

Do introduced North American beavers *Castor canadensis* engineer differently in southern South America? An overview with implications for restoration

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ABSTRACT

1. Twenty-five pairs of North American beavers *Castor canadensis* Kuhl were introduced to Tierra del Fuego Island in 1946. The population has expanded across the archipelago, arriving at the Chilean mainland by the mid-1990s. Densities range principally between 0.5–2.05 colonies/km. They have an impact on between 30–50% of stream length and occupy 2–15% of landscape area with impoundments and meadows. Beaver impacts constitute the largest landscape-level alteration in subantarctic forests since the last ice age.

2. The colonization pattern, colony densities and impacted area indicate that habitat in the austral archipelago is optimal for beaver invasion, due to low predator pressure and suitable food resources. *Nothofagus pumilio* forests are particularly appropriate habitat, but a more recent invasion is occurring in adjacent steppe ecosystems. Nonetheless, *Nothofagus* reproductive strategies are not well adapted to sustain high beaver population levels.

3. Our assessment shows that at the patch-scale in stream and riparian ecosystems, the direction and magnitude of exotic beaver impacts are predictable from expectations derived from North American studies, relating ecosystem engineering with underlying ecological mechanisms such as the relationships of habitat heterogeneity and productivity on species richness and ecosystem function.

4. Based on data from the species' native and exotic range, our ability to predict the effects of beavers is based on: (i) understanding the ecological relationships of its engineering effects on habitat, trophic dynamics and disturbance regimes, and (ii) having an adequate comprehension of the landscape context and natural history of the ecosystem being engineered.

5. We conclude that beaver eradication strategies and subsequent ecosystem restoration efforts, currently being considered in southern Chile and Argentina, should focus on the ecology of native ecosystems rather than the biology of this invasive species *per se*. Furthermore, given the nature of the subantarctic landscape, streams will probably respond to restoration efforts more quickly than riparian ecosystems.

Keywords: *Castor canadensis*, ecosystem engineer, exotic, invasion, *Nothofagus*, Patagonia

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BACKGROUND

The North American beaver *Castor canadensis* Kuhl was brought to the Argentine portion of Tierra del Fuego Island (TDF) in southern South America in 1946. The one-off introduction consisted of 25 mating pairs released into the Claro River near Fagnano Lake (Daciuk, 1978; Sielfeld & Venegas, 1980; Lizarralde, 1993) (Fig. 1). The goal of the introduction was to promote a fur industry, but curiously the hunting of beavers was not officially authorized in Argentina until 1981 (Lizarralde, 1993). In Chile, the beaver was declared a nuisance or harmful species in 1993; thus, authorizing its hunting year-round (D.S. 133 – Chilean Hunting Law).

By the 1960s, the population had expanded across the Beagle Channel to Chile, into what is today the Cape Horn Biosphere Reserve, and progressively colonized the islands of Navarino, Hoste, Picton, Nueva and Lennox (Fig. 1) (Sielfeld & Venegas, 1980; Lizarralde, 1993; Anderson *et al.*, 2006a; Moorman *et al.*, 2006; Skewes *et al.*, 2006; Wallem *et al.*, 2007). On Dawson Island in the Strait of Magellan between TDF and the mainland, personnel from the Chilean Navy reported the first beaver colonies in 1989 (Skewes *et al.*, 2006). Further-

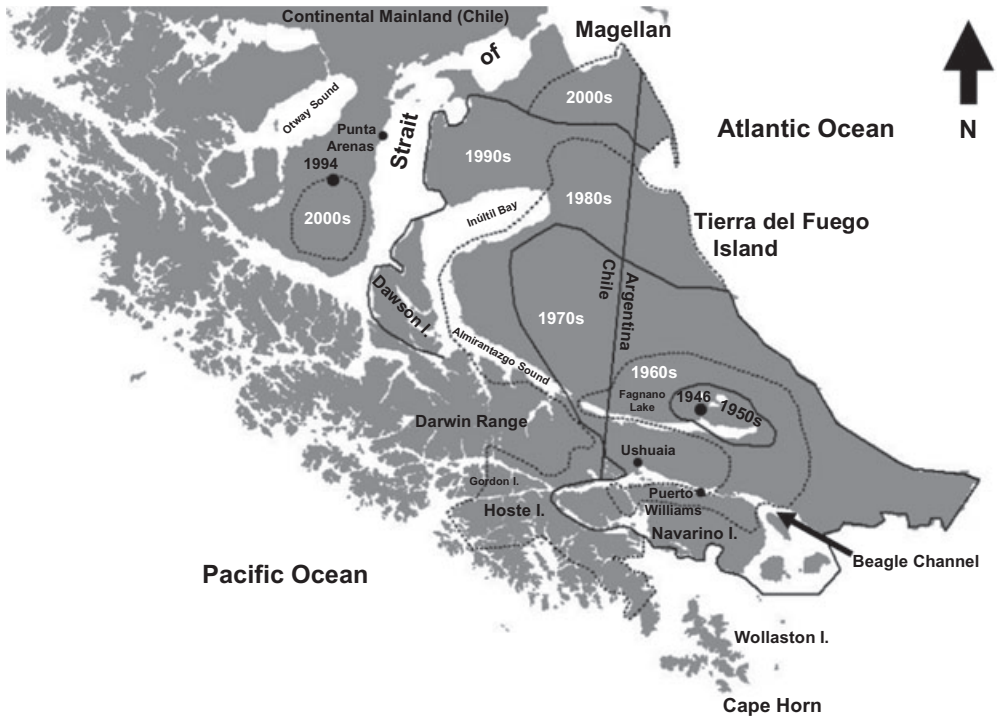


Fig. 1. Map of the archipelagic region of southern South America, showing the approximate dates of expansion of *Castor canadensis* throughout the area. The initial introduction of 25 pairs of beavers in 1946 took place near Fagnano Lake on Tierra del Fuego, an island shared between Argentina and Chile. By the 1960s, invasive beavers had reached the Chilean islands south of the Beagle Channel, and today a resident population is also found on mainland Chile.

more, colonies have been detected on the Chilean mainland (Brunswick Peninsula) since the 1990s (Wallem *et al.*, 2007). However, the Wollaston Island Group (Cape Horn National Park) and the extreme western portion of the archipelago (Agostini National Park) have not been colonized by beavers to date, perhaps due to intrinsic ecological barriers making the habitat undesirable (Anderson *et al.*, 2006a; Moorman *et al.*, 2006).

