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The effects of invasive North American beavers on riparian plant communities in Cape Horn, Chile

Do exotic beavers engineer differently in sub-Antarctic ecosystems?

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ABSTRACT

North American beavers (*Castor canadensis*) were introduced into southern South America in 1946. Since that time, their populations have greatly expanded. In their native range, beavers shape riparian ecosystems by selectively feeding on particular plant species, increasing herbaceous richness and creating a distinct plant community. To test their effects as exotic engineers on sub-Antarctic vegetation, we quantified beaver impacts on tree canopy cover and seedling abundance and composition, as well as their impacts on herbaceous species richness, abundance and composition on Navarino Island, Cape Horn County, Chile (55°S). Beavers significantly reduced forest canopy up to 30 m away from streams, essentially eliminating riparian forests. The tree seedling bank was greatly reduced and seedling species composition was changed by suppressing *Nothofagus betuloides* and *Nothofagus pumilio*, but allowing *Nothofagus antarctica*. Herbaceous richness and abundance almost doubled in meadows. However, unlike beaver effects on North American herbaceous plant communities, much of this richness was due to invasion by exotic plants, and beaver modifications of the meadow vegetation assemblage did not result in a significantly different community, compared to forests. Overall, 42% of plant species were shared between both habitat types. Our results indicate that, as predicted from North American studies, beaver-engineering increased local herbaceous richness. Unlike in their native range, though, they did not create a unique plant community in sub-Antarctic landscapes. Plus, the elimination of *Nothofagus* forests and their seedling bank and the creation of invasion pathways for exotic plants together threaten one of the world's most pristine temperate forest ecosystems.

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1. Introduction

Exotic species are a primary cause of global ecological change (Vitousek et al., 1996). Sub-Antarctic islands are particularly vulnerable to species invasions and are also the site of some of the most significant effects of global climate change, such as warming and UV-B exposure (Chapuis et al., 2004). Predicting the impacts of particular introduced species, therefore, on ecosystem level processes requires understanding the mechanisms of invasion and linking species with their ecosystem-level consequences (Jones and Lawton, 1994; Courchamp et al., 2003).

In southern Chile's Cape Horn County, which includes the archipelago south of Tierra del Fuego Island, terrestrial mammals and freshwater fish assemblages are dominated by exotic species. Greater than 50% of taxa in these groups are introduced (Anderson et al., in press). An important consequence is that intact, pristine ecosystems are embedded in a landscape that is replete with potential invaders. One species in particular has merited a great deal of attention from scientists, wildlife managers and governmental authorities: the North American beaver (*Castor canadensis* Kuhl).

Beavers were brought to the Argentine portion of Tierra del Fuego Island near Fagnano Lake in 1946 as part of a government effort to economically "enhance" the species-poor Fuegian landscape by introducing exotic furbearers, including beavers, muskrats and minks. While only 25 mating pairs were released initially, by the 1950s the expanding population had entered into the Chilean portion of the island, and by the 1960s they had succeeded in crossing channels to the adjacent Chilean archipelago, including Navarino and Hoste Islands (Sielfeld and Venegas, 1980); (Fig. 1). Beaver densities

rapidly increased to very high levels (0.2–5.8 colonies km⁻¹; Lizarralde, 1993; Skewes et al., 1999; Briones et al., 2001), compared to North American densities (0.08–1.4 colonies km⁻¹; Gurnell, 1998). Today, beavers inhabit nearly every available watershed on most of these islands (Sielfeld and Venegas, 1980; Lizarralde, 1993; Skewes et al., 1999), except a few uncolonized refuges in the far southern and western portions of the archipelago (Anderson et al., in press).

The ecological context and natural history of sub-Antarctic broad-leafed *Nothofagus* (Fagaceae) forests are important to understand the effects of beavers in this non-native ecosystem. *Nothofagus* forests on the islands near Cape Horn are embedded in a complex mosaic of habitats that includes several bog types, such as *Sphagnum* peatlands, cushion bogs and rush wetlands (Rozzi et al., 2004a). In addition, the forested portions have relatively low native flora and fauna diversity, compared to similar latitudes in the Northern Hemisphere. Many islands completely lack terrestrial mammalian predators (Venegas and Sielfeld, 1998), and the regional plant assemblage is relatively simple and homogeneous (Moore, 1983; Martínez Pastur et al., 2002). In the absence of a common evolutionary history with beaver, *Nothofagus* trees lack the types of defensive mechanisms and reproductive strategies (Rebertus and Veblen, 1993; Cuevas and Arroyo, 1999) that are found in North American forests to deal with the impacts caused by beaver foraging and flooding (Basey et al., 1988; Johnston and Naiman, 1990). Finally, a more diverse riparian assemblage in North America includes taxa such as conifers, which are not part of the sub-Antarctic assemblage, and that are avoided by beaver simply due to their lower nutritional quality and palatability (Jenkins, 1980; Johnston and Naiman, 1990).

