

# Pine afforestation changes more strongly community structure than ecosystem functioning in grassland mountain streams

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## ABSTRACT

In the past decades, afforestation of grassland landscapes has gained importance both as an economic activity and a mechanism to mitigate anthropogenic carbon emissions. This study evaluates the effect of pine afforestation on grassland streams analyzing changes in two integrative ecological indicators: leaf litter breakdown and primary production. We compare those results with changes in structural attributes of benthic biota (primary producers and invertebrates). Six contiguous first-order streams were selected in the upper basin of the Ctalamochita river (Córdoba, Argentina): three reference streams draining grasslands and three streams draining *Pinus elliottii* afforestations. Two in situ experiments were performed to compare leaf litter breakdown and primary production between grassland and afforested streams. Additionally, invertebrate assemblages in leaf litter and riffles, and periphyton standing stock were sampled and assessed. Nine out of 26 structural indicators showed differences between stream types but indicators measuring changes at the basal level of the food web (i.e. detritus and primary producers) were less sensitive than those recording changes in consumers. Our attempt to measure direction and magnitude of changes on stream functioning following afforestation was halted by our simple implemented methodology (i.e. leaf pack method for leaf litter decay and biofilm accrual on natural stone substrates for primary production assessments); only 1 out of 4 indicators differed. We argue that the lack of strong differences in elemental measurements of primary production and needle decay between afforested and grassland streams resulted from compensating opposing forces controlling such processes, i.e. higher grazing vs. higher sunlight in grassland streams and higher shredding vs. lower microbial decomposition mediated by lower temperature in afforested streams. Attributes related to the invertebrate compartment showed the highest sensitivity to afforestation, emphasizing their value as biological indicators of stream ecological integrity.

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## 1. Introduction

The integrity of lotic ecosystems is threatened by multiple human impacts of physical (e.g. dams, channelization), chemical (e.g. pollutants), and biological (e.g. invasive species) nature (Allan and Castillo, 2007). Land use changes can affect lotic ecosystems through all these pathways, being particularly intense in the case of grassland converted to tree plantations. While this vegetation transition may provide valuable benefits to societies (e.g. labor economy, timber production, flood regulation), several studies have quantified negative impacts, such as reduction in water

quantity (Jackson et al., 2005; Little et al., 2009) and quality (Farley et al., 2008), and to a lower extent impaired functioning of lotic systems (Ress and Ribbens, 1995; Thompson and Townsend, 2004).

Catchment afforestation with species that have contrasting ecological characteristics compared to those commonly found in their hosting environment may have strong effects on aquatic ecosystems. On the one hand, direct changes in hydrology have already been acknowledged with negative 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

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their better known benefits of wood, runoff regulation, erosion control, and carbon sequestration. On the other hand, changes on biotic components associated to afforestations have been more elusive. In New Zealand, Thompson and Townsend (2003) found little effects of land use at the catchment scale on structural components of stream food webs when comparing native mixed forests vs. pine plantations, but strong changes between native grassland and pines. In Ireland, Giller and O'Halloran (2004) reviewed the magnitude of changes resulting from pine afforestations in moorlands and showed that negative effects on the ecology of streams were regionally dependent and not always deleterious for the environment, probably because of the ecological nature of moorlands.

The establishment of evergreen conifers in grassland landscapes is expected to produce strong stream impacts, not only as a consequence of large inputs of coarse organic matter such as leaf litter and woody material but also by imposing heavy shading and affecting stream sunlight and temperature year around. Additionally, conifer needles break down slowly (Webster and Benfield, 1986; Robinson et al., 2000) since they have thick waxy cuticles containing large amounts of compounds that inhibit or delay matter cycling by aquatic decomposers and detritivores (Bärlocher and Oertli, 1978a,b). Therefore, afforestation of grassland streams is expected to have direct strong effects on energy and matter fluxes through stream food webs, which should be expressed both in terms of community attributes (abundance and composition) and also on key ecosystem processes (i.e. stream primary production and organic matter decomposition).

Generating information about the direction and magnitude of the ecological impact of afforestations becomes essential since an integrative understanding of the influence of tree plantations on ecosystem services will help to develop suitable management strategies and more sustainable forestry systems and policies (Jobbágy et al., 2006). Catchment management practices that alter energetic linkages between aquatic and terrestrial habitats can affect associated ecosystem processes, and ultimately the provision of ecosystem services of importance to humans. Such effects might not always be inferred from common biomonitoring schemes, which are typically based on assessment of community structural parameters rather than functional attributes related to important ecosystem-level processes (Mckie and Malmqvist, 2009).

Impacts of anthropogenic activity on ecosystems can affect both structural and functional components but these broad groups of attributes do not necessarily respond with the same sensitivity and timing. Stressors might cause changes to structure but not function (Death et al., 2009), to function but not structure (Mckie and Malmqvist, 2009; Riipinen et al., 2009), or to both (Friberg et al., 2009; Young and Collier, 2009). Adequate characterization of ecosystems requires information on both structure and function since both aspects provides a more complete picture of ecosystem health than either aspect alone (Gessner and Chauvet, 2002; Young et al., 2008; Riipinen et al., 2009; Feio et al., 2010). Although functional indicators have been suggested to be considered as complementary to traditional monitoring tools (Young et al., 2008; Friberg et al., 2009) their response to anthropogenic stressors has yet been little assessed.

Headwaters streams in Sierras de los Comechingones (Córdoba, Argentina) drain grasslands that were afforested with pines in the late 1970s. This marked vegetation shift may have important implications on the structure and functioning of the aquatic environments. Previous research in the study streams has reported a reduction in annual water yield of nearly 50% in afforested watersheds (Jobbágy et al., 2013), but no evidence of stream water acidification (Farley et al., 2008) or changes in ions loading (Jobbágy, unpublished data) associated to biogeochemical changes from pine plantations were found. This study aims to evaluate the effect of pine afforestation on key ecosystem-level processes

in grassland (control) streams by analyzing changes in leaf litter breakdown and primary production. Additionally, we compared those findings with changes in commonly used structural attributes of benthic biota (invertebrates and primary producers) to assess ecological effects of pine plantations. Pine afforestation of grassland streams are expected to cause: (i) lower primary production due to a lesser exposure to sunlight in afforested compared to grassland streams, and as a consequence lower abundance of periphyton feeders (i.e. scrapers), (ii) higher pine needle decay rate as a result of the large ambient abundance of coarse organic matter (needles and woody material) which is anticipated to support large abundance of decomposers and detritivores (e.g. shredders). Alternatively, afforested streams may present lower total invertebrate abundance and richness if invertebrate communities originally inhabiting grassland streams were inefficient or unable of consuming the low-quality pine needles. Finally, we discuss the tradeoffs of implementing structural or functional indicators in stream ecosystem biomonitoring.

