

Research Article

Organic matter characterization and decomposition dynamics in sub-Antarctic streams impacted by invasive beavers

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ABSTRACT. Despite being a relatively remote and well conserved area, the sub-Antarctic ecoregion faces pressing global threats from climate change, the ozone hole and introduced species. Its freshwater ecosystems are one of the least studied components of this biome, but they are known to confront a host of invasive taxa including trout and beavers. We set out to understand the basic characterization and dynamics of organic matter processing and decomposition in sub-Antarctic streams under natural forest (NF) conditions and in ponds constructed by North American beavers (*Castor canadensis*) (BP). We found these streams have a naturally stable benthic organic matter regime throughout the year with a peak in leaf input from *Nothofagus pumilio* in autumn. Beaver ponds significantly increased the retention of organic matter and caused significantly higher decomposition rates, probably associated with increased density and biomass of *Hyaella* spp. As expected, leaf decay rates for *N. pumilio*, a deciduous species, were higher (NF: $-0.0028 \text{ day}^{-1} \pm 0.0001 \text{ SE}$; BP: $-0.0118 \text{ day}^{-1} \pm 0.0009 \text{ SE}$) than *N. betuloides* (a broad-leaf evergreen) (NF: $-0.0018 \text{ day}^{-1} \pm 0.0005 \text{ SE}$; BP: $-0.0040 \text{ day}^{-1} \pm 0.0003 \text{ SE}$). Overall these results indicate that the naturally low decomposition rates (slower than 89% of a global survey of decay rates) for these cold, oligotrophic streams are being modified by introduced beavers to resemble more temperate latitudes.

Keywords: *Castor canadensis*, carbon cycle, decay rate, decomposition, leaf packs, *Nothofagus*.

Caracterización de la materia orgánica y la dinámica de descomposición en arroyos subantárticos impactados por castores invasores

RESUMEN. A pesar de ser una zona relativamente remota y bien conservado, la ecorregión subantártica se enfrenta a presiones por amenazas globales por el cambio climático, el agujero de ozono y las especies introducidas. Los ecosistemas de agua dulce son uno de los componentes menos estudiados de este bioma, pero se sabe que enfrentan una serie de taxones invasivos como la trucha y los castores. El propósito de este estudio es entender la caracterización básica y dinámica de descomposición de la materia orgánica en arroyos subantárticos de bosques naturales (NF) y condiciones de los estanques construidas por diques del castor norteamericano (*Castor canadensis*) (BP). Todos los arroyos estudiados presentaron un régimen naturalmente estable de materia orgánica bentónica, durante todo el año, con un mayor ingreso de hojas de *Nothofagus pumilio* en el otoño. La retención de materia orgánica aumentó significativamente en BP y causó una mayor tasa de descomposición, probablemente asociada a una mayor densidad y biomasa de *Hyaella* spp. Como era de esperar, las tasas de descomposición de hojas de *N. pumilio*, una especie de hoja caduca, fueron mayores (NF: $-0,0028 \text{ día}^{-1} \pm 0,0001 \text{ SE}$; BP: $-0,0118 \text{ día}^{-1} \pm 0,0009 \text{ SE}$) que las de *N. betuloides*, un árbol de hoja ancha perenne (NF: $-0,0018 \text{ día}^{-1} \pm 0,0001 \text{ SE}$; BP: $-0,004 \text{ d}^{-1} \pm 0,0003 \text{ SE}$). En general, estos resultados que las bajas tasas de descomposición natural (menores al 89% de los casos reportados), para estas corrientes frías y oligotróficas, están siendo modificadas por los castores introducidos, haciéndolas parecerse a aquellas provenientes de arroyos de latitudes más templadas.

Palabras clave: *Castor canadensis*, ciclo de carbono, tasa de descomposición, descomposición, paquete de hojas, *Nothofagus*.

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INTRODUCTION

Streams in forested biomes depend heavily on allochthonous material inputs for their energy and material budgets (Wallace *et al.*, 1997). While overall little is known about lotic ecosystems in southern South America, it has been found that the sub-Antarctic streams that drain the world's southernmost forested watersheds in the Tierra del Fuego Archipelago depends on allochthonous organic material as the base of their benthic food web (Anderson & Rosemond, 2007). In particular, the majority of the energy flow in these food webs comes specifically from fine benthic organic material (250 μm <FBOM <1 mm) (Anderson & Rosemond, 2010). Consequently, the benthic macroinvertebrate assemblage is dominated by taxa belonging to the collector-gatherer functional feeding group that feeds on FBOM. Shredders, which consume coarse benthic organic matter (CBOM >1 mm), largely made up of leaves and other material derived from riparian vegetation, are conspicuously scarce in these streams (Anderson & Rosemond, 2007; Simanonok *et al.*, 2011). These trends contrast with the general expectations for forested ecosystems in the Northern Hemisphere, where shredders are common and play important roles in the processing of organic matter (Huryn & Wallace, 2000). However, the lack of shredders coincides with reports from New Zealand streams (Winterbourn & Ryan, 1994), which share a similar geomorphology and common (but remote) evolutionary history of their flora and fauna as remnants of Gondwana (Winterbourn & Ryan, 1994). Such similarities and differences between the structure and function of sub-Antarctic streams with expectations from comparable sites in Northern and Southern Hemisphere led to the underlying motivation of this paper: to determine how sub-Antarctic streams process and transform organic matter.

In this context, it is important to recognize that in the Tierra del Fuego Archipelago, located south of the Magellan Strait, at the southern tip of the Americas, one of the largest and most dramatic impacts to streams that could affect ecosystem processes such as organic matter retention and decay, has been the invasion of North American beavers (*Castor canadensis* Kuhl, 1820). During the last sixty years, this invasion has arguably been the largest

modification to riparian forests in Tierra del Fuego in the Holocene, *i.e.* since the retreat of the last glaciations, approximately 10-12,000 years BP (Anderson *et al.*, 2009). Indeed, the impact of beavers, as introduced ecosystem engineers, has been shown to be even greater than forestry practices, when these are well managed and maintain a riparian buffer (Simanonok *et al.*, 2011). Beavers affect the structure and function of benthic macroinvertebrate communities in these streams as well as ecosystem-level processes, like the flow of carbon in food webs (Anderson & Rosemond, 2007, 2010).