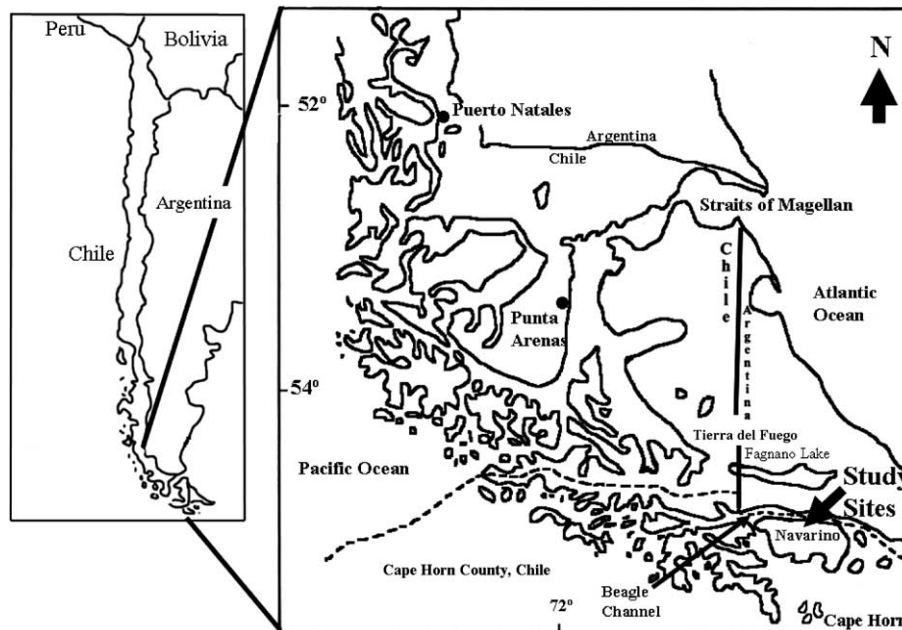


Fig. 1 – Map of southern South America. Dashed line delimits Cape Horn County, Chile, which also corresponds to the sub-Antarctic archipelago area of the Cape Horn Biosphere Reserve. The arrow indicates the study areas located on the north coast of Navarino Island.

As a consequence beaver herbivory and wetland creation in North America promotes the persistence of an unpalatable stand of riparian trees that remains and regenerates (Naiman et al., 1988; Müller-Schwarze et al., 1994) and creates a more complex and diverse habitat and herbaceous species assemblage (Pollock et al., 1995; Wright et al., 2002). In sharp contrast, the forests of the Cape Horn area have only three major tree species, all in the genus *Nothofagus*, which are broad-leaved trees that are all eaten by beavers (Sielfeld and Venegas, 1980). Furthermore, these forests 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 and Arroyo, 1999). Also *Nothofagus* forests in general have problems regenerating when under a systematic or permanent disturbance, making them extremely vulnerable to persistent disturbance (Rebertus and Veblen, 1993). Furthermore, only one species (*N. antarctica*) is adapted for boggy soil conditions (Ramírez et al., 1985).

Such profound differences in the natural history of sub-Antarctic *Nothofagus* forests leads to the questions: as ecological engineers, how do introduced beavers affect sub-Antarctic riparian forests? And, what are the implications for the conservation of one of the world's largest and most pristine temperate forests (Mittermeier et al., 2001; Rozzi et al., 2004a)?

Therefore, we tested the hypothesis that beaver activities in this novel ecosystem would increase riparian plant species richness and diversity and create beaver-specific community assemblages, as expected from studies conducted in its native range (Pollock et al., 1995; Wright et al., 2002; Wright and Jones, 2004). Furthermore, knowing that the vegetation of this archipelago is otherwise largely intact and pristine (Mittermeier et al., 2001), we analyzed the impact of beaver disturbance with relation to altered forest succession and the invasion by exotic plants.