## 2. Materials and methods

### 2.1. Study area

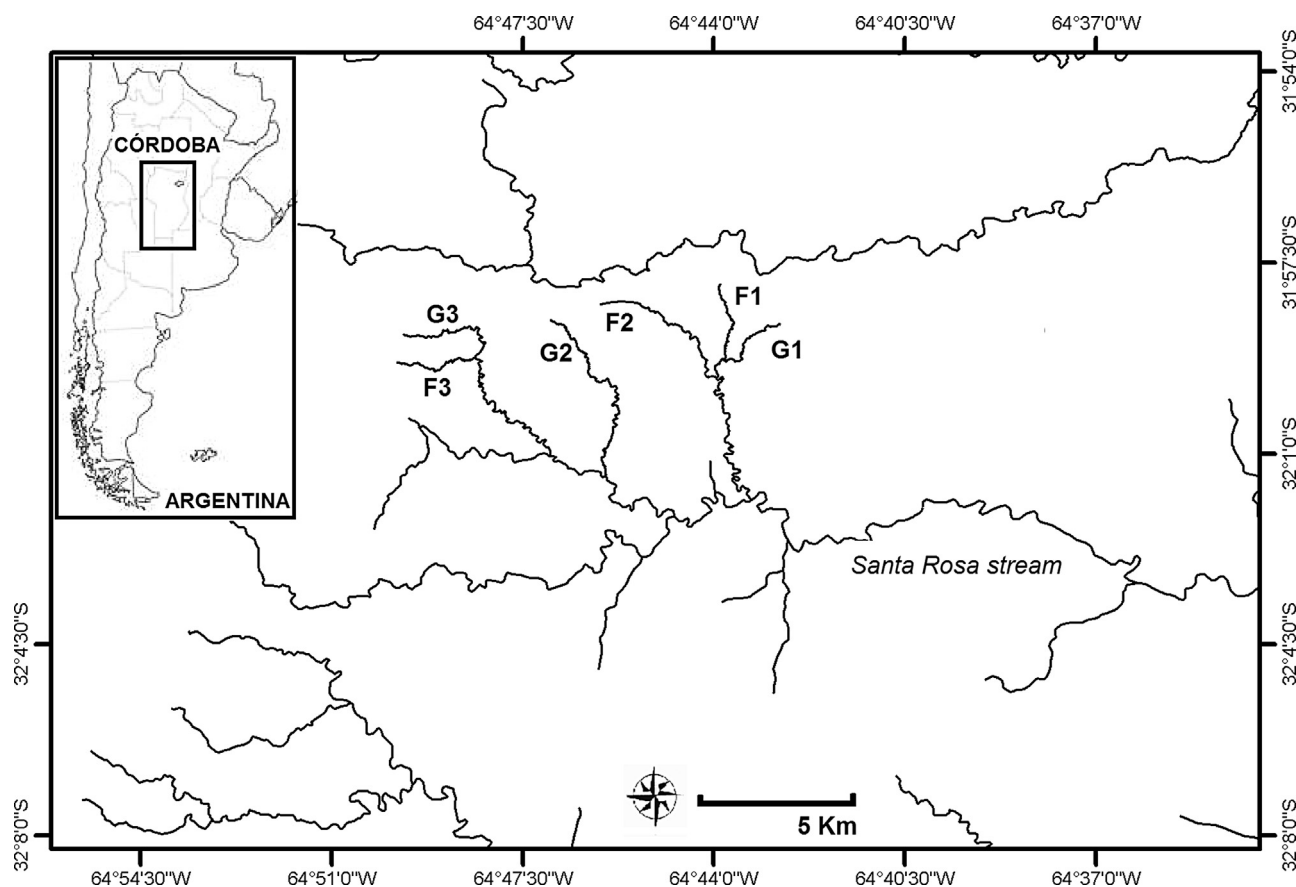
The study was carried out in streams of the Ctlamochita river upper basin, Córdoba, Argentina (Fig. 1). Annual precipitation in the region reaches 725 mm occurring mostly between spring and the end of summer (October–March) (Cabido et al., 2003) whereas maximum temperature reaches 34°C in summer (December–March)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

Six first-order streams with similar drainage area were selected in the Santa Rosa stream sub-basin (which belongs to the Ctlamochita river basin). Three streams drain grasslands (control streams) and each one has a contiguous stream that drains plantations of *Pinus elliottii* (afforested streams) (Fig. 1, Table 1). Study sites in each stream were selected considering stream reaches with similar slope, altitude and orientation. Grasslands at this altitude are dominated by *Festuca hieronymi*, *Nassella filiculmis*, *Schizachyrium condensatum* and *Eragrostis airoides* (Oggero and Arana, 2012) and they are primarily used for extensive livestock grazing. Although the largely established idea has been that these grasslands are climatically determined and that their characteristics respond mainly to natural abiotic factors (Cabido et al., 1987), more recent studies have suggested that they have, at least in part, an anthropogenic origin (Cingolani et al., 2008). The long periods of domestic grazing with associated fire (used as a management tool to favor grass regrowth) and the increased erosion processes have led to the modification of floristic composition and structure of natural grasslands (Cingolani et al., 2003).

Most afforested areas in the region were established in the late 70s as a result of a tax deferral plan implemented by the Córdoba government. Currently, nearly 36,000 ha of the Sierras de los Comechingones in Córdoba are afforested with pines between 900 and 1600 m a.s.l. (Plevich et al., 2002). In the study area, *Pinus elliottii* is the dominant tree in the plantations followed by *Pinus radiata* and *Pinus taeda*.

### 2.2. Experimental procedure and field and laboratory methods

Between May and August 2008, two in situ experiments were performed at each of the six study streams to compare leaf litter breakdown and primary production between grassland ( $n=3$ ) and pine afforested ( $n=3$ ) streams. Experiments were carried out



**Fig. 1.** 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).

**Table 1**  
Characterization of study streams. Average values of physicochemical variables measured during the experimental period are shown.

