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### Excess of nitrogen reduces temporal variability of stream diatom assemblages

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#### Abstract

Nutrient enrichment degrades water quality and threatens aquatic biota. However, our knowledge on (dis)similarities in temporal patterns of biota among sites of varying level of nutrient stress is limited. We addressed this gap by assessing temporal (among seasons) variation in algal biomass, species diversity and composition of diatom communities in three streams that differ in nutrient stress, but are otherwise similar and share the same regional species pool. We monitored three riffle sections in each stream bi-weekly from May to October in 2014. Temporal variation in water chemistry and other environmental variables was mainly synchronous among riffles within streams and often also among streams, indicating shared environmental forcing through time. We found significant differences in diatom community composition among streams and, albeit less so, also among riffles within streams. Diatom communities in the two nutrient-enriched streams were more similar to each other than to those in the nutrient-poor stream. Taxa richness did not differ consistently among the streams, and did not vary synchronously at any spatial scale. Temporal variation in diatom community composition decreased with increasing DIN:TotP ratio, likely via a negative effect on sensitive taxa while maintaining favorable conditions for certain tolerant taxa, irrespective of season. This relationship weakened but remained significant even after controlling for stochastic effects, suggesting deterministic mechanisms between nutrient levels and diatom community stability. After controlling for stochastic effects temporal variability was best explained by DIN suggesting that excess of nitrogen reduces temporal variability(intra-annual beta diversity) of diatom communities. The high temporal variation, and especially the

lack of temporal synchrony at the within streams scale, suggests that single sampling at a single site may be insufficient to reliably assess and monitor a complete stream water body. Our results also showed that measures including species identity outperform traditional diversity metrics in detecting nutrient stress in streams.

Keywords: anthropogenic stress, beta diversity, community homogenization, eutrophication, intra-annual, temporal variability

#### 1. Introduction

Nutrient enrichment degrades water quality and is considered to be among the major threats to aquatic biota. Despite widespread recognition of the problem, and consequent national and continental-scale actions to improve the situation, nutrient levels are still exceeding the natural base concentrations, and even increasing in many regions (Bennett et al. 2001, Canfield et al. 2010). The earlier view of singleresource limitation has shifted towards prevalence of co-limitation by multiple resources, but phosphorus and nitrogen are generally the most critical nutrients limiting primary production in both aquatic and terrestrial ecosystems (Harpole et al. 2011). Aquatic algae respond readily to increased availability of limiting nutrients, potentially altering ecosystem processes and food-web interactions, and thereby causing loss or reduction in the services that these systems provide (Smith et al. 1999, Dodds 2006). Nutrient enrichment may lead to local extinctions or decreasing abundances of sensitive taxa and concurrent colonization and strong increase of tolerant taxa (Taylor et al. 2014). Consequently, waters differing in nutrient concentrations differ often also in species composition, regardless of ecosystem type, taxonomic group or trophic level (e.g. Jeppesen et al. 2000, Nelson et al. 2013, LeBrun et al. 2018, Zhang et al. 2019). Even a relatively modest increase in nutrient inputs, and especially in their relative concentrations, may induce shifts in community composition of primary producers and related ecosystem functioning (Nelson et al. 2013). However, our knowledge of the similarity, or lack thereof, in temporal dynamics of biological variables among sites of varying level of anthropogenic stress is rather limited.

Nutrient enrichment has also been related to biodiversity loss and change. Species richness does not necessarily show a consistent pattern of increase or decrease as a result of nutrient enrichment

(Mittelbach et al. 2001, Biggs & Smith 2002), but nutrients can erode spatial beta diversity, i.e. reduce compositional heterogeneity of biotic assemblages among sites (Eskelinen & Harrison 2015), and this can happen already at relatively low concentrations (Donohue et al. 2009). Such biotic homogenization has been observed in many ecosystems and is considered one of the leading causes for biotic impoverishment (Olden et al. 2004, Olden & Rooney 2006, McGoff et al. 2013). A recent study by Cook et al. (2018) suggests that community homogenization due to nutrient enrichment may hold true also temporally, with sites of higher nutrient concentration showing less seasonal variability in community composition.