2. Materials and methods

2.1. Study site description

This study was carried out on Navarino Island (2528 km²) (Fig. 1), near the town of Puerto Williams, Chile, located south of the Beagle Channel between Tierra del Fuego Island and Cape Horn National Park (approximately 55°S). Cape Horn County, Chile is South America's (and the world's) southernmost political unit and hosts the world's southernmost forested ecosystems. It was recently declared by UNESCO as the Cape Horn Biosphere Reserve (see Rozzi et al., 2004a).

These forests are dominated by three broad-leaved species of the genus *Nothofagus* (Pisano, 1977). Two of the species are deciduous (*N. pumilio* and *N. antarctica*), and one is evergreen (*N. betuloides*). The natural forest understory has low species richness (Moore, 1983), but habitat diversity is high, composed of a heterogeneous mosaic of ecosystems compacted over an abrupt topography and complex geography (Pisano, 1977; Rozzi et al., 2004a).

The main stems of four separate, predominantly forested watersheds (Ukika, Róbaló, Mejillones and Farallones) were chosen for study along 35 km of the north coast of the island. Sample sites ranged from 0.5 to 2 km from the coast,

and all were below 150 m elevation. In each watershed, two study reaches of at least 100 m were chosen that represented: (1) a natural, mature riparian forest with no history of beaver impact either in the stream or in the riparian zone; and (2) a beaver-created meadow along a reach that was previously forested before the beaver's arrival, which was determined by evidence of standing, dead trees up to the stream edge. The study meadows were made by abandoned beaver dams that were less than 5 years old, which was determined by personal observation. Both sites in each catchment were within 1 km of one another and on the main stem of the catchment. Their slopes, measured with a stadia rod and surveyor's level, were not significantly different (forest stream slope = 0.03 ± 0.008 , Meadow stream slope = 0.02 ± 0.001 , $P = 0.25$). Field work was carried out from February to March 2003 and April 2004, the austral summer months.

2.2. Field methods

To quantify the effects of beaver on forest canopy cover as a function of distance from the stream, ten 1 × 50 m transects spaced 10 m apart were run perpendicularly to the stream edge at each study reach. Shaded cover was recorded with a spherical densitometer at 10 m intervals along each transect and averaged for each study stream. Additionally, twenty 0.5 m² plots were placed in 10 m intervals along the stream edge at each habitat type per stream to survey herbaceous layer (plants < 1 m in height) vegetation. Species accumulation curves, created using PCOrd version 2.0, leveled off at 50 plots in forests and at 65 in meadows, which gave confidence that 80 plots per habitat type was sufficient to capture the species assemblage of these ecosystems. Within each plot, herbaceous species were identified and relative percent coverage was estimated to the nearest 5% with a grid. Tree seedlings also were counted and identified in each plot in order to determine the quantity and type of regeneration of forest species in these two different sites. Most specimens were determined to genus and species in the field or were collected and returned to the Universidad de Magallanes for later identification using Moore (1983).

2.3. Statistical analysis

We first calculated species richness, Shannon-Weiner diversity and several similarity indices (Morisita-Horn and Bray-Curtis), using EstimateS (Colwell, 2004). In addition, we quantified the percentage of survey plots containing exotic species and the percent coverage of six plant categories (monocotyledons, forbs, bushes, trees, bryophytes and exposed soil/leaf litter) to demonstrate the relative abundance of different groups to community composition. Then using JMP version 5.0.1 (SAS Institute Inc., 1994), significant differences were tested between forest and meadow sites with (a) Student's t-test (richness, diversity and regeneration), (b) a two-way ANOVA with a Tukey-Kramer test for significance (percentage canopy cover as a function of distance per site), and (c) a one-way ANOVA with a Tukey-Kramer test for significance (similarity indices between and within habitat types). Community similarity was also analyzed using a non-metric

multidimensional scaling approach (PCOrd version 2.0, McCune and Grace, 2002).

3. Results

3.1. Riparian forest removal and regrowth

Beavers significantly reduced tree canopy cover to 30 m away from the stream edge in the meadow study areas (habitat*distance $F = 57.02$, $df = 5$, $P < 0.0001$ with Tukey-Kramer test $P < 0.05$ to 30 m). The regeneration of the riparian forest likewise was affected by beaver activities. *Nothofagus* seedling abundance in natural riparian forests was significantly greater [7.36 ± 2.52 seedlings per plot (mean \pm SE)] than in meadows, where seedlings were nearly eliminated (0.91 ± 0.17 seedlings per plots; t -test = 2.55, $df = 6$, $P = 0.04$) (Fig. 2).

