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RESEARCH ARTICLE



Pine afforestation affects key primary producers in mountain grassland streams in Córdoba, Argentina

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ABSTRACT

We evaluated changes in benthic algal community in grassland mountain streams converted to exotic pine afforestation. Three headwater streams draining grasslands and three draining plantations of *Pinus elliottii* were selected in a semiarid mountain watershed (Córdoba, Argentina). Hydraulic and physicochemical variables were recorded and benthic algal samples were collected in each stream at two hydrological periods (high and low flow). Light intensity was lower in afforested streams. Community composition differed between grassland and afforested streams. Algal abundance and richness, richness of chlorophytes and cyanobacteria, and the indicator taxa were reduced in afforested streams. Diversity, evenness and biomass were higher in the high water period but did not differ between riparian vegetation types. The observed changes in benthic algal attributes may have implications in ecosystem functioning because of the central role that algal biofilms play in the productivity of these fluvial systems, as sources of food, energy and oxygen.

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KEYWORDS

Exotic pines; headwater streams; hydrological period; light; periphyton

Introduction

Human activity has impaired many aquatic systems around the world. Headwater streams, key ecosystems for water production, nutrient retention and transformation, and habitat for biota are vulnerable to human alteration of their catchments, riparian zones and channels (Richardson & Danehy 2007; Studinski et al. 2012). Vegetation changes in riparian zones alter river functioning (Martínez et al. 2013), particularly in small streams, which are highly connected with and strongly influenced by terrestrial landscapes (Fausch et al. 2010).

The conversion of natural grasslands to plantations has occurred over extensive areas of the Southern Hemisphere (Richardson et al. 1994) promoted by the undoubted appeal of their ecosystem service as a carbon sequestration mechanism which adds to direct forestry incomes (Laclau 2011). The notion that this vegetation change may strongly affect ecosystem processes, including water yield and nutrient transport from rivers and streams, has

already been demonstrated (Farley et al. 2005; Jackson et al. 2005; Mátyás & Sun 2014). In the mountain ranges of semiarid regions, annual water yield in afforested watersheds may be reduced by 50% compared to grassland watersheds (Jobbágy et al. 2013), because of increased water interception by dense forest canopy (evaporating before reaching the ground) and absorption by deep tree roots compared to grasslands. Very little research has focused on the alteration of basal resources of stream food webs such as algal community composition and structure resulting from the conversion of grassland landscapes into pine forestations (Quinn et al. 1997). However, considerable work has been done on the effect of logging on benthic invertebrate communities and river functioning (Kiffney & Bull 2000; Kedzierski & Smock 2001; Death et al. 2003; Boothroyd et al. 2004; Thompson et al. 2009). Headwater streams flowing through afforested grasslands are more vulnerable than larger streams because of their strong lateral link with terrestrial landscapes (Richardson & Danehy 2007). In such small streams, afforestation can switch a system in which basal resources are dominated by production of benthic algae to one dependent on allochthonous plant litter altering aquatic food web structure (Thompson & Townsend 2005).

Light, nutrients, grazing and current velocity are considered the major factors controlling benthic algae in stream ecosystems (Wellnitz & Rader 2003; Lange et al. 2011). The availability of light depends on stream width, depth and on the riparian vegetation type. In open mountain streams, benthic algae represent the primary production supporting food webs (Roberts et al. 2004); thereby dense canopy over the streams due to afforestation is expected to deeply affect benthic algal communities with consequences for stream biodiversity and productivity. In a previous study, Cibils et al. (2015) found that functional diversity of algal traits was affected differently by pine afforestation, and afforested streams showed a higher proportion of low-profile and small species.

The present study aimed to evaluate differences in composition and structure of benthic algal communities in grassland streams converted to afforestation. We hypothesised that changes associated with pine afforestation produces a substantial shift in algal communities. Given that with higher light more species can develop (Lowe et al. 1986; Hill 1996; Lange et al. 2011), we expected differences in composition and structure of benthic algal communities, a reduced richness and diversity in afforested streams due to the prevalence of shade-tolerant taxa including cyanobacteria, and lower biofilm biomass given the low sunlight availability year round. Moreover, as pine afforestation may reduce discharge particularly during summer (i.e. high water period, Jobbágy et al. 2013), we expected major differences between afforested and grassland streams to occur at this period. Summer is the season with higher precipitation in the area and pine afforestation can reduce discharge due to higher evapotranspiration and accumulated litter which buffer floods. As a result, grasslands are expected to have more fluctuations in discharge in the high water period (Jobbágy et al. 2013).

This study corresponds to the final stage of the productive forestry cycle, since logging has begun in the last years. Hence, this study represents a baseline that would provide tools to evaluate the ecological status of headwater streams and to contribute to the decisions for management and land use planning (Sabater et al. 2015).

Materials and methods

Study area

The study was carried out in streams of the Ctalamochita River upper basin, Córdoba, Argentina (Figure 1). Annual precipitation in the region reaches 725 mm, occurring mostly between spring and late summer (October–March) (Cabido et al. 2003) whereas the maximum air temperature reaches 34°C in summer (December–March), and decreases to as low as –5°C in winter (June–September). The lithology is dominated by granite, but localised patches of metamorphic rocks (gneiss, schist, migmatite) are also present.

