Stream macroinvertebrate communities change with grassland afforestation in central Argentina

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ABSTRACT

Lotic ecosystems are highly affected by land use changes such as afforestation of natural areas for management or commercial purposes. The aim of this study was to analyze the effect of pine plantations on benthic invertebrate communities in mountain grassland streams. Additionally, we assessed if the hydrological period modifies the effect of afforestation on stream invertebrates. Three headwater streams draining grasslands (reference streams) and three draining plantations of *Pinus elliottii* were selected in a mountain watershed of Córdoba province (Argentina). Hydrologic and physicochemical variables were registered and benthic invertebrate samples were collected in each stream at two different hydrological periods. Total invertebrate abundance, richness and diversity were reduced in afforested streams as well as the number of indicator taxa. In addition, invertebrate functional structure (i.e. taxonomic richness and total and relative abundance of functional feeding groups, FFG) showed differences between streams with different riparian vegetation and between hydrological periods. Total abundance of all FFGs was lower in afforested streams and scrapers' relative abundance was higher in grassland streams at the low water period. In addition, in most FFGs richness was diminished in afforested streams. Changes in light intensity, hydrology and coarse organic matter inputs produced by afforestation alter fluvial habitats and consequently the composition and trophic structure of invertebrate communities in grassland streams of Córdoba mountains.

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Introduction

Natural terrestrial ecosystems are altered by human activities encompassing broad-scale land-use changes related to natural resource acquisition (forestry, agriculture and mining) or urban and industrial development (settlements and transport infrastructures) (Foley et al., 2005). These alterations can have strong and long lasting ecological impacts on fluvial systems (Allan and Flecker, 1993; Fausch et al., 2010). Low-order open streams are characterized by communities based on the availability of sunlight establishing "green" food webs (i.e. primary producers-based) (Delong and Brusven, 1998; Thompson and Townsend, 2004a). Modifications in watershed vegetation and, most directly, in riparian areas can alter the quantity, quality and seasonality of external resource inputs into streams (e.g. altering sunlight regimes, allochthonous organic matter dynamics) (Naiman et al., 2005) as well as affecting the

regime of environmental stressors (e.g. sediment inputs and loading, temperature and chemistry concentrations). Those changes may have strong effects on the feeding rates, growth, densities and survival of aquatic populations resulting in changes in their communities both in taxonomic and functional attributes (Sponseller et al., 2001; Thompson and Townsend, 2004a; Richardson, 2008).

In recent centuries, reafforestation and afforestation have become common practices to recover or convert new lands to timber production or to reduce erosion. These forestry practices result in significant landscape alterations, impacting the catchments that drain plantations (van Dijk and Keenan, 2007). In particular, the replacement of natural grassland with pines alters sunlight regimes and organic matter dynamics. Perennial tree species shade lotic systems throughout the year and also cause an increase in the income of coarse particulate organic matter (CPOM), mainly leaves, branches and trunks in the streams (Giller and O'Halloran, 2004). The pine needles have a very low decaying rate (Webster and Benfield, 1986) due to their thick cuticle and the presence of resins that can function as inhibitory substances for decomposers and detritivores (Bärlocher and Oertli, 1978a, 1978b). Thereby, pine needles and trunks accumulate and create natural dams

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which modify fluvial habitats (Hilderbrand et al., 1997; Collier and Halliday, 2000).

Catchment afforestation with species that have contrasting ecological characteristics compared to those commonly found in their hosting environment may also have strong effects on water yield. Large leaf biomass and the high growth rate of the conifers may increase evapotranspiration by two ways, a greater evaporative capacity of the canopy by interception and a better access to soil water (Jobbágy et al., 2006). Direct changes in hydrology have already been acknowledged with detrimental effects of exotic plantations (pines) replacing native temperate forests in the water yield of large catchments in Chile (Little et al., 2009). Similarly, Farley et al. (2005) found that tree plantation in grasslands and shrublands reduced up to 40% and 75% (pines and eucalyptus, respectively) of the annual water discharge. These studies pointed out that the effects were proportionally stronger in low flow periods, raising concern on the environmental costs that afforestations face while delivering their better known benefits of wood, runoff regulation, erosion control, and carbon sequestration. In this way, afforestation provides new productive opportunities but it may also alter essential services that ecosystems provide such as water supply or watershed hydrological regulation (Jobbágy et al., 2006; Little and Lara, 2010).

The evaluation of forestry impacts is essential for the implementation of management strategies and the conservation of water resources and biota in headwater streams. The use of benthic invertebrate communities as an indicator of land use effects in a catchment as well of direct perturbation in the aquatic environment is widespread in many regions of the world (Roy et al., 2003; Gabriels et al., 2010; Dos Santos et al., 2011; Ansah et al., 2012). Aquatic macroinvertebrates have proven to be an efficient diagnostic tool in monitoring water quality and ecological integrity of river systems (Rosenberg and Resh, 1993; Bonada et al., 2006) because they integrate anthropogenic impacts across different spatial and temporal scales.

In the seventies, Argentine's federal laws promoted afforestation with introduced fast-growing species (primarily pines, eucalyptus and Salicaceae) in vast regions originally occupied by grasslands (Jobbágy et al., 2006). For instance, large extensions of semi-arid grasslands in mountainous landscapes in central Argentina were afforested with pines, which were also planted into riparian areas, with potential negative effects on the structure and functioning of watercourses. Several studies have reported that in catchments dominated by deciduous forests or gramineous vegetation, pine plantations alter both composition of aquatic invertebrate assemblages and organic matter dynamics (Death et al., 2003; Thompson and Townsend, 2004a; Richardson, 2008; Miserendino and Masi, 2010). Although the conversion of grasslands to implanted forest of exotic pines should produce strong environmental changes in aquatic systems, (e.g. altering sunlight regime, moderating temperature and increasing the amount of organic matter inputs) affecting the quantity and quality of resources, the response of stream invertebrate communities remains unstudied.

