlorophyll *a* (chl *a*) concentrations over two years with the goal of determining the relationship between eutrophication and  $\beta_t$ . We hypothesized that increasing nutrient inputs would decrease the degree to which macroinvertebrate assemblages partitioned temporal niche space, resulting in lower  $\beta_t$  with increasing

eutrophication. We also considered other environmental variables that are known to influence macroinvertebrate assemblage composition as potential additional drivers of  $\beta_t$ . As temporal trends can be driven by forces acting on either inter- or intra-annual time scales, we explored the possibility that the trends observed in  $\beta_t$  were the result of an aseasonal signal by also examining  $\beta_{\text{spat}}$  across the two-year study period.

## MATERIALS AND METHODS

### *Study area and site characterization*

We studied 35 mid-order (third to fifth) stream reaches in the Ozark Highlands and Boston Mountains Level III ecoregions of Oklahoma and Arkansas, USA within the Illinois River drainage basin and surrounding area every other month for two years (Appendix S1: Fig. S1; 12 sampling events from June 2014 to April 2016). Study sites were selected both to capture the steep P gradient present in the region, as well as to minimize among site habitat variability. We targeted reaches of streams and rivers with open canopies, riffle-run channel units, and cobble-dominated substrate. We collected a suite of in-stream and riparian habitat variables to characterize each site, and focused on total phosphorus (TP) and chlorophyll *a* (chl *a*) as measures of eutrophication. Increases in benthic biomass associated with nutrient enrichment in this region is dominated by filamentous green algae (Chlorophyta), cyanobacteria (Cyanophycota), and diatoms. Data gathered during a concurrent study indicated that periods of peak productivity were associated with rapid uptake of P with little change in ambient N concentrations, high N:P ratios (20–2000, typically >100) in the surface water indicative of P rather than N limitation (Dodds and Smith 2016), and proliferation of species known to be associated with P enrichment (*Cladophora glomerata*; Dodds and Gudder 1992).

We collected instantaneous water grab samples in triplicate upstream of macroinvertebrate and periphyton collection activity to quantify TP ( $\mu\text{g/L}$ ) during each site visit. Water samples were analyzed pursuant to EPA QA/QC standards and APHA/CRASR protocols (APHA 2005; Center for Reservoir and Aquatic Systems Research, Waco, Texas, USA). Water temperature ( $^{\circ}\text{C}$ ) and turbidity (NTU) were measured using a YSI multiprobe (YSI, Yellow Springs, Ohio, USA) at the grab sample location. We recorded wetted width (m) at each transect, as well as current velocity (m/s) and canopy cover (0–100%) at the midpoints of each transect. Current velocity was measured using a Marsh-McBirney flowmeter (Loveland, Colorado, USA) following USGS protocols, and canopy cover was estimated using a densiometer. Substrate embeddedness (0–100%) was visually estimated at each Hess sample location (transect delineation as described in *Periphyton sampling*). We calculated a measure of physical habitat disturbance

(scouring) as the number of times we sampled within 10 d of a discharge event exceeding five times median base flow as determined from USGS gauges. For sites that were ungauged (15 of 35 sites), we associated flow data from neighboring sites that possessed similar hydrology and spatial proximity. While we were unable to directly measure bed stability (Schwendel et al. 2011), the proximity of sampling to high discharge events was included as a relative measure because physical disturbance could lead to higher variation in community composition (Tonkin and Death 2012). There were no impoundments above or below any study site save for several low-water crossings that did not impede water flow. Elevation (m) and catchment area (km<sup>2</sup>) were estimated using a 30-m digital elevation model (USGS National Elevation Dataset; *available online*)<sup>4</sup> and a point shapefile of stream-reach locations as outlets. A flow accumulation raster was generated using the flow-wacc function and, subsequently, catchment boundaries were delineated using the watershed function in ArcGIS 10.1 (ESRI, Redlands, California, USA). Catchment areas were estimated using the cumulative areas of the 30-m pixels within each catchment boundary.

