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Which environmental factors best explain variation of species richness and composition of stream bryophytes? A case study from mountainous streams in Madeira Island

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ABSTRACT

Freshwater ecosystems and their associated organisms are among the most endangered in the world. Here we focus on bryophyte communities in streams characterized by a strong altitudinal gradient. The main purpose of this study was to determine the most important environmental variables affecting bryophyte species richness and composition and to quantify the relative importance of different sets of environmental variables. We studied bryophyte communities at upstream, intermediate and downstream sections of 16 streams distributed on the northern and southern side of Madeira Island in the Atlantic Ocean. We found that bryophyte species richness and composition was strongly affected by the measured environmental variables. Of particular importance were the geomorphological and hydrological variables as well as the chemical and physical properties of the streams. Temperature (or altitude) was highly correlated with other variables reflecting clear altitudinal gradients. While upstream communities were generally in a rather natural condition and rich in bryophyte species, downstream communities had less species and often anthropogenically modified stream banks. Due to the confounding of downstream areas with human influences and other variables such as temperature, the separate effects of these variables are not known. The relationship and the distributions of some bryophyte species/communities across the altitudinal range suggest that these riparian bryophyte communities may be sensitive to global warming.

1. Introduction

Freshwater habitats occupy less than 1% of the earth's surface and contain approximately only 0.01% of the World's water (Strayer and Dudgeon, 2010). Nevertheless, these habitats are hotspots of biodiversity and their associated biota are among the most endangered in the world as they are also hotspots for human activities leading to widespread habitat degradation (Darwall et al., 2008).

Bryophytes are an important component of freshwater biodiversity. They can attain high cover values, especially in streams, and may thus fulfill important ecosystem functions such as the stabilization of the margins of the water courses or the provision of sheltered habitats for microfauna (Richardson and Danehy, 2007; Strayer and Dudgeon, 2010). Bryophyte communities of freshwater habitats can be rich in bryophyte species and some species are even restricted to this habitat (Lang and Murphy, 2012). However, there is considerable variation in species richness and community composition of bryophytes in streams and a number of factors, may be responsible for this variation. Furthermore, streams are quite complex habitats with distinct bryophyte communities from permanently submerged to terrestrial conditions (Muotka and Virtanen, 1995; Luís et al., 2010; Lacoul and Freedman, 2006). Physical and chemical variables are well known to be an important driver of bryophyte species richness and composition in streams (Ceschin et al., 2012). Nutrient status, temperature, conductivity and pH have been shown to significantly affect bryophyte species communities and bryophytes are thus used to assess stream water quality (Vanderpoorten, 2003; Ah-Peng and Rausch de Traubenberg, 2004). For example, it has been shown that streams with high nutrient contents due to inputs from agricultural areas

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have a very impoverished bryophyte flora (Vanderpoorten, 2003; Lujan et al., 2013). Geomorphological and hydrological properties of streams further affect the occurrence of bryophytes (Fritz et al., 2009; Lang and Murphy, 2012; Vieira et al., 2012). For example, velocity of the water or the kind of substrates available (e.g. blocks, sand) strongly influence bryophyte communities (Muotka and Virtanen, 1995; Tremp et al., 2012). Effects of these variables on bryophyte communities are mostly indirect by determining or modulating disturbance regimes. Macroclimatic factors like temperature or precipitation may have direct effects on water temperature and on stream flow. While temperature directly influences physiological processes, precipitation determines stream flow and the strength and frequency of disturbance regimes. For the stream-border bryophytes, which are rarely submerged, climatic factors may be even more important since they are more exposed to climatic conditions than instream communities. Aranda et al. (2014) have recently shown that climatic factors are predominantly responsible for species richness patterns on Macaronesian Islands.

Generally, community ecology of stream bryophytes has been in the focus of a number of studies (Söderström, 2006; Richardson and Danehy, 2007; Lang and Murphy, 2012; Tremp et al., 2012). However, there is considerable bias in these studies with respect to the type of streams studied as emphasized by Lang and Murphy (2012).

Here we focus on bryophyte communities in stream habitats on the Island of Madeira, as a model for mountain streams with a strong altitudinal gradient. Madeira is a mountainous and volcanic Island in the Atlantic Ocean belonging to Macaronesia. Typical for volcanic Islands, streams are dropping strongly in altitude over very short horizontal distances (Hughes and Malmqvist, 2005). The mountain streams of Madeira represent a high stream gradient characteristic for Macaronesian Islands. It was previously shown that Madeiran streams contain 34% of the total bryophyte flora of Madeira (Luís et al., 2010) and are thus considered as important elements for bryophyte conservation on Madeira. Bryophyte species composition and richness of these streams are affected by the habitat (instream vs. stream-border) and by the position in the stream (upstream vs. downstream) as well as by the location of the stream in the Island (northern slope vs. southern slope; Luís et al., 2010). Here we scrutinize in more detail which environmental factors affect the bryophyte communities of Madeiran mountain streams, and what is the individual contribution of distinct sets of environmental variables on species richness and species composition.

