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Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile

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Abstract Species invasions are of global significance, but predicting their impacts can be difficult. Introduced ecosystem engineers, however, provide an opportunity to test the underlying mechanisms that may be common to all invasive engineers and link relationships between changes in diversity and ecosystem function, thereby providing explanatory power for observed ecological patterns. Here we test specific predictions for an invasive ecosystem engineer by quantifying the impacts of habitat and resource modifications caused by North American beavers (*Castor canadensis*) on aquatic macroinvertebrate community structure and stream ecosystem function in the Cape Horn Biosphere Reserve, Chile. We compared responses to beavers in three habitat types: (1) forested (unimpacted) stream reaches, (2) beaver ponds, and (3) sites immediately downstream of beaver dams in four streams. We found that beaver engineering in ponds created taxonomically simplified, but more productive, benthic macroinvertebrate assemblages. Specifically, macroinvertebrate richness, diversity and number of functional feeding groups were reduced by half, while abundance, biomass and secondary production increased three- to fivefold in beaver ponds compared to forested sites. Reaches downstream of beaver ponds were very similar to natural forested sections. Beaver invasion effects on both community and ecosystem parameters occurred predominantly via increased retention of fine particulate organic matter, which was associated with reduced macroinvertebrate richness and diversity (via homogenization of benthic microhabitat) and increased macroinvertebrate biomass and production (via greater food availability). Beaver modifications to macroinvertebrate community structure were largely confined to ponds, but increased benthic production in beaver-modified habitats adds to energy retention and flow for the entire stream ecosystem. Furthermore, the effects of beavers on taxa richness (negative) and measures of macroinvertebrate biomass (positive) were inversely related. Thus, while a generally positive relationship between diversity and ecosystem function has been found in a variety of systems, this work shows how they can be decoupled by responding to alterative mechanisms.

Keywords Ecosystem engineer · Exotic · Invasion · Secondary production · Subantarctic

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Introduction

Invasive exotic species and their associated impacts constitute a principal part of global environmental change (Vitousek et al. 1996). Species invasions can alter communities and ecosystems via a number of pathways such as changing resource availability, energy flow dynamics and disturbance regime (Vitousek 1990). Moreover, it has been

recognized that an additional process by which invasive species may impact an entire ecosystem is via ecosystem engineering, i.e., creating, destroying or modifying habitat (Jones et al. 1994; Crooks 2002). However, while invasion is a widely documented phenomenon, the ability to predict its consequences is often difficult (Sax et al. 2005). In this context, the framework provided by the ecosystem engineer concept (Jones et al. 1994) may also allow the development of greater predictive power regarding the impacts of invasive species by identifying key mechanisms that are generally applicable and explain observed ecological patterns.

The Cape Horn Biosphere Reserve (CHBR) in southern Chile is an area replete with exotic species (Anderson et al. 2006a), even though it is otherwise considered one of the world's most pristine wilderness areas, due to its low human population density and its largely intact native vegetation cover (Mittermeier et al. 2002; Rozzi et al. 2006). The introduced fauna include approximately half of terrestrial mammals (12 of 22 species) and freshwater fish (two of five species) (Anderson et al. 2006a; Moorman 2007), as well as two non-native birds and an introduced earthworm (Anderson and Hendrix 2002; Anderson et al. 2006a). Among these exotics, the North American beaver (*Castor canadensis* Kuhl), introduced in 1946, stands out for being an ecosystem engineer that has invaded most of the archipelago at relatively high densities (Lizarralde 1993; Skewes et al. 2006; Anderson et al. 2006a; Wallem et al. 2007).

An invasive ecosystem engineer (IEE), such as the beaver, can be a particularly strong modifier of the environment. The effects of IEEs on taxa richness are predicted to be a function of their influence on physical resources, such that richness is expected to increase or decrease as habitat heterogeneity is enhanced or reduced, respectively (Crooks 2002). In this respect, ecosystem engineers may be crucial for maintaining biodiversity in some landscapes (Badano and Cavieres 2006). Alternatively, richness may be expected to be a function of an engineer's effect on the productivity of a system, whereby richness increases to a peak after which greater production results in a decrease in the number of taxa (Wright and Jones 2004). Previous research in the beaver's native range indicates that their engineering enhances landscape diversity of terrestrial and aquatic assemblages via the creation of a patchy mosaic of habitats (Naiman et al. 1988; Pringle et al. 1988; Wright et al. 2002). The role of an ecosystem engineer in a particular place, however, is a question of scale and context, depending upon the surrounding natural landscape and regional species pool in which the engineering activity is embedded (Crooks 2002; Rosell et al. 2005). In an area such as southern South America where wetlands occur naturally, we would therefore expect beaver-created habitats to potentially have less influence on landscape heterogeneity, compared to their effects where wetlands are absent or less abundant.

In addition to altering community structure, invasive species also modify food web dynamics by affecting resource availability (e.g., Vitousek et al. 1987), or they may dominate energy flow due to their sheer numbers and biomass (e.g., Strayer et al. 1999). By influencing resource quality, availability and productivity, ecosystem engineers too can have trophic effects that are unrelated to their actual membership in the food web (Jones et al. 1994; Wright and Jones 2004). The engineering activities of beavers in their native range make stream ecosystems more retentive of organic material (Naiman et al. 1986) and nitrogen (Naiman and Melillo 1984), which also leads to increased biomass of stream macroinvertebrates (McDowell and Naiman 1986). Similar effects should be expected of beavers as invasive exotics, as they increase retention in streams and thus enhance food resources to consumers.