#### *Periphyton sampling*

We collected composite periphyton samples at each site using three transects that spanned the width of the riffle-run habitat because within-reach sampling has shown that streams are heterogeneous in terms of biomass and community composition (Heino et al. 2012). Five equidistant points were selected along each transect, and a cobble nearest to each point 0.5 m upstream of the transect line was collected (totaling 15 cobbles per site per visit). Benthic periphyton was removed from the cobbles by vigorous scrubbing and washing, and placed in dark bottles on ice for further processing. Cobble surface area was estimated using the aluminum foil mass-to-area conversion method (Lamberti et al. 1991). To ensure a representative sample all periphyton slurries were thoroughly homogenized with a hand-blender until no large particles or filaments remained, after which the slurry was suspended at a high rate of stirring. Volumetric pipette tips were widened to prevent clogging before three aliquots of 2–5 mL were filtered onto 0.8- $\mu$ m glass fiber filters for chl *a* (mg/m<sup>2</sup>) determination following Biggs and Kilroy (2000).

#### *Macroinvertebrate sampling*

We estimated benthic macroinvertebrate assemblage structure by sampling the same three transects used for periphyton determination using 0.086-m<sup>2</sup> Hess samplers (Wilco, Yulee, Florida, USA). After periphyton sampling, taking care to choose undisturbed streambed 0.5 m upstream of the removed cobbles, we took 15 Hess

samples per site visit (totaling 1.29 m<sup>2</sup> of sampled benthos). Samples were aggregated and preserved in buffered formalin (5% by volume). In the lab, samples were rinsed through a large (4.75 mm) sieve and the retained organisms were identified in full. The sample was further rinsed through a medium (2 mm) sieve, and the retained organisms subsampled by homogenizing the organisms in a flooded, large diameter PVC pipe with a 363- $\mu$ m screen at one end. As the water evacuated the pipe, organisms were evenly distributed on the screen, which allowed us to partition the subsample into quarters. Equal divisions of subsample were processed until both a fixed-area (at least 25% of the total sample) and a fixed-count minimum (at least 300 individuals) were reached for the 2-mm fraction. Using a coupled fixed-area/fixed-count approach has been shown to provide a representative sample of the entire assemblage (King and Richardson 2002). Concentrating on large-bodied taxa (>2 mm) potentially excluded some smaller size classes and meiofauna, but allowed us to rigorously sample over a wide temporal and spatial extent while still capturing the majority of taxa contributing to local diversity (we detected 61 of 69 taxa at overlapping sites as compared to Petersen et al. (2014), a regional survey, with 85 additional taxa observed in our study that they did not detect). Macroinvertebrate specimens were counted and identified to the lowest operational taxonomic unit, typically genus (except for Chironomidae, Hydrachnidia, and Oligochaeta; Stewart and Stark 2002, Merritt et al. 2008). During identification, 10 individuals of each taxa were randomly selected and measured using either an ocular micrometer or Vernier calipers for total length or head capsule width for biomass determination using length-mass regressions (Sample et al. 1993, Benke et al. 1999, Baumgärtner and Rothhaupt 2003, Edwards et al. 2009, Méthot et al. 2012). In instances where taxa could not be reliably associated with published regressions, we either dried and weighed organisms to create our own, or directly weighed dried organisms (four taxa; see in Appendix S3: Table S1 for a complete listing). We averaged taxa-specific biomass by site and event, and multiplied this by their counts standardized to the area sampled (1.29 m<sup>2</sup>). All site-specific biomass was summed to calculate mean total biomass (cumulative site biomass/number of site visits).

#### *Measures of temporal $\beta$ diversity*

Measures of  $\beta$  diversity can broadly be divided between values derived directly from classical metrics of  $\alpha$  and  $\gamma$  and multivariate measures that are calculated from pairwise dissimilarity values (sensu Anderson et al. 2011). We calculated the exponentiated Shannon index (also referred to as Hill numbers; Jost 2007) for both cumulative temporal diversity ( $\gamma_t$ ) and mean time-point specific diversity ( $\bar{\alpha}$ ) for each sampling site, which yields a metric of  $\beta_t$  diversity that incorporates relative

<sup>4</sup><https://nationalmap.gov/elevation.html>

abundance information ( $\beta_t$  [Shannon] =  $\gamma/\bar{x}$ ). We also calculated  $\beta_t$  (Richness) in a similar manner to the above, but used cumulative site richness and mean site richness ( $\beta_t$  [Richness] = cumulative richness/mean site richness). Though  $\beta_t$  (Richness) excludes abundance information, we included it both to determine if any trends observed in the study were driven by a richness gradient across the region, and for comparative purposes between our study and others.

