



Alteration of hydrogeomorphic processes by invasive beavers in southern South America



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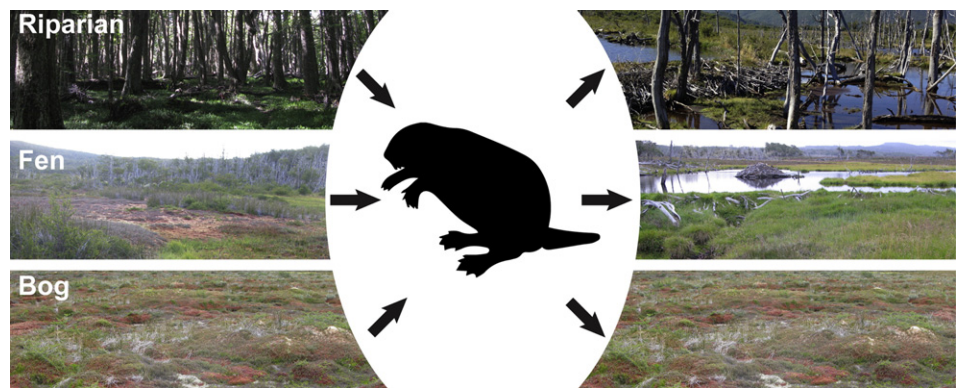
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HIGHLIGHTS

- Invasive beaver occupy all wetland and aquatic habitat except large rivers and bogs.
- Beaver alter hydrogeomorphic processes in ways antithetical to meadow theory.
- Beaver dig and pile large volumes of sediment into dams, reshaping valleys.
- Damming leads exotic grasses to replace native moss in groundwater-fed peatlands.
- Restoration proposals have previously overlooked impacts to peatlands.

GRAPHICAL ABSTRACT



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ABSTRACT

The North American beaver (*Castor canadensis*) is an invasive species in southern Patagonia, introduced in 1946 as part of a program by the Argentine government to augment furbearers. Research focus has turned from inventorying the beaver's population and ecosystem impacts toward eradicating it from the region and restoring degraded areas. Successful restoration, however, requires a fuller determination of how beavers have altered physical landscape characteristics, and of what landscape features and biota need to be restored. Our goal was to identify changes to the physical landscape by invasive beaver. We analyzed channel and valley morphology in detail at one site in each of the three major forest zones occurring on the Argentine side of Tierra del Fuego's main island. We also assessed 48 additional sites across the three forest biomes on the island to identify a broader range of aquatic habitat occupied and modified by beaver. Beaver build dams with *Nothofagus* tree branches on streams, which triggered mineral sediment accretion processes in the riparian zone, but not in ways consistent with the beaver meadow theory and only at a few sites. At the majority of sites, beavers actively excavated peat and mineral sediment, moved thousands of cubic meters of sediment within their occupied landscapes and used it to build dams. Beaver were also common in fen ecosystems where pond formation inundated and drowned peat forming mosses and sedges, and triggered a massive invasion of exotic plant species. Results highlight that restoration of fen ecosystems is a previously unrecognized but pressing and challenging restoration

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need in addition to reforestation of *Nothofagus* riparian forests. We recommend that decision-makers include the full ecosystem diversity of the Fuegian landscape in their beaver eradication and ecosystem restoration plans.

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1. Introduction

Among the biota that affect ecosystems, beavers (*Castor canadensis* and *C. fiber*) are among the best known for creating, destroying and modifying riverine habitats, and so are considered to be ecosystem engineers (sensu Jones et al., 1994). Beavers 'engineer' largely by building dams across low order streams to create ponds that retain water and provide protection from predators, expand foraging areas, and store their winter food supply (Baker and Hill, 2003). In the northern hemisphere, dam building results in the alteration of key ecological, hydrologic and geomorphic processes that transform riverine ecosystems from lotic to lentic habitats and terrestrial zones to wetlands (Butler and Malanson, 2005; Brown and Fouty, 2011; Johnston, 2012; Polvi and Wohl, 2012; Burchsted and Daniels, 2014; de Visscher et al., 2014). Beavers can also occupy lake and large river margins, mineral soil wetlands, peatlands and groundwater-fed sites that lack channels (Johnston, 2012; Westbrook et al., 2013; Morrison et al., 2015), although their impacts on these ecosystems are less studied.