Six first-order streams located in sites with similar altitude, slope, exposure to sunlight and drainage area were selected in the Santa Rosa stream sub-basin (which belongs to the Ctalamochita river basin). Three streams drain grasslands (G1: 31°58'56"S, 64°43'25"W; G2: 31°58'52"S, 64°46'29"W; G3: 31°58'47"S, 64°48'41"W) and each one has a neighbour stream that drains 40-year-old plantations of *Pinus elliottii* (F1: 31°58'12"S, 64°43'49"W; F2: 31°58'24"S, 64°45'15"W; F3: 31°59'22"S, 64°48'44"W) (Figure 1). Drainage area of the study streams ranged from 27 to 142 ha (mean watershed size, grassland: 69 ha; afforested: 86 ha, fully covered by pine plantations) and were located at about 1100 m a.s.l. Grasslands at this altitude are dominated by the native species *Festuca hieronymi*, *Nassella filiculmis*, *Schizachyrium condensatum* and *Eragrostis airoides* (Oggero & Arana 2012) and they are primarily used for extensive livestock grazing (effective stocking rates can vary from 0.1 to

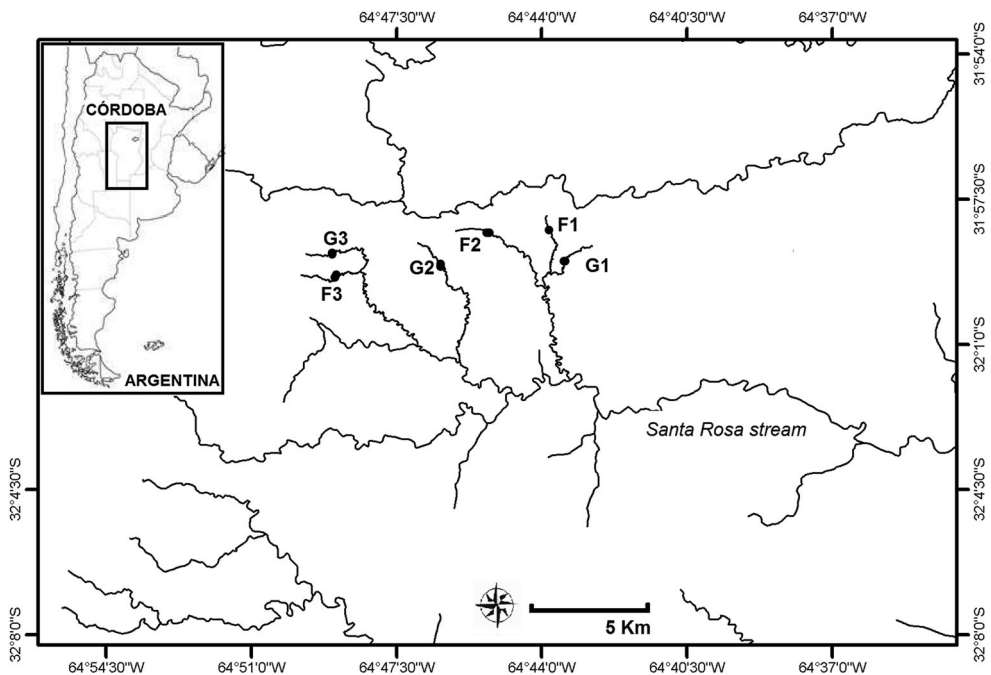


Figure 1. Study streams belonging to Santa Rosa stream sub-basin (Córdoba, Argentina). Three streams drain grasslands (G1, G2, G3) and the other three streams run through pine plantations (F1, F2, F3). Sampling points are indicated.

2 cow equivalent ha^{-1} , Teich et al. 2005). In the study area, *P. elliottii* is the dominant tree in the plantations followed by *Pinus radiata* and *Pinus taeda*, all of them exotic species.

Field and laboratory methods

Samples were collected at each stream during low (July 2008) and high water period (February 2009). In each sampling occasion, hydraulic and physicochemical variables were measured to characterise grassland and afforested streams. Water temperature, pH and conductivity were recorded with portable sensors once in each stream and hydrological period at midday. Depth, width and current velocity were measured with a Global Flow Probe at the reaches where benthic algae were collected. Discharge data were obtained from Jobbágy et al. (2013) using values of three months during low water period (August 2004, 2005, 2006) and three months during high water period (March 2005, January 2006, February 2007). The PAR (photosynthetically active radiation) intensity was measured with a QSL-2100 Irradiance Sensor (4 Pi, Biospherical Instruments, Inc., San Diego, California) at midday along a 50 m reach in each stream only during the high water period. One water sample was obtained in each stream and hydrological period and brought back to the laboratory for chemical analysis. The analyses of total dissolved solids (TDS), carbonate, bicarbonate, nitrate and hardness were carried out by the hydrology laboratory of the Department of Geology, National University of Río Cuarto, according to standard methods (APHA 1998). Carbonate and bicarbonate were measured by potentiometric titration with a Thermo Orion-selective electrode. Nitrate were determined by potentiometry using an ion selective electrode (Orion Model 9307), a reference electrode and an Orion potentiometer 710 A. To calibrate the potentiometer six benchmarks (5, 10, 25, 50, 100 and $300 \text{ mg l}^{-1} \text{ NO}_3^-$) were used. The detection limit for NO_3^- was 0.2 mg l^{-1} and the analytical error was 0.5%.

Benthic algae samples were collected from four randomly selected cobbles at each stream and hydrological period in a 50 m reach. Cobbles superior surfaces were scrubbed with a stiff brush and clean water and then measured to estimate area. The sample obtained from each rock was analysed as a separate sample. The slurry was kept refrigerated in darkness in individual plastic bags. In the laboratory, total sample volume was recorded, then homogenised and fractionated in three subsamples. One fraction was fixed with 4% formalin for later species identification and cell density calculation. Another fraction was filtered through a pre-incinerated and pre-weighed glass-fiber filter MF/C ($1.2 \mu\text{m}$ nominal pore size, Munktell, Sweden), dried for 48 h at 60°C and burned to obtain ash-free dry mass (AFDM). The third fraction was used to extract and quantify chlorophyll *a* (Chl *a*) concentration by 90% ethanol extraction in a hot bath and spectrophotometry (Nusch 1980). Results were expressed per unit surface area of inorganic substrate (Biggs & Kilroy 2000). Chl *a* and AFDM were used to calculate an autotrophic index ($\text{AI} = \text{AFDM}/\text{Chl } a$) (Weber 1973) for each riparian vegetation type and hydrological period. This index is indicative of the proportion of the community composed of heterotrophic (plus organic non-living matter) and autotrophic organisms. AFDM represents the combined mass of heterotrophic and autotrophic biomass (and organic detritus), and Chl *a* reflects the autotrophic component.