We also calculated the multivariate dispersion (MVD) around site centroids in multivariate ordination space as a proxy of  $\beta_t$  using the betadisper function in R (Anderson et al. 2006). In the MVD method, community abundance data is compressed into a pairwise dissimilarity measure of choice, after which group dispersion is calculated in multivariate space from a principal coordinates ordination (PCO). We used a Bray-Curtis dissimilarity matrix due to its proven behavior along ecological gradients using abundance data. Also, we  $\log(x + 1)$ -transformed macroinvertebrate counts to incorporate abundance information without manifold increases in abundant taxa clouding the contribution of rare taxa (McCune and Grace 2002). As above, groups were considered as the aggregate of all sampling events of an individual site, with points in PCO space denoting the individual, locality-specific sampling events. The mean distances to group centroids were calculated, which we denote as  $\beta_t$  (MVD).

### Modeling

We first determined if any richness trends were present along our main gradient of interest by directly regressing mean site richness, cumulative site richness, and  $\beta_t$  (Richness) on mean TP and chl *a* using generalized linear models (GLMs). We then utilized GLMs within an iterative information-theoretic framework to examine the effect of eutrophication and other contributing or confounding variables on  $\beta_t$  (Shannon) and  $\beta_t$  (MVD) (Zuur et al. 2009). We visually screened variables known to influence macroinvertebrate diversity through a series of biplots and multivariate bubble plots, which included the two measures of eutrophy with measures of habitat variability, watershed area, frequency of scour, and mean total and snail macroinvertebrate biomass. This, coupled with correlation matrices, enabled us to select variables for model inclusion as well as assess collinearity and potential interactive effects. Although macroinvertebrate biomass was potentially non-independent, we viewed its use in the model as logical because the objective of this study was to characterize the effect of stream eutrophication on  $\beta_t$ , and a large amount of eutrophy-driven biomass could be sequestered in the macroinvertebrate compartment. Also, the dominant grazers in the region were operculate snails (Pleuroceridae) and, due to top-down suppression of benthic algal biomass, could potentially confound one measure of eutrophication (chl *a*). For these reasons, mean total macroinvertebrate as well

as mean snail biomass were each evaluated separately in modeling efforts. Because TP and chl *a* are highly correlated, each was modeled and reported separately for  $\beta_t$  (Shannon) and  $\beta_t$  (MVD).

As a measure of physical habitat variability through time, we calculated the MVD of temporal centroids based on a Euclidean distance matrix constructed from five instream and riparian variables; canopy cover, wetted width, midpoint current velocity, substrate embeddedness, and turbidity (all variables standardized to mean = 0 and SD = 1; Astorga et al. 2014). Composite measures sometimes have failed to yield significant relationships with community variation, so we also considered individual predictors (interquartile range of the five environmental variables, IQR) as potential drivers of  $\beta_t$  (Heino et al. 2015a).

In summary, the GLMs modeled both  $\beta_t$  (Shannon) and  $\beta_t$  (MVD) in response to TP and chl *a* with potential covariates. We specified a gamma distribution with a log-link function due to variance behavior, distributions of the residuals from each model, and positively bound continuous response variables. Covariates were sequentially removed and the Akaike information criterion corrected for sample size (AIC<sub>c</sub>) values examined in conjunction with deviance explained (%) to select the simplest models that explained the most variation in the response. We considered models with  $\Delta AIC_c < 2$  to be comparable in explanatory power (Bolker 2008). In cases where the most parsimonious model included covariates, we generated response surfaces examining the behavior of one predictor while holding the other predictors static.

As the analysis above is insensitive to the nature of the temporal trend (vectoral vs. cyclic sensu Korhonen et al. [2010]), we needed to verify our hypothesis that any change to  $\beta_t$  in response to eutrophication was driven by the collapse of a seasonal signal rather than the presence of an interannual one. We revisited the MVD analysis framework, and specified sampling time points as groups, with the distance to multivariate centroid interpretable as the degree of assemblage differentiation between spatial localities during a given sampling event;  $\beta_{\text{spat}}$  (MVD). If present, an interannual signal would manifest as the absence of any trend in  $\beta_{\text{spat}}$  plotted against the day of year. The vegan package was used to implement the betadisper function, and the classical measure of  $\beta_t$  was calculated using functions written in the R language environment (S. C. Cooke, *unpublished scripts*; version 3.3; R Core Team [2016]). All calculations, modeling, and plotting was also conducted in R.

