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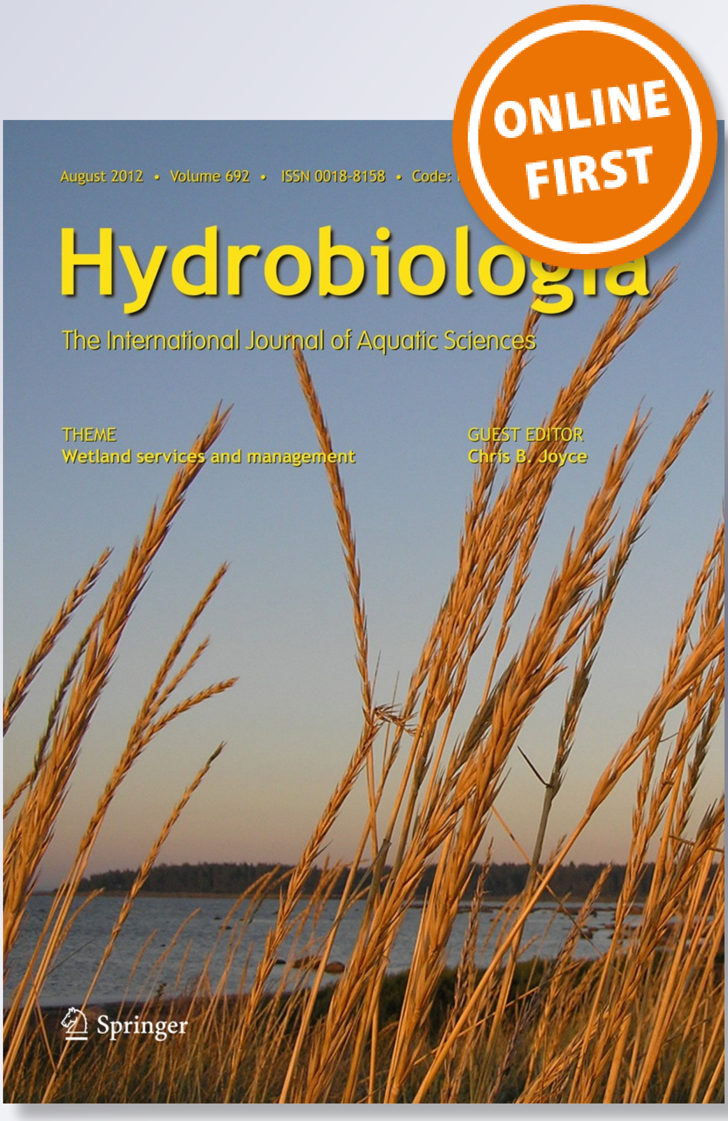

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PRIMARY RESEARCH PAPER

Invasive *Salix fragilis* alters benthic invertebrate communities and litter decomposition in northern Patagonian streams

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Abstract Invasion by exotic trees into riparian areas has the potential to impact aquatic systems. We examined the effects of the exotic *Salix fragilis* (crack willow) on the structure and functioning of small streams in northern Patagonian Andes via a field survey of benthic invertebrates and leaf litter and an in situ experiment. We compared leaf decomposition of the native *Ochetophila trinervis* (chacay) and *S. fragilis* in reaches dominated by native vegetation versus reaches dominated by crack willow. We hypothesized that *S. fragilis* affects the quality of leaf litter entering the streams, changing the aquatic biota composition and litter decomposition. Our study showed that crack willow leaves decomposed slower than chacay, likely related to leaf properties (i.e., leaf toughness). Benthic leaf litter mass was similar between the two riparian vegetation types, though in stream reaches dominated by crack willow, leaves of this species represented 82% of the total leaf litter. Benthic invertebrate abundance and diversity were similar between reaches but species composition differed. Our study found little evidence for strong impacts of crack willow on those small streams. Further studies on other aspects of ecosystem functioning, such as primary production, would enhance our understanding of the impacts of crack willow on Patagonian streams.

Keywords *Ochetophila trinervis* · Riparian vegetation · Exotic · Willow · Detritivores

Introduction

Many scientific studies indicate that biological invasions have negative effects on ecosystem functioning (Lockwood et al., 2007). However, only a limited number of these studies are from developing countries where conservation efforts are most needed and biological invasions can have the largest impact on biodiversity (Nuñez & Pauchard, 2010). Invasion by exotic trees into riparian areas has the potential to impact terrestrial and aquatic systems (Reinhart & Vande Voort, 2006). Riparian vegetation provides shelter and food and acts as a corridor for terrestrial wildlife. It also strongly influences river ecosystems by shaping channel morphology, exchanging nutrients,

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and providing shade and organic matter (leaves, wood, and fruits) for aquatic organisms (Wallace et al., 1999). In small streams, with more riparian vegetation influence (Richardson & Danehy, 2007), canopy buffers in-stream thermal regimes and also reduces primary production. This promotes the establishment of benthic communities dominated by detritivores which play a primary role in breaking down leaf litter and recycling litter nutrients (Hall et al., 2000). The quality and quantity of leaf litter depends on the taxonomy and phenology of the plant community, which determine its chemical and physical properties. Influence of litter quality on litter processing by invertebrates is indirect, through the direct influence of litter quality on microorganism colonization (Webster & Benfield, 1986).

If a plant species invades the riparian zone and significantly changes its species composition and physiognomy, it may alter the detritus cycling dynamics, thus affecting the diversity, trophic structure and dynamics of the stream's benthic communities (Reinhart & Vande Voort, 2006; Going & Dudley, 2008; Hladyz et al., 2011). In particular, *Salix* (willow) invasion have major effects on the ecological properties as it can alter channel morphology, increase flood propensity, and reduce water quantity (due to its higher evapotranspiration rate compared to native species) (Groninger & Bohanek, 2000; Cremer, 2003; Doody & Benyon, 2011). However, consequences of willow invasion appear to be site-dependent. While several studies have shown negative effects on the biota (aquatic invertebrates: Lester et al., 1994; Read & Barmuta, 1999, terrestrial invertebrates: Greenwood et al., 2004; riparian birds: Holland-Clift et al., 2011), other have shown positive effects on fish, which apparently benefit from having access to both terrestrial and aquatic invertebrates that exploit willow as a refuge or food resource (Glova & Sagar, 1994; Jayawardana et al., 2010).

In Patagonia, the southernmost portion of South America, a large number of species has been introduced intentionally or by chance since the first European settlements. Of these, several plant species have become invaders (Correa, 1984; Damascos & Gallopín, 1992; Norambuena et al., 2000; Sarazola et al., 2006; Budde et al., 2011). The effects of invasive species in Patagonia are likely to be extensive, even in protected areas. For example, 25% of plants (257 species) catalogued recently in a protected area in northwestern Patagonia, the Nahuel Huapi National Park (NHNP), were exotic (Escurra & Brion, 2005). Of the four *Salix* species (*S. alba* var. *vitellina* (L.) Stokes, *S. caprea* L., *S. fragilis* L., and *S. viminalis* L.) introduced from the Northern Hemisphere and already naturalized in Argentina, *S. fragilis* (crack willow) is the most abundant in the NHNP (J. Grossfeld & C. Brion, pers. comm.). The distribution of crack willow has increased significantly along the margins of rivers in northern Patagonia. The major cause appears to be their successful asexual reproduction (Budde et al., 2011) that involves vegetative hydrochory in which stems break off and are washed downstream where they take root. Moreover, a recent study has uncovered the expanded distribution of an individual female genotype of *S. fragilis* ranging up to 760 km between the most distant members of this clone (Budde et al., 2011).