Determining detritus decomposition dynamics was a clear need within limnological research in southern South America, particularly the effects of the introduced and invasive North American beaver. The goals of this study were to: i) determine natural organic matter composition and dynamics in sub-Antarctic streams, ii) link detritus with its associated benthic macroinvertebrate assemblage, and iii) evaluate the effects of invasive beavers on organic matter decomposition and associated fauna. Based on previous findings, we expected that the increased retention of organic matter caused by beaver engineering would increase the abundance of benthic macroinvertebrates, due to an increase in resource availability, but decrease their diversity, due to habitat homogenization (Anderson & Rosemond, 2007). We also was expected that leaf litter would decompose more slowly and be less of a resource for macroinvertebrates in beaver pond habitats, due to increased accumulation of material which could create anoxic conditions (Naiman *et al.*, 1986).

MATERIALS AND METHODS

Study site

The extreme southern portion of the Tierra del Fuego Archipelago stands out as one of the few remaining unfragmented temperate forests on the planet (Silander, 2000). Yet, paradoxically this otherwise "remote" area has been the foci of a series of species introductions; particularly in streams (see Anderson *et al.*, 2006). Among this exotic assemblage, the North American beaver (*C. canadensis*), introduced in 1946, has come to play a dominant role in engineering the structure and function of freshwater ecosystems

throughout most of the archipelago (Anderson & Rosemond, 2007, 2010).

The study was conducted from 29 May to 19 November 2008 in the Róbaló River (Fig. 1; 54°56.3'S, 63°37.7'W). The area's climate is characterized by mean monthly temperatures that fluctuate from 1.9° to 9.6°C and an annual precipitation of approximately 467.3 mm (Rozzi *et al.*, 2006). The sub-Antarctic forests are very poor in trees species, consisting of three main broad leaf taxa from the genus *Nothofagus*, including two deciduous species *N. pumilio* (lenga) and *N. antarctica* (ñirre), and the evergreen *N. betuloides* (coigüe). A fourth species *Drimys winterii* (Winter's bark) is also found associated with *coigüe* in the wetter portions of the archipelago (Pisano 1977). The replicate unit in this field experiment was the leaf pack ($n = 4$ per date), which were deployed in two habitat types: 1) Natural Forest (NF): a natural pool in a stream segment without influence from beaver or humans and whose intact natural riparian forest vegetation was a mix of co-dominant *N. pumilio* and *N. betuloides*, and 2) Beaver Pond (BP): a stream segment impacted by the direct action of *C. canadensis*, including both damming and foraging of the adjacent riparian mixed forest. The NF site was approximately 1.5 km downstream from the BP site; there are no watersheds without beavers in the archipelago. Temperature data were available between May to October 2008 from HoboTM data loggers placed in the stream as part of a concurrent study (Contador, 2011), to determine mean daily temperature = $1.75^{\circ}\text{C} \pm 0.08$ during the leaf pack experiment, but more precise information was not available from our specific sites to include in the decay rate model. A previous study (Anderson, 2006) also characterized the general habitat characteristics of these study reaches (Table 1).

Characterization of benthic organic matter

This study was carried out from January to December 2009. In each stream segment, benthic organic material (BOM) was characterized as percent BOM coverage on the stream bed using a 0.5 m² quadrat, divided into 100 sub-squares (0.005 cm² each). This quadrat was placed every 5 m in a longitudinal transect along each study reach to obtain a total of 50 measurements on each site during each season of the year. We used a 30 cm diameter cylinder to estimate organic matter standing crop, agitating and extracting material for 3 min, using a cup. Four core samples were taken on each site during each season. Later, in the laboratory, these samples were separated into fine benthic organic material ($250 \mu\text{m} < \text{FBOM} < 1 \text{ mm}$), and course benthic organic matter (CBOM $> 1 \text{ mm}$).

This last category was further divided into four sub-groups: coigüe leaves (*N. betuloides*), lenga leaves (*N. pumilio*), sticks, and unidentified material; which was composed of other bush species or leaves that were undistinguishable due to advanced decomposition. Then, samples were dried for 48 h at 60°C to obtain their dry weight (g m⁻²). These data were then analyzed in JMP version 7 (SAS Institute Inc.), to determine differences between annual and/or seasonal means of response variables (% cover and g DM biomass) between habitats using one-way analysis of variance (ANOVA). Within the NF sites, the same analysis was performed to detect an effect of season upon these variables.

Decomposition of leaf packs

The rate of decomposition of leaf litter was studied using the leaf pack methodology developed by Benfield (1996). During autumn, leaves were collected from lenga just before abscission. Leaves from the evergreen broad-leaf coigüe were collected from the forest floor in the freshest possible state. The leaves were air dried at room temperature for 8 days. We constructed a total of 128 plastic mesh bags with 5 mm apertures to hold 5 g of dry leaf material, weighed on an analytical balance ($\pm 0.0001 \text{ g}$). Bags contained only a single species (coigüe or lenga). Each bag was identified with an aluminum tag and an individualized number that identified replicate, species and day of incubation to be removed from the stream. After weighing leaf packs, and to avoid excess loss and breakage, the leaf packs were wet with distilled water to soften them for transport and placed in re-sealable, plastic bags.

In the field, we placed 64 leaf packs in each habitat type: NF and BP. Each bag was anchored to the stream bed with metal stakes to keep them submerged. Four replicate packs of each species (coigüe and lenga) were removed after 0 (designated as "blanks" to calculate error due to handling loss by manipulation in transport to the study site), 7, 15, 30, 60, 90, 120 and 150 days. The study was conducted to coincide with leaf fall into streams in late May (austral autumn). From each sample, leaf packs were rinsed in a 250 μm sieve to remove inorganic material and benthic macroinvertebrates. The organic matter portion of samples was then placed in plastic bags and frozen at -20°C. Macroinvertebrates were preserved in 70% ethanol until final processing in the laboratory at the Instituto de la Patagonia, Universidad de Magallanes, Punta Arenas, Chile.

