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Flow regimes filter species traits of benthic diatom communities and modify the functional features of lowland streams - a nationwide scale study

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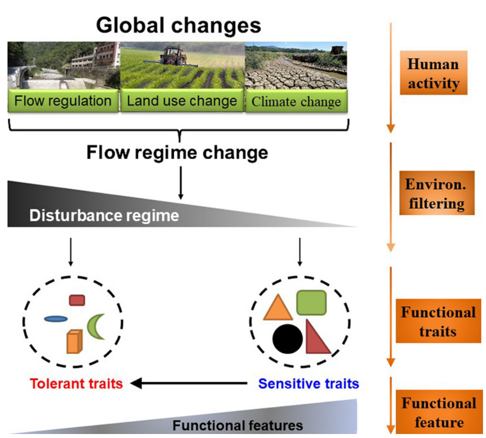
HIGHLIGHTS

- The responses of functional traits of benthic diatoms to flow regime changes are studied.
- Species turnover is the dominating process during high flow regime changes.
- Functional redundancy and diversity are mediated mainly by high and low flow magnitude.
- Median daily flow magnitude shows a consistent positive relationship with functional redundancy and richness indices.
- Our study highlights the robustness of trait-based approaches for identifying flow regime changes in streams.

GRAPHICAL ABSTRACT



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ABSTRACT

Changes in land use, climate and flow diversion are key drivers of river flow regime change that may eventually affect freshwater biodiversity and ecosystem functions. However, our knowledge is limited on how the functional features of stream organisms vary along the gradient of hydrological disturbance (i.e. flow regime changes) and how flow regimes mediate the functional features in lowland streams. We analyzed the functional traits of benthic diatoms (unicellular siliceous algae) that are most sensitive and tolerant to flow regime changes along a nationwide scale of 246 sites in Denmark. We combined RLQ and fourth-corner analyses to explore the co-variation between hydrological variables (R table) and species traits (Q table), constrained by the relative abundance of each species (L table) as observed in each of the sampling sites. Further, we examine the relationships between functional features (i.e., functional redundancy and diversity) and hydrological variables by multivariate statistical analyses. Results show that species turnover with displacement of sensitive species by tolerant species was the dominating process in benthic diatom communities during high flow disturbances. Functional features, as indicated by functional diversity and redundancy indices, were mediated mainly by high and low flow magnitude. Median daily flow magnitude shows a consistent positive relationship with functional redundancy and richness

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indices indicating that larger streams are more resilient to flow perturbations. In addition flow regime changes are less important than median daily flow magnitude and show inconsistent correlation to functional features likely due to the interaction of multiple environmental stressors. Our study highlights the robustness of trait-based approaches for identifying flow regime changes in streams, and strongly suggests that biodiversity conservation and water resource management should focus on protecting natural base flow in headwater streams and generally reduce flow regulation for sustaining stream ecosystems under future global changes.

1. Introduction

Global changes in land use and climate have caused dramatic changes to the hydrologic cycle causing immensely pressure to freshwater ecosystems worldwide. Conversion of land use and land cover can influence catchment properties and processes, including infiltration, water yield, surface runoff, lateral flow, groundwater recharge and water quality (Guse et al., 2015; Palamuleni et al., 2011). Deforestation can induce higher streamflow generation and reduce the time lag between precipitation and runoff leading to increased peak flow. In contrast, reforestation can dramatically decrease the streamflow generation while trigger an increase in flow concentration time. Climate change is another critical driver that can intensify the hydrologic cycle causing rivers to become flashier with larger swings between drought and flood conditions on seasonal and annual scales (Grimm et al., 2013). In addition, flow diversion due to for instance dam construction and river regulation is a key driver of flow regime change (Arheimer et al., 2017) and can disrupt the river's natural connectivity and impede the cycling of carbon and nutrient as transport downstream (Jenkins and Boulton, 2003).

The flow regime of rivers is one of the most important environmental variables, which controls the diversity and distribution of aquatic species through physical processes and habitat conditions and can alter nutrient cycling and export (Munn et al., 2010; Wu et al., 2016). Understanding ecosystem responses to environmental stressors is a long-standing interest in ecology and environmental management, and the relationships between river organisms and environmental conditions have been investigated with a long history. Nevertheless, previous studies and biomonitoring campaigns focused mostly on local physicochemical variables such as nutrients (Kelly and Whitton, 1995; Lange et al., 2011) as well as species dispersal (Leibold et al., 2004). Less attention has been paid to hydrological factors such as flow magnitude and flow changes (Qu et al., 2018; Sun et al., 2018), although some studies have shown that aquatic organisms are linked to the flow regime (Kuemmerlen et al., 2015; Wenger et al., 2011; Wu et al., 2016). With human-mediated fast global change, studying the river organisms in relation to abiotic factors, and identifying their driving mechanisms has become a major research focus of community ecology, since these are basis for prioritizing global and regional conservation efforts (Myers et al., 2000; Wang et al., 2016). Yet a profound understanding of the interaction of hydrological variables and benthic organism communities is still missing.