Cell counts were performed by direct methods at $400\times$ magnification with slide and coverslip of $24 \times 50 \text{ mm}$ following transects along the coverslip. The counting unit was

an individual cell for unicellular and coenobial organisms, and a cell equivalent of 30 μm length for filaments and of $30 \times 30 \mu\text{m}$ area for colonies. Soft algae were identified in this count, and diatoms lumped into a single taxonomic category. For diatom species identification, organic matter was digested using 40% hydrogen peroxide and permanent slides were prepared according to Hasle (1978), using ZRAX (1,7) as slide-mounting medium. At least 600 units (one frustule or two valves) were counted and identified in each sample using a light microscope with 1000 \times magnification. The abundances of all diatom taxa observed were expressed as percentages, which were converted to number of individuals, based on the total count of diatoms. Counts were converted to density of cells per surface area of rocks (number of cells cm^{-2}) based on Villafañe and Reid (1995), accounting for the volume of sample counted in each slide, the area of transects in slides, the volume of sample and the cobble area. For taxonomic analysis, specific bibliography of each particular group was used and names were updated following Spaulding et al. (2010), Komárek and Hauer (2013) and Guiry and Guiry (2014).

Data analysis

To compare physicochemical variables measured at each vegetation type and hydrological period once in each stream (T° , pH, conductivity, TDS, carbonate, bicarbonate, nitrate and hardness), one-way repeated-measures analysis of variance (ANOVA) were performed. For those variables measured at the sites where benthic algae were collected (depth, width and current velocity), a nested, repeated-measures ANOVA (between-subjects factor: vegetation type; nested factor: sample (within vegetation type); within-subjects factor: hydrological period) was performed. One-way ANOVA was used to compare PAR measurements, taken only at the high water period, between grassland and afforested streams.

Abundance ($\ln(x+1)$ transformed) and richness of algal divisions were compared between stream types and hydrological periods using nested, repeated-measures ANOVA (between-subjects factor: vegetation type; nested factor: sample (within vegetation type); within-subjects factor: hydrological period). Non-metric multidimensional scaling (NMDS), using the Bray–Curtis similarity coefficient, was performed to visually describe differences in benthic algae on both vegetation types and between hydrological periods (Quinn & Keough 2002). Species with relative abundances higher than 1% were retained, and density values were $\log(x + 1)$ transformed prior to analysis. Permutational multivariate analysis of variance (PERMANOVA, Anderson 2001; McArdle & Anderson 2001) was performed to statistically test differences between groups, with 999 permutations. We considered vegetation type as a fixed factor, samples nested within vegetation type and hydrological period as a repeated-measures factor. To check that differences between groups in terms of their centroids are not induced by differences in variances, we used analysis of multivariate homogeneity of group dispersions (PERMDISP, Anderson 2001). All statistical analyses described above were performed in R version 3.3.2, using vegan library (Oksanen et al. 2013; R Core Team 2013).

Indicator taxa were obtained using the IndVal method (IndVal, Dufrene & Legendre 1997), which combines measurements of the degree of specificity of a species to a habitat type, and its fidelity within that habitat. Good indicator species are those that are always present at certain sites and never occur in other sites. The

indicator value ranges from 0 to 100; the later corresponds to a perfect indication. Significance of the indicator value for each taxa was tested using Monte Carlo test with 1000 permutations. Species with significant ($P < .05$) indicator value and greater than 70% were considered indicators, representing species characteristics of that stream type (McGeoch et al. 2002). Those species resulting indicators combine high specificity (present only under a particular stream type) and high fidelity (abundant in all samples of that stream type). Species with other combinations of specificity and fidelity, however, may also be useful indicators, and are named detector species (see McGeoch et al. 2002). When monitoring environmental change, species that spread along a range of ecological states may be more useful indicators of the direction of the change than highly specific species restricted to a single state. Thus, detector species will provide information complementary to that provided by indicator species (McGeoch et al. 2002). Species that were selected as detectors of changes produced by afforestation were those with indicator values between 5 and <50% in grassland streams, and between 50% and 70% in afforested streams. These species were judged as sufficiently uncharacteristic of the conditions of grassland streams so as to potentially show an increase in the indicator value under the environmental changes caused by afforestation (McGeoch et al. 2002). IndVal was carried out using PC-ORD version 5.0 (McCune & Mefford 1999).

Rank abundance curves were constructed for grassland and afforested streams and each hydrological period with selected species (relative abundance >1%). Relative abundance (π) was calculated and species ordered from the commonest to the less abundant in each stream type and hydrological period. Hence, these curves visually represent the changes in dominant species between streams.

Structural attributes of the community were calculated: total abundance, richness, Shannon's (H') diversity index, evenness (J'), Chl a , AFDM and AI. To test our hypothesis in relation to the structure of the algal community, we examined the relationships between each response variable (structural attributes) and explanatory variables (riparian vegetation type and hydrological period) using nested, repeated-measures ANOVA (between-subjects factor: vegetation type; nested factor: sample (within vegetation type); within-subjects factor: hydrological period). The assumptions of parametric test were analysed graphically and using the Shapiro–Wilks normality test and Bartlett's test for homoscedasticity and variables were transformed when needed. ANOVAs were carried out using the R statistical program version 3.3.2, ez library (Lawrence 2016; R Core Team 2013).

Results

Physicochemical variables did not show marked differences between grassland and afforested streams (Table 1). However, PAR intensity was 70% lower in afforested streams. Water temperature ranged from 12°C to 21°C in grassland streams and from 10°C to 19°C in afforested streams. pH was circumneutral, with similar values for grassland and afforested streams. Afforested streams were narrower and had lower current velocity during the low water period. Mean discharge values in afforested streams were 0.007 l s^{-1} at low water period and 0.01 l s^{-1} at high water periods. In grassland, streams were 0.01 l s^{-1} at low water period and 0.27 l s^{-1} at high water period.

Table 1. Physicochemical variables measured at each riparian vegetation type (grass: grassland streams, aff: afforested streams) and hydrological period.

