

Engineering by an invasive species alters landscape-level ecosystem function, but does not affect biodiversity in freshwater systems

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ABSTRACT

Aim Ecological theory predicts that invasive ecosystem engineers like the American beaver (*Castor canadensis*) in Tierra del Fuego (TDF) affect landscape-level biodiversity and ecosystem function (BEF) when engineered habitats are novel or extensive. We tested these hypotheses on freshwater BEF, sampling benthic habitat and macroinvertebrates in natural lotic (forest and grassland streams) and natural lentic habitats (bogs, lakes) and beaver-modified lentic ecosystems (active and abandoned ponds).

Location Tierra del Fuego Archipelago (Chile and Argentina).

Methods To determine effects on patch-scale BEF, we assessed two drivers: substrate diversity (H') and benthic organic matter standing crop (BOM, g m^{-2}). Extent of impact was estimated as relative stream length (%) for each patch type in four 1000 ha images.

Results The freshwater landscape was 56% free-flowing streams (natural lotic), 13% bogs and lakes (natural lentic) and 31% active and abandoned beaver ponds (beaver lentic). While engineering significantly modified lotic habitats (converting them to ponds), the beaver ponds were largely similar to natural lentic systems, but engineered lentic patches retained more BOM. While benthic biodiversity in beaver ponds was less than streams, the assemblage contained no habitat-specific taxa and was a subset of the natural lentic community.

Main conclusions Invasive beavers engineer habitats whose biodiversity is similar to the landscape's natural lentic habitats, but by increasing the surface area and unit area retention of BOM via its impoundments, this invasion augments carbon standing stock approximately 72% in watersheds. While this invasion is considered the largest alteration to TDF's forested biome in the Holocene, here we discover that its impact is to ecosystem function, rather than biodiversity in the aquatic landscape.

Keywords

Beaver, benthic macroinvertebrate, biodiversity–ecosystem function, *Castor canadensis*, non-native, Patagonia.

INTRODUCTION

Understanding the role of species in ecosystems is an important question with theoretical and applied dimensions that

relate to both ecological science and conservation practice (Jones & Lawton, 1995). We know that nonlinearities exist in these relationships; some species display particular traits or behaviours that result in greater impact than would be

expected from their numbers or biomass alone (e.g. keystone species, Power *et al.*, 1996). Ecosystem engineering is one conceptual proposal to describe and explain specifically how certain species affect ecosystems by changing the physical environment via the creation, modification and destruction of habitat (Jones *et al.*, 1994). In so doing, ecosystem engineers influence patterns and processes of biodiversity and ecosystem function (BEF) (Wright *et al.*, 2002; Wright & Jones, 2004; Anderson & Rosemond, 2007; Badano & Marquet, 2008). Concepts such as ecosystem engineering can help ecological research effectively formulate research questions and develop predictive understandings of ecological outcomes like explaining the direction and magnitude of changes in the structure and function of ecosystems.

In addition to linking species identity with BEF, it is also important to integrate the effects of scale. For example, ecosystem engineers can influence species richness by affecting landscape-scale habitat heterogeneity (Wright *et al.*, 2002) and/or patch-scale habitat productivity (Wright & Jones, 2004). Basic ecological theory then allows us to predict the direction and magnitude of these impacts, based on understanding the relationship between patch- versus landscape-level conditions. If the engineered ecosystem constitutes a unique landscape unit with a habitat-specific biotic community, compared with surrounding patches, the role of the ecosystem engineer would be expected to enhance gamma diversity in the landscape. Similarly, if the extent of the impact were great enough to dominate the entire landscape, then we would also anticipate that the magnitude of the effect to biodiversity would be large in either a positive or negative direction, depending on the relative difference between the engineered and unmodified habitats. Finally, while the impact of an ecosystem engineer on landscape-level

patterns of species diversity depends on the surrounding context of habitat-specific species assemblages and the similarity between communities, the addition of novel habitat conditions in a landscape could be expected to produce cumulative effects on ecosystem function (e.g. increases or decreases in rates and standing crops of materials and energy).

