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# Tropical stream diatom communities – The importance of headwater streams for regional diversity

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#### ABSTRACT

Understanding how species are distributed in space and time is a focal element guiding conservational efforts under ongoing climate change and the Holocene extinction. Freshwater habitats are currently one of the most threatened ecosystem types, and studies aiming to unravel factors that govern biodiversity of tropical stream micro-organisms are especially scarce. Diatoms play an important role as primary producers in streams and are widely used as ecological indicators. However, relatively little is known about which factors affect diatom communities in the tropics.

Here, we studied benthic diatom diversity across 67 tropical streams spanning stream orders 1–5 in Kenya. We examined whether the hypothesis of latitudinal diversity gradient applies for benthic diatoms, i.e. whether tropical streams encompass more species than boreal streams using a comparable boreal dataset. In addition, we studied which environmental, land use and spatial factors control benthic diatom communities using redundancy analysis. We also examined the nestedness and turnover components of beta diversity, factors contributing to diatom species richness, and the uniqueness of the communities across stream orders by using boosted regression trees and local contribution to beta diversity. Finally, we studied whether environmental heterogeneity and beta diversity are related across stream orders and tested their relationship using tests of homogeneity of dispersion and regression analysis.

Species richness was not higher in tropical streams than in boreal ones. Tropical diatom communities were controlled jointly by local environmental and spatial factors. Although water chemistry was the most important controlling factor, also physical variables contributed significantly to community variation. Land use had also a significant effect on diatom communities as broad leaved forest streams harboured different diatom communities compared with streams with higher human impact and conductivity, stressing the importance of forests to water quality and diatom biodiversity. Headwater streams encompassed the highest species turnover, whereas nest-edness was higher in higher order streams. Species richness was significantly higher in higher order streams than in headwaters, whereas the uniqueness of the communities peaked in headwaters. Environmental heterogeneity was the highest in headwater streams and was related to high beta diversity, which highlights the importance of habitat heterogeneity to biodiversity. Our results stress the management and conservational importance of headwater streams and tropical montane forests as these environments harbour unique diatom communities important for regional diversity.

#### 1. Introduction

How species are distributed across the Earth in space and time remains a fundamental topic guiding conservation efforts under ongoing climate change and the Holocene extinction (Pimm et al., 1995; Thomas et al., 2004). The extinction threat concerns not only terrestrial ecosystems but also aquatic communities. Freshwater habitats harbour a disproportionately large species richness in relation to habitat area in many taxonomic groups and freshwater biodiversity is more threatened than biodiversity in other ecosystems (IUCN, 2009; Strayer and Dudgeon, 2010; Wiens, 2016). Thus, an understanding of the drivers that maintain species diversity is urgently needed in order to combat the severe biodiversity losses taking place at the present.

While studies aiming to unravel the determinants of macro-organismal biodiversity have been extensive (Rosenzweig, 1995), microbial communities (e.g. bacteria, unicellular algae and fungi) have received

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less attention in this regard (Green et al., 2004; Zeglin, 2015). For example, whereas latitudinal diversity gradients are well documented for macro-organisms (Gaston, 2000; Hillebrand, 2004; Lawton, 1999), the existence of such a pattern for micro-organisms remains a controversial issue (Hillebrand and Azovsky, 2001; Passy, 2010; Salinas et al., 2015). Furthermore, microbial biodiversity studies in boreal and temperate regions have been far more numerous than in the tropics but see for example (Bellinger et al., 2006; Bere, 2014; Bojorge-Garcia et al., 2014; Mangadze et al., 2015).

The diversity and composition of microbial communities are affected by a wide range of determinants and there is still no consensus as to whether the key drivers are more related to the local environment (Gothe et al., 2013; Maloufi et al., 2016) or spatial factors (Crump et al., 2007; Soininen et al., 2004). Also land use (Bere and Tundisi, 2011; Carpenter and Waite, 2000) or climatic factors (Pajunen et al., 2016) may affect aquatic microbial communities. Finally, the spatial scale of the study influences the factors which govern microbial communities (Lindstrom and Langenheder, 2012), and communities may thus often be described by the shared influence of spatial and environmental factors, with increasing spatial influence in larger studies (Heino et al., 2014; Soininen et al., 2016; Verleyen et al., 2009).

Freshwater organisms may be especially vulnerable to changes in precipitation and possible droughts can quickly alter a freshwater habitat and thus its biodiversity (Wiens, 2016). Streams encompass a disproportionately high biodiversity (Vinson and Hawkins, 1998; Vorosmarty et al., 2010), and the stream network provides an excellent environment to study diversity patterns via its hierarchic dendritic organization (Grant et al., 2007). The river continuum concept (RCC) predicts biological diversity to peak at mid-order streams, whereas headwaters and large rivers should be less diverse (Vannote et al., 1980). However, while this prediction might hold true for alpha (local) diversity, beta (between-site) and gamma (regional) diversity may show different patterns as especially headwater streams (orders 1-2) may harbour a greater proportion of biodiversity compared with higher order stream branches (Meyer et al., 2007). Moreover, human induced disturbances usually increase with increasing stream order (Januchowski-Hartley et al., 2011), which may affect biodiversity. Headwater streams may also be more physically variable promoting environmental heterogeneity and subsequently also beta diversity (Finn et al., 2011). Consequently, possible environmental homogenization in higher order streams may decrease beta diversity compared with headwaters.