To determine the role of beavers as invasive exotic ecosystem engineers, we assessed their modification of stream habitat (physical, chemical and geomorphological) and basal resources (quantity and quality). We then quantified how the beaver's ecosystem engineering altered benthic macroinvertebrate community structure (richness, diversity, similarity, density and assemblage) and ecosystem function (macroinvertebrate biomass and secondary production). We tested our hypotheses regarding beaver impacts by comparing these parameters among three habitat types: (1) natural, forested stream sections that were not modified by beavers; (2) beaver ponds; and (3) reaches downstream of ponds. The 60-year history of North American beaver presence in southern South America gave us an excellent opportunity to test predictions concerning the effects of IEEs on recipient ecosystems. Our data also allowed us to make comparisons between the structure and function of stream ecosystems worldwide with those from the CHBR for which very little previous information is known (Rozzi et al. 2006).

Materials and methods

Site description

This study was conducted on Navarino Island (55°S) in the CHBR, which hosts the world's southernmost forested ecosystem (Appendix 1). Short, cool summers (mean 9°C) and long, cold winters (mean 2°C) characterize the study site, which receives about 500–650 mm of precipitation annually (Tuhkanen et al. 1989). Four streams (Robalo, Estrella, Mejillones and Faraones) were studied on the island's north coast at elevations below 100 m in mixed forest–bog watersheds. Catchments are relatively short (<15 km). Study reaches were established on the main channels with widths ranging from approximately 4.5 to 8 m (mean 6.6 ± 0.9 m),

and beaver damming increased channel width (mean 29.6 ± 10.2 m).

Each stream had three sampling locations that represented: (1) a natural, forested reach not impacted by beavers (forested); (2) an active beaver pond (pond); and (3) a site immediately downstream of the beaver dam, whose riparian zone was foraged by beavers, but with a flowing stream current (downstream). The beaver-impacted sites were previously forested before beaver colonization, as evidenced by the geomorphology of the site and the presence of standing dead tree trunks, and forested sites were located approximately 1 km from beaver ponds (downstream in the case of Robalo and Faraones and upstream for Estrella and Mejillones).

Most samples were collected monthly, bimonthly or during three seasons [spring (October), summer (January) and fall (May)] from January to December 2003. For several variables [temperature, specific conductivity, dissolved oxygen (DO), wood and seston biomass and carbon:nitrogen ratio for coarse benthic organic matter (CBOM), very fine benthic organic matter (VFBOM) and seston] data were lacking from Estrella Stream and therefore reflect a smaller sample size.

Habitat characterization

Physical

Riparian forest canopy cover was estimated seasonally at 10-m intervals along each study reach with a spherical densiometer. Mean daily stream temperature was recorded with Hobo dataloggers, taking measurements every 15 min in three streams (Robalo, Mejillones and Faraones). Degree days were calculated as the sum of daily averages over 0°C for 1 year for only the Robalo River, due to lost data at the other sites since they could not be accessed in July (winter) due to deep snow.

Chemical

Stream water samples were collected bimonthly at each site using a syringe-mounted membrane filter (Millipore 0.45-μm pore size). Samples were frozen and transported to the Analytical Chemistry Lab at the Institute of Ecology, University of Georgia (UGA), Athens, Georgia. Nitrate and soluble reactive phosphorus (SRP) were measured using an Alpkem RFA 300. Dissolved organic carbon (DOC) concentrations were measured with a Shimadzu TOC-5000A. We used an YSI 85D meter to measure DO and specific conductance (SC), and a Beckman 250 probe was used to determine pH once at each site.

Substrate

Substrate characteristics were determined at each site using Wolman pebble counts to quantify particle size distribution (Harrelson et al. 1994). These values were then used to calculate substrate diversity by applying a Shannon–Weiner diversity index to the abundance of particular size classes of substrate found during the pebble counts.

Basal resources

Quantity

The standing crops of basal resources were measured seasonally. CBOM, fine benthic organic matter (FBOM) and VFBOM were collected using a core sampler (0.07 m^2). The number of sub-samples was determined by the size of the stream with three stream-width transects and one sample per meter in forested and downstream sites (usually nine to 12) and ten replicates in ponds. Contents of the sampler were removed to a depth of 10 cm and passed through two sieves: 1 mm and 250 μm. The total >1-mm portion was collected and constituted the CBOM; FBOM was the fraction of the sample collected by the 250-μm sieve. VFBOM was collected in a bucket under the sieve, a sub-sample of which was passed through pre-ashed filter (0.7 μm, Whatman GF/F). Biofilm was collected seasonally using a stiff brush and core sampler on three to five rocks (sub-samples) in downstream and forested sites; rocky substrates were not available in ponds. The slurry was removed and pipetted through a pre-ashed filter. Seston (suspended organic material >0.7 μm) was collected in spring 2005 on a pre-ashed filter. Estimates of wood biomass were also made at each site in spring 2005 using the method of Wallace and Benke (1984) to determine wood volume, which was then converted to biomass with specific weight values for *Nothofagus* spp. (CONAF 1988). All samples were frozen until they could be transported to the laboratory at the University of Magallanes (UMAG), Punta Arenas, Chile, where they were dried at 60°C, weighed, ashed at 500°C and reweighed to determine g ash-free dry mass (AFDM) m^{-2}.

Quality

Samples of all resources were also collected at each collection period for carbon:nitrogen ratio analysis. All were dried at UMAG and transported to UGA, where they were homogenized with a CertiPred 8000-D ball mill, weighed on a Sartorius M2P micro-balance and analyzed for carbon:nitrogen ratio with a Costech elemental analyzer. We determined total nitrogen content of resources by multiplying resource quantity by its carbon:nitrogen ratio for each basal resource type.