Considering that benthic invertebrates in mountain streams of Córdoba province (central Argentina) are adapted to a broad spectrum of spatio-temporal environmental gradients (Corigliano, 1998; Principe et al., 2007), afforestation of grassland catchments may produce varied responses in benthic communities. Changes in both resources and environmental variables might lead to a lower diversity in afforested streams, with the disappearance of sensitive species and the increased abundance of tolerant species. In relation to functional groups, the abundance of shredders may increase in afforested streams due to the large inputs of riparian coarse particulate organic matter. However it has been observed that shredders are not abundant in these mountain streams (Principe et al., 2010).

Moreover, changes in light intensity entering the stream may affect algal abundance and production. In that way, scrapers are expected to decrease in afforested environments. Oppositely, if invertebrates in grassland streams are generalists, periphyton and allochthonous organic matter could be used alternatively as a food resource with little changes in invertebrate communities at both taxonomic and functional levels.

The abiotic environment set the main stage for evolutionary development of specific traits and associated life-history strategies in ecosystems (Lytle and Poff, 2004). Water current exerts a drag force on individual organisms and, due to episodic fluctuations and substrate dislodgement, can be a powerful disturbance force as well. However, current benefits the biota through mass transfer processes and transporting food resources to animals. In that way, community structure is highly determined by flow conditions (Biggs et al., 2005). Water temperature, which determines species distribution, also affects community structure. Stream temperature is expected to be moderate during summer months under shading of implanted pines which may either alleviate physiological stress of sensitive species imposed to high temperatures occurring in grassland streams or may delay invertebrate feeding and growth or both with consequences for species fitness (Huryn et al., 2008).

Our aim was to analyze the effect of grassland replacement by pine plantations on benthic invertebrate communities in mountain grassland streams. Our study region is characterized hydrologically by two contrasting periods, a rainy season occurring between spring and late summer (Austral region) when stream flows and occasional spates are high and a dry season with low stream flow between autumn and winter. Recently, Jobbágy et al. (2013) demonstrated a 50% reduction in the annual water yield in those afforested catchments compared to their paired grassland ones occurring during the rainy season in coincidence with seasonal tree growth. Water temperature is also higher during spring-summer, potentially resulting in higher differences in stream thermal regimes than in autumn-winter. Considering that higher environmental differences are expected during the rainy season, we hypothesize that the direction and magnitude of changes in invertebrate community structure are to be emphasized between afforested and grassland streams compared to the dry season.

Materials and methods

Study area

The study was carried out in streams of the Ctalamochita river upper basin, Córdoba, Argentina (Fig. 1). This river is one of the main tributaries of the Carcarañá river and belongs to La Plata river basin. Headwaters of the Ctalamochita river are located in grasslands of the Comechingones mountains between 800 and 1500 m a.s.l. The lithology is dominated by granitic rocks but localized patches of metamorphic rocks (gneiss, schist, migmatite) can also be found. Annual precipitation in the region reaches 725 mm occurring mostly between spring and the end of summer (Austral region: October–March) (Cabido et al., 2003) determining a relatively dry mountainous landscape. Maximum air temperature reaches 34 °C in summer (December–March) and decreases up to −5 °C in winter (June–September). Grasslands are dominated by *Festuca hieronymi*, *Nassella filiculmis*, *Schizachyrium condensatum* and *Eragrostis airoides* (Oggero and Arana, 2012). They are primarily used for cattle and sheep grazing and other human activities like extraction of medicinal and aromatic herbs and fauna that contribute to landscape modification (Cabido et al., 2003).

Most afforested areas in the region were established in the late 1970s as a result of a tax deferral plan implemented by the Córdoba government. Currently, 36,000 ha of the Sierras de los
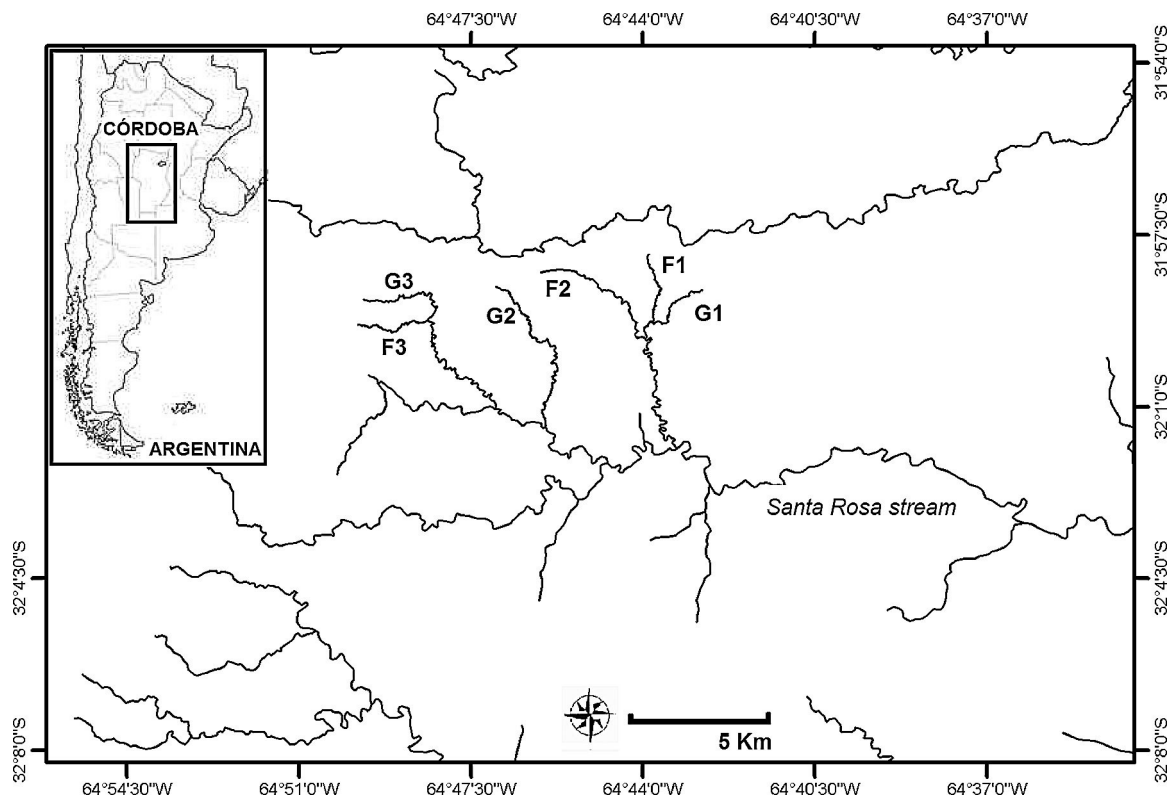
Fig. 1. Paired study streams belonging to Santa Rosa stream sub-basin (Córdoba, Argentina). Three streams drain grasslands (G1, G2, G3) and the other three streams drain pine plantations (F1, F2, F3). Numbers 1, 2 and 3 correspond to different sites.