### RESULTS

Mean TP and chl *a* ranged from 7.25 to 107.44  $\mu\text{g/L}$ , and 43.53 to 638.91  $\text{mg/m}^2$ , respectively (Appendix S2: Table S2). One site was exposed to untreated wastewater discharge during the study, resulting in near complete

macroinvertebrate mortality, and was excluded from analysis. We catalogued 212 unique taxa (Appendix S3: Table S1), and mean and median richness per sample was 26.15 and 26, respectively. Cumulatively, we identified 331,728 individuals over the course of the study, and mean and median counts per sample were 829 and 545, respectively. Cumulative site richness ranged from 52 to 97, and displayed no trend with either measure of eutrophy, while mean site richness and  $\beta_t$  (Richness) exhibited a weak but increasing ( $P = 0.03$ , 1.2% deviance explained) and sharply decreasing trend ( $P = 0.003$ , 25.1% deviance explained) with TP, respectively (Appendix S1: Fig. S2). Both  $\beta_t$  (Shannon) and  $\beta_t$  (MVD) showed sharp decreases in response to increasing TP and chl *a*, and displayed responses to secondary predictors including temperature variability (IQR), temporal habitat heterogeneity, disturbance frequency, and both total macroinvertebrate and snail biomass.

The model selection process resulted in three models of similar explanatory power using TP, and four models of similar explanatory power using chl *a* as the measure of eutrophy. Below we report the most parsimonious models for both measures of  $\beta_t$  (see Appendix S2: Table S1 for a complete listing). Secondary predictors that remained after model selection included temperature variability and two measures of macroinvertebrate biomass (mean total and snail biomass). The most parsimonious GLM of all models considered included an interactive effect between mean total macroinvertebrate biomass and TP (Fig. 1,  $P < 0.0001$ , deviance explained = 71.74%), and showed  $\beta_t$  (MVD) declining in response to both TP and mean total macroinvertebrate biomass. Macroinvertebrate biomass played a particularly large explanatory role at low to moderate levels of P enrichment, and showed a wedge-shaped response with increasing P enrichment.

The most parsimonious model using chl *a* as the measure of eutrophy included total macroinvertebrate biomass and temperature variability to predict  $\beta_t$  (Shannon) (Fig. 2,  $P < 0.0001$ , deviance explained = 67.45%).  $\beta_t$  (Shannon) declined in response to increased macroinvertebrate biomass, and increased in response to temperature variability. However, total macroinvertebrate biomass did not provide as large a boost in explanatory power over snail biomass when using chl *a* as the measure of eutrophy. Instead, mean total macroinvertebrate and mean snail biomass provided comparable explanatory power for both  $\beta_t$  (Shannon) and  $\beta_t$  (MVD) when chl *a* and temperature variability were included as covariates, with  $\Delta AIC_c$  scores between models of 1.39 and 1.88, respectively.

$\beta_{\text{spat}}$  illustrates differences in the macroinvertebrate assemblages across the TP gradient during a particular sampling event, and tracked with seasonally driven changes in water temperature (Fig. 3a, b). The cyclic tracking of  $\beta_{\text{spat}}$  with water temperature, highlighted by the GAM smoother, indicates that declines in  $\beta_t$  stem from losses in seasonally generated biodiversity. When