The introduction of the North American beaver to southern South America has arguably engendered the largest alteration to the forested portion of this landscape since the recession of the last ice age approximately 10 000 years ago. Greater areas have been affected only in the adjacent steppe ecosystem by sheep and cattle grazing. Awareness of the consequences of this invasion has grown over time, as a social-scientific process has developed amongst scientists, authorities and the general community. As a result, national control programmes in Chile and Argentina have been attempted to mitigate the detrimental effects of this invasive ecosystem engineer in subantarctic ecosystems. In addition, a parallel series of bi-national working groups in 2006 led to an International Workshop on Beaver Control in the Fuegian Archipelago and a nascent commitment to approach the issue in a holistic, transborder manner.

However, while the impacts of beavers are recognized as large, widespread and visually dramatic, until recently it was not possible to produce a synthesis of their effects across various taxa and ecosystems to determine whether this invasion has a generally negative or positive effect on subantarctic biota and habitats. Likewise, a review of the habitat-level effects of invasive beavers, based on current understanding, can help answer the general question of whether the introduced North American beaver engineers differently in southern South America or whether it follows expectations from ecological theory developed in its native range? Here, we synthesize the available literature about the North American beaver in southern Chile and Argentina, addressing its role as an invasive exotic ecosystem engineer, to compare it to its habitat-level effects in North America and to provide information relevant to regional eradication of beavers and restoration efforts in this ecosystem.

BEAVERS AS EXOTIC ECOSYSTEM ENGINEERS

Exotic species generally fall under a pall of negative perceptions, given their widely accepted role as agents of global ecological change (Vitousek *et al.*, 1997), biotic homogenization (McKinney & Lockwood, 1999) and economic harm (Pimentel *et al.*, 2000). Consequently, most research has been focused on the deleterious effects of exotic species, creating a body of literature since the mid-1980s in the sub-discipline of invasion ecology (see Lockwood, Hoopes & Marchetti, 2007). Most of this research is based on the underlying supposition that invasive exotic species have innate differences from native recipient communities or even their natural populations of origin that makes them harmful (but see Meiners, 2007). Recently, the utility of the invasion metaphor has been called into question (Larson, 2005), due to its inherently value-laden connotations, and a call has been made that species invasions be evaluated more objectively, broadening the types of ecologically relevant questions that can be asked about introduced species (Brown & Sax, 2004).

In this context, studying the role of the North American beaver as both an exotic and native ecosystem engineer gives us the opportunity to ask questions relevant to both general ecology and potential invasive species management efforts. The case of the beaver allows us to use the framework of the ecosystem engineer concept to address *how* beavers modulate the availability of resources and habitat to other species by causing physical state changes in biotic or abiotic materials (Jones, Lawton & Shachak, 1994, 1997). Fortunately, a great deal is known about the ecology of *C. canadensis* in North America (e.g., Naiman, Johnston &

Kelley, 1988, 1994; Johnston & Naiman, 1990; Rosell *et al.*, 2005). As an introduced species that has successfully colonized most of the archipelago south of the Strait of Magellan in the last 60 years, we can also approach our understanding of the beaver's influence as an exotic ecosystem engineer under the rubric of species invasions.

Vitousek (1990) set out a list of basic ecological mechanisms one can evaluate regarding the consequences of introduced species, including their effect in: (i) altering resource availability or quality, (ii) changing food-web dynamics, and (iii) modifying disturbance regimes. Crooks (2002) extended this list to include changes wrought to the physical structure of the ecosystem itself by ecosystem engineers, which may affect each of the three mechanisms proposed by Vitousek (1990). Combining insights from these frameworks, we can predict that the physical state effects of invasive ecosystem engineers should cause alteration in habitat heterogeneity (linked to species richness) and/or productivity (linked to trophic effects and/or species richness) (Crooks, 2002; Wright & Jones, 2004; Anderson & Rosemond, 2007).

At the same time, though, we know that the effects of an ecosystem engineer, such as the beaver, are determined by the context of the landscape in which they are embedded (Wright, Jones & Flecker, 2002; Rosell *et al.*, 2005). In that sense, the role of beavers in subantarctic ecosystems could differ in terms of magnitude of impacts between terrestrial and aquatic ecosystems, as on the one hand beaver ponds may replicate natural lentic features of the post-glacial landscape, while on the other hand the flooding and herbivory caused by beavers may have no parallel in the evolutionary history of this region's riparian vegetation.

By reviewing the mass of literature that now exists, we use the invasion of introduced beavers in the Fuegian Archipelago to address the questions: (i) are the directions and magnitudes of change caused by beavers the same in North and South America; and (ii) are the mechanisms by which beavers engineer ecosystems and resulting ecological responses the same between riparian and aquatic ecosystems? These questions are relevant to both general ecology and invasion biology. Furthermore, answering them will inform our understanding of introduced beavers and subantarctic ecosystems, thereby providing urgent information for policy-makers regarding the bi-national (Chilean–Argentine) beaver eradication programme being proposed for the archipelago.

Terrestrial effects

Riparian plant community structure

As in North America, the beaver in TDF is a generalist herbivore with certain preferences expressed broadly in its pattern of colonization of the archipelago. The summer diet of both native and introduced beavers has been identified as principally containing herbaceous species, while in winter woody species dominate (Svendson, 1980; Roberts & Arner, 1984; Castillo, 2006; Wallem *et al.*, 2007). The beaver's diet on TDF also includes bryophytes and marine algae, which have not been reported in their native habitat (Briones *et al.*, 2001; Andrade, 2005).