The species composition of the seedling bank was influenced by beavers, as well. Natural riparian forests contained exclusively *N. pumilio* (3.71 ± 1.11 per plot) and *N. betuloides* (3.65 ± 1.48 per plot) seedlings in the understory. The average number of seedlings for both species was significantly reduced in beaver meadows to near zero (*N. betuloides* = 0.08 ± 0.06 and *N. pumilio* = 0.6 ± 0.2 ; t -test = 2.791, $df = 6$, $P = 0.03$ and t -test = 2.41, $df = 6$, $P = 0.05$, respectively). On the other hand, beaver-impacted riparian zones were the exclusive site of *N. antarctica* seedling establishment, but this was also a very small number (mean seedlings per plot 0.28 ± 0.08) (Fig. 2). Beaver meadows overall had very few *Nothofagus* seedlings near the stream bank, and we observed an assemblage shift from *N. pumilio*–*N. betuloides* to *N. pumilio*–*N. antarctica*.

3.2. Riparian vegetation community characteristics

Meadows had significantly greater plant species richness and diversity than natural forests. A total of 67 plant taxa were identified in the herbaceous layer for all riparian study sites

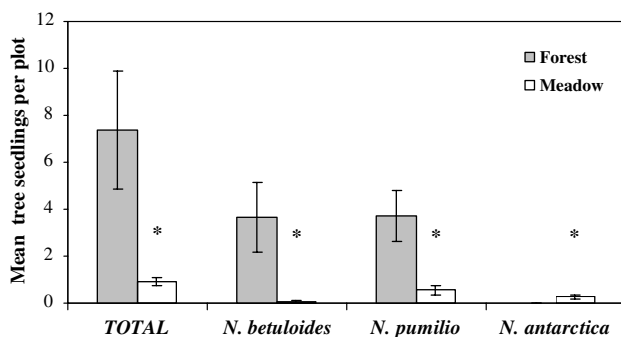


Fig. 2 – Mean *Nothofagus* seedlings per plot in natural and beaver impacted sites (± 1 SE). Beaver meadows showed an overall decrease in the regeneration of *Nothofagus* seedlings ($P = 0.04$). A large impact was found on *N. betuloides*, which is virtually eliminated in meadows ($P = 0.05$). *N. antarctica*, however, demonstrated an opposite trend, only establishing itself (but in very low numbers) in the riparian area after beaver meadows removed the naturally co-dominant forests of *N. betuloides*–*N. pumilio*.

(Table 1). In beaver meadows 63 species were found (94% of all surveyed riparian species). Only 28 species (41% of the total riparian assemblage) inhabited forested riparian zones. Herbaceous species richness per survey plot significantly increased in meadows, when compared to forested sites, by nearly doubling from an average of 3.6 ± 0.66 species per plot in natural areas to 6.94 ± 0.89 in meadows (t -test = -2.99 , $df = 6$, $P < 0.02$; Fig. 3). The overall diversity calculated for each habitat showed the same result with significantly higher diversity in meadows ($H' = 2.42 \pm 0.07$ SD) than forests ($H' = 1.89 \pm 0.16$ SD) (t -test = -3.15 , $df = 6$, $P = 0.02$).

The meadows also had a more abundant herbaceous layer with an average of 86.5% plant coverage per plot, while only 32.2% of forested sites were covered with vegetation. The remaining 13.5% and 67.8%, respectively, for meadows and forests, was bare ground and leaf litter (Fig. 5). Meadows specifically were inhabited by abundant forbs (49.1%), exotics (16%) and native grasses/monocots (14.1%), while forested sites' coverage was dominated by forbs (20.5%), mosses and liverworts (bryophytes: 4.8%), and young woody species (shrubs: 4.4% and trees: 1.8%) (Fig. 4).