The most plausible mechanisms behind the erosion of beta diversity as a result of nutrient enrichment are related to stress, productivity and environmental heterogeneity (Hawkins et al. 2015). From a temporal perspective (i.e. site-specific temporal β-diversity), it is likely that increased stress due to excess of nutrients will have a negative effect on sensitive and positive effect on tolerant taxa, leading to reduced beta diversity if tolerant taxa are temporally common (i.e. exhibit little intra-annual/annual variability; Cook et al. 2018). Increased productivity can increase community stability (i.e. reduce temporal beta diversity) by allowing more species to co-exist or, alternatively, it can decrease stability by promoting opportunistic responses of individual species leading to unstable population dynamics (Chase 2010, Stegen et al. 2013). Environmental heterogeneity may also have a twofold effect: it may increase temporal beta diversity by providing more habitats or by favoring different species at different times (niche sorting) or it may stabilize communities by providing refugia against predation or disturbances (Brown 2003).

We explored intra-annual temporal dynamics of epilithic benthic algae in boreal streams with differing level of anthropogenic nutrient inputs, based on the finding that temporal variation in aquatic communities, including algal communities, is often stronger within than among years (Korhonen et al. 2010, Andrus et al. 2013). Our key aim was to study whether anthropogenic nutrient enrichment influences taxonomic composition of stream diatoms and the level and pattern of their intra-annual variability. Benthic diatoms have species-specific ecological requirements and short generation times, being therefore one of the most widely used groups in freshwater bioassessment. We hypothesized that nutrient enrichment homogenizes algal community composition through time, with nutrient enriched sites

exhibiting less intra-annual variability in occurrences and relative abundances of diatom species in comparison to sites of low nutrient concentrations. In addition to quantifying the degree of similarity in intra-annual dynamics of biological variables among streams (and among riffles within streams) of differing nutrient input, we also explored similarity of dynamics in physico-chemical variables. Even if sites differ in absolute values of variables, their temporal dynamics may be synchronous, reflecting concurrent highs and lows at different sites through time. This could be especially clear in boreal ecosystems where the dynamics of environmental conditions translate to seasonal oscillations in community composition (Tonkin et al. 2017). Therefore, we expected i) similar temporal oscillations of physico-chemical variables across streams and riffles within streams if they are driven by the inherent seasonality of boreal streams; and ii) consequently, synchronous temporal oscillations of biological variables across sites among or within streams if they are then driven by such synchronously varying environmental variables.

From an applied perspective, we assessed if temporal variability in benthic diatom assemblages affects the status assessment of a site, testing whether i) a defined ecological status of a site (reference vs. degraded) is temporally constant, and ii) separate riffles of a stream yield the same status classification (i.e. temporal / spatial representativeness of a single time point / site, respectively). In addition, we compared the performance of different biodiversity metrics in identifying nutrient enrichment. Recent studies by Larsen et al. (2018; consumers) and Hillebrand et al. (2018; primary producers) reported on failures of simple richness measurements to detect a systematic change in biodiversity. Thus, we hypothesized that metrics including information on species' identity and abundance patterns outperform a mere species number in detecting human impact on stream biodiversity.

#### 2. Materials and methods

#### 2.1. Study sites and design

Benthic algae, along with concurrent data on environmental variables, were collected from three riffle sites in each of three boreal streams (Juuvanjoki, Muhosjoki, Tyrnävänjoki). Sampling was conducted 11 times in

two-week intervals over six months, covering the algal growing season from spring (May) to late autumn (October) 2014. The study sites are in 3rd order streams in the Middle Boreal ecoregion in northern Finland and they drain into the Bothnian Bay of the Baltic Sea (Fig. S1). All three streams have sparsely populated catchments, but they differ strongly in the degree of agricultural nutrient input. Juuvanjoki represents a near-natural catchment with negligible agricultural pressure (< 1% agricultural land use), the other two streams having a higher pressure with 9% and 11% agricultural land use in Muhosjoki and Tyrnävänjoki catchments, respectively. Otherwise the streams are closely similar in their natural characteristics and share the same potential species pool.

#### 2.2. Algal community sampling

We used a portable fluorometric probe, BenthoTorch (bbe Moldaenke GmbH, Schwentinental) to measure algal biomass via chlorophyll *a* concentration in 15 randomly chosen cobble-sized stones per riffle and averaged these measurements to obtain site- and time-specific estimates of total benthic algal biomass. Estimation of total algal biomass by BenthoTorch has been shown to be closely similar to more conventional methods, e.g. brushing stones and measuring chl-a content with spectrophotometer, whereas the relative contribution of different algal groups to benthic algal biomass was shown to differ between BenthoTorch and microscope observations (Kahlert & McKie 2014).