	Grassland 1	Pine forest 1	Grassland 2	Pine forest 2	Grassland 3	Pine forest 3
Drainage area (ha)	31.2	27.0	88.4	142.5	86.7	88.9
Altitude (m a.s.l.)	1036	1111	1159	1130	1227	1196
Wet width (m)	1.12	0.94	1.15	1.03	1.41	1.58
Depth (m)	0.09	0.06	0.09	0.09	0.07	0.08
Current velocity (m/seg)	0.22	0.17	0.17	0.21	0.26	0.28
Temperature (°C)	14.5	12.2	14.8	10.7	12.5	9.8
Cumulate degree days (°C)	1409	1223	1439	1075	1194	971
pH	8.3	8.2	8.8	8.1	8.7	8.4
Conductivity ( $\mu\text{S}/\text{cm}$ )	103	233	74	197	76	93

in the low flow period to avoid the influence of high flow on biotic instream components and therefore on measured ecosystem level processes. Primary production was estimated as biofilm development and accumulation in sterilized rocks (used as introduced substrates) and measured as chlorophyll *a* (Chl *a*) and ash free dry mass (AFDM) accumulation per surface and time unit. In each stream, ten rocks of similar size (~10 cm), roughness and lithology (flat metamorphic rocks) were collected and subsequently scrubbed and autoclaved (3 periods of 30 min at 121 °C and 0.75 atm) to remove all attached material. The rocks were then placed in the bottom of each stream (10–20 cm below the surface) and collected after 30 days. Afterwards they were individually scrubbed and the collected slurry (algae plus amorphous organic matter) preserved refrigerated in dark conditions to quantify periphyton abundance. The slurry was processed as follows: (i) ten to 20 mL per sample, depending on concentration, were filtered through pre-incinerated and pre-weighed microglass fiber filters (1.2  $\mu\text{m}$  pore size, Munktell, Sweden), dried for 48 h at 60 °C

and burned to obtain AFDM; (ii) 1 mL was placed in a container with 9 mL ethanol for extraction and quantification of Chl *a* by spectrophotometric reading (Biggs and Kilroy, 2000). The results were expressed by inorganic substrate area. Although this method estimates primary production resulting from algal accrual ignoring possible losses by grazing and other pathways, it is still suitable for comparative purposes on short periods of time (Biggs and Kilroy, 2000). Once during the experimental period, PAR (photosynthetically active radiation) intensity was measured with a QSL-2100 Irradiance Sensor (Biospherical Instruments, Inc., San Diego, California) at midday along a 20 m reach at the six streams. PAR was reduced more than 70% in afforested streams (average grassland streams: 2028  $\mu\text{E m}^{-2} \text{s}^{-1}$ ; average afforested streams: 533  $\mu\text{E m}^{-2} \text{s}^{-1}$ ).

Leaf packs were used to measure litter processing rates and macroinvertebrates that colonized these packs were also assessed. Leaves used in experiments were collected in the study area from one individual of *P. Elliottii* to reduce variability. In each stream,

ten packs with conditioned needles of *P. elliotti* equivalent to 5.00 g dry mass (weighed to the nearest 0.01 g) were tied with plastic seals and placed in riffles. Needles were air-dried for three weeks and moistened to avoid breakage before the packs were placed in the streams. Leaf litter was not oven-dried to avoid overestimation of decay rates (Gessner and Dobson, 1993). Instead, an independent set of samples was dried to estimate the initial dry mass. Leaf packs were removed from the streams after 98 days of exposure (seven packs were recuperated from each stream) and returned to the laboratory where remaining dry mass and abundance of invertebrates were measured. Leaf remaining dry mass was obtained for each pack by drying it at 60 °C for 96 h and then burning it to obtain AFDM. Decay rate was estimated using an exponential decay model:

$$W_t = W_i e^{-k_d t}$$

where  $W_t$  is dry mass at a given time  $t$ ,  $W_i$  is the initial dry mass,  $k_d$  is the breakdown rate and  $t$  is time, measured in days and also in degree-days. According to Benfield (2006), cumulate degree-days (DD) were estimated from fortnight water temperature recordings over the incubation period and entering this value in the model instead of days. Mean values between dates:  $t_0-t_{15}$ ,  $t_{15}-t_{30}$ ,  $t_{30}-t_{45}$ ,  $t_{45}-t_{60}$ ,  $t_{60}-t_{75}$  and  $t_{75}-t_{98}$ , were obtained assuming as mean water temperatures over those periods and cumulated to obtain DD. We assumed an exponential decay model for fitting needle mass losses against time or degree-days elapsed *sensu* previous decay rate estimation reports for different pine species (Webster and Benfield, 1986; Albariño and Balseiro, 2002; Collier and Smith, 2003).

Invertebrates were separated from the packs and preserved in ethanol 70% for later identification and counting. Taxa were assigned to Functional Feeding Groups (FFGs) considering available literature (Berg, 1995; Lopretto and Tell, 1995; Merritt and Cummins, 2006; Merritt et al., 2008; Tomanova et al., 2006). Leaf packs were examined in search of signals of invertebrate feeding such as bites in the needles and the number of packs presenting these signals was quantified.

Simultaneously to the experiments, structural attributes of stream communities were also measured. Periphyton was sampled in each stream by collecting five rocks in riffles. The rocks were individually scrubbed and the slurry (algae plus amorphous organic matter) preserved refrigerated in dark conditions to quantify AFDM and Chl *a* following the same procedure used in the primary production experiment. Macroinvertebrate communities inhabiting riffles were also assessed collecting four Surber samples (0.09 m<sup>2</sup>, 300 μm mesh size) in each stream. Invertebrates were identified, counted and assigned to Functional Feeding Groups (FFGs) likewise to those in leaf packs. Physicochemical variables were also measured during the experimental period to characterize study streams and to obtain cumulated degree days. Depth and current velocity were measured with a digital water velocity meter (Global Flow probe FP101–FP202) in each stream on a transect along stream width (four measurements per stream). Stream width was also measured and temperature, conductivity and pH measurements were taken with portable sensors. Water temperature was measured fortnightly and conductivity and pH were measured three times in each stream during the experimental period.

### 2.3. Data analyses

Functional and structural variables were compared with linear mixed models (LMM) in a hierarchical design to assess differences between grassland and afforested streams. Riparian vegetation type was considered as a fixed factor and Stream as a random factor nested within Vegetation type. Analyses were performed using InfoStat that implements an interface of platform R for

estimating linear mixed models (Di Rienzo et al., 2011, 2012). Validations of simple assumptions of the models were performed reviewing standardized residuals vs. predicted and the normal Q–Q plot of standardized residuals. Heterogeneity of variances between treatments was observed for richness and abundance of invertebrates in leaf packs and the model had the best fit (using the AIC and BIC criterion) using a variance function (varIdent) with 'vegetation' as grouping criteria. Di Rienzo–Guzman–Casanoves test (DGC test), a hierarchical method which controls type I error while maintaining acceptable power, was used for a posteriori comparisons.