The comparison of community similarity between the two habitat types (forest–meadow) was not significantly different from comparisons made within habitat types (forest–forest, meadow–meadow) (Table 2 and Fig. 5), meaning that beaver-engineered assemblages were not significantly different than naturally occurring communities. These data showed that forest–forest habitat comparisons were naturally heterogeneous, and that natural riparian zone community composition was variable at the 0.5 m^2 scale due to the sparse herbaceous vegetation cover in primary riparian forests. Furthermore, the lack of a significantly distinct or obligate beaver-associated meadow community was further shown by substantial overlap between the two habitats. Forty-two percent of the total community assemblage was shared between both habitat types. Only four species (or 5.9%) were unique to forested riparian zones. The four forest-obligate species were the perennial herbs *Lagenophora hariotii* (Asteraceae), *Luzula alopecuarius* (Juncaceae), *Macrachaenium gracile* (Compositae) and *Senecio acanthifolius* (Compositae). Those species only found in meadows tended to be grasses, exotic species and the tree *N. antarctica* (Table 1).

3.3. Exotic riparian plants

We also observed an increase in exotic plant species richness and abundance in beaver meadows, compared to forests. Ten exotic plant species inhabited meadow habitats, but only one species was found in natural, forested riparian zones (Table 1). The richness per sample area of exotic plants was significantly greater in meadows as well (t -test = -3.31 , $df = 6$, $P = 0.02$), ranging from an average of 0.03 ± 0.01 exotic species per plot in forests to 0.66 ± 0.2 in meadow plots. Additionally, introduced species occurred more frequently in meadows. For example, more than half of the eighty beaver meadow survey plots contained at least one exotic species (Table 3). Dandelion (*Taraxacum officinale* [Compositae]) and the herb *Cerastium fontanum* (Caryophyllaceae) were the two most common exotic plants in the herbaceous layer, occurring in 31.3% and 28.8% of meadow plots, respectively (Table 3). The remaining

Table 1 – Total plant species list for both natural forested (F) and beaver-impacted riparian meadows (M)

Species name	Forest	Meadow	Exotic
<i>Acaena magellanica</i> (Lam.) Vahl	F	M	
<i>Adenocaulon chilense</i> Poepp. ex Less.	F	M	
<i>Agrostis capillaris</i> L.		M	E
<i>Agrostis</i> sp.		M	
<i>Alopecurus magellanicus</i> Lam.		M	
<i>Bellis perennis</i> L.		M	E
<i>Berberis buxifolia</i> Lam.	F	M	
<i>Berberis ilicifolia</i> L.f.	F	M	
<i>Blechnum penna-marina</i> (Poiret) Kuhn	F	M	
<i>Carex banksii</i> Boott		M	
<i>Carex curta</i> Gooden		M	
<i>Carex</i> sp.		M	
<i>Cerastium fontanum</i> Baumg.	F	M	E
<i>Cerastium arvense</i> L.		M	
<i>Chilotrichum diffusum</i> (Forster f.) O. Kuntze	F	M	
<i>Codonorchis lessonii</i> (D'Urv.) Lindley	F	M	
<i>Cotula scariosa</i> Franch.		M	
<i>Deschampsia antarctica</i> Desv.		M	
<i>Deschampsia kingii</i> (Hooker f.) Desv.		M	
<i>Deschampsia</i> sp.		M	
<i>Dysopsis glechomoides</i> (A. Richard) Muller Arg.	F	M	
<i>Empetrum rubrum</i> Vahl.	F	M	
<i>Epilobium australe</i> Poeppig & Hausskn. ex. Hausskn.		M	
<i>Festuca magellanica</i> Lam.		M	
<i>Festuca</i> sp.		M	
<i>Galium aparine</i> L.		M	
<i>Gamochaeta spiciformis</i> (Sch. Bip) Cabrera		M	
<i>Gaultheria pumila</i> (L. f.) Middleton	F	M	
<i>Gunnera magellanica</i> Lam.	F	M	
<i>Juncus scheuchzerioides</i> Gaudich		M	
<i>Koeleria fueguina</i> Calderón		M	
<i>Lagenophora hariotii</i> Franch.	F		
<i>Luzula alopecurus</i> Desv.	F		
<i>Lycopodium magellanicum</i> (P. Beav.) Swartz		M	
Lichens	F	M	
Liverworts	F	M	
<i>Macrachaenium gracile</i> Hooker f.	F		
<i>Maytenus disticha</i> (Hooker f.) Urban	F	M	
Mosses	F	M	
Mushrooms	F	M	
<i>Nothofagus antarctica</i> (Forster f.) Oersted		M	
<i>Nothofagus betuloides</i> (Mirbel) Oersted	F	M	
<i>Nothofagus pumilio</i> (Poeppig & Endl.) Krasser	F	M	
<i>Osmorhiza chilensis</i> Hooker & Arn.	F	M	
<i>Pernettya mucronata</i> Gaud.	F	M	
<i>Phleum alpinum</i> L.		M	
<i>Poa fuegiana</i> (Hooker f.) Hackel ex Dusén		M	
<i>Poa pratensis</i> L.		M	E
<i>Poa</i> sp.		M	
<i>Poa trivialis</i> L.		M	E
<i>Primula magellanica</i> Lehm.		M	
<i>Ribes magellanicum</i> Poiret		M	
<i>Rubus geoides</i> Sm.	F	M	
<i>Rumex acetosella</i> L.		M	E
<i>Sagina procumbens</i> L.		M	E