As a recognized component of global ecological change, it is imperative that we develop a better understanding of how invasive species drive BEF patterns and processes, and the lack of such a predictive understanding has been a major critique of the field of invasion biology (Davis *et al.*, 2011). In this context, the ecosystem engineer concept provides an explanatory mechanistic framework regarding the role of invasive species in novel ecosystems (Crooks, 2002; Anderson *et al.*, 2009). Specifically, it offers a way to test the indirect and broader-scale impacts of invasive species on ecosystems and landscapes, rather than focusing on their direct impacts related to predation or competition (Valenzuela *et al.*, 2014).

The North American beaver (*Castor canadensis* Kuhl 1820) is an emblematic invasive ecosystem engineer that has received substantial scientific, conservation and media attention in the Tierra del Fuego (TDF) Archipelago (Choi, 2008; Anderson *et al.*, 2011). Fifty beavers were introduced near Fagnano Lake in 1946 (Fig. 1), and since that time, the population has expanded to inhabit most of the archipelago, and on the mainland, it has colonized as far north as Puerto Natales, Chile (Valenzuela *et al.*, 2014). In southern Patagonia, beavers fill a unique ecological niche; there are no ecologically or evolutionarily equivalent species that forage and physically alter streams in the same way. However, natural lentic habitats, such as lakes and peat bogs, are abundant in this post-glacial landscape. These natural lentic landscape

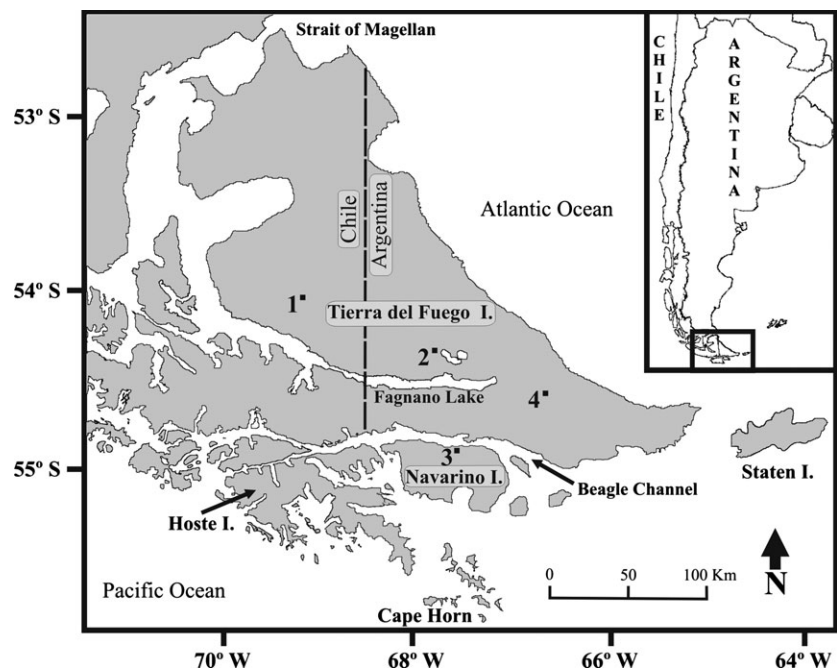


Figure 1 Map of southern South America with a detailed projection of the Tierra del Fuego Archipelago (Argentina & Chile). Study sites are indicated with closed circles and were distributed along a west–east gradient from (1) Karukinka, (2) Kareken, (3) Navarino and (4) Malvinera.

units may or may not be equivalent to beaver ponds, as it is unknown whether the key physical characteristics of natural impoundments are similar to those engineered by the beaver. On the other hand, regardless of whether beaver ponds are quantitatively and qualitatively similar to unmodified impoundments, their damming activities would be expected to increase the retention of materials and alter ecosystem processes in invaded watersheds (Anderson & Rosemond, 2007; Anderson & Rosemond, 2010; Ulloa *et al.*, 2012). Therefore, we predict that the beaver's influence on biodiversity will depend on the landscape's broader context, while the effect on ecosystem function is expected to be cumulative.