Few studies have evaluated the impact of exotic plants on streams and rivers in Patagonia. In large streams invaded by crack willow, Miserendino & Pizzolón (2004) found lower abundance of shredders and higher abundance of filtering-collectors (fine particle filtering feeders) than in streams in *Nothofagus* forests. However, in this study the authors acknowledged that agricultural land use, and not just crack willow, might have played a role in their results. Thus, our knowledge of the effects of crack willow on Patagonian streams is limited even though this species already dominates riparian vegetation communities in much of Patagonia. Our general objective was to study the possible effects of crack willow on the structure of stream invertebrate communities and on leaf litter decomposition. We compared stream invertebrate communities in stream reaches dominated by native riparian vegetation with communities in reaches dominated by crack willow via field survey. We simultaneously compared decomposition of *Ochetophila trinervis* (Gillies ex Hook. & Arn.) Reiche (chacay) and crack willow leaf litter via a field experiment and compared the decomposition of both species in stream reaches dominated by native riparian vegetation and in reaches dominated by crack willow.

Methods

Study area

The study was conducted in the eastern area of the Nahuel Huapi National Park (NHNP) in the North

Andean-Patagonian region of Argentina (40°46′S–40°48′S and 71°6′W–71°8′W; Fig. 1). Bare ground comprises 20% of the study area and the terrestrial vegetation is dominated by grasses (*Festuca pallescens* (St. Yves) Parodi, *Jarava chrysophylla* (E. Desv.) Peñail) and shrubs (*Mulinum spinosum* (Cav.) Persoon., *Baccharis salicifolia* (Ruiz & Pav.) Pers, *Berberis darwini* (Hook.), *Berberis microphilla* (G. Forst.), *Discaria chacaye* (G. Don) Tortosa, *Ochetophila trinervis*, and *Schinus patagonica* (Phil.) IM Johnst). Individual trees (e.g., *Maytenus boaria* (Molina) and *Nothofagus antarctica* (G. Forst.) Oerst.) are mostly associated with riparian habitats while, above 1100 m a.s.l., *Nothofagus pumilio* (Poepp. & Endl.) Krasser extends along the headwaters (Mermoz et al., 2000). Land use in this area of the National Park is restricted to low density cattle grazing belonging to a few settlers.

As it was not possible to find lower stream reaches lacking the presence of crack willow, the impact of this exotic species was tested by comparing benthic communities and decomposition in lower stream reaches invaded by crack willow and upper reaches with only native riparian vegetation. Thus, two field sites were established in each stream (Fig. 1): native riparian vegetation reaches (designated NatRV hereafter) in the upper reaches, and downstream reaches dominated by crack willow (designated ExotRV hereafter). This sampling and experimental design may limit the interpretation of results, due to longitudinal up–down stream connectivity, which might result in little variation in decomposition rates among reaches within a stream (Tiegs et al., 2009).

Three tributary streams of the Limay river (Cornelios, Horquetas, and Cóndores, Fig. 1), with similar environmental characteristics were chosen as replicates for field surveys and decomposition experiments. In selecting streams and sites we attempted to find localities that had comparable physical characteristics both at the catchment and reach scales. All selected streams had a permanent water regime, similar orientation (to the East) and streambed grain-size (means cobble–boulder bottom with sparse patches of pebble-gravel–sand), and relatively similar size. The sites were georeferenced with a GarminMap 60CSx GPS instrument while simultaneously obtaining the altitude above sea level (between 713 and 855 m a.s.l).

Field survey

Field surveys were conducted in winter 2009. Physical and chemical environmental variables were recorded at each site. Depth and width of the wet channel were measured in six transects (five equidistant measures per transect), every 5 m in a 30-m length stream reach. Temperature, conductivity, and dissolved oxygen concentration (DO) were measured with a multiprobe instrument (YSI 85). Discharge was measured by adding a conservative tracer to the stream and recording conductivity changes through time sensu Gordon et al. (2004).

Benthic organic matter and invertebrates were collected with a Surber sampler (mesh size of 200 µm and surface area of 0.063 m^2) ($N = 4$ per site) and transported to the laboratory where they were fixed and preserved in 5% formalin for further processing. Samples were washed through 0.5- and 1-mm sieves to facilitate detritus and invertebrate sorting and also cleaning organic matter from inorganic materials. Organic matter larger than 1 mm was classified as coarse particulate organic matter (CPOM). We identified three categories among CPOM: leaf litter (which was sorted according to species), woody material (wood, bark, and woody fruits and seeds), and miscellaneous matter (unidentifiable organic fragments). The different fractions of detritus were quantified by drying organic matter at 60°C for 48 h and weighing it on an analytical balance (Sartorius 2004 MD) to obtain their dry mass (DM) (accuracy ± 0.001 g). Leaf species were weighed separately to calculate abundance, species richness, and the Shannon diversity (H') index.

Invertebrates (>500 µm) present in Surber samples were collected and preserved in 70% ethanol for taxonomic identification and enumeration. Individuals were observed under a stereoscopic microscope (Leica Wild M8) and identified following keys for North American (Merritt & Cummins, 1996) and South American taxa (Domínguez & Fernández, 2009). The identification was made to the lowest possible taxonomic level. Invertebrates were assigned to the functional feeding groups (FFG) sensu Merritt & Cummins (1996): shredder, scraper, filtering-collector, gathering-collector and predator, according to previous local studies (Albariño & Valverde, 1998; Albariño & Díaz Villanueva, 2006; Miserendino, 2007). We gave particular attention to shredders as