Community analysis

Beaver impacts on macroinvertebrate communities are typically driven by the trophic guilds, or functional feeding

groups (FFG), of macroinvertebrates that can benefit from changes in food resources, particularly collector–gatherers and predators (McDowell and Naiman 1986). We sampled benthic macroinvertebrates seasonally with three sub-samples taken at each study reach with a core sampler. The contents were passed through a 250-μm sieve, and collections were transported in jars of ethanol to the laboratory, where invertebrates were separated from detritus under a dissecting microscope (63×) and stored in 70% ethanol. Taxa were identified to the lowest possible level, and FFGs, i.e., collector–gatherer (gatherer), collector–filterer (filterer), scraper, shredder and predator, were determined using Merritt and Cummins (1996), Miserendino and Pizzollo (2000), Fernández and Domínguez (2001) and by other experts for particular taxa (see Acknowledgements). Mean richness, Shannon–Weiner diversity, Bray–Curtis community similarity (using presence–absence and biomass) and abundance were calculated using EstimateS (Colwell 1997).

Ecosystem function

During identification of macroinvertebrates, the lengths of specimens were measured to the nearest millimeter under a dissecting scope, and biomass was determined for each taxon using length–mass regressions developed by Benke et al. (1999) and Miserendino (2001). Mean annual biomass, expressed as mg AFDM m^{-2}, was calculated for each taxon and functional feeding group in each habitat type in the four streams on a seasonal basis.

Benthic macroinvertebrate secondary production was calculated for the Robalo and Mejillones streams, which were chosen because they reflected two distinct stream types: clear water and tannin-enriched water, respectively. Samples for secondary production were taken as above, although in this case four, rather than three, sub-samples were collected at each stream/habitat type on a monthly basis from January to December 2003; no collections were made in August due to deep snow. Macroinvertebrates were collected, identified, and measured for biomass as described above. We then used the size-frequency method (Hamilton 1969) with the cohort production interval (CPI) correction factor (Benke 1979) to calculate secondary production, expressed as mg AFDM m^{-2} $year^{-1}$. Size distributions, graphed using each sample date, showed that cohorts were asynchronous, and we used CPIs derived for similar taxa from analogous streams in New Zealand (Huryn 1996, 1998). For a few taxa, we used an estimated CPI based on reported values or general life history information [Amphipoda (Pickard and Benke 1996); Bivalvia (Winterbourn 1973); Copepoda, Gastropoda and Ostracoda (Thorp and Covich 1991); Simuliidae (M. Mercado, Laboratorio Benthos, Chile, personal communication)].

Analyses

Macroinvertebrate data (abundance, richness, diversity and biomass) and basal resource standing crops were log-transformed to achieve normality. They and other physical, chemical and geomorphological variables were converted to mean annual values based on seasonal samples and compared between habitat types with a randomized complete block design (stream = block; habitat = main factor). Significant main effects were followed by Tukey HSD tests of significance. Since biofilm was only measured in forested and downstream sites, comparisons were made with a *t*-test. pH was expressed as the median value for each habitat. Secondary production of macroinvertebrates was compared qualitatively among habitat types and with other published values for the two streams for which it was determined.

To examine predicted physical versus resource pathways by which beavers altered community and ecosystem-level properties, we conducted regression analyses to test our hypotheses regarding the relative importance of habitat diversity and resource quantity and quality on macroinvertebrate community structure and function. Dependent variables were mean annual values per stream per habitat for: (1) benthic macroinvertebrate richness (no. of taxa m^{-2}), as our indicator of community-level change; and (2) macroinvertebrate biomass (mg AFDM m^{-2}), as the indicator of ecosystem-level change. We used biomass as a surrogate for secondary production since it was available from all sites, and the two variables were significantly related ($r^2 = 0.85$, $P = 0.01$, $n = 6$). We tested whether: (1) substrate heterogeneity (H'), or (2) macroinvertebrate biomass (mg AFDM m^{-2}) were useful in explaining variation in taxa richness among habitat types, based on a priori predictions that richness would be related to habitat diversity (Crooks 2002) or potentially to overall productivity (Wright and Jones 2004). To test which factors were important drivers of ecosystem function, we examined relationships between macroinvertebrate biomass (as a dependent variable) and resource quantity (g AFDM m^{-2}) and nutrient content [g nitrogen m^{-2}] of basal resources (as independent variables). These tests were based on hypotheses that macroinvertebrate biomass should be related to carbon and/or nutrient standing crop (Wallace et al. 1997; Cross et al. 2006). We also analyzed these relationships differentiating between size fractions of organic matter to determine which component was most important in driving impacts on benthic production. All statistical analyses were performed with JMP 5.0.1 (SAS Institute, Cary, N.C.).

Results

Habitat characterization

Forested study reaches were heavily shaded, and beavers significantly reduced canopy cover at both pond and downstream sites (Table 1). Temperature, however, did not differ significantly among habitat types, but daily temperate range and degree days did show an increasing trend from forested to downstream to beaver pond sites (Table 1).

Water chemistry did not differ among habitat types (Table 1). Nitrate concentrations were uniformly low and unaffected by beaver modifications; SRP was undetectable; DOC was similar between habitats in the same stream; and median pH was circumneutral in all habitat types (Table 1). SC values were also low, while DO was supersaturated (Table 1).

Substrate differed in beaver ponds compared to the other two habitats (Table 1). Pond sites contained almost exclusively organic material, lacking natural rocky substrate, while the downstream site retained the same particle size profile as forested reaches. Consequently, pond sites had a significantly lower substrate diversity index than both forested and downstream reaches (Table 1).

Basal resources

In ponds, beavers increased the standing crop of wood six-fold, CBOM 43-fold, FBOM 44-fold and VFBOM 22-fold compared to forested reaches, but organic matter standing crops at sites immediately downstream of beaver ponds were similar to forested reaches (Table 2). The quantity of seston and biofilm did not vary among habitat types (Table 2).

The quality of benthic organic matter did not differ among habitat types. However, the greatest differences in carbon:nitrogen ratio were for FBOM and VFBOM, which showed a trend toward lower quality (i.e., higher carbon:nitrogen ratio) in ponds, compared to downstream and forested sites (Table 2).