To test this hypothesis, we compared the patch- and landscape-level effects of invasive beavers on BEF in freshwater bodies in TDF. We predicted that if the patch-level habitat conditions of beaver-impacted streams were largely the same as natural lentic features, then beavers would not significantly alter stream biodiversity at the landscape scale, despite its large and negative effect at the patch scale compared to unmodified streams (Anderson & Rosemond, 2007). At the same time, this invasion's influence on broader processes, such as carbon retention and standing crop, would be expected to be large and a function of the overall magnitude and extent of the engineered ecosystems in the landscape.

METHODS

Study site

The study was conducted between 2003 and 2006 in both the Argentine and Chilean portions of the TDF Archipelago, which encompasses the islands south of the Strait of Magellan. Since their initial introduction in 1946, beavers have colonized most of the archipelago, and as of the 1990s were also established on the mainland (Anderson *et al.*, 2009). As a result of its relatively recent glaciation and fragmented geography, the archipelago's native vertebrate community is relatively species poor, especially potential predators of beavers (Anderson *et al.*, 2006; Valenzuela *et al.*, 2014). At the same time, this glacial history has left a landscape with

natural lentic features including lakes, ponds and bogs. The archipelago's only large native herbivore is the guanaco (*Lama guanicoe* Muller 1776), but there are no ecological equivalents to the beaver's herbivory or dam-building/flooding behaviours.

Patch and landscape characterization

The Fuegian Archipelago includes a mosaic of habitat patches and a precipitation gradient from the Pacific to the Atlantic Oceans (Moore, 1983). To characterize this landscape, we used four 1000 ha Quickbird[®] satellite images taken from across the archipelago at the following sites from west to east: Karukinka (2005), Kareken (2004), Navarino (2002) and Malvinera (2006) (Table 1; Fig. 1). We classified landscape into three major habitat categories: (1) natural lotic, (2) natural lentic and (3) beaver impacted. Natural lotic patches were habitats with free-flowing streams that passed through forests or grasslands. Natural lentic patches were lakes and peat bog ponds. Beaver-engineered lentic habitats included both active and abandoned ponds with constrained water flow. Sites classified as beaver ponds were previously lotic, as evidenced by the surrounding habitat conditions and/or standing dead trees in the pond or riparian zone. No beaver ponds were chosen in natural lentic habitat (e.g. beaver impoundments in lake outflows, *Sphagnum* bogs).

We collected abiotic and biotic data from a total of 55 aquatic patches between 2003 and 2006 (26 in the west, 18 in the south and 11 in the eastern portion of the study area). In each, we assessed substrate diversity and benthic organic matter (BOM) standing crop, which were previously described by Anderson & Rosemond (2007) as being influential in producing observed patterns of taxonomic richness and ecosystem function for benthos. Substrate characteristics were measured at each site with Wolman pebble counts to quantify particle size distribution (Harrelson *et al.*, 1994), and these values were then used to calculate substrate diversity by applying a Shannon–Weiner index to the abundance of particular pebble count size classes. Benthic macroinvertebrates and BOM were collected with a core sampler

Table 1 Patches (and habitat types) were measured as percent (%) of stream length (km) in four 1000 ha satellite images from sites along a west–east gradient in the Tierra del Fuego Archipelago (Chile & Argentina)

Patch						
Habitat type	Karukinka	Kareken	Navarino	Malvinera	Mean	SE
Natural lotic	51.4	58.7	45.8	69.2	56.3	5.9
Forest	45.9	31.5	45.8	64.3	46.9	7.8
Grassland	5.5	27.2	0.0	5.0	9.4	7.0
Natural lentic	25.3	6.3	10.7	10.5	13.2	4.8
Peat bog	22.5	3.1	8.2	9.8	10.9	4.7
Lake	2.8	3.1	2.4	0.8	2.3	0.6
Beaver lentic	23.3	35.0	43.6	20.2	30.5	6.2
Active pond	13.4	15.0	5.3	4.3	9.5	3.2
Abandoned pond	10.0	20.0	38.3	15.9	21.0	7.1