Comechingones in Córdoba are afforested with pines between 900 and 1600 m a.s.l. (Plevich et al., 2002), which correspond to 15% of upland grasslands in the Comenchingones mountains. In the study area, *Pinus elliottii* is the dominant tree in the plantations followed by *P. radiata* and *P. taeda*.

Three paired first-order streams located in three sites with similar altitude, slope, exposure to sunlight and drainage area were selected (Fig. 1). Three of these streams drain grasslands (reference streams) and each one has a contiguous stream that drains plantations of *P. elliottii* (afforested streams). Drainage area of the study streams ranged from 27 to 142 ha (mean grassland watershed size: 69 ha, mean afforested watershed size: 86 ha) and were located at about 1100 m a.s.l. Previous studies showed that pine afforestation did no change water acidity and chemistry of those grassland streams (Farley et al., 2008).

Macroinvertebrate sampling

Benthic samples were collected with a Surber sampler (0.09 m^2; 300 μm mesh size) in riffle habitats. In each stream (3 grasslands and 3 afforested with pines), four samples were taken during high and low water periods (July 2008 and February 2009). We consider these two opposite hydroperiods that varied not only in discharge but also in water temperature as contrasting conditions for stream fauna. Samples were fixed with formaldehyde 4% and then processed in the laboratory. Invertebrates were identified at the lowest possible taxonomic level with specific keys (Domínguez and Fernández, 2009) and counted. Abundance was measured as number of individuals per m^2.

After identification, macroinvertebrates were assigned to a functional feeding group (FFG) (gathering collector, filtering collector, scraper, shredder, predator) using available references (Merritt and Cummins, 2006; Merritt et al., 2008; Tomanova et al., 2006; Principe et al., 2010; Reynaga and Dos Santos, 2012).

Depth and current velocity were measured in each sample site (four measurements per stream) with a digital water velocity meter (Global Flow probe FP101-FP202). Temperature was measured with a mercury thermometer and pH measurements were taken with a portable sensor. Since conductivity values in the study streams were similar and stable through a two years period (2004 and 2005) (E. Jobbágy, unpublished data) in the Result section values taken in 2005 are shown.

Data analyses

To compare physicochemical variables measured at each stream type (grassland/afforested) and hydrological period (low flow/high flow) two-way ANOVAs and DGC (Di Rienzo–Guzman–Casanoves) test a posteriori were performed using Infostat version 2012 (Di Rienzo et al., 2012). Conductivity was log$_{10}$ Y transformed.

Rank abundance curves were built for grassland and afforested streams and for each hydrological period with more abundant species (relative abundance >1%). Species were ordered from the dominant to the less abundant in each stream type and hydrological period. Hence, these curves visually show taxonomical replacement in dominant species and evenness either between streams or hydrological periods.

To evaluate changes in invertebrate community composition and abundance between grassland and afforested streams and hydrological periods, a correspondence analysis (CA) was performed. In addition, two more additional CAs were performed considering the two hydrological periods separately. Abundance data were log$_{10}$(Y+1) transformed for the ordinations and they were carried out using CANOCO 4.5 (ter Braak and Smilauer, 1999). Differences in composition and abundance of invertebrate fauna between grassland and afforested streams were tested by Multiresponse Permutation Procedures (MRPP, a non parametric

Table 1
Physicochemical measurements of grassland and afforested streams during sampling periods (low flow: July 2008, high flow: February 2009). Values correspond to mean values of three grassland and three afforested streams. Standard errors are shown between brackets.

	Low flow period		High flow period	
	Grassland	Pine forest	Grassland	Pine forest
Current velocity (m seg^{-1})	0.21 (0.02)	0.23 (0.04)	0.34 (0.05)	0.29 (0.06)
Channel depth (m)	0.08 (0.01)	0.08 (0.01)	0.08 (0.01)	0.05 (0.01)
Temperature (°C)	12.50 (0.50)	11.30 (0.88)	18.66 (1.17)	18.00 (0.76)
pH	8.50 (0.19)	8.24 (0.08)	7.98 (0.49)	8.16 (0.25)
Conductivity (µS cm^{-1})*	146.4 (71.5)	144.7 (34.9)	141.3 (64.8)	133.6 (29.4)

* Unpublished data provided by E. Jobbagy taken in the study streams in 2005.

procedure for testing the hypothesis of no difference between two or more groups of sampling units).