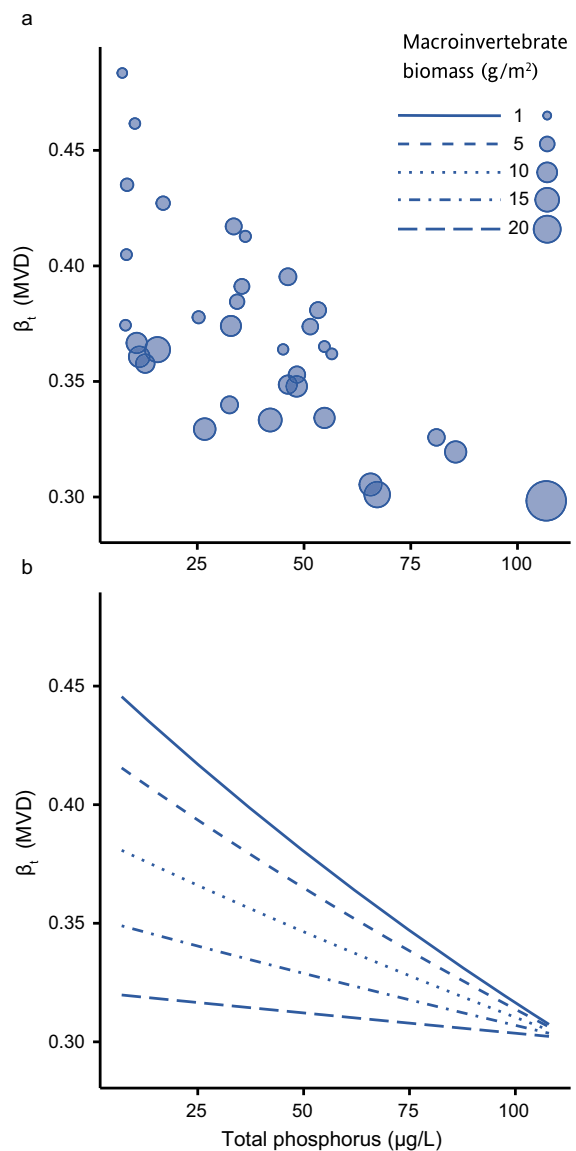


FIG. 1. Temporal  $\beta$  diversity ( $\beta_t$ ) of macroinvertebrate assemblages declined in response to total phosphorus (TP,  $\mu\text{g/L}$ ) and mean macroinvertebrate biomass ( $\text{g/m}^2$ ), which indicates increased temporal homogenization of community composition with increasing nutrient enrichment.  $\beta_t$  was quantified as the multivariate dispersion (MVD) around site centroids in ordination space. (a) Raw data points are sized by mean macroinvertebrate biomass observed at each site over the two-year study duration. The model describing the most variation in  $\beta_t$  (MVD, 71.74% deviance explained) included an interactive effect between TP and macroinvertebrate biomass. (b) The GLM response surface of  $\beta_t$  (MVD) to TP and macroinvertebrate biomass shows the modeled response of  $\beta_t$  (MVD) to TP at different levels of macroinvertebrate biomass (represented by lines ranging from 1 to 20  $\text{g/m}^2$ ).

regressed against mean site water temperature,  $\beta_{\text{spat}}$  was generally higher in the cooler months, and lower in the summer (Fig. 3c,  $P = 0.0318$ , deviance explained = 38.87%).