(0.07 m²) whose contents were passed through a 250-µm sieve. Contents were preserved in 70% ethanol. In the laboratory, macroinvertebrate specimens were separated from BOM and were identified to the lowest taxonomic level, which was usually genus or species (see Appendix S1). For some taxa, such as Chironomidae dipterans, we only arrived to subfamily or tribe level. In addition, the length of each specimen was measured to determine biomass with length–weight regressions developed by Benke *et al.* (1999) and Miserendino (2001). BOM was dried at 60 °C, weighed, ashed at 500 °C and reweighed to calculate g ash-free dry mass (AFDM) m⁻². In each stream, three to four subsamples were taken to determine an average per site, which was then used as the statistical unit of replication.

Analyses

To determine the beaver's effects on patch-level aquatic BEF, we first used JMP 10 (SAS Institute Inc., Cary, NC, USA) to conduct one-way analyses of variance (ANOVAs) with a Tukey's *post hoc* honestly significant difference (HSD) test that compared the means for substrate diversity, BOM, benthic macroinvertebrate taxa richness, benthic macroinvertebrate diversity (Shannon–Weiner) and benthic macroinvertebrate biomass between the three patch types (natural lotic, natural lentic and beaver lentic). To determine the beaver's effects on landscape-level aquatic BEF, we used EstimateS 8.2 (Colwell *et al.*, 2012) to calculate diversity (Shannon–Weiner) and to estimate taxonomic richness (Coleman rarefaction), based on a randomized dataset ($n = 100$) constructed from the percentage contribution of each patch type (natural lotic + natural lentic) and the landscape with beaver impacts (natural lotic + natural lentic + beaver lentic) (Table 1). These results were used to project species accumulation curves using the biodiversity indicators described above (Colwell *et al.*, 2012). Significance between curves was assumed if the 95% confidence interval of the responses did not overlap (Badano & Cavieres, 2006). The natural landscape's patch percentages were determined based on converting the beaver-engineered patches to the habitat type of the adjacent area, which can be determined visually from satellite images.

To compare the similarity and composition of the benthic macroinvertebrate assemblage between the patch types, we employed two detrended correspondence analyses (DCA, Hill & Gauch, 1980) in PC-Ord 5 (McCune & Mefford, 1999). DCA was selected because it is the only ordination technique that simultaneously analyses sampling units and species, thereby allowing the examination of ecological interrelationships, such as species habitat affinities, in a single-step analysis (Ludwig & Reynolds, 1988). In the first DCA, the data matrix included benthic macroinvertebrate species abundance by plot and was processed (1) without down-weighting for rare species and (2) with axis rescaling (Hill, 1979; Greenacre, 1984; Manly, 1994). In the second DCA, which was processed (1) without down-weighting for rare species and (2) without axis rescaling, benthic macroinvertebrate species

abundances were averaged for patch type to highlight differences among species habitat affinities, which were classified by their rarity as the following: singletons (only one specimen collected), rare (2–10 specimens), common (11–100 specimens) and very common (more than 100 specimens). Finally as a complementary methodology, we employed a multiresponse permutation procedure (MRPP, Mielke *et al.*, 1976) to detect differences within and between previously defined groups.

Total BOM standing crop was estimated in the watershed network for each study area, using the calculations of the longitudinal length of each patch type and multiplying this value by the means obtained for patch-specific BOM standing crop (g AFDM m⁻²) for the entire stream network. This estimation is a low representation of the actual amount for the watershed, since using length of the network, we do not account for area. As such, this calculation was based on a 1-m-wide water body, which is an underestimate considering the increase that beavers also create in water body width. From this result, we obtained a total g AFDM value for each study area with and without beavers and calculated the percentage change caused by the presence of beaver-engineered habitats.

RESULTS

Comparison of natural and engineered freshwater habitat patches

Ecosystem engineering by invasive beavers transformed between 20 and 43% of the studied hydrological networks (mean \pm SE = $30.5 \pm 6.2\%$) (Table 1). The Fugian freshwater landscape was conformed primarily of natural lotic stream habitat types that included forests and grasslands, but natural lentic ecosystems were also present along 6–25% of the network's total length. The most extensive beaver impact was abandoned ponds.