	Low water period		High water period		ANOVAs
	Grass	Aff	Grass	Aff	
Temperature (°C)	12.5 (0.71)	11.33 (1.53)	18.6 (2.02)	18 (1.32)	$F_{1,9(\text{veg})} = 1.10, P = .32$; $F_{1,9(\text{per})} = 66.78, P < .0001$
pH	8.51 (0.28)	8.24 (0.14)	7.99 (0.85)	8.16 (0.44)	$F_{1,9(\text{veg})} = 0.07, P = .79$; $F_{1,9(\text{per})} = 1.40, P = .27$
Width (cm)	135 (39)	100 (52)	130 (40)	97 (54)	$F_{1,4(\text{veg})} = 19.85, P = .01$; $F_{1,4(\text{per})} = 1.00, P = .37$
Depth (cm)	8.02 (4.21)	9.83 (6.82)	10.27 (4.33)	6.75 (2.87)	$F_{1,4(\text{veg})} = 0.09, P = .77$; $F_{1,4(\text{per})} = 0.05, P = .82$
Current velocity (m s^{-1})	0.24 (0.05)	0.27 (0.05)	0.29 (0.14)	0.31 (0.21)	$F_{1,4(\text{veg})} = 6.99, P = .06$; $F_{1,4(\text{per})} = 13.27, P = .02$
PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)			2028 (169)	533 (353)	$F_{1,5(\text{veg})} = 51.34, P = .002$
Conductivity ($\mu\text{S cm}^{-1}$)	150.33 (113)	169 (60)	126.77 (114.71)	151.53 (56.78)	$F_{1,9(\text{veg})} = 0.19, P = .67$; $F_{1,9(\text{per})} = 0.17, P = .69$
TDS (mg l^{-1})	135.67 (103.65)	151.67 (54.6)	122.66 (111.39)	139 (48)	$F_{1,9(\text{veg})} = 0.12, P = .73$; $F_{1,9(\text{per})} = 0.08, P = .79$
Carbonate (mg l^{-1})	2.83 (3.91)	0.00	0.00	0.00	$F_{1,9(\text{veg})} = 1.48, P = .25$; $F_{1,9(\text{per})} = 1.48, P = .25$
Bicarbonate (mg l^{-1})	82.1 (69.65)	97.5 (38.49)	76.66 (79.15)	85 (30)	$F_{1,9(\text{veg})} = 0.14, P = .72$; $F_{1,9(\text{per})} = 0.08, P = .78$
Nitrate (mg l^{-1})	0.33 (0.58)	<0.1	1.33 (0.58)	2.33 (1.53)	$F_{1,9(\text{veg})} = 0.41, P = .54$; $F_{1,9(\text{per})} = 10.23, P = .01$
Hardness (meq l^{-1})	1.9 (1.15)	1.53 (0.7)	1.23 (1.36)	1.27 (0.55)	$F_{1,9(\text{veg})} = 0.09, P = .77$; $F_{1,9(\text{per})} = 0.73, P = .41$

Notes: Mean values, standard deviation (in brackets) and ANOVAs results are shown (i.e. F and P values and degrees of freedom for each factor). Significant results are in bold ($P < .05$). For T° , pH, conductivity, total dissolved solids (TDS), carbonate, bicarbonate, nitrate and hardness: one-way repeated measures ANOVA. For depth, width and current velocity: nested, repeated-measures ANOVA. For PAR (photosynthetically active radiation) measurements: one-way ANOVA. per: factor hydrological period, veg: factor riparian vegetation type.

A total of 301 taxa were collected and identified in the study streams. Almost 70% of all taxa were diatoms, followed by cyanobacteria (13%), chlorophytes (9%) and charophytes (8%). ANOVAs showed that abundance and richness of all algal divisions were affected by both factors. Abundance of all algal divisions was higher in grassland streams ($P < .01$, Figure 2). Diatom richness was higher in the afforested stream at the high water period ($F_{1,6(\text{vegetation} \times \text{period})} = 34.55, P = .001$) while chlorophytes, charophytes and cyanobacteria showed the highest richness in grassland streams at the high water period ($F_{1,6(\text{veg})} = 39.23, P < .001$ and $F_{1,6(\text{period})} = 20.76, P = .004$; $F_{1,6(\text{veg} \times \text{period})} = 29.28, P = .001$; $F_{1,6(\text{veg} \times \text{period})} = 6.03, P = .04$; respectively).

Benthic algal communities of grassland and afforested streams were separated in the NMDS ordination (Figure 3; stress = 0.15, PERMANOVA, $F_{1,44} = 7.48, P = .001$). However, some samples from afforested stream collected at site 3 during the high water period were not separated from grassland samples. Community composition also differed between hydrological periods (PERMANOVA, $F_{1,44} = 4.09, P = .002$). In addition, differentiations among groups were not due to differences in dispersion within groups (PERM-DISP, $F_{1,46} = 0.96, P = .34$).

Grassland and afforested streams were characterised by different sets of indicator taxa obtained by the IndVal method (Table 2). Thirteen indicator species were identified for grassland streams and two for afforested streams. Additionally, *Eunotia minor* (Kützing) Grunow was identified as a detector of changes produced by afforestation.