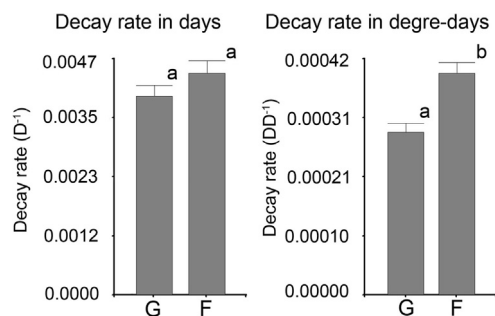
Univariate analyses were performed in both functional and structural response variables. Functional variables tested by LMM were: AFDM accrual and Chl *a* accrual obtained in the primary production experiment, and decay rate  $k_d$  (days<sup>-1</sup>) and  $k_{dd}$  (degree-days<sup>-1</sup>) obtained in the leaf litter breakdown experiment. Structural variables were: AFDM and Chl *a* of periphyton standing stock and a set of variables from invertebrate assemblages in riffles and in leaf packs: richness, total abundance, richness of the Ephemeroptera–Plecoptera–Trichoptera group (EPT richness), total EPT abundance, %EPT (relative to total invertebrate abundance) and the abundance of each FFG (shredders, scrapers, predators, gathering collectors and filtering collectors).

Structural variables (i.e. for invertebrate community) were also analyzed by multivariate methods considering assemblage composition. Correspondence Analyses (CA) and the Multiresponse Permutation Procedures (MRPP, a non parametric procedure for testing the hypothesis of no difference between two or more groups of sampling units) were carried out to examine differences between grassland and afforested streams in: invertebrate assemblages colonizing leaf packs (i) and invertebrates in riffles (ii). Abundance data were  $\log(y+1)$  transformed for the CAs and these analyses were carried out with CANOCO (TerBraak and Smilauer, 1999). Jaccard distance measure was used for performing the MRPP. The indicator value method (IndVal method) proposed by Dufrene and Legendre (1997) was used to identify indicator taxa in leaf packs and riffles for grassland and forested streams. Both MRPP and the IndVal method were performed using PC-Ord for Windows 4.25 (McCune and Mefford, 1999). Finally, differences in FFG composition between grassland and afforested streams were also evaluated by MRPP in leaf packs and riffles.

### 3. Results

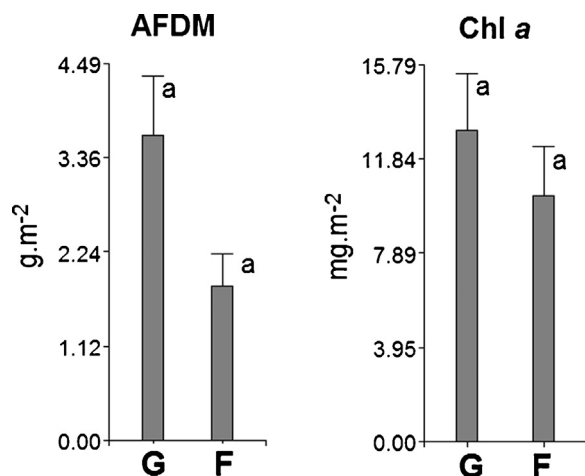
In the primary production experiment, periphyton AFDM accrual and Chl *a* concentration did not differ between grassland and afforested streams (LMMs: AFDM,  $F_{1,54} = 0.32$ ,  $p = 0.600$ , mean value forest = 1.05 g m<sup>-2</sup> d<sup>-1</sup>, mean value grassland = 1.34 g m<sup>-2</sup> d<sup>-1</sup>; Chl *a*,  $F_{1,30} = 0.02$ ,  $p = 0.900$ , mean value forest = 6.19 mg m<sup>-2</sup> d<sup>-1</sup>, mean value grassland = 6.46 mg m<sup>-2</sup> d<sup>-1</sup>). In the needle breakdown experiment, the estimated decay rate  $k$ , considering days as independent variable, did not either differ between stream types (LMM:  $F_{1,36} = 0.64$ ,  $p = 0.467$ ). However, pine needles decayed 29% faster in afforested streams when corrected by cumulative degree-days (LMM:  $F_{1,36} = 11.02$ ,  $p < 0.029$ ) (Fig. 2). In afforested streams, 52% of leaf packs in average presented signals of invertebrate feeding whereas only 14% of packs from grassland streams had these signals.

With regard to structural variables, periphyton standing stock did not show differences between grassland and afforested streams, though AFDM was marginally significant (LMMs: AFDM,  $F_{1,23} = 5.10$ ,  $p = 0.087$ ; Chl *a*,  $F_{1,23} = 0.69$ ,  $p = 0.454$ ) (Fig. 3). In contrast, invertebrate community attributes were different depending on the selected metrics. For instance, EPT richness and EPT abundance in leaf packs from afforested streams were 50% and 74% lower (respectively) relative to grassland ones (LMMs: EPT richness,  $F_{1,30} = 25.75$ ,  $p = 0.007$ ; EPT abundance,  $F_{1,30} = 17.78$ ,



**Fig. 2.** Mean values of needles decay rate  $k$  measured in days and degree-days in grassland (G) and pine afforested (F) streams. Error bars represent  $\pm 1$  standard error and different letters indicate significant differences at  $p < 0.05$  (DGC post hoc test).

$p = 0.013$ ) whereas taxonomic richness, total abundance and %EPT were marginally significant (LMMs: Richness,  $F_{1,30} = 4.77$ ,  $p = 0.094$ ; Total abundance,  $F_{1,30} = 4.60$ ,  $p = 0.098$ ; % EPT  $F_{1,30} = 4.38$ ,  $p = 0.104$ ) (Fig. 4). Functional Feeding Groups composition in leaf packs also differed between stream types (MRPP:  $A = 0.058$ ;  $p < 0.001$ ). Scrapers and predators were more abundant in grassland streams (LMMs: Scrapers,  $F_{1,30} = 8.38$ ,  $p = 0.044$ ; Predators,  $F_{1,30} = 11.32$ ,  $p = 0.028$ ) whereas the abundance of shredders, gathering collectors and filtering collectors did not differ statistically (LMMs: Shredders,  $F_{1,30} = 0.44$ ,  $p = 0.542$ ; Gathering collectors,  $F_{1,30} = 0.84$ ,  $p = 0.412$ ; Filtering collectors,  $F_{1,30} = 2.00$ ,  $p = 0.230$ ) (Fig. 5A). Scrapers represented 11% of the assemblage in grassland streams and they were only 3% in afforested streams. The relative abundance of shredders in leaf packs was lower in