As expected, beaver-impacted patches displayed significantly different physical and biotic characteristics than natural lotic habitats, and they displayed both similarities and differences with natural lentic patches. For example, beavers significantly reduced substrate diversity compared with flowing streams, but displayed very similar parameters to the natural conditions recorded for peat bog ponds and lakes (Table 2). Ecosystem engineering by invasive beavers caused BOM standing crop to significantly increase, while benthic macroinvertebrate diversity and richness significantly decreased, compared with natural lotic habitats (Table 2). Meanwhile, natural lentic patches occupied an intermediate position. Benthic macroinvertebrate biomass was greater in both beaver-impacted and natural lentic patches, compared with natural lotic sections, but this result was not statistically significant.

Patch- versus landscape-level effects on BEF

DCA results showed a segregation of plots between lotic and lentic patch groups (Fig. 2a), which was driven by

Table 2 Habitat and biotic variables and ANOVA results for natural lotic and lentic patches and beaver lentic areas of freshwater ecosystems in Tierra del Fuego

Variable	Unit	Natural Lotic	Natural Lentic	Beaver Lentic	d.f.	F	P
Substrate heterogeneity	H'	1.8 (0.1) ^A	0.2 (0.1) ^B	0.6 (0.2) ^B	2, 52	29.7	<0.0001
Total BOM	g AFDM m ⁻²	6.1 (2.5) ^A	16.6 (3.3) ^{AB}	38.4 (9.1) ^B	2, 52	8.7	0.0006
Macroinvertebrate richness	taxa m ⁻²	10.3 (0.7) ^A	8.4 (0.6) ^{AB}	8.0 (0.4) ^B	2, 52	4.9	0.01
Macroinvertebrate diversity	H'	1.5 (0.1) ^A	1.2 (0.0) ^{AB}	1.1 (0.1) ^B	2, 52	5.5	0.007
Macroinvertebrate biomass	g AFDM m ⁻²	0.4 (0.1)	0.5 (0.1)	0.6 (0.2)	2, 52	1.9	0.16

BOM: benthic organic matter. Bold and italics indicate significant ANOVA p values, and different letters indicate significantly different means with a Tukey's HSD *post hoc* test ($P < 0.05$).