To describe the composition of epilithic diatom assemblages we sampled benthic periphyton from 5 stones used for chl-*a* measurement by brushing the upper stone surface with a toothbrush and rinsing the diatoms from the toothbrush to river water in a container for one combined sample per time and site. Samples were preserved in ethanol (final concentration 70%). Diatom cells were cleaned using strong acid solution (HNO<sub>3</sub>+ H<sub>2</sub>SO<sub>4</sub>; 2:1) and mounted in Naphrax. Four hundred diatom valves per sample were identified to the lowest feasible taxonomic level using light microscopy equipped with differential interference condenser. Taxonomic identification was based on Krammer & Lange-Bertalot (1986-1991),

Lange-Bertalot (2000-2011), and Hofmann et al. (2011). Singletons as well as taxa consisting < 1% of total abundance were excluded prior to any statistical analyses.

#### 2.3. Environmental measurements

We collected water samples and measured local environmental variables at the same time with algal sampling. Water samples were analyzed for major nutrients: total nitrogen (TotN), inorganic N (NO<sub>2</sub> + NO<sub>3</sub> and NH<sub>4</sub>), total phosphorus (TotP) and phosphate P (PO<sub>4</sub>). All nutrient analyses as well as determination of water color and turbidity were conducted in an accredited laboratory following Finnish national standards (https://www.finas.fi/Documents/T003\_M40\_2019.pdf). In addition, we measured water temperature, pH, conductivity and dissolved oxygen in the field using YSI Professional Plus -meter (YSIInc., Yellowsprings, Ohio, USA). We delineated catchments for each site in ArcMap and calculated percentages of various land uses in each catchment from Corine 2012 data. Mean discharge for each site for a 14-d period prior to sampling was obtained from the national hydrological model VEMALA (Huttunen et al. 2016). A 14-d period was chosen to describe average discharge conditions between samplings. Only little variation has been observed in explanatory power of discharge parameters from 3 to 45 days before sampling (Jacobsen et al. 2014). The full list of descriptive variables and their site-specific mean values are presented in Table 1 and site-specific temporal variation across the study period in a supplementary Table S1.

#### 2.4. Data analysis

Diatom assemblage structure was described by calculating taxonomic richness and evenness for each sample. In addition, we used nonmetric multidimensional scaling (NMDS) ordination and analysis of similarity (ANOSIM) to visualize and statistically test, respectively, temporal and spatial patterns in assemblage composition based on relative abundance data. To study whether the spatio-temporal patterns of core taxa differed from those of the entire assemblage we further examined variability in the occurrence of stream type-specific taxa (Aroviita et al. 2008), based on a nationally established list of diatom species

that commonly occur in natural or near-natural streams in a given stream type (here, peatland-draining medium-sized streams; Aroviita et al. 2012). Absence of type-specific taxa is considered to indicate anthropogenic impairment. The number of type-specific taxa is routinely used in bioassessment and corresponds to comparison of observed and expected taxa in other bioassessment applications (Moss et al. 1987, Hawkins 2006).

We quantified temporal variation in diatom assemblage composition, i.e. temporal species turnover ( $\beta$ -diversity), using two different methods. First, we computed temporal variation for each site by calculating pairwise dissimilarities across all consecutive time points and then averaged these values to yield each site a mean dissimilarity value. Second, we calculated multivariate dispersion around group centroids in multivariate ordination space, describing variation through time across all time points, using betadisper function in R (package vegan; Oksanen et al. 2014), a 'group' consisting of samples from the same site collected at different times. Multivariate dispersion describes the level of within-group variation, calculated in a multivariate space based on principal coordinates ordination constructed from pair-wise sample distances (Anderson et al. 2006). Distances of each sampling time to group centroid were averaged to gain single site-specific values describing the level of temporal variation in diatom assemblage composition (mean distance to group centroid, MDGC). For both methods, in addition to using raw observed dissimilarities, we used the difference between the observed and expected assemblage to control for the effect of differences in species richness (i.e.  $\alpha$  diversity) between samples. This was done using a null model approach (e.g. Chase et al. 2011). Using function nullmodel and algorithm swsh\_both\_r in vegan package we constructed a quantitative null model retaining original sample-specific species richness and total abundances, and stream-specific species frequencies and gamma diversity. Mean expected measure of assemblage variability was then calculated across 1000 iterations and departure from null expectation (i.e., effect size:  $\beta = (\beta obs - \beta exp)/SD \beta exp$ ) was used as the final measures of variability. Null models were constructed separately for each stream. Null expectation for riffles within each stream was drawn from these stream-specific null models.