Indicator taxa were obtained using the IndVal method (IndVal, Dufrêne and Legendre, 1997). 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 and the later corresponds to a perfect indication. Significance of each taxa was tested using Monte Carlo test with 1000 permutations and species with significant indicator values ($p < 0.05$) were considered indicators of each stream type. The IndVal method and the MRPP were carried out using PC-ORD version 5.0 (McCune and Mefford, 1999).

Structural attributes of the community were calculated: total abundance, richness, Shannon diversity index (H') and evenness (J'). To examine the relationships between each response variable (structural attributes) and explanatory variables (riparian vegetation and hydrological period) we used linear mixed models (LMM) in a hierarchical design. We included "site", "stream" and "replicates" as nested random factors, since we collected four Surber samples in each stream, and streams corresponded to three different sites ("replicate nested within stream nested within sites") and "riparian vegetation" and "hydrological period" were included as fixed factors. Validations of simple assumptions of the models were performed reviewing standardized residuals vs. predicted and the normal Q–Q plot of standardized residuals. Total abundance was $\log_{10} Y$ transformed.

Total abundance, relative abundance and richness of the FFGs were analyzed with the same statistical analysis previously explained. Total abundance of each FFG and relative abundance of shredders and scrapers was $\log_{10} Y$ transformed. LMMs were carried out using the R statistical program version 3.0.1 (R Core Team, 2013) and DGC (Di Rienzo–Guzman–Casanoves) test a posteriori was performed using Infostat version 2012 (Di Rienzo et al., 2012).

Results

Physicochemical variables were mostly similar between stream types (Table 1). Current velocity and channel depth were slightly lower in pine afforested streams during high flow period (i.e. summer sampling), though no significant (ANOVA: current velocity $F_{1,8(vegetation)} = 0.97$, $p = 0.354$; $F_{1,8(period)} = 0.56$, $p = 0.475$; Channel depth: $F_{1,8(vegetation)} = 2.24$, $p = 0.173$; $F_{1,8(period)} = 1.62$, $p = 0.238$). Water temperature was nearly 1 °C lower in afforested streams than in grassland streams and it was significantly higher in high water period (ANOVA: water temperature $F_{1,7(period)} = 45.66$, $p = 0.0003$). Overall, water pH was basic and water conductivity was relatively low and similar among sampling conditions (i.e. ~140 µS cm^{-1}) (ANOVA: water pH $F_{1,7(vegetation)} = 0.02$, $p = 0.894$; $F_{1,7(period)} = 0.87$, $p = 0.381$; conductivity $F_{1,8(vegetation)} = 0.12$, $p = 0.74$; $F_{1,8(period)} = 0.01$, $p = 0.915$).

A total of 89 taxa were found in grassland streams whereas 87 taxa were registered in afforested streams. In the low water period, the black fly *Simulium* spp. was the most abundant taxa in both stream types (Fig. 2). In grassland streams, the non-biting midge

Rheotanytarsus spp. and the caddisfly *Smicridea* spp. presented high densities whereas the mayfly *Americabaetis* spp. and the freshwater shrimp *Hyalella curvispina* were very abundant in afforested streams. In the high water period, differences between assemblages from streams with different riparian vegetation were more noticeable. In grassland streams, the freshwater shrimp *H. curvispina* was the dominant species followed by the non-biting midges *Pseudochironomus* spp. and *Rheotanytarsus* spp. (Fig. 2). In afforested streams, the community were dominated by the mayfly *Caenis* spp., the sludge worm *Naidinae* spp. and the freshwater shrimp *H. curvispina*.

Grassland streams communities differed from those in afforested streams by the first axis of correspondence analysis (Fig. 3) and differences between hydrological periods were also observed. The first four axes of the ordination explained 40.4% of total variability of species composition (Eigenvalues, axis 1:
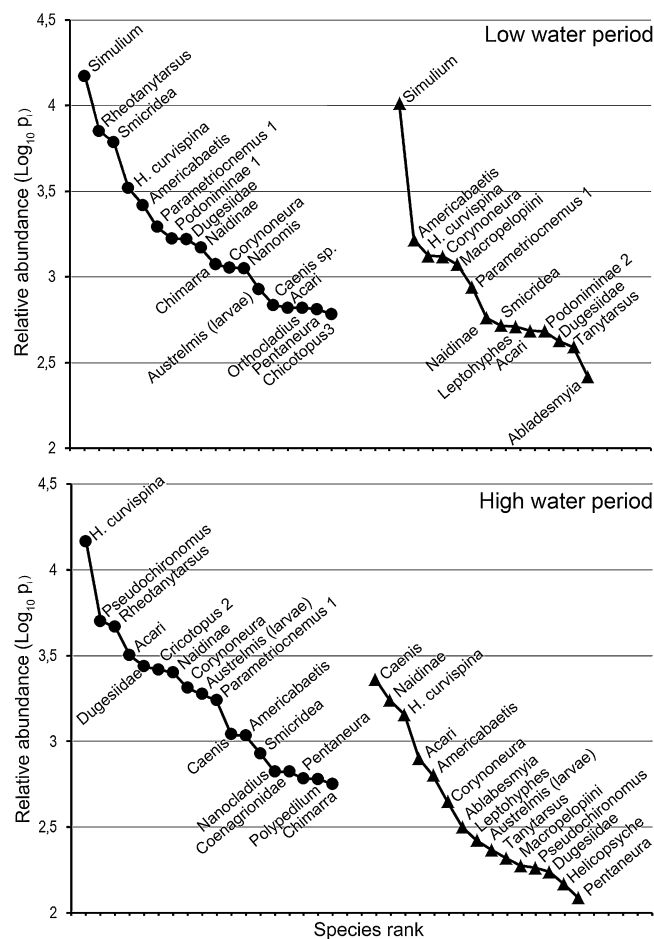