As the most abundant and diverse group of life on Earth, benthic diatom communities have been increasingly used as reliable environmental indicators in streams and rivers globally (Stevenson et al., 2010) due to their many merits, e.g., short-term life cycle, easy sampling, cosmopolitan with well-known autecology. Consequently, many assessment methods based on benthic diatoms have been developed in several countries and regions (Siddig et al., 2016). Generally, these assessment methods were mostly based on taxonomic composition, which are under strong micro-evolutionary constraints (Soininen et al., 2016) and do not fully meet the urgent demands for studies on global environmental change. Therefore, new approaches for biomonitoring purposes are required. Trait-based approaches applied to benthic diatom community ecology have led to a considerable advance in understanding the effect of environmental stressors on species assembly (Jung et al., 2010; Wu et al., 2017) because they give insights into underlying mechanisms driving community and ecosystem processes along the gradients of influential factors including responses to global change (Litchman and Klausmeier, 2008). In fact, traits have been used for different purposes in terrestrial plants (Grime, 1979; Tilman, 1980) and macroinvertebrate (Menezes et al., 2010), but have only very recently been considered for freshwater algae, particularly for benthic diatom community (Lange et al., 2016; McGill et al., 2006; Tapolczai et al., 2016). Besides, mechanisms driving species traits filtering in benthic diatom communities between different flow regimes is still poorly documented, especially from large scale studies. Thus, quantifying the responses of benthic algal assemblages to flow regime along temporal and spatial scales can promote an advanced understanding of how flow regimes affect river ecosystem structure and functioning.

A growing number of benthic algae surveys have adopted trait-based approaches and a range of traits are currently in use. A broadly accepted morphological and life form trait is diatom guilds (i.e., low profile, high profile, motile and planktonic), which can reflect not only the difference of dispersal ability, but also the environmental adaptability (Passy, 2007; Rimet and Bouchez, 2012). Meanwhile, other biological traits based on cell sizes, life history, physiology, behavior and morphology have been proposed and summarized recently (Lange et al., 2016; Wu et al., 2017). Trait-based approaches allow the estimation of many important components of ecosystem functioning (Hooper et al., 2005), such as functional diversity (FD) and functional redundancy (FR). Unlike traditional measures of species richness or diversity, FD presupposes a positive mechanistic link between diversity and the ecological function in question and is increasingly appearing in the literature (Cadotte et al., 2011). FR is also a promising functional index because it links positively to stability, resistance and resilience of ecosystems (Bruno et al., 2016; Hooper et al., 2005). However, mitigation of the ecological consequences of environmental change requires a deeper and sounder understanding of links between environmental stressors, biodiversity and ecosystem functions (Cardinale et al., 2012). Yet very few studies have investigated how stream ecosystem functions, resilience and stability vary along a gradient of flow regime, but see Neif et al., 2017; Piano et al., 2017; Schneider and Petrin, 2017, and to our best knowledge, none of these include large scale benthic diatom community studies.

Here we identify complementary functional traits, at the community level, that are most sensitive and tolerant to flow regime changes (Fig. 1) along a nationwide scale of 246 sites in Denmark. We combine RLQ and fourth-corner analyses (Dolédec et al., 1996; Dray et al., 2014; Kleyer et al., 2012) to explore the co-variation between hydrological variables (R table) and species traits (Q table), constrained by the relative abundance of each species (L table) as observed in each of the sampling sites. Further, we examine the relationships between functional features (i.e., functional redundancy and diversity) and hydrological variables. We hypothesize that (*Hypothesis 1*) high flow disturbance including high flow frequency, duration and magnitude selects for tolerant functional traits, e.g., small cell size species with low profile and firm attachment to substrate; (*Hypothesis 2*) low flow condition favors sensitive traits, e.g., big cell size species with high profile, filamentous and planktonic taxa; (*Hypothesis 3*) functional features (e.g., functional