Simple linear regression in R was used to examine the relationships between environmental variables and temporal variation in assemblage composition. Since our primary interest was to test the relationship between community dynamics and nutrient enrichment we focused on nutrient concentrations (inorganic N and total P; Bergström 2010) as the key environmental variables potentially related to assemblage variability through time.

To test for similarity of temporal dynamics at different spatial extents (among streams; among riffles within streams) in environmental and biological variables, we calculated the level of coherence (i.e. synchrony) by computing Spearman rank correlation coefficient in R between all possible site pairs (with no time lag) for each variable following the procedure in Huttunen et al. (2014). Spearman coefficient was chosen instead of Pearson, because we were interested in detecting concurrent highs and lows among the sites irrespective of potential differences in absolute values. For each response variable an average value across all possible site pairs at each spatial extent was used as mean coherence. Statistical significance of individual coherence values was estimated by computing bootstrapped 95% confidence intervals for each variable at each spatial extent, resampling time instead of sites (see Lillegård et al. 2005). Instead of individual time points, we resampled moving blocks of two consecutive time points to take into account potential temporal autocorrelation in data structure. Resampling with replacement was run 1000 times for each variable and coherence was deemed statistically significant if the 95% confidence levels across those 1000 runs did not overlap zero.

#### 3. Results

The study streams (and to some degree also riffles within streams) differed in both average level and temporal variation of nutrient concentrations, with the near-natural Juuvanjoki having clearly the lowest and least variable concentrations of both phosphorus and nitrogen (Fig. 1 a-f, Table 1). Of the two nutrientenriched streams Tyrnävänjoki had the highest levels of phosphorus (TotP) and Muhosjoki of dissolved inorganic nitrogen (DIN). The DIN:TotP ratio was clearly highest in Muhosjoki (average across riffles and

time: 7.5), indicating high availability of inorganic nitrogen in relation to phosphorus whereas the other two streams had more equal concentrations (DIN:TotP 2.2 in Juuvanjoki and 2.0 in Tyrnävänjoki). Also benthic algal biomass was higher, and increased through the growing season, in the nutrient-rich streams, whereas in the near-natural Juuvanjoki algal biomass was constantly low (Fig. 1 g-i). Most environmental variables varied across the sampling period (Table S1). Temporal variation in water chemistry variables was highly synchronous among riffles within streams but less so among streams. However, variation in pH and conductivity, along with physical factors such as water temperature and discharge, was temporally coherent also among the streams (Table 2a). Temporal dynamics of algal biomass were synchronous at both among and within-stream scales, especially in both nutrient-enriched streams (Table 2b).

We identified 70 diatom taxa that were observed in more than one sample and consisted >1% of total sample abundance and were thus included in statistical analyses. Site-specific total taxa richness through time,  $\gamma$ -diversity, ranged from 39 to 48, and mean  $\alpha$ -diversity (i.e., taxa number per sampling time) from 13 to 20 taxa. Of all taxa observed, 35 occurred in all three streams at least once during the study period. We found significant among-stream differences in diatom assemblage composition (global R<sub>ANOSIM</sub> = 0.654) and these spatial differences were mostly maintained through time, with the mean among-stream dissimilarity exceeding the within-stream dissimilarity (Fig. 2, Fig. S2). Assemblages in the two nutrient-enriched streams resembled each other more than those in the nutrient-poor stream, as indicated by the greater distance of sample points in the NMDS ordination space and by the lower R<sub>ANOSIM</sub> values (Fig. 2, Table S2). There were differences in assemblage composition also at the within stream scale, but these differences were less pronounced, with the global R<sub>ANOSIM</sub> ranging between 0.206-0.373, assemblage composition among riffles within a stream being most similar in Muhosjoki and least similar in Tyrnävänjoki.

Temporal beta diversity, i.e. variation in diatom assemblage composition through time, was high at most sites (i.e. riffles) but less than spatial variation (i.e. distance between sites; Fig. 2). Diatom assemblages were dominated by few taxa at all sites and at most times whereas a great share of the less abundant taxa changed from one time to another, causing temporal variation based on species

presence/absence data to be higher compared to relative abundance data (average dissimilarity 0.53 and 0.34, respectively). Especially in the nitrogen-enriched Muhosjoki the identity and relative abundance of dominant taxa (mainly *Achnanthidium minutissimum* (Kützing) Czarnecki *sensu lato*) remained stable throughout the study, making assemblage composition very persistent (Table S3). Correspondingly, the proportion of total abundance contributed by the three most abundant taxa was clearly highest for Muhosjoki (on average 79%), followed by the phosphorus-enriched Tyrnävänjoki (72%) and nutrient-poor Juuvanjoki (66 %).