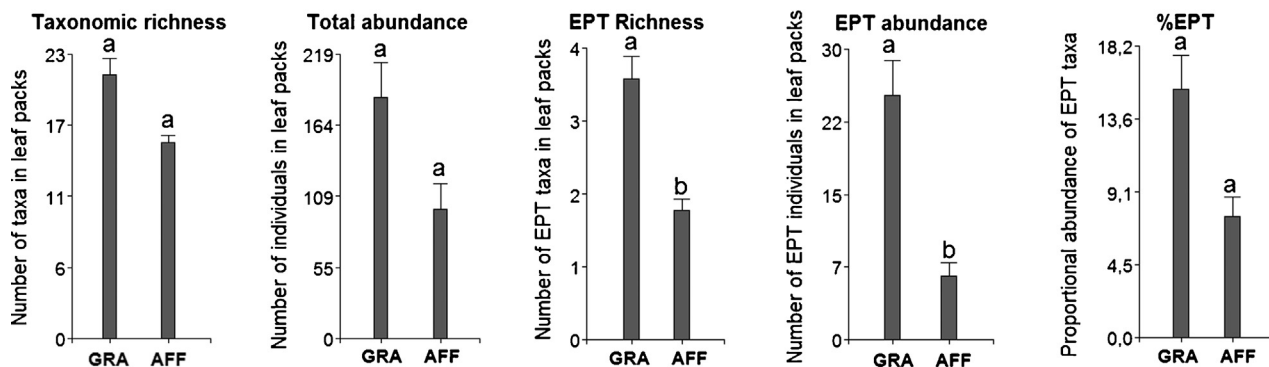


**Fig. 3.** Mean values of AFDM and Chl  $a$  of periphyton standing stock from grassland (G) and pine afforested (F) streams. Error bars represent  $\pm 1$  standard error and different letters indicate significant differences at  $p < 0.05$  (DGC post hoc test).

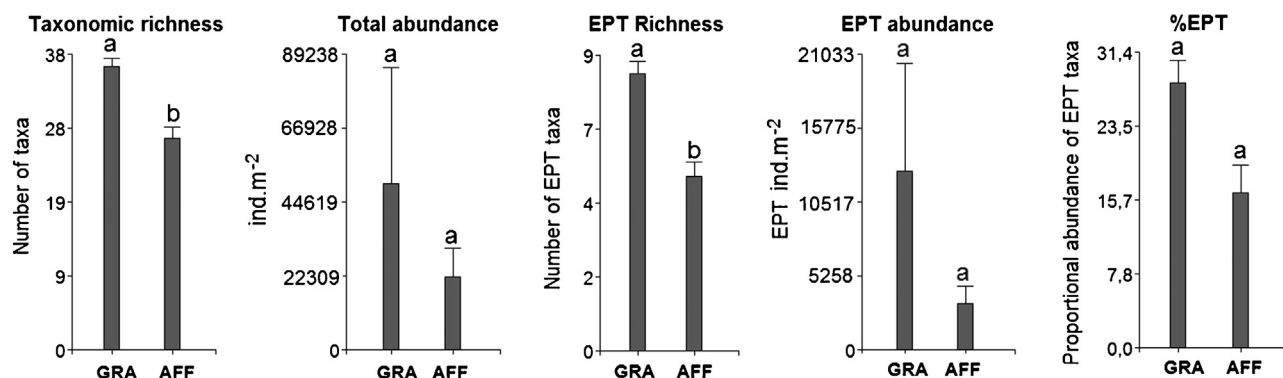
grassland streams (4% in grassland streams and 12% in afforested streams) except in one of the grassland streams in which the highest abundance of shredders was recorded (25%) mainly due to a large number of *Hyalella curvispina* colonizing needle packs.

Community richness in riffles was 25% lower in afforested streams (LMM:  $F_{1,18} = 16.59$ ,  $p = 0.015$ ) (Fig. 4) and similarly, EPT richness was 37% lower in these streams (LMM:  $F_{1,18} = 23.60$ ,

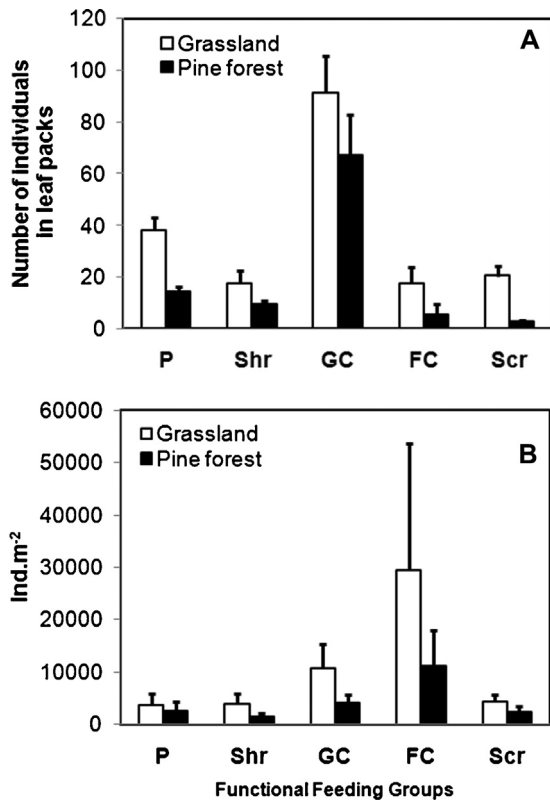
## LEAF PACKS



## RIFFLES



**Fig. 4.** Mean values of richness, abundance, EPT richness, EPT abundance and % EPT in experimental leaf packs (upper plots) and riffles (lower plots) from grassland (GRA) and pine afforested (AFF) streams. Error bars represent  $\pm 1$  standard error and different letters indicate significant differences at  $p < 0.05$  (DGC post hoc test).



**Fig. 5.** Mean abundance of FFGs in experimental leaf packs (A) and riffles (B) of grassland and pine afforested streams. Error bars represent  $\pm 1$  standard error. P: Predators, Shr: Shredders, GC: Gathering collectors, FC: Filtering collectors, Scr: Scrapers.