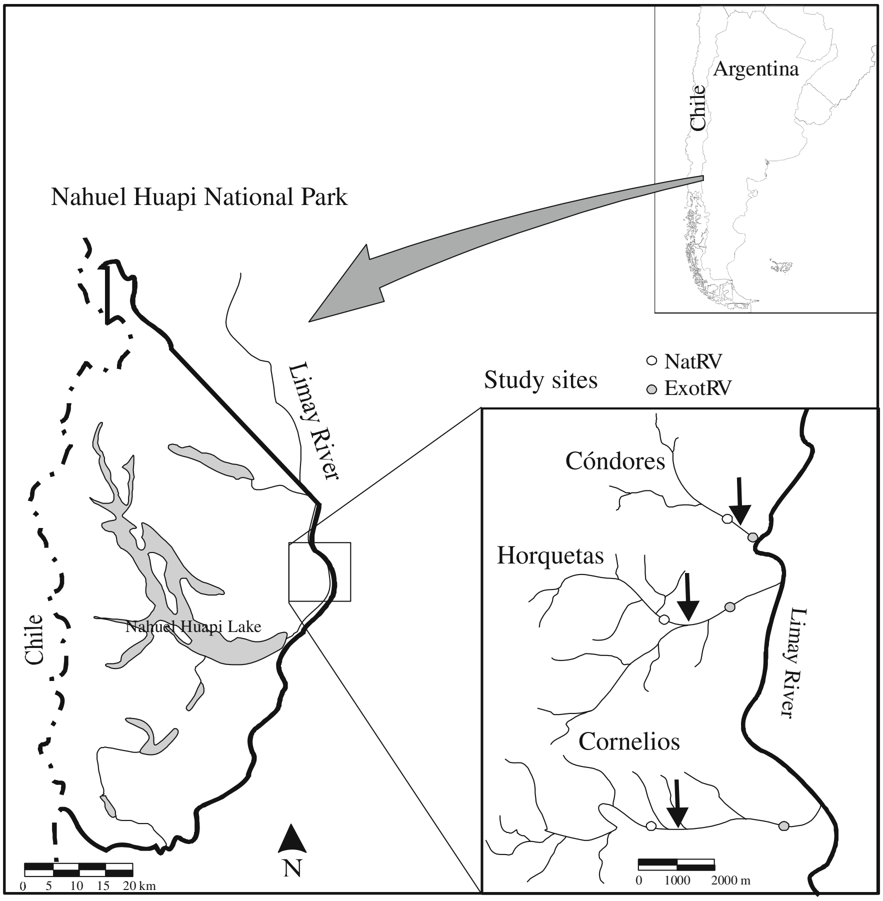

Fig. 1 Study sites in the three tributaries of the Limay river, western border of Nahuel Huapi National Park, northern Patagonia, Argentina. *Arrows* indicate the location of the last willow found upstream in each stream

they are responsible for CPOM processing. Invertebrate abundance was expressed as individuals per m^2. Although some taxa could not be identified to the species level, different morpho-species were counted and taxonomic richness and the Shannon diversity (H') indices were calculated.

Experimental procedures

For the experimental study, the riparian native species *O. trinervis* (chacay) was selected as a representative of native taxa because of its dominance in non-invaded plant stands. Both the native and exotic species used in the experiments have similar phenology (peaks of leaf abscission in autumn), which is an important ecological aspect when comparing streamside plant effects (Bañuelos et al., 2004).

Freshly fallen undamaged leaves of both the native and the exotic species were collected from the riparian floor in the study catchments in April 2009 (at the time of leaf abscission). In the laboratory, leaves were dried at room temperature and stored until needed. Artificial drying was avoided as it accelerates decomposition rate (Gessner & Dobson, 1993).

Leaching

We measured the loss of soluble substances of leaf litter by immersing four replicates of 3 g fresh mass (FM) of each leaf type ($N = 4$) in individual containers with 6 l of stream water. Water was renewed three times a day, thus simulating the renewal of water in a stream. After 48 h, leaf litter was dried at 60°C for 48 h. The difference between initial and final mass, expressed as percentage of initial mass, was considered the mass lost by leaching (Bärlocher, 2005a). Initial DM was estimated from a correction factor (DM/FM) calculated for each species ($N = 4$) by drying the stored leaf litter at 60°C for 48 h.

Leaf toughness

The necessary force for a metal rod of known diameter to perforate plant tissue (Bärlocher, 2005b) was estimated using a penetrometer (expressed in g mm^{-2}, Albariño & Balseiro, 2001). We took four measurements per crack willow leaf ($n = 12$), which were averaged before further analysis. Due to the small size of chacay leaves we could only take one measurement per leaf. Therefore, we took measurements for 48 leaves and then averaged four randomly selected units in order to obtain the same number of observations (12) as for crack willow. The same procedure was performed with leaves after 30 days of submergence in the stream to calculate resistance at t_{30}.

Leaf mass loss

We designed a three-factorial experiment considering the riparian vegetation of the site (two levels: native and exotic vegetation), leaf species (two levels: crack willow and chacay), and stream (three levels: Cornelios, Horquetas, and Cóndores) as factors. Each combination of treatments (riparian vegetation × plant species × stream) received three replicates. Each experimental unit consisted of leaf bags (19 × 12 cm) 70% of 5- and 30% of 2-mm mesh size. These mixed mesh bags have been used previously to retain leaves and leaf fragments smaller than 5 mm while simultaneously allowing entry of aquatic invertebrates that naturally colonize these accumulations (Albariño & Balseiro, 2002). Each bag contained 3 g FM of leaf litter from a single species, which is similar to its mean annual benthic mass per m^2 (Albariño et al., 2009). To prevent leaf litter from breaking during the preparation and handling of litter bags in the field, leaves were previously submerged in stream water for 24 h to regain elasticity (Bärlocher, 2005b).

The experimental units were placed in the streambed of each site in June (late autumn) and secured by metal rods. We considered t_0 when leaf litter was submerged to regain elasticity. After 30 days in the stream, bags were retrieved and transported to the laboratory in sealed and labeled plastic bags adequately labeled. In the lab the remaining litter was carefully removed from the bags, aquatic invertebrates were separated and preserved in 70% ethanol for further taxonomic identification and enumeration, and leaf litter was dried at 60°C for 48 h to obtain final DM. Leaf mass loss was calculated as the difference between initial and final mass, expressed as percentage of initial mass.

With this experiment we were able to quantify leaf litter colonization by invertebrates which use leaves as a food source as well as a refuge (Moore et al., 2004). Invertebrates were identified as previously described. Abundance was expressed as individuals per gram of leaf litter DW within each litter bag. Taxonomic richness and Shannon diversity (H') index were also calculated and all individuals were assigned to their corresponding FFG.

Statistical analysis

The physical variables of the different stream reaches and the community attributes of benthic invertebrates (abundance, taxonomic richness, Shannon diversity index) were compared using two-way nested ANOVAs with streams and riparian vegetations (nested within streams) as factors (Quinn & Keough, 2002). Leaf physical attributes were compared with two-way ANOVA (leaf species × time). Decomposition (% leaf mass loss) and abundance, taxonomic richness, and Shannon diversity indices of invertebrates in the litter bags were analyzed using three-way nested ANOVAs with streams, riparian vegetation (nested within streams), and leaf species as factors. Normality and variance homogeneity were confirmed before the analysis. When significant differences were found a posteriori Tukey tests were run. The coefficient of variation of leaf mass loss was calculated across all leaf litter bags per leaf species, independently of stream.

The relationship between shredder abundance and leaf litter mass loss in the experiment was analyzed by calculating the Pearson correlation coefficient (r). Univariate analysis was performed using the statistical package STATISTICA 7 (StatSoft 1984-2005, Tulsa USA).