Temporal beta diversity, measured either as pairwise dissimilarities across consecutive time points or as mean distance to group centroids based on all possible sampling times, was related to nutrient concentrations. The level of temporal beta diversity decreased with increasing DIN:TotP ratio (i.e. high inorganic nitrogen concentration in relation to total phosphorus; Fig. 3a, Fig. S3a), independent of total algal biomass. This relationship weakened but remained statistically significant even after controlling for stochastic effects, suggesting deterministic mechanisms between nutrient levels and diatom assemblage stability (Fig. 3b, Fig. S3b). Also, average DIN concentration (especially NO<sub>2</sub>+NO<sub>3</sub>) and its temporal variation (CV) was related to temporal beta diversity (departure from null (SES); R<sup>2</sup>=0.57 (p=0.02) and R<sup>2</sup>=0.46 (p=0.04), respectively), suggesting that assemblage variability was more likely dictated by the amount of inorganic nitrogen than phosphorus, with assemblage composition being less variable at sites of constantly high concentrations of inorganic nitrogen. The results were closely similar also when PO<sub>4</sub> was used instead of TotP, the only difference being that the relationship between temporal beta diversity and the nutrient ratio was weaker after controlling for stochastic effects, further highlighting the key role of nitrogen.

Opposite to diatom assemblage composition, taxonomic richness did not differ consistently among the streams (or riffles) although on average the nutrient-poor stream had somewhat higher diversity than the other two streams (Fig. 4a-c). Evenness was on average lower in the nutrient-enriched Muhosjoki, but otherwise differences among streams or riffles were small and inconsistent (Fig. 4d-f). Consequently, variation in community metrics was not positively coherent at any spatial scale (Table 2b). Instead, the most downstream riffle of river Tyrnävänjoki had an opposite temporal pattern of species

richness compared to the other two riffles, resulting in significant negative coherence at the within-stream scale. Temporal variation was independent both among and within streams also when based on type-specific taxa only (Fig. 4g-i, Table 2b). However, the nutrient-poor stream Juuvanjoki had on average more type-specific taxa than the two nutrient-enriched streams, indicating the near-natural conditions of this stream. Status assessment based on type-specific taxa varied through time in all three streams, including the nutrient-poor stream. Consequently, sites within the two nutrient-enriched streams as being in a degraded condition (Fig. 4g-i). However, in late summer surveys, i.e. the recommended time for sampling in routine bioassessment in Finland (Aroviita et al. 2012), sites were in most cases classified according to expectations based on the level of anthropogenic stress.

#### 4. Discussion

Freshwater eutrophication from anthropogenic nutrient inputs may change the composition of aquatic communities and alter ecosystem functions and food-web interactions. Regarding the pervasiveness of eutrophication, our understanding of the effects of nutrients on the temporal dynamics of freshwater assemblages is still limited. Our study demonstrates that anthropogenic nutrient enrichment influences stream periphyton both by altering its taxonomic composition and by affecting its intra-annual dynamics. However, each stream, and even separate riffles within a stream, behaved individually through time, with no consistent temporal patterns.

In accordance with the existing literature we reported decreasing synchrony from physicochemical to biological variables and from the among-streams to within-stream spatial extent (Magnuson et al. 1990, Arnott et al. 2003, Huttunen et al. 2014). Most of the measured physical and chemical variables behaved synchronously through time, especially at the within stream extent but among streams as well, suggesting that the study sites were experiencing similar temporal variation of abiotic factors. This is expected since boreal environments experience strong and predictable seasonality regarding air and water

temperature, precipitation and availability of light and nutrients (Tonkin et al. 2017, Snell et al. 2019). Seasonality in the abiotic environment may then be expected to control community composition and ecosystem processes. Accordingly, algal biomass at nutrient-enriched sites increased rather steadily until late autumn, starting to drop during the last sampling occasions, leading to high synchrony both among streams and among riffles within each stream for the two nutrient-enriched streams. Primary production generally responds strongly and rather consistently to nutrient enrichment (Johnson et al. 2009, Nelson et al. 2013) but, in addition to mean differences in algal biomass, intra-annual dynamics of algal biomass seemed to differ as well. There were clear differences in algal biomass among streams differing in nutrient concentrations, with clearly lower biomass in the nutrient-poor stream where, opposite to the nutrientenriched streams, algal biomass did not increase throughout the study period. Benthic diatoms did not show any consistent temporal patterns regarding community diversity or species identity but exhibited a low level of synchrony in all biological attributes except biomass. This is somewhat surprising considering the strong shared environmental forcing. All biodiversity measures investigated, particularly species richness, fluctuated from one sampling time to another without any consistent pattern, even among riffles within a stream, as indicated by low synchrony at all spatial scales.