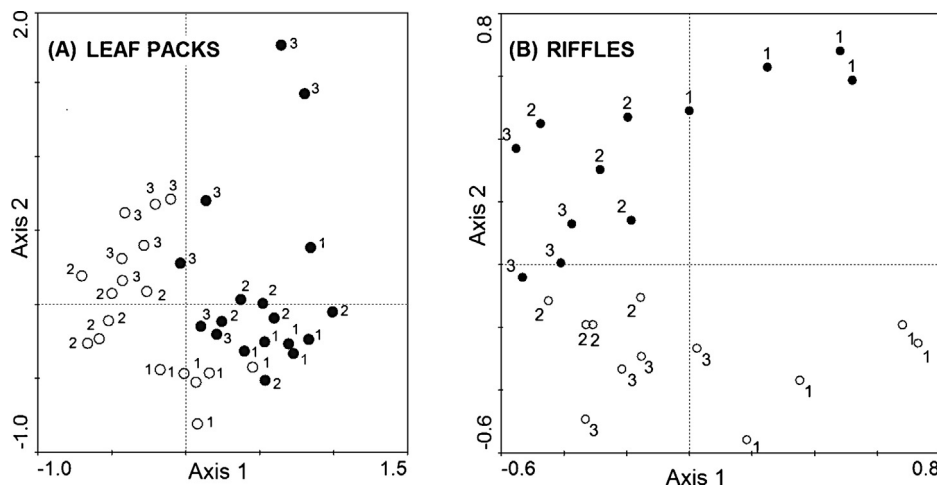
$p=0.008$ ). % EPT was marginally significant and total abundance and EPT abundance did not differ between stream types (LMMs: %EPT,  $F_{1,18} = 6.1$ ,  $p = 0.068$ ; Total abundance,  $F_{1,18} = 0.47$ ,  $p = 0.530$ ; ETP abundance,  $F_{1,18} = 1.07$ ,  $p = 0.359$ ) (Fig. 4). The MRPP did not show differences in Functional Feeding Groups composition from riffles between stream types (MRPP:  $A = 0.015$ ;  $p = 0.130$ ) and similarly the abundance of each FFG did not either differ (LMMs: Scrapers,  $F_{1,18} = 0.82$ ,  $p = 0.417$ ; Shredders,  $F_{1,18} = 0.37$ ,  $p = 0.577$ ; Predators,  $F_{1,18} = 0.10$ ,  $p = 0.770$ ; Gathering collectors,  $F_{1,18} = 1.08$ ,  $p = 0.356$ ; Filtering collectors,  $F_{1,18} = 0.37$ ,  $p = 0.577$ ) (Fig. 5B). Scrapers represented 20% of the benthic community in riffles of grassland

streams and 11% in pine afforested streams. Shredders had similar low relative abundances in grassland and afforested streams, representing in average 4 and 9%, respectively of the total benthic community.

Invertebrate assemblages in leaf packs and riffles were different between afforested and grassland streams (Fig. 6). In the CA ordination of leaf packs, axis 1 mainly separated packs of afforested streams from those of grassland and 46.7% of taxa abundance was accounted by the first four ordination axes (Eigenvalues: Axis 1: 0.200, Axis 2: 0.181, Axis 3: 0.142, Axis 4: 0.095; Total inertia: 1.324). The differences between leaf pack assemblages of afforested and grassland streams were significant according to MRPP ( $A = 0.03$ ,  $p = 0.002$ ). In the CA ordination of riffle samples, the first four ordination axes accounted for 52.7% of taxa abundance (Eigenvalues: Axis 1: 0.167, Axis 2: 0.144, Axis 3: 0.093, Axis 4: 0.068; Total inertia: 0.895). The MRPP confirmed that differences between the assemblages were significant ( $A = 0.035$ ,  $p = 0.002$ ).

In grassland streams, invertebrates colonizing leaf packs presented 13 indicator taxa (IndVal method, Table 2). The scrapers *Helicopsyche* sp. and larvae of *Austrelmis* sp. had the higher indicator values (*IndVals*: >70%). In contrast, only 3 taxa belonging to Chironomidae and Hirudinea were indicators of afforested streams with *IndVals* lesser than 70%. In riffles, thirteen indicator taxa of grassland streams were also found with the scraper *Nanomis* sp. having the highest *IndVal* (97.4%) (Table 2). In contrast, in riffles of afforested streams only 2 Chironomidae taxa were found as indicators.

The functional attributes measured in this study did not show important changes caused by afforestation (Table 3). Only leaf litter decay rate measured in degree days showed a magnitude of response of 29%. On the other hand, nine structural indicators showed differences between stream types (Table 4). Indicators measuring changes on basal levels of food web (i.e. detritus and primary producers) were less sensitive than those recording changes in the consumer compartment. One out of six metrics (17%) was statistically significant between vegetation conditions for basal trophic levels (Tables 3 and 4). In contrast, 9 out of 24 (37%) differed for consumers and some of them reflected losses in biodiversity in afforested streams. Regarding the magnitude of changes in the indicators, any functional indicator changed more than 50% respect to the reference condition (Table 3). In contrast, 3 structural indicators had differences higher than 50%. When comparing basal vs. consumer trophic levels, no indicators for the base of the food web changed more than 50% against 3 indicators for consumers (Tables 3 and 4). In this study, only one third (10 out of 30) of



**Fig. 6.** CA ordinations of invertebrate samples obtained from experimental leaf packs (A) and riffles (B) in grassland (open symbols) and pine afforested streams (filled symbols). Numbers correspond to the study streams.

**Table 2**  
Indicator values (*IndVals*) for invertebrate taxa in leaf packs and riffles 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. FFG: Functional Feeding group assigned to the taxon (Scr: scraper, Shr: Shredder, P: Predator, GC: Gathering collector, FC: Filtering collector).

