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Does grazing change algal communities from grassland and pine afforested streams?: A laboratory approach

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ABSTRACT

Drastic changes in the composition and physiognomy of riparian vegetation, such as the conversion of grassland to forest, are expected to alter interactions among light availability, primary producers and herbivores. Our aim was to examine in laboratory the influence of a ubiquitous grazer on periphyton grown in a grassland unshaded stream (reference) vs. periphyton from a nearby pine afforested stream. Besides, we evaluated how the community responds to the removal of grazing. Given that grassland streams are exposed to higher light intensity and grazers are more abundant compared to afforested streams, we proposed that if biofilm grown in the afforested stream are dominated by grazing-vulnerable algal species, grazing pressure by *Helicopsyche* sp. should be stronger. In addition, if biofilm from the afforested stream has low quality or is less abundant as food for consumers, the effects of *Helicopsyche* sp. may be stronger or weaker depending on their feeding decisions. *Helicopsyche* sp. caused a decrease in richness and diversity in periphyton grown in the grassland stream and its net grazing effect on chlorophyll *a* (Chl *a*) was higher. Algal community composition from grassland stream was strongly changed after grazing, with a decrease in the proportion of overstory algae. In contrast, algal community structure of periphyton from the afforested stream was neither affected by grazing nor by grazing exclusion. *Helicopsyche* sp. produced significant changes in a short time in structural attributes of algal communities, mainly in periphyton from the grassland stream suggesting that herbivory, as a functional factor, is diminished following afforestation.

Introduction

Land use changes at the catchment scale affect stream habitat condition, productivity and biotic interactions, and consequently alter stream functioning, water quality and ecosystem services (Allan and Castillo, 2007). In open-canopy streams, benthic algal community is the main source of organic carbon in the food web. Changes in the composition and physiognomy of riparian vegetation, such as the conversion of grassland to forest, may affect the availability of light and nutrients, discharge and temperature (Jobbágy et al., 2006, 2013), and hence profoundly alter algal communities (Stevenson, 1996) and food webs (Thompson and Townsend, 2005).

Light in particular has been reported as a limiting factor in shaded streams, changing the physiognomic and taxonomic structure of algal communities (Steinman and McIntire, 1987; Lange et al., 2011). Light reduction leads to slower development, lower cell density and less vertical stratification of epilithic biofilms (Hudon and Bourget, 1983). Wellnitz et al. (1996) found that light level had a strong effect on the abundance of common algae. The green filamentous algae may outcompete diatoms under full light conditions, but in shaded conditions diatoms may be the dominant algal type (Steinman et al., 1989; Melody and Richardson, 2004; Villeneuve et al., 2010). In experimental channels, Bourassa and Cattaneo (2000) found higher proportion of cyanobacteria, single cells and colonial forms in shaded channels whereas filamentous chlorophytes and chain-forming diatoms were prevalent in open channels. Many studies have shown that irradiance can also influence chemical composition (Steinman et al., 1988), photosynthetic

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performance, primary production, and light utilisation efficiency (Boston and Hill, 1991; Hill et al., 1995; Hill and Dimick, 2002) resulting in higher chlorophyll *a* and higher periphyton biomass (Mallory and Richardson, 2005).

Periphyton is subject to complex interactions between top-down and bottom-up forces (Mallory and Richardson, 2005). Herbivore control could be of greater importance in some systems (Hillebrand, 2005; Schneck et al., 2013). Several studies have shown that grazing in lotic ecosystems can substantially influence algal growth form thus controlling assemblage physiognomy (Steinman et al., 1987; Wellnitz and Ward, 1998; Álvarez and Peckarsky, 2005), and reducing biomass significantly (Wallace and Webster, 1996; Álvarez and Peckarsky, 2005; Barbee, 2005). However, relatively few studies (Quinn et al., 1997a,b) have addressed the question of how the implantation of forests in grassland landscapes affects top-down control by grazing of stream algal communities.

The grazers' ability to affect the structure of algal communities is probably related to differences in grazing vulnerability of algal species, which is associated to differences in algal physiognomy, microdistribution and palatability (Steinman, 1996). Grazers reduce the relative abundance of upright, overstory or loosely attached algal taxa, while algal species more closely associated with or tightly attached to the substratum usually increase their relative abundance (Holomuzki et al., 2010). Whereas prostrate growth forms are well adapted to high grazing pressure, upright or large forms are susceptible to it (Steinman, 1992). Large growth forms also may have a competitive advantage for light, as their higher profile enables them to intercept irradiance before the lower profile cells (Hudon and Bourget, 1983). Moreover, chemical composition of algal communities affects grazer–algal interactions since it modifies feeding activity of consumers. Hillebrand et al. (2009) found that individual grazers increase their intakes in response to low food quality but low-nutrient food often reduces herbivore growth efficiency and population growth rate. Therefore, grazing could shift species composition to grazer-tolerant organisms and/or non palatable species, which will be benefited by a higher access to light, nutrients and space (Holomuzki et al., 2010).