Oscillation of environmental factors through time should favor different species at different times (Hutchinson 1961). Andrus et al. (2013) and Snell et al. (2019) reported seasonal variability to be the major gradient along which periphyton communities vary, and they observed a closely similar seasonal trend in community composition at each site, independent of the level of anthropogenic impact. Despite some site-specific temporal changes, we did not observe a systematic change across time in the identity or relative abundance of dominant taxa among sites. Intra-annual variation in diatom assemblage composition was high, but still less than spatial variation, and it was strongly related to nutrient concentrations. The negative relationship between assemblage turnover and DIN:TotP ratio, and especially the key role of DIN after controlling for stochastic effects, suggests deterministic control of algal assemblages by nutrients, with sites with constantly high availability of DIN harboring temporally stable diatom species composition. The observed variation in assemblage composition differed less from that expected by chance at nutrient-

poor sites. This indicates that temporal variation at nutrient-poor sites may be dictated more by stochastic processes of random establishment or local extinctions and sampling effects. Our results thus partly support earlier findings of homogenization of biological assemblages with nutrient enrichment (e.g. Donohue et al. 2009, Leboucher et al. 2019), but they further show that the same pattern may hold true also for temporal β-diversity as was recently reported also by Salgado et al (2018; aquatic macrophytes) and Cook et al. (2018; stream macroinvertebrates).

Cook et al. (2018) suggested that the temporal community variability of stream macroinvertebrates decreases with the increased dominance of generalist taxa that exhibit little seasonal turnover. In our study temporal stability seemed to arise largely from the strong dominance by a highly persistent diatom species complex, Achnanthidium minutissimum s.l., which comprises several small Achnanthidium species (Novais et al. 2015). The existence and significance of species turnover within the A. minutissimum s.l. complex remains unresolved because different morphotypes were not always identified. In general, however, species turnover was rather high, with the identity of rare (i.e. low abundance) species changing from one time to another with little effect on the abundance-based dissimilarity metric. Nelson et al. (2013) found several diatom groups known to be associated to low nutrient levels to exhibit a consistent decline in density with increasing nutrient enrichment. It thus seems likely that excess nutrients cause stress that eliminates, or decreases abundances of, sensitive taxa, resulting in strong and persistent dominance by tolerant taxa. Detecting species-specific threshold responses to nutrient enrichment (see Taylor et al. 2014, 2018) was not the aim of our study, yet consistent differences among streams in algal assemblage composition indicate differences in species' tolerances. Especially sites with high inorganic N concentrations were dominated by Achnanthidium minutissimum s.l., whereas sites with high P levels were often dominated by Fragilaria gracilis Østrup or Karayevia oblongella (Østrup) Aboal, and the nutrient-poor sites by Brachysira neoexilis Lange-Bertalot, a species found rarely and only in low abundance in the two nutrient-enriched streams. The absence of certain species due to nutrient enrichment was also suggested by nutrient-enriched sites supporting a lower number of type-specific taxa, i.e., taxa expected to be present at a site in the absence of human impact. The fact that both A. minutissimum s.l. and F. gracilis occurred

also at near-natural sites, although often less abundantly, whereas nutrient rich sites lacked several taxa, indicates again that the mechanism behind decreasing  $\beta$  diversity with increasing anthropogenic stress is species sorting (for a similar result on spatial  $\beta$ , see Chase 2007, Pound et al. 2019). An alternative explanation to observed patterns of assemblage stability might be that superior competitors (e.g. taxa with faster growth rates) benefit from increased nutrient concentrations, outcompeting less effective taxa. Riffles within the nutrient-enriched Muhosjoki did not differ much in nutrient concentrations: phosphorus and especially inorganic nitrogen levels were high and rather stable throughout the study period. This suggests that in addition to increased stress, temporally and spatially homogenous environment (here, water chemistry) could partly explain the similarity of diatom assemblages among riffles and also through time. Similar findings on the effect of environmental heterogeneity on species turnover were reported in a spatial context by Astorga et al. 2014.