Amongst the three riparian tree species, all in the genus *Nothofagus*, the beaver apparently prefers *Nothofagus pumilio*, and avoids *Drimys winteri* and *Maytenus magellanica* (Wallem *et al.*, 2007, Table 1). Consequently, we find that the far southern and western areas of the archipelago remain largely uninvaded (Anderson *et al.*, 2006a; Moorman *et al.*, 2006, Fig. 1), corresponding to areas where vegetation types are conformed mainly of Magellanic tundra with patches of forest containing *Nothofagus betuloides*, *M. magellanica* and *D. winteri* (Moorman *et al.*, 2006; Rozzi *et al.*, 2006). While these parts of the archipelago are geographically closer to the point of introduction than other sites on the mainland and in the northern steppe ecosystem, to date they have been colonized much less. In addition to having

Table 1. Natural history characteristics of riparian vegetation, the beaver *Castor canadensis* and landscape-level impacts of this invasion in its native range of North America and from its introduced distribution in southern South America (Chile and Argentina)

	North America	South America
Riparian forest regeneration	Variety of species that reproduce by vegetative means as well as seedling banks (Barnes & Dibble, 1988; Naiman <i>et al.</i> , 1988; Johnston & Naiman, 1990)	Mostly from seedling and sapling banks (Cuevas & Arroyo, 1999)
Riparian forest composition	Many forests include various species of deciduous and coniferous woody species (Naiman <i>et al.</i> , 1988)	Riparian forests dominated by three species of broad-leaf <i>Nothofagus</i> (Anderson <i>et al.</i> , 2006b; Martínez Pastur <i>et al.</i> , 2006)
Riparian forest succession	Can speed up succession by releasing less palatable conifers or reverse succession by favoring early colonizers and disturbance adapted species (Barnes & Dibble, 1988; Naiman <i>et al.</i> , 1988; Johnston & Naiman, 1990)	Succession in foraged areas without flooding returns the original ecosystem. In flooded sites, the meadow is not re-colonized by the original forest, instead having herbaceous taxa & <i>Nothofagus antarctica</i> (Anderson <i>et al.</i> , 2006b; Martínez Pastur <i>et al.</i> , 2006)
Diet	Preference for more palatable deciduous species, such as <i>Populus</i> and <i>Salix</i> (Johnston & Naiman, 1990)	Preference for <i>Nothofagus pumilio</i> and avoidance of <i>Drimys winteri</i> (Wallem <i>et al.</i> , 2007)
Foraging distance (m)	Mean 30–45 m (max. 60) (Barnes & Dibble, 1988; Johnston & Naiman, 1990)	Mean 28–60 m (max. 90–120 m) (Ramírez Silva, 2006; Wallem <i>et al.</i> , 2007)
Density (colonies/km)	1.2 in favorable habitat 0.1–0.5 in poor habitat (Gurnell, 1998)	0.5–2.05 (max. 5.38) in forested habitats 0.1–0.6 in ecotone environments (Briones <i>et al.</i> , 2001; Lizarralde, 1993; Skewes <i>et al.</i> , 2006)
Proportion of stream length impacted (%)	30–50% (Naiman & Melillo, 1984)	40–50% (Anderson & Martínez Pastur, unpublished data)
Proportion of landscape impacted (%)	13% (ponds and meadows) in Minnesota (Naiman <i>et al.</i> , 1988)	2–15% (ponds and meadows) on Navarino and Tierra del Fuego Islands (Anderson & Martínez Pastur, unpublished data)
Colonized streams (order)	1st–4th (Gurnell, 1998; Naiman <i>et al.</i> , 1986)	Principally 2 nd (Coronato <i>et al.</i> , 2003)

a different forest type, these areas also have greater rainfall, steeper topography and large areas of peat moorlands (Anderson *et al.*, 2006a; Rozzi *et al.*, 2006).

Overall, beaver foraging for both food and construction activities in *Nothofagus* forests removes overstory trees and changes the riparian community structure resulting in greater understory species richness and productivity (Anderson *et al.*, 2006b; Martínez Pastur *et al.*, 2006). In the beaver's native range, the direction of species richness changes in beaver-impacted riparian areas can be higher (Pollock, Naiman & Hanley, 1998) or the same (Wright *et al.*, 2002), compared to adjacent unimpacted forested zones (Table 2). Wright & Jones

Table 2. The direction of impacts caused by *Castor canadensis* on habitat, community and ecosystem variables, comparing responses from North and South American riparian and stream ecosystems

Riparian	North America	South America	Stream	North America	South America
Habitat – Resource availability (g/m ² and %)					
Soil organic matter	+	+	Benthic organic matter	+	+
Canopy cover	–	–	Canopy cover	–	–
Community – Species richness (taxa/m ²)					
Trees	–	–	Macroinvertebrates	–	–
Herbaceous plants	0, +	+	Fish	+	0
Exotic plants	0, +	+	Exotic fish	NA	0
Ecosystem – Biomass (g/m ²)					
Trees	–	–	Fish	+	+
Herbaceous plants	+	+	Macroinvertebrates	+	+
Dicotyledons	+	+	C-G & Pred	+	+
Monocotyledons	+	+	Sc, Sh & Fil	–	–

NA, not assessed; Macroinvertebrate functional feeding guilds; C-G, collector-gatherer; Pred, predator; Sc, scraper; Sh, shredder; Fil, filterer.

(2004) provided one model to predict the direction of these responses, showing that the influence of an ecosystem engineer on productivity can determine whether richness will increase or decrease. Using this model, the response in our study systems correspond with this proposed mechanism, whereby beaver modifications induce very low productivity forest riparian herbaceous communities to increase their biomass and in the process enhance their species richness.

In the South American studies, a large number of the plant species found in the assemblage that establishes itself in abandoned ponds do not grow in primary forests. However, unlike reports from parts of North America (Wright *et al.*, 2002), many of the plants inhabiting Fuegian beaver meadows were not unique to this habitat type, but rather were characteristic of other non-forested, adjacent environments such as steppe, peat bogs or *Nothofagus ant-arctica* forests (Martínez Pastur *et al.*, 2006). The magnitude of the beaver's effects on species composition, and ultimately landscape level patterns of richness and overlap between habitat types, will depend on the landscape context in which the beaver's engineering is found (Wright *et al.*, 2002; Rosell *et al.*, 2005), but it is apparently less in TDF than in some parts of North America.

In addition, the disturbance caused by beaver invasion in southern South America gave an advantage to introduced plant species (Table 2) (Martínez Pastur *et al.*, 2006; Anderson *et al.*, 2006b), showing how this invasive ecosystem engineer can facilitate further invasions, as has been found in invasive species interactions elsewhere (Simberloff & Von Holle, 1999; Badano *et al.*, 2007). In contrast, the occurrence of introduced plant species is rare in undisturbed riparian forests, but they settle abundantly after any disturbance event, which besides beavers can include timber harvesting (Martínez Pastur *et al.*, 2002). Therefore, the mechanism by which beavers provide avenues for invasion by introduced plants into pristine native forests is driven by the response of pioneer and colonizer species to beaver impacts, as with any other habitat disturbance.