We studied three sets of environmental variables and their effects on riparian bryophyte communities. The three sets are characterized by chemical and physical properties of the water at the sampling locations, by macroclimatic conditions, and by geomorphological and hydrological properties specifically, we focused on the following questions: (i) which environmental factors best explain species richness and composition? (ii) How do different sets of environmental factors influence species richness and composition? Because bryophyte communities in the instream and the stream border habitat are likely to show quite different environmental relationships (Luís et al., 2010), we treated the two habitats separately in all analyses.

2. Methods

2.1. Sampling

The study was performed on Madeira Island, a mountainous and volcanic Island in the Atlantic Ocean belonging to Macaronesia. The sampling was carried out in the main hydrographic basins of the Madeira Island. We selected 16 streams, located in both the northern and southern part of the Island. Each stream was partitioned in three sections (upstream, intermediate and downstream). Within each section two accessible sampling areas were selected. Finally, within each area, the riparian bryophytes were sampled from the stream-border (0–50 cm above the water level in summer, submerged in winter) and the instream habitat (submerged in winter and summer). We thus got 96 plots for the instream and the stream border habitat (16 streams × 3 sections × 2 areas). However, two areas had to be omitted due to the absence of water flow during the summer period (downstream of Ribeira da Cruz). Within each area six subplots of 0.2 m^2 were established and searched for bryophytes. We used the total number of bryophyte species in these six subplots as our species richness measure. For each species, cover was estimated in percentage within each subplot. For ordinations (see below) we used the mean cover within these six subplots as an estimate of species abundance. A more detailed description of the study design can be found in Luís et al. (2010).

Information on 59 environmental variables was either sampled in the field or later compiled from various GIS layers (from the National Sea and Atmosphere Institute). The 49 variables were grouped into three thematic sets: (1) chemical and physical characteristics of the water, (2) climate and (3) geomorphological and hydrological variables (Table 1). Normally each variable refers to the sampling areas. The variables included in the set 'chemical and physical characteristics of the water' refers to each sections (i.e. the two areas in a section have identical values).

In the set 'chemical and physical characteristics of the water' 16 variables were included. However, because each variable has been measured in summer (May–August) and winter (December–January) the final set contains 32 variables (Table 1). The water samples were collected in sterilized polyethylene bottles and preserved in cold for transportation to the lab, although some parameters were determined in situ, namely pH (Lovibond, PC Checkit pH), conductivity (WTW cond 330i), temperature (WTW cond 330i), solids in suspension (WTW cond 330i), dissolved oxygen (WTW oxi 330i) and waterflow (OTT-Nautilus/SENSA Z 300). The following parameters were analyzed in the lab using colorimetric methods (WTW Photolab S12A): NH_4^-, Cl^-, PO_4^-, NO_3^-, NO_2^- and SO_4^-. The concentration of Ca, Mg, K, and Na was determined using graphite furnace atomic absorption spectrometry (GBC 932 Plus) and by flame atomic absorption spectrometry (Varian Techtron AA59), for Cd, Cu, Fe, Hg, Pb and Zn.

The climatic variables included different thermic variables and were obtained from GIS layers provided by the National Sea and Atmosphere Institute. The layers were derived from meteorological recordings (considered time period: 1961–1990) and extrapolated by means of a digital elevation model (resolution 25 m) to the whole of Madeira (National Sea and Atmosphere Institute) (Table 1).

The twelve variables included in the geomorphological and hydrological data set were registered in situ during fieldwork being related to substrate and the size of the streambeds and the water flow, except the slope which was derived from a digital elevation model with resolution 25 m (PRAM, 2002) (Table 1).

Bryophyte nomenclature followed Grolle and Long (2000) for liverworts and hornworts and Hill et al. (2006) for mosses as well as Stech et al. (2008) for *Isothecium prolixum* (Mitt.) Stech, Sim-Sim Tangney & Quandt.

2.2. Statistical analysis

Before starting with statistical analyses, we excluded some variables because they were considered as either ecologically redundant or contained too many zero values (e.g. due to concentrations of chemical variables below the detection limit).