Aquatic invertebrate assemblages from benthic samples and in leaf litter bags were compared using analysis of similarities (ANOSIM with 1000 iterations, Clarke & Warwick, 2001), which assesses the differences between invertebrate assemblages based on the rank similarities from the Bray–Curtis similarity matrices. Benthic invertebrate assemblages were analyzed by one-way ANOSIM, with riparian vegetation as factor. Invertebrate assemblages colonizing leaf litter bags were analyzed by two-way ANOSIM considering riparian vegetation and leaf species as factors. When there were significant differences, we used ANOSIM post hoc tests, with Bonferroni corrections to account for multiple comparisons, to evaluate differences among riparian vegetation types or leaf species. We performed these multivariate analyses using the statistical package PRIMER (version 6.1.6, PRIMER-E Ltd 2006, PML Lutton, England).

When ANOSIM revealed significant differences, we used the species contributions to similarity (SIMPER) function in PRIMER to identify which taxa were responsible for the observed differences in assemblages. SIMPER uses the Bray–Curtis similarity matrix to calculate how much each taxon contributes to the observed dissimilarities between groups and expresses its relative contribution in percentages.

Results

Environmental characteristics of stream reaches

Channel depth and width were similar among stream reaches (ExotRV and NatRV) (Table 1). However, width varied among streams (nested ANOVA, $P < 0.05$); Cóndores stream, with the smallest catchment area, was significantly narrower (Tukey test, $P < 0.05$). Discharge was also similar between stream reaches for the two types of riparian vegetation but did differ among streams, being greater in Horquetas than in Cóndores (Tukey test, $P < 0.05$). Temperature and DO concentration were similar among sites, and among streams, while conductivity differed among streams, being lower in Horquetas (Tukey test, $P < 0.050$; Table 1).

Benthic organic matter

CPOM did not differ between reaches (two-way nested ANOVA, $P = 0.425$) but was highly variable, ranging between 5.10 and 45.10 g m^{-2} in reaches dominated by NatRV and between 11.20 and 25.48 g m^{-2} in ExotRV reaches (Table 2). CPOM abundance was more variable in the NatRV reaches, principally because of the great variability in woody debris distribution. Leaf litter in the stream bottom accounted for 5–33% of total CPOM abundance (Table 2).

With regards to the taxonomic composition of leaf litter in the stream, in ExotRV reaches crack willow represented 82% of the total identifiable leaf litter retained in the benthos (Table 3). In NatRV reaches chacay represented 61% of total leaf litter. When crack willow was excluded from the analyses, the relative

Table 1 Physical characteristics of sampling sites

	Cornelios		Horquetas		Cóndores		Statistical results	
Stream order	3		3		2			
Catchment area (ha)	1715		1556		269			
Position	S: 40° 49.389′ W: 71° 8.635′		S: 40° 47.583′ W: 71° 8.362′		S: 40° 46.676′ W: 71° 7.587′			
Study sites	NatRV	ExotRV	NatRV	ExotRV	NatRV	ExotRV	Stream reaches	Streams
Distance (m)	350	2700	300	1100	200	300		
Altitude (m a.s.l.)	855	748	769	736	727	713		
Width (m)	3.0 ± 0.2	3.3 ± 0.3	2.8 ± 0.3	2.6 ± 0.2	1.8 ± 0.3	1.6 ± 0.3	0.637	**0.003**
Depth (m)	0.27 ± 0.01	0.23 ± 0.05	0.20 ± 0.02	0.20 ± 0.02	0.16 ± 0.06	0.14 ± 0.06	0.886	0.076
Disch. (l s^{-1})	181 ± 92	287 ± 146	178 ± 56	386 ± 97	53 ± 17	61 ± 12	0.133	**0.039**
Cond.(μS cm^{-1})	90.2 ± 7.6	87.4 ± 9.3	72.5 ± 10.1	70.8 ± 9.2	87.7 ± 2.9	87.6 ± 5.5	0.209	**<0.001**
Temp. (°C)	5.9 ± 1.2	6.2 ± 1.4	6.0 ± 1.5	5.4 ± 1.5	6.0 ± 1.5	5.3 ± 1.4	0.892	0.776
[O_2] (%)	93 ± 2	89 ± 4	90 ± 2	90 ± 2	88 ± 1	88 ± 2	0.644	0.413
[O_2] (mg l^{-1})	11.3 ± 0.4	10.5 ± 0.6	10.9 ± 0.6	11.1 ± 0.6	10.7 ± 0.4	10.8 ± 0.6	0.782	0.895

Distance refers to the distance from the sampling site to the last documented individual of crack willow in the stream. Width and depth are means ± 1 SE

Disch Discharge, *Cond.* conductivity, *Temp* temperature, *NatRV* native riparian vegetation, *ExotRV* exotic riparian vegetation (mean ± 1 SE)

Statistical results are *P* values of a two-way nested ANOVA with "stream reach" (nested within stream) and "stream" as factors. *Bold* values show statistical significance among levels of a factor

Table 2 Coarse particulate organic matter (CPOM) and percentage of the three categories at the six sampling sites (mean ± SE)

	Cornelios		Horquetas		Córndores	
	NatRV	ExotRV	NatRV	ExotRV	NatRV	ExotRV
CPOM (g m^{-2})	9.93 ± 4.73	11.19 ± 1.96	45.08 ± 20.1	25.48 ± 13.17	5.08 ± 2.24	23.49 ± 13.08
% Leaf litter	9.36 ± 4.83	9.03 ± 1.69	7.45 ± 3.33	4.55 ± 0.63	27.36 ± 23.23	32.91 ± 22.35
% Wood	39.65 ± 16.51	67.65 ± 8.75	78.89 ± 39.11	82.42 ± 48.55	28.54 ± 10.23	47.51 ± 31.25
% Miscellaneous	50.75 ± 26.28	23.32 ± 7.06	13.66 ± 2.15	13.03 ± 2.51	44.09 ± 10.63	19.58 ± 2.08

NatRV native riparian vegetation, *ExotRV* exotic riparian vegetation

Table 3 Species abundance (g m^{-2}), richness, and diversity of benthic leaf litter found in the six sampling sites

	Cornelios		Horquetas		Cóndores	
	NatRV	ExotRV	NatRV	ExotRV	NatRV	ExotRV
Native						
Baccharis salicifolia	0.12 ± 0.12	0.11 ± 0.11	0.04 ± 0.04	–	–	–
Berberis darwini	–	–	0.3 ± 0.13	–	–	0.01 ± 0.01
B. microphylla	0.14 ± 0.14	–	–	–	–	–
Discaria chacaye	0.46 ± 0.38	–	0.24 ± 0.19	–	0.08 ± 0.05	0.32 ± 0.27
Mutisia sp.	–	–	0.2 ± 0.2	–	–	0.04 ± 0.04
Nothofagus pumilio	0.01 ± 0.01	–	2.34 ± 1.15	0.23 ± 0.19	0.03 ± 0.03	0.01 ± 0.01
Ochetophila trinervis	0.26 ± 0.13	0.053 ± 0.05	0.18 ± 0.11	0.09 ± 0.04	1.28 ± 1.18	0.24 ± 0.15
Exotic						
Rosa rubiginosa	–	–	0.05 ± 0.03	0.32 ± 0.27	0.01 ± 0.01	–
Salix fragilis	–	0.85 ± 0.23	–	0.52 ± 0.34	–	7.16 ± 5.18
Taxonomic richness (R)	1.75 ± 0.48	1.67 ± 0.33	4.75 ± 0.85	2.50 ± 0.50	2.00 ± 0.71	2.50 ± 0.50
Shannon diversity (H')	0.18 ± 0.11	0.17 ± 0.08	0.46 ± 0.09	0.20 ± 0.07	0.15 ± 0.13	0.16 ± 0.08