Community parameters

We identified a total of 35 benthic macroinvertebrate taxa representing all functional feeding groups (Appendix 2). Forested sites had the greatest total richness (33) with ponds being the lowest (28) and downstream reaches intermediate between the other two (31). The assemblage included a total of 15 orders from five classes (Annelida, Arthropoda, Crustacea, Insecta and Mollusca). Most taxa were insects (74%), and Diptera was the most diverse

Table 1 Shown are mean annual values (±SE) for physical, chemical and geological habitat variables at forested reaches, beaver ponds and downstream sites. Values within each row with *different letters* were significantly different with a Tukey HSD post-hoc test ($P < 0.05$) for significant main effects. *SRP* soluble reactive phosphorous, *DOC* dissolved organic carbon, *SC* specific conductivity, *DO* dissolved oxygen

Habitat characteristic	Forested	Beaver pond	Downstream	F[a]	df[a]	P[a]
Canopy cover (%)	69.4 (5.1) A	21.5 (5.7) B	30.2 (7.8) B	21.6	2,6	0.002
Mean daily temperature (°C)	4.5 (0.1)	4.8 (0.4)	4.8 (0.2)	0.93	2,4	0.47
Annual temp. range (°C)	−0.6 to 16	−2 to 20	−0.6 to 18	–	–	–
Annual degree days (>0°C)	1,781	1,853	1,830	–	–	–
Nitrate-nitrogen (p.p.m.)	0.05 (0.01)	0.04 (0.01)	0.05 (0.01)	0.0004	2,6	0.57
SRP (p.p.m.)	Undetectable	Undetectable	Undetectable	–	–	–
DOC (p.p.m.)	13.5 (5.3)	12.2 (5.4)	13.1 (5.5)	0.21	2,6	0.81
SC (μS cm^{-1})	118.2 (25.9)	103.5 (15.8)	77.2 (14.9)	1.32	2,4	0.4
DO (mg l^{-1})	9.6 (0.6)	8.3 (1.5)	10.8 (0.3)	3.48	2,4	0.13
pH	7.5	7.1	7.6	–	–	–
Substrate particle diversity (H')	0.81 (0.08) A	0.14 (0.14) B	0.85 (0.05) A	39.1	2,6	0.0004
Substrate particle type (%)						
Organic	0.5 (0.3) A	88.8 (13) B	5.3 (3.3) A	50.22	2,6	0.0002
Sand	11.0 (5.4)	8.0 (9.2)	11.3 (6.6)	0.18	2,6	0.84
Gravel	37.0 (8.1) A	2.8 (3.2) B	46.8 (6.0) A	40.32	2,6	0.0003
Cobble	45.3 (17.2) A	0.5 (0.6) B	22.0 (6.8)AB	7.61	2,6	0.02
Boulder	0.3 (0.3)	0.0 (0.0)	0.8 (0.9)	1.00	2,6	0.42
Bedrock	6.0 (4.1)	0.0 (0.0)	14.0 (6.7)	2.24	2,6	0.19

[a] F-values and df are from main effects analyzed with a randomized complete block design for all variables except temperature range, annual degree days >0°C and median pH

Table 2 Mean annual basal resource standing crops [g ash-free dry mass (*AFDM*) m^{-2}] and mean annual basal resource quality (carbon:nitrogen ratio) at forested reaches, beaver ponds and downstream sites (±SE)[a]. *CBOM* Coarse benthic organic matter, *FBOM* fine benthic organic matter, *VFBOM* very fine benthic organic matter

Quantity	Forested	Beaver pond	Downstream	*F*	*df*	*P*
Mean annual basal resource standing crops (g AFDM m^{-2})						
Wood	558.4 (37.7) A	3,561.7 (232.8) B	662.9 (245.2) A	23.8	2,4	0.006
CBOM	10.6 (3)	438.2 (134.4)	15.4 (6.7)	5.35	2,6	0.05
FBOM	18.0 (1.3) A	786.8 (63.4) B	66.0 (7.5) A	127.7	2,6	<0.0001
VFBOM	26.0 (6.1) A	574.0 (139) B	34.6 (6) A	309.2	2,6	<0.0001
Biofilm	5.6 (2)	–	7.4 (1.8)	2.3	3	0.1[b]
Seston	0.002 (0.0004)	0.003 (0.001)	0.003 (0.001)	0.2451	2,4	0.79
Mean annual basal resource quality (carbon:nitrogen ratio)						
CBOM	40.8 (3.7)	41.2 (4.4)	39.8 (6.4)	0.02	2,6	0.98
FBOM	21.7 (1.4)	26.7 (1.7)	20.5 (0.7)	5.22	2,6	0.05
VFBOM	14.5 (1.2)	18.7 (1.5)	14.2 (0.9)	4.21	2,6	0.06
Biofilm	9.5 (0.4)	–	9.8 (0.2)	0.88	5	0.42[b]
Seston	12.8 (1.6)	9.4 (0.8)	11.7 (0.4)	2.15	2,4	0.23

[a] ANOVA results are as in Table 1

[b] Indicates *t*-test for data only collected in two habitat types

order (13 morpho-species). Ten species and 14 genera could be determined. The 11 remaining taxa were identified to family or order. Beaver-impacted areas had two taxa that were not found in natural forested sites: the Hemiptera *Corixa* sp. and the bivalve *Pisidium magellanicum* Dall.