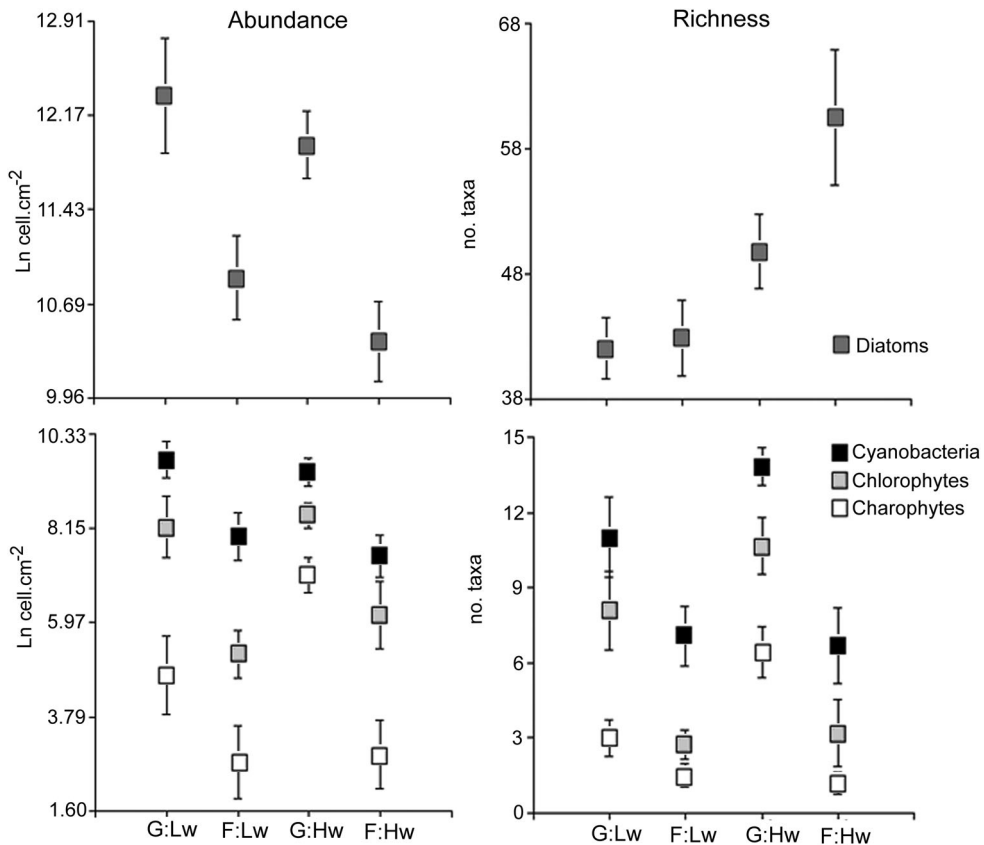


Figure 2. Abundance and richness of the algal divisions in samples from grassland (G) and afforested (F) streams in the high water (Hw) and low water (Lw) hydrological period. Mean and standard error are represented.

Range abundance curves showed that there were different dominant species at each stream type and hydrological period (Figure 4). *Achnanthydium minutissimum* (Kützing) Czarnecki and *Gomphonema pumilum* were abundant in grassland streams while *A. minutissimum*, *Cocconeis placentula* and *Karayevia clevei* were predominant in afforested streams. These species were present in both stream types but their proportions changed between grassland and afforested streams. *A. minutissimum*, *C. placentula* and *K. clevei* showed an increase in afforested streams, while *G. pumilum*, *Fragilaria capucina* Desmazières and *Encyonopsis microcephala* (Grunow) Krammer decreased. Some cyanobacteria species were more common in afforested streams, such as *Oscillatoria subbrevis* Schmidle, *Phormidium* spp. and thin filamentous cyanobacteria genera.

Most structural attributes of algal communities varied between hydrological periods and some of them showed also variations between riparian vegetation types (Figure 5, Table 3). Algal abundance and richness were higher in grassland streams and at the high water period. Diversity and evenness indices, Chl *a* concentration and AFDM were higher at the high water flow period, with no differences due to

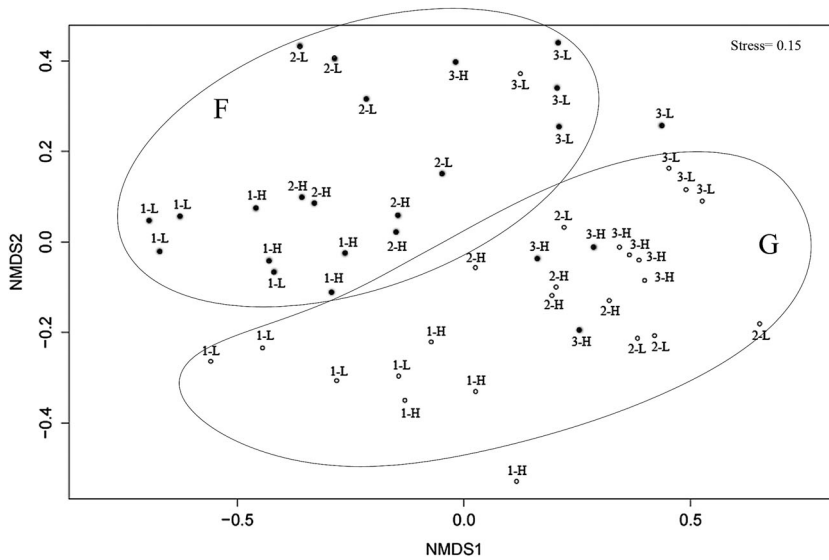


Figure 3. NMDS of algal communities from grassland (open symbols) and pine afforested streams (filled symbols). Numbers correspond to the different sites, H to high water period and L to low water period. Elliptic contours group samples belonging to each vegetation type (G, grassland; F afforestation).

Table 2. Results of IndVal analysis.

Indicator species of grassland streams	IV	P
<i>Ulnaria ulna</i> (Nitzsch) P.Compère	92.6	.0010
<i>Gomphonema pumilum</i> (Grunow) Reichardt & Lange-Bertalot	92.4	.0015
<i>Cymbella cymbiformis</i> C.Agardh	90.9	.0001
<i>Encyonema minutum</i> (Hilse) D.G.Mann	89.9	.0322
<i>Reimeria uniseriata</i> Sala, Guerrero & Ferrario	85.7	.0145
<i>Scenedesmus ecornis</i> (Ehrenberg) Chodat	80.7	.0001
<i>Nitzschia fonticola</i> (Grunow) Grunow	80.4	.0019
<i>Monoraphidium minutum</i> (Nägeli) Komárkova-Legnerová	78.2	.0001
<i>Cocconeis placentula</i> Ehrenberg (var. <i>lineata</i> , var. <i>euglypta</i>)	75.5	.0001
<i>Gomphonema rhombicum</i> Fricke	74.6	.0002
<i>Monoraphidium arcuatum</i> (Korshikov) Hindák	71.4	.0005
<i>Rhoicosphenia abbreviata</i> (C.Agardh) Lange-Bertalot	70.8	.0160
<i>Coleodesmium</i> sp.	70.7	.0001
Indicator species of afforested streams		
<i>Karayevia clevei</i> (Grunow) Round & Bukhtiyarova	77.7	.0091
<i>Denticula kuetzingii</i> Grunow	72.9	.0218
Detector species		
<i>Eunotia minor</i> (Kützing) Grunow	7 grass 53 aff	