Fig. 2. Rank–abundance curves of abundant taxa (relative abundance >1%) from grassland (circles) and afforested (triangles) streams in the high water and low water hydrological period.
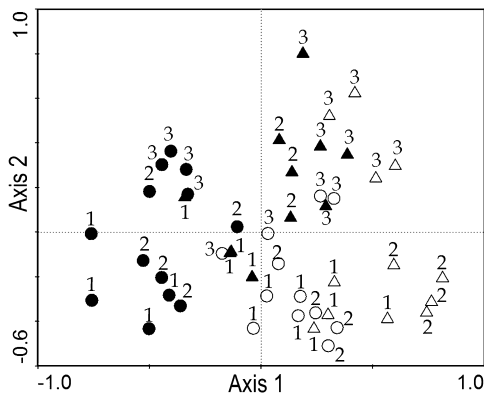
Fig. 3. Correspondence analysis ordination of invertebrate samples from grassland (circles) and pine afforested streams (triangles) collected in two hydrological periods, low water (open symbols) and high water (filled symbols). Numbers correspond to the different sites.

Table 2
Indicator values (IndVals) for invertebrate taxa of pine afforested and grassland streams. Monte Carlo test was used to assess the significance of each taxon as an indicator for a respective stream type. Only taxa with significant indicator values ($p < 0.05$) are listed. Functional feeding group assigned to each taxa is shown. Sd: shredder, Sc: scraper, P: predator, FC: filtering collector, GC: gathering collector.

Taxa	FFG	Indicator value	p-Value
Grassland			
Rheotanytarsus spp.	FC	90.5	0.001
Pseudochironomus spp.	GC	88.1	0.001
Austrelmis spp.	GC	82.3	0.011
Pentaneura spp.	P	82.2	0.002
Cricotopus sp. 1	GC	81.4	0.001
Ambryssus spp.	P	74.2	0.003
Nanocladius spp.	GC	74.2	0.001
Metrichia spp.	GC	73.6	0.002
Hydroptila spp.	GC	70.3	0.001
Helicopsyche spp.	Sc	63.3	0.008
Coenagrionidae	P	61.2	0.020
Cricotopus sp. 2	GC	59.8	0.018
Limonia spp.	Sd	57.0	0.036
Lutrochidae	GC	54.2	0.001
Chimarra spp.	GC	41.0	0.025
Polypedilum spp.	GC	40.5	0.007
Oxyetira spp.	GC	37.0	0.005
Ceratopogonidae sp. 1	P	36.8	0.010
Maruina spp.	GC	35.3	0.033
Camelobaetidius spp.	Sc	33.2	0.006
Podonominae sp. 1	GC	25.0	0.022
Empididae	P	24.8	0.033
Pine forest			
Macropelopiini spp.	P	74.2	0.001
Pentaneuriini spp.	P	74	0.002
Tipulidae	P	40	0.006

0.153, axis 2: 0.101, axis 3: 0.099, axis 4: 0.062). Additionally, the MRPP showed significant differences for invertebrate assemblages between streams with different riparian vegetation ($p < 0.0004$).

Correspondence analyses performed for each hydrological period revealed stronger divergence between assemblages of grassland and afforested streams than the CA carried out with the whole data set (Fig. 4). The first four axes explained 52.1% of total variability of species data in low water period and 48.0% in high water period. MRPP indicated significant differences in invertebrate assemblages between both riparian vegetation (Low water period: Eigenvalues, axis 1: 0.168, axis 2: 0.147, axis 3: 0.096, axis 4: 0.066, MRPP: $p < 0.001$; High water period: Eigenvalues, axis 1: 0.152, axis 2: 0.113, axis 3: 0.073, axis 4: 0.071, MRPP: $p < 0.001$).

Grasslands streams were characterized by a rich community represented by twenty one-indicator taxa (Table 2). The non-biting midges *Rheotanytarsus* spp. (90.5%) and *Pseudochironomus* spp. (88.1%) showed the highest values followed by the riffle beetle *Austrelmis* spp. (83%). In contrast, only three indicator taxa with values lower than 75% were detected by the IndVal method in afforested streams (Table 2) and all the indicator taxa belonged to dipteran families.

Structural community attributes differed between streams with different vegetation type. Total invertebrate abundance, taxonomic richness and Shannon diversity index were significantly reduced in afforested streams (Fig. 5) (LMMs: total abundance: $F_{1,22} = 8.01$, $p = 0.009$; taxonomic richness: $F_{1,22} = 21.12$, $p < 0.001$, diversity: $F_{1,22} = 4.8$, $p < 0.039$; DGC pos hoc test, $p < 0.05$). Community richness increased significantly in the high water period regardless of the vegetation type in the catchment (LMM: taxonomic richness: $F_{1,22} = 10.86$, $p = 0.003$).

Total abundance for each FFG was significantly higher in grassland streams than in afforested ones (Fig. 6) (LMMs: gathering-collectors: $F_{1,22} = 8.42$, $p = 0.008$; filtering-collectors: $F_{1,22} = 6.13$, $p = 0.021$; shredders: $F_{1,22} = 6.24$, $p = 0.02$; predators: $F_{1,22} = 8.07$, $p = 0.009$; scrapers: $F_{1,22} = 7.6$, $p = 0.011$; DGC pos hoc test, $p < 0.05$).