High beta diversity in headwaters may also be caused partly by the more isolated position of headwater streams compared with higher order branches (Finn et al., 2011). Thus, highly connected sites at lower reaches harbour lower beta diversity due to a higher exchange of individuals between sites leading to homogenisation of communities (Lopes et al., 2014). Furthermore, anthropogenic and natural stressors may cause different patterns in beta diversity given that beta diversity under natural disturbances may be caused more by species turnover (i.e. the shared number of species between sites is small), whereas community dissimilarities under anthropogenic stressors may be more generated by nestedness (i.e. poorer assemblages are subsets of those of richer sites) (Gutierrez-Canovas et al., 2013). These patterns are largely unresolved in the tropics, however, as stream beta diversity has not been studied extensively in tropical regions (but see Al-Shami et al., 2013; Tonkin et al., 2016) and microbial communities have received even less attention.

Sub-Saharan Africa is going through an intense land cover change due to human population growth and the subsequent conversion of forests into arable land (Brink et al., 2014; Pellikka et al. 2018). Land cover changes can have severe effects on the environment and natural resources (Alcantara-Ayala et al., 2006; Hohenthal et al., 2015). Furthermore, land use changes in the catchments may have profound effects also on aquatic ecosystems via water scarcity, increased turbidity, and nutrient fluxes (Allan and Castillo, 2007; Hohenthal et al., 2015; Soininen et al., 2015). The human impact on stream communities usually increases downstream, agricultural effects being the most severe threat to biodiversity (US -Environmental Protection Agency, 2000; Vorosmarty et al., 2010). The detrimental anthropogenic effects are increased by poor waste water treatment in many rural areas (Concoran et al., 2010). Indeed, freshwater biodiversity conservation under the increasing human demands for water poses a true challenge (UNESCO, 2009; Wiens, 2016; Vorosmarty et al., 2010).

Benthic diatoms are a pivotal component of stream biodiversity and are widely used as ecological indicators (Hill et al., 2000; Wang et al., 2005). We studied the diversity and composition of stream benthic diatom communities in the Taita Hills. Kenva. The area is considered a biodiversity hotspot with a high rate of endemism of plants (Beentje and Ndiang'ui, 1988; Gereau et al., 2006; Lovett and Wasser, 1993) and animals (Gereau et al., 2006). At the same time, however, the area is affected by intensive land use change along with other anthropogenic pressures threatening ecosystems and their functioning (Pellikka et al., 2013; Pellikka et al., 2009). First (Q1), we were interested in whether there are major richness differences between tropical and boreal stream diatoms. We thus compared diatom species richness between tropical and boreal streams using two data sets with identical sampling methods. We expected that species richness would be higher in the tropics as found for other taxa (Hillebrand, 2004). Second (Q<sub>2</sub>), we studied the effects of local environmental, land use and spatial factors on tropical stream diatom community composition. We expected water chemistry and stream physical variables to have a significant effect on diatom composition (Soininen, 2007) but also that communities are spatially structured (Piano et al., 2017). In addition, we expected land use to affect diatom communities indirectly via affecting water quality (Bere and Tundisi, 2011; Carpenter and Waite, 2000; Potapova and Charles, 2002). We considered the use of diatom diversity as an ecological indicator of land cover change by sampling diatoms in four massifs of the Taita Hills of Kenya, which differ in their land use history but are similar in their bedrock, soil types, forest species composition, agricultural crop composition and climate. Third  $(Q_3)$ , we studied the distribution of diatom biodiversity across stream orders. We expected headwater sites (orders 1-2) to harbour more unique diatom communities and, simultaneously, to have lower species richness than higher stream order sites (Meyer et al., 2007; Sherwood et al., 2000). We also examined beta diversity components, i.e. species turnover and nestedness across stream orders, and expected species turnover to be largest in headwaters while nestedness is largest in downstream sites. Fourth (Q<sub>4</sub>), we examined factors contributing to diatom species richness and the uniqueness of the communities. We expected that species richness is mostly related to conductivity (Heino et al., 2010) and pH (Jyrkankallio-Mikkola et al., 2017), whereas uniqueness would be most related to conductivity and nutrient levels (Pajunen et al., 2017). Finally (Q5), we studied whether environmental heterogeneity and diatom beta diversity are related across stream orders and tested their relationship. We expected headwater streams to harbour higher beta diversity and environmental heterogeneity (Finn et al., 2011; Meyer et al., 2007) than sites at higher order streams.

In this study, we characterized diatom communities using species richness, community composition and the uniqueness of species composition at sites, measured as local contribution to beta diversity

(LCBD) (Legendre and De Caceres, 2013). Since beta diversity provides the most useful measure to understand the processes that generate and maintain biodiversity (Legendre et al., 2005; Qiao et al., 2015; Socolar et al., 2016) we placed most emphasis on beta (between site) diversity in terms of dissimilarities and LCBD.

#### 2. Material and methods

#### 2.1. Study area

The Taita Hills form the northernmost part of the biodiversity

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