Beaver ponds had significantly lower richness and diversity, compared to forested and downstream sites (Table 3). Community similarity indices showed a significant difference between ponds and forested sites, while the downstream reach was intermediate between the two (Down–Down = 0.46 A, Forest–Down = 0.43 A, Pond–Pond = 0.43 A, Forest–Forest = 0.42 A, Down–Pond = 0.35 AB, Forest–Pond = 0.22 B; $F_{5,65} = 6.26$, $P < 0.001$; values separated by *different letters* were significantly different with a post-hoc Tukey HSD test, $P < 0.05$). Macroinvertebrate abundance was 2–5 times higher in downstream and pond sites than forested reaches, but this trend was not statistically significant (Table 3).

Biomass and secondary production

Total benthic macroinvertebrate biomass was significantly higher in beaver ponds (5 times higher) compared to forested sites, and downstream sections were again intermediate between the two, but not significantly different than forested reaches (approximately twice as high) (Table 3). Gatherers were the dominant functional feeding group by biomass in all three-habitat types (Table 4). In ponds, biomass of predators and gatherers was 8–20 times higher, and the biomass of scrapers, shredders and filterers was significantly lower, 5–10 times, in ponds compared to the other two habitats (Table 4). While downstream sites exhibited an increase in total biomass (Table 3), as well as the biomass of every FFG in the order of 1.5 times, compared to forested sites, these increases were not significant (Table 4). The relative contribution of scrapers, shredders and filterers was also significantly decreased in ponds, while the proportion of

Table 3 Benthic macroinvertebrate community variables for forested, beaver pond and downstream sites[a]. Annual means (±SE) are based on seasonal samples for each habitat (forested reaches, beaver ponds and downstream sites) from four streams. *H′* Shannon–Weiner diversity index

Category	Forested	Beaver pond	Downstream	*F*	*df*	*P*
Richness (no. taxa m^{-2})	15.3 (1.7) A	10.0 (0.9) B	15.8 (1.2) A	5.7	2,6	0.04
Diversity (*H′*)	2.0 (0.1) A	1.4 (0.1) C	1.9 (0.1) B	1540.4	2,6	<.0001
Abundance (individuals m^{-2})	2,611.5 (504.9)	14,350 (10,381)	5,086.2 (1,029.8)	0.99	2,6	0.42
Biomass (mg AFDM m^{-2})	257.9 (89.4) A	864.1 (179.8) B	443.3 (68.2) AB	7.2	2,6	0.03

[a] ANOVA results are as in Table 1

Table 4 Mean annual biomass (mg AFDM m^{-2}) and relative annual biomass (%) for each functional feeding group (±SE) based on seasonal samples in three habitat types (forested reaches, beaver ponds and downstream sites) from four streams[a]

	Forested	Beaver pond	Downstream	*F*	*df*	*P*
Mean annual biomass						
Gatherer	149.8 (71.9)	708.0 (180.0)	258.0 (70.2)	3.81	2,6	0.09
Scraper	35.7 (12.1) A	3.0 (3.0) B	45.8 (23) A	18.1	2,6	0.003
Shredder	15.0 (4.0) A	2.8 (1.7) B	37.5 (20.8) A	5.62	2,6	0.04
Filterer	52.2 (16.8)	5.3 (4.1)	84.8 (40.8)	2.99	2,6	0.13
Predator	5.2 (1.3) A	144.3 (43.4) B	17.2 (7.5) A	11.77	2,6	0.008
Relative annual biomass						
Gatherer	53.9 (11.3)	75.8 (6.0)	56.7 (5.2)	1.66	2,6	0.27
Scraper	17.8 (5.2) A	0.4 (0.4) B	12.2 (5.4) A	7.5	2,6	0.02
Shredder	8.2 (0.01) A	0.27 (0.00) B	7.3 (2.9) A	7.05	2,6	0.03
Filterer	22.4 (7.9)	0.7 (0.5)	20.2 (9.7)	2	2,6	0.22
Predator	2.2 (0.1) A	22.8 (7.0) B	3.7 (1.8) A	8.8	2,6	0.02

[a] ANOVA results are as in Table 1

predators significantly increased, compared to forested and downstream sites (Table 4).

In both Robalo and Mejillones, secondary production was highest in ponds and lowest in forested sites (Fig. 1, Appendices 3a, b). The production values for forested sites were similar in both streams. Secondary production at the Mejillones beaver pond was higher than at Robalo, and for the Robalo downstream site was higher than at Mejillones (Fig. 1).

In all habitat types, the gatherer *Hyalella simplex* Schellenberg (Amphipoda: Hyalellidae) and non-Tanypodinae chironomids (Diptera: Chironomidae) were the dominant taxa with regards to secondary production; together they represented >50% of production at all sites. The number of taxa that contributed >1% to total secondary production was reduced in ponds relative to the other habitats. Overall, the assemblage found in beaver ponds was a subset of the total diversity found in forested and downstream sites, rather than a unique assemblage (Appendix 2).

In downstream and forested sites, we found from seven to nine morpho-species at each site were important (i.e., >1%) contributors to production (Fig. 1, Appendices 3a, b). In contrast, beaver ponds had only four taxa (*H. simplex*, Oligochaeta, Tanypodinae and non-Tanypodinae chironomids) that contributed similarly.