Notes: List of indicator taxa of grassland and afforested streams. Taxa with a significant ($P < .05$) indicator value (IV) $> 70\%$ were selected as indicators. Detector taxa and its indicator value in grassland (grass) and afforested (aff) streams are also shown.

riparian vegetation type. AI showed differences between riparian vegetation types in both hydrological periods. AI was significantly higher in grassland streams at low water flow (G 410 vs. F 200) and in afforested streams at high water flow (F 320 vs. G 200).

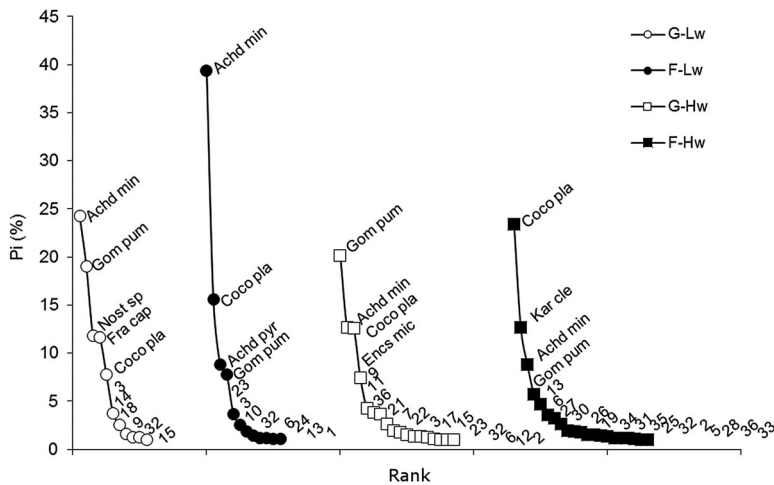


Figure 4. Rank abundance curves of abundant taxa ($P_i > 1\%$) in grassland (G) and afforested (F) streams at low water (Lw) and high water (Hw) periods. References: Achd min *Achnantheidium minutissimum* (Kützing) Czarnecki, Achd pyr *Achnantheidium* aff. *pyrenaicum* (Hustedt) H.Kobayasi, Coco pla *Cocconeis placentula* Ehrenberg (var. *lineata*, var. *euglypta*), Encs mic *Encyonopsis microcephala* (Grunow) Krammer, Fra cap *Fragilaria capucina* Desmazières, Gom pum *Gomphonema pumilum* (Grunow) Reichardt & Lange-Bertalot, Kar cle *Karayevia clevei* (Grunow) Bukhtiyarova, Nost sp. *Nostoc* sp., 1 *Achnanthes* sp., 3 *Achnantheidium deflexum* (C.W.Reimer) J.C.Kingston, 5 *Amphipleura lindheimeri* Grunow, 6 *Amphora pediculus* (Kützing) Grunow ex A.Schmidt, 7 *Chamaesiphon incrustans* Grunow in Rabenhorst, 9 *Coleodesmium* sp., 10 Cyanobacteria filamentous, 11 *Cymbella cymbiformis* C.Agardh, 12 *Cymbella excisa* var. *angusta* Krammer, 13 *Denticula kuetzingii* Grunow, 14 *Encyonema minutum* (Hilse) D.G.Mann, 15 *Encyonema silesiacum* (Bleisch) D.G.Mann, 18 *Fragilaria capucina* var. *mesolepta* (Rabenhorst) Rabenhorst, 19 *Gomphonema acuminatum* Ehrenberg, 21 *Gomphonema rhombicum* Fricke, 22 *Gomphonema subclavatum* (Grunow) Grunow, 24 *Leptolyngbya* sp., 25 *Navicula cryptocephala* Kützing, 26 *Navicula perminuta* Grunow, 27 *Navicula radiosa* Kützing, 28 *Nitzschia dissipata* var. *media* (Hantzsch) Grunow, 30 *Oscillatoria subbrevis* Schmidle, 31 *Phormidium* sp., 32 *Reimeria uniseriata* Sala, Guerrero & Ferrario, 33 *Rhoicosphenia abbreviata* (C.Agardh) Lange-Bertalot, 34 *Stigeoclonium* sp., 35 *Synechocystis* sp., 36 *Ulnaria ulna* (Nitzsch) P.Compère.

Discussion

Afforestation of mountain grassland streams in Central Argentina has led to significant changes in benthic algal community composition, the proportions of different algal taxonomic divisions and the indicator species, which represented different stream conditions. Community structure was also different, according to expectations algal abundance and richness were lower in afforested streams. Hydrological period significantly affected algal community but not as we expected. We had predicted stronger differences between grassland and afforested streams to show up at high water flow, when discharge in afforested catchments is reduced compared to catchments draining grasslands (Jobbágy et al. 2013). According to the results of Jobbágy et al. (2013), discharge values were similar between hydrological periods in afforested stream while in grassland streams more differences between periods were observed. However, for most of our community variables, hydrological period did not interact with terrestrial vegetation in the catchments. This meant that algal community variables that were sensitive to