Table 1 – continued

Species name	Forest	Meadow	Exotic
<i>Senecio acanthifolius</i> Hombron & Jacquinot	F		
<i>Senecio</i> sp.		M	
<i>Spergularia marina</i> (L.) Griseb.		M	E
<i>Taraxacum officinale</i> Weber		M	E
<i>Trisetum lechleri</i> (Steud.) Nicora		M	
<i>Trisetum spicatum</i> (L.) K. Richter		M	
<i>Trifolium dubium</i> Sibthorp		M	E
<i>Uncinia lechleriana</i> Steudel		M	
<i>Uncinia</i> sp.		M	
<i>Veronica</i> sp.		M	
<i>Viola magellanica</i> Forster f.	F	M	
<i>Viola</i> sp.	F	M	
Total = 67	28	63	10

The last column indicates whether the species is exotic (E).

introduced species were found in 10% or fewer plots. The forested area only hosted *C. fontanum*, and it was found in just two plots at one stream (2.5% of total).

4. Discussion

As a major component of global ecological change, quantifying the effects of introduced invasive species is an especially pressing area of ecological research and management policy. The introduction of North American beavers to southern South America provides a special opportunity to study their role as exotic ecosystem engineers in a relatively simple ecosystem. In this way, the islands of the Cape Horn Archipelago offer a valuable natural laboratory to conduct research on biological invasions and their consequences. In particular, the abundant, high quality research done in the native habitat of the beaver provides the context to meaningfully compare its role as both a native and exotic species.

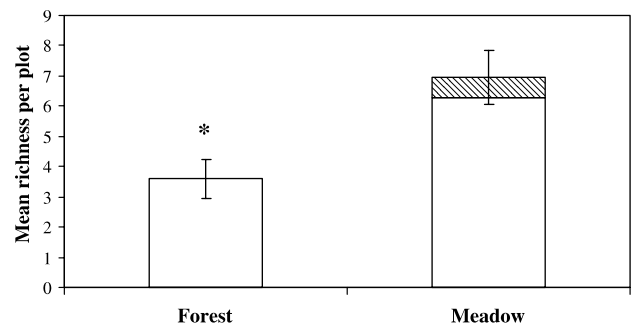


Fig. 3 – Herbaceous layer plant species richness in natural and beaver-impacted sites. Average species richness per plot (±1 SE) was significantly greater in beaver meadow riparian sites than forested reaches ($P = 0.02$). In addition, the number of exotic plants per plot increased in meadows ($P = 0.01$). Shading indicates the contribution of exotic species to average richness per habitat type.

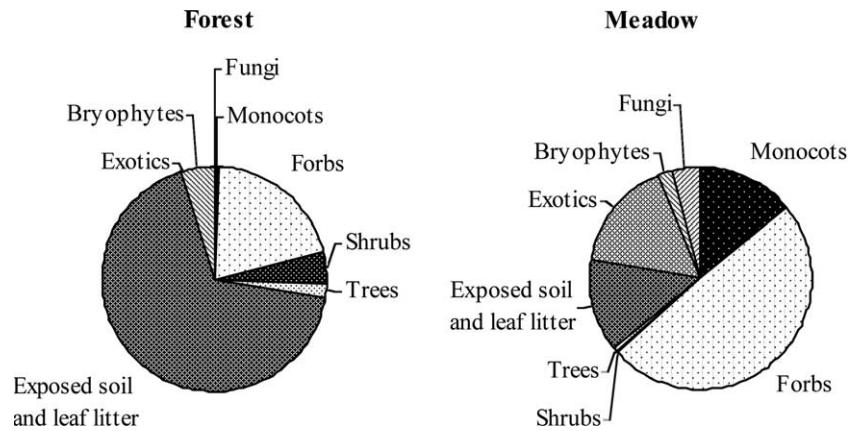


Fig. 4 – Average percent coverage of different plant types in the herbaceous layer of forests and beaver meadows. The natural forest floor is covered primarily with leaf litter, bryophytes and woody plant seedlings, while meadows are dominated by forbs, monocotyledons (mostly grasses) and exotic species.