Beaver-mediated alterations to resources and community and ecosystem properties

There was a positive relationship between macroinvertebrate taxa richness and substrate diversity (Fig. 2a). Greater

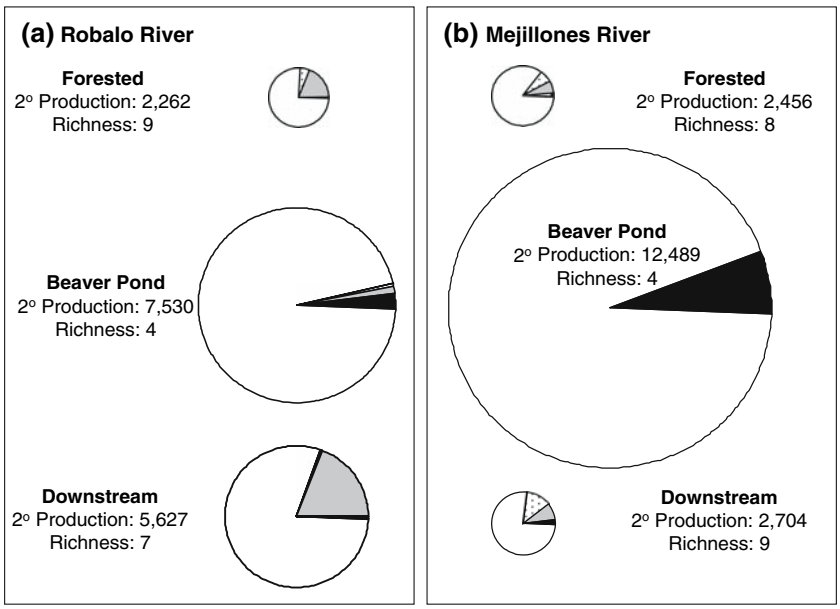

Fig. 1 Annual secondary production [mg ash-free dry mass (AFDM) m^{-2} $year^{-1}$] of stream benthic macroinvertebrates for the period January–December 2003 and proportional representation of functional feeding groups for three habitats (forested, beaver pond and downstream) in the (**a**) Robalo and (**b**) Mejillones watersheds in the Cape Horn Biosphere Reserve, Chile. Richness is the number of taxa that constituted >1% of production. Size of pie chart is proportional to its total secondary production, and each is divided into relative contribution from functional feeding groups: gatherer (□), filterer (▨), shredder (▦), scraper (■) and predator (■)

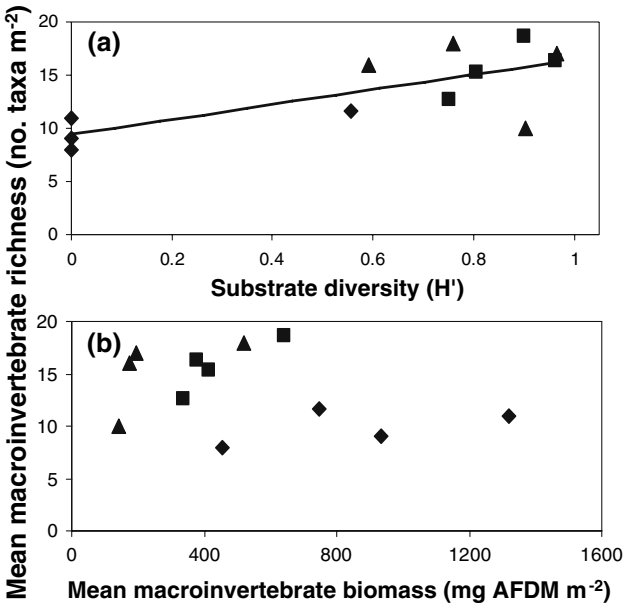

Fig. 2 Mean benthic macroinvertebrate taxa richness was regressed with (**a**) benthic substrate diversity measured with a Shannon–Weiner diversity index (*H'*) and (**b**) mean benthic macroinvertebrate biomass (mg AFDM m^{-2}). Habitat types are indicated as forested (*filled triangle*), beaver pond (*filled diamond*), and downstream (*filled square*). **a** $r^2 = 0.55$, $P = 0.01$; **b** not statistically significant

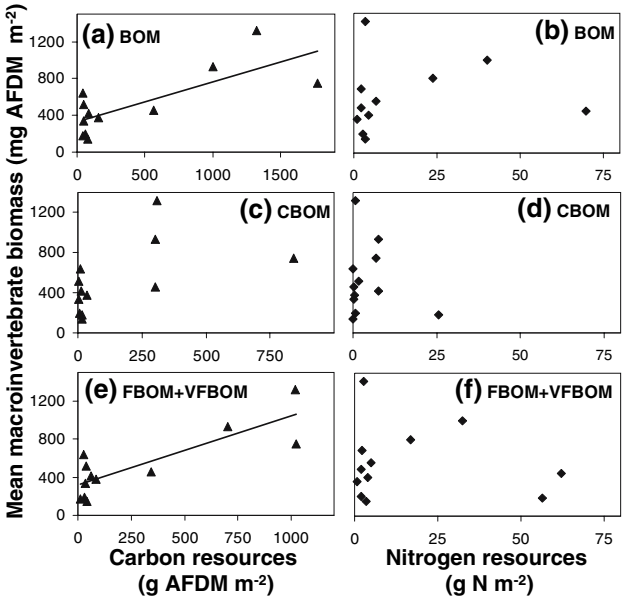

Fig. 3 Mean annual macroinvertebrate biomass (mg AFDM m^{-2}) was regressed against categories of carbon (g AFDM m^{-2}) and nitrogen (g N m^{-2}) resources in total benthic organic matter (*BOM*; **a**, **b**), coarse BOM (*CBOM*; **c**, **d**) and total fine and very fine BOM (*FBOM + VFBOM*; **e**, **f**). Biomass only responded significantly to carbon resource availability (total BOM $r^2 = 0.57$, $P = 0.01$), which was mostly driven by the fine particle fraction (FBOM + VFBOM $r^2 = 0.72$, $P = 0.004$)

macroinvertebrate richness was associated with forested and downstream sites, and the lowest richness was found with lower substrate diversity in beaver ponds. We found no explanatory power comparing macroinvertebrate richness to macroinvertebrate biomass ($R^2 = 0.1$, $P = 0.3$) (Fig. 2b).

Macroinvertebrate biomass, however, was positively related to resource quantity (Fig. 3a, e), but showed no relationship with the quality of organic matter, based on nitrogen content (Fig. 3b, d, f). The effect of benthic organic matter on macroinvertebrate biomass was strongest with fine, rather than coarse, fractions of organic matter (Fig. 3c, e).