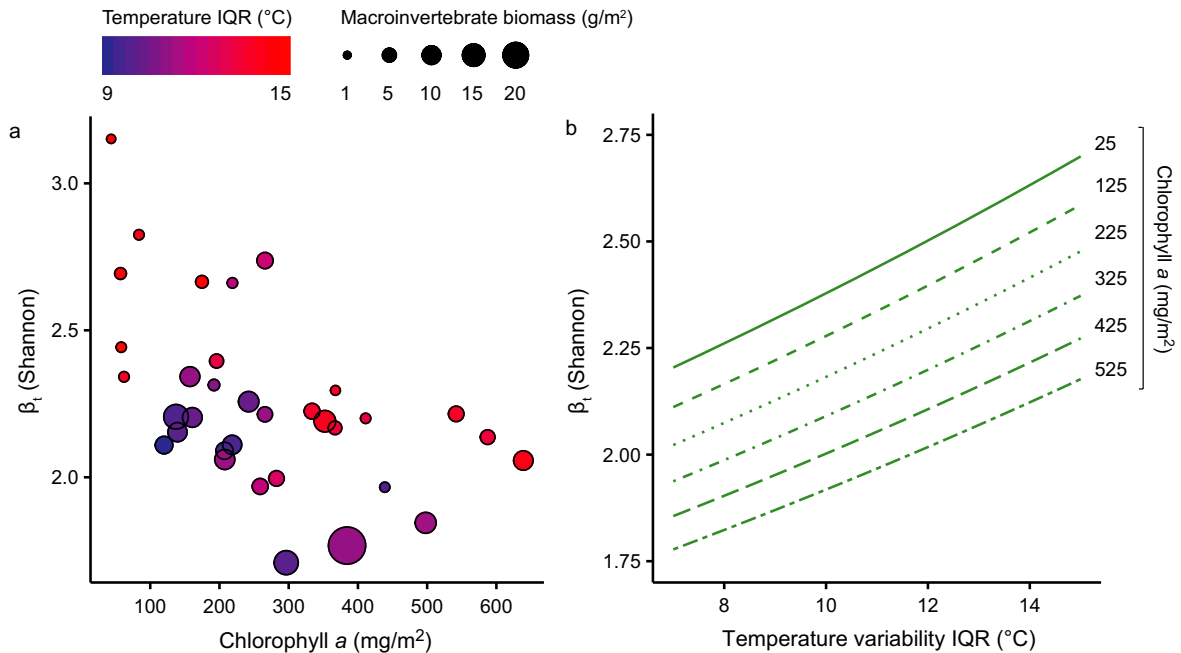


FIG. 2. (a) Temporal  $\beta$  diversity ( $\beta_t$ ) of macroinvertebrate assemblages declined in response to increasing chlorophyll *a* (chl *a*) and mean macroinvertebrate biomass (1–20  $\text{g/m}^2$ , points scaled by size), and showed a positive relationship with increasing temperature variability ( $^{\circ}\text{C}$ , interquartile range [IQR]), with variability decreasing from red to blue.  $\beta_t$  was quantified using the exponentiated Shannon diversity index. (b) The GLM response surface of  $\beta_t$  (Shannon) in response to temperature variability and macroinvertebrate biomass shows the modeled response of  $\beta_t$  (Shannon) to temperature variability at different levels of eutrophication (67.45% deviance explained, chl *a* represented by lines ranging from 25 to 525  $\text{mg/m}^2$ ). Macroinvertebrate biomass was included in the model, and was held constant at the mean observed value across all study sites to calculate the temperature response surface.

## DISCUSSION

Our study shows that eutrophication stemming from anthropogenic nutrient inputs leads to more temporally homogenous communities. Species comprising benthic communities are intimately linked to seasonal cues that govern the timing of reproductive cycles and peak resource assimilation (Wolda 1988, Bêche et al. 2006, Johnson et al. 2012, Bonada and Resh 2013). The cyclic trend of  $\beta_{\text{spat}}$  (Fig. 3) strongly suggests that the decline in  $\beta_t$  with increasing eutrophication was generated by the collapse of naturally occurring seasonal oscillations in community composition.

High values of  $\beta_t$  at the low end of the eutrophication gradient argue for a larger role of temporal niche partitioning (Fig. 1), whereas the decreasing and narrowing range of  $\beta_t$  as eutrophication increases suggests an expansion of temporal niche space dominated by exploitative taxa. Finely partitioned temporal niches are occupied by taxa with life-history strategies that maximize resource utilization by temporally offsetting interspecific competition, or timing periods of peak cohort growth to co-occur with the availability of basal resources or ideal hydrology (Merritt et al. 2008). Freshwater systems are increasingly experiencing novel nutrient concentrations uncharacteristic of their evolutionary

past (King et al. 2011, Radeloff et al. 2015), which release communities from nutrient limitation (Carpenter et al. 1998). Novel increases in nutrient inputs alter the competitive balance of temporal resource exploitation, effectively reducing the benefit that specialist taxa gain by occupying a particular temporal niche. Both experimental evidence (Cross et al. 2006) and observational field studies (Singer and Battin 2007, Evans-White et al. 2009) show that taxa with faster growth rates and higher P demand respond strongly to nutrient enrichment. As nutrient inputs increase, taxa normally constrained by evolutionary P limitation are released to rapidly complete their life cycles (Elser et al. 2000, Brown et al. 2004), which would shift assemblage composition by altering the dominant form of voltinism present in the assemblage.