Leaf packs were dried as before, at air temperature, and weighed to obtain DW. Then, samples were transferred to the drying oven and kept at 60°C for

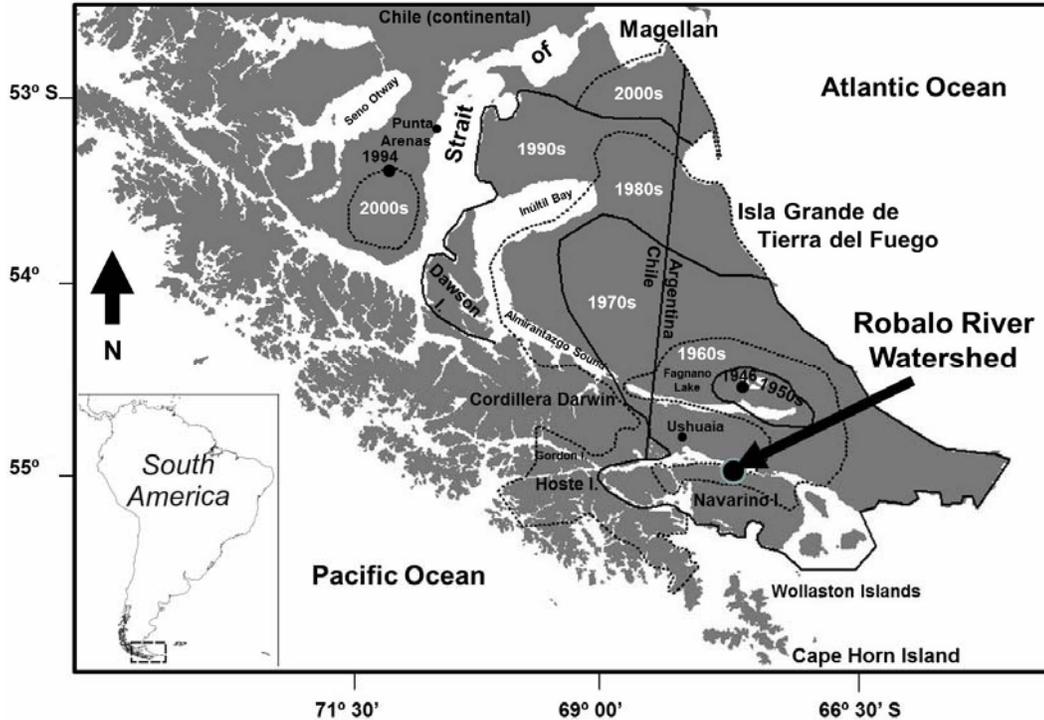


Figure 1. Map of the Tierra del Fuego Archipelago (modified from Anderson *et al.*, 2009). The principal islands of the archipelago are indicated and an arrow demonstrates the site of the Róbalo River watershed. Concentric areas indicate the approximate expansion dates of invasive North American beavers (*Castor canadensis*) in the area.

Figura 1. Mapa del Archipiélago de Tierra del Fuego y Cabo de Hornos (modificado de Anderson *et al.*, 2009). Se destacan las principales islas del archipiélago, indicando con una flecha el lugar de la cuenca del río Róbalo y con áreas concéntricas las fechas aproximadas de expansión y colonización del castor norteamericano (*Castor canadensis*).

Table 1. Habitat variables for natural forested (NF) and beaver pond (BP) reaches of the Robalo River (from Anderson 2006). Values are means (\pm SE). If SE is not shown, then values are from a single sample. SE: standard error.

Tabla 1. Variables de hábitat de bosque natural (NF) y lagunas de castor (BP) en el río Róbalo (de Anderson 2006). Valores son promedios (\pm SE). Si no se indica SE, los valores corresponden a una sola muestra. SE: Error estándar.

Habitat variables	NF	BP
Width (m)	8.3 \pm 1.1	15.3 \pm 2.0
Canopy cover (% shaded)	51.5 \pm 6.4	11.2 \pm 2.4
Slope	0.0016	0.0019
pH	7.71	7.73
Conductivity (μ S)	68.7	85.1
Dissolved oxygen (mg L^{-1})	10.3	10.4

48 h to obtain a constant weight, measured with an analytical balance (0.0001 g). Finally, the percent of initial weight remaining was calculated, correcting for

loss of material through handling. Decomposition was calculated based on percent of remaining organic material (%DW Remaining) = $\text{DW Day}_t / \text{DW Day}_0 \times 100$, successively, where Day_t = sampling dates. Afterwards, we applied a linear regression to these decomposition curves between the ln of percent DW remaining (y-axis), versus days exposed (x-axis). The negative slope of the regression is equal to the decay coefficient ($-k$). We compared the slopes of the two species in the two habitats using analysis of covariance followed by a *post-hoc* Tukey test (Benfield, 1996).

Macroinvertebrate communities

Specimens were identified under dissecting microscopes (4x) to arrive at the lowest possible taxonomic level and classified by functional feeding groups (*sensu* Merritt & Cummins, 1996) as shredders, scrapers/grazers, collector-gatherers, collector-filterers, predators and parasites. We used standard guides and taxonomic keys for identification (Flint, 1982; Fernández & Domínguez, 2001; González, 2003; Merritt & Cummins, 1996). Functional feeding groups

(FFGs) were based on Miserendino & Pizzolon (2003), Anderson & Rosemond (2007) and Merritt & Cummins (1996). We used these data to evaluate benthic assemblage by habitat and leaf treatment, using abundance (# individuals/leaf pack), species richness (# taxa/leaf pack), and Shannon-Weaver diversity index (H' /leaf pack). All calculations were made per collection date and for type of habitat and leaf. These response variables were then compared using ANOVA. FFGs were compared between habitats and expressed as percentage of the entire assemblage based on abundance. All statistical analyses were done in JMP 7 (SAS Institute Inc.).