Some studies have demonstrated that streams in grassland landscapes converted to afforestation present lower algal productivity and higher standing crops of organic matter affecting food web structure (Thompson and Townsend, 2004, 2005). Surveys in our study area have revealed that the afforestation of grassland streams with pines changes macroinvertebrate community composition and abundance reducing grazer densities by half (J. Márquez, unpublished data). Interestingly, benthic biofilm accrual in a field experiment carried out in three catchments did not differ between both stream types, possibly due to higher grazing in grassland streams (R. Principe, unpublished data). However, biofilm standing stock was higher in grassland streams, so it is still unclear if grazers do control algal growth and how this interaction is affected by light regimes altered by pine afforestations.

In this study we aimed at answering how grazing controls periphyton from streams with contrasting light regimes by offering the ubiquitous grazer *Helicopsyche* sp. (Trichoptera, Insecta) biofilm grown both in a grassland (reference) and in a pine afforested stream. Given that grassland streams are exposed to higher light intensity, which favours the development of more productive algal communities (Thompson and Townsend, 2005), and grazers are more abundant compared to afforested streams (J. Márquez, unpublished data), we proposed two non-exclusive hypotheses. If biofilm assemblages grown in the afforested stream are dominated by grazing-vulnerable algal species, grazing pressure by *Helicopsyche* sp. (i.e. biofilm changes relative to the initial biofilm condition) is expected to be stronger than on assemblages grown in grassland streams (i). In addition, if biofilm from the afforested stream has less quality (as low light intensity yields less autotrophic biofilms) or is less abundant as food for consumers, the effects of *Helicopsyche* sp. may be stronger or weaker depending on their feeding decisions (i.e. compensating or not the low food quality with high consumption) (ii).

Materials and methods

Study area

This study is included in a project that aims at assessing the potential changes in biodiversity and ecological processes of headwater streams draining natural grassland catchments converted to pine forests. The study area includes streams belonging to the headwaters of Ctalamochita river, which are situated between 800 and 1500 m a.s.l. on the east side of Córdoba hills, Argentina. Vegetation varies according to altitude, with grassland developing between 1000 and 1500 m a.s.l. (mainly *Festuca hieronymi* Hack. var. *hieronymii* and *Nasella* spp.; Cabido et al., 2003; Oggero and Arana, 2012). The study area is affected by anthropogenic activities, mainly livestock and afforestation with exotic pines. *Pinus elliotti* is the most abundant in plantations.

We selected two streams with different riparian cover, one flowing through grassland (31° 58′ 52″S, 64° 46′ 29″W, 1157 m a.s.l., drainage area 89 ha) and the other flowing through pine afforestations (31° 58′ 24″S, 64° 45′ 15″W, 1121 m a.s.l., drainage area 142 ha). PAR (photosynthetically active radiation) intensity was measured with a QSL–2100 irradiance sensor (Biospherical Instruments, Inc., San Diego, California) at midday along a 50 m reach at each site. PAR was reduced more than 60% in afforested stream (grassland: 2200 μmol m^{-2} s^{-1}; afforested: 900 μmol m^{-2} s^{-1}).

Experimental design and laboratory methods

During the low flow season (August–September 2011), twelve artificial substrata were placed in each stream (grassland and afforested) to allow algal community development under contrasting environmental conditions (i.e. lower light intensity, temperature and grazers abundance in afforested stream). Substrata consisted of sand-blasted glass slides, each measuring 9 cm^2. After 28 days, substrata were collected and transported to the laboratory in dark plastic containers filled with stream water. At the same time, *Helicopsyche* sp. larvae were collected by hand in the grassland stream and transported in similar conditions. This Trichoptera was selected for the experiment since it was reported as indicator (IndVal Method, Dufrêne and Legendre, 1997) of grassland streams in the study area (Márquez et al., 2010) and also is the only taxon of the community assigned as primarily scraper (Merritt and Cummins, 1996; Reynaga, 2009). *Helicopsyche* sp. was only collected in the grassland stream to test how grazers from a reference grassland stream face food resources from the same stream compared to food from an unshaded stream converted to afforestation and how algal assemblages respond to grazing.

In the laboratory, two plastic white trays (5 L volume) were used as microcosms. Each one contained a water pump to create a constant flow (200 L h^{-1}), and plastic beakers to contain glass substrata and grazers acting as experimental units. A 4 × 4 cm opening was cut in two opposite sides of the beakers and screened with 1 mm^2 mesh, which allowed water circulation preventing *Helicopsyche* sp. larvae from escaping (Zanotto Arpellino et al., 2011). Each microcosm was filled with net-filtered water (25 μm mesh) either from the grassland or the afforested stream and was replaced twice daily. Water chemistry was similar between streams (see Farley et al., 2008) and water temperature was kept at 24 °C (±2 °C). Although temperature is lower under afforestations, the experiments were run in late winter when stream water