There were likely additional environmental filters concomitant with high levels of eutrophication that caused direct stress to sensitive taxa; such as diel fluctuations in dissolved oxygen (Carpenter et al. 1998), increased rates of sedimentation (Paulsen et al. 2008), and homogenization of the physical structure of the basal resource compartment (Dodds and Gudder 1992, Goldenberg Vilar et al. 2014). Declines in assemblage variation in response to anthropogenic stressors have primarily been attributed to large reductions in the number of taxa at impacted

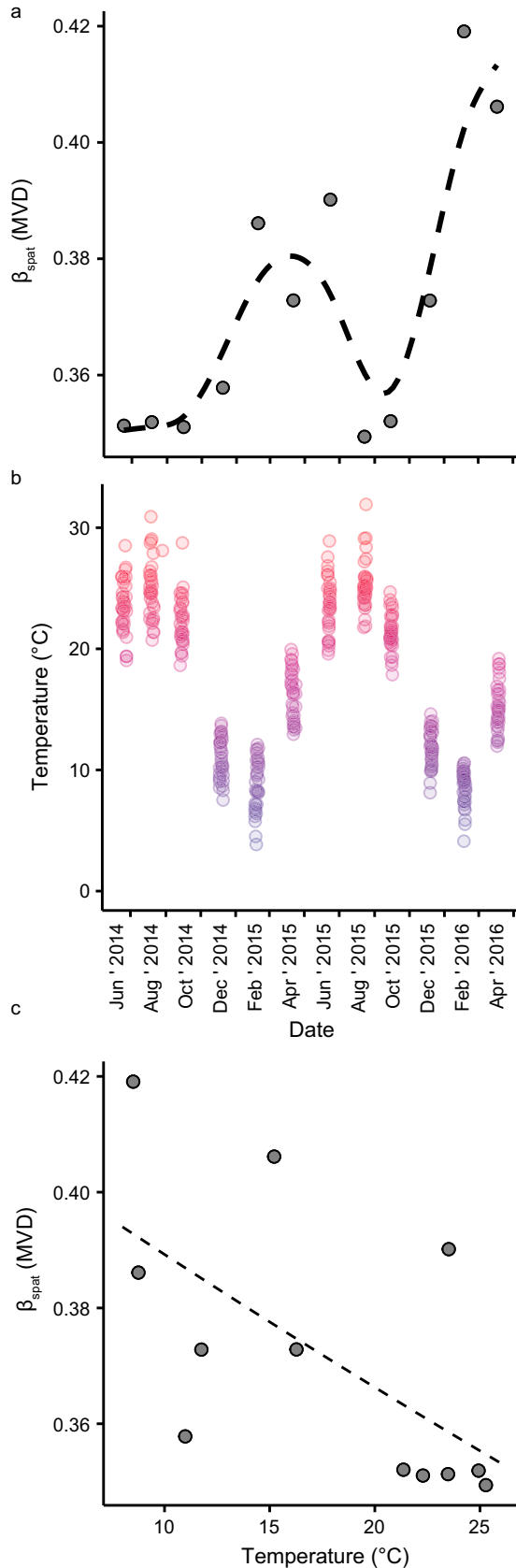


FIG. 3. (a) Spatial  $\beta$  diversity ( $\beta_{\text{spat}}$ ) displayed seasonal oscillations over the two-year study duration, and tracked with (b) site water temperatures ( $^{\circ}\text{C}$ ), which suggests that the declines in temporal  $\beta$  diversity with increasing eutrophication stem from losses in seasonally driven biodiversity.  $\beta_{\text{spat}}$  was quantified as the multivariate dispersion (MVD) around sampling event centroids in ordination space, and represents the degree of assemblage differentiation between spatial localities during a given sampling event.  $\beta_{\text{spat}}$  was overlaid with a GAM smoother (a, dotted line) to highlight the oscillations. (c)  $\beta_{\text{spat}}$  was generally higher in the cooler months than in the summer, and displayed a negative relationship with mean site water temperature (GLM regression,  $P = 0.032$ , 38.87% deviance explained).

sites (Helms et al. 2009, Johnson et al. 2012). While we did not observe any reductions in cumulative site richness with increasing eutrophication, anthropogenic stressors have been shown to have a disproportionate effect on specialist taxa (Gutiérrez-Cánovas et al. 2013). Likely a combination of both direct taxa responses to the eutrophication gradient and indirect effects on interspecific interactions lead to declines in  $\beta_i$ .