RESULTS

Characterization of benthic organic matter

The coverage of organic material accumulated on the stream bed was four times greater in the BP habitat than in the NF stream segment ($F_{7, 32} = 61.4$, $P < 0.001$; Fig. 2a). In BP, seasonal values fluctuated between 18-95.5%, (annual mean: $43 \pm 7.5\%$), while the free flowing lotic habitat was only 4.3-20.3% (annual mean: $10\% \pm 1.8$). Similarly, the standing crop of particulate organic matter was four times greater in BP than in NF. FBOM ranged from seasonal averages of 119.1 to 279.4 g m^{-2} with a yearly mean of $198.5 \pm 33.2 \text{ g m}^{-2}$ in BP, while the NF habitat ranged from seasonal minima and maxima of 43.5 to 54.5 g m^{-2} and a yearly mean of $49.83 \pm 2.3 \text{ g m}^{-2}$ ($F_{3, 12} = 0.46$, $P = 0.72$; Fig. 2b). CBOM similarly showed five times greater standing crop in BP, compared to the NF site. CBOM fluctuated seasonally from 440.9-777.5 g m^{-2} (annual mean = $554.3 \pm 85.1 \text{ g m}^{-2}$) and NF within 73.8-153.5 g m^{-2} (annual mean = $121.34 \pm 16.9 \text{ g m}^{-2}$) ($F_{1, 16} = 24.91$, $P = 0.003$; Fig. 2c)

The seasonal pattern for organic matter dynamics in sub-Antarctic streams under natural conditions (NF) showed no significant differences during the year for FBOM (Fig. 3a) ($F_{3, 12} = 0.46$, $P = 0.72$). On the other hand, separating CBOM into its constituent parts (lenga, coigüe, sticks and unidentifiable material) allowed us to observe that lenga leaves nearly doubled in autumn (Fig. 3b), reaching about $48.0 \pm 4.9 \text{ g m}^{-2}$, and displayed a relatively stable range of 15.5 to 28 g m^{-2} during the rest of the year ($F_{3, 12} = 3.48$, $P = 0.05$). At the same time, coigüe leaves, an evergreen broadleaf, showed no seasonal pattern ($F_{3, 12} = 1.03$, $P = 0.41$; Fig. 3c). These results also demonstrated a natural co-dominance of coigüe and lenga leaves in the CBOM size class of benthic organic material.

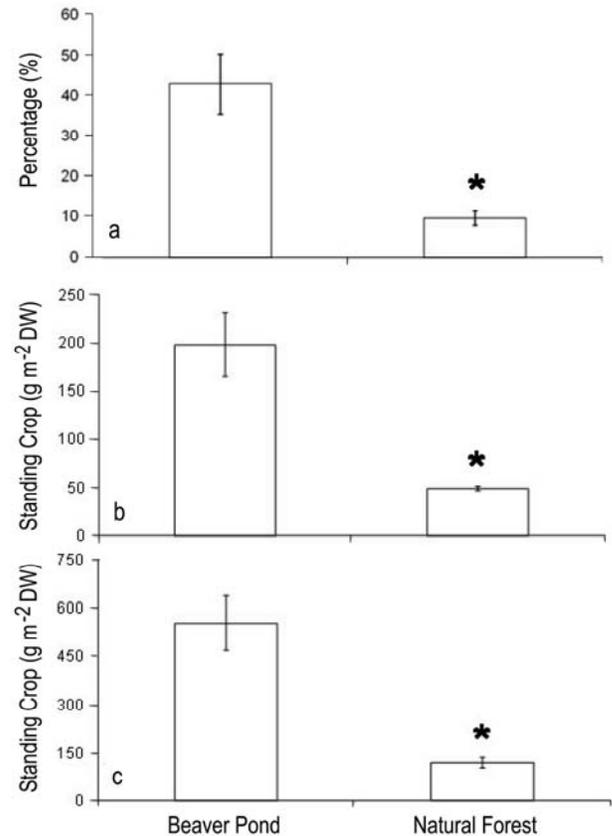


Figure 2. Organic material by type of habitat. * indicates a significant difference ($P < 0.05$) with a one-way ANOVA. a) Percentage of Coverage, b) FBOM = fine benthic organic matter ($250 \mu\text{m} < \text{FBOM} < 1 \text{ mm}$), and c) CBOM = course benthic organic matter (CBOM $> 1 \text{ mm}$).

Figura 2. Materia orgánica por tipo de hábitat. * indica una diferencia significativa ($P < 0.05$) con una prueba ANOVA de un factor. a) Porcentaje de Cobertura, b) FBOM = materia orgánica bentónica fina ($250 \mu\text{m} < \text{FBOM} < 1 \text{ mm}$), y c) CBOM = materia orgánica bentónica gruesa (CBOM $> 1 \text{ mm}$).

Decomposition of leaf packs

Decomposition rates varied by an order of magnitude depending on leaf and habitat combinations, going from -0.0118 d^{-1} in NF-lenga to -0.0018 d^{-1} in BP-coigüe (Table 2). However, within the same leaf species, the effect of the BP habitat was always to increase the decomposition rate (Fig. 4). Also, within habitat type, coigüe was always slower to decompose than lenga; though the difference was not significant in the NF habitat, it was in the BP (Fig. 4).

Macroinvertebrate assemblage

During the experiment, we found a total of twenty one different macroinvertebrate taxa. All were identified to

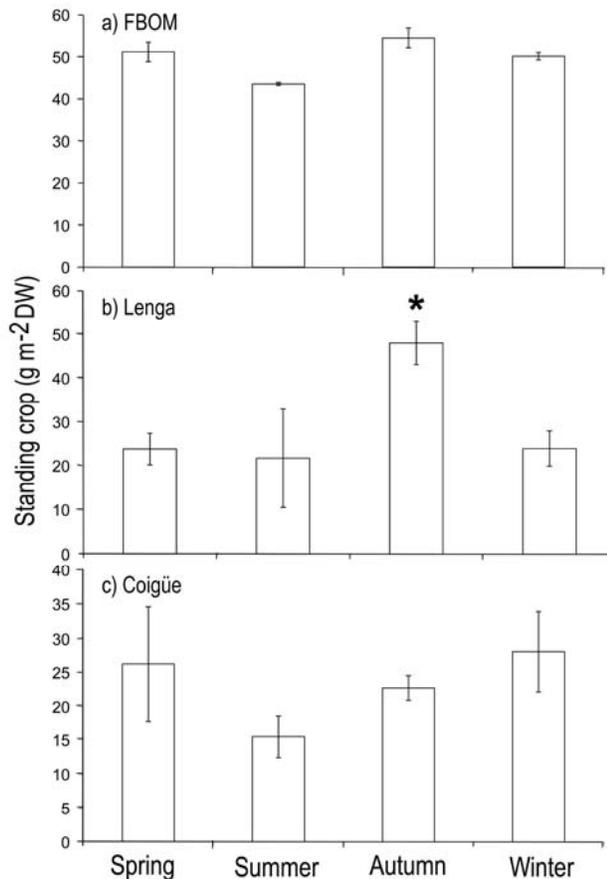


Figure 3. Seasonal dynamic of organic material under natural conditions. * indicates a significant difference ($P < 0.05$) with a one-way ANOVA.