Relative abundance of FFGs gave different results. Gathering-collectors had higher abundance at the high water period (LMM: $F_{1,22} = 6.92$, $p = 0.015$; DGC pos hoc test, $p < 0.05$) and filtering collectors were more abundant at low water period (LMM: $F_{1,22} = 17.27$, $p < 0.001$; DGC pos hoc test, $p < 0.05$). In contrast, scraper relative abundance was higher in grassland streams only at the low water period (Fig. 7) (LMM: Scrapers: $F_{1,22} = 6.94$, $p = 0.015$; DGC pos hoc test, $p < 0.05$).
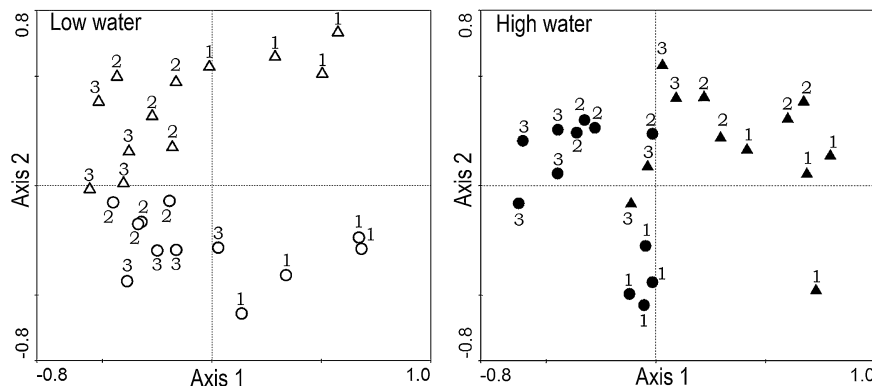

Fig. 4. Correspondence analysis ordinations of invertebrate samples from grassland (circles) and pine afforested streams (triangles) in low water period (left) and high water period (right). Numbers correspond to the different sites.
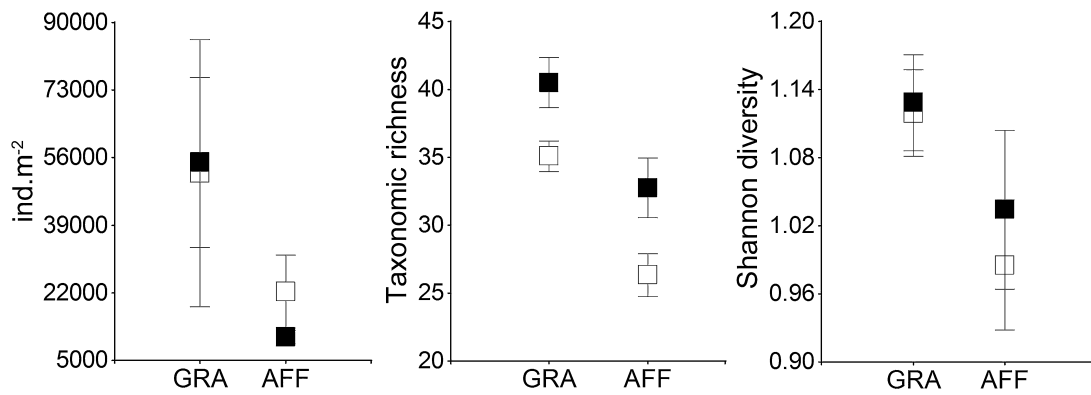
Fig. 5. Total abundance, taxonomic richness and Shannon diversity in grassland (GRA) and afforested streams (AFF) in two hydrological periods: low flow (open symbols) and high flow (filled symbols). Mean values are shown with standard error.
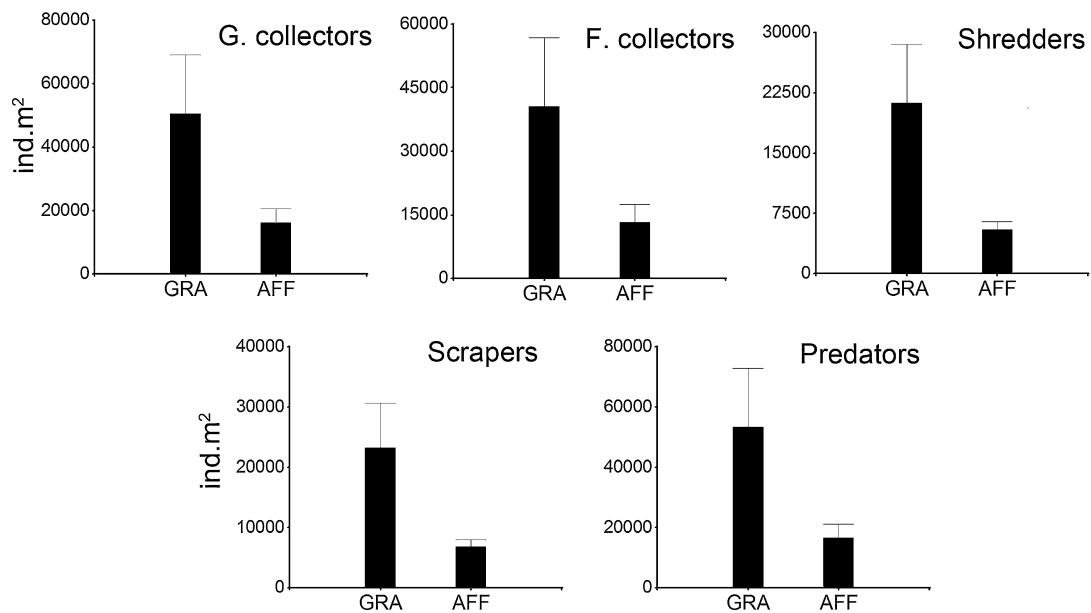

Fig. 6. Total abundance of FFGs in grassland (GRA) and afforested streams (AFF). Mean values are shown with standard error.