Seasonal cues manifest primarily as changes in irradiance and precipitation (Newbold et al. 1994), which can vary widely by latitude and region. The magnitude of seasonality and the predictability of seasonal events govern the degree to which communities have evolved to utilize distinct temporal niches (Tonkin et al. 2017). Though we found a strong relationship between eutrophication and  $\beta_i$ , the degree to which  $\beta_i$  is reduced is likely dependent upon the degree of seasonality present in a given region (Bêche et al. 2006, Bonada and Resh 2013). The spatial extent of the study contains numerous groundwater seeps and several wastewater treatment plant discharges; both of which buffer stream water temperature. Thermal regime is one of the primary controls of macroinvertebrate growth and life history event synchronization, and even closely related taxa can display different optimal thermal conditions (Vannote and Sweeney 1980). Though we did not explicitly test the mechanism of action, it is likely that decreased variability in temperature selects against taxa that utilize fast-seasonal life cycle adaptations (Hawkins et al. 1997, Wood et al. 2005), thereby decreasing  $\beta_i$ .

Both the strength and weakness of community analysis lies in its ability to integrate abiotic conditions and biotic interactions across time, and difficulty arises when the antecedent conditions that led to the sampled community are no longer observable. These findings strongly suggest that treating temporally dynamic communities as relatively static assemblages is a simplification that may fail to detect temporally explicit assemblage-environment relationships (Heino et al. 2015c). Rather, sampling that occurs only annually may generally prove to be inadequate for the study of metacommunity structure at the regional level for a variety of aquatic assemblages with active dispersal capabilities (Erős et al. 2012, Johnson et al. 2012, Fernandes et al. 2014, Hewitt et al. 2016). Incorporating appropriate temporal extent into

study design is vital to address ecological questions that may be influenced by temporal factors, and the majority of studies to date have either focused on a temporal scale too fine to detect seasonality (~1 month duration; Brown 2003), or on a temporal extent aimed at assessing long-term community stability (repeated sampling of the same time point over multiple years; Mykrä et al. 2011). The wide range of  $\beta_t$  observed in this study examined in light of the wide variation in temporal extents of other studies indicate that comparative examinations of  $\beta$  diversity between systems may be exceedingly difficult (see Heino et al. 2015b), and further study of the factors influencing seasonally driven community variation are needed. However, integrating biological data over sufficient time periods has been shown to reveal underlying environment–community relationships that are not readily apparent with single event sampling (e.g., King et al. 2016).

The increased explanatory power of snail biomass in models where chl *a* was the measure of eutrophy highlights the importance of quantifying forces that remove benthic algae. Though chl *a* provides a measure of algal productivity that directly influences macroinvertebrate taxa, it has the drawback of being influenced by both top-down suppression from grazing as well as by physical disturbance. Astorga et al. (2014) reported a lack of significance between chl *a* and  $\beta_{\text{spat}}$  when aggregating multiregional data, and attributed this to the confounding influence of physical disturbance (i.e., scouring events removing periphyton biomass). Our findings support their conclusion, as the temporal homogenization of communities may manifest spatially when comparing regions with different levels of productivity. TP, while being causally removed from direct effects on macroinvertebrate taxa, has the benefit of being robust to both physical and biological disturbance (though rapid uptake by periphyton during bloom conditions may influence nutrient concentrations in the water column).

Measuring biodiversity loss and its impact on ecosystem structure and function is an imperative task that is complicated by the variety of spatial and temporal extents of observational data (Cardinale et al. 2012, Socolar et al. 2016). Our study demonstrates that eutrophication reduces seasonally driven variation in community composition, and adds to a growing body of literature exploring controls on intra-annual succession (Bêche et al. 2006, Bonada and Resh 2013, Steiner 2014, Tonkin et al. 2017). Benthic consumers occupy a key linkage in stream food-webs by remineralizing nutrients and aiding in the breakdown of allochthonous resources (Cross et al. 2005, 2006). Reduced temporal specialization of consumer assemblages could exert a top-down feedback that contributes to decreased ecosystem efficiency caused by increased dominance by generalist consumers. The current prevalence and projected increase in nutrient enrichment (Smith et al. 2006, Paulsen et al. 2008) may therefore have profound and unanticipated effects on the whole aquatic ecosystem that is

significantly underestimated by examining the spatial component of biodiversity alone. More studies examining both the spatial and temporal dimensions of  $\beta$  diversity are needed for a robust understanding of community variation and its effects on aquatic ecosystems.

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#### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecs.2069/supinfo>

#### DATA ACCESSIBILITY

Macroinvertebrate data associated with this study are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3r44n>