Figura 3. Dinámica estacional de material orgánica bajo condiciones naturales. * indica una diferencia significativa ($P < 0,05$) con una prueba ANOVA de un factor.

family, 29% to genus and 38% to species. For the specimens that were not classified to species, they were grouped as morpho-species for the subsequent analysis, based on similar characteristics (see Appendix 1).

Grouping the total results by habitat type and leaf type over the 150 days of the study, we found that abundance of macroinvertebrates was significantly greater in leaf packs made up of lengua leaves in the BP habitat, compared to the other treatment combinations ($F_{3, 140} = 9.78$, $P < 0.0001$; Fig. 5a). Total taxa richness ($F_{3, 140} = 8.98$, $P < 0.0001$; Fig. 5b) and diversity ($F_{3, 137} = 8.65$, $P < 0.0001$; Fig. 5c) followed the opposite pattern, whereby leaf packs including coigüe had a significantly less speciose macroinvertebrate species assemblage in BP, compared to the other treatments. The same patterns were observed for the other

community variables (abundance, richness and diversity), as a function of time and habitat as well ($F_{(\text{leaf}*\text{habitat})1, 123} = 5.34$, $P = 0.02$; Fig. 6a, $F_{(\text{leaf}*\text{habitat})1, 123} = 20.99$, $P = 0.00001$; Fig. 6b, $F_{(\text{leaf}*\text{habitat})1, 123} = 16.62$, $P = 0.0001$; Fig. 6c, respectively).

All of the FFGs were found during the study and presented the same dominance patterns in all habitat and leaf treatments (Fig. 7). The greatest change observed in BP was the increased contribution of predators on both leaf types. Although consistently, collector-gatherers were the most abundant FFG, their relative contribution to the assemblage was reduced in BP (NF-BP lengua = 74-47%; NF-BP coigüe = 62-59%). Predators were the second most abundant FFG at all sites, while shredders, scrapers and parasites were consistently present but in low abundance for all treatments. Filterers were almost never present, being found only in the BP site (coigüe: 0.9% and lengua: 0.3%), which were represented by *Gigantodax* spp. (Simuliidae).

DISCUSSION

The role of beaver ponds in sub-Antarctic streams

The pond habitats that were engineered by introduced beavers (BP) increased the decomposition rate of both leaf species (coigüe and lengua). In the case of lengua (*N. pumilio*), this increase was by an order of magnitude, effectively transforming this ecosystem function from a “sub-Antarctic decay rate” to one more aligned with values found in more temperate latitudes (Table 3). These findings regarding the effects of beaver ponds were contrary to our expectations. Whereas we had hypothesized that beaver ponds would lower processing of organic matter by benthos, via the creation of harsher abiotic conditions including lower DO or increased pH Naiman *et al.*, 1986, what we observed, was an increase in benthic macroinvertebrate abundance that appears to facilitate greater shredding of leaf material. This result could be due to the fact that these sub-Antarctic streams are cold (potentially lowering microbial anaerobic respiration and anoxic conditions in the beaver pond), and the water is super saturated in oxygen (see Table 1 and Anderson & Rosemond, 2007).

In general, we also expected the decomposition rates of organic matter in sub-Antarctic streams to be lower than other values reported around the world, due to the colder temperatures found at high latitudes and the oligotrophic conditions of most water bodies in the Fuegian Archipelago (Moorman *et al.*, 2006;

Table 2. Regression results of decomposition rates per leaf species and habitat (NF: natural forest, BP: beaver pond, SE: standard error).

Tabla 2. Resultados de la regresión entre tasas de descomposición por tipo de hoja y tipo de hábitat (NF: bosque natural, BP: laguna de castor, SE: error estándar).

Habitat	Species	Common name	$-k \text{ day}^{-1}$	SE	R^2	F	P
NF	<i>N. betuloides</i>	Coigüe	-0.0018	0.0005	0.34	14.7	0.0006
NF	<i>N. pumilio</i>	Lenga	-0.0028	0.0001	0.68	107.7	<0.0001
BP	<i>N. betuloides</i>	Coigüe	-0.0040	0.0003	0.84	154.4	<0.0001
BP	<i>N. pumilio</i>	Lenga	-0.0118	0.0009	0.85	168.0	<0.0001

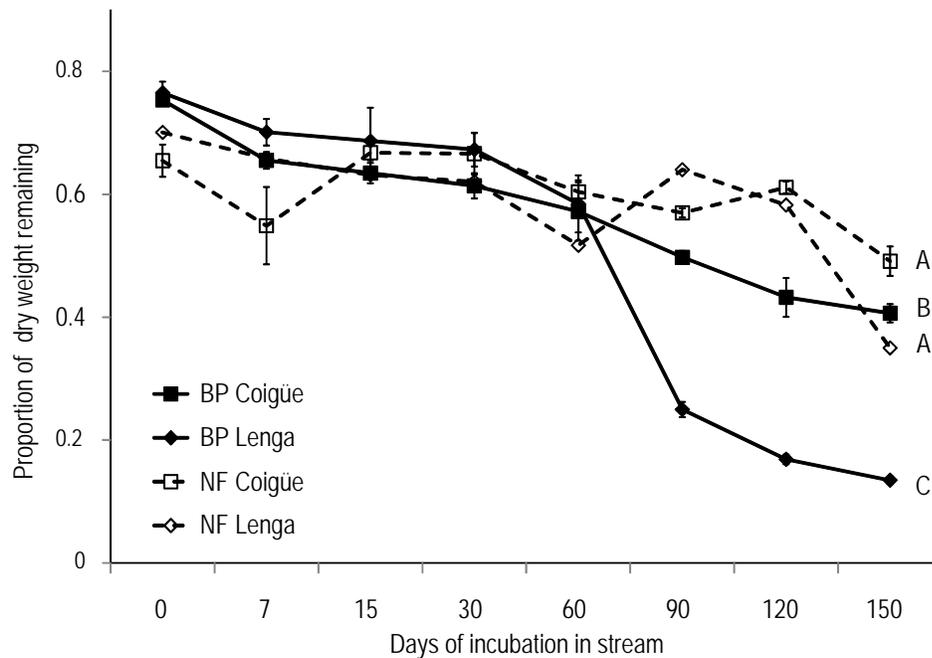


Figure 4. Proportion of dry weight remaining of organic material during the leaf pack decomposition experiment. BP: Beaver Pond; NF: Natural Forest. Different letters indicate significant differences with a *post-hoc* Tukey test.