Leaf packs				Riffles			
Taxa	FFG	IndVal	p-Value	Taxa	FFG	IndVal	p-Value
<b>Grassland</b>							
<i>Helicopsyche</i> sp.	Scr	82.6	0.001	<i>Nanomissp.</i>	Scr	97.4	0.001
<i>Austrelmis</i> sp. (larvae)	Scr	70.1	0.002	<i>Cricotopus</i> sp. 3	GC	94.6	0.001
<i>Nanocladius</i> sp.	GC	68.7	0.001	<i>Rheotanytarsus</i> sp.	FC	90.2	0.005
Dugesidae	P	66.7	0.002	<i>Pentaneura</i> sp.	P	81.0	0.014
<i>Cricotopus</i> sp. 3	GC	66.7	0.007	<i>Pseudochironomus</i> sp.	GC	74.8	0.019
<i>Pseudochironomus</i> sp.	GC	65.7	0.001	<i>Cricotopus</i> sp. 2	GC	72.6	0.002
<i>Rheotanytarsus</i> sp.	FC	65.6	0.001	<i>Helicopsyche</i> sp.	Scr	71.2	0.004
<i>Polycentropussp.</i>	P	60.1	0.004	<i>Nanocladius</i> sp.	GC	65.5	0.003
<i>Tanytarsus</i> sp.	FC	55.0	0.042	<i>Polycentropus</i> sp.	P	65.0	0.020
<i>Leptohyphes eximius</i>	Scr	53.9	0.044	<i>Maruina</i> sp.	GC	50.0	0.014
Limoniinae	Shr	50.0	0.001	Lutrochidae	GC	50.0	0.016
<i>Austrelmis</i> sp. (adult)	GC	43.0	0.004	Podonominae sp. 1	GC	49.9	0.013
<i>Hydroptila</i> sp.	Scr	27.8	0.046	<i>Hydroptila</i> sp.	Scr	41.7	0.035
<b>Pine forest</b>							
<i>Parametrioconemus</i> sp. 2	GC	69.8	0.027	<i>Ablabesmyia</i> sp.	P	92.0	0.001
<i>Apsectrotanypus</i> sp.	P	44.4	0.004	<i>Apsectrotanypus</i> sp.	P	66.6	0.001
Hirudinea	P	33.3	0.018				

the biotic indicators commonly used in studies to measure stream integrity showed significant changes in grassland streams following pine afforestation.

#### 4. Discussion

Our estimations of two opposing ecosystem elemental biotic processes, leaf litter decay and primary producer accrual were little affected by the afforestation of grassland mountain streams (i.e. their absolute values). Contrary to our expectations, pine needles decayed 29% faster in afforested streams only when we removed the effect of water temperature and our proxy of carbon fixation, i.e. the rate of biofilm accrual in benthos, did not differ between both stream types. Structural attributes of stream basal resources such as periphyton standing stock were also similar between the contrasting studied streams. Benthic organic matter was not measured in this study but there was a clear visual contrast in organic matter amount retained in afforested stream channels compared to grassland streams. Up in the food web, the invertebrate compartment, which is responsible of the transference of energy and matter to higher trophic levels (e.g. aquatic and riparian vertebrates), showed different results. Invertebrate communities in stream bottoms and assemblages colonizing the experimental leaf packs were different between grassland and afforested streams and some variables reflected loss in biodiversity in afforested streams. Therefore our functional and structural measurements of ecological indicators at the base of the food web were more elusive than measurements in the consumer fraction, which reflected direct changes of pine afforestation on stream communities.

**Table 3**  
Summary of functional responses to pine afforestation in mountain streams of the Ctalamochita River basin, Argentina. AFF: afforested streams, GRA: grassland streams. The magnitude of the response is expressed as the percentage of variation in afforested streams regarding the reference condition (i.e. grassland streams).

Functional attributes	Ecological indicator	Response	Magnitude of response
Periphyton growth	AFDM accrual [Chl <i>a</i> ] accrual	AFF = GRA AFF = GRA	
Decay rate	$k_d$ $k_{dd}$	AFF = GRA AFF > GRA	29%>

Values of Chl *a* obtained in the primary production experiment were similar to those found in other canopied headwater streams (Kiffney and Bull, 2000; Hill and Dimick, 2002; Roberts et al., 2004). Although we expected primary production to be an appropriate environmental indicator of changes induced by sunlight reduction following afforestation, periphyton growth did not show the anticipated differences. Light, nutrients, grazing and current velocity are considered the major factors controlling periphyton in stream ecosystems (Lange et al., 2011; Wellnitz and Poff, 2012). The availability of light, a prerequisite for algal growth, depends on stream width, depth and on riparian vegetation, which indeed suffer strong

**Table 4**  
Summary of structural responses to pine afforestation in mountain streams of the Ctalamochita River basin, Argentina. AFF: afforested streams, GRA: grassland streams. The magnitude of the response is expressed as the percentage of variation in afforested streams regarding the reference condition (i.e. grassland streams). Coll: collectors.

Structural attributes	Ecological indicator	Response	Magnitude of response
Invertebrate standing stock (Leaf litter)	Assemblage composition	AFF ≠ GRA	
	Richness	AFF = GRA	
	Total abundance	AFF = GRA	
	EPT richness	AFF < GRA	50% <
	EPT abundance	AFF < GRA	74% <
	% EPT	AFF = GRA	
	FFG composition	AFF ≠ GRA	
	Shredder abundance	AFF = GRA	
	Scraper abundance	AFF < GRA	87% <
	Predator abundance	AFF < GRA	62% <
	Gathering coll. abundance	AFF = GRA	
	Filtering coll. abundance	AFF = GRA	
	Invertebrate standing stock (Riffles)	Community composition	AFF ≠ GRA
Richness		AFF < GRA	25% <
Total abundance		AFF = GRA	
EPT Richness		AFF < GRA	37% <
EPT abundance		AFF = GRA	
% EPT		AFF = GRA	
FFG composition		AFF = GRA	
Shredder abundance		AFF = GRA	
Scraper abundance		AFF = GRA	
Predator abundance		AFF = GRA	
Periphyton standing stock	Gathering coll. abundance	AFF = GRA	
	Filtering coll. abundance	AFF = GRA	
	AFDM [Chl <i>a</i> ]	AFF = GRA AFF = GRA	

modifications after afforestation of grassland streams. Our results were unlikely affected by nutrient concentrations since a previous study in these catchments showed that water chemistry is fairly similar in afforested and grassland streams (Farley et al., 2005). Two possible and non-exclusive reasons may explain our results. First, the neutralizing effects of bottom-up and top-down forces, such as shading vs. grazing, may have acted simultaneously as already reported in other studies (Wellnitz et al., 1996; Álvarez and Peckarsky, 2005). Since grazers (mostly ephemeropterans and some trichopterans) were in general two-fold more abundant in grassland than in afforested streams it is likely that grazing pressure had played a key role controlling primary production in the unshaded ones. Secondly, the ability of certain algal functional groups adapted to thrive under the low light intensities imposed by afforestations (Villeneuve et al., 2010) may have compensated algal accrual differences (in terms of Chl *a* concentration) between open and canopied streams.

