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The relationship between water velocity and morphological complexity of stream dwellers

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ABSTRACT

The effects of environmental factors have been considered important for the evolution of morphological complexity in organisms. The water flow exhibits constant disturbance on stream dwellers, independently of their taxonomic group. Thus, we assessed whether two different kinds of organisms (insects and algae) exhibit any ecological similarity by facing stream current. For this, we used several previous studies in order to relate the morphological complexity of insect gills and algal filaments to water velocity, in micro and mesohabitats. The results for micro-scale showed that complex body shape tends to favor taxa that colonize stream areas with lower velocity for both kind of organisms. However, mesohabitats exhibited no relationship between morphology and water velocity. We suggest that morphological complexity in organisms from different lineages (algae and insects) are similarly related to water velocity in stream habitats. Moreover, the methodology of stream samplings must be carefully designed to get more precisely the environmental factors that organisms experience.

1. Introduction

The unidirectional water flow in stream habitats is a constant condition that organisms must be adapted to. The effects of flow are experienced by all stream dwellers and hydraulic features have been considered a remarkable factor responsible for benthic communities organization (Resh et al., 1988; Brooks et al., 2005; Tonetto et al., 2014, 2015). In this scenario, evolutionary mechanisms might favour the occurrence of convergent strategies in different phylogenetic lineages, like animals and plants, in response to environmental factors such as water flow.

An important topic in evolutionary ecology is the understanding of processes shaping morphological complexity. Recent studies suggest that in some niches, evolutionary mechanisms may complexify the body plans of organisms, while in other habitat conditions simpler body plans tend to be selected (Adami, 2002; Auerbach and Bongard, 2014). Hence, organismal morphology is considered an important predictor of persistence in aquatic environments (Webb and Cotel, 2010; Lovvorn et al., 2001). For instance, body shape (or parts of it) is related to acquisition of resources from the surroundings (Hein et al., 1995; McAbendroth et al., 2005; Tonetto et al., 2015), and consequently to niche preferences.

In lotic habitats, filamentous algae exhibit several types of morphology, such as simple filaments, sparsely branched filaments and densely branched filaments (Biggs and Kilroy, 2000). All of these filamentous algae obtain their nutrients from the water flow, but the level of morphological complexity may depend on specific hydraulic conditions to facilitate nutrition (Tonetto et al., 2015). The relationship between structural complexity and hydraulics may also occur in other taxonomical groups that exhibit similar preferences, taking into account their body plans and flow conditions, since most of stream inhabitants maintain their biological functions using dissolved substances from the water column (e.g. O_2, CO_2 and nutrients).

Aquatic insects, for example, absorb oxygen from water flow by using their gills. Some gills of stream insects are structurally quite similar to algal filaments. However, to the best of our knowledge, there are no studies concerning the relationship between morphological complexity of gills and hydraulic conditions, like recently shown for stream algae (Tonetto et al., 2015). Most of previous studies regarding stream invertebrates and hydraulic conditions have considered the

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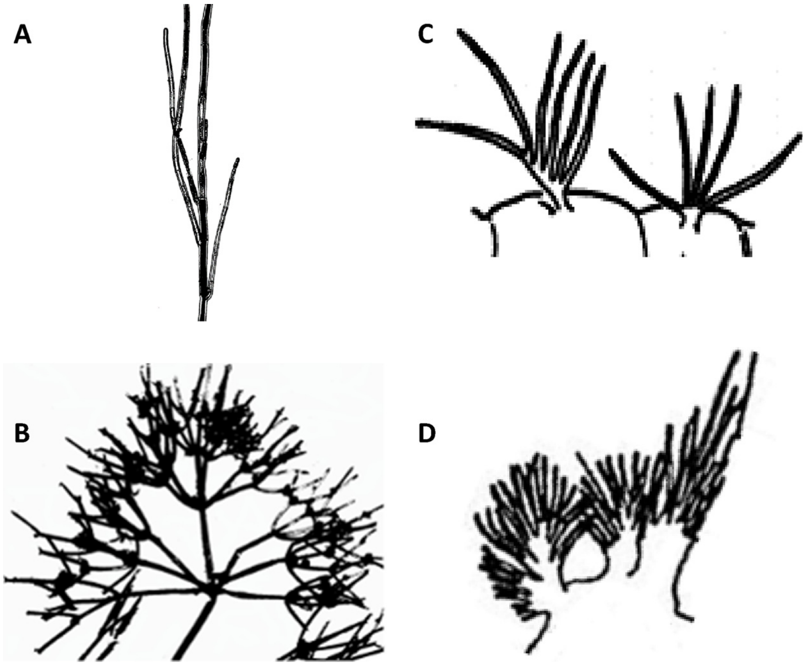