Both environmental factors (i.e. vegetation type and hydrological period) affected richness of different FFGs (Fig. 8). In most FFGs, richness was diminished in afforested streams (LMMs: gathering-collectors: $F_{1,22} = 36.14$, $p < 0.001$; filtering-collectors: $F_{1,22} = 7.61$,

$p = 0.011$; predators: $F_{1,22} = 8.61$, $p = 0.007$; scrapers: $F_{1,22} = 18.63$, $p < 0.001$; DGC pos hoc tests, $p < 0.05$). Richness of predators and scrapers were higher in the high water period (LMMs: predators: $F_{1,22} = 87.49$, $p < 0.001$; scrapers: $F_{1,22} = 15.61$, $p < 0.001$; DGC pos hoc test, $p < 0.05$) whereas shredders showed higher taxonomic richness at the low water period (LMM: shredders: $F_{1,22} = 5.67$, $p = 0.026$; DGC pos hoc test, $p < 0.05$).
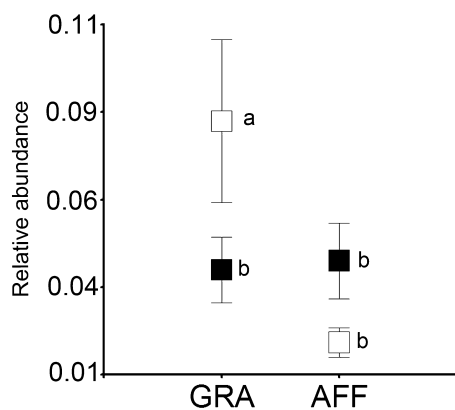
Discussion

One of the main causes of the dramatic transformation of aquatic ecosystems is associated to human activities in the surrounding landscapes, such as afforestation of natural areas. Our study explores grassland afforestation in small catchments and reveals significant modifications in stream invertebrate communities, which are involved in key processes and ecosystem services, such as mediating organic matter breakdown, nutrient cycling and the connection of basal and top levels in food webs (Wallace and Webster, 1996; Graça, 2001; Cross et al., 2005). Invertebrate diversity was reduced in afforested catchments as well as the total abundance and taxonomic richness. Regarding invertebrate functional organization we found higher relative abundance of scrapers in grassland streams only at the low water
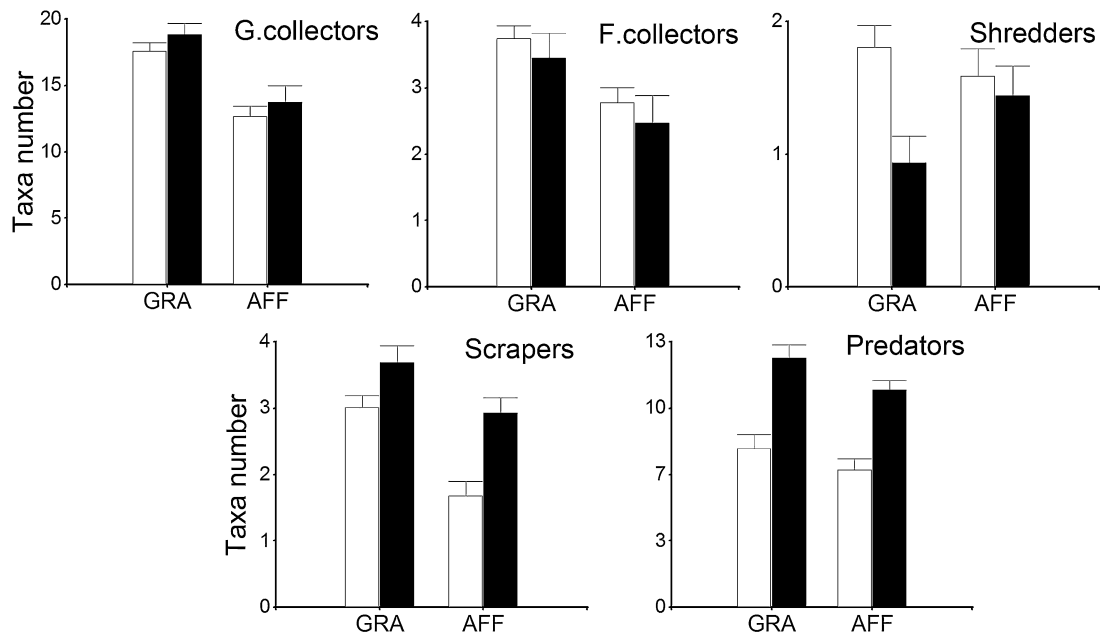

Fig. 7. Relative abundance of scrapers in grassland (GRA) and afforested streams (AFF) in two hydrological periods: low flow (open symbols) and high flow (filled symbols). Mean values are shown with standard error. Different letters indicate statistical differences (DGC pos hoc test, $p < 0.05$).

Fig. 8. Taxonomic richness of FFGs in grassland (GRA) and afforested streams (AFF) in two hydrological periods: low flow (white bars) and high flow (black bars). Mean values are shown with standard error.

period, however shredders did not exhibit changes in their relative abundance between grassland and afforested catchments.

Abundance and taxonomic composition

In our study area, invertebrate communities in grassland streams changed after afforestation, as shown in the ordination analysis and rank–abundance curves. Quinn et al. (1997a) found similar results when pine afforested streams were compared with open pasture ones. Several authors have reported modifications in aquatic invertebrate communities after clear felling of native forests (including riparian zones) for commercial afforestation (Death et al., 2003; Thompson and Townsend, 2005; Richardson, 2008; Miserendino and Masi, 2010). Changes in grassland stream biofilm due to pine afforestation were also reported (Thompson and Townsend, 2004b), but so far, to our knowledge, few studies have reported the response of stream benthic invertebrates to the conversion of grassland streams to afforestations (Thompson and Townsend, 2003).