Figura 4. Proporción de peso seco de materia orgánica remanente luego del experimento de descomposición de paquetes de hojas. BP: Laguna de Castor; NF: Bosque Natural. Letras distintas indican diferencias significativas con una prueba Tukey.

Anderson & Rosemond, 2007). Our results supported this hypothesis with the decay rates from NF sites being lower than 89% of those reported in a global review by Abelho (2001). The remaining 11% of decay rates, in the review, that were similar to those found in this study, were for the following genera (locations): *Acer* (Virginia, USA; southern Poland, Switzerland), *Eucalyptus* (northern Spain), *Acacia* (New South Wales, Australia); *Eugenia*, *Palanguium*, and *Pandanus* (Malaysia), *Quercus* (Virginia, Alaska and New Jersey, USA), *Rhododendron* (North Carolina, USA), *Pinus* (central Spain and Portugal; Michigan and Alaska, USA), and *Fagus* (northern France). Overall, the rates that were similar to ours

were for evergreen species, or those with tough structural properties (*e.g.*, *Rhododendron*, *Quercus* and *Pinus*), or similarly high latitude or elevation sites (*e.g.*, Poland, Switzerland, Michigan and Alaska). However, it should be noted that we were unable to use temperature as part of the decomposition model in this study, and the inter-site comparisons of our results should take this into account. Future stream ecology research here and elsewhere should seek to fully incorporate temperature as an explanatory factor in habitat-specific organic matter decay rates.

Similar to past studies in this biome (Anderson & Rosemond, 2007, 2010), we also found a scarcity of shredders in both habitat types. Recent emphasis on

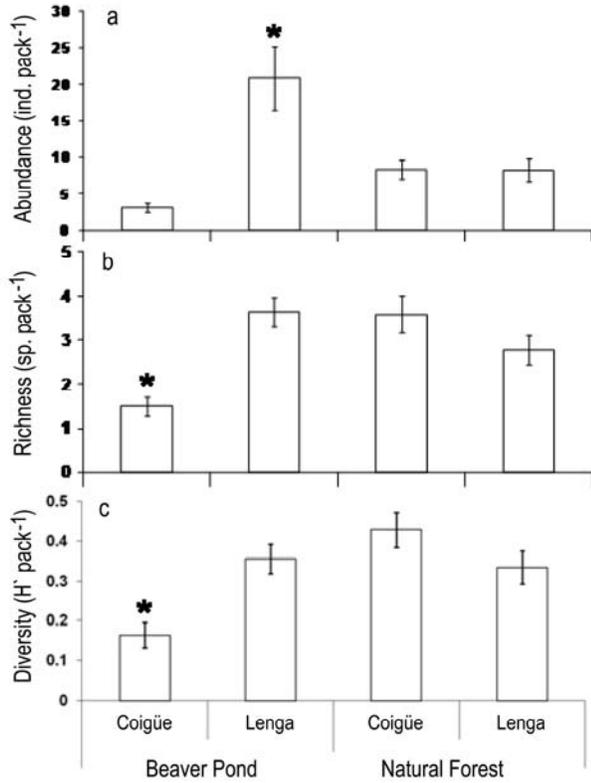


Figure 5. Mean (\pm SE) a) abundance b) taxonomic richness and c) Shannon-Weaver diversity of benthic macroinvertebrates on leaf packs during the entire experiment were compared with a one-way ANOVA to detect significant differences ($P < 0.05$) shown with an *, between treatments of leaf species and habitat. SE: standard error.

Figura 5. El promedio (\pm SE) de a) abundancia b) riqueza taxonómica y c) diversidad de Shannon-Weaver de macroinvertebrados bentónicos durante todo el experimento fueron comparados con una prueba ANOVA de un factor para detectar diferencias significativas ($P < 0,05$), indicados con *, entre los tratamientos de especie de hoja y hábitat. SE: error estándar.

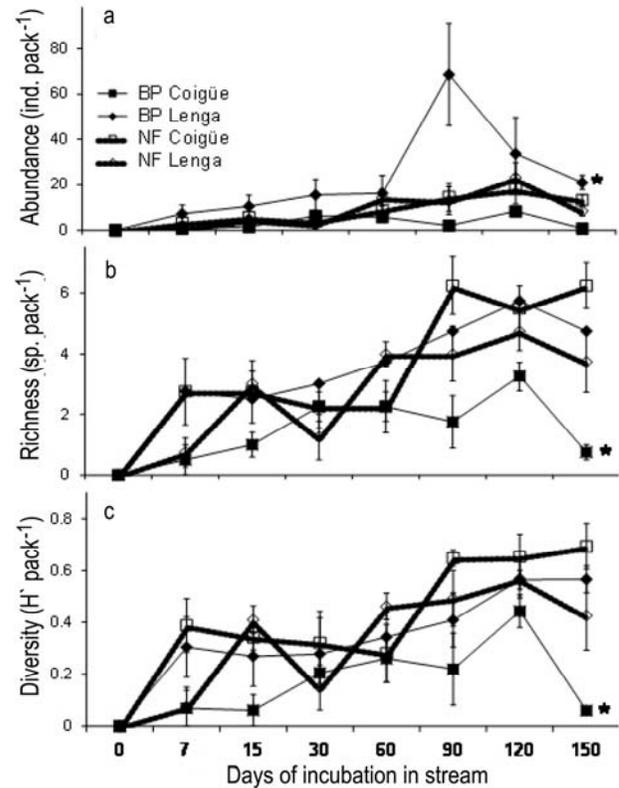


Figure 6. Temporal characteristics of the benthic macroinvertebrate assemblage associated with leaf packs in decomposition. Means (\pm SE) are shown and * indicates a significant difference for the habitat-leaf treatment using an ANCOVA with time as the covariate. SE: standard error.