Decrease of biological diversity has been considered as one of the signs of environmental stress on ecosystems (Odum 1985, Rapport et al. 1985), yet we saw no consistent differences in species richness among sites of differing nutrient input. Diatom richness may not respond linearly to chemical pollution, but rather follow a hump-shaped pattern (Pandey et al. 2017). However, a similar failure of species richness, or its change, to indicate anthropogenic impact was recently reported by Hillebrand et al. (2018) and Larsen et al. (2018). Quite the opposite, there were clear differences among our study streams in the assemblage composition of benthic diatoms. Despite high levels of temporal variation in species composition, spatial differences among streams were maintained through time. The two nutrient-enriched streams were more similar to each other than either of them was with the near-natural stream, indicating that species composition is a robust indicator of anthropogenic stress (see also Korhonen et al. 2013, Taylor et al. 2018). Taking species identity into account by basing richness estimates only on type-specific taxa resulted in a distinct and constant separation of near-natural from human-impacted sites, with the nutrient-poor sites having a higher number of type-specific taxa. Fertilization often decreases community evenness (Hillebrand et al. 2007), and we also observed that the cumulative abundance of key taxa was higher and community evenness lower in the nutrient-enriched streams.

Based on the observed among-stream differences in the number of type-specific taxa, diatoms should be a good indicator group for detecting anthropogenic stress in stream ecosystems. Comparison of observed to expected number of taxa provides a measure of biotic integrity that is used to assess the ecological status of a site (e.g. Hawkins 2006). The status class 'moderate' is the threshold for management actions in the European Water Framework Directive (EC 2000). From an applied perspective, quantifying the degree of temporal variation is a prerequisite for insightful management decisions. Our monitoring of the number of type-specific taxa revealed different assessment outcomes at different times (see also Snell et al. 2019). In addition, riffles within a stream did not always behave synchronously, resulting occasionally in differing assessment outcomes between riffles. Differences among riffles within a stream would be expected if the sites differ in the level of stress they experience. In our case, however, no clear trend of a riffle having constantly lower or higher number of type-specific taxa compared to other riffles in the same stream was observed. These findings challenge the representativeness of a 'one-timeone-site' sampling strategy for assessing the ecological status of a stream (see also Kelly et al. 2009, Huttunen et al. 2012). However, basing the status assessment on samples collected at the recommended time of the season (September) mainly resulted in expected status classifications.

We have demonstrated that despite shared environmental forcing, diatom communities behave rather independently through time even at the within-stream scale, indicating that local, rifflescale, factors override the effect of regional factors on community dynamics. Nutrient enrichment clearly modifies community composition and may dampen natural temporal variability, mainly by having a negative effect on sensitive taxa and maintaining favorable conditions for certain tolerant taxa. Community dissimilarities related to nutrient enrichment persisted through time. Thus, measures including species identity clearly outperform traditional diversity metrics in detecting ecological impacts of nutrient stress in streams.

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Solution

#### Figure captions

**Figure 1.** Seasonal variation in the concentrations of total phosphorus (a-c), inorganic nitrogen (d-f), and total algal biomass (chl-a  $\mu$ g/cm<sup>2</sup>; g-i) at each study site during summer 2014.

**Figure 2.** Spatial and temporal patterns in diatom community composition across 11 biweekly samples according to nonmetric multidimensional scaling ordination based on Bray-Curtis dissimilarity (relative abundance data). The scatter of symbols represents seasonal variation in community composition at each study site. Lines represent site (i.e. riffle) specific 95% confidence ellipses. R<sub>G</sub> signifies global dissimilarity between groups. Juu = Juuvanjoki (nutrient poor), Muh = Muhosjoki (nutrient enriched), Tyr = Tyrnävänjoki (nutrient enriched).

**Figure 3.** Average pairwise dissimilarity between consecutive time points (observed (a) and departure from null (b)), describing site-specific temporal variation in community composition in relation to average levels of DIN:TotP ratio. Symbols are weighted by algal biomass, i.e. the larger the symbol, the higher the mean biomass of algae at a site. Corresponding figures for mean distance to group centroid (MDGC) as a measure of community variability are shown in Fig. S3.

**Figure 4** Seasonal variation in diatom taxa richness (a-c), evenness (d-f) and number of type-specific taxa (gi) at each study site. The horizontal red line in the lowermost panel indicates the threshold between status classes 'good' and 'moderate' below which a site is considered impaired in ecological status assessment. Vertical red lines represent the recommended timing of diatom sampling in the national bioassessment program (Aroviita et al. 2012).