Succession

After beaver pond abandonment, riparian vegetation is expected to begin a process of succession that can follow multiple pathways, which are different from those of other

openings caused by disturbance (Terwilliger & Pastor, 1999). Succession in areas impacted by beavers is influenced by factors related to surrounding vegetation, hydrology, geomorphology, herbivory, and future chances of re-colonization by beavers. In North America, nutrient and carbon accumulation during impoundment has been shown to produce long-term effects on soil structure and function, even after the pond has been drained, resulting in productive wetland and meadow patches in an otherwise nutrient-poor forest (Johnston *et al.*, 1995). These changes in nutrient cycles and decomposition dynamics in North America (Naiman *et al.*, 1988; Johnston *et al.*, 1995; Johnston, 2001) then modify the biomass and composition of the new plant communities, which can either promote colonizer species or release understory, shade tolerant and unpalatable taxa, such as conifers, considered the climax community type in northern boreal forests (Barnes & Dibble, 1988; Johnston & Naiman, 1990).

Beavers in TDF alter the structure of the original *Nothofagus* ecosystem from a closed forest to a grass- and sedge-dominated meadow as well (Table 1). Subsequent to pond abandonment, herbaceous plant richness in North American ecosystems has been shown to decline due to dominance by competitively superior species (Wright, Flecker & Jones, 2003), but beaver meadows in the southern part of TDF presented higher richness in older abandoned ponds (32 plant species) than in the recently created meadows (eight species) (Martínez Pastur *et al.*, 2006).

Forest clearings can return to their original plant community structure through succession after natural disturbances, such as wind throw, but the beavers have also modified the hydrology and the vegetation community that ultimately affect succession. In essence, in the Fuegian Archipelago, riparian vegetation communities are switched from a process of succession based on tolerant species to one of inhibition (P.K. Wallem, C.G. Jones, P.A. Marquet & F.M. Jaksic, unpublished). In North America, meadows may persist for over 70 years once formed (Wright *et al.*, 2002). The *Nothofagus* riparian forests that are foraged, but lie beyond the direct impact of the beaver impoundment, regenerate abundantly (Briones *et al.*, 2001). Nonetheless, on TDF these areas are also vulnerable to herbivory not only from beavers, but also from guanacos *Lama guanicoe* and livestock, which can convert the saplings into deformed shrubs. However, *N. antarctica* does occur in medium-aged meadows (>6 years), but this is not naturally a dominant tree species south of Fagnano Lake (Anderson *et al.*, 2006b; Martínez Pastur *et al.*, 2006) and instead is considered a pioneer species of non-forested environments (rangelands and borders of peat bogs). Over time, though, the establishment of a *N. antarctica* stand could create the necessary conditions for the establishment of other *Nothofagus* species.

Regeneration

The regeneration strategy of *Nothofagus* depends mostly on an understory seedling bank (Cuevas & Arroyo, 1999). While these forests under special ecological conditions, such as at tree-line, can regenerate through vegetative reproduction (stump sprouts, root suckering or layers), this is not a frequent occurrence at lower elevations where beavers are mainly active (Martínez Pastur *et al.*, 2006). As a result of beaver foraging and flooding, therefore, various groups of riparian plants are entirely removed from the riparian assemblage in impacted areas, including secondary trees and shrubs, and also orchids, ferns and some other herbaceous plants (Martínez Pastur *et al.*, 2006).

Regeneration strategies and differences in palatability are important for riparian forest recovery in North America (see review in Rosell *et al.*, 2005), and the absence of such strategies in South American indicates that *Nothofagus* lacks adaptation to long-term beaver impact (Table 1). *Nothofagus* forests are naturally subjected to a number of catastrophic

disturbances (Donoso, 1993; Rebertus *et al.*, 1997), and as such have the capacity to restore the forest after a wide range of natural perturbations (Cuevas, 2000; Martínez Pastur *et al.*, 2002). However, the flooding associated with beaver dams drowns all the seedlings and trees. In addition, deposited sediments completely cover the original forest floor and impede seed germination, making new input of seeds to the abandoned ponds necessary for regeneration. For this reason, forest plant species in the austral archipelago do not regenerate well in meadows for at least 20 years and probably for much longer periods (Martínez Pastur *et al.*, 2006).

Aquatic ecosystems

Habitat

The immediate physical, chemical and geomorphological consequences of beaver engineering activities in streams generally occur in the same direction and magnitude in both North and South America, depending mostly on the context of the catchment. For example, beaver damming activity reduces current velocity and increases retention in all cases, thereby initiating a series of associated effects such as inducing sediment deposition, reducing canopy cover, changing benthic habitat conditions and increasing standing stock of organic matter and nutrients (Table 2) (Butler & Malanson, 1995; Lizarralde, Deferrari & Escobar, 1996; Coronato *et al.*, 2003; Anderson & Rosemond, 2007).

In southern South America, beaver dams increase detrital standing crop and alter the relative contribution from fractional components of benthic organic matter, as one would expect from studies in North America (Naiman, Melillo & Hobbie, 1986; Anderson and Rosemond, in press). While the natural unretentive nature of streams in the Fuegian archipelago, which are often high gradient and flashy, washes out most benthic organic matter, beaver ponds accumulate greater proportions of coarse (44×) and fine (30×) benthic organic material (Anderson & Rosemond, 2007). In contrast to the increase found in basal resource quantity, it was also found that beaver-induced conditions in pond habitats resulted in lower quality (higher C : N) fine benthic organic matter (Anderson & Rosemond, 2007).

Besides being a basal resource with trophic consequences (see *Stream food-webs* below), beaver alteration of the standing crop of benthic organic matter also changes the stream bed habitat by burying natural rocky substrates under a layer of organic debris. In the austral archipelago, beaver engineering changes the substrate characteristics of ponds, but not of stream, and reaches immediately downstream of dams, where riparian zones have been cut, but not impounded (Anderson & Rosemond, 2007). Overall, ponds display a substrate particle size profile that is almost 100% organic material, while natural forested stream and downstream sites maintain similar profiles (Anderson, 2006). As a result, benthic microhabitat heterogeneity is significantly lower in beaver ponds than forested reaches, which would also be an explanation for observed reductions in benthic macroinvertebrate richness in streams in both hemispheres (McDowell & Naiman, 1986; Anderson & Rosemond, 2007).