4.1. The fate of riparian *Nothofagus* forests

With regards to introduced beaver effects on *Nothofagus* forests, we found that the creation of meadows in the Cape Horn area did not result in a modified, but persistent riparian forest that regenerates after herbivory, as has been noted in North America (Naiman et al., 1988). Other studies from Tierra del Fuego Island affirm, however, that certain habitat types do experience abundant regeneration (Briones et al., 2001), but on Navarino Island our results indicated a potentially long-term elimination of trees by suppressing the seedling bank, thus creating an alternative stable state for riparian ecosystems. Furthermore, considering the *Nothofagus* individuals that did persist, seedlings and adults of the evergreen broad-leaf *N. betuloides* were virtually non-existent in meadow riparian sites, which contrasts with the notion that this species is less impacted due to its denser wood (Briones et al., 2001). On the other hand, meadows were the only place where we found the deciduous species *N. antarctica*, which otherwise inhabits natural bogs and extreme areas, such as tree line (Moore, 1983). Consequently, proper management and restoration of impacted sub-Antarctic riparian ecosystems should consider not only stopping the effects of beaver foraging and flooding on *Nothofagus* trees, but also must attempt reforestation as a means to recover natural riparian forest ecosystems.

4.2. Beaver impacts on riparian herbaceous communities

Our findings that beaver-created habitats increased species richness and abundance at the habitat scale contrast with

results in the beaver's native range (Wright et al., 2002), but fit Wright and Jones' (2004) model for predicting the effect of ecosystem engineers on species richness as a function of their influence on ecosystem productivity. Furthermore, in North America, it has been shown that the comparison between forested sites and beaver-impacted areas demonstrated significantly different assemblages (Wright et al., 2002). In their study, Wright et al. (2002) found that 17% of 125 species were shared between the two habitats' assemblages and consequently the Morisita-Horn similarity value between beaver impacted and natural plant communities was <0.1 . In this North American example, the change in plant species composition in beaver-engineered sites led to the conclusion that the beaver wetlands and meadows increased the gamma diversity of plants for the region by creating unique ecological landscape units.

In the Cape Horn Archipelago, we also observed changes in plant richness and abundance between forests and meadows, but while assemblage changes indeed were found that could be ecologically meaningful, the two communities were not

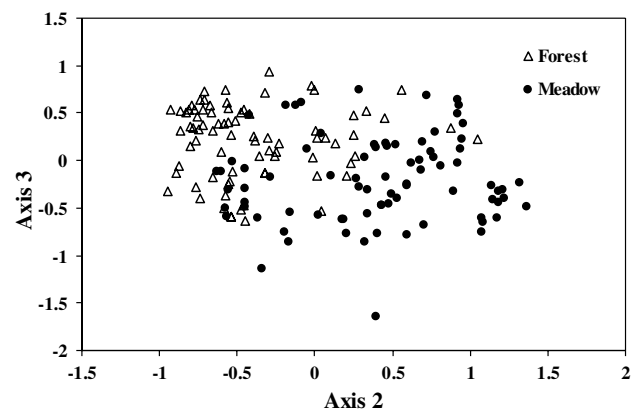


Fig. 5 – Non-metric multidimensional scaling of survey plots from forested and beaver-impacted riparian zones. The lack of differentiation between riparian plant assemblages in natural and beaver-impacted sites is shown by the large degree of overlap of plots from the two habitats.