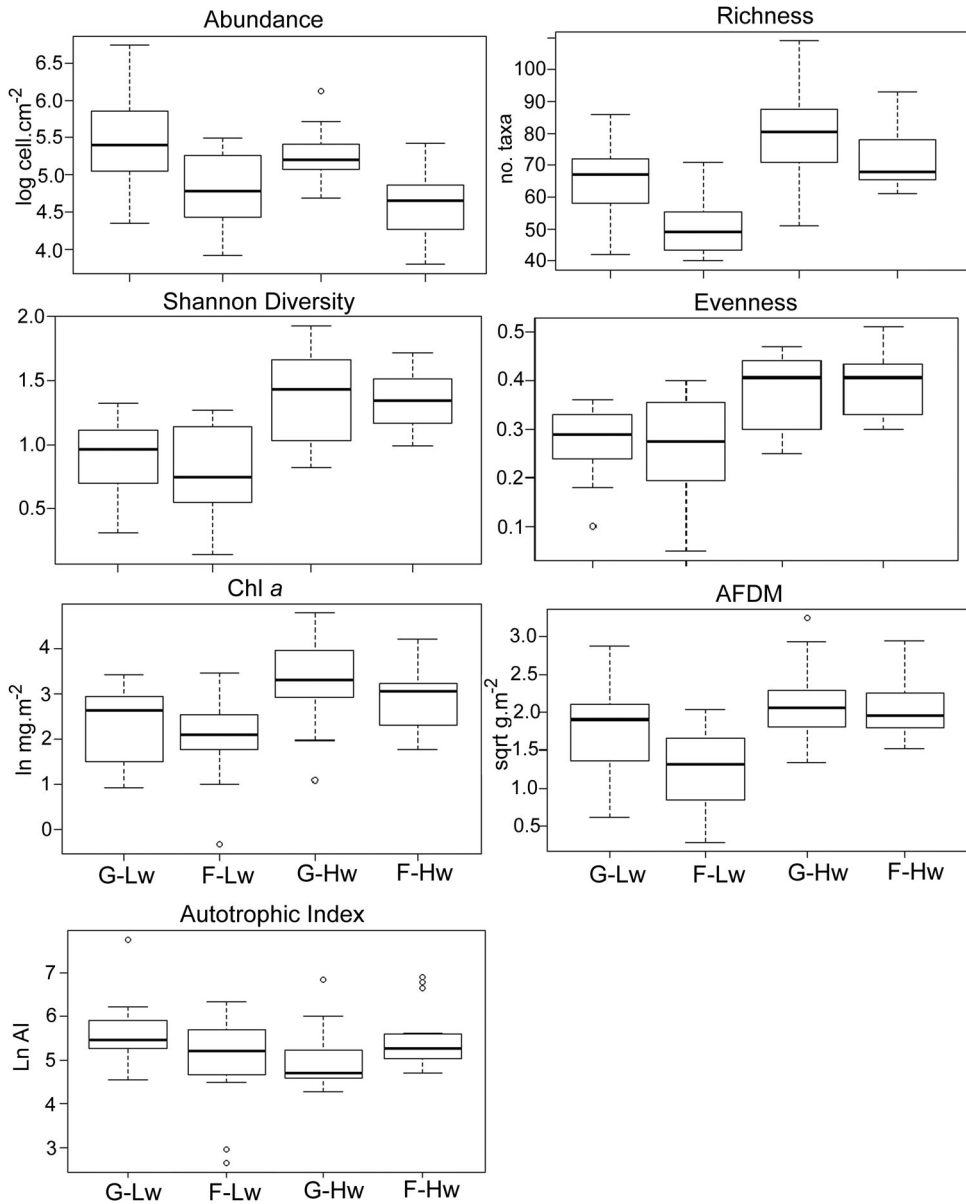


Figure 5. Box-and-whisker plots of structural attributes of algal communities: log abundance, richness, Shannon diversity (H'), Evenness (J'), Ln Chl *a*, squared root AFDM and Ln AI from grassland (G) and pine afforested (F) streams and low (Lw) and high (Hw) water periods.

pine afforestation, responded independently of changes associated to hydrological period (e.g. T°, discharge), and that the effect of hydrological period was important in streams of both vegetation types.

Benthic algae are affected by many abiotic and biotic factors (Stevenson 1996). Light intensity reaching stream bottoms in our studied afforested streams was lower as a consequence of heavy shading by perennial pines in stream margins, and this may be a key

Table 3. Results of nested, repeated-measures ANOVAs for each structural variable.

Variable	Vegetation		Period		Veg*period	
	$F_{1,6}$	P	$F_{1,6}$	P	$F_{1,6}$	P
LogAbundance	23.03	0.003	8.05	0.03	0.07	0.80
Richness	15.01	0.008	96.37	<0.0001	1.48	0.27
Shannon diversity (H') ²	2.79	0.15	34.51	0.001	0.34	0.58
Evenness (J') ²	0.03	0.88	27.30	0.002	0.37	0.57
Ln Chl a	2.01	0.21	12.54	0.01	0.59	0.47
Sqrt AFDM	3.47	0.11	20.76	0.004	2.78	0.15
Ln AI	2.44	0.17	0.05	0.83	10.45	0.02

F (with degrees of freedom) and P values for each factor (between-subjects factor: vegetation type; within-subjects factor: hydrological period and interaction) are shown. Significant results for each analysis are in bold.

factor determining our observed changes. In relation to our first prediction about changes associated with light reduction, we indeed found differences in algal community composition and a prevalence of shade-tolerant taxa in afforested streams. Lange et al. (2011) demonstrated experimentally how light strongly influence community structure; certain diatoms were more abundant under reduced light, such as *C. placentula*, which is in agreement with our results. We found that the ubiquitous small and pioneer diatoms *A. minutissimum* and *C. placentula* and also *K. clevei* increased their proportion in afforested streams while *G. pumilum*, *F. capucina* and *E. microcephala* decreased in shaded streams, in resemblance to the findings of Lange et al. (2011). Green algae usually predominate in open canopy streams as consequence of higher light intensity requirements due to their narrow pigment diversity relative to diatoms and cyanobacteria. Accordingly, we found more chlorophytes growing in our grassland streams and a dominance of diatoms in the afforested ones, similar to the results of other studies (Lowe et al. 1986; Steinman et al. 1989; Guasch & Sabater 1995; Mosisch et al. 2001; Melody & Richardson 2004; Villeneuve et al. 2010).