Overall, the direction of beaver effects on stream habitat in both North and South America is related to converting the stream's physical, chemical and geomorphological conditions to those of a lentic ecosystem (Table 2). The characteristics, persistence and magnitude of these effects will depend on their placement in the catchment, including such conditions as slope and precipitation. In much of North America, however, the ultimate impacts of beaver modifications on streams is to increase the diversity of patch types and to enhance total catchment retention of organic matter and nutrients, leading Naiman *et al.* (1988) to conclude that in their native range beavers increased ecosystem stability and resilience to distur-

bance. In the case of subantarctic ecosystems, the landscape effect of beavers has yet to be assessed, but may not increase habitat diversity for the aquatic portion of the landscape. Instead, beaver-engineered habitats may merely replicate natural lakes and ponds. On the other hand, the expected increases in retention should make streams more resilient and stable, as in North America. However, these changes in the retentiveness of subantarctic streams will also have implications for the transport of material and nutrients to coastal estuaries and for a fauna evolved for high gradient, flashy streams.

Stream food-webs

Beaver engineering increases the dependence of in-stream food-webs on terrestrially-derived organic material, enhancing this allochthonous resource subsidy to stream fauna (McDowell & Naiman, 1986; Anderson, 2006; Anderson & Rosemond, in press). In the case of the Fuegian archipelago, this cross-boundary link may also extend to marine communities, which are known to have an important standing crop of terrestrially-derived organic matter for benthic consumption (Pérez-Barros *et al.*, 2004). The transport of material across ecosystem boundaries, including downstream bays and estuaries, is potentially an unanticipated landscape-level trophic effect of beaver invasion in archipelagic regions. We are unaware of any studies linking the effects of beavers to estuary ecosystems in North America, but this would make for an interesting line of inquiry between the two hemispheres.

Beaver-induced alterations to basal resource availability in streams, as well as changes in physical habitat conditions, modify the structure and function of the aquatic communities found in beaver engineered ecosystems in both hemispheres. In the subantarctic archipelago, as expected from North American studies focused on macroinvertebrate trophic structure and dynamics (McDowell & Naiman, 1986; Clifford, Wiley & Casey, 1993; Margolis, Raesly & Shumway, 2001), a large increase is observed in macroinvertebrate biomass and a shift in dominance towards collector–gatherer and predator functional guilds (Anderson & Rosemond, 2007). The assertions by Pollock *et al.* (1995) that benthic macroinvertebrate assemblages from beaver ponds are characteristic of larger-order streams, and beaver pond communities may be unique in catchments that do not have higher order segments are valid in both North America and southern South America. However, in the subantarctic landscape of southern Chile and Argentina, natural ponds and lakes abound in the headwaters of catchments. A detailed comparison between natural lentic habitats and beaver-engineered ones has not yet been conducted, but in North America it is of note that France (1997) found that even in natural boreal lakes, beavers changed benthic habitat heterogeneity. In this case, their effect was to enhance habitat diversity and thereby increase both diversity and abundance of macroinvertebrate taxa. In the austral archipelago, it has been noted that the community changes in beaver ponds favour a small subset of common taxa found in subantarctic streams, rather than representing a unique, beaver-associated community (Anderson & Rosemond, 2007).

The trophic consequences of the alterations caused by beavers push subantarctic stream benthic ecosystems towards a more heterotrophic food-web, but this is an enhancement of a system already dependent largely on allochthonous organic material (Anderson, 2006). The increased magnitude of energy flows in ponds was primarily through the fine benthic organic material compartment via collector–gatherer taxa and predators, as expected from North America (Hodkinson, 1975; Anderson, 2006). However, this result could not totally be explained based on expectations from resource availability, since the coarse organic material fraction was the basal resource most enhanced by beaver damming. Nonetheless, a concomitant increase in the shredder functional feeding guild was not seen, which may be due to a

relative absence of this functional feeding group in subantarctic ecosystems (Moorman *et al.*, 2006; Anderson & Rosemond, 2007).

In North America, beaver ponds have been shown to enhance fish species richness at the catchment level by adding a lentic habitat type to the lotic stream network (Hanson & Campbell, 1963; Snodgrass & Meffe 1998; Schlosser & Kallemeyn, 2000). However, in North American watersheds with natural lakes, it was found that beaver ponds had lower species richness than the natural lentic habitats, which were deeper and more diverse (Keast & Fox, 1990). Furthermore, beaver dams may also represent an obstacle for some fish species (Collen & Gibson, 2001). The southern South American native fish assemblage includes very few species, including rare and vulnerable species in the genera *Galaxias* and *Aplocheilichthys*. As small taxa that prefer low-gradient runs and pools, these species may be found in habitats created by beavers, but on the other hand these taxa may also be particularly affected by beaver dam barriers (Jowett, 2002). Based on habitat preferences and increased benthic invertebrate biomass, available information at the habitat-scale indicates that beaver ponds favour the puye *Galaxias maculatus*, the most abundant native fish species (Vila, Fuentes & Saavedra, 1999; Moorman, 2007). In contrast, no effect of beaver habitat modification was found on introduced trout species such as rainbow *Oncorhynchus mykiss* and brook *Salvelinus fontinalis* (Moorman, 2007). However, as the native species are catadromous, it is important to consider that the impacts of beaver invasion on native puye may at one scale enhance their abundance, while at the same time creating a landscape level impact by limiting their dispersal and reproduction in interior waters. Furthermore, since native freshwater fish richness is so low in the austral archipelago, it is impossible to compare the influence of beavers on diversity between continents.