NatRV: native riparian vegetation; *ExotRV*: exotic riparian vegetation (mean ± SE)

abundance of chacay in the ExotRV reaches was almost as much as in the NatRV (51%). The presence of crack willow did not alter plant species taxonomic richness or Shannon diversity index in leaf litter packs (two-way nested ANOVA, $P = 0.095$ for taxonomic richness and $P = 0.359$ for diversity; Table 3). The presence of *N. pumilio* leaves in the samples, even though the trees from which these leaves were derived are confined to the uppermost reaches in the catchment (i.e., the species is absent at the NatRV sites), indicates the longitudinal connectivity of these systems.

Benthic invertebrates

Benthic invertebrate abundance differed between the reaches with different riparian vegetation (two-way nested ANOVA $P < 0.05$) and among streams ($P < 0.05$) being higher in the NatRV reaches and in Cornelios stream (Fig. 2a). There were no significant relationships between benthic organic matter or leaf litter and invertebrate abundances (Pearson correlation coefficient, $P = 0.673$).

A total of 32 invertebrate taxa were found, belonging to 17 families of 6 orders and 2 classes (Table 4). Taxonomic richness was similar between native and invaded reaches (two-way nested ANOVA, $P = 0.22$) but differed among streams ($P < 0.05$), being higher in Cornelios than in Cóndores (Tukey test, $P < 0.05$; Table 4). Invertebrate Shannon diversity (H') index showed no significant differences between invaded vs native reaches nor among streams (two-way nested ANOVA, among reaches $P = 0.95$; among streams $P = 0.23$; Table 4). Of the total species found, shredders represented 28% (9 spp), scrapers 28%

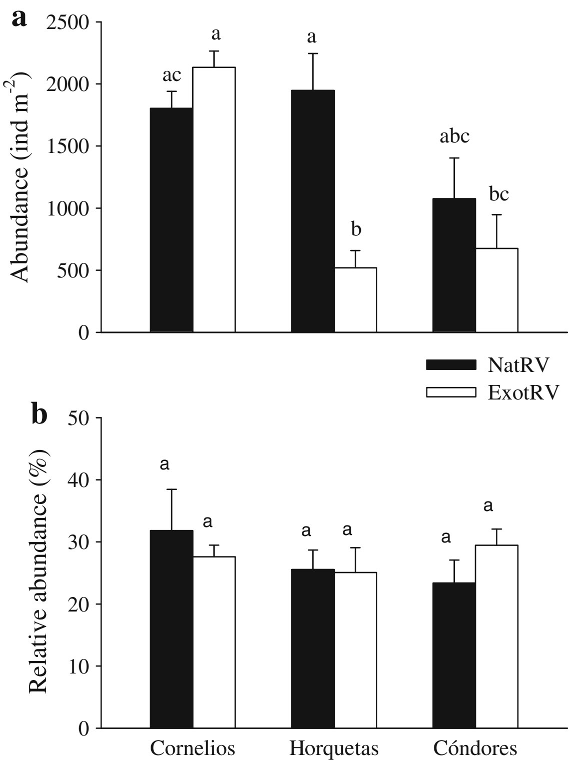

Fig. 2 Total invertebrate abundance (**a**) and shredder relative abundance (**b**) in the benthos of the six study sites (*error bars* 1 SE)

(9 spp), predators 25% (8 spp), and collectors 19% (6 spp). In terms of abundance, shredders were 27%, on average, of the total invertebrate community in both native and invaded reaches (two-way nested ANOVA, $P = 0.07$; Fig. 2b).

Invertebrate community composition differed significantly between the two kinds of riparian vegetation (ANOSIM for riparian vegetation, Global Rho: 0.213, $P < 0.05$). The species that most contributed to the differences in communities, according to SIMPER analysis, were *Smicridea* sp. (12.2%), *Meridialaris chiloeensis* (8.3%), *Nousia bella* (7.4%), *Limnoperla* sp. (6.9%), *Rhitroperla* sp. (6.8%), and *Antarctoperla michaelseni* (6.3%). The most abundant invertebrate was *Smicridea* sp., which was significantly more abundant in the NatRV reaches than in the ExotRV (two-way nested ANOVA, $P < 0.05$). Of the six taxa that contributed most to community dissimilarity, only *Rhitroperla* sp. and *Antarctoperla michaelseni* are shredders. *Smicridea* sp. is a filterer–collector and the other three taxa feed on periphyton as scrapers. Overall, these six species were more abundant in NatRV reaches; however, in Cóndores stream, *Rhitroperla* sp. showed the opposite pattern, with greater relative abundance at the ExotRV site (ExotRV vs. NatRV: 29.0 vs. 19.3%).

Physical properties of leaves

Mass loss by leaching was higher for crack willow than chacay leaves (one-way ANOVA, $P < 0.05$). Crack willow leaves lost 22.2 ± 0.4% (mean ± SE) of their initial mass, while chacay lost 20.6 ± 0.4% (mean ± SE). Toughness of crack willow leaves was higher than that of chacay leaves, at both t_0 and t_{30} (Tukey test, $P < 0.05$; Fig. 3). But after 30 days in the stream crack willow leaves became as tough as chacay leaves at t_0 (two-way ANOVA, interaction term $P < 0.05$; Tukey test, $P < 0.05$; Fig. 3).

Leaf mass loss

Crack willow decomposed more slowly than chacay (three-way nested ANOVA, $P < 0.05$; Fig. 4). At the end of the experiment, crack willow had lost 55% of its initial mass while chacay had lost 62%. In addition, crack willow decomposition was twice as variable as that of chacay (coefficient of variation: chacay 18% vs. crack willow 38%). Finally, leaf litter decomposed differently between streams ($P < 0.05$) but not between stream reaches ($P = 0.98$; Fig. 4).

Invertebrates in litter bags

Invertebrate abundances in leaf litter bags greatly differed among streams (three-way nested ANOVA, $P < 0.05$), being higher in Cornelios (Tukey test $P < 0.05$), where benthic invertebrates were also more abundant than in the other streams. However, abundance was similar in crack willow and chacay treatments ($P = 0.66$). Differences between stream reaches ($P < 0.05$) depended on the stream. In Cóndores, invertebrates that colonized litter were more abundant in the NatRV reach than in the ExotRV reach but in Cornelios the result was the opposite (Fig. 5a).