Discussion

The effects of invasive beavers on stream benthic community structure

The engineering activities of invasive, exotic beavers in the CHBR reduced both macroinvertebrate richness and diversity in beaver ponds relative to unimpacted sections and reaches downstream of ponds. General ecological theory predicts that taxa richness increases with habitat heterogeneity, an assertion which has been supported by studies for multiple taxa, scales and ecosystems (e.g., Kerr and Packer 1997; Downes et al. 1998; Guegan et al. 1998; Kerr et al. 2001). Crooks (2002) extended this concept to ecosystem engineers, positing that the influence of ecosystem engineering on species richness should be related to whether or not the engineer increases or decreases habitat diversity, which in turn is dependent on the surrounding landscape context. Evidence from our study supports this assertion, as beaver engineering activities in pond habitats reduced taxa richness as a function of reduced benthic substrate heterogeneity (Fig. 2, conceptualized in Fig. 4). By burying the stream-bed under a layer of organic matter, beavers reduced the complexity of benthic habitats in ponds, in contrast to unimpacted or downstream sites, where there were a variety of substrates and microhabitats present.

Landscape impacts of beavers on benthic habitat and taxa richness in the Cape Horn Archipelago may not be as strong, however. In contrast to local effects on substrate microhabitat, beaver modifications moderately enhanced heterogeneity along the forested portion of these streams by introducing a new lentic habitat type (beaver ponds). Aggregating all three habitat patches, beavers increased benthic macroinvertebrate richness in otherwise forested stream reaches, given the presence of two additional species, water boatmen (*Corixa* sp.) and bivalves (*P. magellanicum*), found in beaver-impacted habitat and not in natural, forested sections (Appendix 2). However, if we consider the predominant taxa (>1% of biomass) in each habitat, the beaver ponds' macroinvertebrate community represented merely a subset of those inhabiting unimpacted

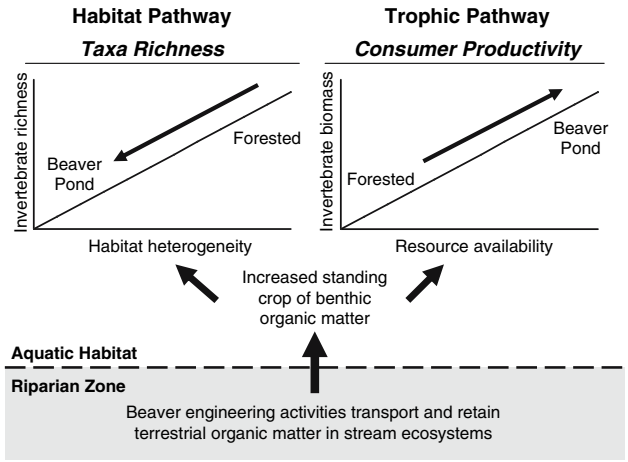

Fig. 4 Underlying mechanisms explaining observed beaver-induced changes to benthic macroinvertebrate richness and production, using proposed pathways for the general effect of invasive ecosystem engineers on community and ecosystem properties (Crooks 2002). *Direction of arrows* indicates trajectories of change from forested to beaver pond habitats. Conditions at sites downstream of beaver ponds were similar to those observed in forested reaches and thus are not shown

sections, while the community at downstream sites was similar to natural conditions. The Cape Horn Archipelago contains a mosaic of forests interspersed among natural lentic habitats such as glacial lakes and peat bogs (Rozzi et al. 2006). In this case, beaver ponds may not be distinct from other lentic habitats found in this forest–bog mosaic, and as would be expected the enhancement of taxa richness we observed along forested reaches was slight. Thus, we believe that beaver modifications to benthic community structure are largely restricted to pond habitats, coinciding with broader scale predictions of weaker ecosystem engineer effects in landscapes in which their impacts are not unique (Wright et al. 2002; Rosell et al. 2005).

In contrast to taxa diversity, however, trophic diversity was enhanced by beaver habitat alterations. In ponds, we observed an increase in both the diversity and biomass of macroinvertebrate predators, while they were virtually absent in forested and downstream sites, indicating that beaver modifications enhanced trophic diversity by adding to secondary consumers. Thus, effects of beavers were propagated through at least three trophic levels: basal carbon, primary consumers and secondary consumers.

The effects of invasive beavers on stream ecosystem function

Our secondary production estimates are the first such values reported for aquatic macroinvertebrates in the temperate forest ecosystems of southern South America. Secondary production at forested sites in our study was lower than 97% of the 58 reported values summarized by Benke (1993) for worldwide streams. However, they fit expectations for other cold, nutrient-poor ecosystems (Huryn and Wallace 2000), and a comparison of subantarctic Chilean streams with other high latitude sites from the Northern and Southern Hemispheres showed similar benthic macroinvertebrate secondary production (Table 5). The effect of beaver introduction resulted in elevating total secondary production values to the median range of estimates for world sites, making these high latitude streams more similar to temperate systems in terms of benthic consumer production.

The contribution to macroinvertebrate production by different functional groupings in our study was analogous to streams in New Zealand, which have a similar biogeographical and evolutionary history to streams in southern Chile. Like New Zealand streams, collector–gatherers were the dominant functional feeding group, and consequently the benthic macroinvertebrate fauna in both the CHBR and the South Island of New Zealand depended largely on the standing crop of fine benthic organic matter (Winterbourn and Ryan 1994), instead of CBOM as in other forested ecosystems (Wallace et al. 1997). The effects of beavers on the biomass and productivity of functional groups varied somewhat between the two study streams. While overall collector–gatherers were dominant at all sites, the clear water stream (Robalo) had greater scraper FFG biomass and production than the tannin-enriched stream (Mejillones). As a result, secondary production at the downstream site at Robalo was nearly twice as great as at the Mejillones site, due to the contribution of scrapers.