Figura 6. Características temporales del ensamblaje bentónico asociado a los paquetes de hojas en el experimento de descomposición. Se demuestran promedios (\pm 1 SE) y un * para indicar diferencias significativas para un tratamiento combinado de hábitat- hoja, usando una prueba ANCOVA con el tiempo como covariante. SE: error estándar.

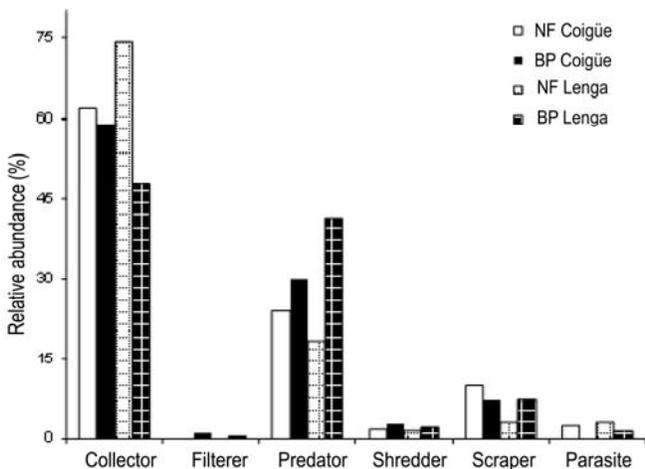


Figure 7. Relative abundance of benthic macroinvertebrate functional feeding groups per type of habitat and leaf treatment.

Figura 7. Abundancia relativa de los gremios alimenticios de los macroinvertebrados bentónicos por tipo de hábitat y tratamiento de hojas.

Table 3. Summary of Southern Hemisphere studies that evaluated decay rate of leaves in streams. * indicates introduced species, † denotes evergreen coniferous species, and § denotes evergreen broadleaf.

Tabla 3. Resumen de estudios del hemisferio sur que evaluaron la tasa de descomposición de hojas en arroyos. * indica especies introducidas, † indica especies de coníferas perennes y § indica especies de hojas anchas perennes.

Habitat	Country	Latitude	Species evaluated	$-k$ day ⁻¹	Reference
River passing through native broad leaf forests and some introduced taxa like <i>Eucalyptus</i>	Argentina	31°4'S	<i>Eucalyptus camaldulensis</i>	0.0131	Gallizzi & Marchese (2009)
Stream passing through native coniferous forest (<i>Austrocedrus chilensis</i>)	Chile	36°3'S	<i>Nothofagus pumilio</i>	0.0072	Valdovinos (2001)
Stream passing through native coniferous forest (<i>A. chilensis</i>)	Chile	36°3'S	<i>Pinus radiata</i> *†	0.0027	Valdovinos (2001)
Stream passing through pasture with scattered riparian planting of <i>Salix</i> and <i>Populus</i> sp.	New Zealand	37°6'S	<i>Aristotelia serrata</i>	0.0055	Quinn <i>et al.</i> (2000)
Stream passing through pasture with scattered riparian planting of <i>Salix</i> and <i>Populus</i> sp.	New Zealand	37°6'S	<i>Populus canadensis</i> *	0.0374	Quinn <i>et al.</i> (2000)
Stream passing through pasture with scattered riparian planting of <i>Salix</i> and <i>Populus</i> sp.	New Zealand	37°6'S	<i>Knighitia excelsa</i> §	0.0167	Quinn <i>et al.</i> (2000)
Stream passing through shrub and pasture	New Zealand	37°6'S	<i>Melicactus ramiflorus</i>	0.0507	Hicks & Laboyrie (1999)
Stream passing through shrub and pasture	New Zealand	37°6'S	<i>Betula pendula</i>	0.0325	Hicks & Laboyrie (1999)
Stream passing through shrub and pasture	New Zealand	37°6'S	<i>Alnus glutinosa</i>	0.0216	Hicks & Laboyrie (1999)
Stream passing through shrub and pasture	New Zealand	37°6'S	<i>Dacrycarpus dacrydoides</i>	0.0160	Hicks & Laboyrie (1999)
Stream passing through shrub and pasture	New Zealand	37°6'S	<i>Nothofagus menziesii</i>	0.0103	Hicks & Laboyrie (1999)
Stream passing through shrub and pasture	New Zealand	37°6'S	<i>Knighitia excelsa</i>	0.0045	Hicks & Laboyrie (1999)
Stream passing through shrub and pasture	New Zealand	37°6'S	<i>Beilschmiedia tawa</i>	0.0036	Hicks & Laboyrie (1999)
Stream passing through native <i>Eucalyptus</i> forest	Australia	37°5'S	<i>Acacia melanoxylon</i>	0.0049	Campbell <i>et al.</i> (1992)
Stream passing through native <i>Eucalyptus</i> forest	Australia	37°5'S	<i>Eucalyptus viminalis</i>	0.0230	Campbell <i>et al.</i> (1992)
Stream passing through native <i>Eucalyptus</i> forest	Australia	37°5'S	<i>Pomaderris aspera</i>	0.0099	Campbell <i>et al.</i> (1992)
Stream passing through native <i>Eucalyptus</i> forest	Australia	37°5'S	<i>Blechnum nudum</i>	0.0045	Campbell <i>et al.</i> (1992)
Stream passing through native <i>Eucalyptus</i> forest	Australia	37°5'S	<i>Correa lawrenciana</i>	0.0130	Campbell <i>et al.</i> (1992)
Stream passing through native deciduous forest of <i>N. pumilio</i>	Argentina	41°8'S	<i>Nothofagus pumilio</i>	0.0033	Albariño & Balsaeiro (2002)
Stream passing through native deciduous forest of <i>N. pumilio</i>	Argentina	41°8'S	<i>Pinus ponderosa</i> *†	0.0017	Albariño & Balsaeiro (2002)
Stream passing through mixed evergreen and deciduous forest (<i>N. pumilio</i> and <i>N. betuloides</i>)	Chile	54°5'S	<i>Nothofagus betuloides</i>	0.0018	Present study
Beaver pond in a mixed evergreen and deciduous forest (<i>N. pumilio</i> and <i>N. betuloides</i>)	Chile	54°5'S	<i>Nothofagus betuloides</i>	0.0040	Present study
Stream passing through mixed evergreen and deciduous forest (<i>N. pumilio</i> & <i>N. betuloides</i>)	Chile	54°5'S	<i>Nothofagus pumilio</i>	0.0028	Present study
Beaver pond in a mixed evergreen and deciduous forest (<i>N. pumilio</i> and <i>N. betuloides</i>)	Chile	54°5'S	<i>Nothofagus pumilio</i>	0.0118	Present study