Of all the species inhabiting the benthos, 39–68% were identified in leaf litter bags (Table 4). Taxonomic richness in litter bags did not differ between leaf species (three-way nested ANOVA, $P = 0.06$; Table 4) or among streams ($P = 0.47$), but it differed between stream reaches ($P < 0.05$), being higher in NatRV.

Table 4 Abundance (indiv. m^{-2}), taxonomic richness and Shannon diversity (H') of invertebrate assemblages in the benthos at the six sampling sites and taxonomic richness and Shannon diversity of invertebrate in litter bags (*ch* chacay, *w* crack willow) (mean ± SE)

Stream		Cornelios		Horquetas		Cóndores	
	FFG	NatRV	ExotRV	NatRV	ExotRV	NatRV	ExotRV
ANNELIDA							
Oligochaeta*	CG	–	96.0 ± 41.6	–	4.8 ± 4.8	4.8 ± 4.8	8.0 ± 4.8
ARTHROPODA							
Insecta							
Coleoptera							
Scirtidae*	CF	27.2 ± 19.2	20.8 ± 4.8	24 ± 9.6	20.8 ± 8	–	4.8 ± 4.8
Diptera							
Athericidae							
Atherix sp.*	P	36.8 ± 11.2	4.8 ± 4.8	8.0 ± 8.0	–	28.8 ± 12.8	12.8 ± 8.0
Blephariceridae							
Edwardsina dispar (Edwards)	S	–	–	–	–	4.8 ± 4.8	–
Ceratopogonidae*	P	–	–	–	–	4.8 ± 4.8	–
Chironomidae							
Chironomidae sp. 1*	CG	<1.6	<1.6	–	<1.6	–	–
Chironomidae sp. 2*	CG	4.8 ± 4.8	16 ± 9.6	–	–	8.0 ± 4.8	–
Chironomidae sp. 3*	CG	–	20.8 ± 14.4	4.8 ± 4.8	4.8 ± 4.8	–	20.8 ± 20.8
Empididae							
Chelifera sp.*	P	<1.6	<1.6	<1.6	–	–	–
Psychodidae							
Pericoma sp.*	P	–	–	–	–	4.8 ± 4.8	–
Simulidae*	CF	27.24.8	171.2 ± .8.8	60.8 ± 30.4	64 ± 25.6	20.8 ± 9.6	16.0 ± 0.0
Tipulidae							
Hexatoma sp.*	P	32.0 ± 0.0	–	4.8 ± 4.8	–	–	12.8 ± 12.8
Ephemeroptera							
Baetidae							
Andesiops sp. 1	S	–	–	8.0 ± 16.0	–	–	–
Andesiops peruvianus (Ulmer)	S	–	16.0 ± 9.6	–	–	–	–
A. torrens (Lugo-Ortiz&McCafferty)	S	48.0 ± 43.2	112.0 ± 49.6	24.0 ± 19.2	12.8 ± 12.8	12.8 ± 8.0	36.8 ± 20.8
Leptophlebiidae							
Leptophlebiidae sp. 1	S	–	–	104.0 ± 104.0	16.0 ± 16.0	–	–

Table 4 continued

	FFG	Cornelios NatRV	Cornelios ExotRV	Horquetas NatRV	Horquetas NatRV	Cóndores ExotRV	Cóndores NatRV
Meridialaris chiloeensis (Demoulin)*	S	308.8 ± 83.2	299.2 ± 38.4	260.8 ± 123.2	52.8 ± 20.8	192.0 ± 36.8	48.0 ± 27.2
Nousia bella (Pescador&Peters)*	S	107.2 ± 19.2	123.2 ± 28.8	84.8 ± 32.0	16.0 ± 11.2	124.8 ± 56.0	20.8 ± 12.8
Hapsiphlebia sp.	S	–	–	4.8 ± 4.8	–	–	–
Plecoptera							
Gripopterygidae							
Antarctoperla alteria (Zwick)*	Sh	–	–	4.8 ± 4.8	–	4.8 ± 4.8	–
A. michaelseni (Klapalek)*	Sh	116.8 ± 32.0	27.2 ± 9.6	68.8 ± 4.8	24.0 ± 24.0	8.0 ± 4.8	24 ± 48.0
Aubertoperla illiesi (Froehlich)*	S	160.0 ± 9.6	208.0 ± 8.8	108.8 ± 1.1	24.0 ± 9.6	108.8 ± 40.0	72.0 ± 40.0
Klapopteryx kuscheli (Illies)*	Sh	–	–	12.8 ± 4.8	8.0 ± 8.0	–	–
Limnoperla sp.*	S	203.0 ± 19.2	140.0 ± 72.0	16.0 ± 22.4	48.0 ± 11.2	132.8 ± 96.0	84.8 ± 62.4
Notoperlopsis femina (*Illies*)*	S	43.2 ± 14.4	219.2 ± 19.2	100.8 ± 22.4	92.8 ± 32.0	32.0 ± 6.4	16.0 ± 6.4
Rhitroperla sp.*	Sh	448.0 ± 115	528.0 ± 60.8	368.0 ± 60.8	80.0 ± 30.4	208.0 ± 65.6	188.8 ± 99.2
Trichoptera							
Hydrobiosidae							
Cailloma sp.	P	4.8 ± 9.6	–	–	–	–	–
Genus x*	P	4.8 ± 4.8	11.2 ± 4.8	–	4.8 ± 4.8	–	–
Hydropsychidae							
Smicridea sp.*	CF	219.2 ± 99.2	4.8 ± 4.8	540.8 ± 76.8	48.0 ± 17.6	156.8 ± 64.0	88.0 ± 44.8
Polycentropodidae	P	–	–	–	–	4.8 ± 8.0	–
Sericostomatidae							
Myotrichia murina (*Schmid*)*	Sh	–	–	–	–	4.8 ± 4.8	4.8 ± 4.8
Parasericostoma cristatum (*Flint*)*	Sh	–	16.0 ± 9.6	16.0 ± 6.4	–	4.8 ± 4.8	–
P. laterale (*Schmid*)*	Sh	–	–	–	–	16.0 ± 9.6	4.8 ± 4.8
P. ovale (*Schmid*)*	Sh	–	–	–	–	<1.6	–
Benthic taxonomic richness		14.33 ± 2.52	15.67 ± 2.08	14.00 ± 2.65	10.67 ± 3.21	12.00 ± 4.36	10.33 ± 0.58
Benthic Shannon diversity		2.14	2.20	2.02	2.05	2.02	2.05
Leaf litter species in bag		ch w	ch w	ch w	ch w	ch w	ch w
Leaf bags taxonomic richness		8.3 7	6.3 7.3	6.3 5.3	6 4.3	8 9	4.7 5

Table 4 continued

Stream		Cornelios				Horquetas				Cóndores			
	FFG	NatRV		ExotRV		NatRV		ExotRV		NatRV		ExotRV	
Leaf bags Shannon diversity		1.85	1.52	1.26	1.40	1.60	1.18	1.62	1.25	1.61	1.97	1.17	1.38

Species found in the experimental bags are marked (*)