Beaver meadow formation theory (BMFT) is a conceptual framework that explains and predicts how beavers influence the hydrogeomorphic and ecological processes that form stream valleys including the riparian zone (Ruedemann and Schoonmaker, 1938; Naiman et al., 1988). BMFT posits that beavers alter plant communities in the initial phase of colonization by impounding water. The ponds inundate adjacent riparian areas that we define as ecosystems created and maintained by the hydrologic and geomorphic processes driven by flowing water (Cooper et al., 2012). Ponding may drown the existing vegetation and facilitate the establishment of wetland species such as sedges. In this way, beaver dams and their ponds, although transient features, create recognizable, enduring signatures in the riparian zone (Westbrook et al., 2013). Since dams function as efficient water and sediment traps, over time they may fill with fine-grained mineral sediment and organic matter (Polvi and Wohl, 2013) that can remain in the pond and on riparian surfaces once the dam breaches (Butler and Malanson, 2005; Cooper et al., 2006; Westbrook et al., 2011). As dams are abandoned or degrade, the water table recedes, and the exposed, moist, and usually nutrient-rich sediment is quickly colonized by herbaceous plants or shrubs, forming what is termed a beaver meadow (Ives, 1942; Johnston and Naiman, 1987). Beaver meadows may be relatively homogeneous (Wright et al., 2002) or heterogeneous (Westbrook et al., 2011) landscape patches with vegetation composition that favors future beaver reoccupation (McMaster and McMaster, 2001). Over hundreds to thousands of years it is thought that beavers contribute to floodplain aggradation (Ruedemann and Schoonmaker, 1938; Wolf et al., 2007; Polvi and Wohl, 2012). The BMFT has never been tested in a place where beaver have been introduced as exotic animals.

North American beaver (*C. canadensis*) were purposefully introduced to the Tierra del Fuego Archipelago of southern South America in 1946 as part of a program by the Argentine government to augment furbearers (Lizarralde et al., 2004). Owing to a lack of natural predators and suitable habitat conditions (Lizarralde, 1993), the introduced population of 20 individuals (Pietrek and Fasola, 2014) achieved high densities (maximum of 168,000 individuals; Whitfield et al., 2015) and a broad distribution across the region (Anderson et al., 2009). Riparian ecosystems in *Nothofagus* spp. dominated forests are reported to be the preferred habitat for beaver in the archipelago (Skewes et al., 2006; Valenzuela et al., 2014), although the term riparian was never defined. By the mid-1990s beaver crossed saltwater in the Strait of Magellan and reached mainland Chile (Wallem et al., 2007); they have since moved at least 200 km northward into continental Patagonia

(Pietrek and Fasola, 2014). As the beaver population continued to grow (Whitfield et al., 2015), their habitat selection pattern changed to include occupation of ecosystems initially less preferred such as the Patagonian steppe (Pietrek and González-Roglich, 2015; Henn et al., 2016). In those landscapes, the only woody plants are small shrubs or none at all.

A significant body of ecological research established the largely negative ecological impacts of beavers to these ecosystems and the threat presented by their continued northern expansion (Anderson et al., 2011). So, in 2008, Argentina and Chile embarked on an ambitious effort to eradicate beavers from the region and restore the affected areas (Choi, 2008; Burns and Giessen, 2014), with pilot programs supported by the Global Environment Facility beginning in 2015 (Malmierca et al., 2011; Ballari et al., 2016). Yet, it remains to be fully determined how beavers have altered the physical landscape of southern South America, and what landscape features and biota need to be restored. In this paper we focus on the following questions: 1) What is the range of aquatic habitat occupied and modified by beaver in the three forest biomes; 2) have the landscape alterations created by beaver triggered mineral sediment accretion processes in their occupied habitats and initiated the formation of beaver meadows; and 3) is the restoration of *Nothofagus* species the only restoration need?

2. Methods

2.1. Study area

We worked in the Argentine portion of Tierra del Fuego's main island, *Isla Grande* (Fig. 1), during the austral summer of 2013. The island has a varied glacial topography with the end of the Andes Mountain Range lying in the south (running east–west) and the low relief Patagonian steppe in the north. Precipitation can exceed 2000 mm on the windward side of the Andes and is usually <400 mm in the eastern Patagonian steppe (Markgraf, 1993). The dramatic climate gradient across the island produces three forest biomes in the Argentine portion – mixed broadleaf evergreen/deciduous forests in the wetter south and west dominated by *Nothofagus betuloides* and *N. pumilio*, a middle zone dominated by the deciduous *N. pumilio*, and a drier northern strip of forest-steppe ecotone that blends *N. pumilio* and *N. antarctica* (Moore, 1983). We chose one valley with existing beaver ponds in each of these forest biomes (Fig. 1) to examine mineral sediment accretion processes and the hydrogeomorphologic formation of beaver meadows. Sites were selected prior to field work based on presence of beaver dams as observed on Google Earth imagery, previous knowledge about the region, proximity to roads, and permission for land access. After working at all three sites, we realized that the effects of beaver are much broader than stream and riparian ecosystems, and established a landscape-scale analysis. We then visited 48 additional sites to provide a representative sampling of beaver inhabited sites throughout the three forest biomes.

2.2. Intensive analysis in each forest biome

The three valleys we analyzed for mineral sediment accretion processes and the hydrogeomorphologic formation of beaver meadows were Lapataia, Escondido and Rivadavia (Fig. 1). Lapataia is a 2.5 m wide stream with a sandy pebble bed that originates on the adjacent Guanaco Mountain. It bisects a 20 ha *N. betuloides*-*N. pumilio* forested area in Tierra del Fuego National Park that is broad and gently sloping (1.25 m per km) with primarily mineral soils. Beaver have occupied

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