Appendix 1. All taxa found during the study and identified to lowest possible taxonomic unit and classified by functional feeding group (FFG). FFG abbreviations: CG: Collector-Gatherers, P: Predators, SCR: Scrapers/Grazers, FC: Filtering-Collectors, SHR: Shredders. X represents a taxon's presence within a habitat type, where NL: Natural-Lenga, NC: Natural-Coigüe, BL: Beaver Pond-Lenga, BC: Beaver Pond-Coigüe.

Appendix 1. Todos los taxa encontrados durante el estudio fueron identificados al nivel más bajo posible y clasificados por grupos funcionales de alimentación (FFG). Abreviaturas FFG: CG: colectores-recolectores, P: Depredadores, SCR: Raspadores / Grazers, FC: Filtrado de Coleccionistas, SHR: desbrozadoras. X representa la presencia de un taxón dentro de un tipo de hábitat, donde NL: Natural-Lenga, NC: Carolina del Norte: Natural-Coigüe, BL: Beaver Pond-Lenga, BC: Beaver Pond-Coigüe.

Class/Order	Family	Sub-Family	Genus	Species	FFG	NL	NC	BL	BC
Annelids									
Clitellata (Oligochaeta)	Tubificidae	Naidinae			CG	X	X	X	X
Hirudinea					P	X	X	X	-
Arachnids									
Trombidiformes (Hydracarina)									
Crustaceans									
Amphipoda	Hyalellidae		<i>Hyalella</i>	spp.	CG	X	X	X	X
Insects									
Coleoptera	Elmidae		<i>Luchoelmis</i>	sp.	SCR	X	X	X	-
Diptera	Chironomidae	Chironomini			CG	X	X	X	X
Diptera	Chironomidae	Orthocladinae			CG	X	X	X	X
Diptera	Chironomidae	Tanypodinae			P	X	X	X	X
Diptera	Ceratopogonidae				P	X	X	X	X
Diptera	Empididae		<i>Hemerodroma</i>	sp.	P	-	X	X	-
Diptera	Simuliidae		<i>Gigantodax</i>	spp.	FC	-	-	X	X
Ephemeroptera	Baetidae		<i>Andestiops</i>	<i>torrens</i> Lugo-Ortiz & McCafferty	SCR	X	X	-	X
Ephemeroptera	Leptophlebiidae		<i>Meridalaris</i>	<i>chiloensis</i> Demoulin	SCR	X	X	X	X
Hemiptera	Corixidae		<i>Corixa</i>	sp.	P	X	-	X	-
Plecoptera	Gripopterygidae		<i>Antarctoperla</i>	<i>michaelseni</i> Klapalek	SCR	X	X	X	X
Plecoptera	Gripopterygidae		<i>Chilenoperla</i>	sp.	SCR	-	X	X	-
Plecoptera	Gripopterygidae		<i>Notoperla</i>	<i>fuergiana</i> Enderlein	SCR	-	-	-	X
Trichoptera	Hydrobiosidae		<i>Rheochorema</i>	<i>magellanicum</i> Flint	P	X	X	X	-
Trichoptera	Limnephilidae	Dicosmoecinae	<i>Monocosmoecus</i>	<i>hyadesi</i> Mabilie	SHR	X	X	X	-
Trichoptera	Glossosomatidae		<i>Matigoptila</i>	<i>brevicornuta</i> Schmid	SCR	-	-	X	-
Odonata	Aeshnidae		<i>Aeshna</i>	<i>variegata</i> Fabricius	SCR	X	X	-	-

latitudinal patterns of the shredder guild has focused on the scarcity of this group in tropical ecosystems (Boyero *et al.*, 2011). Our work and other reports from New Zealand (Winterbourn & Ryan, 1994) would suggest that shredders are also scarce at high latitudes at least in some biomes. However, similar to the tropics, there are other organisms, not normally classified as shredders, may actually fill the functional role of shredders. In particular, it is important to notice the high density and biomass of a taxon that could be key for processing leaf material in this system, the crustacean *Hyalella* spp. This amphipod has been categorized as a collector-gatherer (Miserendino & Pizzolon, 2003; Anderson & Rosemond, 2007), but the fact that the highest decay rate of leaves occurred in the sites with the highest biomass of this organism would indicate that it may be an important consumer of leaves in this ecosystem. Furthermore, preliminary gut analyses conducted in an associated study in 2005, also found leaf fragments as a principal part of *H. simplex* diet (Anderson & Rosemond, 2010). Therefore, further work is needed to link species with the ecosystem level process described here, but our study allows us to determine how the assemblage is influenced by leaf pack decomposition and vice-versa.

Implications for understanding sub-Antarctic stream ecology

In addition to the findings regarding introduced beaver impacts on sub-Antarctic streams, these results provide new insights into the structure and function of lotic ecosystems in South America's highest latitude biome. For example, most components of BOM were stable throughout the year, without marked seasonality. The major exception was the doubling of *N. pumilio* leaves in autumn. This overall stability in the BOM inputs and standing stocks of these streams (particularly coigüe leaves and FBOM), is important to compare with other studies, which until now was impossible. In the most extensive review of organic matter dynamics to date (Abelho, 2001), there is a stark lack of studies from southern South America. Various other works, summarized in Table 3, have helped to fill this latitudinal gap in the Southern Hemisphere, and we hope that the present work furthers our basic and applied understanding of these streams to better value one of the world's frontiers in stream ecology.

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