NatVR native riparian vegetation, *ExotRV* exotic riparian vegetation, *FFG* functional feeding groups, *CG* collector–gatherers, *CF* collector–filterers, *P* predators, *Sh* shredders, *S* scrapers, Genus x is defined in Domínguez & Fernández (2009)

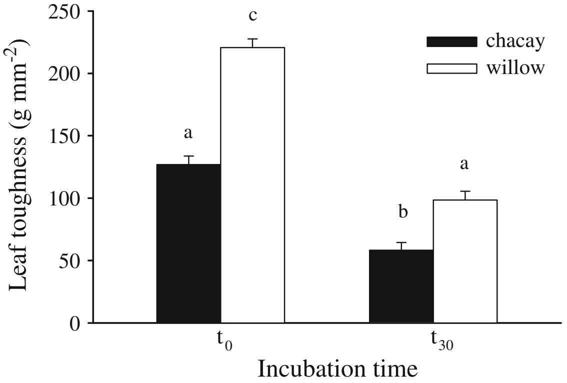

Fig. 3 Leaf toughness of *Salix fragilis* (crack willow; invasive) and *Ochetophyla trinervis* (chacay; native) at the beginning (t_0) and the end (t_{30}) of the decomposition experiment (*error bars* 1 SE)

Neither Shannon diversity (H') index differed between leaf species (three-way nested ANOVA, $P = 0.06$), stream reaches ($P = 0.09$) nor streams ($P = 0.10$). As a consequence, there were no differences in the proportions of the different FFG between leaf-species bags. However, of the total number of taxa that colonized the experimental units, shredders were 48% of the assemblage in the bags in the NatRV reaches and 30% in those of ExotRV. Relative abundance of shredders colonizing litter bags did not differ among stream reaches (three-way nested ANOVA, $P = 0.12$; Fig. 5b) nor between species ($P = 0.99$). Shredder density in the bags was significantly related to leaf litter mass losses only in chacay treatment ($r_{\text{chacay}} = 0.558$, $P = 0.016$; $r_{\text{crack willow}} = 0.287$, $P = 0.248$).

Composition of invertebrate assemblages in leaf litter bags did not differ between leaf species treatments (ANOSIM, Global Rho $= -0.010$, $P = 0.540$) but they did differ between reaches with different riparian vegetation (ANOSIM, Global rho $= 0.218$, $P < 0.05$). The taxa that most contributed to the differences between the assemblages of reaches with different riparian vegetation were Chironomidae sp. 2 (23.7%) and sp. 3 (12.2%), *Rhitroperla* sp. (11.6%), and *Limnoperla* sp. (11.2%). The relative abundance of Chironomidae sp. 2 exceeded 25% in ExotRV reaches, while in NatRV reaches it was lower than 15%. On the other hand, the relative abundance of *Rhitroperla* sp., the only shredder in this group, was higher in NatRV reaches in Cóndores and in crack willow bags from Cornelios. The relative abundance of the grazer *Limnoperla* sp. was more than 10% in NatRV reaches but was less than 10% in ExotRV.

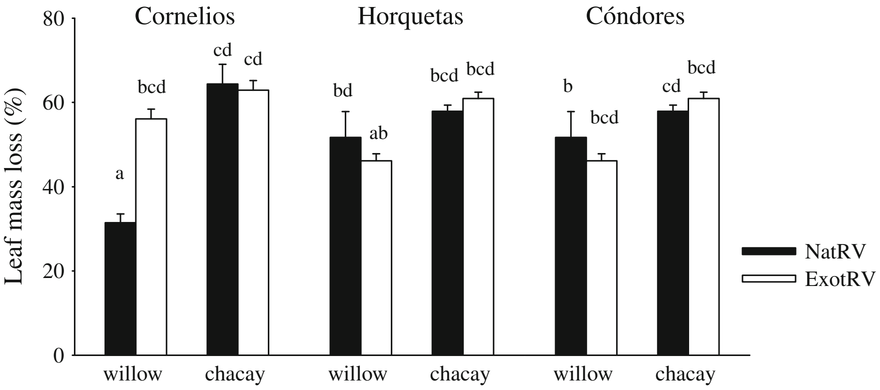

Fig. 4 Leaf mass loss (%) of *Salix fragilis* (crack willow) and *Ochetophyla trinervis* (chacay) in the native riparian vegetation reach (NatRV) and in the exotic riparian vegetation reach (ExotRV) of the three streams (*error bars* 1 SE)

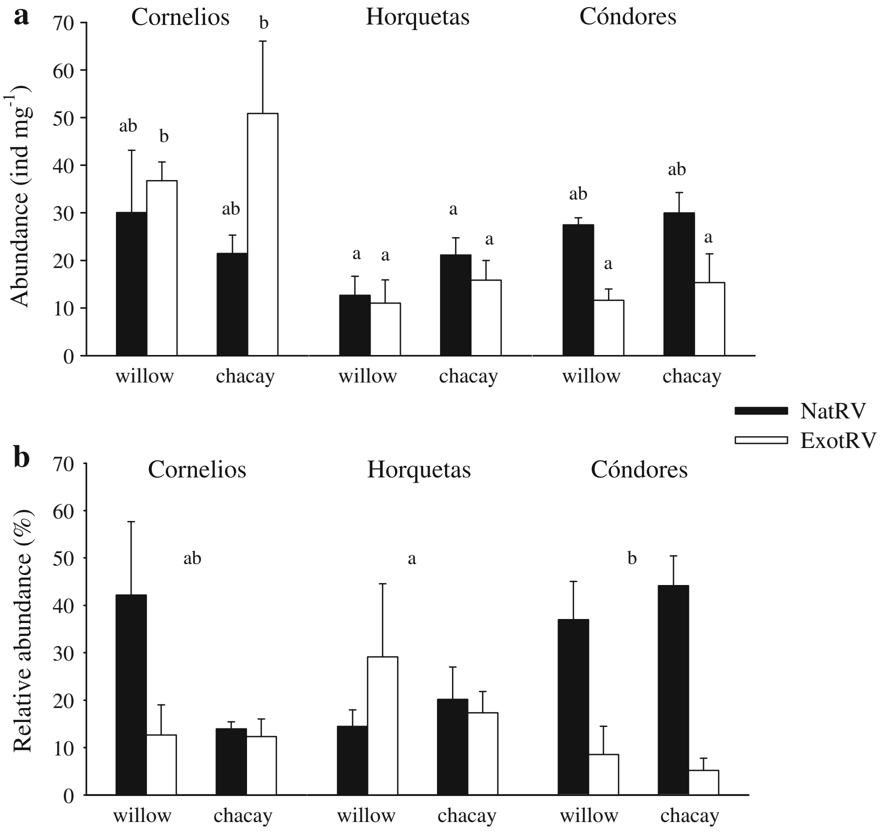

Fig. 5 Total invertebrate abundance (**a**) and shredder relative abundance (**b**) in the experimental units of *Salix fragilis* (crack willow) and *Ochetophyla trinervis* (chacay) in the native riparian vegetation reaches (NatRV) and in the exotic riparian vegetation reaches (ExotRV) of the three streams (*error bars* 1 SE)

Discussion

Decomposition of both leaves species in invaded versus non-invaded reaches

Our field experiment demonstrated that the decomposition rate of willow and chacay litter did not differ between invaded and non-invaded reaches. The fact that the decomposition of the exotic species did not differ as a function of riparian vegetation (NatRV vs. ExotRV) suggests that shredders in the NatRV reaches were able to exploit this new resource as well as they do downstream, where willow litter has been present for longer. Also, this lack of differences between reaches may be attributed to the system connectivity along the longitudinal axes of the stream, as leaves of native species were abundant in the ExotRV reaches, suggesting that the detrital pathway including benthic biota was still supported by leaf litter derived from native species growing in upstream reaches. Impacts to the stream should be stronger as one move in the downstream direction since more stream length has been exposed to the influence of the invasive crack willow.