Understanding beaver engineering mechanisms

Since its introduction in 1946, the beaver has successfully colonized most of the austral archipelago, shared between Chile and Argentina, and more recently the Chilean mainland. At the patch-scale its influence on subantarctic ecosystems is large (see Lizarralde, 1993; Anderson *et al.*, 2006a,b; Martínez Pastur *et al.*, 2006; Skewes *et al.*, 2006; Anderson & Rosemond, in press; Wallem *et al.*, 2007), but is it of greater magnitude than expectations based on impacts from equally suitable habitat in its native range? Exploring mechanisms concerning 'niche opportunity' (Shea & Chesson, 2002) can potentially help to explain the response and effects of the beaver's successful invasion, considering that: (i) on one hand, the beaver in the austral archipelago may be experiencing behavioral changes associated with low predator pressure (Wallem *et al.*, 2007); and (ii) subantarctic riparian vegetation could alternatively be 'naïve' to beaver herbivory and might therefore be more heavily impacted and/or more easily colonized (Anderson *et al.*, 2006a).

Native community of potential predators and competitors

Native terrestrial carnivores in the austral archipelago are neither diverse or abundant (Venegas & Sielfeld, 1999; Anderson *et al.*, 2006a), while in the Northern Hemisphere the beaver has a variety of traditional predators such as wolves, bears, mountain lions, alligators, bobcats, lynx and martens (Potvin & Breton, 1992; Hartmann, 1994; Rosell, Parker & Kile, 1996; Collen & Gibson, 2001). The only prevalent native, terrestrial carnivore on TDF and Hoste Islands is the Fuegian red fox *Pseudalopex culpaeus lycoides*. Previous studies of the red fox's diet have not indicated that the beaver was a component (Atalah, Sielfeld & Venegas, 1980; Jaksic & Yáñez, 1983; Jaksic, Yáñez & Rau, 1983). A more recent work (Andrade, 2005), though, did document the presence of scars on beavers trapped on

Navarino and TDF Islands. While on TDF, two species of fox, including the introduced *Pseudalopex griseus* and the native *P. culpaeus*, are potential predators, on Navarino these marks must have come from dogs *Canis familiaris*, as no foxes are currently found on that island (Anderson *et al.*, 2006a). Another exotic predator found on TDF, Hoste and Navarino Islands is the American mink *Mustela vison*, which can prey on beaver kits (Ibarra, 2007).

The low predator pressure in the area has the potential to cause behavioral changes, leading beavers to increase their home range and consequently exploit a greater area of forest by an individual colony. In its native habitat, the beaver generally feeds in a restricted 'central place', due to the costs and benefits associated with foraging and depredation (Jenkins, 1980). Its foraging area generally concentrates within 30 m of the stream edge, but distances of up to 60 m are not uncommon (Johnston & Naiman, 1990; Barnes & Dibble, 1988). Studies in southern South America have found average distances between 28 and 63 m with a maximum of 90–120 m (Arroyo *et al.*, 1995; Ramírez Silva, 2006). Anderson *et al.* (2006b) did not measure foraging distance directly, but the distance that beavers significantly affected canopy cover was 30 m from the stream edge on Navarino Island, which has the least amount of potential predators (Anderson *et al.*, 2006b) (Table 1).

Furthermore, the percentage of the landscape area affected by beavers in streams in North America can reach as high as 13% in flat topography such as Minnesota (Naiman *et al.*, 1988). On TDF and the Navarino Islands, the beaver impacts about 2–15% of the area (Table 1). Likewise, the affected channel length of streams in North America can be as high as 30–50% (Naiman & Melillo, 1984), which is similar to values of 40–50% found in TDF and on the Navarino Islands (Table 1). Both of these cases provide evidence that establishes a foraging range for beavers in the austral archipelago that would be at the higher end of the ranges described in North America, thus providing support that low predator pressure has released beavers to impact relatively large areas in the subantarctic landscape (Wallem *et al.*, 2007). However, overall this impact is not without precedent in North America, and the beavers on TDF behave as beavers in North America under similar conditions of high quality habitat with low predation.

Natural history of riparian plants in the austral archipelago

The second potential niche related mechanism that could lead to greater impacts by beavers as an invasive species in the austral archipelago is related to the fact that there are important differences in the riparian vegetation of *Nothofagus* forests, compared to similar latitudes in the Northern Hemisphere. The subantarctic landscape's vegetation types include a mosaic of grasslands, bogs (*Sphagnum* peatlands, cushion bogs and rush wetlands) and forests (dominated by only three species in the *Nothofagus* genus) (Moore, 1983; Rozzi *et al.*, 2006). These plant communities have relatively low species diversity, compared to similar latitudes in the Northern Hemisphere, and they display a rather homogeneous forest understory assemblage throughout the landscape (Moore, 1983; Martínez Pastur *et al.*, 2002). The study of beavers in subantarctic ecosystems has concentrated mostly on their effects in forests, but it is important to point out that they have colonized steppe and shrub habitats in northern TDF as well (Wallem *et al.*, 2007). To date, there is little or no published information about beavers in these ecosystem types either from North or South America.

The only three tree species found in the austral archipelago (*N. betuloides*, *N. pumilio* and *N. antarctica*) largely lack the types of defensive mechanisms and reproductive strategies (Rebertus & Veblen, 1993; Cuevas & Arroyo, 1999) that are found in North American forests (Basey, Jenkins & Busher, 1988; Johnston & Naiman, 1990; Muller-Schwarze *et al.*, 1994).

Conifers, which are generally of lower nutritional quality and palatability than broad-leaf species (Jenkins, 1980; Johnston & Naiman, 1990), are also an important part of North American riparian assemblages, while in the subantarctic archipelago they are functionally absent.

As a result of natural history characteristics, such as regeneration strategies and defense mechanisms, in North America the beaver's foraging activities eventually create an unpalatable stand of riparian trees that remains and/or regenerates (Naiman *et al.*, 1988; Muller-Schwarze *et al.*, 1994). In addition, the overall consequence of these changes on plant communities is to engineer a more diverse habitat mosaic and thereby a more species rich riparian plant assemblage at the patch (Pollock *et al.*, 1998) and landscape scales (Wright *et al.*, 2002). *Nothofagus* forests, in contrast, naturally regenerate from sapling banks in a gap dynamic, since seed banks do not persist for long periods in these soils and vegetative reproduction is rare (Cuevas & Arroyo, 1999). Only one species (*N. antarctica*) is adapted for boggy soil conditions (Ramírez *et al.*, 1985), but this species is not naturally a part of most riparian forests. Therefore, this 'naïve' vegetation may have problems in both protecting itself from herbivory and subsequently coming back after an impact caused by the beaver (Table 1).