		Juuvanjoki			Muhosjoki			Tyrnävär		
	up	mid	low	up	mid	low	up	mid		
Catchment area (km²)	3.1	3.4	4.8	4.0	15.8	19.5	24.9	26.8		
Urban (%)	0.1	0.1	0.2	3	1.3	1.4	1.3	2		
Agriculture (%)	0	0	1.2	10.9	7.6	8.8	8.5	10		
Discharge (m <sup>3</sup> /s)	а	0.40	а	0.23	0.77	1.29	0.46	0.54		
Water depth (cm)	29.6	30.7	29.7	30.1	35.2	31.2	33.7	31.7		
Water temperature (°C) <sup>b</sup>	11.8	11.6	10.7	10.7	9.7	11.2	12.6	11.9		
Total P (μg /L)	10	12	20	47	54	62	53	90		
Phosphate P, PO₄ (µg /L)	2	2	5	14	16	20	11	20		
Total N (μg /L)	493	504	664	880	919	877	730	843		
Inorganic N, DIN (μg /L)	14	17	65	395	383	377	71	164		
DIN:TotP ratio	1.5	1.6	3.5	8.4	7.4	6.8	1.4	1.9		
Dissolved O <sub>2</sub> (mg/L) <sup>c</sup>	8.8	8.0	8.4	10.3	10.8	10.2	9.8	8.8		
рН	7.2	7.2	7.0	7.4	7.4	7.5	7.4	7.2		
Conductivity (mS/m)	49.5	52.2	60.4	47.1	57.2	60.4	34.3	67.0		
Colour (mg Pt/L)	147	147	185	199	171	197	253	266		
Turbidity (FNU)	3.2	3.1	6.2	15.9	21.1	19.5	9.6	11.1		
Total algal chl-a (µg/cm²)	0.81	0.91	1.31	1.87	1.73	2.05	1.87	1.49		

**Table 1** Site-specific means of environmental variables. Site-specific temporal variation across the studyperiod (CV) is presented in a supplementary Table S1.

<sup>a</sup> no riffle-based values from Juuvanjoki

<sup>b</sup> based on 10 time points

<sup>c</sup> based on 9 time points

**Table 2.** Means of temporal coherence in (a) physical, chemical and (b) biological variables among streams and among riffles within a stream. Values in bold indicate statistically significant coherence based on bootstrapped 95% confidence intervals. Juu = Juuvanjoki (nutrient poor), Muh = Muhosjoki (nutrient enriched), Tyr = Tyrnävänjoki (nutrient enriched). TS refers to type specific taxa (see text for further explanation).

		Among streams			Within stream		
	average	Juu-Muh	Juu-Tyr	Muh-Tyr	Juu	Muh	Tyr
a) Physical and chemical varia	bles:		0				
Discharge	0.58	0.51	0.63	0.61	а	0.68	0.98
Water depth	0.24	0.24	0.23	0.24	-0.07	0.17	0.14
Water temperature <sup>b</sup>	0.97	0.96	0.99	0.95	0.98	0.97	0.99
Total P	0.08	0.18	0.38	-0.34	0.63	0.57	0.83
Dissolved inorganic N	0.20	-0.06	0.32	0.33	0.34	0.53	0.69
Dissolved O <sub>2</sub> <sup>c</sup>	0.41	0.15	0.57	0.52	0.63	0.62	0.78
рН	0.81	0.82	0.78	0.82	0.81	0.90	0.92
Conductivity	0.56	0.61	0.62	0.44	0.86	0.98	0.61
Colour	0.53	0.56	0.74	0.29	0.82	0.77	0.84
b) Biological variables:							
Total algal biomass	0.03	-0.41	0.07	0.43	0.41	0.71	0.63
Richness (diatoms)	-0.05	-0.01	-0.07	-0.09	-0.11	0.26	-0.22
Evenness (diatoms)	0.09	0.20	0.10	-0.03	0.22	0.51	0.41
Richness (diatoms TS taxa)	0.02	0.06	0.04	-0.03	0.17	-0.19	-0.05

<sup>a</sup> No riffle-based values from Juuvanjoki

<sup>b</sup> Correlations based on 10 time points

<sup>c</sup> Correlations based on 9 time points

Graphical abstract

Highlights

- We studied how nutrient enrichment affects temporal dynamics of diatom communities.
- Community composition differed among streams of differing nutrient input.
- Temporal variation in community composition decreased with increasing DIN:TotP.
- Taxa richness did not differ consistently among the streams.
- Measures including species identity outperform traditional diversity metrics.

Solution





Figure 2



Figure 3