To explain the observed functional response of benthic ecosystems to introduced beaver modifications, we found that macroinvertebrate biomass was positively related to total benthic organic matter standing crop, but not to nitrogen availability. Increased retention of organic matter in ponds by beaver activity enhanced this ecosystem function, indicating that even in these very nutrient-poor systems, stream macroinvertebrates appeared to be more limited by carbon than nitrogen availability.

The relationship between biodiversity and ecosystem function

An underlying assumption when examining the relationships between species diversity and ecosystem functioning is that the loss of species from ecosystems will result in a reduction in ecosystem function (Chapin et al. 2000; Naeem and Wright 2003). While this general concept may likely hold in many ecosystems, particularly in regard to taxa such as foundation species (Ellison et al. 2005), our study showed that reductions in species richness were associated with increased ecosystem function (secondary production). Our findings are illustrative of the type of scenario wherein ecosystem function is determined less by

Table 5 Comparison of secondary production values from high latitude sites in the Northern and Southern Hemispheres

Name, location (country)	Latitude (°)	Temperature[a] (°C)	Habitat type	Secondary production (mg AFDM m^{-2} $year^{-1}$)	Comments	Reference
Northern hemisphere						
Esko River (Norway)	60°N	3	Mixed forest	2,344–3,838	Regulated weir sites	Baekken et al. (1984)
				2,068–8,227		Fjellheim et al. (1989)
Laxá River, North-Iceland (Iceland)	65°N	0.3–2.3[b] 9.5–13[c]	Arctic tundra	32,000–352,000	Only quantifies blackflies at lake outflow sheep farming and volcanic activity in vicinity	Gíslason and Gardarsson (1988)
Kuparuk River, Alaska (USA)	68°N	0[b] 8–10[c]	Arctic tundra	6,000–12,000	Control four dominant taxa	Petersen et al. (1993)
				14,000–19,000	Nutrient addition four dominant taxa	
Oksrukuyik Creek, Alaska (USA)	68°N	0[b] 10–13[c]	Arctic tundra	1,500–2,200	Pre-fertilization experiment three dominant taxa	Harvey et al. (1998)
				2,300–4,400	One to 4 years of nutrient addition three dominant taxa	
Southern hemisphere						
Hinau Stream, North Island (New Zealand)	40°S	11	*Nothofagus* forest with limited disturbance	8,400	Forested	Hopkins (1976)
				32,530	Open canopy	
				73,690	Organically enriched	
Horokiwi Stream, North Island (New Zealand)	41°S	13.5	*Nothofagus* forest heavily disturbed by agriculture	24,630	Forested	
				56,450	Open canopy	
				43,550	Open canopy	
Sutton and Stony Creeks, South Island (New Zealand)	45°S	5.6 to 6	Grasslands	8,503–13,352	Exotic pasture and native tussock grassland	Huryn (1998)
Robalo and Mejillones Streams, Cape Horn Biosphere Reserve (Chile)	55°S	4.5	Subantarctic *Nothofagus* forest-bog mosaic	2,263–2,456	Forested	This study
		4.8		7,530–12,589	Beaver pond	
		4.8		2,704–5,627	Downstream of beaver pond	

[a] Yearly means unless noted otherwise

[b] Ranges for winter temperature

[c] Ranges for summer temperature

individual species traits and more by resource availability (in this case, a beaver-mediated ecosystem-level trait).

The opposing trends observed for benthic richness (negative) and production (positive) in relation to organic matter standing crop in ponds appears to derive from the fact that their drivers, while originating from the same source, operated along different pathways (Fig. 4); both trends arose from an increased quantity of organic matter, which then had two types of impacts. Effects on richness apparently occurred due to a physical/habitat modification pathway (reductions in benthic substrate heterogeneity associated with an increased quantity of organic matter), whereas increased biomass and secondary production of macroinvertebrates were indicative of a trophic/resource availability pathway (increased quantity of benthic food resource availability associated with increased organic matter retention). Both mechanisms are consistent with predictions regarding the effects of IEEs, whose habitat modifications can influence novel ecosystems via: (1) nutrient resources, (2) trophic resources, or (3) physical/habitat resources (Crooks 2002). At the same time, these findings are inconsistent with predicted positive relationships between biodiversity and ecosystem function. These results suggested an overriding importance of habitat and trophic resources in affecting species richness and ecosystem function individually, in contrast to species number and composition being the primary drivers of function.

Conclusion

Previous studies in the Austral Archipelago have addressed the influence of beaver invasion on riparian vegetation, showing that beaver impacts on streamside forests create meadow ecosystems with limited *Nothofagus* regeneration and often permit the invasion of exotic herbaceous plants (Anderson et al. 2006b; Martínez Pastur et al. 2006). Here we found that introduced beavers impacted both benthic community and ecosystem properties of the pond habitats they created, but not at sites immediately below beaver ponds. These results largely coincided with predictions outlined for the effects of IEEs in general (Crooks 2002). The landscape effects of beavers on the benthic macroinvertebrate community may be mitigated in the CHBR since natural lentic habitats exist in these watersheds, which has major implications for the maintenance of native aquatic biodiversity in the face of this invasion. Consequently, questions regarding the management of this invasive exotic species should include: (1) to what extent and density are beaver ponds being constructed across the landscape, and (2) to what degree are beavers dominating these watersheds rather than creating a patchy mosaic? We furthermore found that beaver activity enhanced overall energy production and retention in subantarctic stream ecosystems. Therefore, determining the fate of this increased macroinvertebrate production and its potential links with riparian ecosystems will be an important future area of work in quantifying the role of beavers in the subantarctic landscape.

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