In the Northern Hemisphere it has also been reported that the exploitation of resources by beavers degrades habitat quality, resulting in unstable population dynamics (Hall, 1960; Aleksiuik, 1970). While *N. pumilio*, the beavers preferred food, is very abundant in parts of the archipelago north of the Darwin Range on TDF and on the north coast of Navarino Island, in other areas it is completely absent (Rozzi *et al.*, 2006). Nonetheless, population fluctuations by beavers have not yet been demonstrated in southern South America, but considering the slow regeneration of *Nothofagus*, future limitation in this food resource is certainly possible. Up until now, the beaver has expanded its range and numbers based on the availability of new pristine (high quality) habitat. As optimal habitat is used and degraded, the rate of turnover will become important, and we would expect a population decrease and a new equilibrium based on a less-than-optimal habitat condition.

The outcome of beaver invasion in southern South America has led to a highly invaded landscape with approximately 90% of all streams being occupied in the Argentine portion of Tierra del Fuego from the Chico River in the north to the coast of the Beagle Channel in the south (Lizarralde, 1993). On TDF researchers report between 0.2 to 5.8 colonies/km (Lizarralde, 1993; Briones *et al.*, 2001; Skewes *et al.*, 2006), and the only study on Navarino Island reported 1.1 colonies/km (Skewes *et al.*, 2006). In comparison, colony densities described for beavers in North America range between 0.08 to 1.4 colonies/km (Boyce, 1983; Beier & Barret, 1987; Howard & Larson, 1985; Robel & Fox, 1993), thereby putting the density values for the austral archipelago at the high end of the range expected from the beaver's native range. As stated previously, this would indicate that the invasive beaver lacks some population control factors that are present in parts of its native habitat, but the response of the invasive populations is within expectations for optimal habitat conditions that can also be found in North American forested ecosystems (Table 1).

Such profound differences in the natural history and composition of both predators and riparian plants from North and South America are important considerations when explaining the mechanisms and impacts of beaver invasion in southern Chile and Argentina. However, based on available evidence, it appears that beavers have their widespread impacts principally due to the abundance of optimal habitat and food. These factors could make it easier for beavers to disperse and colonize areas (i.e. invade), thereby increasing the amount of stream networks and new catchments inhabited by beavers, but once established, their

impacts are largely in the direction and magnitude expected based on native habitat with optimal conditions (Table 1).

Restoration implications of possible beaver eradication

Consensus has been built amongst many scientists and authorities in southern Chile and Argentina that an eradication programme of North American beavers should be initiated to protect not only the subantarctic forest's regenerative capacity, but also maintain the region's integrity, singularity and identity. However, when reflecting on the perceived need for exotic species eradication and subsequent ecosystem restoration in the austral archipelago, it should be kept in mind that the introduction of species by humans is a global process that has been occurring for many centuries. We must acknowledge that the majority of introduced species either do not become permanently established, or they cause little effect on the recipient ecosystems and biota. Larson (2005) has also questioned the utility of the 'invasion' metaphor, since in a globalized planet it may cause: (i) an inaccurate perception of introduced species; (ii) social misunderstanding and loss of scientific credibility; and (iii) reinforcement of a militaristic outlook that is counterproductive to conservation itself.

Nonetheless, the current rate and extent of introductions are accompanied by large-scale habitat alteration, which together threaten to create an increasingly homogenized planetary biota (McKinney & Lockwood, 1999), even though on local and regional levels introductions may only enhance species richness (Sax & Gaines, 2003). Furthermore, we suggest that exotic ecosystem engineers in particular merit special attention for their potential to affect changes to entire ecosystems and landscapes. In the case of North American beavers in the subantarctic archipelago, this invasive exotic ecosystem engineer arguably produces a large landscape alteration. Overall though, the direction, magnitude and mechanisms producing its effects are in keeping with expectations from its native range and general ecological principles based on theory from ecosystem engineering and food-web ecology.

The persistence and magnitude of its effects in the subantarctic archipelago differ between terrestrial and aquatic ecosystems. In addition to understanding the underlying mechanisms by which beavers modify ecosystems, it is perhaps equally or more important to have a thorough understanding of the native riparian and aquatic ecosystems in the austral archipelago. Amongst the biotic assemblage found in the austral archipelago, there are species which can be favored or harmed by the presence of beaver-engineered habitats, and the development of community-scale models that assess multiple taxa simultaneously, such as that proposed by Sax, Kinlan & Smith (2005), will be useful in future monitoring efforts to determine the general compensatory effect of beavers and potential mitigation and restoration efforts.

Based on current understanding of this invasion and the ecology of native ecosystems, we put forward the following recommendations regarding beaver eradication and concomitant ecosystem restoration: (i) riparian zone restoration must take into account that the beaver produces two kinds of impacts: direct and largely temporary effects caused by cutting trees for food and dam construction; and indirect and more long-lasting effects caused by the deposition of sediments in impoundments and the standing dead trees that remain for long periods of time; and (ii) regarding the stream ecosystem, the beaver again creates at least two kinds of impacts: a direct and temporary physical effect associated with impounding the stream that creates a lentic ecosystem that lacks flowing water and has associated changes to the physico-chemical regime of the site that affects the associated biotic communities, and a more lasting effect caused by the accumulation of organic matter that changes nutrient and energy cycling, as well as secondary production and decomposition dynamics of the entire ecosystem.

To facilitate succession in both riparian and stream ecosystems, restoration programmes should first include the removal of dams to permit a return to a natural flow-flood dynamic that will rework deposited material in the stream channel. As many of the islands in the archipelago are conformed by relatively steep gradient and short watersheds and their natural flow dynamic includes annual spring freshets, it is likely that they can return to pre-beaver stream conditions in a relatively short period. Since the pond ecosystems may be similar to natural features in the landscape, beavers also probably have less impact on aquatic ecosystems at the landscape level.

The forested riparian areas with direct impact by beaver foraging, but lying outside of the flooded zone, are expected to naturally regenerate in accordance with the patterns that have been described for these forests (Gea *et al.*, 2004; Rosenfeld, Navarro Cerrillo & Guzmán Alvarez, 2006), depending on the degree of canopy opening, site quality and understory composition (Veblen, 1989; Heinemann, Kitzberger & Veblen, 2000; Martínez Pastur *et al.*, 2002). The time required for regeneration to begin will vary depending on cyclical masting events (Kelly, 1994; Monks & Kelly, 2006). This initial period of seedling establishment can vary between 5–20 years to achieve natural abundances of 40–50 cm and 50–300 thousand/ha *Nothofagus* seedlings (Martínez Pastur *et al.*, 1999; Rosenfeld *et al.*, 2006).