Decomposition of crack willow versus chacay leaves

Crack willow leaves decomposed slower than chacay leaves both in ExotRV sites and in stream reaches where they represented a novel resource (NatRV sites). Major physical and chemical properties governing leaf decay are (a) leaf toughness, (b) concentration of nutrients, and (c) chemical defenses (Graça, 2001). These features all have major impacts on colonization and degradation of leaf litter by decomposing microorganisms (Bärlocher, 1992). Both leaf species in our study decomposed fast (sensu Petersen & Cummins, 1974), though crack willow leaves were tougher than chacay leaves, both at the beginning and at the end of the experiment.

With regard to nutrient concentration, though we did not analyze leaf nutrients, species of the genus *Salix* and *Ochetophila* have symbiotic relationships with ecto-mycorrhizae and arbuscular mycorrhizae to promote the absorption of soil nutrients (Chaia, 1997; Hashimoto & Higuchi, 2003; Chaia et al., 2006). This relationship promotes high nutrient concentrations in leaves and roots, thus improving their nutritional quality for consumers and decomposers (Tortosa, 1983; Kull et al., 1998). On the other hand, leaves of some European willow species contain high concentrations of phenols and tannins (Julkunen-Tiitto, 1985; Haapala et al., 2001), which are deterrents to aquatic invertebrates. Future research in Patagonia should look into leaf nutrient contents and deterrent substances of both plant species to assess the relevance of chemical characteristics on the consumption and growth of stream detritivores.

If the invasive species has higher decomposition rates than the native, leaf litter disappears earlier, which results in discontinuity of resource supply for decomposers (Bottollier-Curtet et al., 2011). Conversely, in these Patagonian systems, though the invasive plant has the same phenology as the native, its slower decomposition would provide the community of detritivores a longer temporal availability of OM in the stream benthos. The fact that crack willow leaf toughness after 30 days in the stream was similar to that of chacay leaves at the time it enters the stream, could suggest that after some time of decomposition in the stream crack willow may become functionally equivalent to chacay (based on toughness), increasing OM availability later. However, as both species decompose fast, litter accumulations are unlikely to be found after some time in the stream.

Invertebrate community

Few studies have simultaneously studied the effects of invasions on both community structure and ecosystem functioning in the context of the decomposition process (Reinhart & Vande Voort, 2006; Braatne et al., 2007; Bottollier-Curtet et al., 2011; Hladyz et al., 2011). In this study, community attributes such as total invertebrate density, taxonomic richness, and diversity were insensitive to crack willow invasion. However species composition, both in the benthos and in litter bags, differed between crack willow-invaded and non-invaded reaches. Thus, the hypothesis of crack willow-driven structural changes at the community level in streams could not be rejected.

The lack of differences in total invertebrate abundance and diversity between NatRV and ExotRV stream reaches may be in part the result of stream connectivity, as upstream reaches might supply downstream with the same species. However, the composition of invertebrate assemblage differed between both types of reaches. Two scraper and two shredder species were less abundant in crack willow-dominated reaches, suggesting that habitat/food resource availability was reduced in the presence of crack willows. Miserendino & Pizzolón (2004) have also reported lower abundances of shredder species in crack willow-lined rivers than in native riparian rivers. Our studied streams are dominated by riparian native shrubs of medium height that produce no effective shading on the streambeds. In contrast, reaches invaded by crack willow are heavily shaded during summer, probably producing stronger effects on autotrophy and invertebrate scrapers. One of the most sensitive species to willow presence was the Trichopteran *Smicridea* sp., which had higher abundance in NatRV reaches. As species of this genus are filterers (i.e., they feed on organic particles in suspension, Merritt & Cummins, 1996), further studies should include the sampling of suspended fine particulate organic matter to be able to conclude if this dissimilar distribution may be attributed to a bottom–up control.

Research on the impact of crack willow on stream biota has mostly focused on the abundance and composition of benthic invertebrates and these studies have arrived at different conclusions about the effects of crack willows. In New Zealand, some studies found lower densities of invertebrates in reaches lined with crack willow (Lester et al., 1994; Lester et al., 1996) while others observed the opposite (Glova & Sagar, 1994; Parkyn & Winterbourn, 1997). In Australia, the composition of invertebrates in willow-invaded reaches differed with that at sites with native species (Jayawardana et al., 2006; Jayawardana & Westbrooke, 2010; Jayawardana et al., 2010) or showed minor changes (Schulze & Walker, 1997). It is worth noting that, in at least two studies, exotic willow had positive effects on populations of invasive aquatic fauna: the mud snail *Potamopyrgus antipodarum* (Jayawardana et al., 2006 in Australia) and brown trout *Salmo trutta* (Jayawardana et al., 2006 in Australia, Glova & Sagar, 1994 in New Zealand). The site-specific nature of these results indicates the importance of performing local studies analyzing a suite of ecological metrics in assessing the impacts of invasive species, rather than extrapolating results obtained from other regions.

Invertebrates colonizing litter bags did not show species selectivity as both types of bags were equally colonized, both in abundance and in taxonomic composition. Not only shredders colonized litter bags, but also Chironomids (collector–gatherers) were abundant, which demonstrates that bags are also used as refuge or that FPOM trapped in bags makes the leaf pack in the bag a suitable environment for them.

Final remarks and future research

Freshwater ecosystems are affected both by aquatic and terrestrial invaders. As of now, most studies conducted in Patagonia have assessed the effects of animal invaders, such as the North American beaver *Castor canadensis* Kuhl in streams and rivers of Tierra del Fuego (Simanonok et al., 2011) and Northern Hemisphere salmonids (mostly brown and rainbow trout) in continental lentic and fluvial systems (Reissig et al., 2006; Buria et al., 2010). Our study is the first to assess the impact of a riparian plant invader on Patagonian small streams. The current distribution of crack willow along watercourses in Patagonia has not been formally mapped and studies on ecosystem vulnerability or invader expansion rates are still lacking.

We suggest that further studies are needed on the quality of willow leaves as a food resource, including leaf chemical analysis and experiments on shredder growth, and also studies on the impact on other ecosystem processes such as primary production and herbivory.

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