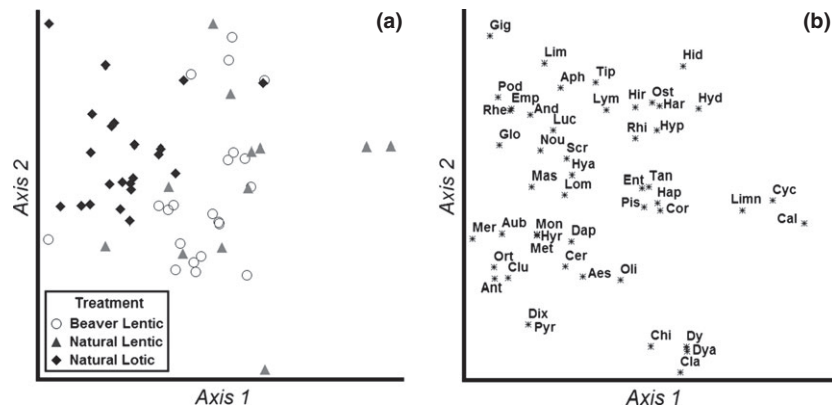


Figure 2 Detrended correspondence analysis (DCA), comparing the similarity of the benthic macroinvertebrate community from samples within and between patch types, found that (a) the lotic samples' assemblage segregated from both lentic patch types, but a high degree of overlap occurred among samples from beaver and natural lentic patches and that (b) species habitat affinities did not demonstrate uniquely beaver-associated taxa. Codes correspond to: Hirudinae (Hir), Oligochaete (Oli), Lumbricidae (Lom), Hydracarina (Hyd), *Hyalella* (Hya), *Daphnia* (Clad), Calanoid (Cal), Cyclopoid (Cyc), Harpactacoid (Har), Colembola (Ent), *Lancetes* (Dyt), *Luchoelmis* (Elm), Hydroptilidae (Hyp), Halipilidae (Hal), Hydrophilidae (Hyp), Scirtidae (Scr), *Aphroteniella* (Aph), Tanypodinae (Tan), Podonominae (Pod), Chironomini (Chi), Tipulidae (Tip), Ceratopogonidae (Cer), Empididae (Emp), *Gigantodax* (Gig), Orthocladinae (Ort), Dixidae (Dix), Syrphidae (Syr), *Andesiops* (And), *Massartellopsis* (Mas), *Meridialis* (Mer), *Metamonius* (Met), *Nousia* (Nou), *Corixa* (Cor), Pyralidae (Pyr), *Aeshna* (Aes), *Antarctoperla* (Ant), *Aubertoperla* (Aub), *Rhithroperla* (Rhi), *Limnoperla* (Lim), *Matigoptila* (Glo), Hydrobiosidae (Hyd), *Monocosmoecus* (Mon), *Rheochorema* (Rhe), *Lymnea* (Lym) and *Pisidium* (Pis). Full taxonomic details in Appendix S1.

habitat-specific species affinities (Fig. 2b) (total variance in the species data = 4.16; axis 1 = eigenvalue 0.7118; axis 2 = eigenvalue 0.2698). For example, blackflies (*Gigantodax* spp.) and glossosomatid caddisflies (*Matigoptila brevicornuta* Schmid) were associated with natural lotic patches, while diving beetles (Dyt: Dytiscidae), midges (Chironomidae) and water fleas (Cladocera) were representative of lentic zones. MRPP indicated that benthic macroinvertebrate community similarity was homogeneous within patch types ($T = -8.218$; $A = 0.048$; $P < 0.001$, Fig. 2a), but significantly different between lotic and both lentic groups. No difference was observed between natural and beaver lentic communities (beaver lentic vs. natural lentic: $T = -1.54$, $A = 0.01$; $P = 0.08$; beaver lentic vs. natural lotic: $T = -8.11$, $A = 0.05$, $P < 0.001$; natural lentic vs. natural lotic: $T = -7.89$, $A = 0.05$, $P < 0.001$).

A closer examination of each patch's species assemblage (by the second DCA, Fig. 3) found that lotic zones not only were the most diverse ecosystems for benthos, but they also hosted a high number of rare and singleton species,

including mayflies (*Massartellopsis irarrazavali* Demoulin, *Metamonius anceps* Eaton), beetles (Scirtidae), caddisflies (*M. brevicornuta*) and stoneflies (*Antarctoperla michaelsoni* Klapálek). Natural lentic areas also had more habitat-specific taxa (e.g. the dragonfly *Aeshna variagata* Fabricius) than beaver-engineered ponds, which were conformed by species that are common elsewhere (e.g. Chironomidae, Oligochaete). *Daphnia* sp. was the only 'rare' taxa associated with beaver-impacted lentic habitats, but its order (Cladocera) was found as very common in both beaver-impacted and unmodified lentic bodies (Fig. 3).

At the landscape-level, we did not find a difference in benthic diversity or richness in landscape scenarios that included only natural habitats and those that had both natural patches and beaver-impacted areas (Fig. 4). In contrast, however, the beaver's influence on the ecosystem function associated with carbon standing crop increased by an average of $71.6 \pm 17.1\%$ (ranging from 43.6% to 111.3%) in the studied watersheds.

enhancing secondary production of benthos by an order of magnitude (Anderson & Rosemond, 2010) and transitioning benthic production and BOM decomposition rates in sub-Antarctic streams to values more similar to temperate zones (Anderson & Rosemond, 2007; Ulloa *et al.*, 2012). It should be noted, however, that the effects of beavers on other ecosystem functions need to be more fully explored, as our analyses have only focused on benthic ecosystems. Furthermore, it is known that adjacent marine food webs incorporate terrestrial organic matter (Romero *et al.*, 2004), but to date, there has been no quantification of this ecosystem process or beaver's role in modifying it.