The abandoned impoundments that were formerly dominated by *Nothofagus pumilio* or *N. betuloides* may not regenerate naturally at desirable time scales, as these species' seedlings present scarce re-establishment in areas of sediment accumulation by beaver dams (Anderson *et al.*, 2006b; Martínez Pastur *et al.*, 2006). However, in these areas, *N. antarctica* seedlings are successfully established in the beaver meadows (Anderson *et al.*, 2006b; Martínez Pastur *et al.*, 2006). It is possible, though, that given very long time periods, forests of *N. antarctica* could cause succession from grasslands to the original forest ecosystems, but from the standpoint of human-scale conservation goals, the restoration of these sites may not be tenable in the short or medium-term.

One alternative for future plans is to consider planting the original forest species in the meadows. Seedling transfers to beaver meadows should be carried out using whole seedlings with bare roots with a maximum above-ground height of 30 cm and come from adjacent forests. Using transplanted seedlings would ensure that any required ectomycorrhizae would also be included, as this has been shown to affect re-establishment of forests in the Northern Hemisphere (Terwilliger & Pastor, 1999). The planting date should occur before spring budding, which varies based on location from September to November. While field trials do not yet exist, one alternative is to consider planting the original riparian tree species (*N. pumilio* or *N. betuloides*) on the upper sides of the old dams and the tail ends of the drained ponds, where less sediment accumulated. The rest of the meadow could be planted with *N. antarctica* at seedling density to mimic natural conditions. These transitional forests could then facilitate the re-establishment of the native understory and the recuperation of the associated fauna. However, the impacted areas will undoubtedly continue to host many exotic species, which were able to invade during the period of colonization by the beaver. Invasive plant species, such as *Cerastium fontanum*, *Veronica serpyllifolia*, *Taraxacum officinale*, *Rumex acetosella*, *Trifolium pratense* and *Bellis perennis*, will not be easily eliminated from the affected ecosystems, but their abundance should diminish significantly when the forest canopy cover recuperates.

Returning to the stream ecosystem, the physical changes caused by beavers, which lead to increased retention of organic matter and increased productivity of benthic organisms, finally result in an overall shift in ecosystem function and processes. Nonetheless, with respect to restoration, Anderson (2006) and Anderson & Rosemond (2007) found that sites down-

stream of beaver ponds, which had foraged riparian zones, but did not have alterations in the flow regime, hosted a benthic macroinvertebrate community whose structure and function were almost identical to the natural, forested stream. This fact indicates that mitigation efforts that return the stream to its natural flow dynamics may be sufficient to restore much of its natural biota and ecosystem processes in the stream, in spite of not completely restoring riparian vegetation in the short-term. Likewise, Moorman (2007) found that while recently impacted sites near beaver impoundments had modified abundances of the native fish species *Galaxias maculatus*, streams running through later successional habitats (meadows and shrublands) had the same fish community structure as unimpacted forested reaches.

In essence, it appears that the most important aspect to consider for the in-stream impacts of beavers on subantarctic streams is the accumulation of benthic organic matter (Anderson & Rosemond, 2007). Therefore, the removal of dams is relatively easy (assuming the beavers were eliminated) and is likely to produce significant results in the medium-term to return these streams to natural conditions regarding benthic ecosystem structure and function. Also, it should ensure proper migration of the native catadromous freshwater fish in the archipelago (Vila *et al.*, 1999; Cussac *et al.*, 2004; Moorman, 2007).

CONCLUSION

Species introductions are a major conservation issue throughout the world (Vitousek *et al.*, 1997), and even remote areas such as the subantarctic forests of Chile and Argentina do not escape this pattern (Lizarralde & Escobar, 2000; Anderson *et al.*, 2006a). At the same time, this phenomenon provides a scenario to test basic questions in ecology, using introductions as 'species addition experiments'. Approaching the issue of invasion in this way can teach us a great deal about the ecology of native ecosystems, as well as implications for conservation and restoration.

We began this review by posing the question: Do exotic North American beavers engineer differently in southern South America? Specifically, we have sought to use the invasion of beavers in the southern archipelago of South America: (i) to compare the direction and magnitudes of impacts in North and South America; and (ii) to evaluate mechanisms and responses to beaver invasion in riparian and aquatic habitats. Based on our current understanding of the habitat-level impacts of beavers in the austral archipelago, we found that the direction and overall extent of their effects are predictable based on expectations from their native habitat in North America in ecosystems with similarly optimal conditions (Tables 1 and 2). Understanding how beavers affect underlying ecological variables such as disturbance, trophic dynamics, habitat heterogeneity and productivity allows us to predict the biotic and ecosystem outcome of these impacts in both native and exotic habitats.

Furthermore, in the context of predicting the effects of invasion and the restoration implications, we conclude it is more important to understand the ecology of native ecosystems, rather than the ecology of invasive beavers *per se*. Also, comparing the changes wrought by beavers in terrestrial and aquatic ecosystems in the Fuegian Archipelago, it appears that the impact and persistence are greater in riparian zones than in stream ecosystems in the subantarctic archipelago. As an ecosystem engineer that affects both terrestrial and aquatic habitats, however, restoration post-eradication will require integrating understanding of both riparian and stream ecology, including short-, medium- and long-term timescales. It is clear, therefore, that restoration efforts demand a better understanding of native ecosystems, rather than more detailed studies of invasive beavers.

It should also be explicit that this information, when used in conservation is part of a value-driven process, whereby management plans are determined to achieve an intentional,

socially desired outcome. To achieve this goal, these restoration activities must be carried out within the context of whole ecosystem management at the watershed level and with long-term commitment. Otherwise, they will not only be ineffective, but could in fact produce greater harm. Poorly implemented control programmes in fact could have an adverse effect if, instead of controlling the population, they merely push colonies to more marginal and previously uncolonized habitats. Such a scenario would not only provoke greater impact, but would also be an inefficient use of conservation resources thereby damaging the credibility of scientists and managers for society.

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