The breakdown assessment did not show differences for pine needle decay rates when considering only elapsed time, but a higher rate (+29%) was observed in afforested streams when temperature effect was eliminated. It has been globally demonstrated that litter breakdown is faster at warmer temperatures and the main effect of temperature is linked to microbial decomposition (Boyero et al., 2011). This suggests that litter decay was similar between grassland and afforested streams because water temperature in the first accelerated microbial activity compensating the effect of shredding invertebrates in the second (i.e. feeding signals on pine needles were 73% higher in afforested streams). Pine needles have thick cuticles and resins that delay decomposer and detritivore activity but needles are ultimately consumed by aquatic invertebrates in streams draining native coniferous forests (Richardson et al., 2005) and the same is likely to occur (Hladysz et al., 2010) or not (Martínez et al., 2013) in streams where this litter is exotic.

Although a higher decay rate was measured in our afforested study streams where a few shredders and opportunist invertebrates were able to feed on needles, the large amounts of coarse organic matter (i.e. leaf litter and wood) present in these streams was not reflected in higher abundances of total invertebrate and detritus feeders compared to grassland streams; i.e. food webs do not seem boosted by these plentiful input and retention of allochthonous organic matter. According to Gessner and Chauvet (2002) a difference less than 50% in decay rates between impacted and reference sites would indicate the maintenance of ecosystem integrity but we argue that our results are associated to the typical low abundance of detritivores in grassland streams able to exploit such abundant allochthonous plant resource. Moreover, it has been recently shown in these catchments that afforestation reduces mean annual stream base flow by 50% (Jobbágy et al., 2013) and the retention capacity of organic matter in streams is inversely associated to water flow (Richardson et al., 2010). All this evidence suggests that such resource is in excess and may accumulate in bottoms of afforested streams without substantial matter transformation into animal tissue and nutrient cycling.

Nutrient concentration in streams is a key bottom-up factor also affecting organic matter decomposition (Castelá et al., 2007; Feio et al., 2010; Woodward et al., 2012). However, litter breakdown in this study was unlikely affected by nutrient concentrations since as we have previously stated, water chemistry is fairly similar in afforested and grassland streams (Farley et al., 2005). Nonetheless, it remains an open question if the similar reported chemistry might result from dissimilar nutrient dynamics in afforested stream bottoms with abundant organic matter and decomposers able to uptake nutrients from the water column.

The benthic invertebrate compartment, in which structural attributes were analyzed in riffles and needle packs, showed

significant differences between grassland and afforested streams. Those changes were mainly expressed by metrics of the EPT group. From the univariate indexes, EPT richness and EPT abundance were lower in leaf packs of afforested streams and total richness and EPT richness were also lower in riffles of these streams. Similarly, the IndVal method showed that ephemeropterans and trichopterans were among the 13 indicator taxa characterizing grassland streams whereas exclusively chironomids and Hirudinea represented pine afforested streams. As the EPT group reflects good water quality whereas dipterans and Hirudinea are commonly found in impaired environments (Bonada et al., 2006; Moya et al., 2011), our results may reveal environment degradation in afforested streams. Functional feeding group composition also differed between stream types, more significantly in leaf packs than in riffles. Changes in basal resources from periphytic algae to allochthonous organic matter may lead to consequent changes in consumers and, as a result, trophic linkages become disrupted.

Periphyton, leaf litter and benthic invertebrates were analyzed in this study as different ecosystem components from which different ecological attributes emerge. The ecological effects of converting grassland catchments to pine afforestation on streams were better detected by structural metrics. Although in part, this may reflect the low number of replicates used in this study (i.e. 3 streams per treatment), other authors have also found that community structure responds to human-driven stress more strongly than stream functioning (Bergfur et al., 2007; Death et al., 2009). However, leaf litter breakdown has been pointed out as a key indicator responding to changes in land use (Dangles et al., 2004; Mckie and Malmqvist, 2009; Riipinen et al., 2009) and nowadays there is more consensus about the use of quality indexes that combine functional and structural measures to obtain a complete assessment of stream integrity (Castelá et al., 2007; Clapcott et al., 2010; Feio et al., 2010; VandeWalle et al., 2010; Moya et al., 2011). But unfortunately, both kinds of ecological indicators may result inconsistent across seasons as has been recently shown by Masese et al. (2014).

Although the inclusion of leaf litter packs in biomonitoring schemes may cost additional time in placing and processing leaf packs samples, indicators related to invertebrate assemblages colonizing these leaf packs showed valuable information compared to indicators obtained from assemblages inhabiting riffles. Assemblages in leaf packs showed much lower densities and richness than the benthic community in riffles resulting in faster processing of the complete sample unit. In addition, it is important to consider that indicator obtained from leaf packs were measured on more homogeneous conditions (e.g. identical litter bags, needles of only one tree to reduce variability) while structural attributes were directly sampled in the stream bottom and probably reflected more heterogeneous conditions. In fact, results showed much lower dispersion measures in leaf packs, so the detection of changes in these variables may be possible with a less number of sampling units. A similar argument is in favor of the use of stone substrate colonization for assessing periphyton (see suggestions below). Finally, the inclusion of litter packs may allow to monitor the breakdown process in the study area to evaluate potential changes when facing new environmental conditions (i.e. harvesting) or to explain underlying mechanisms responsible of no differences in the breakdown process between stream types.

Indicators describing changes on basal levels of the food web (i.e. detritus and primary producers) were, on average, less sensitive than those recording changes in the consumer compartment (17 vs. 39%, respectively); hence invertebrate indicators emerged here as better to detect differences. These results support the wide use of benthic invertebrates in the monitoring of human impact on freshwater ecosystems (Bonada et al., 2006; Menezes et al., 2010). We argue that the little/null differences of both primary



production and needle litter breakdown between streams were related to the opposing effects of abiotic (water temperature and shading) and biotic (benthic invertebrate feeding activity) forces acting in concert in a particular ecosystem, reducing absolute differences in the target variables. Thus, we suggest implementing those approaches by incorporating the experimental exclusion of invertebrates (Hauer and Lamberti, 2006); e.g. leaf litter bag method with fine mesh bags or J-inverted racks to keep substrates for biofilm accrual far from stream bottom.

Our study is the first to compare the effects of pine afforestation on structural and functional attributes of small mountainous grassland streams in South America. While afforestations have been little managed since planting, harvesting has recently begun in some catchments and stronger negative effects on streams may occur associated to whole catchment canopy reduction and riparian canopy removal, large organic matter entrance to streams, increased erosion and sedimentation, and hydrology and channel morphology alteration (Kreutzweiser et al., 2005; Studinski et al., 2012) affecting aquatic biota as well (Death et al., 2003; Reid et al., 2010). The ecological indicators that reflected biotic changes after afforestation in this study are of great importance in biomonitoring programs for the management and restoration of harvested catchments.

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