Taxonomic changes in afforested catchments could be accounted for the modification of the resources that enter and predominate in the stream. Forest implantation strongly alters the quantity and quality of organic matter and primary production dynamics in the stream channel through the continuous supply of woody debris and the reduction in sunlight intensity (Naiman et al., 2005; Giller and O'Halloran, 2004; Richardson, 2008). Consequently, these changes modify the characteristic invertebrate assemblages in grassland streams. In addition, our study reported 22 taxa characteristic of grassland streams (IndVal Method) whereas only three taxa were indicators of afforested streams. This may indicate that macroinvertebrate fauna could neither efficiently exploit the new resources that afforestation provides nor tolerate the new environmental conditions generated by plantations. Comparing indicator taxa with values higher than 70% in both streams types, it can be appreciated that grassland streams were characterized by species belonging to Diptera, Coleoptera, Hemiptera and Trichoptera. These groups represent a great diversity of life forms and feeding behaviors, with primary consumers and predators which may suggest an equilibrated

trophic web. By contrast, in afforested streams only two indicator taxa were detected with an IndVal value higher than 70%, both belonging to the dipteran family Chironomidae. Since dipterans are commonly found in deteriorated environments (Rosenberg and Resh, 1993), our results may suggest environment degradation in afforested streams.

Structural community attributes

In addition to the taxonomic changes in the invertebrate communities, our study showed a significant reduction in total abundance, taxonomic richness and diversity in afforested streams. Quinn et al. (1997a) found greater invertebrate density in open streams with pasture management than in afforested ones, but no richness changes were reported. Similarly, other studies performed in New Zealand and Argentina reported no significant changes in invertebrate richness and diversity in afforested streams (Death et al., 2003; Thompson and Townsend, 2003, 2004a; Miserendino and Masi, 2010).

Open streams, such as those in our study area, have low allochthonous riparian plant inputs, and stream fauna is adapted to feed on autotrophic organisms (Delong and Brusven, 1998) and fine particulate organic matter. The conversion of stream margins from grassland to pine forest reduces stream algal productivity by shading (Thompson and Townsend, 2004b), and the reduction in invertebrate taxonomic richness may be related with this condition (Quinn et al., 1997b). Additionally, our study showed that fine particulate organic matter feeders, scraper and predator richness were diminished in afforested streams and we found a high relative abundance of scrapers in grassland streams in low water period. These results suggest that pine afforestation modifies basal resources that affect invertebrate community structure and function. Furthermore, streams food webs may become altered (Thompson and Townsend, 2003) since grassland food webs are longer, have more algal species and display greater internal connectance, whereas forest food webs tend to be based on detritus, with a simple food web structure dominated by short food chains and with low prey: predator ratios (Thompson and Townsend, 2004a).

Functional feeding groups

In spite of the fact that herbaceous riparian vegetation may be an important allochthonous energy resource to small streams in non-forested catchments (Menninger and Palmer, 2007), shredder invertebrates were found to be scarce and with low densities in Córdoba streams (Principe et al., 2010) similar to our results. Contrary to what we expected, shredders showed higher total abundance in grassland streams but this result may be underplayed by the great difference in total invertebrate abundance between grassland and afforested streams (i.e. three times higher, mean total invertebrate abundance: 53,416 ind m^{-2} vs. 16,578 ind m^{-2}, respectively). Thompson and Townsend (2004a) found higher shredder richness in afforested streams than in grassland ones. It is worth mentioning that pine afforested streams in that study had originally been native forest streams where shredders inhabited naturally. What is more, many invertebrate species have been reported to behave as facultative shredders (Thompson and Townsend, 2003). Although in Argentina some studies on the feeding preference of aquatic invertebrates have been conducted (Albariño and Díaz Villanueva, 2006; Reynaga, 2009; Reynaga and Dos Santos, 2012), it is widely accepted that these preferences change regionally and depending on resource availability (Cummins et al., 2005; Tomanova et al., 2006). Although in central Argentina information about the trophic behavior of aquatic invertebrates is still lacking, our results suggest that invertebrate community of grassland mountain streams are not able to track stream resource changes (i.e. periphyton based vs. detritus based food web) following afforestation. Future studies will expand the knowledge about trophic behavior and diet of invertebrates therefore allowing to link this information with taxonomic changes in afforested catchments and to establish the role of these organisms in key ecosystem processes such as degradation of organic matter.

Variation between hydrological periods

Hydrologic alteration in stream draining pine afforested catchments is likely to be responsible for changes in invertebrate assemblage characteristic of grassland streams. In our study area, Jobbágy et al. (2013) showed that water flow reduction of afforested streams compared to paired grassland ones mostly happens during the rainy summer season (i.e. high water period). However, hydrological seasons exerted strong contrast in our study not only in stream water flow but also in water temperature. Therefore, our comparison of benthic invertebrate community attributes between hydrological periods incorporate the simultaneous effect of both abiotic factors. Although water temperature and flow may have synergic or antagonistic effects on species, taxa composition in both stream types differed more notoriously during the high water period according to CA ordinations and rank abundance curves. However, some structural and functional traits (e.g. FFGs variables) varied in relation to hydrologic period regardless vegetation type. In afforested streams the great quantities of coarse organic matter (trunks, branches and needles) in the streambed may reduce the frequency and intensity of floods occurring during the high water period. Floods are considered a natural process that influence stream communities (Poff et al., 1997; Biggs et al., 2005), controlling species interactions, increasing habitat heterogeneity and favoring thereby more diverse communities. Thus, plantations may alter this natural process affecting sensitive species and reducing diversity.

The types of aquatic community attributes and ecosystem processes that are altered by afforestation, and the magnitude of changes, vary geographically and according to the type of practice (Richardson, 2008). In this way, our study provides new information on how afforestation of natural semi-dry grasslands affects stream macroinvertebrates. The changes of riparian vegetation type affect benthic community structure and ecosystem functioning as a result of tight abiotic and biotic coupling between small streams and the surrounding land (Sweeney et al., 2004). Our study ratifies the differences between grassland and afforested streams considering that invertebrate assemblages change after afforestation. Furthermore, this work reports indicator taxa of afforested aquatic environments which could be important in freshwater monitoring and in the application of restoration strategies of altered systems and management of harvested catchment.

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