Table 2 – Analysis of variance of community similarity response to beaver impacts, comparing the Morisita-Horn Similarity Index between vegetation communities in forest-forest, meadow-meadow and forest-meadow sites

Term	df	SS (Type I)	F	P
Site-site similarity	2	0.1651079	2.0983	0.1437
Error	25	0.9835902		
C. Total	27	1.1486981		

Table 3 – The percentage of survey plots containing exotic plants for each habitat-type

Exotic species	% Meadow plots	% Forest plots
<i>Agrostis capillaris</i> L.	5	
<i>Bellis perennis</i> L.	5	
<i>Cerastium fontanum</i> Baumg.	28.8	2.5
<i>Poa pratensis</i> L.	10	
<i>Poa trivialis</i> L.	1.3	
<i>Rumex acetosella</i> L.	2.5	
<i>Sagina procumbens</i> L.	1.3	
<i>Spergularia marina</i> (L.) Griseb.	3.8	
<i>Taraxacum officinale</i> Weber	31.3	
<i>Trifolium dubium</i> Sibthorp	1.3	
Total	53.8%	2.5

A total of 10 exotic plant species were recorded in the forested and beaver meadow riparian zones. All 10 were found in meadows, while only one was in forested sites.

significantly different using beta diversity indices. These findings are corroborated by another study of beaver impacts on Tierra del Fuego Island with a wider range of meadow ages (0–20 years) that discovered the natural forested and beaver-impacted habitats shared 73% of their plant species (Lencinas et al., 2001). Here, we found 42% of the species were the same between forested riparian zones and relatively young beaver meadows.

Thus, while beavers are increasing species richness and abundance of both native and exotic plants, we did not find a beaver-specific assemblage, as was found in North America. This difference between Northern and Southern examples can perhaps be explained due to their respective ecological contexts. Throughout much of the beaver's range in North America natural wetlands are often mostly associated with beavers. As a result "wetland" species are only found with beaver engineered habitats. In the Cape Horn Biosphere Reserve, the landscape includes a diverse mosaic of bogs and forested habitats under natural conditions prior to beaver invasion (Rozzi et al., 2004a). Additionally, the plant assemblage is a simple, relatively homogeneous community (Moore, 1983). Therefore, it is not surprising that due to evolutionary, biogeographical and natural history differences, we did not find a beaver-associated community that represented a unique ecological unit in the sub-Antarctic ecosystem.

4.3. Facilitating exotic species

In addition to impacting riparian forests, beaver meadows provided opportunities for exotic plant species by creating disturbed habitat and dispersal corridors along stream banks. On Navarino Island and in much of the Cape Horn Archipelago, human disturbance is localized around coastal settlements and ranches (Rozzi et al., 2004a,b). Consequently, exotic plants associated with livestock and humans, such as grasses, daisies and dandelions, are generally confined to such areas. By opening avenues of early successional, disturbed habitats from the coast towards the interior of the island along river basins, beavers are providing an important

mechanism for the introduction of weedy plant species into the forested catchments away from the coast. Several comparable studies in the United States showed little or no significant increase in exotic species associated with beaver ponds and meadows (Feldman, 1995; McMaster and McMaster, 2000), while still others indicated that beaver impoundments could likewise provide the opportunity for particular invasive plants to establish themselves and even reduce the native plant species richness (Perkins and Wilson, 2005). The beaver engineering activities in sub-Antarctic riparian forests appear to be facilitating the establishment and spread of exotics, thereby threatening the region's still highly pristine ecosystems and native biodiversity (Rozzi et al., 2004b), further illustrating the need for proper control and restoration measures.

5. Conclusions

In conclusion, our comparison of riparian plant communities in the Cape Horn area of Chile with studies in North America has shown that the impacts of *C. canadensis* were initially similar. In both cases, beavers converted forests to early successional gaps and changed plant assemblages to include more species rich and abundant herbaceous layer. However, we also found that beaver activities on Navarino Island are causing long-term alterations by almost eliminating *Nothofagus* forest regeneration, which unlike North American forests is not evolved to regenerate under this kind of disturbance. Additionally, the pristine character of the sub-Antarctic ecosystem is itself being threatened by ecosystem alteration and the invasion of introduced plant species, whose expansion to unsettled parts of the islands is facilitated by beaver-disturbed corridors along rivers. Furthermore, we did not find that plant communities in beaver habitats were unique assemblages in the sub-Antarctic landscape, as they often are in North America. Understanding the role of introduced beavers in creating an alternative stable state for sub-Antarctic riparian ecosystems, therefore, is extremely important for the management and conservation of the Cape Horn Archipelago, identified as one of the world's largest and most pristine remaining wilderness areas (Mittermeier et al., 2001) and recently designated the Cape Horn Biosphere Reserve (Rozzi et al., 2004a,b).

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