Indicator species are characteristic of each stream type and can be used to monitor the assemblage response to afforestation (McGeoch et al. 2002). Indicator species of grassland streams were mostly diatoms, but they were also chlorophytes and a cyanobacterium. *Coleodesmium* sp., in particular, is common in the epilithon of mountain areas, in clear, unpolluted creeks (Komárek & Hauer 2013). Most indicator species of our grassland streams are widely distributed in freshwater systems; some of them are common in the epilithon of low nutrient, circumneutral streams and lakes (e.g. *G. pumilum*, *E. minutum*, *Coleodesmium* sp., Kelly et al. 2005), coinciding with the characteristics of our studied streams. *Eunotia minor* was found to be detector of changes produced by afforestation, and other species of this genus were more frequent and abundant in our afforested streams. We found only two species characteristic of afforested streams (*K. clevei* and *D. kuetzingii*) which may reflect the overall low affinity of local algal assemblages to the conditions imposed by afforestation. Even when some species were common in all streams (e.g. *A. minutissimum*, *C. placentula*), there were changes in proportions of species and in the identity of dominant species among streams that lead to the differences in community composition.

Shading by implanted trees in stream margins should negatively affect benthic algal biomass in contrast to open canopied streams (Kiffney & Bull 2000; Boothroyd et al. 2004). In our study, we found lower abundance and richness in afforested streams,

coinciding with the expected results. However, we did not find differences in Chl *a* concentration or AFDM between grassland and afforested streams. On the one hand, the summer light levels measured in afforested streams (mean of 533 micromol m⁻² s⁻¹) might not have been low enough to have a strong effect on periphyton biomass (Quinn et al. 1997). On the other hand, several studies have demonstrated the interactive effects between resources and disturbances such as light, nutrients, current velocity and grazing on algal communities (Rosemond et al. 2000; Mallory & Richardson 2005; Liess et al. 2009; Villeneuve et al. 2010; Lange et al. 2011; Cibils Martina et al. 2014). Previous studies in the area have already shown heavy reduction of benthic invertebrate herbivores (specifically scrapers) in afforested streams (Márquez et al. 2015) and in a recent laboratory experiment, we showed a greater effect of grazers controlling algal communities developed in a grassland stream compared to that of an afforested stream (Cibils Martina et al. 2014). Additionally, an *in situ* stream experiment showed that biofilm development rate was similar between grassland and afforested streams (Principe et al. 2015). This suggests a compensation of opposing forces happening in grassland open streams (high light levels plus strong grazing) vs. the same opposing forces but with different direction occurring in pine streams (low light and weak grazing) (Principe et al. 2015). Consequently, these interactions may be responsible for cancelling differences in algal biomass between grassland and afforested streams. Many studies have reported the simultaneous top-down and bottom-up control of periphyton, revealing the importance of the interactive effects of grazing and light (Feminella et al. 1989; Wellnitz & Ward 1998, 2000; Rosemond et al. 2000; Hillebrand 2005; Mallory & Richardson 2005; Díaz Villanueva et al. 2010).

Regarding our second prediction, we expected that in afforested streams there would be a discharge reduction (Jobbágy et al. 2013) that lead to higher differences between grassland and afforested streams at the high water period. However, we did not find the expected result. Some variables, such as abundance and richness, showed differences between stream types in both hydrological periods. Other variables showed higher differences between hydrological periods instead of between riparian vegetation types. We found higher diversity, evenness and biomass at the high water period. This way, higher water flow could have benefited algal growth and colonisation both in grassland and afforested streams given the stimulation of algal metabolism (Stevenson 1996). According to Boulétreau et al. (2006), the dynamics of epilithic biomass is mainly conducted by hydrodynamics, but further studies could explore the role of temperature and flow disturbances on periphytic communities' development. In a previous study in the area, Cibils et al. (2015) found that most algal traits showed higher diversity at the high water period and found differences between periods for both stream types, similar to our results for algal community composition and structure. Similar to the present study, hydrological period had an important influence on the functional responses of algal communities under different riparian vegetation.

We found an interactive effect between vegetation type and hydrological period only for the AI, with higher values of AI in grassland streams in the low water period and in the afforested in the high water period. This could suggest a change in the proportion of autotrophs and heterotrophs in both riparian vegetation types between hydrological periods. Nevertheless, Biggs and Close (1989) stated that AI values of up to 100 generally indicate a community dominated by viable algae, and over 400 a community dominated by heterotrophs and/

or organic detritus. We found that mean values in all cases were lower than 400, indicating that epilithic communities were always autotrophic. Further research could explore the heterotrophic portion of the community and the use of AI as an indicator of water quality as in Fernandes and Esteves (2003) and Leandrini and Rodrigues (2008).

Headwater ecosystems are threatened by human activities and are inadequately protected, in part, because they are usually remote and unmapped. Plantation of exotic pines in grassland landscapes is growing over extensive areas of the Southern Hemisphere. Alien trees contribute significantly to the economies of many countries and are frequently seen positively from an aesthetical perspective, especially in arid or semiarid landscapes (Nijnik et al. 2012). However, there are also important costs associated with ecosystem services (less water yields, high fire frequency and/or severity, potentially altered nutrient cycling, changes or reduction in biota diversity) and the invasive spread of trees from plantations into natural and semi-natural habitats, where they have large impacts on a wide range of ecosystem properties and functions (Richardson 1998; Farley et al. 2005; Simberloff et al. 2010). In our study region, extensive areas are already afforested with introduced pine species which can be effective invaders of grasslands, increasing the potential impacts on natural ecosystems (Pollice et al. 2013). Furthermore, this study corresponds to the final stage of the productive forestry cycle, since logging has begun in the last years. Hence, this study represents a baseline that would allow modelling long-term dynamics of afforested semiarid mountain streams and the effects of plantation design and management to ensure no negative effects on biodiversity.

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