Fig. 1. Images used for fractal dimension calculations. These figures illustrates two contrasting morphological complexities of algal and gills. Algae: A – Sporophytic stage 'Chantransia'; B – *Nitella mucronata*; Gills: C – *Petrophila* sp.; D – *Kempnyia* sp.

richness and abundance (Jowett, 2003; Brooks et al., 2005), and body size or morphological categories in response to flow exposure (Growns and Davis, 1994; Sagnes et al., 2008; Brooks, 2016). Thus, the morphology of gills have not been used for the understanding of spatial distribution of stream invertebrates at microhabitat scales.

In freshwater stream ecology, most studies have been conducted at macro- and mesohabitat scales. Nevertheless, key biological and physical processes, such as hydrological forces and nutrient uptake, operate at micro scale. Studies on freshwater biodiversity using mesohabitat underestimate the influence of hydrological forces (Tonetto et al., 2015). Therefore, here we aimed at combining microhabitat conditions and morphological features into a single and unique description of a biological process: the adaptation of morphological complexity. Morphological fractal structures are conservative and genetically coded (Isaeva, 2009). In other words, similar mechanisms are responsible for complexity in distant taxa. Hence, we expected that morphological complexity of both algae and insect gills would exhibit a similar relationship with water flow conditions and that microscales would display greater effects on the organisms than mesoscales. Furthermore, we believe that a robust perspective on the relationship between organismal morphology and hydrological function of stream microhabitats will contribute to the understanding of how evolutionary forces select complex shapes of bodies and structures.

2. Material and methods

In order to assess the relationship between morphological complexity of both algae and insect gills and water velocity in streams (micro- and mesoscales), we made a survey of previous published data: algae (e. g. Tonetto et al., 2014, 2015; Branco and Necchi, 1996, 1998; Necchi, 1993; Necchi et al., 1999; Vieira et al., 2002; Vieira and Necchi, 2002; Sheath et al., 1989; Sheath and Cole, 1996; Sherwood, 2006) and insects (Monahan and Caffrey, 1996; Oliveira et al., 1997; Nelson and Lieberman, 2002; Bispo et al., 2002, 2006; Dudgeon, 2006; Arango et al., 2008; Dudgeon, 2012; Rawi et al., 2013; Cardona-Duque, 2014). The data used for the analyses was limited to filamentous algae with macroscopic thallus because they experience more the effect of water column than microscopic species (Tonetto et al., 2014, 2015). The algal species include representatives of Cyanobacteria (blue-green algae), Chlorophyta (green algae), Rhodophyta (red algae) and Ochrophyta divisions. For insect, there are taxa from the orders Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Odonata, Lepidoptera and Diptera. For both organisms, we used the most common taxonomic groups found in stream habitats (Allan and Castillo, 2007).

For both algae and insects, we separated microhabitat studies from those that assessed mesohabitat conditions. For both scales, we listed the taxa registered and the water velocity where they were sampled. Furthermore, we used in our analysis a great range of morphological complexity by selecting organisms with simpler morphology and those with higher structural complexity. After we have selected the taxa, we selected the images of algal filaments and insect gills. We used the original images from the papers or specialized literature with well-defined scale for all species images (algae and gills). In order to measure morphological complexity, we transformed all images to black and white color scale (Fig. 1). Thus, we used these images in the program Fractalyse 2.4 © to measure the fractal dimension (level of complexity) of each taxon by applying a grid method (Tonetto et al., 2014, 2015) (Fig. 1). Recently, fractal dimension has become widely applied in ecology and has been frequently used to measure complexity (Thomaz et al., 2008; Tonetto et al., 2014, 2015).

For macroinvertebrates, we obtained the microhabitat data from 100 random samples in a natural stream habitat (Bocaina stream, State Park of Intervales, São Paulo State - S: 24°16´20.1´´| W: 48°27´18.1´´). First, we collected a substrate area with a sampler (diameter of 10 cm and 250 μm mesh), then we measured the water velocity using an electronic flow meter (Soft) as close as possible of the sampled area. We selected the data of the microhabitats where the organisms were present for the analysis.

We applied Linear Regression tests to determine the relationship between algae and gills with different morphological complexity and different water velocity. When the assumptions of Linear Regression was not attended, a Spearman Test was used. We made the analyses for micro and mesohabitat to assess the effect of scale. All analyses was made using R statistical software, version 2.13 (R Development Core Team, 2011).