At the same time, various studies elsewhere have provided evidence that ecosystem engineering has a positive landscape-level effect on species richness (Wright *et al.*, 2002; Lill & Marquis, 2003; Castilla *et al.*, 2004; Badano & Cavieres, 2006). However, our results help confirm that this is not a characteristic of the ecosystem engineering *per se*. Rather, the proportion and similarities/differences of modified and unmodified habitats in the broader landscape context determine the magnitude and direction of ecosystem engineering impacts by native or exotic species (Wright *et al.*, 2004). We found, therefore, that the beaver's impact on landscape-level stream biodiversity was predictable by combining the ecosystem engineering framework with basic ecological understanding (i.e. the relationship between habitat heterogeneity and species diversity). In addition, as beavers did not transform all of the natural lotic streams into ponds, their patch-level effect of decreasing stream benthic macroinvertebrate diversity was not generalized for the entire landscape as part of this invasion.

At the same time, the beaver's invasion still can be considered a large and important landscape-level phenomenon. Therefore, rather than concluding from these data that the invasive beaver is not harmful to TDF because it 'merely' engineers ponds whose benthic biodiversity is similar to natural lentic habitats, we can now more precisely determine the actual way it has transformed this landscape, which is via effects on ecosystem processes. Other studies have also shown that this invasive species not only changes standing crops, but increases decomposition rates of BOM (Ulloa *et al.*, 2012).

What we still need to know about invasive beavers in Tierra del Fuego

As a result of the beaver's impacts in what is otherwise considered a largely pristine wilderness area (Mittermeier *et al.*, 2003), conservationists and environmental managers have worked to define control and/or eradication programmes for the beaver in southern Patagonian forests (Malmierca *et al.*, 2011). In this scenario, a number of important research areas still remain to be explored regarding the role of this invasive species in engineering a novel Fuegian landscape, particularly areas related to management and social perceptions of beavers (Anderson *et al.*, 2011). However, specifically regarding

the ecological role of invasive beavers, it is important to consider further how these changes to ecosystem processes can include even potential and fundamental ecosystem state shifts. For example, by retaining sediments and organic matter in the stream, beavers can ultimately modify the hydrogeomorphology that connects floodplains and streams (Westbrook *et al.*, 2011).

Furthermore, the role of exotic beavers in affecting patch-versus landscape-level patterns and processes of riparian ecosystems and biota requires a modification of our hypotheses, but we believe still should be predictable based on the basic conceptual model used here of the role of invasive ecosystem engineers. While the effect of beavers to freshwater biota and ecosystems may be to produce patches that are very similar to the natural lentic habitats already found in the Fuegian landscape, we would not anticipate *a priori* that this would be the case for riparian BEF. As the beaver's flooding and foraging habits have no evolutionary or ecological equivalent for the adjacent terrestrial zone, unlike the introduction of *C. canadensis* to Europe where *C. fiber* previously evolved, this modified habitat would not be expected to have analogues in the landscape. Indeed, we have determined that these riparian zones also are not resilient to beaver disturbance (Wallem *et al.*, 2010), and one of the most important ecological research areas for the future of riparian restoration efforts will be to determine effective and efficient ways to regenerate the BEF of these modified terrestrial habitats (Anderson *et al.*, 2009).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Benthic macroinvertebrate taxa described per habitat.

BIOSKETCH

Christopher B. Anderson is a socio-ecologist working on research, education and conservation projects in southern Patagonia's Tierra del Fuego Archipelago for over a decade. Building on initial natural history and community ecology studies of native and exotic flora and fauna, today he works to integrate (1) scale and (2) 'human-nature' dimensions to the study and management of these socio-ecosystems.

Author contributions: The project was a collaborative effort that transcended political borders and institutional affiliations. C.B.A., P.K.W. and G.M.P. conceived the idea; C.B.A. and M.P.S. conducted most field and laboratory work; C.B.A., M.V.L., P.K.W. and A.E.J.V. lead statistical analyses; and all authors participated in the writing and contextualization of results and discussion.

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